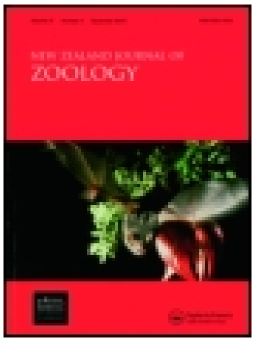

New Zealand Journal of Zoology

ISSN: 0301-4223 (Print) 1175-8821 (Online) Journal homepage: http://www.tandfonline.com/loi/tnzz20

A working list of breeding bird species of the New Zealand region at first human contact

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To cite this article: Richard N. Holdaway , Trevor H. Worthy & Alan J. D. Tennyson (2001) A working list of breeding bird species of the New Zealand region at first human contact, New Zealand Journal of Zoology, 28:2, 119-187, DOI: 10.1080/03014223.2001.9518262

To link to this article: http://dx.doi.org/10.1080/03014223.2001.9518262

Published online: 30 Mar 2010.

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New Zealand Journal of Zoology, 2001, Vol. 28: 119–187
0301–4223/01/2802–0119 $7.00/0 © The Royal Society of New Zealand 2001

A working list of breeding bird species of the New Zealand region at first human contact

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Abstract We present an annotated working list of the bird species breeding in New Zealand during the late Pleistocene and Holocene, up to the time of human contact. New Zealand is defined as including the three main islands and the surrounding smaller islands, plus outlying island groups from Norfolk Island in the northwest, the Kermadec, Chatham, Bounty, Antipodes, Campbell, Auckland, Snares, to Macquarie Islands, but excluding islands south of Macquarie Island and the Ross Dependency. Inclusions or exclusions of species from the list were based on specified criteria. We include only species with a breeding population and not vagrants that occur in New Zealand but which breed elsewhere. Species with validly published names were included if there was fossil evidence for a breeding population before human contact. Species with a breeding population at the time of European contact were included unless contrary evidence from the fossil record indicates that they actually colonised after human settlement. Species without a fossil record were included if a breeding population exists on a relatively undisturbed island within the New Zealand archipelago as defined above. Species now present on the main islands were excluded if they are absent from all well-documented fossil faunas. Species were excluded from the breeding fauna and treated as vagrants where sustained breeding has not been demonstrated. The phylogenetic species concept is applied both to fossil and to living taxa. The late Quaternary fossil record of birds in New Zealand is excellent, and the contribution of extinct taxa to the total list is understood at least as well as that of the surviving taxa. Many taxa presently recognised at subspecific level are treated here as full species. Twelve extinct species whose former presence is known from fossil evidence, but for which no description has been published, are listed under informal species designations. Taxonomic considerations limited the extent to which the main list could reflect present understanding of the diversity of the avifauna; some undescribed species are at present subsumed under one species name. Where previous taxonomic publications provide precedence, available names at the species-level have been used. A supplementary hypothetical species list includes all nomenclatural changes signalled in extensive annotations to the main list. In this list we accept 245 species in 110 genera representing 46 families; 176 species were endemic to the archipelago. Preliminary biogeographic analyses based on the composition of the supplementary list show that there were four separate regional faunas: a northern subtropical fauna (Norfolk, Kermadecs); the major fauna of the main islands (North, South, Stewart, and offshore islands); a Chathams fauna (Chatham Islands only); and a subantarctic fauna on the southern islands. Species with wider distributions formed link groups. The origin and compositions of the regional avifaunas and their endemic species differ with their

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Z99045
Received 2 November 1999; accepted 18 January 2001

geographic position, climate, and proximity to source faunas. Instances of speciation in groups such as the *Coenocorypha* snipe and *Petroica* flycatchers, and adaptive radiations in groups including moa and acanthisittid wrens, show that there are many avenues for research on the rate of evolution in island and mainland populations of New Zealand birds and that there are large gaps in knowledge of even common taxa. A brief case study demonstrates the inadequacies of using species lists that do not include Holocene fossil species. Species-area curves based on the total fauna differ substantially from those developed in previous studies based on incomplete, or biased, lists. Pleistocene glaciations caused the pattern of distribution of species on the main islands to change in concert with vegetation changes. Other possible effects include the elimination of warm climate species early in the cooling phase more than 1 million years ago, the speciation in groups including waders and parrots as new habitats (e.g., braided riverbeds and alpine areas) appeared, and the appearance regularly during the Pleistocene of islands that were potential staging points for colonisation of the Chatham Islands. For at least the past 100 000 years, until 2000 years ago, the fauna appears to have been very stable in composition, despite strong cyclic fluctuations in climate and vegetation. The effects of extinctions within the past 2000 years on the composition of the present fauna include the elimination of most of the endemic taxa from all but the subantarctic faunas. Only 169 species of the original late Holocene breeding fauna survive. The extinctions have resulted in a strong bias towards marine and coastal taxa in the present avifauna, in contrast to the balanced representation of terrestrial and marine species in the Pleistocene and Holocene fauna. The importance of systematic studies and the determination of the status of island populations to conservation and basic ornithological research is emphasised. The systematic status of many New Zealand birds is poorly known at present.

Keywords avifauna; list; breeding species; phylogenetic species concept; New Zealand; extinction; evolution; biogeography; new synonymy

INTRODUCTION

Biogeographic studies of the New Zealand regional avifauna (e.g., Fleming 1962; Diamond & Veitch 1981; Williams 1981, 1984; Diamond 1984; East & Williams 1984) have had to rely on interpretation of checklists of extant taxa that included introduced species and vagrants. Yet, the biogeographically interesting and significant fauna of New Zealand must be that which occupied the archipelago before human influences changed the distribution and abundance of many species only within the past two millennia (Holdaway 1989; McGlone 1989). Before humans arrived, New Zealand's avifauna had been stable in composition, and largely in distribution, since the end of the Otiran glaciation about 10,000 years ago (Worthy 1999a). There is no evidence for colonisation by birds from outside the archipelago or extinction during that time, although there may have been alterations of range and colonisations within the archipelago.

To achieve a meaningful analysis of the biogeography and evolution of the New Zealand avifauna requires knowledge of the original regional avifaunas. The taxa in these faunas did not evolve in the much-altered environment resulting from the very recent effects of mammalian predators and human settlement (Anderson 1991; Holdaway 1996, 1999a, b; Higham et al. 1999). The use of the plural 'faunas' is deliberate; New Zealand consists of several distinct geographic regions, each with its own fauna with a separate and distinctive evolutionary history. The differences stemmed from marked regional differences in geological longevity of the land masses, climate, geography, and proximity to source faunas.

Unresolved problems in the systematics of New Zealand birds make it impossible at present to prepare definitive lists for the various archipelagoes. The common view is that the relationships and taxonomy of the New Zealand avifauna are well understood, but this view is being challenged by work in New Zealand and elsewhere. The present compilation makes the gaps and inconsistencies abundantly clear. The recent revision of the albatrosses (Robertson & Nunn 1997) shows that much has yet to be learned about even supposedly well-known groups. For taxa known only as fossils, the problems are intrinsically greater, but progress has been made, especially with the perennially difficult moas (Millener 1982; Worthy 1988a, b, 1989a, b, 1992) and waterfowl (Worthy 1995, 1998b; Worthy et al. 1997; Johnson & Sorenson 1999; Kennedy & Spencer 2000). Work is proceeding on other groups as well (e.g., Trewick 1996).

New Zealand has one of the best late Quaternary fossil records of birds in the world. The abundance of fossils and widespread distribution of deposits especially in the North, South, and Chatham Islands, provide levels of detail in the distribution and changes in distribution, that can rarely be obtained elsewhere. The broad pattern of the original distributions of most species, at least on the main islands, is now reasonably well known (e.g., Millener 1981; Horn 1983; Worthy & Holdaway 1993, 1994, 1995, 1996; Holdaway & Worthy 1997; Worthy 1997a, 1998a,b,c, d, e; 1999a,b). Analysis of former distributions also leans to some extent on information from archaeological sites, although human transport of some material (for example to Stewart Island – Worthy 1998d) has been a source of error in the past. Worthy (1997b, 1998b, d) has reviewed progress to date on reassessing the archaeological faunal material. The distribution of the living species is based on information in Oliver (1955), Schodde et al. (1983), Bull et al. (1985), Marchant & Higgins (1990) and Turbott (1990), unless noted otherwise.

Information is lacking most obviously for the offshore islands, for many of which there are only incomplete lists and no known fossil sites. The vegetation, and presumably the avifauna, of many islands in the group recognised here as "northern offshore", has been so altered that the original avifauna may never be known. Inferences may be drawn, however, from historic records for islands such as Stephens Island in Cook Strait, whose original fauna was – briefly – available for scientific study in the 1890s. Distributions given in this paper must necessarily be tentative and incomplete for these islands.

Until a definitive list for New Zealand can be prepared, we offer the following working list as a summary of the composition of the avifauna that had evolved or established breeding populations here before human interference. We have developed it to indicate present knowledge, and lack of knowledge, of the living and extinct taxa. We hope that it will be a useful tool in analyses of human impact, evolutionary and conservation biology, and biogeography of the Australasian and Pacific areas. It is also a convenient forum for reviewing current understanding of the New Zealand avifauna.

Despite the example set by Oliver (1930), it was not until the most recent New Zealand bird checklist (Turbott 1990) that species recently extinct but known only from fossils were included on equal terms with living species in official checklists. Their inclusion as an appendix to the previous list (Kinsky 1970) was justified on the basis of "greatly extended interest in archaeology throughout New Zealand" and not because of the intrinsic value of an integrated systematic list. A separation of living and extinct species characterised lists until 1990, as most checklists were presented more as tools for field observers and editors than as baselines for work in diverse fields. All studies were tied to the nomenclatural base of the then-current checklist, and the inherent biases in treatment were reflected in research, in New Zealand and elsewhere.

Even the archaeological studies that were supposed to be facilitated (Kinsky 1970), were affected by the peripheral treatment of the extinct taxa. Cassels (1984), Anderson (1989), and Holdaway (1989) depended on the 1970 checklist. Oliver (1955) might have been a better source because, although he dealt with the extinct species separately, they were given the same level of treatment as extant species. The general impression given by the near exclusion of extinct taxa in the 1953 (Fleming 1953a) and 1970 (Kinsky 1970) checklists was that only living taxa were significant entities in the fauna. The extinct species which had constituted a large proportion of the avifauna when humans arrived may have been theoretically interesting to the compilers but were given less apparent importance in the lists than species recorded once, well outside their normal range. Such impressions seem to have influenced most faunal, biogeographic, and evolutionary analyses into the 1980s (e.g., Williams 1981, 1984; Diamond 1984), and are still influencing them today.

The historical development of the New Zealand avifaunal list was summarised by Kinsky and his coworkers (Kinsky 1970: 10–11). More recently, bare lists of the passerines (Holdaway 1988) and of the whole avifauna (Holdaway 1991a) have been published to emphasise that avian systematics and taxonomy in New Zealand are not as advanced or settled as commonly believed, and that new information such as the DNA-DNA hybridisation results of Sibley & Ahlquist (references cited in Holdaway 1991a) might alter present perceptions of relationships within the avifauna.

Much of the work on systematics of New Zealand birds is still done elsewhere (e.g., Christidis et al. 1996; Houde et al. 1997), and much that is of relevance to the New Zealand avifauna is not published in the local literature (e.g., work on the adzebills – Weber & Hesse 1995; Weber & Krell 1995; and teal – Kennedy & Spencer 2000). In addition to integrating the extinct taxa and concentrating solely on the breeding fauna, the list we present here also attempts to bring together as much of the new literature as necessary to reflect current views and recent research. It includes the faunas of all archipelagoes in the New Zealand region.

Protocols for inclusion of taxa

1. *Fossil evidence for a breeding population of a taxon in New Zealand before human contact.* For example, beach-wrecked sea birds contribute substantially to dune deposits. Oceanic species that are rare in dune deposits and unknown in other fossil deposits are considered to be vagrants or seasonal migrants and improbable breeders on the island concerned, as with the *Aptenodytes patagonicus* recorded from the Chatham Islands (Scarlett 1976). A particularly good example of an abundant non-breeding visitor that has a high likelihood of appearing in dune deposits is *Puffinus tenuirostris*, so, for example, the records of that species from Mason Bay, Stewart Island (Worthy 1998a) are presumed to be of birds wrecked on migration. For birds recently washed up on beaches, the total number of *P. tenuirostris* recorded over 45 years was nearly 20% of that of the locally breeding *P. griseus* (Powlesland & Pickard 1992). Where seabirds are listed in Turbott (1990) as being present as fossils on an island, but do not appear in either our main list or our Appendix 2, we have assumed that the remains were derived from beach-wrecks and not from a breeding population on that island. We have treated marine taxa found as fossils in inland caves as probably derived from breeding populations in that area.
2. *Valid taxonomic differentiation from related taxa elsewhere* (see notes below for discussion of treat ment of species). Where our treatment differs from that in Turbott (1990), only names and combinations that have been previously published are used in the main list. Explanations of differences in usage between the present list and Turbott (1990) are given in the notes. Undescribed taxa are listed where there is evidence for taxonomic distinction (or, in some instances, such as the Norfolk and Campbell Island snipe, this evidence includes a strong expectation based on levels of differentiation in other forms within the genus). Changes to present names made necessary by the taxonomic decisions advocated in the SYSTEMATIC LIST (below) are listed in Appendix 2.
3. *Presence of a contemporary breeding population on relatively unmodified islands* (there are no completely unmodified islands in the New Zealand region), even without fossil evidence.
4. *Presence of a breeding population at European contact* unless (as in *Anas rhynchotis*, *Porphyrio porphyrio*, *Botaurus poiciloptilus*, and *Circus approximans*) there is contrary evidence from the fossil record.

Protocols for exclusion of taxa currently on the New Zealand list

1. *Absence from all known large and well-documented fossil faunas* in sites where the taxon might have been expected, from its known ecology, to be included at the time of deposition.
2. *Lack of evidence of sustained breeding,* for example, *Aythya australis*, *Chlidonias leucoptera*, *Recurvirostra novaehollandiae*, and *Artamus personatus* on the main islands, and *Phalacrocorax melanoleucos* on Campbell Island.
3. *Taxonomic disputes.* Taxa of questionable taxonomic standing are excluded only if a definite statement as to their inadmissability has been published in a taxonomic work. In some instances, we have noted our reasons why we consider a species biologically invalid, but have had to include it in the systematic list in the absence of a published treatment of the problem.

Geographic limits

The list includes all species thought to have been breeding in the New Zealand region at the time of human discovery. Geographic abbreviations are: Norfolk Island, with Nepean and Philip Islands (Nf), the Kermadec Islands (K), northern offshore islands (NO), North Island (N), South Island (S), southern offshore islands (SO), Stewart Island and outliers including the Solanders (St), the Chatham Islands (Ch), and the subantarctic islands of the Snares, Bounty, Antipodes, Auckland, Campbell, and Macquarie Island groups (Sub), but excluding the Antarctic continent or its inshore islands.

Although Norfolk Island and Macquarie Island are politically Australian territories, biogeographically and geologically they have closer affinities to New Zealand. The placement of the Macquarie Island avifauna as part of the New Zealand avifauna is widely accepted, for example by Abbott & Simpson (1972) and Turbott (1990), although the inclusion of the Norfolk avifauna is not (Abbott & Simpson 1972). Williams (1971) regarded Norfolk Island as having a "predominantly Australian" avifauna but, as for the Kermadecs, the list presented here demonstrates a closer relationship with the New Zealand avifauna and a strong tropical Pacific influence. The avifauna of the Australian territory of Lord Howe Island has close links with that of Norfolk Island (e.g., Hutton 1986), but we have excluded it from this list because, unlike Norfolk Island, it lacks key mainland New Zealand groups (*Coenocorypha*, *Hemiphaga*, *Nestor*).

Islands in Cook Strait (except Kapiti and Mana) are regarded as being biologically part of the South Island and are listed as southern offshore islands. Those in Foveaux Strait are regarded as outliers of Stewart Island. The Southern Offshore (S) islands category extends therefore from the Marlborough Sounds to Puysegur Point in southern Fiordland and Chaslands Mistake in eastern Southland. Norfolk and the Kermadecs, and the subantarctic islands are, of course, artificial groupings, but they have been pooled here for convenience of analysis. Hence, the adopted arrangement of northern (subtropical) islands, the three main islands (with their outliers separately), the Chathams, and the southern (subantarctic) islands. We define offshore islands as those included in NO and SO, and outlying islands as those included in Nf, K, Ch, and Sub.

Systematic conventions and notes

The list is presented in the higher taxonomic order used in the current New Zealand checklist (Turbott 1990), for convenience of comparison. The lowest taxonomic unit listed is the species, with higher taxonomic levels usually as in Turbott (1990), even though we do not necessarily agree with them. In particular, the arrangement is not followed for the raptors or *Turnagra*. Where our systematic treatment differs from those in Turbott (1990) and Schodde et al. (1983), it represents our views based on references cited here. In all instances the usage in the main list has a precedent in earlier literature such as Oliver (1955).

We have not erected any new names or made new combinations in the *main* list. However, in Appendix 1 we make one formal new combination and list the taxa whose status we have changed from subspecies to species, on the basis of (mostly unpublished) morphological and genetic evidence, and two taxa that we believe cannot be supported on present evidence. Based on these decisions, and on comments made in the notes to the main text, we offer in Appendix 2 a list incorporating predictions of future taxonomic changes. Taxa that we believe will be eliminated by future research are underlined and omitted from the biogeographic analysis. Where we have elevated a subspecies to species rank in Appendix 1 and there is no previous published revision that can be cited in justification, the name is given in **bold** type in Appendix 2 (as discussed in the notes to the main list), and the taxa are treated as separate species in the counts and analysis. The single new combination is flagged in the Appendix 2 list.

The present paper is not the place to revisit the long-standing debate on how to determine whether a population, particularly an island population, should be accorded species rank (e.g., Mayr 1963; Cracraft 1983), but there are obvious problems in attempting to reconcile treatment of living species with that of extinct species known only from fossil remains. New Zealand and other oceanic islands such as Hawaii, are unusual in that large percentages of their recent terrestrial avifaunas are now extinct. Faunas on continents dominated by taxa that are now extinct are much older, at least 10 000 years old in the case of North America, site of the most recent major continental extinction event (Martin 1984). For fossil faunas, all taxa have to be assessed purely on perceived differences in morphology; for living species, there is a wider choice of species concepts to which one might appeal (see, for example, the viewpoints presented in the anthology edited by Ereshefsky (1992) and the papers in Claridge et al. (1997)). A major problem for the systematics of New Zealand birds is the abundance of allopatric forms in groups such as the snipe and tomtits. For previous lists, personal judgment of the systematist has been the final arbiter of the rank adopted for each population, usually with at least a tacit acknowledgment of the biological species concept.

In the present work, we lean more towards the phylogenetic or diagnostic species concept of Cracraft (1983, 1997). Hence, we use the criterion of diagnostic taxa, rather than the biological species concept which emphasises the generally untestable ability to interbreed (Mayr 1963) (except the work on *Cyanoramphus* by, for example, Taylor et al. (1986)). However, the ability to interbreed may be misleading, as again shown by *Cyanoramphus* (Boon et al. 2000). Among proponents of the phylogenetic species concept, the ability to interbreed is viewed as a shared-primitive attribute and of no consequence in the recognition of species (Mayden 1997). For example, few would doubt that the widely interbreeding *Anas platyrhynchos* and *A. superciliosa* are full species. It has been tacitly agreed that if a taxon can be diagnosed by external morphological characters that it will be a biological species (Mayr 1963). However, the reverse does not hold, as cryptic species can be extremely difficult to identify from morphology and there is usually insufficient knowledge of genetic and other variation in most of the avifauna to recognise them: see, for example, the recent suggestion of such forms in the kiwi (Baker et al. 1995). The diagnostic species concept maintains that a taxon should be accorded species rank if all members of its constituent populations share a unique combination of characters, which may be morphological, behavioural, ecological, or molecular. It does not require the presence of autapomorphies (characters unique to the taxon) to provide an effective operational definition. To do so would negate the acceptance of a living parent species, because only the derived taxon could be defined in this way. Wiens & Servedio (2000) have suggested a technique for quantitatively assessing the strength of evidence for species distinction, which has potential for the application of the phylogenetic concept.

The precepts of the diagnostic species concept have been adopted by the Dutch committee on avian systematics (Comissie Systematiek Nederlandse Avifauna, CSNA), an organisation supported by both the Netherlands Ornithologists' Union and the Dutch Birding Association, and Sangster et al. (1999) contains a detailed summary of the issues and their practical resolution. Some of the determinations made by the committee (Sangster et al.1999) are relevant to the New Zealand list: treatment of the soft-plumaged petrel complex as separate species (*Pterodroma mollis*; *P. feae*; *P. madeira*), recognition of the Balearic shearwater (*Puffinus mauretanicus*) as distinct from the Manx shearwater (*P. puffinus*), the separation of Cory's shearwater (*Calonectris borealis*) from Scopoli's shearwater (*Calonectris diomedea*), the recognition of separate species of *Porphyrio* rather than one polytypic species (*Porphyrio melanotus*), the recognition of *Casmerodius* for *Egretta* for the great white egret, *Pluvialis fulva* for the Pacific golden plover (already adopted), and the separation of Richard's pipit (*Anthus richardi*) from the New Zealand pipit (*Anthus novaeseelandiae*).

In New Zealand, North and South Island representatives of species pairs of different groups of passerines differed sufficiently in their ecology and behaviour to have responded differently to introduced predators (which may themselves, however, have differed in their ecology between habitat types and at different altitudes). In some instances (e.g., *Callaeas*), one of the two congeneric species proved to be fatally vulnerable to changes that the other survived (Holdaway 1999a); in others (*Philesturnus*, *Turnagra*), both taxa were equally vulnerable. In some songbirds, such as the *Petroica* robins, there are significant differences in body size between island populations, but we have accepted species status only where differences in ecology, skeletal morphology, or plumage support the size differences. In *Philesturnus*, *P. carunculatus* has a separate juvenile stage — once recognised as a different species — that is lacking in *P. rufusater*, and the two species differ also in adult plumage pattern, as well as body size.

We believe, following Cracraft (1997), that the emphasis of taxonomy should be on taxa as the *results* of the evolutionary processes rather than on the process itself. A key outcome of applying the phylogenetic species concept is that several taxa recognised as subspecies in the current New Zealand checklist (Turbott 1990) are elevated here to full species, just as Oliver (1955) did in relation to the checklist of that time (Fleming 1953a). We have tried to apply our judgment on the rank of species equitably to both living and fossil forms. Obviously, discrepancies in treatment will remain.

Again, our list points to the need for much more work on the systematics of New Zealand birds using modern techniques of character analysis. In particular, the promise of molecular biology is that the problems of defining degree of differentiation within and among both fossil and living taxa can be assessed from repeatable and comparable data. The widespread use of "evolutionary significant units" in conservation and management requires that the unit be definable: we feel that the criteria suggested by Cracraft (1983, 1997) provide a useful framework for recognition of the evolutionary units in the New Zealand avifauna.

Composition of regional avifaunas

Although the purpose of this paper is to present a list of the New Zealand avifauna based on the most recent information, a preliminary analysis of the local patterns within that fauna is appropriate. The effect of revising the list, and of including recently extinct taxa, on biogeographical treatments of the total fauna is also briefly explored.

Faunal groupings were investigated using the program TWINSPAN (Hill 1979). Regions were grouped according to shared taxa, and taxa were grouped according to their distribution within the greater archipelago. The composition of both the original and the extant avifaunas were examined. Results are presented as dendrograms showing degrees of association of regions and of species (Fig. 2–3), which provide a formal framework for what has normally been an intuitive process of assigning species to local faunas. Lists of taxa endemic to each fauna are given in Appendix 3. Acronyms for taxa in Fig. 3 are given in Appendix 4.

Institutional abbreviations

MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; CM, Canterbury Museum, Christchurch.

SYSTEMATIC LIST

The taxa recognised in this list are not numbered consecutively as in the formal checklists (Fleming 1953a; Kinsky 1970; Turbott 1990), because frequent changes made necessary by new systematic research rapidly makes any such system unwieldy and unworkable. Numbering seems to have little practical use. Totals are given for numbers of species in families and orders as recognised in the lists. Taxa that are extinct in New Zealand are indicated by †, global extinctions by ††. Distributions given in the list, are for **breeding populations** at the time of human contact.

Within genera, species are listed first within groupings (such as brown kiwis before spotted kiwis), then geographically from north to south, according to their breeding distribution in here and in Appendix 2. Nf, Norfolk, Nepean, and Philip; K, Kermadecs; NO, northern offshore; N, North, S, South; southern offshore; St, Stewart and outliers (including Solanders); Ch, Chathams; Sub, Snares, Bounty, Antipodes, Auckland, Campbell, Macquarie.

Order Dinornithiformes (11)

Family Emeidae (8)

Subfamily Anomalopteryginae (5)

Anomalopteryx didiformis††	–	–	N	S	–	–	–	–
Megalapteryx didinus††	–	–	–	S	–	–	–	–
Pachyornis mappini††	–	–	N	–	–	–	–	–
Pachyornis elephantopus††	–	–	–	S	–	–	–	–
Pachyornis australis††	–	–	–	S	–	–	–	–

Subfamily Emeinae (3)

Euryapteryx curtus††	–	NO	N	–	–	–	–	–
Euryapteryx geranoides††	–	NO?	N	S	–	–	–	–
Emeus crassus††	–	–	–	S	–	–	–	–

Family Dinornithidae (3)

Dinornis struthoides††	–	NO	N	S	SO	St	–	–
Dinornis novaezealandiae††	–	–	N	S	SO	–	–	–
Dinornis giganteus††	–	–	N	S	SO	–	–	–

Notes Moa are known exclusively from fossil and archaeological evidence and are (or were) endemic to the central archipelago of New Zealand. There are Stewart Island records of *Pachyornis elephantopus*, *Emeus crassus*, and *Euryapteryx geranoides*, and a single bone of *Anomalopteryx didiformis* (Turbott 1990), but they are exclusively from archaeological sites or of archaeological age (Worthy 1998d). On taphonomic grounds the material of each was probably imported to the island, mainly as joints of meat (Worthy 1998d). *Dinornis struthoides* does, however, appear to have had a population on Stewart Island (Worthy 1998d).

Pachyornis elephantopus is reported from the North Island in Turbott (1990) but the records were based on the misidentification of other taxa (Worthy 1987, 1988b, 1990). The record of *Euryapteryx curtus* for NO is MNZ S34025, Great Barrier Island; Law (1972) records *Euryapteryx geranoides* from archaeological site N30/5 at Harataonga on Great Barrier Island but the identification has not been checked and is probably not sustainable. The record of *Dinornis struthoides* from NO is based on Weetman (1897) and Hutton (1891). *D. struthoides* from SO is based on a juvenile specimen from a dune deposit on D'Urville Island (THW, unpubl. data). Millener (1981) recorded *Dinornis novaezealandiae* from Great Barrier Island (NO) but the specimen (Auckland University Anthropology Department, unregistered) was from the archaeological site N30/5, so may not have been killed on the island. The SO record is based on material from D'Urville Island in CM and in MNZ (S820).

The record of *D. giganteus* from SO is a specimen from D'Urville Island (MNZ S34004). Several records from islands close to the North Island mainland (Moturua, Motukawanui, Motutapu, and Tiritiri Matangi) have been omitted from this list because they are midden records (Millener 1981: 794–780; THW, unpubl. data), and the carcases were probably transported to the sites from the adjacent mainland. The same applies to records of moa bone from Mana Island (Miskelly 1999).

The Portland Island record of *D. giganteus* (Millener 1981: 825) is omitted because it is older than Holocene age (THW, unpubl. data) and therefore falls outside the parameters of this study. Fossil records from Quarantine and Scinde Islands at Napier (Millener 1981: 828–829) are also excluded because those "islands" are attached to the mainland, and the deposits are probably of Pleistocene age (Worthy et al. 1991).

Order Apterygiformes (5)

Family Apterygidae (5)

Apteryx mantelli	–	NO	N	–	–	–	–	–
Apteryx australis	–	–	–	S	SO	St		–
Apteryx "eastern South Is."††	–	–	–	S	–	–	–	
Apteryx owenii	–	–	N	S	SO	–	–	–
Apteryx haastii	–		–	S	–	–	–	–

Notes In the brown kiwi, we recognise a northern (North Island) species, and a southern species on Stewart Island and in the southwest of the South Island (Bartlett 1852). These are presently listed as subspecies of *A. australis* (Turbott 1990) but further work is needed. A relict population near Okarito in Westland and the North Island form may together deserve species rank (Baker et al. 1995), but no formal name changes were proposed. A small, stout kiwi separable from both brown and little spotted kiwi is known from fossils from Canterbury, Otago, and Southland (Worthy 1997a, 1998c, 1998d). Lack of skeletal material of the Okarito kiwi precludes comparison between the fossil and living forms, but they could be the same as the eastern taxon. *A. mantelli* is listed for NO, because Palma (1991) showed that it was an original part of the fauna of Little Barrier Island. We assume that the North Island population of *A. owenii* that went extinct at the end of the 19th century was the same species as that presently on Kapiti and D'Urville islands and that which occupied the South Island until the late 20th century, but variation may not be apparent in the limited material available and there has as yet been no attempt to extract its DNA.

Order Podicipediformes (2)

Family Podicipedidae (2)

Podiceps cristatus	–	–	N	S	–	–	–	–
Poliocephalus rufopectus			N	S				

Notes Millener (1991) suggested that both species might be recent immigrants. However *P. rufopectus* was present at Pyramid Valley 3000 years ago (Holdaway & Worthy 1997) and is a distinct endemic species. Horn (1983) recorded *P. cristatus* from Layers 2 and 3 at Poukawa which were dated by volcanic ash layers to 1000–4000 and 4000–7000 years B.P. respectively.

Order Procellariiformes (53)

Family Diomedeidae (12)

Diomedea sanfordi	–	–	–	–	–	–	Ch	–
Diomedea chionoptera	–	–	–	–	–	–	–	Sub
Diomedea exulans	–	–	–	–	–	–	–	Sub
Diomedea epomophora	–	–	–	–	–	–	–	Sub
Thalassarche bulleri	–	–	–	–	–	St	–	Sub
Thalassarche eremita	–	–	–	–	–	–	Ch	–
Thalassarche sp. 1	–	–	–	–	–	–	Ch	–
Thalassarche impavida	–	–	–	–	–	–	–	Sub
Thalassarche cauta	–	–	–	–	–	–	–	Sub
Thalassarche salvini	–	–	–	–	–	–	–	Sub
Thalassarche chrysostoma		·	–	–	–	–	–	Sub
Phoebetria palpebrata	–	–	–	–	–	–	–	Sub

Notes Our acceptance of several full species not recognised by Turbott (1990) follows the review by Robertson & Nunn (1997). Most existing breeding islands (except Chathams, Enderby, and Macquarie) have no known fossil records, but almost all of this group are endemic to the region so presumably evolved here. The large, pale "wandering" albatross *D. chionoptera* breeds only at Macquarie Island in the New Zealand region (Marchant & Higgins 1990). A smaller, darker, more northerly-breeding "wanderer" (*D. exulans*) breeds on Antipodes, Auckland, and Campbell Islands in the New Zealand region. Robertson & Warham (1992) recognised the Antipodes and Campbell birds as a subspecies *antipodensis*, distinct from the Auckland Island birds (*gibsoni*). Robertson & Nunn (1997) have elevated each to full species. However, the plumage and measurements of Antipodes, Campbell, and Auckland Island birds show considerable overlap and many are not distinguishable in the hand (see Robertson & Warham 1992, 1994), so we have not recognised them here as being distinct, pending further information. Some fossil bones of large albatrosses from the Chatham Islands have previously been referred to *D. exulans* (see Turbott 1990; Robertson 1991) or *D. epomophora* (Imber 1994; Robertson & Nunn 1997) but all that have been examined by us fall within the size range of *D. sanfordi* (AJDT, unpubl. data), which still breeds on the Chathams.

The small population of *D. sanfordi* at Taiaroa Head on the South Island was established in the early twentieth century (Richdale 1939) and as yet there is no fossil evidence for the former presence of a breeding population on the South Island.

Thalassarche melanophris currently breeding in the New Zealand's subantarctic has been excluded because it is probably a recent colonist (Tennyson et al. 1998). *T. melanophris* takes precedence over the often-used *T. melanophrys* (see Christidis & Boles 1994), in accordance with Article 32 Cii of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). We use *Thalassarche cauta* and include *T. steadi* in its synonymy because the character used to separate these as species (that wing lengths do not overlap, Robertson & Nunn 1997) was based on *T. steadi* having a wing length of > 600 mm, which is incorrect (Marchant & Higgins 1990). Robertson & Nunn (1997) accord species rank to both currently recognised races of *Thalassarche bulleri*, but point out that the name *platei* used for the northern (Chatham Islands) birds is based on a juvenile of the southern form. We refer to the Chatham Island form here as *Thalassarche* sp. 1, but it is only questionably separable from *T. bulleri* at the species level, and Robertson & Nunn (1997) present little information on how the forms can be distinguished. The small breeding population (referred to as *"Diomedea* *bulleri platei*") on Rosemary Rock in the Three Kings group to the north of the North Island (Wright 1984; McCallum et al. 1985) seems to be of recent origin, as it was not reported by earlier observers.

Records of larger *Thalassarche* are sufficiently abundant in middens on the eastern and southern coasts of the South Island for it to be possible that populations bred there into Polynesian times (Worthy unpubl. data); evidence of breeding sites is required to confirm this suggestion.

Family Procellariidae (36)

Subfamily Procellariinae (15)

Puffinus pacificus	Nf,K	–	–	–	–	–	–	–
Puffinus carneipes		NO	–		SO		–	
Puffinus bulleri	–	NO	–	–		–		–
Puffinus griseus	–	NO	N	S	SO	St	Ch	Sub
Puffinus gavia	–	NO	N	S	SO	–		–
Puffinus huttoni	–	–		S	–	–		–
Puffinus spelaeus††	–			S	–	–	–	
Puffinus assimilis	Nf,K	NO	N	–	–		–	
Puffinus elegans	–		–	–	–	–	Ch	Sub
Pelecanoides urinatrix	–	NO	N	S	SO	St	Ch	Sub
Pelecanoides georgicus	–	–	–	–	–	St	Ch	Sub
Procellaria parkinsoni	–	NO	N	S	–	–	–	–
Procellaria westlandica		–	–	S	–	–	–	–
Procellaria aequinoctialis	–	–	–	–	–	–	–	Sub
Procellaria cinerea	–	–	–	–	–	–	–	Sub

Notes A fossil from Southland attributed to *Puffinus bulleri* by Worthy (1998e) has been re-assessed and could represent one of several medium-sized petrel species (AJDT, unpubl. data). Holdaway & Worthy (1994) described the West Coast, South Island, population of small *Puffinus* as *Puffinus spelaeus*. "Fluttering shearwaters" reported by Millar & Jones (1997) on an unnamed island off the Kaihoka coast, northwest South Island, within the prehistoric range of *P. spelaeus*, in the 1996/97 summer have been identified from bones (MNZ 25764) as *P. gavia* (AJDT, unpubl. data). "Fluttering shearwater type" calls heard by M. Lark (pers. comm. to AJDT) at Scott's Lookout, North Westland, on 1 December 1996 are also within the former range of both *P. gavia* and *P. spelaeus* (Holdaway & Worthy 1994) and the site requires further examination. *P. gavia* is known from sites in northwest Nelson and elsewhere in the South Island (Holdaway & Worthy 1994; Worthy 1997a).

P. gavia and *Pelecanoides urinatrix* were recorded as likely to have bred in the North Island by Millener (1981: 265); *P. urinatrix* was formerly widespread in the South Island (Worthy & Holdaway 1993, 1995, 1996; Worthy 1997, 1998c, d); one *P. assimilis* was recorded from a North Island cave by Millener (1981: 422).

The *Puffinus assimilis* species complex is widely distributed around the world, and the species are separated on size, plumage, and genetic differences (Fleming & Serventy 1943; Marchant & Higgins 1990; Austin 1996). Future reviews will probably treat all current races as full species using these data, primarily the small size of *P. a. assimilis*, and because *P. a. kermadecensis* and *haurakiensis* differ from each other in their lice (Pilgrim & Palma 1982) and calls (AJDT, unpubl. data) (see Appendix 2). Pending formal nomenclatural changes, we accept two species and three subspecies in the main list. *P. elegans* (Giglioli & Salvadori, 1869) is treated here as a full species, as it was originally named, because it is larger and has a darker plumage than other races.

A possible new shearwater species from the Chatham Islands (MNZ 24154) (Tennyson 1991a) now seems more likely to be a hybrid (possibly ♀ *P. griseus* × ♂ *P. bulleri*) (AJDT, unpubl. data).

Two local forms of diving petrel (*Pelecanoides u. urinatrix*; *P. u. chathamensis*) were synonymised without explanation in Turbott (1990). The northern (*P. u. urinatrix*), southern (*P. u. chathamensis*), and subantarctic (*P. u. exsul*) populations of *P. urinatrix* have discrete size distributions, with the northern nominate form being significantly larger (Marchant & Higgins 1990; Worthy & Jouventin 1999). It may be necessary, when DNA and ecological data are available, to recognise these as two separate species. The more similar southern forms would then become *P. exsul* (Salvin, 1896), which was originally described as a full species. A worldwide review of the six races of *Pelecanoides urinatrix* recognised by Marchant & Higgins (1990) is required to determine how the New Zealand forms are related to the others.

Subfamily Fulmarinae (21)

Daption capense	–	–	–	–	–	–	–	Sub
Macronectes halli	–	–	–	–	–	St	Ch	Sub
Macronectes giganteus	–	–	–	–	–	–	–	Sub
Pachyptila turtur	–	NO	N	S	SO	St	Ch	Sub
Pachyptila vittata	–	–	–	S	SO	St	Ch?	Sub
Pachyptila crassirostris	–	–	–	–	–	–	Ch	Sub
Pachyptila desolata	–	–	–	–	–	–	–	Sub
Halobaena caerulea	–	–	–	–	–	–	–	Sub
Pterodroma pycrofti	Nf	NO	–	–	–	–	–	–
Pterodroma cervicalis	K	–	–	–	–	–	–	–
Pterodroma alba	K?	–	–	–	–	–	–	–
Pterodroma neglecta	Nf,K	–	–	–	–	–	–	–
Pterodroma solandri	Nf	–	–	–	–	–	–	–
Pterodroma nigripennis	Nf?,K	NO?	–	–	–	–	Ch?	–

Pterodroma macroptera		NO	N	–		–	–	–
Pterodroma cookii	–	NO	N	S	–	St	–	–
Pterodroma inexpectata	–	–	N	S	SO	St	–	Sub
Pterodroma axillaris		–	–	–		–	Ch	–
Pterodroma magentae		–	–	–	–	–	Ch	–
Pterodroma sp. 1††	–	–	–	–		–	Ch	–
Pterodroma lessonii	–	–	–	–		–	–	Sub

Notes *Pachyptila turtur* has been recorded from cave sites in the North Island (Millener 1981: 422) and bred abundantly at some South Island sites (e.g., Worthy & Holdaway 1993). *Pachyptila vittata* may have colonised the Chathams after humans changed the environment and lowered the populations of other species (Tennyson & Millener 1994; AJDT, unpubl. data). *P. cookii* and *P. inexpectata* are both known from non-archaeological sites in the North and South Islands (Millener 1981: 268; Worthy & Holdaway 1993). Worthy (1993) lists ?*Pterodroma nigripennis* and *P. pycrofti* from Honeycomb Hill Cave, northwest Nelson. The record of *P. nigripennis* was based on material from Canterbury Museum mentioned in Millener (1984) but this has not been traced and is probably a mis-identification. The specimen attributed to *P. pycrofti* (MNZ S23606) appears to be an immature *P. cookii* (AJDT, unpubl. data).

"*Pterodroma* Norfolk Island" listed by Meredith (1985, 1991) is *Pterodroma neglecta* (Holdaway & Anderson in press), which appears to have been abundant on the island before European colonisation and now breeds on Phillip Island (M. Christian, pers. comm.). The former status of *Pterodroma nigripennis* at the Chathams and on the northern offshore islands is unclear, although it has recently colonised several sites (Tennyson 1991b).

P. mollis is probably a recent colonist, as it was not recorded at a New Zealand breeding colony until 1969 and has since increased (Imber et al. 1998; AJDT, unpubl. data). *Pterodroma* sp. 1 was formerly regarded as *P. inexpectata* (Turbott 1990), but it is larger than that species and does not match any of the *Pterodroma* species known to breed in the New Zealand region (Tennyson & Millener 1994; Millener 1996; AJDT, unpubl. data). A record of *Pterodroma leucoptera* "from one site" (unspecified) (Millener 1981: 441) does not appear in his appendix, where there is instead a record of *Pterodroma hypoleuca* from Haurangi #17 cave at Martinborough which we refer tentatively to *P. cookii*.

Family Hydrobatidae (5)

Oceanites maorianus††	–	–	N	S	–	–	–	–
Garrodia nereis	–	–	–	S	–	–	Ch	Sub
Pelagodroma marina	Nf,K	NO	N	S	SO	St	Ch	Sub
Fregetta tropica	–	–	–	–	–	–	–	Sub
Fregetta grallaria	Nf?,K	–	–	–	–	–	–	–

Notes The inclusion of *Oceanites maorianus* follows Oliver (1955) but its breeding ground was never located. We have tentatively attributed to *O. maorianus* the fossil material from the Holocene of the West Coast of the South Island formerly attributed to *Fregetta tropica* (Worthy & Holdaway 1993), bones of *Oceanites* from a late Pleistocene deposit near Gisborne (MNZ S35739), and an unregistered skeleton from Martinborough formerly attributed to *Garrodia nereis* (Yaldwyn 1956; Millener 1981: 441). *O. oceanicus* does not breed closer than Heard Island and the limb bone proportions of the Heard Island and New Zealand specimens differ both from each other and from northern hemisphere specimens of *O. oceanicus* (Worthy 2000).

There are confirmed records of *Garrodia nereis* from South Island cave and owl sites (Worthy & Holdaway 1996; Worthy 1997a, 1998c). We have retained the genus *Garrodia* rather than placing it as a subgenus in *Oceanites* as listed without comment in Turbott (1990). Both *Garrodia* and *Pelagodroma* were submerged in *Oceanites* by Olson (1985a), but we retain the different genera (following Oliver 1955 and others) pending a full review. Only single fossil bones of *Pelagodroma marina* are known from caves in the North Island (Millener 1981: 442) and South Island (Worthy 1998c).

The Kermadec Island storm petrel is distinct from both the New Zealand and Australian forms (Murphy & Irving 1951), but is closer to the latter. Evidence (Tennyson et al. 1989) suggests that it does breed on the Kermadecs, contra Imber (1984). Its distinctive appearance should justify its separation as a full species. Consequently, the records from Norfolk and Lord Howe Islands (Meredith 1991) presumably refer to a form more closely related to the Australian or Kermadec populations than to the more southern New Zealand form (see Appendix 2). The possible record of *Fregetta grallaria* from Norfolk Island is from Meredith (1985, 1991).

Order Sphenisciformes (10)

Family Spheniscidae (10)

Aptenodytes patagonicus	–	–	–	–	–	–	–	Sub
Pygoscelis papua	–	–	–	–	–	–	–	Sub
Megadyptes antipodes	–	–	–	S	SO	St	–	Sub
Eudyptula minor	–	NO	N	S	SO	St	Ch	–
Eudyptes pachyrhynchus	–	–	–	S	SO	St	–	–
Eudyptes "Chatham Islands"††		–	–	–	–	–	–	Ch

Eudyptes filholi	–	–	–	–	–	–	–	Sub
Eudyptes schlegeli	–	–	–	–	–	–	–	Sub
Eudyptes robustus	–	–	–	–	–	–	–	Sub
Eudyptes sclateri	–	–	–	–	–	–	–	Sub

Notes Of the larger penguins, only *Eudyptes pachyrhynchus* and *Megadyptes antipodes* are accepted in the fossil record from the South Island (Worthy 1997b) but fossils from the North Island attributed to the larger penguins have not been reassessed. It is likely that both species bred at least as far north as the Manawatu and Wairarapa coasts, as they were common in the northern South Island (Worthy 1997b). *Eudyptes filholi* Hutton, 1879 is recognised, following the original description, as a full species on the basis of its distinctive appearance (Tennyson & Miskelly 1989; Marchant & Higgins 1990). *E. schlegeli* is treated as a full species distinct from *E. chrysolophus*, following Marchant & Higgins (1990). An undescribed species of *Eudyptes* bred on the Chatham Islands (Tennyson & Millener 1994; AJDT, unpubl. data).

Order Pelecaniformes (15)

Notes Material of *Pelecanus* (Pelecanidae) from New Zealand does not differ in dimensions from that of the Australian species, *P. conspicillatus*. Although there is a chance that some may have bred in New Zealand before humans arrived, the few fossil specimens are best treated as vagrants (Worthy 1998b).

Suborder Phaethontes (1)

Family Phaethontidae (1)

Phaethon rubricauda	Nf,K	–	–	–	–	–	–	–

Suborder Pelecani (14)

Superfamily Suloidea (14)

Family Sulidae (3)

Sula dactylatra	Nf,K	–	–	–	–	–	–	–
Sula tasmani††	Nf	–	–	–	–	–	–	–
Morus serrator	–	NO	N	–	SO	St	–	–

Notes We regard *Sula tasmani* (van Tets et al. 1988) as being based on material from the upper size range of *Sula dactylatra* (RNH, unpubl. data) (see Appendix 2). The population of *Morus serrator* has increased substantially and several new colonies have formed this century (Wodzicki et al. 1984), including that on Farewell Spit (S) (Hawkins 1988), but its prehuman breeding distribution is unclear from the fossil record as presently known.

Family Phalacrocoracidae (11)

Phalacrocorax carbo	–	NO	N	S	SO	St	Ch	–
Phalacrocorax varius	–	NO	N	S	SO	St	–	–
Phalacrocorax melanoleucos		NO	N	S	SO	St	–	–
Leucocarbo carunculatus	–	–	N	S	SO	St	–	–
Leucocarbo onslowi	–	–	–	–	–	–	Ch	
Leucocarbo ranfurlyi	–	–	–	–	–	–	–	Sub
Leucocarbo colensoi	–	–	–	–	–	–	–	Sub
Leucocarbo campbelli	–	–	–	–	–	–	–	Sub
Leucocarbo purpurascens	–	–	–	–	–	–	–	Sub
Stictocarbo punctatus	–	NO	N	S	SO	St	–	
Stictocarbo featherstoni	–	–	–	–	–	–	Ch	–

Notes There is no fossil record of *Phalacrocorax sulcirostris*; the species was collected in the Bay of Islands in 1840, but was rare during the 19th century (Oliver 1955) and was probably not part of the prehuman fauna. The fossil record of phalacrocoracids in New Zealand has not been studied intensively. *Leucocarbo carunculatus* includes *L. chalconotus*. Remains of *L. carunculatus* found as far north as Tokerau Beach (Worthy 1996), North Cape, and at other widespread sites between there and the relict South Island population (THW, unpubl. data), indicate a former New Zealand-wide population. Central and southern New Zealand populations are relicts, contra Falla (1974). Siegel-Causey (1988) maintained a specific separation between *L. chalconotus* and *L. carunculatus* without examining material of the latter. *L. purpurascens* is recognised as a full species following Marchant & Higgins (1990). The full classification presented by Siegel-Causey (1988) placed *P. melanoleucos* in *Microcarbo*, *P. varius* in *Hypoleucos*, *L. campbelli* in *Nesocarbo*, *L. purpurascens* in *Notocarbo*, and the other New Zealand species of *Leucocarbo* in *Euleucocarbo*. Siegel-Causey (1988) treated all three island populations of *Leucocarbo* (=*Euleucocarbo*) as full species, as we do.

Order Ciconiiformes (3)

Suborder Ardeae (3)

Family Ardeidae (3)

Subfamily Ardeinae (2)

Egretta sacra	–	NO	N	S	SO	St	Ch?	–
Casmerodius albus	–	–	N	S	–	–	–	–

Subfamily Botaurinae (1)

Ixobrychus novaezelandiae††	–	–	N	S	–	–	Ch	–

Notes *Casmerodius* is used for the great white egret for the reasons given by Sangster et al. (1999). The former presence of a breeding colony of *C. albus* in the Far North is indicated by immature bones in the dune deposits (Millener 1981, 1991; Turbott 1990). It is also known from the lake site at Pyramid Valley (Holdaway & Worthy 1997). Also, during the Holocene, it bred at Te Aute in southern Hawke's Bay, where immature bones have also been found

(Worthy 2000). *Egretta sacra* is rare as a fossil. Breeding has never been reported from the Chathams, but the early history of the species there is unclear. Although Turbott (1990) listed only one Chatham record in about 1985, Travers & Travers (1873) included it in their list and there is a 1928 skin (Fleming 1939; MNZ 4772). *Botaurus poiciloptilus* is unknown outside recent fossil deposits (Turbott 1990; Millener 1991) and appears to be a recent colonist from Australia. There are no *Botaurus* fossils from the Chathams despite its being reported there by Travers & Travers (1873). *Ixobrychus novaezelandiae* fossils are now known from several sites, including two on Chatham Island (MNZ S29632; CM Av31320) (Horn 1983; Millener 1996; Holdaway & Worthy 1997). The reported possible presence of *Dupetor flavicollis* at Poukawa (Horn 1980) has been shown to be a misidentification of *Ixobrychus novaezelandiae* (Horn 1983).

Order Anseriformes (18)

Family Anatidae (18)

Subfamily Anserinae (3)

Cygnus atratus†	–	NO	N	S	SO	St	Ch	–
Cnemiornis gracilis††	–	–	N	–	–	–	–	–
Cnemiornis calcitrans††	–	–	–	S	–	–	–	–

Subfamily Tadorninae (2)

Tadorna variegata	–	–	N	S	SO	St	–	–
Tadorna "Chathams"††	–	–	–	–	–	–	Ch	–

Subfamily Anatinae (13)

Hymenolaimus malacorhynchos	–	–	N	S	–	–	–	–
Anas superciliosa	Nf?,K	NO	N	S	SO	St	Ch	Sub
Anas gracilis	–	–	N	S	–	–	–	–
Anas chlorotis	–	NO	N	S	SO	St	Ch	–
Anas aucklandica	–	–	–	–	–	–	–	Sub
Anas nesiotis	–	–	–	–	–	–	–	Sub
Anas "Macquarie"††	–	–	–	–	–	–		Sub
Pachyanas chathamica††	–	–	–	–	–	–	Ch	–
Euryanas finschi††	–	–	N	S	–	–	–	–
Malacorhynchus scarletti††	–	–	N	S	–	–	Ch	–
Aythya novaeseelandiae	–	NO	N	S	–	–	Ch	–
Mergus australis††	–	NO	N	S	–	St	Ch	Sub
Biziura delautouri††	–	–	N	S	–	–	–	–

Notes *Cygnus sumnerensis* is not accepted here: Worthy (1998b) casts serious doubt on its validity, finding mainland swan bones to be indistinguishable from *C. atratus* in morphology and size. However, the prehistoric Chatham Island population is said to have had smaller wings and a stouter bill (Millener 1996), and may yet require specific status if morphological comparisons support the preliminary observations. The New Zealand population was probably not genetically isolated from the Australian population because of periodic influxes of Australian birds. The most recent was about the same time as the deliberate re-introduction of the species by Europeans in the 19th century (Turbott 1990). The New Zealand population of the black swan has the unique history of having been eliminated by humans hunting for meat, re-introduced naturally and by humans, and then branded as a pest in the new agricultural landscape, and controlled by hunting and egg-collecting (Heather & Robertson 1996).

Recent work (Worthy et al. 1997; THW, unpubl. data) has shown that the two forms of *Cnemiornis* were distinct in skeletal structure as well as size. Although Marchant & Higgins (1990) list *Tadorna variegata* as resident on Great and Little Barrier Islands, the only breeding population is based on a human introduction (Bell 1976), and there is no evidence of their former presence on any northern island. The record from Mana Island in Miskelly (1999) is from a midden and the material could have been brought from the mainland. Millener (pers. comm.) and Tennyson & Millener (1994) suggest that the Chatham Island *Tadorna* was a distinct species.

The breeding status of *Anas superciliosa* on Norfolk Island before human contact is unclear (Marchant & Higgins 1990). Schodde et al. (1983) treat it as having been present when Europeans arrived in 1788, but no fossils are known (RNH, unpubl. data). *Anas gracilis* apparently was rare in New Zealand when Europeans arrived. It was not recognised here until 1866 (Oliver 1955) and has sometimes been regarded as a recent colonist (Olson 1977a). Recent increases and spread have been attributed to influxes from Australia (Turbott 1990), but it was certainly part of the prehuman fauna because it was breeding at Pyramid Valley about 3000 years B.P. (Holdaway & Worthy 1997). Perhaps the decline in *A. chlorotis* on the mainland in the 19th century allowed the smaller species to expand in numbers. Despite a record of *A. gracilis* from the Chatham Islands in 1951 (MNZ 1256), there is no evidence that it was ever established there since references to fossil material (Turbott 1990; Millener 1991) have not been substantiated.

The populations of small *Anas* from Auckland (*A. aucklandica*) and Campbell (*A. nesiotis*) Islands are treated here as full species after Oliver (1955), Livezey (1990), and Marchant & Higgins (1990). Johnson & Sorenson (1999) and Kennedy & Spencer (2000) showed that the New Zealand radiation of teal is separate from, and possibly earlier than, the separation of chestnut (*Anas castanea*) and grey teal in Australia. Kennedy & Spencer (2000) concluded that the New Zealand teal all warrant full species status. There is evidence of a further (now extinct) undescribed teal that was endemic to Macquarie Island (AJDT & P. Scofield, unpubl. data) (see Appendix 2).

Malacorhynchus scarletti has recently been found among collections of fossil bones from the Chatham Islands in Canterbury Museum and the Museum of New Zealand (THW unpubl. data). The *Aythya* record for NO is based on Williams (1981). The Chatham Islands and mainland specimens of *Mergus* may be separable from the Auckland Islands bones (Millener 1991, 1996), but this requires a detailed analysis. The NO record for *Mergus* is based on MNZ S36845.

Anas rhynchotis was present when Europeans arrived but has not been found as fossils older than 1000 years and is probably a relatively recent immigrant (Holdaway & Worthy 1997). Although the New Zealand population has been recognised as a distinct subspecies, its absence from the fossil record accords with the findings of Marchant & Higgins (1990), who could discern no clear differences between New Zealand and Australian birds, and indicates that there is no need for taxonomic recognition of the New Zealand birds. *Oxyura australis* was reported from the lake deposit at Poukawa (Horn 1983; Turbott 1990), but the material is referable to *Mergus* and *Malacorhynchus* (THW, unpubl. data) and to *Aythya* (Millener 1991).

Order Accipitriformes (3)

Family Accipitridae (3)

Circus eylesi††		–	N	S	–	–	–	–
Accipiter cf. *fasciatus*†	Nf	–	–	–	–	–	–	–
Harpagornis moorei††	–	–	–	S	–	–	–	–

Notes The Orders Accipitriformes and Falconiformes are separated here because of the fundamental differences in their osteology (Jollie 1976, 1977a, b, c; Holdaway 1994) and karyotype (de Boer 1976). *Circus approximans* is not accepted as part of the prehuman avifauna because all supposed occurrences predating Polynesian settlement have been shown to be of *Circus eylesi* (RNH, unpubl. data). The status of the forms then inhabiting the North and South Islands (described as species by Forbes, without adequate descriptions) has not been resolved (RNH, unpubl. data). Meredith (1985, 1991) reported three *Accipiter* bones from Norfolk Island and suggested that they were referable to the Australian *A. fasciatus* but recently collected specimens are not separable from *Accipiter fasciatus vigilax* of New Caledonia (RNH & R. Varman, unpubl. data.). Examination of material from the North Island attributed to *Harpagornis moorei* (Millener 1981; Holdaway 1991b) has shown that there is no valid evidence that the species was ever present in the North Island. Eagle fossils reported by Hamilton (1889) from the late Glacial site at Te Aute were misidentifications of *Circus eylesi* (Worthy 2000). A record of *H. moorei* from Stewart Island is from an archaeological site and is probably imported industrial bone (Worthy 1999b). There are several reasons to consider the few bones described as *Haliaeetus australis*, reportedly from the Chatham Islands as being mistakenly attributed to this locality (Millener 1996) and it is not accepted here as part of the fauna.

Order Falconiformes (1)

Family Falconidae (1)

Falco novaeseelandiae	–	NO	N	S	SO	St	Ch	Sub

Order Galliformes (2)

Family Phasianidae (1)

Coturnix novaezelandiae††	–	NO	N	S	–	St	–	–

Notes Remains of the New Zealand quail are abundant in deposits dating from the past 1000 years but less so in earlier horizons, presumably because of the greater extent of forest rather than shrub and grasslands before Polynesian deforestation about 600–800 years ago (McGlone et al. 1994). They are found regularly in Pleistocene deposits also, when shrublands and grasslands would have been more widespread than in the Holocene, before Polynesian settlement. The NO record is based on Oliver (1955). Fossil remains have been found on Red Mercury Island (Millener 1981: 798), and on Mana Island (Miskelly 1999): both records are from middens but are likely to be of locally obtained birds.

Family Megapodiidae (1)

Megapodius sp.†	K	–	–	–	–	–	–	–

Notes Cheeseman (1891) included a megapode in his list of Raoul Island (Kermadecs) birds, based on a report by a former settler on the island. The settler, named Johnson, described having taken eggs and young birds from 600–900 mm-high mounds built by large birds in the crater. Johnson said that the birds had been present until a large eruption in 1876 covered the floor of the crater with mud and destroyed them. On this basis, Cheeseman (1891) suggested that a megapode may have been present there until the late nineteenth century. The report has not been substantiated by fossils in the archaeological sites excavated so far, but a pigeon also reported by Johnson (in Cheeseman 1891) but not seen by scientists or collected, has been confirmed by the recent discovery of a humerus in an archaeological site (Worthy & Brassey 2000). This adds weight to the megapode sightings by indicating that Johnson was a reliable observer. The lack of terrestrial endemic species on the Kermadec Islands suggests that the megapode is most likely have been a population of an extant form of *Megapodius*, rather than an endemic Kermadec taxon, especially as the island has been devastated repeatedly by massive rhyolitic volcanic eruptions (Latter et al. 1992) that would have destroyed populations of terrestrial birds. The 1876 eruption was tiny by comparison with other events in the past 5000 years.

Order Gruiformes (19)

Family Aptornithidae (2)

Aptornis otidiformis††	–	–	N	–	–	–	–	–
Aptornis defossor††	–	–	–	S	–	–	–	–

Notes Although some recent authors (e.g., Olson 1985b; Livezey 1994) have suggested that the correct name for these birds is *Apterornis*, we retain *Aptornis*. *Apterornis* has been placed on the Official Index of Rejected and Invalid Names in Zoology [Opinion 1874, *Aptornis* Owen, 1848 (Aves): conserved as the correct original spelling (Bulletin of Zoological Nomenclature 54(2): 142–143) (1997)]. Analyses of mitochondrial DNA have shown *Aptornis* to be basal to the rails, and, contra Livezey (1998), not closely related to the kagu *Rhynochetus* of New Caledonia (Houde et al. 1997) which supports the observations of Parker (1866) that *Aptornis* was close to *Psophia*. The family is therefore placed before the rails, contra Turbott (1990).

Family Rallidae (17)

Gallirallus philippensis	Nf?/K?	NO	N	S	SO	St	–	–
Gallirallus "Norfolk Island"††	Nf	–	–	–	–	–	–	
Gallirallus australis	–	NO	N	S	SO	St	–	–
Gallirallus dieffenbachii††	–	–	–	–	–	–	Ch	–
Gallirallus macquariensis††	–	–	–	–	–	–	–	Sub
Capellirallus karamu††	–	–	N	–	–	–	–	–
Cabalus modestus††	–	–	–	–	–	–	Ch	–
Diaphorapteryx hawkinsi††	–	–	–	–	–	–	Ch	–
Dryolimnas muelleri	–	–	–	–	–	–	–	Sub
Porzana tabuensis	Nf,K	NO	N	S	–	–	Ch	–
Porzana pusilla	–	–	N	S	–	–	Ch	–
Gallinula hodgenorum††	–	–	N	S	–	–	–	–
Porphyrio mantelli††	–	–	N	–	–	–	–	–
Porphyrio hochstetteri	–	–	–	S	–	–	–	–
Porphyrio sp.	Nf	–	–	–	–	–	–	–
Fulica prisca††	–	–	N	S	–	–	–	–
Fulica chathamensis††	–	–	–	–	–	–	Ch	–

Notes We follow Olson (1973a), Marchant & Higgins (1993), and Livezey (1998) in using *Gallirallus* rather than *Rallus* for *G. philippensis* and many of its derivative species, and in recognising *G. dieffenbachii* as a full species. *Gallirallus philippensis* is rare as a fossil, and has been considered to be a recent colonist (Millener 1981, 1990, 1991), but it was present in deposits of Otiran glacial age at Honeycomb Hill Cave (Worthy 1993) and the New Zealand birds differ from other races in plumage and size (Marchant & Higgins 1993). Cheeseman (1891) recorded *G. philippensis* from the Kermadec Islands, but there are no other records from there. Two species of *Gallirallus* have been reported from Norfolk Island (Schodde et al. 1983; Meredith 1985, 1991). Meredith (1985, 1991) reported seven bones of an apparently new (still undescribed) species, plus two others tentatively attributed to this species. Further material in collections made by R. Varman from Cemetery Bay (under study by RNH) show it was flightless, larger than *G. philippensis*, and distinct from other rails in the region (RNH & R. Varman, unpubl. data). The former status of *G. philippensis* on Norfolk Island is unclear. A rail was painted by Hunter in 1790 at the time of the first European settlement, but which species has yet to be determined. Hindwood (1965) was not aware of the former presence of another rail when he attributed it to *G. philippensis* (under *Hypotaenidia*). At present, *G. philippensis* seems to be a regular visitor rather than a permanent member of the fauna (Schodde et al. 1983). *Gallirallus minor* is a synonym of *G. australis* (Olson 1975; Holdaway & Worthy 1997). The distinctive Macquarie Island form (Marchant & Higgins 1993) is recognised as a full species, as it was originally described (Hutton 1879). In view of the presence of rails on the Auckland group and Macquarie Island, it is possible that a rail was present on Campbell Island before Norway rats were introduced in the early nineteenth century.

This list follows Olson (1973a, b) in attributing the Auckland Island rail to *Dryolimnas*, and it is recognised as a full species as originally described (Rothschild 1893) because of its distinctive plumage and smaller size (Marchant & Higgins 1993). The two *Porzana*s are very rare as fossils, and Millener (1991) has suggested that they are recent colonists. Both species are extremely vagile: *P. pusilla* is found throughout Eurasia and southeast Asia, and *P. tabuensis* has colonised many islands in the wider Pacific area. These distributions, combined with the low likelihood that small rails would be exposed to predation by the falcon or owl responsible for most aggregations of small fossils in New Zealand, leads us to retain both species provisionally on the original list. *Gallinula hodgenorum* is used in preference to *G. hodgeni*, contra Turbott (1990), following the conclusions of Olson (1987). *Porphyrio melanotus*, the Australian swamphen (as differentiated from various subspecies of *P. porphyrio* in the tropical Pacific) is often assumed to be a member of the prehuman avifauna, but all fossil occurrences are in sites younger than 400 years (Worthy & Holdaway 1996). There is no evidence that the species was present in the main islands of New Zealand before people arrived (Holdaway & Worthy 1997). It was probably excluded by the suite of rails already present, and perhaps by a shortage of the short grass and raupo (*Typha*) swamp habitats the species prefers, because it is certainly vagile enough to reach New Zealand regularly. A dead pukeko (MNZ 23979) found on L'Esperance Rock, a tiny, isolated rock in the Kermadec group more than 200 km from the nearest resident population (Tennyson & Taylor 1989) demonstrates the remarkable ability of this species to disperse over water. Bones in a prehistoric archaeological site on Norfolk Island indicate the presence of a population of *Porphyrio* species on the island but the remains are too fragmentary for specific identification. The two endemic forms of *Porphyrio* on the mainland islands are specifically distinct (Trewick 1996). The extinct mainland and Chatham Island populations of *Fulica* are maintained as distinct species because of consistent differences in the skeleton (Worthy & Holdaway, unpubl. data).

Order Charadriiformes (30)

Family Haematopodidae (3)

Haematopus unicolor	–	NO	N	S	SO	St	–	–
Haematopus finschi	–	–	–	S	–	–	–	–
Haematopus chathamensis	–	–	–	–	–	–	Ch	–

Notes *Haematopus finschi* is recognised as specifically distinct from *H. ostralegus* (see Turbott 1990) and *H. longirostris* (see Hayman et al. 1986) following McKean (1978) and Marchant & Higgins (1993), and in accordance with the original description by Martens (Oliver 1955).

Family Recurvirostridae (1)

Himantopus novaezelandiae	–	–	N	S	–	–	–	–

Notes Fossil records of stilts in New Zealand are rare: inland Hawke's Bay (Worthy & Holdaway 2000); Marfells Beach (Worthy 1998b); Pyramid Valley Swamp (Holdaway 1995; Holdaway & Worthy 1997); and Otago (Worthy 1998c). The proportions of the wing and leg bones of the adult Pyramid Valley specimen are such that it had been free of any degree of introgression with *Himantopus leucocephalus*. *H. leucocephalus* probably did not colonise New Zealand until after the major habitat changes accompanying the Polynesian colonisation (Holdaway 1995).

Family Charadriidae (4)

Charadrius obscurus	–	NO	N	S	–	St	–	–
Charadrius bicinctus	–	NO	N	S	–	St	Ch	Sub
Charadrius novaeseelandiae		NO	N	S	–	–	Ch	Sub
Anarhynchus frontalis	–	–	–	S	–	–	–	–

Notes The banded dotterel from the Auckland Islands, *Charadrius bicinctus exilis*, should be included as a full species because of its greater weight and longer legs (Falla 1978; Pierce 1980, see Appendix 2). *Thinornis novaeseelandiae* and *Anarhynchus frontalis* should be included in *Charadrius*. The genus *Thinornis* was distinguished by the bill being longer than the mid-toe, and the tail being "graduated" rather than rounded as in *Charadrius* (Oliver 1955), but in all other respects *C. novaeseelandiae* is a typical *Charadrius* and is placed in that genus here following Bock (1958). The bent bill of *Anarhynchus frontalis* is not sufficient basis for generic separation as it is an adaptation to feeding in stony river beds (Burton 1972; Pierce 1979). Burton (1972) found that, apart from the laterally bent bill, the cranium is in all respects like that of a typical *Charadrius*. We have retained *Anarhynchus* in the main list but make the new combination in Appendix 1 and have used *Charadrius* in Appendix 2. A plover collected at the Auckland Islands by the *Erebus* and *Terror* expedition in late 1840 was described as *Thinornis rossii*; it is often considered as either a vagrant or mislabelled *Thinornis* (=*Charadrius*) *novaeseelandiae* (Turbott 1990). Whether it was a vagrant or represented a resident population might be resolved from further research on the fossil deposits at Enderby Island. The possibility that it was distinct from the mainland or Chatham Island populations could be tested by molecular analysis of material from the specimen.

Family Scolopacidae (8)

Subfamily Scolopacinae (8)

Coenocorypha "Norfolk Island"††	Nf	–	–	–	–	–		
Coenocorypha barrierensis††	–	NO	N	–	–	–	–	
Coenocorypha iredalei ††	–	–	–	S	–	St	–	–
Coenocorypha chathamica††	—	–	–	–	–	Ch	–	
Coenocorypha pusilla	–	–	–	–	–	–	Ch	–
Coenocorypha huegeli	–	–	–	–	–	–	–	Sub
Coenocorypha aucklandica	–	–	–	–	–	–	–	Sub
Coenocorypha "Campbell Island"			–	–	–	–	–	Sub

Notes The systematics of the *Coenocorypha* complex need work. The arrangement used here is provisional, pending further morphological and genetic study, but follows the recommendation in Higgins & Davies (1996) that *C. a. huegeli* and *C.a. iredalei* and possibly *C. a. meinertzhagenae* and *C. a. barrierensis* warrant species status (see Appendix 2).

The Norfolk Island record is based on fossil material (a humerus, three tibiotarsi) reported by Meredith (1985, 1991). The population was as far from the North Island as the Chathams are from New Zealand, and away from the prevailing winds, so the Norfolk Island population is treated here as an unnamed species. An extinct scolopacid from New Caledonia may extend the range of *Coenocorypha* further north again but available material (a single humerus) is insufficient for a full diagnosis (Balouet & Olson 1989). There is now also a record of a species of an unidentified fossil *Coenocorypha* from Fiji (THW, unpubl. data).

We assume that the extinct North Island population was conspecific with the remnant population that survived on Little Barrier Island until about 1870, and which was described as a subspecies of *Coenocorypha aucklandica* by Oliver (1955). We use *Coenocorypha barrierensis* **new status** for the North Island and northern offshore island populations of snipe, as we consider that the differences between those and *Coenocorypha aucklandica* to be sufficient to warrant species status for the northern birds.

The extinct snipe population on the South Island was probably conspecific with *C. iredalei* as no other taxonomic distinctions can be made between Stewart Island and South Island populations of other birds. Cook Strait was certainly a barrier for many species so *C. iredalei* is likely to have been distinct from *C. barrierensis*. Higgins & Davies (1996) proposed that *C. a. barrierensis* (here *C. barrierensis*) was a subspecies of *iredalei* but the two forms are separable using plumage and measurements (Miskelly 1988; Higgins & Davies 1996). DNA studies may help to resolve the issue of relationships within the genus, including the extinct populations.

A form recently discovered on Jacquemart islet off Campbell Island (Miskelly 1997) is presumed to be the remnant population of a "missing" form that lived on the main Campbell Island until rats were introduced before 1867 (King 1990).

Family Stercorariidae (1)

Catharacta skua	–	–	–	S	–	St	Ch	Sub

Family Laridae (13)

Subfamily Larinae (3)

Larus dominicanus	–	NO	N	S	SO	St	Ch	Sub
Larus novaehollandiae	–	NO	N	S	SO	St	Ch	Sub
Larus bulleri		–	N	S	–	–	–	–

Subfamily Sterninae (10)

Sterna fuscata	Nf,K	–		–	–	–	–	–
Sterna striata	–	NO	N	S	SO	St	Ch	Sub
Sterna albostriata	–	–	N?	S	–		–	
Sterna caspia	–	–	N	S	–	–	–	–
Sterna nereis	–	–	N	S	–		–	
Sterna vittata	–	–	–	–	–	St	Ch?	Sub
Anous stolidus	Nf,K?	–	–	–	–	–	–	–
Anous minutus	Nf,K	–	–	–	–	–	–	–
Procelsterna cerulea	Nf,K	–	–	–	–	–	–	–
Gygis alba	Nf,K	–	–	–	–	–	–	–

Notes Sibson (1992) suggested that *Sterna caspia* may be a recent immigrant, but Millener (1981) listed its presence in several fossil sites. The record of *Sterna vittata* on Chatham Island (Turbott 1990; Millener 1991) needs clarification. *Sterna nereis* was formerly more widespread (Parrish & Pulham 1995), but five fossil bones from Chatham Island (MNZ S28900, 28911, 28961, 30774; CM Av 32738) and a chick (CM Av 1917) that are supposed to be that species (Turbott 1990; Millener 1991), were misidentified (AJDT, unpubl. data). *Anous stolidus* may be a recent colonist at the Kermadec Islands, as it was first recorded there only in 1989 (Turbott 1990). We use *A. minutus* in preference to *A. tenuirostris* following Higgins & Davies (1996). *Procelsterna cerulea* appears to be only a recent colonist on islands off the northern coast of the North Island (Falla 1970).

Order Columbiformes (4)

Family Columbidae (4)

Hemiphaga spadicea††	Nf	–	–	–	–	–	–	–
Hemiphaga novaeseelandiae	K	NO	N	S	SO	St	–	–
Hemiphaga chathamensis	–	–	–	–	–	–	Ch	–
Gallicolumba sp. ? *norfolciensis*††	Nf			–	–	–	–	–

Notes The extinct Norfolk Island pigeon originally described as *Columba spadicea* (Latham, 1802) is here treated as a full species and not a subspecies of *H. novaeseelandiae*. The date of publication follows the explanation given in Browning & Monroe (1991). *Hemiphaga chathamensis* differs from the New Zealand species in plumage and size and is recognised as a full species following Oliver (1955)and Millener & Powlesland (2001). The identity of the large pigeon reported from Raoul Island in the Kermadecs (Oliver 1955) was uncertain until recently as no specimens had been collected. A humerus collected in 1998 is indistinguishable from *H. novaeseelandiae* (Worthy & Brassey 2000).

Meredith (1985) reported two bones (coracoid, tarsometatarsus) of a species of *Gallicolumba* from deposits in the Cemetery Bay dunes on Norfolk Island, and attributed them to *G. norfolciensis*, named from descriptions and a painting done in 1788–1790 (see Christidis & Boles 1994). Meredith (1985) also listed one bone of the living species *Chalcophaps indica* but did not include it in the list in Meredith (1991). Further material of small doves has been collected by R. Varman but awaits identification (RNH & R. Varman, unpubl. data). Schodde et al. (1983) suggest that *Chalcophaps indica* was self-introduced to Norfolk Island in the nineteenth century.

Order Psittaciformes (11)

Family Psittacidae (11)

Subfamily Strigopinae (1)								
Strigops habroptilus	–	–	N	S	SO	St	–	–
Subfamily Nestorinae (4)								
Nestor productus††	Nf	–	–	–	–	–	–	–
Nestor meridionalis	–	NO	N	S	SO	St	–	–
Nestor notabilis	–	–	–	S	–	–	–	–
Nestor "Chatham Islands"††	—	–	–	–	–	Ch	–	
Subfamily Platycercinae (6)								
Cyanoramphus cookii	Nf	–		–		–	–	–
Cyanoramphus novaezelandiae	K	NO	N	S	SO	St	Ch	Sub
Cyanoramphus auriceps	–	NO	N	S	SO	St	–	Sub
Cyanoramphus malherbi	–	NO	N	S	–	–	–	–
Cyanoramphus forbesi	–	–	–	–	–	–	Ch	–
Cyanoramphus unicolor	–		–	–	–		–	Sub

Notes No fossils of *Strigops habroptilus* have been found on Stewart Island. Williams (1956) suggested that the population of *S. habroptilus* on Stewart Island resulted from an introduction in the late nineteenth century. Williams also reported that residents of the island thought that the species was not native to the island, and that all reports of its presence related to the present century, culminating in the capture of an individual in 1949. Russ (1978) gave the time of the introduction as the 1880s, when individuals from Fiordland on board the *Kekeno* and bound for the Dunedin Exhibition were put ashore at Port Pegasus in poor condition after bad weather delayed the passage. He also thought it unlikely that Maori (or, presumably, sealers) had introduced the species in the early nineteenth century. Dawson (1962) reported that a specimen in Paris appears to have been collected on Stewart Island in or before 1847 and Williams (1960) and Russ (1978) further noted that two specimens at Leiden may have been collected on Stewart Island in the early nineteenth century, but these records lack full authentication. However, Powlesland et al. (1995) suggested that the population of about 100 birds in the mid 1970s was too large to have arisen from introductions because of its low fecundity. Fossils are known from dunes on D'Urville Island (SO) (THW, unpubl. data). The record from Waiheke Island (Millener 1981: 798) is excluded as being probably a midden bone imported from the mainland.

The reported differences in plumage and size between the North and South Island kaka (*Nestor meridionalis septentrionalis* and *N. m. meridionalis*) (Oliver 1930, 1955) are not consistently present. There are no morphological differences in the skeleton (Holdaway & Worthy 1993) which overlap in size (THW, unpubl. data), so at present we maintain the two forms as subspecies of *N. meridionalis*. The single record of *Nestor notabilis* from a North Island deposit is assumed to be of late Pleistocene age; there is no evidence that the species bred in the North Island in the Holocene (Holdaway & Worthy 1993). The Chatham Island *Nestor* is probably specifically distinct from the mainland *N. meridionalis* (Tennyson & Millener 1994; Millener 1996).

The systematics of the *Cyanoramphus novaezelandiae*/*C. auriceps* complex are highly controversial. Long regarded as a race of *C. novaezelandiae*, the Norfolk Island *C. cookii* has now been recognised as a full species (McAllan & Bruce 1989; Boon et al. in press), part of a subgroup including the New Caledonian *C. saisseti*.

Cyanoramphus malherbi was accepted as a distinct species by Triggs & Daugherty (1996), contrary to earlier suggestions that it is a colour morph of *Cyanoramphus auriceps* (Nixon 1981; Taylor 1985; Taylor et al. 1986). Although Taylor (1998) then argued again for its being a colour morph, Boon et al. (2000) present new biochemical evidence and further biological evidence (assortative mating) supporting the recognition of *C. malherbi* as a distinct species related most closely to *C. novaezelandiae*. We therefore accept *C. malherbi* in this list.

We accept *C. forbesi* as a separate species because of its larger size and distinctive plumage (Oliver 1955; Higgins 1999) and biochemical differences (Boon et al. 2000). The level of hybridisation between *C. forbesi* and *C. novaezelandiae* (Taylor 1975) has obscured its status (Triggs & Daugherty 1996; Boon et al. 2000). Some island forms traditionally regarded as races of *C. novaezelandiae* may also be specifically separable. For example, Boon et al. (in press) present biochemical evidence that the Macquarie and Auckland Island populations belong to a single species distinct from *C. novaezelandiae.* Oliver (1955) provisionally regarded the Antipodes and Macquarie Island populations as inseparable at the subspecific level but thought that further work was necessary. Presumably the Auckland Islands population of *C. novaezelandiae* was supplemented regularly by vagrants from the South and Stewart Islands not to have diverged significantly. The extinction of the Macquarie Island population (Taylor 1979) means that the Antipodes Islands hold unique populations of two distinct species of *Cyanoramphus*. Campbell Island, midway between Macquarie and the Antipodes, may have had a resident parakeet until Norway rats (*Rattus norvegicus*) were introduced in the early nineteenth century. This may eventually be confirmed by fossils, but they would be unlikely to provide data to resolve the question as to whether *C. novaezelandiae* or the Antipodes/Macquarie species was present.

Order Cuculiformes (2)

Family Cuculidae (2)

Chrysococcyx lucidus	Nf	NO	N	S	SO	St	Ch	–
Eudynamys taitensis	–	NO	N	S	SO	St	–	–

Notes Both cuckoos are extremely rare as fossils. They are, however, unlikely to have been taken regularly by the predators from whose prey deposits most of the fossils of small arboreal taxa have come (Holdaway & Worthy 1996). *Eudynamys* is, however, common in deposits accumulated by *Tyto alba* on Vatulele Island, Fiji (THW, unpubl. data). Material of *Eudynamys* from Norfolk Island includes a tentatively identified humerus, a femur, and a tarsometatarsus (Meredith 1985), but its breeding status there is unclear (Schodde et al. 1983).

Order Strigiformes (2)

Family Strigidae (2)

Ninox novaeseelandiae	Nf	NO	N	S	SO	St	–	–
Sceloglaux albifacies††	–	NO?	N	S	–	St	–	–

Notes Fossils of both taxa are widespread but uncommon, as is usual for predators. *Ninox novaeseelandiae undulata* from Norfolk Island has occasionally been accorded specific rank (see Christidis & Boles 1994; Higgins 1999). The present population is derived from the last remaining female, mated with a male *N. n. novaeseelandiae* from New Zealand. Holdaway (1989), Turbott (1990) and Millener (1991) have suggested that *Ninox* may be a recent immigrant to New Zealand, but *Ninox* is at least as common as *Sceloglaux* in deposits here (Worthy & Holdaway 1993, 1994, 1995). *Ninox* is known from the Pyramid Valley deposit laid down at least 3000 years B.P. (Holdaway & Worthy 1997) and from deposits in Babylon Cave of possible Otiran glacial age (Worthy & Holdaway 1993). The possible NO record for *Sceloglaux* is based on Hutton (1869).

Order Caprimulgiformes (1)

Family Aegothelidae (1)

Aegotheles novaezealandiae††	–	–	N	S	SO	–	–	–

Notes We agree with Olson et al. (1987) that the use of the genus *Megaegotheles* is not justified . A fossil is known from a dune site on D'Urville Island (THW, unpubl. data).

Order Coraciiformes (1)

Family Alcedinidae (1)

Subfamily Daceloninae (1)

Todiramphus sanctus	Nf/K	NO	N	S	SO	St	–	–

Notes The few fossils of *T. sanctus* in New Zealand (Millener 1981, 1991) suggest that it was confined to coastal habitats before the major episode of deforestation 400–600 years B. P. Turbott (1990) and Millener (1990, 1991) suggest that it is a recent immigrant, but there is fossil material from caves near Kaikoura (including one that was sealed at the time of European arrival) in the Canterbury Museum (THW, RNH, unpubl. data). The combination *Todiramphus sanctus* follows the conclusions of Christidis & Boles (1994) that the Australasian species presently placed in *Halcyon* are generically distinct from the African and Asian members of that genus.

Order Passeriformes (44)

Suborder Oligomyodi (7)

Family Acanthisittidae (7)

Acanthisitta chloris	–	NO	N	S	SO	St	–	
Xenicus longipes††	–	–	N	S	–	St	–	–
Xenicus gilviventris	–	–	N	S	–	–	–	–
Traversia lyalli††	–	–	N	S	SO	–	–	–
Pachyplichas jagmi††	–	–	N	–	–	–	–	–
Pachyplichas yaldwyni††	–	–	–	S	–	–	–	–
Dendroscansor decurvirostris††	–	–	–	S	–	–	–	

Notes *Pachyplichas jagmi* was described from a small series: it differed from *P. yaldwyni* only in size (Millener 1988). The larger sample size now available (THW, unpubl. data) suggests that the North and South Island forms are not separable. *Dendroscansor decurvirostris* was described by

Millener & Worthy (1991), and is known from only three sites in the northwest of the South Island and one in Southland (Worthy 1998e).

Suborder Polymyodi (37)

Family Motacillidae (1)

Anthus novaeseelandiae	-	NO	N	S	SO	St	Ch	Sub

Notes Foggo et al. (1997) concluded that the outlying island forms were populations of a separate species from those on the mainland, but that relationships with more distant populations were yet to be clarified. *Anthus aucklandica* (G.R. Gray, 1862) is available as the oldest name for the island form but such a distribution of species is anomalous in comparison to that of other taxa, and begs the question as to how such as situation could have arisen. With further study, it is likely that other island forms will be recognised at the species level, particularly the Chatham Island form (see Appendix 2). We suspect that the differences are masked by convergent evolution which has resulted in separately derived island forms that are superficially similar.

Family Campephagidae (1)

Lalage leucopyga††	Nf	-	-	-	-	-	-	-

Family Muscicapidae (1)

Subfamily Turdinae (1)

Turdus poliocephalus††	Nf	-	-	-	-	-	-	-

Notes Schodde et al. (1983) list *T. poliocephalus* as extremely rare and perhaps extinct. As there have been no confirmed sightings since 1975 (Schodde et al. 1983; Hermes et al. 1985), we treat it as extinct.

Family Sylviidae (3)

Bowdleria punctata	-	NO	N	S	SO	St	-	-
Bowdleria rufescens††	-	-	-	-	-	-	Ch	-
Bowdleria caudata	-	-	-	-	-	-	-	Sub

Notes *Bowdleria rufescens* is distinct in both plumage and osteology (Olson 1990a). We also recognise the resident population on the Snares as a full species, *B. caudata* (Buller, 1894) as originally described, based on its larger size and more uniform brown coloration (Oliver 1955). The systematics of the genus on the three main islands are poorly known, and even the distinctive form on Codfish Island (*B. p. wilsoni*) may require full species status.

Family Pachycephalidae (4)

Subfamily Pachycephalinae (1)

Pachycephala xanthoprocta	Nf	-	-	-	-	-	-	-

Subfamily Mohouinae (3)

Mohoua albicilla	-	NO	N	-	-	-	-	-
Mohoua ochrocephala	-	-	-	S	SO	St	-	-
Mohoua novaeseelandiae	-	-	-	S	SO	St	-	-

Notes The Norfolk Island *Pachycephala* was described as *P. xanthoprocta* Gould, 1838. *Mohoua ochrocephala* and *M. novaeseelandiae* are known from many fossil deposits (Millener 1981; Worthy & Holdaway 1993, 1994, 1995, 1996; Worthy 1997a) contra Turbott (1990). The submergence of *Finschia* in *Mohoua* (Turbott 1990) was supported by Olson (1990b).

Family Acanthizidae (3)

Subfamily Acanthizinae (3)

Gerygone modesta	Nf	-	-	-	-	-	-	-
Gerygone igata	-	NO	N	S	SO	St	-	-
Gerygone albofrontata	-	-	-	-	-	-	Ch	-

Notes Until recently, there was little evidence of *Gerygone igata* in fossil sites (Worthy, in Holdaway 1989). However, analysis of predator deposits has revealed a substantial fossil history for the species (Worthy & Holdaway 1993, 1994, 1995, 1996; Worthy 1997a).

Family Monarchidae (1)

Subfamily Rhipidurinae (1)

Rhipidura fuliginosa	Nf	NO	N	S	SO	St	Ch	-

Family Petroicidae (7)

Petroica multicolor	Nf	-	-	-	-	-	-	-
Petroica toitoi	-	NO	N	-	-	-	-	-
Petroica macrocephala	-	-	-	S	SO	St	Ch	Sub
Petroica dannefaerdi	-	-	-	-	-	-	-	Sub
Petroica longipes	-	NO	N	-	-	-	-	-
Petroica australis	-	-	-	S	SO	St	-	-
Petroica traversi	-	-	-	-	-	-	Ch	-

Notes Evidence cited in Schodde & Miller (1999) suggests that *Petroica multicolor* should be recognised as distinct from Australian populations. *Petroica toitoi* (Lesson, 1828) is recognised as a full species following the original description and other works such as Oliver (1955). The degree of differentiation shown by the two subantarctic populations of *Petroica* (Fleming 1950a, b) is sufficient to justify their recognition as separate species, but only *P. dannefaerdi* has been recognized previously as a full species (Oliver 1955) (see Appendix 2). The Auckland Islands *P. macrocephala marrineri* is treated as a full species in Appendix 2.

Fleming (1950a, b) monographed the genus *Petroica* in New Zealand. He solved the long-standing puzzle of *P. dannefaerdi* from the Snares, showing that it was a derivative of the *P. macrocephala* stock rather, like *P. traversi*, being a sister species of *P. australis*. All the island forms of *P. macrocephala* were treated as subspecies (Fleming 1950a, b), a classification that has been followed by most recent workers (e.g., Kinsky 1970; Turbott 1990). The considerable morphological variation implies a greater degree of differentiation than is expressed by recognition at the subspecies level, and an origin deeper in time. Our proposition to treat most forms as species could be tested using DNA and other modern techniques.

It is arguable that the two robins should be separated from the tomtits at the generic level, rather than subgeneric (as *Miro*) as was done, for example, by Oliver (1930, 1955). The species of *Petroica* occuring outside New Zealand (Pizzey 1980; Sibley & Monroe 1990) all resemble the New Zealand tomtits, and the robins are at least as different from the tomtits (including *P. multicolor*) as are the species of *Eopsaltria*, *Microeca*, *Melanodryas*, and *Poecilodryas* in Australia and New Guinea. We consider that *P. longipes* should be separated from *P. australis*, as in Oliver (1930), because of its consistently different plumage pattern and smaller size, which is particularly evident in the skeleton (AJDT & THW, unpubl. data).

Family Zosteropidae (2)

Zosterops albogularis	Nf	–	–	–	–	–	–	–
Zosterops tenuirostris	Nf	–	–	–	–	–	–	–

Notes Both taxa are endemic to Norfolk Island. *Zosterops albogularis* may be extinct. It was described as "very rare and restricted" by Schodde et al. (1983) who recorded sightings in 1978. However, Hermes et al. (1985) noted that no birds had been seen after late 1979, despite "extensive observation and low-level netting ... in 1983–1985". Moore (1999) refers to sight records up to at least 1994. The widespread *Z. lateralis* does not seem to have been able to colonise the New Zealand region before the inception of environmental change and the reduction or elimination of possible competitors (Diamond & Veitch 1981). There is no fossil evidence for the presence of *Zosterops lateralis* in New Zealand, where it was reported as arriving in 1856, but may have been present in some areas before that (Oliver 1955). It is possible that its recent establishment on Norfolk Island was similarly assisted by the environmental change there, and that birds had been reaching the island regularly but failing to colonise in the face of competition from the two species already resident in the natural vegetation.

Family Meliphagidae (4)

Notiomystis cincta	–	NO	N	–	–	–	–	–
Anthornis melanura	–	NO	N	S	SO	St	–	Sub
Anthornis melanocephala††	–	–	–	–	–		Ch	–
Prosthemadera novaeseelandiae	K	NO	N	S	SO	St	Ch	Sub

Notes Bartle & Sagar (1987), followed by Turbott (1990), preferred not to recognise *A. melanocephala* (Gray, 1843) as specifically distinct, despite noting many differences. We regard the differences listed by Oliver (1955) and Bartle & Sagar (1987) as being sufficient to accord the form species rank, as it was originally described. Oliver (1955) described differences between the mainland and Chatham Island forms of *Prosthemadera*. The differences could support recognition of the two forms as separate species, but a fuller review is required.

Family Sturnidae (1)

Aplonis fusca††	Nf	–	–	–	–	–	–	–

Family Callaeatidae (5)

Callaeas wilsoni	–	NO	N	–	–	–	–	–
Callaeas cinerea††	–	–	–	S	SO	St	–	–
Philesturnus rufusater	–	NO	N	–	–	–	–	–
Philesturnus carunculatus	–	–	–	S	SO	St	–	–
Heteralocha acutirostris††	–	–	N	–	–	–	–	–

Notes The North and South Island forms of *Callaeas* are accepted as full species following Oliver (1955). The supposed races of *Callaeas* appear to have had different ecologies (Holdaway & Worthy 1997); in conjunction with the differences in plumage and wattle colour. *C. cinerea* is probably extinct. In *Philesturnus* we accept two species (*Philesturnus carunculatus* (Gmelin, 1789) and *P. rufusater* (Lesson, 1828)) as originally described, based on the different adult plumage patterns and markedly different sizes, as well as the presence of a distinctive juvenile plumage only in *P. caruncalatus* (Oliver 1955).

Family Turnagridae (2)

Turnagra tanagra††	–	–	N	–	–		–	–
Turnagra capensis††	–	–	–	S	SO	–	–	–

Notes The North and South Island forms are here each regarded as good species (as maintained by Oliver 1955) based on the major differences between their plumages. Although Olson et al. (1983) argued that *Turnagra* is a part of the bowerbird assemblage, details of the skeleton, pterylosis, eggs, reproductive biology, and vocalisations do not support this conclusion (RNH, unpubl. data), and it is referred here to a monotypic family as advocated by Christidis et al. (1996) who found *Turnagra* to be basal to several groups, including the bowerbirds, and not close to either the Australian pachycephaline lineage or the cnemophiline birds of paradise.

Family Corvidae (2)

Corvus "mainland"††	–	NO	N	S	–	St	–	Sub?
Corvus moriorum††	–	–	–	–	–	–	Ch	–

Notes There are no differences in the skeleton that justify recognising *Palaeocorax* as distinct from *Corvus* (RNH, unpubl. data). The mean long bone lengths of the North and South Island forms are significantly smaller than in samples from the Chatham Island population (RNH, unpubl. data), but some mainland individuals are as large as some Chathams Island birds (RNH cf. AJDT, unpubl. data). Otiran glacial specimens from the main islands are also about the same size as Chatham Island birds (AJDT, unpubl. data); the complex obviously needs further study. Forbes recognised size differences between the North and South Island forms but did not publish descriptions (Oliver 1955). Pending detailed biochemical and morphological research on the relationships between the island and mainland forms, we accept the Chatham bird as a full species. The record for NO refers to a fossil *Corvus* bone from Motuopao Island, Northland (MNZ S23199). The presence of *Corvus moriorum* or a related form on the Auckland Islands depends on a single tarsometatarsus reported by Dawson (1964), and confirmed as being *Corvus* (Dawson, pers. comm. to AJDT 1999).

SUMMARY

In all, we recognise 245 species in the late Holocene breeding avifauna of New Zealand (Appendix 2; Tables 1–3; Fig. 1). At least 176 (72%) of species were endemic to the archipelago. Not surprisingly, the South Island, with the largest land area (150,000 km^2) and greatest range of habitats, had the most breeding species (113), followed (in size order) by the North Island (100, 114,700 km^2) and Stewart Island (65, 1735 km^2). The Chathams and the subantarctic groups have roughly equal total areas (975 and c. 830 km^2, respectively) and they had about the same number of breeding species (60, 68, respectively). Largely because of the number of breeding species of petrels, even the small combined areas of the Kermadecs and the Norfolk group had more than 40 species (Table 1; Fig. 1), of which Norfolk (34.5 km^2) had 34 species and the Kermadecs (c. 32 km^2) at least 21. The highest degrees of endemism at the species level were in the Chathams (26 of 60 species, 43.3%), subantarctic (25 of 68 species, 36.8%), and Norfolk (12 of 34 species, 35.3%) faunas (Table 3). Endemism was lower, but still significant, on the main islands (South Island, 18 of 113 species = 15.9%; North Island, 8 of 100 = 8%). Of the 132 species breeding on the core archipelago (NO, N, S, St, SO), 82 (62.12%) were endemic. The low levels of endemism in the faunas of the Kermadecs, Stewart Island, and the northern and southern offshore islands (Appendix 3) and the high numbers shared with the main islands (Appendix 2) show that these faunas are clearly derivatives of those on the closest main islands.

The species listed represent 46 of the bird families listed in Turbott (1990) (Table 1, 2; mean 5.33 species per family, range 1–39). If the arrangement of Sibley et al. (1988) is followed, then the species would be included in 36 families (mean 6.81, range 1–55), with the main differences being in the treatment of the petrels and passerines (Holdaway 1991a). In an earlier treatment of the pre-human avifauna, Holdaway (1989) recognised 168 species in the fauna without Norfolk Island or the Kermadecs. That list is, however, outdated and should not be used for faunal studies. Detailed breakdowns of the fauna presented here are tentative only, especially with respect to the species present on the offshore islands, where the record is, as noted before, incomplete. In addition, the former status of species such as *Egretta sacra* on outlying groups is unknown.

Of 46 families recognised (Appendix 2), seven were endemic to the New Zealand archipelago (actually to the main islands and their immediate offliers) (Table 1). In just half of the families (23), all species on the New Zealand list were endemic to the archipelago (Table 1). Only five families included no endemic forms. One family with species apparently represented elsewhere is the Monarchidae, where the New Zealand fantails (*Rhipidura fuliginosa*) are regarded as being conspecific with the Australian grey fantail. This family warrants further study; they may be specifically distinct under the criteria used here. The other families without local endemic species (Phaethontidae, Sulidae, Stercorariidae, Alcedinidae) are of strong-flying marine or freshwater birds. Since human contact, several other species have established populations in New Zealand that are conspecific with the Australian source populations, but these are not regarded as being part of the original avifauna.

The present (2000) avifauna includes 169 species that bred in New Zealand at the time of first human contact, plus 16 species that have arrived naturally since then, and 37 species that were introduced by Europeans in the mid-nineteenth to early twentieth centuries (Appendix 5). At least 76 species (31%) of the original fauna are now extinct or have no natural populations in the archipelago; 29.4% of the original species are globally extinct (Table 1–3; Fig. 1a-c). Of the 174 endemic species, 72 (41.4%) are extinct. Four of the seven endemic families (57.1%) are extinct, and the other three have suffered 40, 60, and 66.7% extinction of their constituent species, respectively. There are now no representatives of 12 (26.1%) of the original 46 families in the living fauna. Of the 108 genera we recognise in the list, 35 are endemic to the New Zealand archipelago: 37 of the 108 genera (34.3%) are extinct, as are 20 of the 35 (57.1%) endemic genera.

When the avifaunas of the island group regions recognised in the study were analysed according to the distributions of breeding species, the results for before and after human intervention were similar (Table 2; Fig. 2a, b). The only difference was in the association between the faunas of the North Island and northern offshore islands: initially the presence of moa (and other species) grouped the North and South Island faunas together with the northern offshore island, and Stewart and the southern offshore islands as a separate grouping. After the extinction of most of the main island endemics, and the survival of some relicts in the southern South Island, the North Island and South Island faunas each became more similar to that of its offshore islands than to the other large island. The subtropical, subantarctic, and Chathams faunas retained their distinctiveness and order of difference despite the loss of many species from the northern groups. Enough oceanic species remained that were characteristic of the different water bodies that the faunas did not "collapse" into broader regional groupings.

Four major regional faunas (northern subtropical, mainland New Zealand, Chathams, and subantarctic) were recognisable in the groupings of species by coassociation (TWINSPAN analysis) in the late Holocene avifauna before human contact (Fig. 3a). However, the principal division was between the subtropical fauna and the southern faunas, with the southern faunas all sharing more taxa than any did with the northern fauna. Five more widespread species whose main distribution is northern formed two groups to the northern fauna. Two, spotless crake (*Porzana tabuensis*) and sacred kingfisher (*Todiramphus sanctus*), were more often associated with the northern endemics than were three taxa — grey duck (*Anas superciliosa*), red-crowned parakeet (*Cyanoramphus novaezelandiae*), tui (*Prosthemadera novaeseelandiae*) — which all occur farther south and east than the main islands.

There were also two separate groupings in the southern associations, with a group containing the mainland and Chathams taxa being a separate entity from the subantarctic association. Three species with northern affiliations — banded rail (*Gallirallus philippensis*), New Zealand pigeon *Hemiphaga novaeseelandiae*), morepork (*Ninox novaeseelandiae*) — were more often associated with taxa in the mainland-Chatham group than in either the subtropical or the subantarctic faunas.

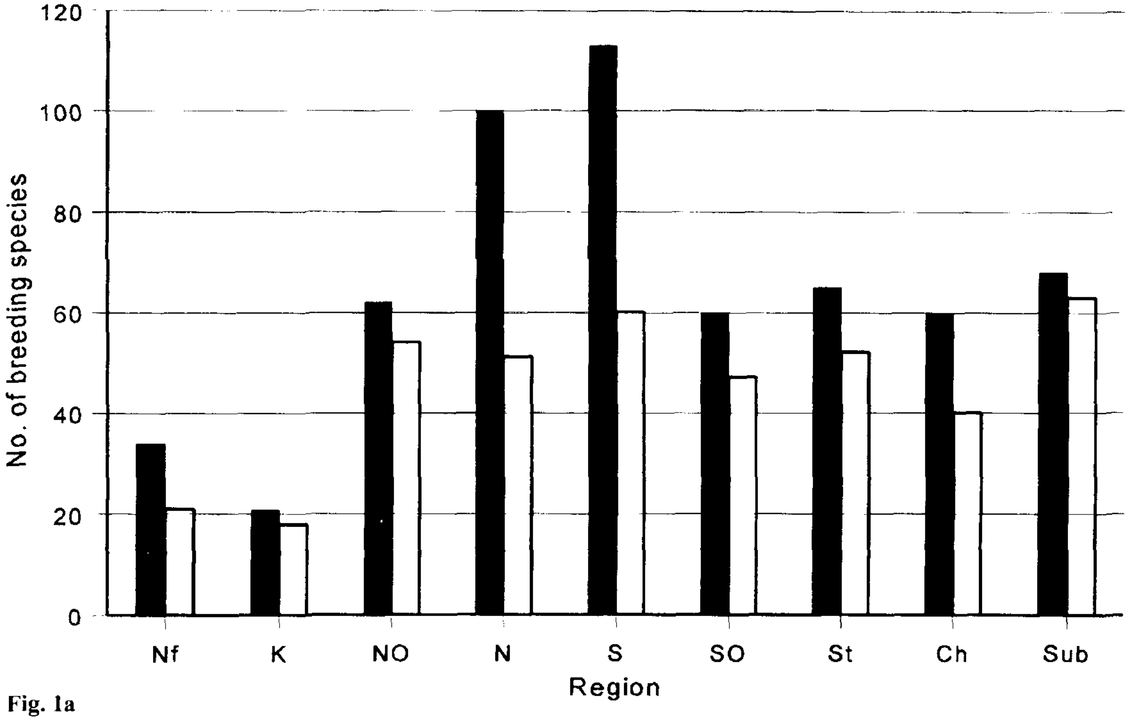
Taxa in the subantarctic fauna were themselves more often found together with a group of 13 species that might be termed "southern ubiquitous", including seabirds and three landbirds — falcon (*Falco novaeseelandiae*), yellow-crowned parakeet (*Cyanoramphus auriceps*), bellbird (*Anthornis melanura*) — that are widely distributed but lack populations on the Kermadecs or Norfolk. Two taxa — the shining cuckoo (*Chrysococcyx lucidus*) and fantail (*Rhipidura fuliginosa*) — link the southern fauna as a whole to the northern faunas, being found on the Chathams and on Norfolk, but not on the Kermadecs and hence form a separate basal satellite group in the southern branch of the cluster diagram (Fig,. 3a).

The indigenous component of the present fauna, that remaining after human intervention, is still divided into two groups, northern (Norfolk and the Kermadecs) and southern, but the loss of many endemics has collapsed the major groupings within the southern association (Fig. 3b; Table 3). The northern fauna still has its satellite group of spotless crake and kingfisher, but the other satellite of more southerly-distributed species is now more similar in its associations to the former southern satellite containing shining cuckoo and fantail. Indeed, the combined association of these species together with the former mainland satellite group (banded rail, pigeon, morepork) now form a major branch: the mainland, Chathams, and subantarctic faunas have been collapsed onto a single branch, because there are fewer island endemics with which to form discrete associations. Within the new southern/mainland fauna, there is still a dichotomy between the subantarctic and the rest. It is, perhaps, surprising, given the climate and the presence of albatrosses and subantarctic petrels that the Chatham Island fauna is now closer to the mainland fauna, but apart from the endemics, most of the species there are shared with the mainland and not with the landbird depauperate faunas farther south. In Fig. 3b, the Chatham Island fauna component is grouped separately to emphasise its origin as a separate, distinct entity.

Table 1 Representation of breeding birds in the New Zealand late Holocene avifauna by avian family with numbers of species surviving, and percentage of extinct species: based on Appendix 2. "Extinct" refers to any species without a known extant *natural* population, i.e., includes species now represented entirely by translocated populations.

		Endemic		Living		Percentage of original fauna extinct			
Family	Original	No.	%	No.	%	Local	Global	Endemic	Total
Emeidae	8	8	100	0	0	0	100	100	100
Dinornithidae	3	3	100	0	0	0	100	100	100
Apterygidae	5	5	100	3	60	0	40	40	40
Podicipedidae	2	1	50	2	100	0	0	0	0
Diomedeidae	12	7	58.3	12	100	0	0	0	0
Procellariidae	39	18	46.15	36	92.31	2.56	5.13	11.1	7.69
Hydrobatidae	6	2	33.33	5	83.33	0	16.67	50	16.67
Spheniscidae	10	6	60	9	90	0	10	16.67	10
Phaethontidae	1	0	0	1	100	0	0	0	0
Sulidae	2	0	0	2	100	0	0	0	0
Phalacrocoracidae	11	7	63.64	11	100	0	0	0	0
Ardeidae	3	1	33.33	2	66.67	0	33.33	100	33.33
Anatidae	18	15	83.33	8	54.44	5.56	50	60	55.56
Accipitridae	3	2	66.67	0	0	33.33	66.67	100	100
Falconidae	1	1	100	1	100	0	0	0	0
Phasianidae	1	1	100	0	0	0	100	0	100
Megapodiidae	1	0	0	0	0	100	0	100	100
Aptornithidae	2	2	100	0	0	0	100	100	100
Rallidae	17	13	76.47	6	35.29	0	64.71	83.3	64.71
Haematopodidae	3	3	100	3	100	0	0	0	0
Recurvirostridae	1	1	100	1	100	0	0	0	0
Charadriidae	5	5	100	5	100	0	0	0	0
Scolopacidae	9	9	100	5	55.56	0	44.44	44.44	44.44
Stercorariidae	1	0	0	1	100	0	0	0	0
Laridae	13	3	23.08	13	100	0	0	0	0
Columbidae	4	4	100	2	50	0	50	50	50
Psittacidae	12	12	100	8	66.67	0	33.33	33.33	33.33
Cuculidae	2	0	0	2	100	0	0	0	0
Strigidae	2	2	100	1	50	0	50	100	50
Aegothelidae	1	1	100	0	0	0	100	100	100
Alcedinidae	1	0	0	1	100	0	0	0	0
Acanthisittidae	6	6	100	2	33.33	0	66.67	66.67	66.67
Motacillidae	3	2	66.67	3	100	0	0	0	0
Campephagidae	1	1	100	0	0	0	100	100	100
Muscicapidae	1	1	100	0	0	0	100	100	100
Sylviidae	3	3	100	2	66.67	0	33.33	33.33	33.33
Pachycephalidae	4	4	100	4	100	0	0	0	0
Acanthizidae	3	3	100	3	100	0	0	0	0
Monarchidae	1	0	0	1	100	0	0	0	0
Petroicidae	8	8	100	7	87.5	0	12.5	16.67	12.5
Zosteropidae	2	2	100	2	100	0	0	0	0
Meliphagidae	4	4	100	3	75	0	25	25	25
Sturnidae	1	1	100	0	0	0	100	100	100
Callaeatidae	5	5	100	2	40	0	60	60	60
Turnagridae	2	2	100	0	0	0	100	100	100
Corvidae	2	2	100	0	0	0	100	100	100
TOTAL	245	176	71.84	169	68.98	1.63	29.39	41.38	31.02

Note: For families such as the Recurvirostridae, Rallidae, Psittacidae, and Callaeatidae the total extinct taxa would be greater without the intervention of conservation efforts (see Holdaway 1999a).


120
100
80
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No. of breeding species
Nf
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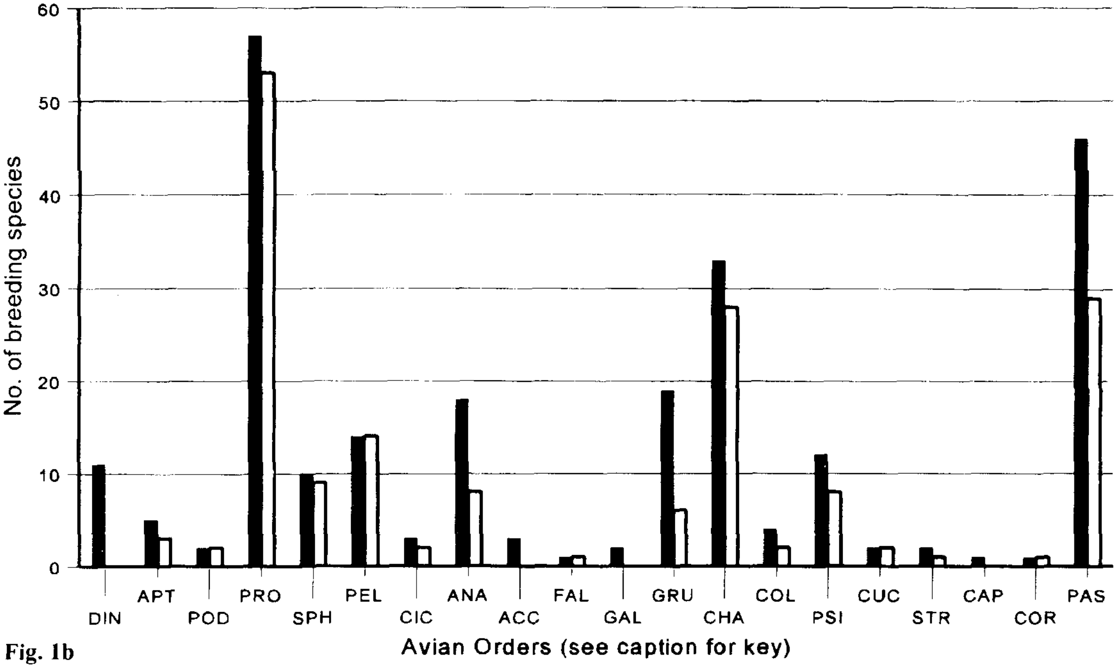
Fig. 1a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Avian Orders (see caption for key)

Fig. 1b

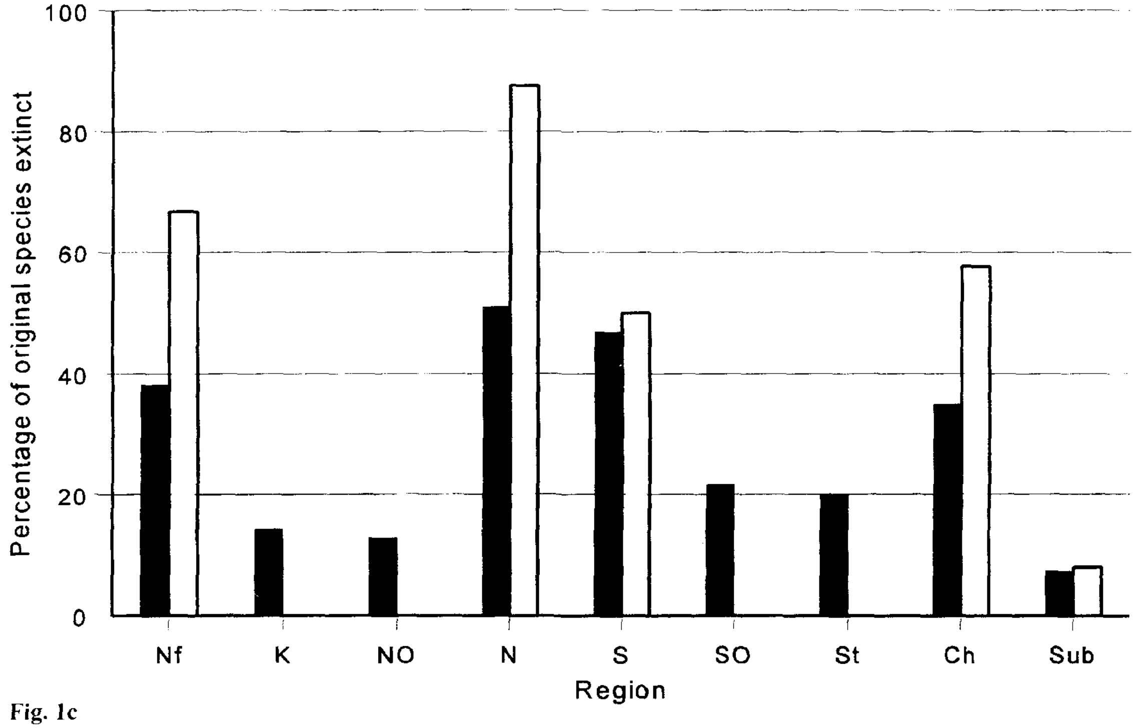

Fig. 1c

Fig. 1 (a-c) Based on list in Appendix 2. **a**, Number of breeding species of birds in New Zealand in the late Holocene avifauna (solid bars) and at present (open bars), by region: Nf/K, Norfolk/Kermadecs; NO, northern offshore islands; N, North Island; S, South Island; SO, southern offshore islands (including all islands in Cook Strait); St, Stewart Island, including islands in Foveaux Strait); Ch, Chatham Islands; Sub, Subantarctic Islands, including The Snares, Bounty Islands, Antipodes Islands, Auckland Islands, Campbell Island, Macquarie Island. **b**, number of breeding bird species in late Holocene and present avifaunas, by Order: DIN, Dinornithiformes; APT, Apterygiformes; POD, Podicipediformes; PRO, Procellariiformes; SPH, Sphenisciformes; PEL, Pelecaniformes; CIC, Ciconiiformes; ANA, Anatiformes; ACC, Accipitriformes; FAL, Falconiformes; GAL, Galliformes; GRU, Gruiformes; CHA, Charadriiformes; COL, Columbiformes; PSI, Psittaciformes; CUC, Cuculiformes; STR, Strigiformes; CAP, Caprimulgiformes; COR, Coraciiformes; PAS, Passeriformes. **c**, percentage of original late Holocene breeding avifauna of the New Zealand archipelago that has been lost since first human contact, by region: black bars, percentage of total species; open bars, percentage of species endemic to each region now extinct.

Likewise, the "southern ubiquitous" group is now part of the subantarctic fauna and is figured separately withing that group to emphasise its former status. It contains species that are now considered to be "subantarctic", especially the sooty shearwater (*Puffinus griseus*), but which are (or were) so widespread that they constitute a separate faunal entity within the New Zealand fauna.

Overall, the compositions of the regional faunas defined by the TWINSPAN analysis were much the same as could have been formulated by inspection of a list. However, the greater discrimination possible with the clustering algorithm allowed the separation of the faunas and those species with distributions that transcended regions. Northern and southern components were found to be not simple entities but with various linking groups and taxa whose distribution was apparently controlled by factors other than climate.

Another way of assessing the relationships within the fauna is based on lists (Appendix 3) of species endemic to subsets of the nine regions defined in the archipelago. There are 511 potential ways of grouping the regions as centres of endemism, but inspection of the lists in Appendix 3 shows that only 31 (6.07%) of these had endemic species in the Holocene. Fifteen "centres" contained only a single endemic, hence only 16 (3.13%) contained the bulk (159) of the endemic species. Such a non-random distribution of endemicity underlines the importance

Table 2 Numbers of breeding bird species in each family represented in each region of the New Zealand archipelago, with totals for each family, number presently existing in each family, percentage existing in each family, and percentage extinct in each family; based on Appendix 2. O, original (= late Holocene) avifauna; L, living (number of species in the present avifauna of that region, excluding recent colonists and those with no remaining natural populations); %Ext, percentage of original breeding species total now extinct). Regions: Nf, Norfolk Island (including Nepean and Philip Islands); K, Kermadecs; NO, northern offshore islands (to the northern side of Cook Strait, including Kapiti and Mana Islands but not The Brothers); N, North Island; S, South Island; SO, southern offshore islands (including Cook Strait islands from The Brothers south and west, to the northern shore of Foveaux Strait); St, Stewart Island (with all outliers, including those in Foveaux Strait); Ch, Chatham Islands; Sub, subantarctic islands (The Snares, Bounty, Antipodes, Auckland, Campbell, and Macquarie Islands).

	Total number of species for each subregion																		Total		
	Nf		K		NO		N		S		SO		St		Ch		Sub				
Taxon	O	L	O	L	O	L	O	L	O	L	O	L	O	L	O	L	O	L	O	L	%Ext
Emeidae					1	0	4	0	6	0									8	0	100
Dinornithidae					1	0	3	0	3	0	3	0	1	0					3	0	100
Apterygidae					1	1	2	1	4	2	2	1	1	1					5	3	40
Podicipedidae							2	1	2	1									2	2	0
Diomedeidae													1	1	3	3	9	9	12	12	0
Procellariidae	5	4	6	5	11	11	9	2	11	3	8	8	8	8	11	9	16	15	39	36	8.1
Hydrobatidae			2	2	1	1	2	0	3	0	1	1	1	1	2	2	3	3	6	5	16.7
Spheniscidae					1	1	1	1	3	3	3	3	3	3	2	1	7	7	10	9	11.1
Phaethontidae	1	1	1	1															1	1	0
Sulidae	1	1	1	1	1	1	1	1			1	1	1	1					2	2	0
Phalacrocoracidae					4	4	5	4	5	5	5	5	5	5	3	3	4	4	11	11	0
Ardeidae					1	1	3	1	3	2	1	1	1	1	1	0			3	2	33.3
Anatidae			1	1	5	3	12	6	12	5	4	2	5	2	8	2	5	3	18	8	55.6
Accipitridae	1	0					1	0	2	0									3	0	100
Falconidae					1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0
Megapodiidae			1	0															1	0	100
Phasianidae					1	0	1	0	1	0			1	0					1	0	100
Aptornithidae							1	0	1	0									2	0	100
Rallidae	4	2	1	1	3	3	8	4	7	5	2	0	2	2	6	2	3	1	17	6	60
Haematopodidae					1	1	1	1	2	2	1	1	1	1	1	1			3	3	0
Recurvirostridae							1	0	1	1									1	1	0
Charadriidae					3	2	3	2	4	2			2	2	2	2	1	1	5	5	0
Scolopacidae	1	0			1	0	1	0	1	0	0	0	1	0	2	1	4	4	9	5	44.44
Stercorariidae									1	1			1	1	1	1	1	1	1	1	0

Table 1 continued

	Total number of species for each subregion																		Total		
	Nf		K		NO		N		S		SO		St		Ch		Sub				
Taxon	O	L	O	L	O	L	O	L	O	L	O	L	O	L	O	L	O	L	O	L	%Ext
Laridae	5	5	4	4	3	3	6	6	7	6	3	3	4	4	3	3	4	4	13	13	0
Columbidae	2	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1			4	2	50
Psittacidae	2	0	1	1	4	3	5	2	6	4	4	3	4	3	3	2	4	4	12	8	33.33
Cuculidae	1	1			2	2	2	2	2	2	2	2	2	2	1	1			2	2	0
Strigidae	1	0			1	1	2	1	2	1	1	1	2	1					2	1	50
Aegothelidae							1	0	1	0	1	0							1	0	100
Alcedinidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1					1	1	0
Acanthisittidae					1	1	5	1	6	2	2	1	2	1					6	2	66.67
Motacillidae					1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3	0
Campephagidae	1	0																	1	0	100
Muscicapidae	1	0																	1	0	100
Sylviidae					1	1	1	1	1	1	1	1	1	1	1	0	1	1	3	2	33.3
Pachycephalidae	1	1			1	1	1	1	2	2	2	1	2	1					4	4	0
Acanthizidae	1	1			1	1	1	1	1	1	1	1	1	1	1	1			3	3	0
Monarchidae	1	1			1	1	1	1	1	1	1	1	1	1	1	1			1	1	0
Petroicidae	1	1			2	2	2	2	2	2	2	2	2	2	2	1	2	2	8	7	14.29
Zosteropidae	2	2																	2	0	0
Meliphagidae			1	1	3	3	3	2	2	2	2	2	2	2	2	1	2	2	4	3	25
Sturnidae	1	0																	1	0	100
Callaeatidae					2	2	3	1	2	0	2	0	2	0					5	2	60
Turnagridae							1	0	1	0	1	0							2	0	100
Corvidae							1	0	1	0			1	0	1	0	0	0	2	0	100
TOTAL	34	21	21	18	62	54	100	51	113	60	60	47	65	52	60	40	68	63	245	169	31
% extant		61.8		85.7		87.1		49		53.1		78.3		80		66.67		92.6		69	

Note: The populations of *Pachyptila turtur* and *Pterodroma inexpectata* extant in the South Island (Turbott 1990; Loh 2000) are relicts in sites inaccessible to introduced mammalian predators. No natural populations of *Apteryx owenii*, *Strigops habroptilus*, or *Philesturnus carunculatus* are known, although the species survive as translocated and managed populations elsewhere.

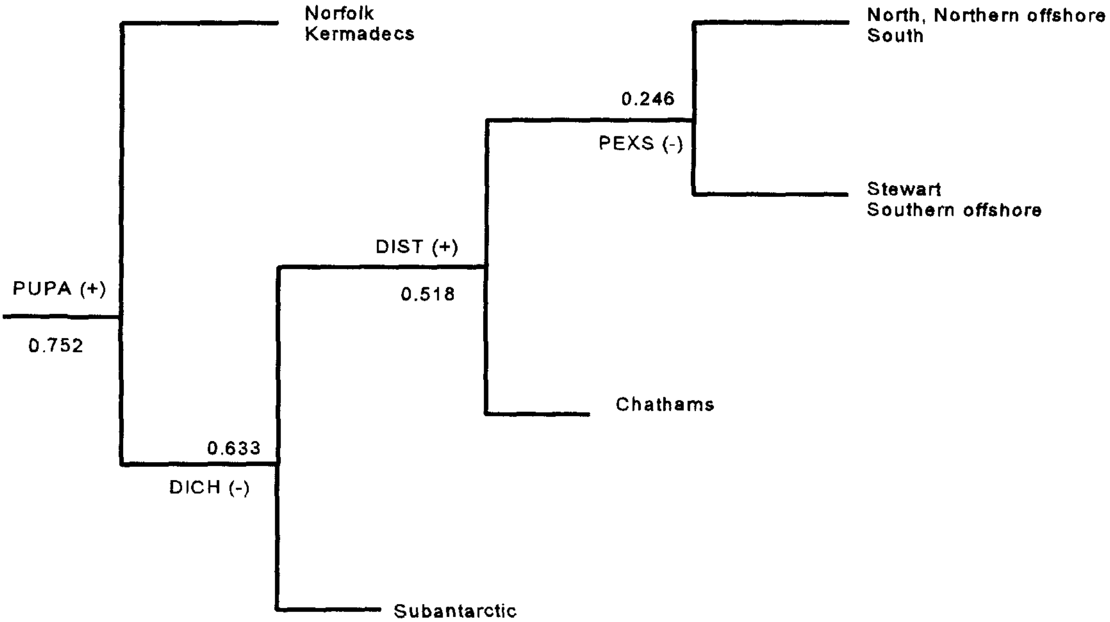

Fig. 2 a

Fig. 2 (a, b) TWINSPAN (Two-way Indicator Species Analysis) clustering of regions in the New Zealand archipelago, based on: **a**, the distribution of species of breeding birds in the late Holocene fauna; and **b**, the distribution of breeding bird species in the present fauna. Lists of taxa endemic to each region are given in Appendix 3. Decimal numbers at branch points are the eigenvalues for the separation of the branches at that point. Taxon code at branch points denotes indicator species, with branch (+, up) or (-, down) for which the taxon discriminates.

of the main island groupings in supporting diversity, and the tendency of taxa to spread to closer islands rather than erratically to distant parts of the archipelago. In a smaller area, the distribution of species within New Zealand reinforces the view based on fossils that the largely disjunct present distributions of many bird species in the wider Pacific area are artefacts of human intervention (Steadman 1989). Species rarely "jump" islands with suitable habitat in colonising more distant islands. Apparent gaps in distribution are invitations to further study of the fossil record.

Introduced and self-introduced species

At least 16 species of bird are known to have established viable populations in New Zealand since human intervention began, and people have successfully introduced another 37 (Appendix 5). The distribution of higher taxa in the lists reflects the kind of niches that opened for new arrivals and the desires of the new human colonists. Only two (12.5%) of the self-introduced species are passerines, against 15 (40.5%) introduced by Europeans in the nineteenth century. Only one duck succeeded in establishing itself naturally in the past thousand years, in contrast to the results of deliberate attempts over less than a century to introduce waterfowl for shooting (three species, 9.1%). Upland game birds (seven species, 18.9%) and waterfowl together (birds imported to hunt) constitute about 30% of the introduced species. The other large category of human introductions was cage and fancier birds, pigeons and parrots, which together comprise nearly 20% of the successful introductions.

DISCUSSION

New Zealand avifauna

It is not sufficient merely to present a new list of New Zealand birds without comment. The information must be placed in context of time, space, and other disciplines. The late Holocene breeding avifauna consisted of several distinctive geographical and evolutionary faunas. Each island group had a fauna with distinctive compositions, bound to the greater New Zealand fauna by common elements. On a wider scale, the avifaunas of Australia, the tropical

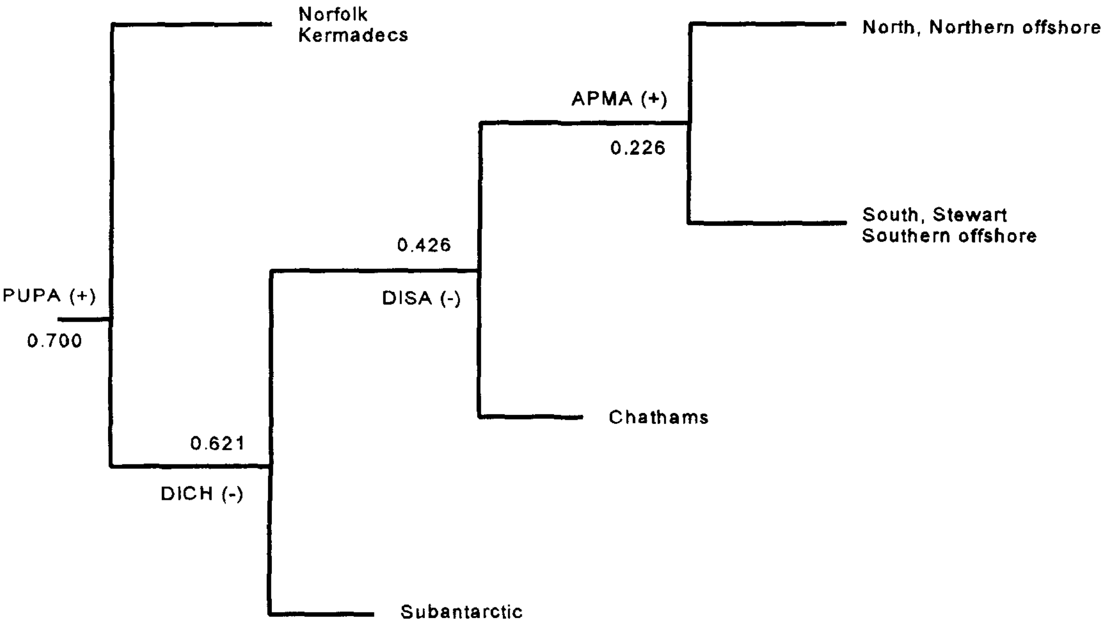

Fig. 2 b

Pacific, and New Zealand meet on Norfolk Island, and the tropical Pacific and New Zealand faunas contribute to the more depauperate Kermadec fauna.

The main islands supported a complex mixture of faunal elements, including several apparent Gondwanan groups such as the moas, kiwis, and wrens (Fleming 1979; Cooper & Cooper 1995). The Australian influence is very strong, but the presence of several endemic orders and families and many endemic genera and species indicates that the avifauna has been isolated for a long time (Fleming 1962). The fauna has, however, been shown to be able to resist invasion of potential colonists from Australia except where and when the environment has been changed to the extent that native species are disadvantaged (Diamond & Veitch 1981). An example is the absence in the fossil record of *Porphyrio melanotus* until after the effective removal of *P. mantelli*, *P. hochstetteri* and other rails from the fauna. The absence of *Anas rhynchotis* until Polynesian times is another possible example. Extinction of endemics and replacement with immigrant and introduced species (Appendix 5) has been a major factor in shaping the present avifauna.

Farther to the east, the distinctive avifauna of the Chatham Islands has much potential for research on speciation rates and multiple colonisations (Trewick 1997a, 1997b). The subantarctic islands in the New Zealand region have depauperate land bird faunas but are remarkable for the abundance and variety of petrels and penguins. In the archipelago as a whole, the petrels, penguins, and shags/cormorants reach levels of diversity unknown elsewhere.

Some groups such as the waterfowl have strong continuing contacts with Australia, as shown by banding recoveries of *Anas superciliosa* in both directions, and of Australian *Anas gracilis* in New Zealand (Heather & Robertson 1996). The link is of long standing as several of the New Zealand species are sister species of living Australian species (Worthy et al. 1997) and many of these relatives, such as *Tadorna tadornoides* and *Chenonetta jubata*, still reach New Zealand as vagrants (Heather & Robertson 1996). The black swan almost certainly reintroduced itself in the mid-nineteenth century, after being exterminated in the Polynesian period (Worthy 1998b), at about the same time that Europeans deliberately introduced it (Williams, in Turbott 1990). Species in several other groups, including grebes, petrels, herons, raptors, rails, and wading birds have continued to colonise unaided since human contact.

The presence of other southern islands and island groups during the Pleistocene glaciations (Fleming 1979: 82) complicates explanations of the patterns of arrival and speciation on islands east and south of the South Island. Fleming (1979: 106) used the currently accepted "degree of systematic difference"

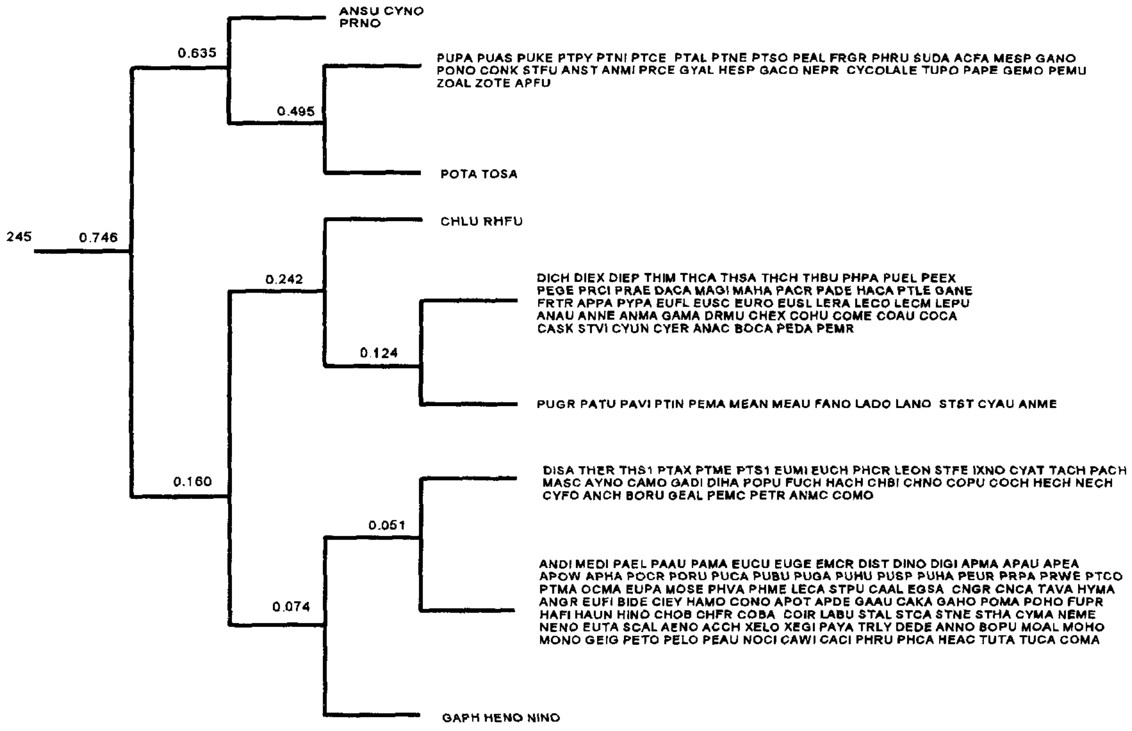

Fig. 3 a

Fig. 3 (**a, b**) TWINSPAN clustering of breeding bird species in: **a**, the late Holocene avifauna, and: **b**, the present avifauna of New Zealand, showing composition of original and current regional faunas, as well as indicating the groupings of more widespread taxa. Four-letter species codes are the first two letters of each of the generic name and specific epithet, for example *Apteryx owenii* becomes APOW: codes are explained in Appendix 4. For unnamed species, the first three letters of a genus or of the location (e.g., **Nor**folk) and a number are substituted. Where duplication is possible, such as between *Anthornis melanura* and *Anthornis melanocephala*, both of which would be ANME, the second of the pair has been modified to avoid confusion. Decimal numbers at branch points are the eigenvalues for the separation of the branches at that point.

as a "yardstick of time". Application of molecular and morphological techniques, integrated with a greater understanding of the timing and extent of environmental, geographical and geological history of the islands may allow the "yardstick" to be calibrated for different groups in the avifauna (and other parts of the biota). The systematic arrangements offered in this paper are testable, there are many opportunities for further study.

Regional avifaunas

Norfolk Island

The Norfolk/Kermadecs region (Fig. 2a) was characterised by the presence of six subtropical petrels, a tropicbird, a booby, a goshawk, five tropical terns, and the Pacific and Australian songbirds on Norfolk Island (Fig. 3a). Norfolk Island is the most recent manifestation of a succession of islands that have been exposed south of New Caledonia during the Tertiary (Rich et al. 1983). The basement is basalt, and the present islands are only 2–3 million years old (Jones & McDougall 1973). There has been inhabitable land present long enough in the immediate area for the evolution of endemic species. Four families, the Campephagidae, Muscicapidae, Zosteropidae, and Sturnidae, reach their natural southeastern limit at Norfolk Island, as does *Accipiter*, the almost cosmopolitan genus of bird-eating hawks. *Accipiter* reaches Fiji farther north, but the

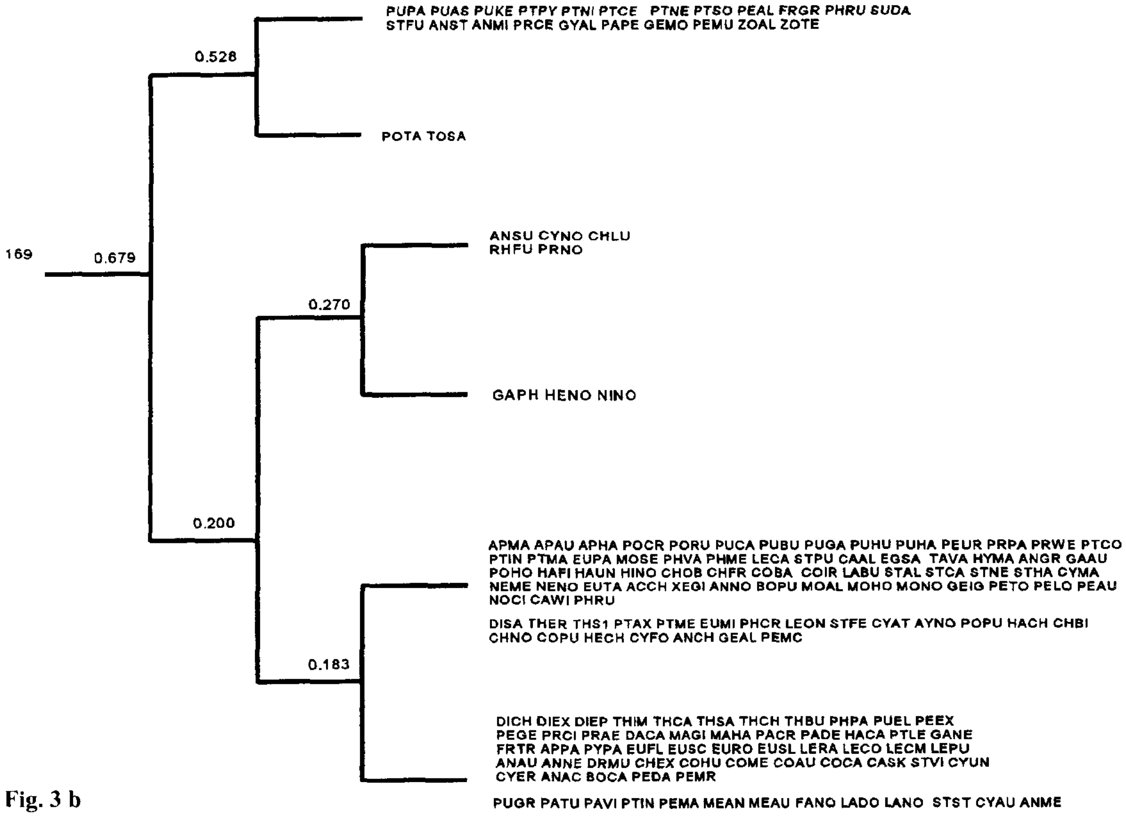

Fig. 3 b

over-water distances involved are much less than that involved in getting to New Zealand. Its ecological niche ('bird hawk') in the main islands of New Zealand was taken by the very large *Circus eylesi.*

Even in the restricted avifauna of a tiny and remote island, the source faunas interdigitate. New Zealand elements include *Pterodroma pycrofti*, a *Coenocorypha* snipe, a *Nestor* parrot, a *Cyanoramphus* parakeet, and a *Hemiphaga* pigeon. Typical Australian elements include two *Zosterops*, and *Petroica multicolor*. A *Lalage*, *Pachycephala xanthoprocta*, and *Accipiter* all have Australian and Pacific relatives. The wider Pacific is represented by *Puffinus pacificus*, *Gygis alba*, *Sterna fuscata*, *Anous* spp., *Procelsterna*, *Sula dactylatra*, *Turdus*, *Gallirallus* spp., *Gallicolumba*, and *Aplonis*. Birds with links to both Australia and New Zealand include *Puffinus assimilis*, *Ninox novaeseelandiae*, *Rhipidura fuliginosa*, and *Gerygone*. Twelve species were endemic to the Norfolk Island group (Appendix 2).

Kermadecs

More isolated still, at 600 km east of Norfolk and 800–1000 km northeast of the North Island, the Kermadecs appear to have missed most species coming from the west. Their avifauna is a mixture of New Zealand and Pacific species. Unfortunately, little is known of the fauna before human contact. Even reports by residents in the 19th century present problems. Cheeseman's (1891) report of the former occurrence of a megapode has not been substantiated by fossils in the archaeological sites excavated so far, although the pigeon has (see above).

All the surviving Kermadec land birds are derived from New Zealand ancestors and there are no endemic species (Cheeseman 1891; Sorenson 1964). The difference in complements of breeding species between Norfolk Island and the Kermadecs may be related to the greater isolation of the Kermadecs, and also their relative youth. The Norfolk group is the exposed remains of a basaltic volcano at the southern end of a previously emergent ridge (Rich et al.

1983), whereas the Kermadecs are violently eruptive rhyolite volcanoes. There have been regular catastrophic eruptions on Raoul and Macauley islands in the past 5000 years (Latter et al. 1992; Lloyd & Nathan 1981; Lloyd et al. 1996). In contrast to the older and volcanically quiescent Norfolk Island, terrestrial species may have been repeatedly wiped out, and had to recolonise after each cataclysmic event, so there has never been time for the evolution of distinctive species. Loss or diminution of source populations may have prevented some species, such as *Hemiphaga* pigeons, recolonising. Chance alone would mean that the new terrestrial avifauna that developed after a major eruption might differ substantially from the previous one. In contrast, endemic seabirds have evolved, perhaps because long-lived seabirds such as *Pterodroma cervicalis* could survive the temporary destruction of the site of their breeding colony. Only one species (*P. cervicalis*) is certainly endemic but, if the storm petrel found as fossil on Norfolk and Lord Howe Islands is not *Pelagodroma albiclunis* and the *Puffinus assimilis* race is a full species (as advocated in this paper), there would be three, all seabirds.

North, South, Stewart, and adjacent islands

The mainland "core" fauna consisted of 132 species, 82 of which were confined to the main islands and those immediately adjacent (Appendix 2). A subset of 40 species of those were endemic to one or both of the North and South Islands themselves: North, 7; South, 19; both, 14 species. The dominance of endemic species in the mainland avifauna reflects both the greater age and size of the islands, all fragments of the Gondwana continental mass, and the ability of the intact ecosystems to resist invasion by species from elsewhere.

The South Island had more than twice as many endemic species as the North, which may reflect the greater variety of habitats available as a result of higher relief that developed over the last 6 million years, and consequent climatic differences between east and west in the South Island. The topography grew more extreme during the Kaikoura Orogeny and the development of the Southern Alps. Three and perhaps four (*Megalapteryx didinus*, *Pachyornis australis*, *Xenicus gilviventris*, possibly *Dendroscansor decurvirostris*) of the endemics were almost confined to montane areas; the present mainly alpine distribution of *Nestor notabilis* is an artefact of extinction, as the species is abundant as a fossil in lowland sites (Holdaway & Worthy 1997). Another three (*Haematopus finschi*, *Charadrius frontalis*, *Chlidonias albofrontata*) were associated with the extensive braided river beds of the eastern South Island, and three more (*Emeus* crassus, *Pachyornis elephantopus*, *Harpagornis moorei*) were found only in the drier mosaic forests of the eastern and southern South Island (or — *Harpagornis moorei* — occasionally in open montane areas as well).

A further difference between the North and South Island endemics is that all of the solely North Island species are extinct. Only 11 of the 19 South Island species are extinct (12, if *Porphyrio hochstetteri*, which has survived probably only because of intensive management, is counted). Three of the survivors (*Haematopus finschi*, *Charadrius frontalis*, *Sterna albostriata*) are fresh water species, two (*Procellaria westlandica*, *Puffinus huttoni*) are petrels (the first being large and subject to predation by only the

Table 3 Number and percentage of all species and endemic species in the original (late Holocene) avifauna that have become extinct since first human contact (including species with no surviving natural populations); based on Appendix 2. Species distributions queried are scored as absent here.

	Number of species			Percentage		
Region	Original	Extinct	Endemic	Extinct	Endemic	Extinct endemic
Norfolk	34	13	12	38.24	35.3	66.7
Kermadecs	21	3	3	14.3	14.3	0
Northern offshore	62	8	1	12.9	1.61	0
North	100	51	7	51.0	8.0	87.5
South	113	51	19	46.9	15.9	50.0
Southern offshore	60	13	0	21.67	0	0
Stewart	65	13	0	20.0	0	0
Chathams	60	21	26	35.0	43.3	57.7
Subantarctic	68	5	25	7.35	36.8	8.0
TOTAL	245	76	174	31.0	71.0	41.4

largest introduced predators and the second has a relict breeding distribution in montane grasslands), and another is a parrot (*Nestor notabilis*). The list of species presently restricted to one or both main islands will decline as the former faunas of the offshore islands become better known.

Many of the species confined to the two main islands were flightless or flew poorly (Appendix 2). A few flightless species (such as moa) on offshore islands indicate the former presence of land bridges to those islands, mostly during the low sea stands of the late Pleistocene. Only two flightless species are known unequivocally from the northern offshore islands, whereas seven lived on Stewart Island and the southern offshore islands, all of which would have been connected to the mainland of the South Island during the low seastand 18 000 years ago. Stewart Island is unusual for so large a land mass so recently connected to the South Island, in that the only flightless species recorded from there are *Dinornis struthoides*, *Gallirallus australis*, *Apteryx australis*, and *Strigops habroptilus*. And some doubt remains about the latter two, as there are persistent reports from Stewart Island residents that both were introduced there in the 19th century. In contrast, there are records of these species plus *Dinornis giganteus*, *Dinornis novaezealandiae*, and *Aegotheles novaezealandiae* (a poor flier) from D'Urville Island, a much smaller area at the other end of the South Island, which is both closer to the South Island and may have retained more of its vegetation during full glacial time.

Chatham Islands

The late Holocene Chathams Islands fauna was composed of two groups; an endemic group including five petrels, a penguin, two shags, two ducks, four rails, three waders, a pigeon, two parrots, and five passerines, and a non-endemic group including eight species shared with the mainland islands. The rails provide ample evidence of the long-standing isolation of Chatham Island birds. *Diaphorapteryx hawkinsi* and *Cabalus modestus* were highly modified (Andrews 1896; Olson 1975). The two snipe, also, suggest at least two invasions from the mainland. The level of differentiation of the duck *Pachyanas chathamica* and the local species of parakeet, parrot, pigeon, bellbird, robin, warbler, and fernbird all indicate rare colonisations followed by isolation from source populations over long periods. The former presence of islands between the South Island and the Chathams, where the Veryan and Mernoo banks now stand, show that not all species would necessarily have had to cross the present distance from the mainland. Whether there was vegetation on those islands that allowed them to act as "stepping stones", and whether there were source populations on the nearest points of the mainland during the times of lowest sea stand, are unknown. Recent self-colonisations from the main islands (see below) indicate that distance per se is not a problem for some taxa: suitable habitat and lack of competition from resident species are probably important factors that have limited diversity on outlying island groups.

Although there would seem to be little chance of direct colonisation from Australia, because any birds flying east would have to pass over the main islands of New Zealand, that may have been possible for some of the strongest fliers. Both cattle egrets (*Bubulcus ibis*; Freeman 1994) and chestnut-breasted shelducks (*Tadorna tadornoides*; Tennyson 1998) have been reported from the Chatham Islands, although neither now has a breeding population established in New Zealand. These highly mobile species could have spent time on the main islands before continuing east to the Chathams. The records do show that it is not *necessary* for a species to breed on the main islands for a potentially viable group to have reached any of the outlying islands.

Even allowing for the possibility of reaching the group direct from a range of sources, the Chatham Island terrestrial avifauna was derived mostly from the mainland New Zealand fauna through dispersal of ancestral forms, yet its fauna is distinctive enough to be recognised as separate from the subantarctic islands. Indeed, the degree of radiation and endemism of both marine and terrestrial species within the group sets it apart from all other islands in the New Zealand region. Completing the original Chatham Islands fauna are the widespread species grouped in the basal branches of that section of the diagram (Fig. 3a), such as the ubiquitous *Cyanoramphus novaezelandiae*, *Petroica macrocephala*, *Prosthemadera novaeseelandiae*, and the northern vagiles *Pelagodroma marina*, *Egretta sacra*, *Porzana tabuensis*, *P. pusilla*, *Chrysococcyx lucidus*, and *Rhipidura fuliginosa*. Colonisation by *Ardea novaehollandiae*, *Porphyrio melantos*, *Vanellus miles*, *Zosterops lateralis*, and 11 Eurasian passerines (see below) less than a century after establishment of source populations on the North and South Islands gives some indication of the frequency at which viable groups of vagrants have reached the Chatham Islands. *Ardea* and *Vanellus* needed a bare half century to become established on both the mainland and the Chathams.

The level of differentiation recognised taxonomically in the Chatham terrestrial avifauna has varied over the past century. Most Chathams forms were described originally as species, in part because the subspecies concept was not available until the early twentieth century. An example of the changes made in the status of one species is that of the fernbird, which Buller (1869) described as *Sphenoeacus rufescens*. Oliver (1930, 1955) also treated it as a species of the genus *Bowdleria*, but it was relegated to a subspecies of *B. punctata* by Fleming (1953). Olson (1990a) pointed to substantial differences between it and the mainland populations, and Turbott (1990) again recognised it as a species. In the past, other Chatham species have been put in monotypic genera, including *Hapolorhynchus* for the warbler *Gerygone albofrontata* (e.g., Oliver 1930), and the rails "*Nesolimnas*" (=*Gallirallus*) *dieffenbachii*, and "*Palaeolimnas*" or "*Nesophalaris*" (=*Fulica*) (see Olson 1977).

Campbell (1996) suggested that the Chathams Islands initially formed as a large volcano about 70 million years ago. It is possible that the successive volcanoes active in the group since then have provided a continuity of land in the Chathams area since that time, on which a terrestrial fauna could evolve. However, the present arrangement of islands may have been achieved less than two million years ago, and for a period before that, most of the present land area was submerged. In addition, any land that was present 2.15 million years ago would have been subjected to the full effects of tsunami generated by the impact of the *Eltanin* asteroid off Tierra del Fuego 2.15 million years ago (Gersonde et al. 1997). The tsunami was at least 40 metres high, and possibly much higher if the object was at the high end of the 1–4 km range in diameter predicted from evidence in the sea floor sediments.

Therefore, the total time available for speciation of land birds has been relatively short: most if not all of the diversity originating in the group must have been achieved in less than two million years. During that time, climatic events may have further constrained the radiation of at least the terrestrial birds. Although some species, including the flightless rail *Diaphorapteryx*, were present on both sides of Pitt Strait, others, such as *Pachyanas chathamica* were endemic to Chatham Island itself (Millener 1996). Presence of suitable habitat has been apparently more important in determining species compositions than the dates of isolation of the different islands. Fleming (1979) suggested that the endemic species were able to survive in shrubland when the coastal forest was suppressed by cool climate during the last glaciation. In his view, birds typical of forest were at best subspecifically distinct from their mainland relatives. Application of independent measures of phylogenetic distance to a range of taxa may help to determine how fast speciation has proceeded in the forest taxa. If speciation has proceeded at a constant rate in the different lineages, the Chatham Islands terrestrial avifauna may be a useful tool in elucidating the tempo of evolution in birds.

Marine rather than land birds would have been able more easily to maintain populations despite the changes in the conformation and areas of land above water at any particular time. Both shags in the Chathams are endemic to the group. Even if the main islands of the group are geologically very young in their present form, volcanic islands and rock outcrops probably provided nesting areas for shags and shallow water as feeding grounds for a much longer period of time than they did as habitat for landbirds. And the diversity of petrels, despite being rather lower than reported by Bourne (1967), reflects the diverse marine environments made available by the position of the archipelago within easy flying distance of rich feeding grounds at the Subtropical Convergence and in the subantarctic zone. Characterised by a surface temperature drop of 4°C from north to south (Brodie 1973), the convergence east of New Zealand follows the crest of the Chatham Rise, and passes a little to the north of the islands.

Subantarctic islands – Snares, Bounty, Auckland, Antipodes, Campbell, Macquarie

The avifaunas of the six groups of subantarctic islands have links to those of Australia, South America, and Antarctica, as well as to the New Zealand mainland. In general, farther links are seen in the seabirds, while the terrestrial birds, with lower over-water dispersal capacity, are derived from a small subset of the New Zealand fauna. The decreasing representation of mainland terrestrial birds with increasing distance from mainland New Zealand islands may be mainly a result of the increasingly inclement climate that supports lower habitat diversity in the southernmost islands. Less structure and variety in the habitat may limit the prospects for colonisation by vagrants that do arrive, more than the over-water dispersal ability of the mainland species. The New Zealand endemic species whose ancestors reached the more distant islands are (a) either those more obviously closely related to Australian species and hence likely to be relatively recent immigrants with a history of vagility (species of *Petroica*), or (b) species that are still strong fliers and which move about above the canopy (e.g., *Cyanoramphus* parakeets and honeyeaters).

Although the subantarctic islands lie downwind from Australia, there has been little direct colonisation from there. Only the Auckland Island rail (*Dryolimnas muelleri*) seems to have successfully colonised the islands directly, although Foggo et al. (1997) considered that subantarctic and Chatham Island pipits may be derived from ancestors living elsewhere than on the New Zealand mainland. Most of the terrestrial fauna – snipe, ducks, dotterel, falcon, parakeets, tomtits and robins, and honeyeaters – are clearly derived from New Zealand ancestors. Even Macquarie Island, far to the southsouthwest, had a *Cyanoramphus* parakeet. Horning & Horning (1974) noted that records of introduced species and New Zealand natives on the subantarctic islands must relate to vagrants from New Zealand to the north rather than from Australia to the northwest despite the prevailing westerly airflows. However, birds have obviously reached the subantarctic islands direct from Australia in the past, and still do so. An example of a probable early colonisation is the Auckland Island (now only Adams and Disappointment islands; Marchant & Higgins 1993) rail which has no known counterpart living or fossil on the main islands of New Zealand, but was included as a subspecies of the Lewin rail (*Dryolimnas pectoralis*) by Oliver (1955) and Turbott (1990).

Records of Australian vagrants in the subantarctic have become more common as researchers spend more time on the remote islands. Examples include the record of a white eyed duck (*Althya australis*) and an Australian wood duck (*Chenonetta jubata*) from The Snares in the 1980s (Miskelly et al. 2001) and an influx of black shags (*Phalacrocorax carbo*) on The Snares in November 1976 which Sagar (1977) suggested may have come directly from Australia. Five cattle egrets and six Australian tree martins (*Hirundo nigricans*) have reached The Snares (Miskelly et al., 2001); chestnut-breasted shelducks have reached The Snares, Auckland Islands, and Campbell Island, including a flock of 22 on Campbell Island in 1984–1985 (Tennyson 1998); and a hoary-headed grebe (*Poliocephalus poliocephalus*) which certainly came direct from Australia was recorded from The Snares before any had been noticed on the main islands (Best 1976). Without a date, it is not possible to assign an origin to one of the farthest landfalls, that of an Australian coot (*Fulica atra*) on Macquarie Island (Turbott 1990).

Strong flight, ease of movement over water masses, and flocking increase the probability of wider dispersal of birds introduced to the main islands of New Zealand in the mid to late nineteenth century. Since that time, 11 species of Eurasian passerines have colonised the Chathams, subantarctic islands and even the Kermadecs and Norfolk (e.g., Bailey & Sorenson 1962; Kinsky 1969; Turbott 1990). Many other casual visits have not (yet) resulted in colonisation. Seven of the successful colonisers were also established in Australia at the same time, but the dunnock (*Prunella modularis*), yellowhammer (*Emberiza citrinella*), chaffinch (*Fringilla coelebs*), and redpoll (*Carduelis flammea*) populations must be derived from the New Zealand stocks. To the north, all the European passerines that reached Norfolk Island could have come from Australia; in contrast, those that reached the Kermadecs were more likely to have arrived from New Zealand, as the redpolls and yellowhammers certainly did, or from Pacific islands to the north. Similarly, the dunnocks and redpolls that reached the Auckland Islands, Campbell Island, and the Antipodes, and the dunnocks on far-flung Macquarie all came south (and for Macquarie, southwest) over hundreds of kilometres of stormy ocean from the main islands. Of the southern islands, the Chathams have 11 breeding species of introduced passerine, The Snares have five, the Aucklands seven, Campbell six, the Antipodes three, and Macquarie has two.

All these species have migratory populations in the northern hemisphere, and hence are both strong fliers and behaviourally willing to cross ocean barriers. Most also fly in flocks, so are more likely to arrive as viable propagules. The difference between the lists of breeding introduced species from islands with different vegetation patterns is an indication of the probable role of habitat availability in deciding which of the vagrant species can establish breeding populations. The Auckland group has about half the area of the Chathams and just over half the species list; both have areas of heath, grassland, and low forest. Twice as many breed on Campbell Island as on Antipodes even though both groups are about the same distance from the main islands (disregarding the presence of the Auckland group closer to Campbell). The species present on the Antipodes are the dunnock, redpoll, and starling (*Sturnus vulgaris*), all of which can live in open country, heath, and grassland. Chaffinches, blackbirds (*Turdus merula*), and song thrushes (*T. philomelos*) need taller, at least shrubby vegetation and breed only on the islands with scrub (*Dracophyllum* on Campbell Island) and are absent or very rare on the Antipodes, which has only grassland. Only starlings and redpolls have breeding populations in the windswept grasslands on Macquarie Island. The Bounties are only bare rocks, lacking plants other than algae and lichens. Despite reports of the arrival of starlings (Turbott 1990), and the presence of breeding populations both to the north (Chathams) and south (Antipodes), the species has not become established.

The group of species characteristic of the subantarctic regional fauna was dominated by seabirds, including 20 petrels, five penguins, and four marine shags (Fig. 3a). The remainder of the core group consisted of three ducks, a rail, three waders, a parakeet, and three songbirds. It is to be expected that petrels and penguins were most strongly represented on these island groups. The assemblage appears to be truly subantarctic, because only five species that breed in the Antarctic region (including the Antarctic peninsula up to South Georgia) are included: *Macronectes giganteus*, *Pachyptila desolata*, *Halobaena caerulea*, *Pygoscelis papua*, *Catharacta skua*. Most of the petrels, penguins, shags, and charadriiforms of the subantarctic groups breed north of the Antarctic convergence, and the islands contain a large percentage of the circum-polar subantarctic species.

The presence of well-differentiated terrestrial taxa, such as the two or three subantarctic teal, the Antipodes Island parakeet, and the distinct forms of snipe on the southern islands, raises the question of the age of the southern faunas. Fleming (1979) suggested that the southern faunas were restricted to those able to survive in grassland and open ground, and hence that the woody vegetation and the fauna that depended on it had been lost entirely. He also pointed out that the endemic taxa of invertebrates on the Auckland Islands are characteristic of grassland and not forest (Fleming 1979). The period of differentiation of island forms from their presumed mainland ancestors, as indicated by molecular data, may give clues both to the rate of speciation in the different groups, and the likely date of origin of the distinctive southern ecosystems.

Speciation and adaptive radiations in the New Zealand avifauna

Although there is no evidence for dramatic adaptive radiations from a single ancestor, such as that of the Hawaiian honeycreepers (James & Olson 1991), there are significant levels of speciation and radiation within some families and genera. Some of the radiations here have not been fully recognised, because we are haunted by previous taxonomic decisions.

For others, there are insufficient data on former distributions. A prime example for both is the snipe genus *Coenocorypha*, which now may include perhaps eleven species on islands from the tropics (Fiji) and subtropics (New Caledonia) to the subantarctic. A recent review (Higgins & Davies 1996) suggests that most if not all of the recognised forms are separate species and only the two Chatham Island forms were sympatric.

Snipe

The elevation of two of the surviving forms of snipe on the southern islands to species level and the discovery of another at Campbell Island means that there are at least three more species of *Coenocorypha* with small, vulnerable populations (*C. huegeli*, *C. meinertzhagenae*, *C.* "Campbell") than are recognised in the present checklist. From a practical conservation standpoint, potentially three more species on small land areas, in addition to the snipe surviving on the Chathams, may need extra resources in the future. The New Zealand Department of Conservation ranks and prioritises taxa for conservation on the basis of many attributes, in addition to taxonomic distinctiveness, so the difference between a species and a subspecies makes only one point difference to the overall score for each taxon (Molloy et al. 1994). Worldwide, species level taxa are given more weight on that criterion alone (e.g., Collar et al. 1994). Higher level classification also affects conservation ranking in New Zealand, in that the second highest score for the distinctiveness criterion is awarded if the taxon is the only species in its genus (Molloy et al. 1994). Using that criterion, two taxa, other Charadriiformes, would both lose a point under the taxonomy adopted here, if both *Anarhynchus* and *Thinornis* are submerged in *Charadrius*.

More work is required on the morphology, behaviour, and biochemistry of New Zealand snipe, and of many other endangered birds, to assess the real level of diversity in the group. Conservation of biodiversity is now recognised as being a high priority globally (Wilson 1992). In the instance of the New Zealand snipe, a newly recognised level of diversity means that instead of one or two species with dispersed island populations providing buffers against individual catastrophes, we now have five separate island populations, each now considered unique and vulnerable. Two populations – probably species – out of nine in the New Zealand snipe radiation (*C. aucklandica barrierensis, C. aucklandica iredalei*), have become extinct in the past 150 years. Both extinctions followed the introduction of mammalian predators to previously predator-free islands (Atkinson & Bell 1978; Holdaway 1999a), although their respective mainland populations were extinguished in pre-European time.

Parakeets and parrots

Evidence for radiation within the *Cyanoramphus* parakeets has been masked by their propensity to produce inter-specific hybrids when ecological barriers are broken down, because the isolating mechanisms that have developed are primarily pre-zygotic (Taylor 1975, 1985; Nixon 1994). Biochemical and morphological evidence suggests, however, that there were indeed three species on the main islands (with two ranging farther afield), and another (*C. forbesi*) on the Chathams, as well as the well-differentiated Antipodes Island species (*C. unicolor*), and another species only recently recognised as distinct (Boon et al. in press) on the southern subantarctic islands. It is surprising that there has been no parakeet recorded from Campbell Island. The recent discovery of a relict population of snipe on a small island offshore from the main Campbell Island (Miskelly 1997), and the presence of populations of parakeets on all other island groups with vascular vegetation, suggests that there was a parakeet there which disappeared unnoticed in the early years of sealing and whaling. If so, it may have been the same taxon now on Antipodes and was formerly on Macquarie Island (Boon et al. in press). The radiation of *Cyanoramphus* parakeets parallels that of the snipe in extending beyond New Zealand to New Caledonia (*C. saisseti*) and the Society Islands (*C. ulietanus* and *C. zealandicus*). Other species are likely to have existed on islands between these extremes before human intervention.

The *Nestor* parrots provide an example of a small radiation accompanying dispersal through the main islands: *N. productus* on Norfolk; *N. meridionalis* and *N. notabilis* on mainland New Zealand; and *N.* n. sp. on the Chatham Islands. The apparent absence of *Nestor* from Raoul Island is anomalous given its (former) presence on Norfolk and the Chathams. Further analysis of fossil deposits is needed.

Penguins and petrels

The penguin radiation is of long standing. The rich penguin fossil record shows that the coasts of proto-New Zealand have been a primary centre of penguin diversity since at least the later Eocene (Fordyce & Jones 1990; Fordyce 1991). Living New Zealand species range from the smallest to the second largest extant forms, and those that breed solitarily under cover or in burrows as well as colonial, open ground breeders. Whether the petrels also radiated in the New Zealand region is doubtful, the one early fossil here that could be from a petrel (*Manu antiquus* Marples, 1946) is of Oligocene age, by which time there was apparently a petrel fauna (in the broad sense) in the North Atlantic (Olson 1985b). Other, unstudied, pre-Holocene material of petrels is known to exist (J. McKee pers. comm. to THW). However, the range of marine conditions at present, the presence of suitable breeding islands in the region throughout the Cenozoic, the present high diversity in the three petrel families (which include more species than in any comparable area elsewhere) and the suites of closely related species such as the small *Puffinus* shearwaters, all suggest that the New Zealand region may have been a centre of speciation for some genera.

Shags and cormorants

van Tets (1976) suggested that the Australasian region as a whole was the base for the radiation of the present diversity of shags (marine species) and cormorants (fresh water species). Siegel-Causey (1988) presented a classification that would require the recognition of two radiations within New Zealand, as well as the arrival of representatives of other radiations of the Phalacrocoracidae. He considered the Campbell Island shag *Leucocarbo (=Nesocarbo) campbelli* to be a sister species to the *Euleucocarbo* group, and therefore part of an older split in the New Zealand region. According to Siegel-Causey, the two New Zealand *Stictocarbo* shags are seen as the most derived members of the cliff shags, which are themselves a derived group of the Leucocarboninae. If this classification is adopted, then New Zealand was not only home to its own radiation within the shags but also shared the results of radiations of cormorants and shags elsewhere.

Moas

Moas have been the focus of most of the research into extinct birds in New Zealand. In the past 20 years, a clearer picture of their diversity has emerged, helped by new techniques of radiocarbon dating and morphological analysis. One result has been a winnowing of the number of species down from 24 in 1970 to the present total of 11, in six genera. Another has been to clarify the distributions of each species in space and time. The earlier history of the moas is still little known for, although there is an abundant fossil record for the past 40,000 years and perhaps a little longer, there are few really old fossils – about two dozen bones of which the oldest is about 2.5 million years (Worthy et al. 1991). This scanty record does show that at least one modern species seems to have been present as early as 2.5 million years ago, so part of the radiation must have started even earlier.

Cooper & Cooper (1995) have suggested that the Oligocene land area bottleneck 30 million years ago was a key factor in speciation in some of the 'older' elements in the New Zealand fauna. Whatever the cause behind their origin, the 11 moa species were present in ecologically separated assemblages in the Holocene. In *Pachyornis* there was a North-South Island species pair, but the three *Dinornis*, *Euryapteryx geranoides*, and *Anomalopteryx didiformis* were found in both main islands; the remaining species were confined either to the North Island (*E. curtus*) or to the South Island, which with more area, accommodated a larger share of three endemic species. There, the subalpine species (*Megalapteryx didinus* and *Pachyornis australis*) must have developed their niche preference some time in the past 6 million years, as the Southern Alps were formed. The eastern lowland South Island endemic *Emeus crassus* was perhaps the ecological counterpart of *E. curtus*. The New Zealand ratites were confined to the main islands and a few of the closest and largest offshore islands.

Waterfowl

With 15 endemic species, the waterfowl represent the third largest group (after rails and songbirds) of non-oceanic birds within New Zealand, but they are not evidence of a major radiation. The ability of most waterfowl to fly strongly, and the diversity of species upwind of New Zealand in Australia, supplied New Zealand with a range of waterfowl, several of which have become differentiated into good species. Other species such as the swan *Cygnus atratus* are so vagile that persistent dilution of the New Zealand gene pool by new immigrants prevented the evolution of endemic taxa. Most that did were simple, monospecific derivatives of the assumed parent species (such as *Malacorhynchus scarletti* from the ancestor of *M. membranaceus*). There are two pairs of allopatric species within New Zealand (the two *Tadorna*s and the two *Cnemiornis*), but members of one genus, *Anas*, have radiated to fill a niche for a small dabbling species on several islands. *Anas chlorotis*, *A. aucklandica*, *A. nesiotis*, and *Anas* "Macquarie" may have been derived separately from different colonising groups, presumably by ancestral grey teal (*Anas gracilis*) (Johnson & Sorenson 1999; Kennedy & Spencer 2000) and not the chestnut teal (*A. castanea*) as has been believed until recently, on the basis of similarity of plumage (e.g., Williams 1995). Alternatively, at least the Auckland and Campbell Island birds were successive colonisations (before each parent stock became flightless) from one original colonisation (the same one that gave rise in the first instance to *A. chlorotis*). As with the snipe, the recognition of these populations as separate species has conserquences for their conservation status. It is possible that the present parlous state of *Anas chlorotis* on the main islands is a result of official neglect in the past because it was seen from 1953 to 1999 as the mainland representative of a more widely distributed speceis. Subconsciously at least, because the distribution of the nominate race under the then-prevailing nomenclature was centred on the relatively "safe" islands of the Auckland group, the mainland population may have been seen as not worthy of attention at the time when its decline was becoming apparent.

Rails

Seven species of rail apparently derived from ancestral *Gallirallus philippensis* forms are known in the region, from Norfolk and Macquarie islands to the Chathams. The species have all diverged more or less from the ancestral morphology, more so than many isolated species of rail elsewhere in the Pacific (Olson 1975; Diamond 1991; Trewick 1997b; Livezey 1998). On the three main islands of New Zealand, *G. australis* has barely differentiated populations. In the North Island, there is also the highly derived *Capellirallus karamu*, which is little studied but is currently considered to to be an earlier derivative of the *G. philippensis* stock.

The Chatham Islands had their own series of three *Gallirallus*-type rails. The most specialised, and perhaps the oldest, was *Diaphorapteryx hawkinsi*. *Gallirallus dieffenbachii* is usually assumed to have been the most recent colonist of the three, because it was the least specialised or least differentiated from *G. philippensis* and it has often been treated as a race. By this view, *Cabalus modestus*, which is more specialised than *G. dieffenbachii*, must also represent an earlier immigration. In contrast, Trewick (1997a) proposed that the rail which originally colonised the Chathams (apparently the common ancestor of today's *G. philippensis* population) has remained relatively unchanged (as *G. dieffenbachii*), but that a second colonisation from the same parent population resulted in a more differentiated species in the same genus (as *G. modestus*). The new colonising population did not interbreed with the previous colonist but diverged rapidly in morphology. We do not see how a small founding group, in the presence of an established population of birds that had differentiated only slightly from the parent form, could stay separate long enough to establish a very different morphology and, presumably, ecological position. The study also did not include either *Capellirallus karamu* or *Diaphorapteryx hawkinsi*, whose absence from the analysis limited the range of possibilities for relationships within the group. The point deserves further research, and indeed the New Zealand and Chathams *Gallirallus*-derived rails are a study in miniature of the vast radiation of the same stock throughout the Pacific (Steadman 1989). Along with *Porzana*, and *Porphyrio* they are the most vagile of the rails (Olson 1973b). The New Zealand *Gallirallus* and related rails would be ideal candidates for a comprehensive interdisciplinary study using ancient DNA (Trewick 1997b) and morphology.

Of the other rails, one group at least had successive waves of immigration. Of the probably volant (extinct) coots, at present the mainland form *Fulica prisca* is separated from the Chatham Islands form *F. chathamensis* at species level, but no differences have been noted between the North and South Island populations of *F. prisca*. In contrast, it has been proposed that the North and South Island takahe arose independently from separate invasions of pukeko-like stock (Trewick 1996). Trewick asserts that the flightless North Island takahe and the Australian swamphen or pukeko (*Porphyrio melanotus)* are sister species, but the North Island/South Island takahe pair are not, as had been assumed, but his conclusion was not supported by a later morphological analysis (Livezey 1998: 204). Although *Porphyrio porphyrio* and related forms are widespread throughout the Pacific (Steadman 1988), apparently no population was established on the Chathams at the time of human colonisation. *Gallinula* did not colonise the Chathams either, and its North and South Island populations had apparently not diverged, despite both being flightless.

Passer ines

The 'older' endemic songbirds present a range of adaptations. The seven described species of acanthisittid wren were confined to the main islands and the offshore islands, which suggests that poor flight ability evolved in this group before the outlying islands in their present form were available for colonisation. The relationships within the family are not well known (Cooper 1994). Much of the diversity within the Acanthisittidae is at genus level, which implies a considerable time depth to the radiation. This conclusion was supported by Cooper & Cooper (1995) who speculated, on the basis of genetic differences, that the New Zealand wrens speciated when the Oligocene marine transgressions left New Zealand as a series of low-lying islands. The long bill of *Dendroscansor decurvirostris* is unique in the family; too little is known of the species to allow firm inferences to be made about its habitat and niche, but it was flightless, as were *Traversia* and *Pachyplichas*. This radiation of flightless songbirds is unique.

The other notable mini-radiation of songbirds is that of the callaeatids, a family with unknown affinities within the Superfamily Corvoidea (Holdaway 1988, 1991a). The three genera have different bills and presumably fed in different ways, although there is only anecdotal evidence for the way the sexes of huia (*Heteralocha acutirostris*) used their different length bills (Jamieson & Spencer 1996). Both species of kokako (*Callaeas*) are (or were) mainly folivorous and frugivorous, but take some insects. The saddlebacks (*Philesturnus*) are insectivores and have strong pointed bills. *Heteralocha* was insectivorous, taking beetle larvae from tree trunks and limbs. Like the wrens, this group was confined to the main and inshore islands. Thus, their poor flight and inability or unwillingness to cross water gaps presumably pre-dates the present arrangement of islands, which was attained only about 0.45 million years ago. The same conclusion could be drawn for the piopio (*Turnagra*).

The largest radiation among the songbirds was that of the *Petroica* complex. This radiation is also likely to have been the most recent with island populations distinguishable only at the species level. In view of the differences between the robins and the tomtits and the similarity of the tomtits to Australian species, Fleming (1950a, b; 1962) may well been correct to postulate two separate invasions by petroicids. The eight species that we include in the *Petroica* group in New Zealand (Appendix 2) occupy all the island groups with woody vegetation, except the distant Kermadecs and Campbell. Only the tomtits have reached outlying islands south of the New Zealand mainland. Of the outlying islands, only the Chathams does not have a tomtit population that is not readily separable (on morphology) from the main island species closest to it. The Norfolk Island species is the only one that appears not to constitute part of the radiation from New Zealand.

Shaping the Holocene fauna — effects of the Pleistocene glaciations

The Pleistocene glaciations of the past 2–3 million years almost certainly reduced diversity of the avifauna of the Miocene and Pliocene, although admittedly there is almost no supporting fossil record at the moment. A deterioration in the climate during the Miocene, interpreted as a general cooling after the middle Miocene (Cooper & Cooper 1995) was reflected in Central Otago by a change from a moist environment flora dominated by *Nothofagus* to a flora dominated by Casuarinaceae and Asteraceae indicating a drier or cooler (or both) climate (Pole & Douglas 1998). *Eucalyptus* was part of the flora in the early Miocene (Pole 1993), and other plants that are today found no closer than Australia, such as *Acacia*, lived in New Zealand until the mid Pleistocene. That the Miocene avifauna may have been radically different to that of the late Pleistocene (Fleming 1962) is indicated by fossils of other groups not now part of the New Zealand fauna, such as a crocodilian (Molnar & Pole 1997).

Apart from penguins (Fordyce & Jones 1990), little is known about pre-Pleistocene bird faunas. Removal of major habitat types by climatic and vegetation change is likely to have been accompanied by extinctions in the avifauna. A small undescribed fauna of waterbirds is known from the Miocene of St Bathans, in central Otago (Douglas et al. 1981; Fordyce 1982, 1991). Pelagornithid seabirds were present in the Pliocene of North Canterbury (Howard & Warter 1969) and Hawera (Scarlett 1972; McKee 1985). Moas are known from deposits of Pliocene to early Pleistocene age (Worthy et al. 1991). At least one genus of rail was present during the mid-Pleistocene and was extinguished before the Aranuian (latest interglacial) (Worthy 1997c). It was a member of a small fauna from the mid-Pleistocene at Marton dated at 1 million years ago which also included another rail and a kiwi that are not known from late Pleistocene faunas (Worthy 1997c; AJDT, unpubl. data).

After an initial 'shaking down' process involving the elimination of warmer-climate taxa, some degree of stasis seems to have developed by the late Pleistocene, including only species that could cope with the recurring variations in the climate and vegetation patterns. The patchy fossil record from earlier interglacials and glacials suggests that the composition of the late Pleistocene fauna was stable for the past 100,000 years or so, through the last glacial and its various interstadials (Worthy & Holdaway 1993, 1994, 1995, 1996; Holdaway & Worthy 1997; Worthy 1997a, 1999a,b, 2000). The distributions of regional faunas changed in concert with the varying vegetation patterns driven by climatic fluctuations, but there were few or no extinctions and as few colonisations during the last glacial-interglacial cycle (Holdaway & Worthy 1997).

The earlier losses were balanced to some extent by endemic speciation in genera, driven by the geographical and climatic effects of the Pleistocene glaciations (Fleming 1979). Perhaps the greatest influence may be seen in the shorebirds, including the gulls and terns. The wrybill, shore plover, black stilt, black-billed gull, and black-fronted tern can all be regarded as having nesting requirements adapted to the conditions prevailing on periglacial tundra and braided river beds. Of the five, only the black-billed gull can be regarded as moderately common now. Two, the black stilt and shore plover, are now extremely rare and endangered (Collar et al. 1994).

The small radiation in the parrots of the genus *Nestor* has been linked to the effects of the glaciations. Fleming (1979) presented a scenario for the evolution of the two mainland species, *Nestor meridionalis* and *N. notabilis*, during the early Pleistocene, when the North and South Islands were separated by a "Manawatu Strait". As the land rose and closed the strait, *N. meridionalis* reached the South Island. Its apparent separation from *N. notabilis* by altitude is contradicted by the sympatry of the species in lowland forests in the Holocene (Holdaway & Worthy 1997) and the separation is probably by subtler differences in their ecologies. *N. notabilis* may have ventured north at the same time. It was certainly present in the North Island during the Otiran glaciation (Holdaway & Worthy 1993) when the islands were separated by a narrow but persistent marine gap (Worthy & Holdaway 1994), as well as by a wider barrier of windswept tundra and grassland. The differentiation of the North and South Island races of *N. meridionalis* could have taken place after the formation of Cook Strait about 0.5 million years ago.

Biased lists and biogeography – short-comings in the data

There are obvious inadequacies in the data available for preparing this list. Earlier lists used in studies paid little attention to the original fauna even as then known, and hence did not reflect the real diversity of the New Zealand avifauna. Studies of the relationships of the fauna as a whole, the factors that governed its composition, and its responses to new influences, including introduced taxa, must be based on the actual fauna that existed before human intervention.

Olson (1990c) and Steadman (1991) have called attention to the errors introduced to biogeographic analysis of Pacific island birds that result from using the incompletely known avifaunas in the area. The data from bird distributions in the Pacific have been used to generate island biogeographic theory. In turn, this body of theory has been used to design reserves, not without accompanying controversy (see Quammen 1996). A spate of papers on the biogeography of New Zealand birds and the design of reserves for their conservation began with Williams (1981) which relates number of species to area. Williams based his analysis on a list prepared from Falla et al. (1979) and Kinsky (1970) which lacked nearly 50% of the original avifauna. An example of the effects of using an inadequate list can be seen if the full prehuman list is used to prepare a substitute for fig. 3 in Williams (1981). Almost all the offshore islands would have had larger faunas. With the full list of species for each, the points for the North and South Islands would lie on the line of best fit for the offshore islands, instead of being some distance below it (see our Fig. 4). On Williams's figure, Stephens Island (Takapourewa) is far above the line and is excluded from further analysis as being anomalous. It is likely that Stephens Island still had more of its original fauna when first described by Europeans than did other islands that had been colonised by Polynesians, or populations of the Pacific rat (*Rattus exulans*).

In the early 1890s, Stephens Island (1.5 km^2) had resident populations of kokako, saddleback, piopio, and Lyall's wren, amongst many other bird species in the coastal *Dysoxylum* and *Streblus* forest that capped the island above steep sea cliffs (Atkinson & Bell 1973). All these birds became extinct on the island within at the most five years of its occupation by lighthouse keepers and their families. If one of the keepers, Lyall, had not noticed the wren and informed Buller, and the surveyors not been required to submit a full report on the island (including its wildlife), the diversity of the island's original avifauna would never have been suspected. No fossil deposits are known or might be expected on the island.

The situation on Stephens Island begs the question of the constitution of the faunas of other islands of similar or larger size. If kokako and piopio could maintain viable populations in coastal forest on about 1.5 km^2 in the harsh climate of Cook Strait, they may well have been present on other islands before those were affected by human occupation and intervention. A more southern example is that of Big South Cape Island (8 km^2), southwest of Stewart Island, on which there were, until 1964, viable – even abundant – populations of saddleback, bush wren, snipe, fernbird, and robin in a forest that is different in composition to that on Stephens Island (*Olearia* and *Metrosideros*, plus *Dacrydium*/*Weinmannia* forest in sheltered valleys) but at least as exposed (Atkinson & Bell 1973; Bell 1978). There are no known fossil deposits on Big South Cape. If the island had been first visited by naturalists 10 years after the invasion of *Rattus rattus* in the early 1960s (Bell 1978), the impoverished fauna that survived the rat plague would have been regarded as the 'natural' fauna of forest birds.

Codfish Island (c. 14 km^2) is nearly twice the size of Big South Cape, only 50 km to the north has a similar vegetation (Atkinson & Bell 1973). At European contact, Codfish Island lacked at least four species from the probable original fauna (*Coenocorypha iredalei*, *Xenicus longipes*, *Petroica australis*, and *Philesturnus carunculatus*): their inclusion is an increase of about 21% over the list used by Williams (1981). There are dunes on the island but to date no significant fossil deposits have been reported, hence the former presence of those species cannot yet be confirmed. The argument that they were prevented from colonising from Stewart Island by the steepness of the Ruggedy Range (Blackburn 1968) is hardly credible. It is far more likely that all species were eliminated by *Rattus exulans* after that rodent became established on Codfish Island, probably early in the 19th century (Holdaway 1999a, b) after the beginning of modern mutton-birding (Anderson 1997).

These examples may reflect the course of events on some of the larger central and northern islands such as the Chetwodes, Kapiti, Mercury, Poor Knights, Hen, Cuvier, and others larger than Stephens Island. Fossils and archaeological bird bones have been found on islands as small as Mana Island (217 ha), off the Wellington west coast, Stanley (120 ha) (Mercury group), Motuopao (30 ha), and Te Haupa (6 ha), (Miskelly 1999; Tennyson & Taylor 1999; AJDT, unpubl. data), and on larger islands such as Great Barrier and D'Urville Islands (authors' unpubl. data), but so far few extensive deposits (particularly natural deposits) have been found. The record is likely to show that many offshore islands had more diverse faunas than are apparent today, after the gross changes in habitat that have accompanied human occupation or exploitation, and the introduction of terrestrial mammals to many islands. For example, it may be that the massive numerical dominance of the bellbird (*Anthornis melanura*) population in the forest on Aorangi, Poor Knights islands (Bartle & Sagar 1987) is a result of the removal of forest and long-term occupation by Maori (Hayward 1993) during which time other species may have been eliminated. The reason for the present dominance of bellbirds is unknown but may be a result of chance in the survival of a small population on the cliffs or some factor in the composition of the present vegetation.

For his biogeographic study, Williams (1981) used the list of land and freshwater birds present when Europeans arrived, so he credited the North Island with 50 species and the South Island with 47 (Williams 1981: table 1) whereas the real numbers in the original faunas were closer to 90 for both. Problems with using modern lists for biogeographic analysis were noted by Holdaway (1990), who found that bird diversity was higher not only in the prehuman environment, but it was also higher than predicted by studies of living communities (McLay 1974; Flux 1989).

Diamond (1984) used Williams's list (Williams 1981: appendix 1), with minor alterations, when he too assessed the species compositions of islands in the New Zealand archipelago in terms of island biogeographic theory. Apart from the biases arising from using a modern list, his analysis was also hampered by limited information on the dispersal ability of species and size of island required to maintain populations of some taxa. The first problem is illustrated by the classification of some species, such as dabchick (*Poliocephalus rufopectus*) and Haast's eagle (*Harpagornis moorei*), kea (*Nestor notabilis*), and fantail (*Rhipidura fuliginosa*) as poor over-water colonisers even though they can fly long distances over land. For example, kea have visited fishing boats several kilometres off the northwest Nelson coast (THW, unpubl. data) and were part of the North Island fauna during the Otiran Glaciation (Worthy & Holdaway 1993). Dabchicks (*Poliocephalus rufopectus*) have crossed Cook Strait to the South Island occasionally since their extinction there (Heather & Robertson 1996). The eagle has never been found in North Island deposits of any age, although it obviously flew very well (Holdaway 1991b). Fantails colonised The Snares after the mid-1970s (Johns et al. 1983). Secondly, the size of islands required by some species may have been over-estimated. For example, Diamond (1984: table 2) gave 10–100 km^2 as the minimum island area required for a 50% chance of recording both piopio and kokako. The presence of both species on Stephens Island before the destruction of its forests suggests either that both species had some over-water dispersal ability, or that stable populations of both could be maintained on an island nearly an order of magnitude smaller than he supposed. There is still a need for a comprehensive biogeographic analysis of the New Zealand avifauna based on the original set of breeding species present before human disturbance.

Williams (1981) ignored the prehistorically extinct taxa which resulted in the general underestimation of the species numbers on the main islands (Williams 1981: appendix 2, fig. 2–4), and the numbers on offshore islands were probably underestimated as well if he used the same criteria for them. We compare the list in Williams (1981: appendix 1) with our interpretation of the terrestrial and freshwater avifauna in Appendix 6). Our Fig. 4 is based on fig. 3 of Williams (1981). As examples of the effects of using the full list, we have plotted the full species complements for five islands (North, South, Stewart, Stephens, and Codfish) as detailed in this paper, with arrows showing the change of position from Williams's for each island. Even allowing for the logarithmic scaling, the changes for the two largest islands are sufficient to alter the slope of the line presented by Williams for 17 offshore islands (Fig. 3): S (number of species) = A (island area, km^2) $^{0.28}$ ($r^2 = 0.76$, $P < 0.001$). Adding the main islands to the offshore island, the species-area relationship is $S = 7.288A^{0.183}$ ($r^2 = 0.748$). Hence, increasing the scale of the analysis to include the larger islands results in a value of z of 0.183 as against 0.28, which, as Williams pointed out, was very close to the theoretical value of 0.27 calculated by Preston (1962) and McArthur & Wilson (1967). Hence, the New Zealand avifauna, departs from expectation when ALL the New Zealand islands are included.

When data for islands for which revised lists are available (Fig. 4) are included, the relationship becomes $S = 5.929A^{0.201}$ ($r^2 = 0.7243$), with the slightly greater slope (0.201) and lower intercept (5.929) resulting from the effects of the greater numbers on the two main islands. If, as an approximation and assuming that other islands as small as Stephens might have had a similar-sized fauna, the species number for Stephens Island (23) is allocated to all islands of that size or greater (0.193 km^2), the relationship is $S = 19.35A^{0.099}$ ($r^2 = 0.892$), with an even lower value of z than before. There would be, of course, a very steep decline in species number for even smaller islands, but there are too few data to support a cutoff size for higher species diversity. The lower slope of the curve when it is assumed that small islands could have larger faunas (as evidenced by Stephens Island), shows that species number was actually less sensitive to island size than was suggested by the present species lists used by Williams. If smaller islands could and did support more species than expected from the present faunas, then there are consequences for conservation theory.

Williams (1981) resorted to special pleading to fit Stephens Island to the curve established from the depauperate present lists from other islands. Instead of plotting the data he had, he suggested that the early reports as to the number of species resident on the island were in error. He plotted the present number of species and maintained that it "is much more in line with what would be expected". We believe that the number of species on other small islands are artificially low as a result of extinctions in pre-European times: the curve was based on incomplete but unquestioned data from the other small islands. The greater number of species accepted here for the North and South Islands raises doubts about the validity of the species-area curve derived from the data used by Williams. The rejection of the reported number of species in favour of a number that fitted the model obscured patterns in the distribution of New Zealand birds that he found unacceptable.

Extinctions

The list presented here emphasises the high level of extinctions of species and of higher taxa in New Zealand faunal history. It replaces the summary of extinctions at species, genus, and family level given by Holdaway (1989), and corrects several errors in that list (for example, deletes the "sea eagle" from the Chathams, and keeps *Circus eylesi*). The dates of the known extinctions, and the basic attributes of the species lost and of those that survived are given in Holdaway (1999a).

Of the 245 breeding species in the New Zealand avifauna when humans arrived, 76 (31%) are now locally or globally extinct (Table 1, Fig. 1). Island groups within the New Zealand region have suffered greater or lesser levels of extinction (Tables 1, 2; Fig. 2), leaving depauperate faunas. Levels of extinction were greatest on the main islands and least on the more remote island groups and where human influences were minimal (Fig. 2). The present faunas of the various components of the wider archipelago are consequently more similar to each other now in total species number, and species number is no longer related to the total land area of the regions (Fig. 1). The greatest percentage loss was from the North Island fauna, at about 51% of the original breeding species; the figure could be even higher if, as is likely, species such as the yellow-eyed penguin (*Megadyptes antipodes*) and New Zealand crested penguin (*Eudyptes pachyrhynchus*) formerly bred on the North Island.

The losses amongst endemics were even greater than losses from the New Zealand as a whole; at least 41.4% of the endemic species thought to have bred in New Zealand as a whole in the late Holocene are now extinct (Table 3). The greatest numbers were lost from island groups that were inhabited prehistorically, and which have been invaded by mammalian predators (Holdaway 1999a). The mean percentage extinction of endemics on the North, South, Norfolk/Kermadec (mostly on Norfolk), the Chathams, and the subantarctic islands was 52.3% (calculated from Table 3).

The New Zealand fauna before human arrival was different in many ways from the fauna that survives. In terms of numerical dominance of species groups rather than speciation or radiation within the endemic fauna, the breeding list we present here is weighted differently from the present checklist (Turbott 1990). For example, the avifauna in Turbott (1990) is dominated by an extensive list of migratory — usually vagrant — charadriiforms. Although many of the migratory species undoubtedly visited New Zealand in the past, as they do today, they represent an ephemeral component of the avifauna. The two most abundant species, the bar-tailed godwit (*Limosa lapponica*) and knot (*Calidris canutus*) are very important members of the estuarine community during the southern summer, and rather less so in winter, where they share the habitat with local breeders such as Finsch's oystercatcher (*Haematopus finschi*) (Robertson 1999). Perhaps the most significant role of the visiting species in the pre-human avifauna was to limit the range of niches available to breeding species that might otherwise have exploited the habitat.

The removal of species from all regions by extinctions since first human contact has affected the relationships and distinctions between the original regional faunas, primarily by removing the characteristic — usually endemic — taxa. The more widespread species now form more link groups (Fig. 3). It is significant that the major faunas (subtropical,

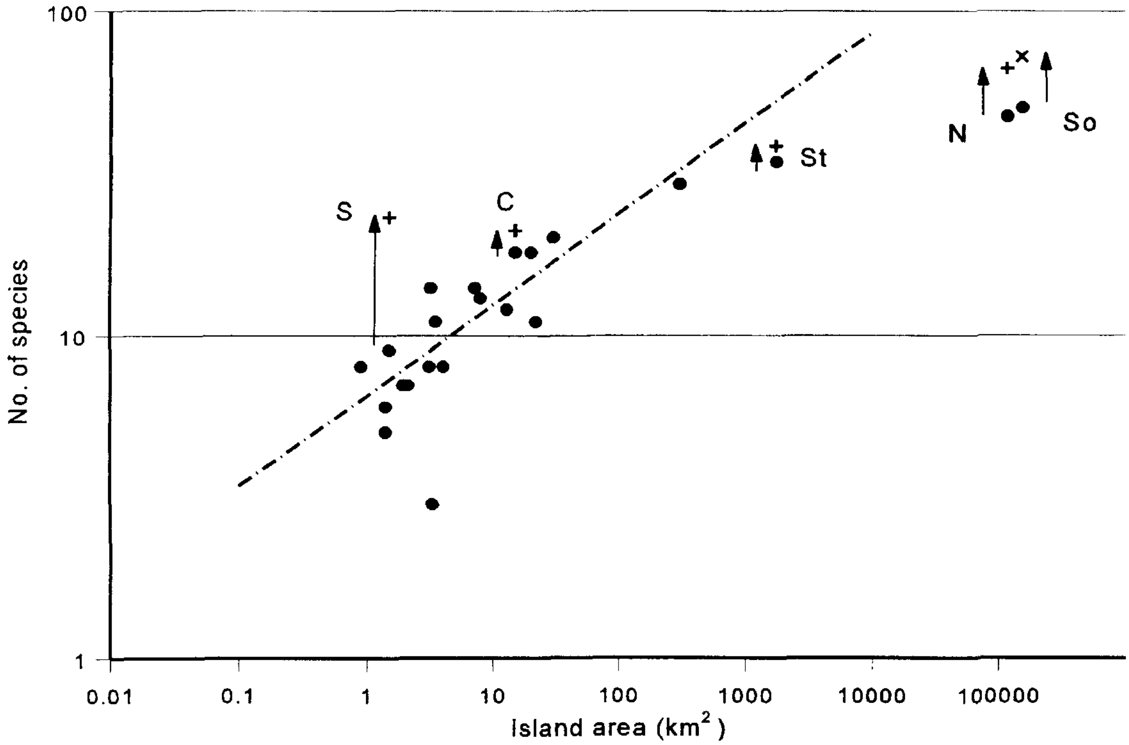

Fig. 4 Species-area plot for the terrestrial and freshwater avifauna of New Zealand archipelago (no. of species v. island area in km^2) based on fig. 3 of Williams (1981), with only the main and closer offshore islands plotted. Islands replotted with species numbers accepted in this papers are plotted as crosses, Williams's data as filled circles. Arrows indicate displacement of values for replotted islands, directed towards the new values. S, Stephens Island; C, Codfish Island; St Stewart Island; N, North Island; So, South Island. The line is the relationship derived by Williams between species and area for 17 offshore islands (i.e. not including the main islands), details of equations in text.

mainland New Zealand, Chathams, and subantarctic) remain as clear entities, despite the magnitude of the losses. The relative importance, in terms of species numbers, has changed, in that the natural subantarctic fauna now rivals that of the natural avifauna of the main islands. The enduring presence of endemic seabirds has buffered the subtropical and Chatham faunas, particularly the former, from collapsing to a more or less characteristic depauperate fauna of island tramps. The Chatham fauna is no longer most similar to the mainland fauna but is part of a broader subantarctic group.

Extinctions among the landbirds has increased the dominance of coastal and oceanic species in the avifauna. Now, an analyst is struck by the dominance of seabirds and waders and the scarcity of indigenous songbirds, waterfowl, and rails. The petrels were a major element in the past as they are now, with almost the same number of species but, before the extinctions began, they were nearly balanced by the total number of species in the other three groups. Many of the mainland extinctions of seabirds were offset by the survival of relict breeding populations on small islands (so that they do not appear as total losses in a summary of extinctions for the archipelago), but the total numbers of individuals must have been greatly reduced. However, although the level of global extinctions of marine species is lower than that for some other groups (Table 1, 2, 3), it is still higher than has been generally appreciated. The hardest hit of the non-marine groups were the terrestrial herbivores, small songbirds, and the terrestrial predators. Several terrestrial species teeter on the brink. For example, there are persistent records of the survival of *Zosterops albogularis* on Norfolk Island (e.g., Moore 1999) but there seem to be no plans to determine its status or to design potential conservation measures, despite previous concerns

(Hermes 1990). Other species may have already gone: the grey-headed blackbird (*Turdus poliocephalus*) was last seen on Norfolk Island in 1975 (Schodde et al. 1983). On the main islands, few believe that the South Island kokako (*Callaeas cinerea*) still hangs on. The two species totally lost in the Big South Cape Island catastrophe in the early 1960s (bush wren and Iredale's snipe: Bell 1978) serve as reminders of how fragile many of the remaining refuges are.

The composition of the original breeding avifauna was weighted towards those taxa from Australia that could colonise across major water gaps. The present New Zealand checklist (Turbott 1990) also includes many vagrants that could not colonise permanently for good ecological reasons, and so is inflated in the representation of tropical and subtropical forms. Fewer terrestrial species had island refuges; some that did, such as Lyall's wren, did not survive for long after the arrival of Europeans.

Holdaway (1999a), using an earlier version of the present list for the three main islands (North, South, Stewart), discussed the vulnerability of the avifauna to various influences and concluded that introduced predators, including humans, were responsible for most if not all of the extinctions. Overall, assuming that extinctions before European arrival were evenly distributed from AD 1300 (the approximate time of first settlement: Higham et al. 1999), the average rate of extinction before 1770 was 0.09% per year, as against 13.5% per year after 1770 (Holdaway 1999a). However, most of the largest taxa do not appear in Classic Period Polynesian sites (Holdaway 1999a; Worthy 1999b; Holdaway & Jacomb 2000), and the rate of extinction before European arrival was probably much greater in the first century or two after colonisation, when the instantaneous rate would have been higher than at any other time since first human contact (Holdaway 1999a). In addition, several of the species most in danger at present began their decline very soon after initial Polynesian settlement; only relict populations remained by the nineteenth century (Holdaway 1999a).

Although this is only a preliminary analysis of the relationships within and between the faunas of the main island groups in the New Zealand avifauna, it does show the main characteristics of each fauna and how human impacts have changed those characteristics and interrelationships. In particular, it demonstrates that the present over-representation of petrels and other marine species and the increased dominance of the subantarctic fauna, are artefacts of the extinctions of land birds that have accompanied settlement by people. The original fauna was centred firmly on endemic groups in the main islands and the Chathams. What remains is a small selection of the most resilient — or luckiest — of the endemics amongst a greater number of more widespread or generalist species.

CONCLUSIONS

Recent research has provided new information on the species level diversity of the New Zealand avifauna at first human contact. Further studies, particularly of fossil faunas on offshore islands, are needed, but there is now a secure basis for biogeographical and evolutionary studies. However, it has become obvious that there are large gaps in our knowledge of the systematics of New Zealand birds. Even the species level diversity of the living New Zealand (natural) avifauna is still far from completely known. For example, we recognise 12 species (5%) that are yet to be formally named. As birds are supposedly the best known higher vertebrates in the fauna, it is somewhat disturbing that the first stage of documenting the diversity at species level is still incomplete.

There is no agreement about how many species should be recognised in several major groups of the pre-human avifauna. In our view, The stability of the New Zealand bird checklist has for many decades been a result of inertia and tradition rather than real and advancing knowledge. If the avifauna is one of the best known groups, and there is such a gap in our knowledge, then there is obviously a need for greater research and documentation of the present and past diversity of the whole fauna if we are to know what the true richness once was, before more of it is lost.

We must know what is and was here, before we can understand how the systems worked, and how they evolved, but the evolutionary histories of New Zealand birds are poorly known. There is ample scope for research. The New Zealand avifauna is as amenable as any to studies that can throw light on fundamental evolutionary and biogeographical processes, and the process of extinctions. Indeed, because the true extent of the unmodified fauna is potentially so accessible, it may be one of the best natural laboratories in the world. However, as a result of past inertia, we are only now about to detect some of these species and thereby recognise the real level of diversity. In some cases, recognition may be coming after their extinction, as it did with Iredale's snipe.

This working list of breeding species focuses attention on the lack of basic information on the systematics of many groups and species in the New Zealand avifauna. Indeed, just how many species should be included in this "well known" group was often a matter of considerable uncertainty in the preparation of the list. Amongst many groups (in particular kiwis, diving petrels, small shearwaters, snipe, parrots, pipits, and the tomtits and robins), there is great need for research to disclose the full measure of species level diversity in the fauna. The treatment used here suggests that there are many more species, and consequently more rare and vulnerable species, than is appreciated at present. There are obvious opportunities for further study using new techniques in biochemistry and morphological analysis, so that the real diversity of the avifauna can be revealed. This paper is a summary of present knowledge. It is not intended as an end of itself. It will achieve its purpose if it is taken as a starting point, and a guide for future research.

ACKNOWLEDGMENTS

We thank Sandy Bartle, John Yaldwyn, and Elliot Dawson for help in determining the correct specific name for *Thalassarche melanophris*. Sandy Bartle was helpful in locating references, and for providing comments on the list. Geoff Tunnicliffe kindly provided access to the Canterbury Museum collections. The manuscript was greatly improved by comments and suggestions by Ricardo Palma, Mike Imber, and two other (anonymous) referees. We espeically appreciate the patience shown by the editor in dealing with this large and complex MS, and her valuable and insightful comments on it.

REFERENCES

Abbott, J. J.; Simpson, K. N. G. 1972: Avifaunal affinities of Macquarie, Norfolk, Phillip, and Lord Howe Islands. *Emu 72*: 178.

Anderson, A. J. 1989: *Prodigious birds: Moa and moa hunting in prehistoric New Zealand.* Cambridge, Cambridge University Press. 238 p.

Anderson, A. J. 1991: The chronology of colonization in New Zealand. *Antiquity 65*: 767–795.

Anderson, A. J. 1997: Historical and archaeological aspects of muttonbirding in New Zealand. *New Zealand Journal of Archaeology 17*: 35–55.

Andrews, C. W. 1896: On the extinct birds of the Chatham Islands. Part 1. The osteology of *Diaphorapteryx hawkinsi. Novitates Zoologicae 3*: 73–84.

Atkinson, I. A. E.; Bell, B. D. 1973: Offshore and outlying islands. Pp. 372–392 *In*: Williams, G. R. *ed. The natural history of New Zealand: an ecological survey.* Wellington, A. H. & A. W. Reed. 434 p.

Austin, J. J. 1996: Molecular phylogenetics of *Puffinus* shearwaters: preliminary evidence from mitochondrial cytochrome *b* gene sequences. *Molecular Phylogenetics and Evolution 6*: 77–88.

Bailey, A. M.; Sorenson, J. H. 1962: Subantarctic Campbell Island. *Denver Museum of Natural History, Proceedings no. 10.*

Baker, A. J.; Daugherty, C. H.; Colbourne, R.; McLennan, J. L. 1995: Flightless brown kiwis of New Zealand possess extremely subdivided population structure and cryptic species like small mammals. *Proceedings of the National Academy of Sciences, USA 92*: 8254–8258.

Balouet, J. C.; Olson, S. L. 1989: Fossil birds from late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology 469*: 1–38.

Bartle, J. A.; Sagar, P. M. 1987: Intraspecific variation in the New Zealand bellbird *Anthornis melanura. Notornis 34*: 253–306.

Bartlett, A. D. 1852: On the genus *Apteryx*. Proceedings of the Zoological Society of London [1850] XVIII (ccxviii): 274–276.

Bell, B. D. 1976: Status of Great Barrier Island birds. *Notornis 23*: 310–319.

Bell, B. D. 1978: The Big South Cape Islands rat irruption. Pp. 33–40 *In*: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. *ed. The ecology and control of rodents in New Zealand nature reserves. New Zealand Department of Lands and Survey information Series No. 4.*

Best, H. A. 1976: First sightings of the hoary-headed grebe (*Podiceps poliocephalus*) in New Zealand. *Notornis 23*: 182–183.

Blackburn, A. 1968: The birdlife of Codfish Island. *Notornis 15*: 51–65.

Bock, W. J. 1958: A generic review of the plovers (Charadriinae, Aves). *Bulletin of the Museum of Comparative Zoology, Harvard 118*: 27–97.

Boon, W. M.; Daugherty, C. H.; Chambers, G. K. In press: The Norfolk Island green parrot and New Caledonian red-crowned parakeet are distinct species. *Emu.*

Boon, W. M.; Kearvell, J. C.; Daugherty, C. H.; Chambers, G. K. 2000: Molecular systematics of New Zealand *Cyanoramphus* parakeets: conservation of orange-fronted and Forbes' parakeets. *Bird Conservation International 10*: 211–239.

Bourne, W. R. P. 1967: Subfossil petrel bones from the Chatham Islands. *Ibis 109*: 1–7.

Brodie, J. W. 1973: The ocean environment. pp. 61–92 *In*: Williams, G. R. *ed. The natural history of New Zealand: an ecological survey*. Wellington, A. H. & A. W. Reed. 434 p.

Browning, M. R.; Monroe, B. L. 1991: Clarifications and corrections of the dates of issue of some publications containing descriptions of North American birds. *Archives of Natural History 18*: 381–405.

Bull, P. C.; Gaze, P. D.; Robertson, C. J. R. 1985: *The atlas of bird distribution in New Zealand*. Wellington, Ornithological Society of New Zealand.

Buller, W. L. 1869: On some new species of New-Zealand birds. *Ibis (1869)*: 37–43.

Burton, P. J. K. 1972: Some anatomical notes on the wrybill. *Notornis 19*: 26–32.

Campbell, H. 1996: Geology. pp. 34–48 *In*: Anonymous *ed. The Chatham Islands: heritage and conservation*. Christchurch, Canterbury University Press and New Zealand Department of Conservation. 136 p.

Cassels, R. 1984: The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific islands. Pp. 741–767 *In*: Martin, P. S.; Klein, R. G. *ed. Quaternary extinctions: a prehistoric revolution*. Tucson, University of Arizona Press. 892 p.

Cheeseman, T. F. 1891: On the birds of the Kermadec Islands. *Transactions and proceedings of the New Zealand Institute 23*: 216–226.

Christidis, L.; Boles, W. E. 1994: The taxonomy and species of birds of Australia and its Territories. *Royal Australasian Ornithologists Union Monograph 2*. Melbourne, RAOU.

Christidis, L.; Leeton, P. R.; Westerman, M. 1996: Were bowerbirds part of the New Zealand fauna. *Proceedings of the National Academy of Sciences USA 93*: 3898–3901.

Claridge, M. F.; Dawah, H. A.; Wilson, M. R. *ed.* 1997: *Species: the units of biodiversity*. Chapman & Hall, London. 439 p.

Collar, N. J.; Crosby, M. J.; Stattersfield, A. J. 1994: *Birds to watch 2 – The world list of threatened birds. Birdlife Conservation Series no.4*. Cambridge.

Cooper, A. 1994: Ancient DNA sequences reveal unsuspected phylogenetic relationships within New Zealand wrens (Acanthisittidae). *Experientia 50*: 558–563.

Cooper, A.; Cooper, R. A. 1995: The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society of London B 261*: 293–302.

Cracraft, J. 1983: Species concepts and speciation analysis. Pp. 159–187 *In*: Johnston, R. *ed. Current Ornithology 1*. Plenum Press, New York.

Cracraft, J. 1997: Species concepts in systematics and conservation biology – an ornithological viewpoint. Pp. 325–339 *In*: Claridge, M. F.; Dawah, H. A.; Wilson, M. R. *ed. Species: the units of biodiversity*. London, Chapman & Hill. 439 p.

Dawson, E. W. 1962: An early specimen of the kakapo (*Strigops habroptilus*) from Stewart Island. *Notornis 10*: 85–86.

Dawson, E. W. 1964: Antarctic oceanography. *Antarctic (June)*: 430–432.

de Boer, L. E. M. 1976: Karyological heterogeneity in the Falconiformes (Aves). *Experientia 31/10 (15.10.1975)*: 1138–1139.

Diamond, J. M. 1984: Distributions of New Zealand birds on real and virtual islands. *New Zealand Journal of Ecology 7*: 37–55.

Diamond, J. M. 1991: A new species of rail from the Solomon Islands and convergent evolution of insular flightlessness. *Auk 108*: 461–470.

Diamond, J. M.; Veitch, C. R. 1981: Extinctions and introductions in the New Zealand avifauna: cause and effect? *Science 211*: 499–501.

Douglas, B. J.; Linqvist, J. K.; Fordyce, R. E.; Campbell, J. D. 1981: Early Miocene terrestrial vertebrates from Central Otago. *Geological Society of New Zealand Newsletter 53*: 17.

East, R.; Williams, G. R. 1984: Island biogeography and the conservation of New Zealand's indigenous forest-dwelling birds. *New Zealand Journal of Ecology 7*: 27–35.

Ereshefsky, M. (*ed.*) 1992: *The units of evolution: essays on the nature of species*. Cambridge, Massachusetts, MIT Press. 405 p.

Falla, R. A. 1970: Grey ternlets in the Bay of Plenty. *Notornis 17*: 83–86.

Falla, R. A. 1974: Rare birds and conservation. Pp. 121–134 *In*: Robertson, C. J. R. *ed. Birds in New Zealand*. Wellington, A. H. & A. W. Reed. 135 p.

Falla, R. A. 1978: Banded dotterel at the Auckland Islands: description of a new subspecies. *Notornis 25*: 101–108.

Falla, R. A.; Sibson, R. B.; Turbott, E. G. 1979: *The new guide to the birds of New Zealand*. Collins, Auckland. 247 p.

Fleming, C. A. 1939: Birds of the Chatham Islands. Part 1. *Emu 39*: 380–413.

Fleming, C. A. 1950a: New Zealand flycatchers of the genus *Petroica* Swainson. Part I. *Transactions of the Royal Society of New Zealand 78*: 14–47.

Fleming, C. A. 1950b: New Zealand flycatchers of the genus *Petroica* Swainson (Aves). Part II. *Transactions of the Royal Society of New Zealand 78*: 127–160.

Fleming, C. A. 1953a: Checklist of New Zealand birds. Ornithological Society of New Zealand.,Wellington. 80 p.

Fleming, C. A. 1953b: Materials for a Recent geochronology of New Zealand. Pp. 114–125 *In*: Black, M. A. *ed.* Seventh Science Congress, Christchurch, Christchurch, May 15–21, 1951. 256 p.

Fleming, C. A. 1962: History of the New Zealand land bird fauna. *Notornis 9*: 270–274.

Fleming, C. A. 1979: *The geological history of New Zealand and its life*. Auckland, Auckland University Press and Oxford University Press. 141 p.

Fleming, C. A.; Serventy, D. L. 1943. The races of *Puffinus assimilis* in Australia and New Zealand. *Emu 43*: 113–125.

Flux, J. E. C.; 1989: Biogeographic theory and the number and habitat of moas. *New Zealand Journal of Ecology 12 (supplement)*: 35–37.

Foggo, M. N.; Hitchmough, R. A.; Daugherty, C. H. 1997: Systematic and conservation implications of geographic variation in pipits (*Anthus*: Motacillidae) in New Zealand and some offshore islands. *Ibis 139*: 366–373.

Fordyce, R. E. 1982: The fossil vertebrate record of New Zealand. Pp. 630–698 *In*: Rich, P. V.; Thompson, E. M. *ed. The fossil vertebrate record of Australasia.* Monash Offset Printing Unit, Clayton, Victoria, Australia. 759 p.

Fordyce, R. E. 1991: A new look at the fossil vertebrate record of New Zealand. Pp. 1191–1316 *In*: Vickers-Rich, P.; Monaghan, J. M.; Baird, R. F.; Rich, T. H. *ed. Vertebrate palaeontology of Australasia.* Melbourne, Pioneer Design Studio and Monash University. 1437 p.

Fordyce, R. E.; Jones, C. M. 1990: Penguin history and new fossil material from New Zealand. Pp. 419–446. *In*: Davis, L. S.; Darby, J. *ed. Penguin biology.* San Diego, Academic Press. 467 p.

Freeman, A. N. D. 1994: Landbirds recorded at the Chatham Islands, 1940 to December 1993. *Notornis 41 (supplement)*: 127–141.

Gersonde, R.; Kyte, F. T.; Bleil, U.; Diekmann, B.; Flores, J. A.; Gohl, K.; Grahl, G.; Hagen, R.; Kuhn, G.; Sierro, F. J.; V''lker, D.; Bostwick, J. A. 1997: Geological record and reconstruction of the late Pliocene impact of the Eltanin asteroid in the Southern Ocean. *Nature 390* : 357–363.

Gray, G. R. 1862: A list of the birds of New Zealand and the adjacent islands. *Ibis (1862)*: 214–252.

Hamilton, A. 1889: Notes on a deposit of moa-bones in the Te Aute Swamp, Hawke's Bay. *Transactions and Proceedings of the New Zealand Institute 21*: 311–318.

Hawkins, J. M. 1988: The Farewell Spit gannetry — a new sea level colony. *Notornis 35*: 249–260.

Hayman, P.; Marchant, J.; Prater, T. 1986: Shorebirds: an identification guide to the waders of the world. Surry Hills, Australia, Croom Helm. 412 p.

Hayward, B. W. 1993: Prehistoric archaeology of the Poor Knights Islands, northern New Zealand. *Tane 34*: 89–105.

Heather, B. D.; Robertson, H. A. 1996: *The field guide to the birds of New Zealand.* Auckland, Viking. 432 p.

Hermes, N. 1990: White-breasted white-eye. Pp. 136–137 *In*: Brouwer, J.; Garnett, S. *ed. Threatened birds of Australia: an annotated list.* Royal Australasian Ornithologists' Union and Australian National Parks and Wildlife Service, Moonee Ponds, Victoria. 178 p.

Hermes, N.; Evans, O.; Evans, B. 1985: Norfolk Island birds: a review 1985. *Notornis 33*: 141–149.

Higgins, P. J. (ed.) 1999: *Handbook of Australian, New Zealand and Antarctic birds, vol. 4. Parrots to Dollarbird.* Melbourne, Oxford University Press.

Higgins, P. J.; Davies, S. J. J. F. *ed.* 1996: *Handbook of Australian, New Zealand & Antarctic birds, Vol. 3 – Snipe to Pigeons.* Melbourne, Oxford University Press.

Higham, T.; Anderson, A. J.; Jacomb, C. 1999: Dating the first New Zealanders: the chronology of Wairau Bar. *Antiquity 73* :420–427.

Hill, M. O. 1979: *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell University, Ithaca, New York.

Hindwood, K. A. 1965: John Hunter: a naturalist and artist of the First Fleet. *Emu 65*: 83–95.

Holdaway, R. N. 1988: The New Zealand passerine checklist: what if Sibley & Ahlquist are right? *Notornis 35*: 63–70.

Holdaway, R. N. 1989: New Zealand's pre-human avifauna and its vulnerability. *New Zealand Journal of Ecology 12 (supplement)*: 11–25.

Holdaway, R. N. 1990: Changes in the diversity of New Zealand forest birds. *New Zealand Journal of Zoology 17*: 309–321.

Holdaway, R. N. 1991a: Sibley et al.'s (1988) classification of living birds applied to the New Zealand list. *Notornis 38*: 152–164.

Holdaway, R. N. 1991b: Systematics and palaeobiology of Haast's eagle (*Harpagornis moorei* Haast, 1872) (Aves: Accipitridae). Unpublished PhD thesis. Department of Zoology, University of Canterbury, Christchurch, New Zealand. 472 p.

Holdaway, R. N. 1994: An exploratory phylogenetic analysis of the genera of the Accipitridae, with notes on the biogeography of the family. Pp. 601–649 *In*: Meyburg, B.-U.; Chancellor, R. D. *ed. Raptor conservation today*. Berlin, WWGBP/The Pica Press.

Holdaway, R. N. 1995: A fossil record of the black stilt *Himantopus novaezelandiae* Gould, 1841. *New Zealand natural sciences 22*: 69–74.

Holdaway, R. N. 1996: Arrival of rats in New Zealand. *Nature 384*: 225–226.

Holdaway, R. N. 1999a: Introduced predators and avifaunal extinction in New Zealand. Pp. 189–238 *In*: McPhee, R. D. E. *ed. Extinctions in near time: causes, contexts, and consequences. Advances in paleobiology*. New York, Kluwer Academic/Plenum Press. 394 p.

Holdaway, R. N. 1999b: A spatio-temporal model for the invasion of the New Zealand archipelago by the Pacific rat *Rattus exulans*. *Journal of the Royal Society of New Zealand 29*: 91–105.

Holdaway, R. N. Anderson, A. J. In press: The avifauna of the Emily Bay archaeological site, Norfolk Island, South-west Pacific: a preliminary account. *Records of the Australian Museum Special Issue*.

Holdaway, R. N.; Jacomb, C. 2000: Rapid extinction of the moa (Aves: Dinornithiformes): model, test, and implications. *Science 287*: 2250–2254.

Holdaway, R. N.; Worthy, T. H. 1993: First North Island fossil record of kea, and morphological and morphometric comparison of kea and kaka. *Notornis 40*: 95–108.

Holdaway, R. N.; Worthy, T. H. 1994: A new fossil species of shearwater *Puffinus* from the late Quaternary of the South Island, New Zealand, and notes on the biogeography and evolution of the *Puffinus gavia* superspecies. *Emu 94*: 201–215.

Holdaway, R. N.; Worthy, T. H. 1996: Diet and biology of the laughing owl *Sceloglaux albifacies* (Aves: Strigidae) on Takaka Hill, Nelson, New Zealand. *Journal of Zoology, London 239*: 545–573.

Holdaway, R. N.; Worthy, T. H. 1997: A reappraisal of the late Quaternary fossil vertebrates of Pyramid Valley Swamp, North Canterbury, New Zealand. *New Zealand Journal of Zoology 24*: 69–121.

Horn, P. L. 1980: Probable occurrence of the black bittern, *Dupetor flavicollis* (Linnaeus), in New Zealand. *Notornis 27*: 401–403.

Horn, P. L. 1983: Subfossil avian remains from Poukawa, Hawke's Bay, and the first record of *Oxyura australis* (Blue-billed duck) from New Zealand. *Journal of the Royal Society of New Zealand 13(1/2)*: 67–78.

Horning, D. J.; Horning, C. J. 1974: Bird records of the 1971–1973 Snares Islands, New Zealand, expedition. *Notornis 21*: 13–24.

Houde, P.; Cooper, A.; Leslie, E.; Shand, A. E.; Montano, G. A. 1997: Phylogeny and evolution of 12S rDNA in gruiformes (Aves). Pp. 117–154 *In*: Mindell, D. P. *ed. Avian molecular evolution and systematics*. San Diego, Academic Press. 382 p.

Howard, H.; Warter, S. L. 1969: A new species of bony-toothed bird (Family Pseudodontornithidae) from the Tertiary of New Zealand. *Records of the Canterbury Museum 8*: 345–357.

Hutton, F. W. 1879: On a new species of rail from Macquarie Island. *Ibis (1879)*: 454–456.

Hutton, F. W. 1891: The moas of New Zealand. *Transactions and proceedings of the New Zealand Institute 24*: 93–172.

Hutton, I. 1986: *Discovering Australia's World Heritage Lord Howe Island*. Australian Capital Territory, Conservation Press.

Imber, M. J. 1984: Migration of the white-faced storm petrel *Pelagodroma marina* in the South Pacific and the status of the Kermadec subspecies. *Emu 84*: 32–35.

Imber, M. J. 1994: Seabirds recorded at the Chatham Islands, 1960 to May 1993. *Notornis 41 (supplement)*: 97–108.

Imber, M. J.; Tennyson, A. J. D.; Taylor, G. A.; Johnston, P. 1998: A second intact specimen of the Chatham Island taiko (*Pterodroma magentae*). *Notornis 45*: 247–254.

International Commission on Zoological Nomenclature 1999: *International Code of Zoological Nomenclature, 4th. ed.)*. London, The International Trust for Zoological Nomenclature. 306 p.

James, H. F.; Olson, S. L. 1991: Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part II. Passerines. *Ornithological monographs no. 46*: 1–88.

Jamieson, I. G.; Spencer, H. G. 1996. The bill and foraging behaviour of the huia (*Heteralocha acutirostris*): were they unique? *Notornis 43*: 14–18.

Johns, P. M.; Butts, C. A.; Miskelly, C. M.; Pettigrew, C. H. 1983: Snares Island Expedition 1982–83 Report. Unpublished report, Department of Zoology, University of Canterbury.

Johnson, K. P.; Sorenson, M. D. 1999: Phylogeny and biogeography of dabbling ducks (Genus *Anas*): a comparison of molecular and morphological evidence. *Auk 116(3)*: 792–805.

Jollie, M. 1976: A contribution to the morphology and phylogeny of the Falconiformes, part 1. *Evolutionary theory 1*: 285–298.

Jollie, M. 1977a: A contribution to the morphology and phylogeny of the Falconiformes, part 2. *Evolutionary theory 2(4)*: 115–208.

Jollie, M. 1977b: A contribution to the morphology and phylogeny of the Falconiformes, part 3 *Evolutionary theory 2(5)*: 209–300.

Jollie, M. 1977c: A contribution to the morphology and phylogeny of the Falconiformes, part 4. *Evolutionary theory 3(1)*: 1–141.

Jones, J. G.; McDougall, I. 1973. Geological history of Norfolk and Philip Islands, Southwest Pacific Ocean. *Journal of the Geological Society of Australia 20*: 239–254.

Kennedy, M.; Spencer, H. G. 2000: Phylogeny, biogeography, and taxonomy of Australasian teals. *Auk 117(1)*: 154–163.

King, C. M. (*ed.*) 1990: *The handbook of New Zealand mammals*. Auckland, Oxford University Press.

Kinsky, F. C. 1969: New and rare birds on Campbell Island. *Notornis 16*: 225–236.

Kinsky, F. C. (convener). 1970: *Annotated checklist of the birds of New Zealand including the birds of the Ross Dependency*. A. H. & A. W. Reed, for the Ornithological Society of New Zealand, Wellington. 96 p.

Latter, J. H.; Lloyd, E. F.; Smith, I. E. M.; Nathan, S. 1992: Volcanic hazards in the Kermadec Islands and at submarine volcanoes between southern Tonga and New Zealand. *Volcanic hazards information series 4*. Wellington, New Zealand Ministry of Civil Defence. 44 p.

Law, G. 1972: Archaeology at Harataonga Bay, Great Barrier Island. *Records of the Auckland Institute and Museum 9*: 81–123.

Livezey, B. C. 1990: Evolutionary morphology of flightlessness in the Auckland Islands teal. *Condor 92*: 639–673.

Livezey, B. C. 1994: The carpometacarpus of *Apterornis* [sic]. *Notornis 41(1)*: 51–60.

Livezey, B. C. 1998: A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). *Philosophical transactions of the Royal Society of London: Biological sciences series B, 353 (1378)*: 2077–2151.

Lloyd, E. F.; Nathan, S. 1981: Geology and tephrochronology of Raoul Island, Kermadec group, New Zealand. *New Zealand Geological Survey bulletin 95*. 105 p.

Lloyd, E. F.; Nathan, S.; Smith, I. E. M.; Stewart, R. B. 1996: Volcanic history of Macauley Island, Kermadec Ridge, New Zealand. *New Zealand journal of geology and geophysics 39*: 295–308.

Loh, G. 2000: A mainland breeding population of fairy prions (*Pachyptila turtur*), South Island, New Zealand. *Notornis 47*: 119–122.

MacArthur, R. H.; Wilson, E. O. 1967: *The theory of island biogeography* Princeton, Princeton University Press.

Marples, B. J. 1946: Notes on some neognathous bird bones from the Early Tertiary of New Zealand. *Transactions of the Royal Society of New Zealand 76*: 132–134.

Marchant, S.; Higgins, P. J. (co-ordinators) 1990: *Handbook of Australian, New Zealand & Antarctic birds, vol. 1 – Ratites to Ducks*. Melbourne, Oxford University Press.

Marchant, S.; Higgins, P. J. (co-ordinators) 1993: *Handbook of Australian, New Zealand & Antarctic birds, vol. 1 – Raptors to Lapwings*. Melbourne, Oxford University Press.

Martin, P. S. 1984: Prehistoric overkill: the global model. pp. 354–403 *In*: Martin, P. S.; Klein, R. G. (*ed.*) *Quaternary extinctions: a prehistoric revolution*. University of Arizona Press, Tucson. 892 p.

Mayden, R. L. 1997: A hierarchy of species concepts: the denouement in the saga of the species problem. pp. 381–424 *In*: Claridge, M. F.; Dawah, H. A.; Wilson, M. R. (*ed.*) *Species: the units of biodiversity*. London, Chapman & Hill. 439 p.

Mayr, E. 1963: *Animal species and evolution*. Harvard University Press, Cambridge, Massachusetts.

McAllan, I. A. W.; Bruce, M. D. 1989. *The birds of New South Wales – a working list*. Turramurra, Biocon Research Group.

McCallum, J.; Brook, F.; Francis, M. P. 1985: Buller's mollymawks on Rosemary Rock, Three Kings Islands, in 1985. *Notornis 32(3)*: 257–259.

McGlone, M. S. 1989: The Polynesian settlement of New Zealand in relation to environmental and biotic changes in New Zealand. *New Zealand journal of ecology 12 (supplement)*: 115–129.

McGlone, M. S.; Anderson, A. J.; Holdaway, R. N. 1994: An ecological approach to the Polynesian settlement of New Zealand. pp. 136–163 *in*: Sutton, D. G. (*ed.*) *The origins of the first New Zealanders*. Auckland, Auckland University Press. 269 p.

McKean, J. L. 1978: Some remarks on the taxonomy of Australasian oystercatchers, *Haematopus* spp. *Sunbird 9*: 3–9.

McKee, J. W. A. 1985: A pseudodontorn (Pelecaniformes: Pelagornithidae) from the middle Pliocene of Hawera, Taranaki, New Zealand. *New Zealand Journal of Zoology 12*: 181–184.

McLay, C. L. 1974: The species diversity of New Zealand forest birds: some possible consequences of the modification of beech forests. *New Zealand Journal of Zoology 1*: 179–196.

Meredith, C. W. 1985: The vertebrate fossil fauna of Norfolk Island, and the phylogeny of the genus *Pterodroma*. Unpublished PhD thesis. Department of Earth Sciences, Monash University, Clayton, Victoria, Australia.

Meredith, C. W. 1991: Vertebrate fossil faunas from islands in Australasia and the Southwest Pacific. Pp. 1345–1382 *In*: Vickers-Rich, P. V.; Monaghan, J. M.; Baird, R. F.; Rich, T. H. *ed. Vertebrate palaeontology of Australasia*. Pioneer Design Studios in cooperation with the Monash University Publications Committee, Melbourne. 1437 p.

Millener, P. R. 1981: The Quaternary avifauna of the North Island, New Zealand. Unpublished PhD thesis. Department of Geology, University of Auckland, Auckland, New Zealand. 897 p.

Millener, P. R. 1982: And then there were twelve: the taxonomic status of *Anomalopteryx oweni* (Aves: Dinornithidae). *Notornis 29*: 165–170.

Millener, P. R. 1984: Honeycomb Hill Cave: A survey of scientific and scenic resources. Unpublished report to New Zealand Forest Service and National Museum of New Zealand. Wellington. 99 p.

Millener, P. R. 1988: Contributions to New Zealand's Late Quaternary avifauna. I: *Pachyplichas*, a new genus of wren (Aves: Acanthisittidae), with two new species. *Journal of the Royal Society of New Zealand 18*: 383–406.

Millener, P. R. 1990: Evolution, extinction and the subfossil record of New Zealand's avifauna. Pp. 93–100 *In*: Gill, B. J.; Heather, B. D. *ed. A flying start*. Auckland, Random Century. 217 p.

Millener, P. R. 1991: The Quaternary avifauna of New Zealand. Pp. 1317–1344 *In*: Vickers-Rich, P. V.; Monaghan, J. M.; Baird, R. F.; Rich, T. H. *ed. Vertebrate palaeontology of Australasia*. Melbourne, Pioneer Design Studios in cooperation with the Monash University Publications Committee. 1437 p.

Millener, P. R. 1996: Extinct birds. pp. 113–120 *In*: Anonymous (*ed.*) *The Chatham Islands: heritage and conservation*. Christchurch, Canterbury University Press and New Zealand Department of Conservation. 136 p.

Millener, P. R.; Powlesland, R. G. 2001: The Chatham Islands pigeon (Parea) deserves full species status; *Hemiphaga chathamensis* (Rothschild, 1891); Aves; Columbidae. *Journal of the Royal Society of New Zealand 31*: in press.

Millener, P. R.; Worthy, T. H. 1991: Contributions to New Zealand's Late Quaternary avifauna. II: *Dendroscansor decurvirostris*, a new genus and species of wren (Aves: Acanthisittidae). *Journal of the Royal Society of New Zealand 21*: 179–200.

Miller, I.; Jones, C. 1997: Nelson/Marlborough. *Rarebits [New Zealand Department of Conservation Threatened Species Unit newsletter] 25*: 17–22.

Miskelly, C. M. 1988: The Little Barrier Island snipe. *Notornis 35*: 273–281.

Miskelly, C. M. 1997: Campbell Island snipe discovered. *OSNZ news No. 85*: 1.

Miskelly, C. M. 1999: *Mana Island Ecological Restoration Plan*. Wellington, Department of Conservation.

Miskelly, C. M.; Sagar, P. M.; Tennyson, A. J. D.; Scofield, R. P. 2001: Birds of the Snares Islands, New Zealand. *Notornis 48*: 1–40.

Molloy, J.; Davis, A.; Tisdall, C. 1994: Setting priorities for the conservation of New Zealand's threatened plants and animals, 2nd. ed. Wellington, New Zealand Department of Conservation. 64 p.

Molnar, R. E.; Pole, M. 1997: A Miocene crocodilian from New Zealand. *Alcheringa 21*: 65–70.

Murphy, R. C.; Irving, S. 1951: A review of the frigate petrels (*Pelagodroma*). *American Museum Novitates 1506*: 1–17.

Moore, J. L. 1999: Norfolk Island bird notes, 1977 to 1997. *Notornis 46*: 354–364.

Nixon, A. J. 1981: The external morphology and taxonomic status of the orange-fronted parakeet. *Notornis 28*: 292–300.

Nixon, A. J. 1994: Feeding ecology of hybridizing parakeets on Mangere Island, Chatham Islands. *Notornis 41 (Supplement)*: 5–18.

Oliver, W. R. B. 1930: *New Zealand birds*. Wellington, Fine Arts (NZ). 539 p.

Oliver, W. R. B. 1955: *New Zealand birds*. A. H. & A. W. Reed, Wellington. 661 p.

Olson, S. L. 1973a: A classification of the Rallidae. *Wilson bulletin 85*; 381–416.

Olson, S. L. 1973b: Evolution of rails of the South Atlantic Islands (Aves: Rallidae). *Smithsonian contributions to zoology 152*: 1–53.

Olson, S. L. 1975: A review of the extinct rails of the New Zealand region. *National Museum of New Zealand records 1(3)*: 63–79.

Olson, S. L. 1977a: The identity of the fossil ducks described from Australia by C. W. De Vis. *Emu 77*: 127–135.

Olson, S. L. 1977b: A synopsis of the fossil Rallidae. pp. 339–373 *In*: Ripley, S. D. *Rails of the world: a monograph of the family Rallidae*. Boston, David R. Godine.

Olson, S. L. 1985a: Early Pliocene Procellariiformes (Aves) from Langebaanweg, south-western Cape Province, South Africa. *Annals of the South African Museum 95*: 123–145.

Olson, S. L. 1985b: The fossil record of birds. Pp. 79–252 *In*: Farner, D. S.; King, J. R.; Parkes, K. C. *ed. Avian biology, Vol. VIII*. New York, Academic Press.

Olson, S. L. 1987: [Letter] More on the name *Rallus hodgenorum*. *Notornis 34*: 167–168.

Olson, S. L. 1990a: Osteology and systematics of the fernbirds (*Bowdleria*: Sylviidae). *Notornis 37*: 161–171.

Olson, S. L. 1990b: Comments on the osteology and systematics of the New Zealand passerines of the genus *Mohoua*. *Notornis 37(3&4)*: 157–160.

Olson, S. L. 1990c: The prehistoric impact of man on biogeographical patterns of insular birds. Pp. 45–51 *In*: International Symposium on Biogeographical aspects of Insularity. Atti dei convegni lincei 85, Accademia Nazionale dei Lincei, Roma.

Olson, S. L.; Balouet, J. C.; Fisher, C. J. 1987: The owlet-nightjar of New Caledonia, *Aegotheles savesi*, with comments on the systematics of the Aegothelidae. *Le Gerfaut 37*: 341–352.

Olson, S. L.; Parkes, K. C.; Clench, M. H.; Borecky, S. R. 1983: The affinities of the New Zealand passerine genus *Turnagra*. *Notornis 30*: 319–346.

Palma, R. L. 1991: A new species of *Rallicola* (Insecta: Phthiraptera: Philopteridae) from the North Island brown kiwi. *Journal of the Royal Society of New Zealand 21*: 313–322.

Parker, W. K. 1866: On the structure and development of the skull in the ostrich tribe. *Philosophical transactions of the Royal Society of London clvi*: 113.

Parrish, G. R.; Pulham, G. A. 1995: Population size, productivity and post-breeding movements of the New Zealand fairy tern. *Tane 35*: 175–181.

Pierce, R. J. 1979: Foods and feeding of the wrybill (*Anarhynchus frontalis*) on its riverbed breeding grounds. *Notornis 26*: 1–21.

Pierce, R. J. 1980: Habitats and feeding of Auckland Island banded dotterel (*Charadrius bicinctus exilis* Falla, 1978) in autumn. *Notornis 27*: 309–324.

Pilgrim, R. L. C.; Palma, R. L. 1982: A list of the chewing lice (Insecta: Mallophaga) from birds in New Zealand. *National Museum of New Zealand miscellaneous Series No. 6*.

Pizzey, G. 1980: *A field guide to the birds of Australia*. Collins, Sydney. 460 p.

Pole, M. 1993: Early Miocene flora of the Manuherikia Group, New Zealand. 7. Myrtaceae, including *Eucalyptus*. *Journal of the Royal Society of New Zealand 23*: 313–328.

Pole, M.; Douglas, B. 1998: A quantitative palynostratigraphy of the Miocene Manuherikia Group, New Zealand. *Journal of the Royal Society of New Zealand 28(3)*: 405–420.

Powlesland, R. G.; Pickard, C. R. 1992: Seabirds found dead on New Zealand beaches in 1988, and a review of *Puffinus* species recoveries, 1943 to 1988. *Notornis 39*: 27–46.

Powlesland, R. G.; Roberts, A.; Lloyd, B. D.; Merton, D. V. 1995: Number, fate, and distribution of kakapo (*Strigops habroptilus*) found on Stewart Island, New Zealand, 1979–92. *New Zealand journal of zoology 22*: 239–248.

Preston, F. W. 1962: The canonical distribution of commonness and rarity. *Ecology 43*: 185–215, 410–432.

Quammen, D. 1996: *The song of the dodo: Island biogeography in an age of extinctions*. London, Hutchinson. 702 p.

Rich, P. V.; van Tets, G.; Orth, K.; Meredith, C.; Davidson, P. 1983: Prehistory of the Norfolk Island biota. pp. 7–29 *In*: Schodde, R.; Fullagar, P.; Hermes, N. *A review of Norfolk Island birds: past and present*. Canberra, *Australian National Parks and Wildlife Service Special Publication no. 8*. 119 p.

Richdale, L. E. 1939: A royal albatross nesting on the Otago Peninsula, New Zealand. *Emu 39*: 467–488.

Robertson, H. A. ed. 1999: Wader studies in New Zealand. *Notornis 46*.

Robertson, C. J. R. 1991: Questions on the harvesting of toroa in the Chatham Islands. *Science and Research Series no. 35*. Wellington, New Zealand Department of Conservation.

Robertson, C. J. R.; Nunn, G. B. 1997: Towards a new taxonomy for albatrosses. Pp. 13–19 *In*: Robertson, G.; Gales, R. *ed. Albatross biology and conservation*. Chipping Norton, Surrey Beatty & Sons.

Robertson, C. J. R.; Warham, J. 1992: Nomenclature of the New Zealand wandering albatrosses *Diomedea exulans*. *Bulletin of the British Ornithologists' Club 112*: 74–81.

Robertson, C. J. R.; Warham, J. 1994: Measurements of *Diomedea exulans antipodensis* and *D. e. gibsoni*. *Bulletin of the British Ornithologists' Club 114*: 132–134.

Rothschild, W. 1893: *Rallus muelleri*, sp.n. *Bulletin of the British Ornithologists' Club 1*: 40.

Russ, R. 1978: Stewart Island kakapo. *Wildlife – a review 9*: 37–42.

Sagar, P. M. 1977: Birds of the 1976–77 Snares Islands Expedition. *Notornis 24*: 205–210.

Sangster, G.; Hazevoet, C. J.; Van Den Berg, A. B.; Roselaar, C. S.; Sluys, R. 1999: Dutch avifaunal list: species concepts, taxonomic instability, and taxonomic changes in 1977–1998. *Ardea 87*: 139–165.

Scarlett, R. J. 1972: Bones of a presumed odontopterygian bird from the Miocene of New Zealand. *New Zealand Journal of Geology and Geophysics 15(2)*: 269–274.

Scarlett, R. J. 1976: King penguins at the Chatham Islands. *Notornis 23*: 355.

Schodde, R.; Mason, I. 1999: *Directory of Australian birds – Passerines*. Canberra, CSIRO Publishing.

Schodde, R.; Fullagar, P.; Hermes, N. 1983: *A review of Norfolk Island birds: past and present*. Canberra, *Australian Parks and Wildlife Service Special Publication 8*.

Sibley, C. G.; Ahlquist, J. E.; Monroe, B. L. 1988: A classification of the living birds of the world based on DNA-DNA hybridisation studies. *Auk 105*: 409–425.

Sibley, C. G.; Monroe, B. L. 1990. *Distribution and taxonomy of birds of the world*. Yale University press, New Haven. 1111 p.

Sibson, R. B. 1992: Some thoughts on Caspian terns in New Zealand. *Notornis 39*: 87–93.

Siegel-Causey, D. 1988: Phylogeny of the Phalacrocoracidae. *Condor 90*: 885–905.

Sorenson, J. H. 1964: Birds of the Kermadec Islands. *Notornis 11*: 69–81.

Steadman, D. W. 1988: A new species of *Porphyrio* (Aves: Rallidae) from archeological sites in the Marquesas Islands. *Proceedings of the Biological Society of Washington 101*: 162–170.

Steadman, D. W. 1989: Extinction of birds in eastern Polynesia: a review of the record, and comparisons with other Pacific island groups. *Journal of Archaeological Science 16*: 177–205.

Steadman, D. W. 1991: Fossil birds and biogeography in Polynesia. *Acta XIX Congressus Internationalis Ornithologici 2*: 1526–1534.

Taylor, R. H. 1975: Some ideas on speciation in New Zealand parakeets, *Notornis 22*: 110–121.

Taylor, R. H. 1979: How the Macquarie Island parakeet became extinct. *New Zealand journal of ecology 2*: 42–45.

Taylor, R. H. 1985: Status, habits and conservation of *Cyanoramphus* parakeets in the New Zealand region. Pp. 195–211 *In*: Moors, P. J. *ed. Conservation of island birds. International Council for Bird Preservation Technical Publication no. 3.*

Taylor, R. H. 1998: A reappraisal of the orange-fronted parakeet (*Cyanoramphus* spp.) – species or colour morph? *Notornis 45*: 49–63.

Taylor, R. H.; Heatherbell, E. G.; Heatherbell, E. M. 1986: The orange-fronted parakeet (*Cyanoramphus malherbi*) is a colour morph of the yellow-crowned parakeet (*C. auriceps*). *Notornis 33*: 17–22.

Tennyson, A. J. D. 1991a: A new shearwater on the Chathams. *Forest and Bird (August)*: 6.

Tennyson, A. J. D. 1991b: The black-winged petrel on Mangere Island, Chathams Islands. *Notornis 38*: 111–116.

Tennyson, A. J. D. 1998: Chestnut-breasted shelducks and other wetland birds at Tupuangi, Chatham Islands. *Notornis 45*: 226–228.

Tennyson, A. J. D.; Millener, P. R. 1994: Bird extinctions and fossil bones from Mangere Island, Chatham Islands. *Notornis 41 (supplement)*: 165–178.

Tennyson, A. J. D.; Miskelly, C. M. 1989: "Dark-faced" rockhopper penguin at the Snares Islands. *Notornis 36*: 183–189.

Tennyson, A. J. D.; Taylor, G. 1989: A visit to the southern Kermadec Islands. *OSNZ News 50*: 5.

Tennyson, A. J. D.; Taylor, G. A. 1999: History, fauna and flora of Te Haupa (Saddle) Island, Hauraki Gulf. *Tane 37*: 69–89.

Tennyson, A. J. D.; Imber, M. J.; Taylor, R. H. 1998: Numbers of black-browed mollymawks (*Diomedea m. melanophrys*) and white-capped mollymawks (*D. cauta steadi*) at the Antipodes Islands in 1994–95 and their population trends in the New Zealand region. *Notornis 45*: 157–166.

Tennyson, A. J. D.; Taylor, G.; Scofield, P. 1989: Another visit to Macauley Island. *OSNZ News 52*: 4–5.

Travers, H. H.; Travers, W. T. L. 1873: On the birds of the Chatham Islands. *Transactions and proceedings of the New Zealand Institute 5*: 212–222.

Trewick, S. A. 1996: Morphology and evolution of two takahe: flightless rails of New Zealand. *Journal of Zoology, London 238*: 221–237.

Trewick, S. A. 1997a: Sympatric flightless rails *Gallirallus dieffenbachii* and *G. modestus* on the Chatham Islands, New Zealand: morphometrics and alternative evolutionary scenarios. *Journal of the Royal Society of New Zealand 27*: 451–464.

Trewick, S. A. 1997b: Flightlessness and phylogeny amongst endemic rails (Aves: Rallidae) of the New Zealand region. *Philosophical transactions of the Royal Society of London B*: 429–446.

Triggs, S. J.; Daugherty, C. H. 1996: Conservation and genetics of New Zealand parakeets. *Bird Conservation International 6*: 89–101.

Turbott, E. G. (Convener) 1990: *Checklist of the birds of New Zealand and the Ross Dependency, Antarctica, 3rd. ed.* Auckland, Random Century and the Ornithological Society of New Zealand. 247 p.

van Tets, G. F. 1976: Australasia and the origin of the shags and cormorants. Phalacrocoracidae. *Proceedings of the XVI International Ornithological Congress (1974)*: 121–124.

van Tets, G. F.; Meredith, C. W.; Fullagar, P. J.; Davidson, P. M. 1988: Osteological differences between *Sula* and *Morus* and a description of an extinct new species of *Sula* from Lord Howe and Norfolk Islands, Tasman Sea. *Notornis 35*: 35–57.

Weber, E.; Hesse, A. 1995: The systematic position of *Aptornis*, a flightless bird from New Zealand. *Courier Forschuninstitut Senckenberg 181*: 293–301.

Weber, E.; Krell, F. 1995: *Aptornis* Owen, 1848 (Aves): proposed conservation as the correct original spelling. Case 2839. *Bulletin of Zoological Nomenclature 52*: 170–174.

Weetman, S. 1887: Notes on some moa remains found at the Great Barrier Island during February 1886. *Transactions and proceedings of the New Zealand Institute 19*: 193–194.

Wiens, J. J.; Servedio, M. R. 2000: Species delimitations in systematics: inferring diagnostic differences between species. *Proceedings of the Royal Society of London, B*: 267: 631–636.

Williams, G. R. 1956: The kakapo (*Strigops habroptilus*, Gray): a review and re-appraisal of a near-extinct species. *Notornis 7*: 29–56.

Williams, G. R. 1960: Distribution of specimens of the kakapo, *Strigops habroptilus* Gray, in some museums throughout the world. *Records of the Dominion Museum 3*: 219–227.

Williams, G. R. 1971: Birds Pp. 304–333 *In*: Williams, G. R. *ed. The natural history of New Zealand: an ecological survey.* Wellington, A. H. & A. W. Reed.

Williams, G. R. 1981: Aspects of avian island biogeography in New Zealand. *Journal of Biogeography 8*: 439–456.

Williams, G. R. 1984: Has island biogeography theory any relevance to the design of biological reserves in New Zealand. *Journal of the Royal Society of New Zealand 14*: 7–10.

Williams, M. J. 1995: Social structure, dispersion and breeding of the Auckland Island teal. *Notornis 42*: 219–262.

Wilson, E. O. 1992: *The diversity of life.* Cambridge, Mass., Belknap Press of Harvard University Press.

Wodzicki, K.; Robertson, C. J. R.; Thompson, H. R.; Alderton, C. J. T. 1984: The distribution and numbers of gannets (*Sula serrator*) in New Zealand. *Notornis 31*: 232–261.

Worthy, T. H. 1987: Sexual dimorphism and temporal variation in the North Island moa species *Euryapteryx curtus* (Owen) and *Pachyornis mappini* Archey. *National Museum of New Zealand records 3*: 59–70.

Worthy, T. H. 1988a: An illustrated key to the main leg bones of moas (Aves: Dinornithiformes). *National Museum of New Zealand Miscellaneous Series No. 17.* 37 p.

Worthy, T. H. 1988b: A re-examination of the moa genus *Megalapteryx. Notornis 35(2)*: 99–108.

Worthy, T. H. 1989a: Validation of *Pachyornis australis* Oliver (Aves; Dinornithiformes), a medium sized moa from the South Island, New Zealand. *New Zealand Journal of Geology and Geophysics 32*: 255–266.

Worthy, T. H. 1989b: An analysis of moa bones (Aves: Dinornithiformes) from three lowland North Island swamp sites: Makirikiri, Riverlands and Takapau Road. *Journal of the Royal Society of New Zealand 19*: 419–432.

Worthy, T. H. 1990: An analysis of the distribution and relative abundance of moa species (Aves: Dinornithiformes). *New Zealand Journal of Zoology 17*: 213–241.

Worthy, T. H. 1992: A re-examination of the species *Euryapteryx geranoides* (Owen) including comparisons with other emein moas (Aves: Dinornithiformes). *Journal of the Royal Society of New Zealand 22*: 19–40.

Worthy, T. H. 1993: *Fossils of Honeycomb Hill.* Museum of New Zealand / Te Papa Tongarewa. 56 p.

Worthy, T. H. 1995: Description of some post-cranial bones of *Malacorhynchus scarletti*, a large extinct pink-eared duck from New Zealand. *Emu 95*: 13–22.

Worthy, T. H. 1996: Holocene populations of shags *Leucocarbo* spp. in the far north, New Zealand. *New Zealand Journal of Zoology 23*: 89–95.

Worthy, T. H. 1997a: Quaternary fossil fauna of South Canterbury, South Island, New Zealand. *Journal of the Royal Society of New Zealand 27*: 67–162.

Worthy, T. H. 1997b: The identification of fossil *Eudyptes* and *Megadyptes* bones at Marfell's Beach, Marlborough, South Island. *New Zealand Natural Sciences 23*: 71–85.

Worthy, T. H. 1997c: A mid-Pleistocene rail from New Zealand. *Alcheringa 21*: 71–78.

Worthy, T. H. 1998a: Fossils indicate *Pelecanoides georgicus* had large colonies at Mason Bay, Stewart Island, New Zealand. *Notornis 45*: 229–246.

Worthy, T. H. 1998b: A remarkable fossil and archaeological fauna from Marfells Beach, Lake Grassmere, South Island, New Zealand. *Records of the Canterbury Museum 12*: 79–176.

Worthy, T. H. 1998c: Quaternary fossil faunas of Otago, South Island, New Zealand. *Journal of the Royal Society of New Zealand 28*: 421–521.

Worthy, T. H. 1998d: Fossil avifaunas from Old Neck and Native Island, Stewart Island – Polynesian middens or natural sites? *Records of the Canterbury Museum 12*: 49–82.

Worthy, T. H. 1998e: The Quaternary fossil avifauna of Southland, South Island, New Zealand. *Journal of the Royal Society of New Zealand 29*: 537–589.

Worthy, T. H. 1999a: The role of climate change versus human impact — avian extinction on South Island, New Zealand. *Smithsonian Contributions to Paleobiology 89*: 111–123.

Worthy, T. H. 1999b: What was on the menu – avian extinction in New Zealand. *New Zealand Journal of Archaeology 19*: 125–160.

Worthy, T. H. 2000: Two late-Glacial avifaunas from eastern North Island – Te Aute and Wheturau Quarry. *Journal of the Royal Society of New Zealand 30*: 1–26.

Worthy, T. H.; Brassey, R. 2000: New Zealand pigeon (*Hemiphaga novaeseelandiae*) on Raoul Island, Kermadec Group. *Notornis 47*: 36–38.

Worthy, T. H.; Holdaway, R. N. 1993: Quaternary fossil faunas from caves in the Punakaiki area, West Coast, South Island, New Zealand. *Journal of the Royal Society of New Zealand 23*: 147–254.

Worthy, T. H.; Holdaway, R. N. 1994: Quaternary fossil faunas from caves in Takaka Valley and on Takaka Hill, northwest Nelson, South Island, New Zealand. *Journal of the Royal Society of New Zealand 24*: 297–391.

Worthy, T. H.; Holdaway, R. N. 1995: Quaternary fossil faunas from caves on Mt Cookson, North Canterbury, South Island, New Zealand. *Journal of the Royal Society of New Zealand 25*: 333–370.

Worthy, T. H.; Holdaway, R. N. 1996: Quaternary fossil faunas, overlapping taphonomies, and palaeofaunal reconstruction in North Canterbury, South Island, New Zealand. *Journal of the Royal Society of New Zealand 26*: 275–361.

Worthy, T. H.; Holdaway, R. N. 2000: Terrestrial fossil vertebrate faunas from inland Hawke's Bay, North Island, New Zealand. Part 1. *Records of the Canterbury Museum 14*: 89–154.

Worthy, T. H.; Jouventin, P. 1999: The fossil avifauna of Amsterdam Island, Indian Ocean. *Smithsonian Contributions to Paleobiology 89*: 39–65.

Worthy, T. H.; Edwards, A. R.; Millener, P. R. 1991: The fossil record of moas (Aves: Dinornithiformes) older than the Otira (last) Glaciation. *Journal of the Royal Society of New Zealand 21*: 101–118.

Worthy, T. H.; Holdaway, R. N.; Sorenson, M. D.; Cooper, A. C. 1997: Description of the first complete skeleton of the extinct New Zealand goose *Cnemiornis calcitrans* (Aves: Anatidae) and a reassessment of the relationships of *Cnemiornis*. *Journal of Zoology, London 243*: 695–723.

Wright, A. E. 1984: Buller's albatrosses breeding at Three Kings Islands. *Notornis 31*: 203–207.

Yaldwyn, J. C. 1956: A preliminary account of the subfossil avifauna of the Martinborough Caves. *Records of the Dominion Museum 3*: 1–7.

Yaldwyn, J. C. 1958: Notes on the environment and age of the sub-fossil deposits of the Martinborough area. *Records of the Dominion Museum 3*: 129–133.

Notes added in proof

1. The South Island record for *Pachyptila vittata* is based on worthy (1998e).
2. A fossil record of *Pterodroma pycrofti* from Lord Howe Island needs confirmation. If correct, the taxon would not be a New Zealand endemic.
3. Records of *Ardea pacifica* at Poukawa (Horn 1983) appear to have been re-identified as *Casmerodius albus* by P. R. Millener.
4. We recognise the Norfolk Island forms of *Lalage* (Campephagidae) and *Turdus* (Turdidae) as distinct, endemic species, following differences summarised by Schodde et al. (1983).

Appendices over page

Appendix 1 Summary of species recognised here whose nomenclatural status has been changed in this paper (**A**), undescribed taxa, taxa that have not been determined to species but which are recognised as having been part of the original avifauna of New Zealand (**B**), and nominal species that we do not recognise as being valid (**C**).

A. Changes to nomenclature

Order Procellariiformes	
Puffinus kermadecensis Murphy, 1927	New status
[=*Puffinus assimilis kermadecensis* Murphy, 1927]	
Puffinus haurakiensis Fleming and Serventy, 1943	New status
[=*Puffinus assimilis haurakiensis* Fleming and Serventy, 1943]	
Pelagodroma albiclunis Murphy and Irving, 1951	
[=*Pelagodroma marina albiclunis* Murphy and Irving, 1951]	New status
Order Charadriiformes	
Charadrius frontalis (Quoy and Gaimard, 1830)	**New combination**
[=*Anarhynchus frontalis* Quoy and Gaimard, 1830]	
Charadrius exilis Falla, 1978	New status
[=*Charadrius bicinctus exilis* Falla, 1978]	
Coenocorypha barrierensis Oliver, 1955	New status
[=*Coenocorypha aucklandica barrierensis* Oliver, 1955]	
Coenocorypha iredalei Rothschild, 1921	New status
[=*Coenocorypha aucklandica iredalei* Rothschild, 1921]	
Coenocorypha meinertzhagenae Rothschild, 1927	New status
[=*Coenocorypha aucklandica meinertzhagenae* Rothschild, 1927]	
Order Passeriformes	
Anthus chathamensis Lorenz-Liburnau, 1902	New status
[=*Anthus novaezealandiae chathamensis* Lorenz-Liburnau, 1902]	
Petroica marrineri (Mathews and Iredale, 1913)	New status
[=*Myiomoira macrocephala marrineri* (Mathews and Iredale, 1913)]	

B. Undescribed or undetermined taxa

Order Apterygiformes
- *Apteryx* "Eastern South Island"

Order Procellariiformes
- *Thalassarche* sp. 1
- *Pterodroma* sp. 1

Order Sphenisciformes
- *Eudyptes* "Chatham Islands"

Order Anseriformes
- *Tadorna* "Chathams"
- *Anas* "Macquarie"

Order Accipitriformes
- *Accipiter* cf. *fasciatus*

Order Galliformes
- *Megapodius* sp. (Raoul Island)

Order Gruiformes
- *Gallirallus* "Norfolk Island"
- *Porphyrio* sp. (Norfolk Island)

Order Charadriiformes
- *Coenocorypha* "Norfolk Island"
- *Coenocorypha* "Campbell Island"

Order Psittaciformes
- *Nestor* "Chatham Islands"

Order Columbiformes
- *Gallicolumba* ?*norfolciensis*

Order Passeriformes
- *Corvus* "Mainland"

C. Nominal taxa not recognised here

Sula tasmani van Tets, Meredith, Fullagar, and Davidson, 1988 [= *Sula dactylatra* Lesson, 1831]
Pachyplichas jagmi Millener, 1988 [= *Pachyplichas yaldwyni* Millener, 1988]

Appendix 2 A systematic list of the late Holocene avifauna, incorporating changes for which there is presently no nomenclatural precedent, but which in the authors' opinion are justified. The list is presented as an attempt to identify the true species diversity of the New Zealand avifauna at the time of first human contact. This list is the basis for the analysis of regional groupings in the avifauna. Taxa tentatively recorded from a region, including taxa that have probably recently colonised that region, are excluded from the analysis, but those that are likely to have become extinct have been included. _Cygnus atratus_ is recorded as extinct because it was exterminated before European arrival. Common names recommended by the authors are also listed. Extensive lists of other common and indigenous names are available in Marchant & Higgins (1990, 1993), Turbott (1990), Higgins & Davies (1996), Heather & Robertson (1996), and Higgins (1999). We have used "island" in common names consistently only within genera when there are several species from different island groups in the fauna. *, endemic; †, extinct in the New Zealand fauna; ††, extinct globally; $^{\mathrm{LD}}$, species that still exist, but which have no natural populations (logged as extinct in the biogeographic analysis). Names of taxa that we raise to to full species for the first time since their publication as subspecies are listed in **bold** type. Taxa that we do not recognise as being distinct, but for which no revision has been published, are underlined..

Order Dinornithiformes (11)										
Family Emeidae (8)										
Subfamily Anomalopteryginae (5)										
Anomalopteryx didiformis††*	Little bush moa	–	–	–	N	S	–	–	–	–
Megalapteryx didinus††*	Upland moa	–	–	–	–	S*	–	–	–	–
Pachyornis mappini††*	Mappin's moa	–	–	–	N*	–	–	–	–	–
Pachyornis elephantopus††*	Heavy-footed moa	–	–	–	–	S*	–	–	–	–
Pachyornis australis††*	Crested moa	–	–	–	–	S*	–	–	–	–
Subfamily Emeinae (3)										
Euryapteryx curtus††*	Coastal moa	–	–	NO	N	–	–	–	–	–
Euryapteryx geranoides††*	Stout-legged moa	–	–	NO?	N	S	–	–	–	–
Emeus crassus††*	Eastern moa	–	–	–	–	S*	–	–	–	–
Family Dinornithidae (3)										
Dinornis struthoides††*	Slender bush moa	–	–	NO	N	S	SO	St	–	–
Dinornis novaezealandiae††*	Large bush moa	–	–	–	N	S	SO	–	–	–
Dinornis giganteus††*	Giant moa	–	–	–	N	S	SO	–	–	–
Order Apterygiformes (5)										
Family Apterygidae (5)										
_Apteryx mantelli_*	Northern brown kiwi	–	–	NO	N	–	–	–	–	–
_Apteryx australis_*	Southern brown kiwi	–	–	–	–	S	SO	St	–	–
Apteryx "East South Is"††*	Eastern kiwi	–	–	–	–	S*	–	–	–	–
_Apteryx owenii_*$^{\mathrm{LD}}$	Little spotted kiwi	–	–	–	N	S	SO	–	–	–
_Apteryx haastii_*	Great spotted kiwi	–	–	–	–	S*	–	–	–	–
Order Podicipediformes (2)										
Family Podicipedidae (2)										
Podiceps cristatus	Southern crested grebe	–	–	–	N	S	–	–	–	–
_Poliocephalus rufopectus_*	New Zealand dabchick	–	–	–	N	S	–	–	–	–
Order Procellariiformes (57)										
Family Diomedeidae (12)										
_Diomedea sanfordi_*	Northern royal albatross	–	–	–	–	–	–	–	Ch*	–
Diomedea chionoptera	Snowy albatross	–	–	–	–	–	–	–	–	Sub
Diomedea exulans	Wandering albatross	–	–	–	–	–	–	–	–	Sub
_Diomedea epomophora_*	Southern royal albatross	–	–	–	–	–	–	–	–	Sub*
_Thalassarche bulleri_*	Southern Buller's albatross	–	–	–	–	–	–	St	–	Sub
_Thalassarche eremita_*	Chatham Island albatross	–	–	–	–	–	–	–	Ch*	–
Thalassarche sp. 1*	Northern Buller's albatross	–	–	–	–	–	–	–	Ch*	–
_Thalassarche impavida_*	Campbell Island albatross	–	–	–	–	–	–	–	–	Sub*
Thalassarche cauta	White-capped albatross	–	–	–	–	–	–	–	–	Sub
_Thalassarche salvini_*	Salvin's albatross	–	–	–	–	–	–	–	–	Sub*
Thalassarche chrysostoma	Grey-headed albatross	–	–	–	–	–	–	–	–	Sub
Phoebetria palpebrata	Light-mantled sooty albatross	–	–	–	–	–	–	–	–	Sub
Family Procellariidae (39)										
Subfamily Procellariinae (18)										
Puffinus pacificus	Wedge-tailed shearwater	Nf	K	–	–	–	–	–	–	–
Puffinus carneipes	Flesh-footed shearwater	–	–	NO	–	–	SO	–	–	–
_Puffinus bulleri_*	Buller's shearwater	–	–	NO*	–	–	–	–	–	–

Puffinus griseus	Sooty shearwater	–	–	NO	N	S	SO	St	Ch	Sub
*Puffinus gavia**	Fluttering shearwater	–	–	NO	N	S	SO	–	–	–
*Puffinus huttoni**	Hutton's shearwater	–	–	–	–	S*	–	–	–	–
Puffinus spelaeus††*	Scarlett's shearwater	–	–	–	–	S*	–	–	–	–
*Puffinus assimilis**	Norfolk Island little shearwater	Nf*	–	–	–	–	–	–	–	–
Puffinus kermadecensis*	Kermadec Island little shearwater		–	K*	–	–	–	–	–	–
Puffinus haurakiensis*	North Island little shearwater	–	–	NO	N	–	–	–	–	–
Puffinus elegans	Subantarctic little shearwater	–	–	–	–	–	–	–	Ch	Sub
Pelecanoides urinatrix	Northern diving petrel	–	–	NO	N	S	SO	–	–	–
Pelecanoides exsul	Richdale's diving petrel	–	–	–	–	–	SO	St	Ch	Sub
Pelecanoides georgicus	South Georgian diving petrel	–	–	–	–	–	–	St	Ch	Sub
*Procellaria parkinsoni**	Parkinson's petrel	–	–	NO	N	S	–	–	–	–
*Procellaria westlandica**	Westland petrel	–	–	–	–	S*	–	–	–	–
Procellaria aequinoctialis	White-chinned petrel	–	–	–	–	–	–	–	–	Sub
Procellaria cinerea	Grey petrel	–	–	–	–	–	–	–	–	Sub
Subfamily Fulmarinae (21)										
Daption capense	Cape petrel	–	–	–	–	–	–	–	–	Sub
Macronectes halli	Northern giant petrel	–	–	–	–	–	–	St	Ch	Sub
Macronectes giganteus	Southern giant petrel	–	–	–	–	–	–	–	–	Sub
Pachyptila turtur	Fairy prion	–	–	NO	N	S	SO	St	Ch	Sub
Pachyptila vittata	Broad-billed prion	–	–	–	–	S	SO	St	Ch?	Sub
Pachyptila crassirostris	Fulmar prion	–	–	–	–	–	–	–	Ch	Sub
Pachyptila desolata	Antarctic prion	–	–	–	–	–	–	–	–	Sub
Halobaena caerulea	Blue petrel	–	–	–	–	–	–	–	–	Sub
*Pterodroma pycrofti**	Pycroft's petrel	Nf	–	NO	–	–	–	–	–	–
*Pterodroma cervicalis**	White-naped petrel	–	K*	–	–	–	–	–	–	–
Pterodroma alba†	Phoenix petrel	–	K?	–	–	–	–	–	–	–
Pterodroma neglecta	Kermadec petrel	Nf	K	–	–	–	–	–	–	–
Pterodroma solandri	Providence petrel	Nf	–	–	–	–	–	–	–	–
Pterodroma nigripennis	Black-winged petrel	Nf?	K	NO?	–	–	–	–	Ch?	–
Pterodroma macroptera	Grey-faced petrel	–	–	NO	N	–	–	–	–	–
*Pterodroma cookii**	Cook's petrel	–	–	NO	N	S	–	St	–	–
*Pterodroma inexpectata**	Mottled petrel	–	–	–	N	S	SO	St	–	Sub
*Pterodroma axillaris**	Chatham petrel	–	–	–	–	–	–	–	Ch*	–
*Pterodroma magentae**	Chatham taiko	–	–	–	–	–	–	–	Ch*	–
Pterodroma sp. 1††*	Unnamed petrel	–	–	–	–	–	–	–	Ch*	–
Pterodroma lessonii	White-headed petrel	–	–	–	–	–	–	–	–	Sub
Family Hydrobatidae (6)										
Oceanites maorianus††*	New Zealand storm petrel	–	–	–	N	S	–	–	–	–
Garrodia nereis	Grey-backed storm petrel	–	–	–	–	S	–	–	Ch	Sub
Pelagodroma albiclunis*	Kermadec storm petrel	Nf?	K	–	–	–	–	–	–	–
Pelagodroma marina	White-faced storm petrel	–	–	NO	N	S	SO	St	Ch	Sub
Fregetta tropica	Black-bellied storm petrel	–	–	–	–	–	–	–	–	Sub
Fregetta grallaria	White-bellied storm petrel	Nf?	K	–	–	–	–	–	–	–
Order Sphenisciformes (10)										
Family Spheniscidae (10)										
Aptenodytes patagonicus	King penguin	–	–	–	–	–	–	–	–	Sub
Pygoscelis papua	Gentoo penguin	–	–	–	–	–	–	–	–	Sub
*Megadyptes antipodes**	Yellow-eyed penguin	–	–	–	–	S	SO	St	–	Sub
Eudyptula minor	Little penguin	–	–	NO	N	S	SO	St	Ch	–
*Eudyptes pachyrhynchus**	New Zealand crested penguin	–	–	–	–	S	SO	St	–	–
Eudyptes "Chatham Islands"††*	Chatham crested penguin	–	–	–	–	–	–	–	Ch*	–
Eudyptes filholi	Eastern rockhopper penguin	–	–	–	–	–	–	–	–	Sub
*Eudyptes schlegeli**	Royal penguin	–	–	–	–	–	–	–	–	Sub*
*Eudyptes robustus**	Snares crested penguin	–	–	–	–	–	–	–	–	Sub*
*Eudyptes sclateri**	Erected-crested penguin	–	–	–	–	–	–	–	–	Sub*
Order Pelecaniformes (14)										
Suborder Phaethontes (1)										
Family Phaethontidae (1)										
Phaethon rubricauda	Red-tailed tropicbird	Nf	K	–	–	–	–	–	–	–

Suborder Pelecani (13)										
Superfamily Suloidea (13)										
Family Sulidae (2)										
Sula dactylatra	Masked booby	Nf	K	–	–	–	–	–	–	–
Sula tasmani										
Morus serrator	Australasian gannet	–	–	NO	N	–	SO	St	–	–
Family Phalacrocoracidae (11)										
Phalacrocorax carbo	Great cormorant	–	–	NO	N	S	SO	St	Ch	–
Phalacrocorax varius	Pied cormorant	–	–	NO	N	S	SO	St	–	–
Phalacrocorax melanoleucos	Little cormorant	–	–	NO	N	S	SO	St	–	–
*Leucocarbo carunculatus**	King shag	–	–	–	N	S	SO	St	–	–
*Leucocarbo onslowi**	Chatham Island shag	–	–	–	–	–	–	–	Ch*	–
*Leucocarbo ranfurlyi**	Bounty Island shag	–	–	–	–	–	–	–	–	Sub*
*Leucocarbo colensoi**	Auckland Island shag	–	–	–	–	–	–	–	–	Sub*
*Leucocarbo campbelli**	Campbell Island shag	–	–	–	–	–	–	–	–	Sub*
*Leucocarbo purpurascens**	Macquarie Island shag	–	–	–	–	–	–	–	–	Sub*
*Stictocarbo punctatus**	Spotted shag	–	–	NO	N	S	SO	St	–	–
*Stictocarbo featherstoni**	Pitt Island shag	–	–	–	–	–	–	–	Ch*	–
Order Ciconiiformes (3)										
Suborder Ardeae (3)										
Family Ardeidae (3)										
Subfamily Ardeinae (2)										
Egretta sacra	Reef heron	–	–	NO	N	S	SO	St	Ch?	–
Casmerodius albus	Great white egret	–	–	–	N	S	–	–	–	–
Subfamily Botaurinae (1)										
Ixobrychus novaezelandiae††*	New Zealand little bittern	–	–	–	N	S	–	–	Ch	–
Order Anseriformes (18)										
Family Anatidae (18)										
Subfamily Anserinae (3)										
Cygnus atratus†	Black swan	–	–	NO	N	S	SO	St	Ch	–
Cnemiornis gracilis††*	North Island goose	–	–	–	N*	–	–	–	–	–
Cnemiornis calcitrans††*	South Island goose	–	–	–	–	S*	–	–	–	–
Subfamily Tadorninae (2)										
*Tadorna variegata**	Paradise shelduck	–	–	–	N	S	SO	St	–	–
Tadorna "Chathams"††*	Chatham Island shelduck	–	–	–	–	–	–	–	Ch*	–
Subfamily Anatinae (13)										
*Hymenolaimus malacorhynchos**	Blue duck	–	–	–	N	S	–	–	–	–
Anas superciliosa	Grey duck	Nf?	K	NO	N	S	SO	St	Ch	Sub
Anas gracilis	Grey teal	–	–	–	N	S	–	–	–	–
*Anas chlorotis**	Brown teal	–	–	NO	N	S	SO	St	Ch	–
*Anas aucklandica**	Auckland Island teal	–	–	–	–	–	–	–	–	Sub*
*Anas nesiotis**	Campbell Island teal	–	–	–	–	–	–	–	–	Sub*
Anas "Macquarie"††*	Macquarie Island teal	–	–	–	–	–	–	–	–	Sub*
Pachyanas chathamica††*	Chatham Island duck	–	–	–	–	–	–	–	Ch*	–
Euryanas finschi††*	Finsch's duck	–	–	–	N	S	–	–	–	–
Malacorhynchus scarletti††*	Scarlett's duck	–	–	–	N	S	–	–	Ch	–
*Aythya novaeseelandiae**	New Zealand scaup	–	–	NO	N	S	–	–	Ch	–
Mergus australis††*	New Zealand merganser	–	–	NO	N	S	–	St	Ch	Sub
Biziura delautouri††*	New Zealand musk duck	–	–	–	N	S	–	–	–	–
Order Accipitriformes (3)										
Family Accipitridae (3)										
Circus eylesi††*	Eyles's harrier	–	–	–	N	S	–	–	–	–
Accipiter cf. *fasciatus*†	Brown goshawk	Nf	–	–	–	–	–	–	–	–
Harpagornis moorei††*	Haast's eagle	–	–	–	–	S*	–	–	–	–
Order Falconiformes (1)										
Family Falconidae (1)										
*Falco novaeseelandiae**	New Zealand falcon	–	–	NO	N	S	SO	St	Ch	Sub
Order Galliformes (2)										
Family Phasianidae (1)										
Coturnix novaezelandiae††*	New Zealand quail	–	–	NO	N	S	–	St	–	–

Family Megapodiidae (1)										
Megapodius sp.†	Megapode	–	K	–	–	–	–	–	–	–
Order Gruiformes (19)										
Family Aptornithidae (2)										
Aptornis otidiformis††*	North Island adzebill	–	–	–	N*	–	–	–	–	–
Aptornis defossor††	South Island adzebill	–	–	–	–	S*	–	–	–	–
Family Rallidae (17)										
Gallirallus philippensis	Banded rail	Nf?	K?	NO	N	S	SO	St	–	–
Gallirallus "Norfolk Island"††*	Norfolk Island rail	Nf*	–	–	–	–	–	–	–	–
*Gallirallus australis**	Weka	–	–	NO	N	S	SO	St	–	–
Gallirallus dieffenbachii††*	Dieffenbach's rail	–	–	–	–	–	–	–	Ch*	–
Gallirallus macquariensis††*	Macquarie Island rail	–	–	–	–	–	–	–	–	Sub*
Capellirallus karamu††*	Snipe rail	–	–	–	N*	–	–	–	–	–
Cabalus modestus††*	Chatham Island rail	–	–	–	–	–	–	–	Ch*	–
Diaphorapteryx hawkinsi††*	Hawkins' rail	–	–	–	–	–	–	–	Ch*	–
*Dryolimnas muelleri**	Auckland Island rail	–	–	–	–	–	–	–	–	Sub*
Porzana tabuensis	Spotless crake	Nf	K	NO	N	S	–	–	Ch	–
Porzana pusilla	Baillon's crake	–	–	NO?	N	S	–	–	Ch	–
Gallinula hodgenorum††*	Hodgens' waterhen	–	–	–	N	S	–	–	–	–
Porphyrio mantelli††*	North Island takahe	–	–	–	N*	–	–	–	–	–
Porphyrio hochstetteri^{LD}*	South Island takahe	–	–	–	–	S*	–	–	–	–
Porphyrio sp.	Swamphen	Nf	–	–	–	–	–	–	–	–
Fulica prisca††*	New Zealand coot	–	–	–	N	S	–	–	–	–
Fulica chathamensis††*	Chatham Island coot	–	–	–	–	–	–	–	Ch*	–
Order Charadriiformes (32)										
Family Haematopodidae (3)										
*Haematopus unicolor**	Variable oystercatcher	–	–	NO	N	S	SO	St	–	–
*Haematopus finschi**	Finsch's oystercatcher	–	–	–	–	S	–	–	–	–
*Haematopus chathamensis**	Chatham Island oystercatcher	–	–	–	–	–	–	–	Ch*	–
Family Recurvirostridae (1)										
*Himantopus novaezelandiae**^{LD}	Black stilt	–	–	–	N	S	–	–	–	–
Family Charadriidae (5)										
*Charadrius obscurus**	New Zealand dotterel	–	–	NO	N	S	–	St	–	–
*Charadrius bicinctus**	Banded dotterel	–	–	NO	N	S	–	St	Ch	–
Charadrius exilis*	Auckland Island banded dotterel	–	–	–	–	–	–	–	–	Sub*
*Charadrius novaeseelandiae**	Shore plover	–	–	NO	N	S	–	–	Ch	Sub?
Charadrius frontalis **n. comb.***	Wrybill	–	–	–	–	S*	–	–	–	–
Family Scolopacidae (9)										
Subfamily Scolopacinae (9)										
Coenocorypha "Norfolk Is"††*	Norfolk Island snipe	Nf*	–	–	–	–	–	–	–	–
Coenocorypha barrierensis††*	North Island snipe	–	–	NO	N	–	–	–	–	–
Coenocorypha iredalei ††*	Iredale's snipe	–	–	–	–	S	–	St	–	–
Coenocorypha chathamica††*	Forbes' snipe	–	–	–	–	–	–	–	Ch*	–
*Coenocorypha pusilla**	Chatham Island snipe	–	–	–	–	–	–	–	Ch*	–
Coenocorypha huegeli*	Snares Island snipe	–	–	–	–	–	–	–	–	Sub*
Coenocorypha meinertzhagenae*	Antipodes Island snipe	–	–	–	–	–	–	–	–	Sub*
*Coenocorypha aucklandica**	Auckland Island snipe	–	–	–	–	–	–	–	–	Sub*
Coenocorypha "Campbell"*	Campbell Island snipe	–	–	–	–	–	–	–	–	Sub*
Family Stercorariidae (1)										
Catharacta skua	Subantarctic skua	–	–	–	–	S	–	St	Ch	Sub
Family Laridae (13)										
Subfamily Larinae (3)										
Larus dominicanus	Kelp gull	–	–	NO	N	S	SO	St	Ch	Sub
Larus novaehollandiae	Red-billed gull	–	–	NO	N	S	SO	St	Ch	Sub
*Larus bulleri**	Black-billed gull	–	–	–	N	S	–	–	–	–
Subfamily Sterninae (10)										
Sterna fuscata	Sooty tern	Nf	K	–	–	–	–	–	–	–
*Sterna striata**	White-fronted tern	–	–	NO	N	S	SO	St	Ch	Sub
*Sterna albostriata**	Black-fronted tern	–	–	–	N?	S	–	–	–	–
Sterna caspia	Caspian tern	–	–	–	N	S	–	–	–	–
Sterna nereis	Fairy tern	–	–	–	N	S	–	–	–	–

Sterna vittata	Antarctic tern	–	–	–	–	–	–	St	Ch?	Sub
Anous stolidus	Brown noddy	Nf	K?	–	–	–	–	–	–	–
Anous minutus	Black noddy	Nf	K	–	–	–	–	–	–	–
Procelsterna cerulea	Grey noddy	Nf	K	–	–	–	–	–	–	–
Gygis alba	White tern	Nf	K	–	–	–	–	–	–	–
Order Columbiformes (4)										
Family Columbidae (4)										
Hemiphaga spadicea††*	Norfolk Island pigeon	Nf*	–	–	–	–	–	–	–	–
*Hemiphaga novaeseelandiae**	New Zealand pigeon	–	K	NO	N	S	SO	St	–	–
*Hemiphaga chathamensis**	Chatham Island pigeon	–	–	–	–	–	–	–	Ch*	–
Gallicolumba ?norfolciensis††*	Norfolk Island ground dove	Nf*	–	–	–	–	–	–	–	–
Order Psittaciformes (12)										
Family Psittacidae (12)										
Subfamily Strigopinae (1)										
*Strigops habroptilus**^{LD}	Kakapo	–	–	–	N	S	SO	St	–	–
Subfamily Nestorinae (4)										
Nestor productus††*	Norfolk Island kaka	Nf*	–	–	–	–	–	–	–	–
*Nestor meridionalis**	Kaka	–	–	NO	N	S	SO	St	–	–
*Nestor notabilis**	Kea	–	–	–	–	S*	–	–	–	–
Nestor "Chatham Is"††*	Chatham Island kaka	–	–	–	–	–	–	–	Ch*	–
Subfamily Platycercinae (7)										
*Cyanoramphus cookii**^{LD}	Norfolk Island green parrot	Nf*	–	–	–	–	–	–	–	–
*Cyanoramphus novaezelandiae**	Red-crowned parakeet	–	K	NO	N	S	SO	St	Ch	Sub
*Cyanoramphus auriceps**	Yellow-crowned parakeet	–	–	NO	N	S	SO	St	–	Sub
*Cyanoramphus malherbi**	Orange-fronted parakeet	–	–	NO	N	S	–	–	–	–
*Cyanoramphus forbesi**^{LD}	Forbes' parakeet	–	–	–	–	–	–	–	Ch*	–
*Cyanoramphus erythrotis**	Hochstetter's parakeet	–	–	–	–	–	–	–	–	Sub*
*Cyanoramphus unicolor**	Antipodes Island parakeet	–	–	–	–	–	–	–	–	Sub*
Order Cuculiformes (2)										
Family Cuculidae (2)										
Chrysococcyx lucidus	Shining cuckoo	Nf	–	NO	N	S	SO	St	Ch	–
Eudynamys taitensis	Long-tailed cuckoo	–	–	NO	N	S	SO	St	–	–
Order Strigiformes (2)										
Family Strigidae (2)										
Ninox novaeseelandiae	Morepork	Nf	–	NO	N	S	SO	St	–	–
Sceloglaux albifacies††*	Laughing owl	–	–	NO?	N	S	–	St	–	–
Order Caprimulgiformes (1)										
Family Aegothelidae (1)										
Aegotheles novaezealandiae††*	New Zealand owlet-nightjar	–	–	–	N	S	SO	–	–	–
Order Coraciiformes (1)										
Family Alcedinidae (1)										
Subfamily Daceloninae (1)										
Todiramphus sanctus	Sacred kingfisher	Nf	K	NO	N	S	SO	St	–	–
Order Passeriformes (46)										
Suborder Oligomyodi (6)										
Family Acanthisittidae (6)										
*Acanthisitta chloris**	Rifleman	–	–	NO	N	S	SO	St	–	–
Xenicus longipes††*	Bush wren	–	–	–	N	S	–	St	–	–
*Xenicus gilviventris**	Rock wren	–	–	–	N	S	–	–	–	–
Traversia lyalli††*	Lyall's wren	–	–	–	N	S	SO	–	–	–
Pachyplichas jagmi										
Pachyplichas yaldwyni††*	Stout-legged wren	–	–	–	N	S	–	–	–	–
Dendroscansor decurvirostris††*	Long-billed wren	–	–	–	–	S*	–	–	–	–
Suborder Polymyodi (40)										
Family Motacillidae (3)										
*Anthus novaeseelandiae**	New Zealand pipit	–	–	NO	N	S	SO	St	–	–
Anthus chathamensis*	Chatham Island pipit	–	–	–	–	–	–	–	Ch*	–
*Anthus aucklandicus**	Subantarctic pipit	–	–	–	–	–	–	–	–	Sub*
Family Campephagidae (1)										
Lalage leucopyga††*	Long-tailed triller	Nf*	–	–	–	–	–	–	–	–

Family Muscicapidae (1)										
Subfamily Turdinae (1)										
Turdus poliocephalus††*	Grey-headed blackbird	Nf*	–	–	–	–	–	–	–	–
Family Sylviidae (3)										
*Bowdleria punctata**	New Zealand Fernbird	–	–	NO	N	S	SO	St	–	–
Bowdleria rufescens††*	Chatham Island fernbird	–	–	–	–	–	–	–	Ch*	–
*Bowdleria caudata**	Snares Island fernbird	–	–	–	–	–	–	–	–	Sub*
Family Pachycephalidae (4)										
Subfamily Pachycephalinae (1)										
Pachycephala xanthoprocta	Norfolk Island whistler	Nf	–	–	–	–	–	–	–	–
Subfamily Mohouinae (3)										
*Mohoua albicilla**	Whitehead	–	–	NO	N	–	–	–	–	–
*Mohoua ochrocephala**	Yellowhead	–	–	–	–	S	SO	St	–	–
*Mohoua novaeseelandiae**	Brown creeper	–	–	–	–	S	SO	St	–	–
Family Acanthizidae (3)										
Subfamily Acanthizinae (3)										
*Gerygone modesta**	Norfolk Island warbler	Nf*	–	–	–	–	–	–	–	–
*Gerygone igata**	Grey warbler	–	–	NO	N	S	SO	St	–	–
*Gerygone albofrontata**	Chatham Island warbler	–	–	–	–	–	–	–	Ch*	–
Family Monarchidae (1)										
Subfamily Rhipidurinae (1)										
Rhipidura fuliginosa	Grey fantail	Nf	–	NO	N	S	SO	St	Ch	–
Family Petroicidae (8)										
Petroica multicolor	Scarlet robin	Nf	–	–	–	–	–	–	–	–
*Petroica toitoi**	White-breasted tomtit	–	–	NO	N	–	–	–	–	–
*Petroica macrocephala**	Yellow-breasted tomtit	–	–	–	–	S	SO	St	Ch	–
*Petroica dannefaerdi**	Snares Island tomtit	–	–	–	–	–	–	–	–	Sub*
Petroica marrineri*	Auckland Island tomtit	–	–	–	–	–	–	–	–	Sub*
*Petroica longipes**	North Island robin	–	–	NO	N	–	–	–	–	–
*Petroica australis**	South Island robin	–	–	–	–	S	SO	St	–	–
*Petroica traversi**^{LD}	Chatham Island robin	–	–	–	–	–	–	–	Ch	–
Family Zosteropidae (2)										
*Zosterops albogularis**	White-breasted white-eye	Nf*	–	–	–	–	–	–	–	–
*Zosterops tenuirostris**	Long-billed white-eye	Nf*	–	–	–	–	–	–	–	–
Family Meliphagidae (4)										
*Notiomystis cincta**	Stitchbird	–	–	NO	N	–	–	–	–	–
*Anthornis melanura**	New Zealand bellbird	–	–	NO	N	S	SO	St	–	Sub
Anthornis melanocephala††*	Chatham Island bellbird	–	–	–	–	–	–	–	Ch*	–
*Prosthemadera novaeseelandiae**	Tui	K	NO	N	S	SO	St	Ch	Sub	
Family Sturnidae (1)										
Aplonis fusca††*	Norfolk Island starling	Nf*	–	–	–	–	–	–	–	–
Family Callaeatidae (5)										
*Callaeas wilsoni**	North Island kokako	–	–	NO	N	–	–	–	–	–
Callaeas cinerea††*	South Island kokako	–	–	–	–	S	SO	St	–	–
*Philesturnus rufusater**	North Island saddleback	–	–	NO	N	–	–	–	–	–
*Philesturnus carunculatus**^{LD}	South Island saddleback	–	–	–	–	S	SO	St	–	–
Heteralocha acutirostris††*	Huia	–	–	–	N*	–	–	–	–	–
Family Turnagridae (2)										
Turnagra tanagra††	North Island piopio	–	–	–	N*	–	–	–	–	–
Turnagra capensis††*	South Island piopio	–	–	–	–	S	SO	–	–	–
Family Corvidae (2)										
Corvus "mainland"††*	New Zealand raven	–	–	NO	N	S	–	St	–	Sub?
Corvus moriorum††*	Chatham Island raven	–	–	–	–	–	–	–	Ch*	–

Appendix 3 Species endemic to regions within the New Zealand archipelago based on Appendix 2 list: *, flightless. **Bold**, extinct (includes species with no natural populations). Uncertain distribution records are excluded.

NORTH ISLAND

Pachyornis mappini*, Cnemiornis gracilis*, Aptornis otidiformis*, Capellirallus karamu*, Porphyrio mantelli*, Heteralocha acutirostris, Turnagra tanagra.

NORTH AND NORTHERN OFFSHORE

Euryapteryx curtus*, _Apteryx mantelli*_, _Puffinus haurakiensis_, **_Coenocorypha barrierensis_**, _Mohoua albicilla, Petroica toitoi, Petroica longipes, Notiomystis cincta, Callaeas wilsoni, Philesturnus rufusater._

NORTHERN OFFSHORE

Puffinus bulleri.

SOUTH ISLAND

Megalapteryx didinus*, Pachyornis elephantopus*, Pachyornis australis*, Emeus crassus*, Apteryx Eastern*, _Apteryx haastii*, Puffinus huttoni,_ **_Puffinus spelaeus_**, _Procellaria westlandica,_ **_Cnemiornis calcitrans*, Harpagornis moorei_**, _Porphyrio hochstetteri*,_ **_Aptornis defossor*_**, _Haematopus finschi, Charadrius frontalis, Sterna albostriata, Nestor notabilis,_ **_Dendroscansor decurvirostris*_**.

SOUTH AND SOUTHERN OFFSHORE

Turnagra capensis.

SOUTH AND STEWART

Coenocorypha iredalei

SOUTH, STEWART, AND SOUTHERN OFFSHORE

Apteryx australis*, Eudyptes pachyrhynchus*, Mohoua ochrocephala, Mohoua novaeseelandiae, Petroica australis, **_Callaeas cinerea*, Philesturnus carunculatus, Turnagra capensis_**.

SOUTH, STEWART, SOUTHERN OFFSHORE, AND CHATHAMS

Petroica macrocephala.

SOUTH, STEWART, SOUTHERN OFFSHORE, AND SUBANTARCTIC

Megadyptes antipodes*.

STEWART AND SUBANTARCTIC

Thalasarche bulleri

NORTH AND SOUTH ISLANDS

Anomalopteryx didiformis*, **_Euryapteryx geranoides*_** _Poliocephalus rufopectus,_ **_Oceanites maorianus_**, _Hymenolaimus malacorhynchos,_ **_Euryanas finschi*, Biziura delautouri, Circus eylesi, Gallinula hodgenorum*, Fulica prisca_**, _Himantopus novaezelandiae, Larus bulleri, Sterna albostriata,_ **_Pachyplichas yaldwyni*_**, _Xenicus gilviventris._

NORTH, SOUTH, AND NORTHERN OFFSHORE

Procellaria parkinsoni, Cyanoramphus malherbi.

NORTH, SOUTH, AND SOUTHERN OFFSHORE

Dinornis novaezealandiae*, Dinornis giganteus*, Apteryx owenii*, Aegotheles novaezealandiae*, Traversia lyalli*.

NORTH, SOUTH, AND STEWART

Sceloglaux albifacies, Xenicus longipes.

NORTH, SOUTH, STEWART, AND SOUTHERN OFFSHORE

Leucocarbo carunculatus, Tadorna variegata, **_Strigops habroptilus*_**.

NORTH, SOUTH, NORTHERN OFFSHORE, AND SOUTHERN OFFSHORE

Puffinus gavia.

NORTH, SOUTH, STEWART, NORTHERN OFFSHORE

Pterodroma cookii, **_Coturnix novaezelandiae_**, _Charadrius obscurus,_ **_Corvus_ Mainland**.

NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, AND SOUTHERN OFFSHORE

Dinornis struthoides*, _Stictocarbo punctatus, Gallirallus australis*, Haematopus unicolor, Hemiphaga novaeseelandiae, Nestor meridionalis, Sceloglaux albifacies, Eudynamys taitensis, Acanthisitta chloris, Anthus novaeseelandiae, Bowdleria punctata, Gerygone igata._

NORTH, SOUTH, AND CHATHAMS

Ixobrychus novaezelandiae, Malacorhynchus scarletti.

NORTH, SOUTH, NORTHERN OFFSHORE, AND CHATHAMS

Aythya novaeseelandiae, Charadrius novaeseelandiae.

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NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, AND CHATHAMS
Charadrius bicinctus.

NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, SOUTHERN OFFSHORE, AND CHATHAMS
Anas chlorotis.

NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, CHATHAMS, AND SUBANTARCTIC
Mergus australis.

NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, SOUTHERN OFFSHORE, CHATHAMS, AND SUBANTARCTIC
Falco novaeseelandiae.

NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, SOUTHERN OFFSHORE, AND SUBANTARCTIC
Cyanoramphus auriceps, *Anthornis melanura*.

NORTH, SOUTH, STEWART, SOUTHERN OFFSHORE, AND SUBANTARCTIC
Pterodroma inexpectata.

NORFOLK
Gallirallus* Norfolk, ***Coenocorypha* Norfolk**, ***Hemiphaga spadicea***, ***Gallicolumba norfolciensis***, ***Nestor productus***, ***Lalage leucopyga***, ***Turdus poliocephalus***, *Pachycephala xanthoprocta*, *Gerygone modesta*, *Petroica multicolor*, *Zosterops albogularis*, *Zosterops tenuirostris*, ***Aplonis fusca***.

NORFOLK AND NORTHERN OFFSHORE
Pterodroma pycrofti.

KERMADECS
Puffinus kermadecensis, *Pterodroma cervicalis*, *Pelagodroma albiclunis*?.

CHATHAMS
Diomedea sanfordi, *Thalassarche eremita*, *Thalassarche* sp 1, *Pterodroma axillaris*, *Pterodroma magentae*, ***Pterodroma* sp 1**, ***Eudyptes* Chatham Islands***, *Leucocarbo onslowi*, *Stictocarbo featherstoni*, ***Tadorna* Chathams**, ***Pachyanas chathamica****, ***Gallirallus dieffenbachii****, ***Cabalus modestus****, ***Diaphorapteryx hawkinsi****, ***Fulica chathamensis***, *Haematopus chathamensis*, ***Coenocorypha chathamica***, *Coenocorypha pusilla*, *Hemiphaga chathamensis*, ***Nestor* Chatham Islands**, *Cyanoramphus forbesi*, *Anthus chathamensis*, ***Bowdleria rufescens***, *Gerygone albofrontata*, ***Petroica traversi***, ***Anthornis melanocephala***, ***Corvus moriorum***.

SUBANTARCTIC
Diomedea epomophora, *Thalassarche impavida*, *Thalassarche salvini*, *Eudyptes schlegeli**, *Eudyptes robustus**, *Eudyptes sclateri**, *Leucocarbo ranfurlyi*, *Leucocarbo colensoi*, *Leucocarbo campbelli*, *Leucocarbo purpurescens*, *Dryolimnas muelleri*, *Anas aucklandica**, *Anas nesiotis**, ***Anas* Macquarie***, ***Gallirallus macquariensis****, *Coenocorypha huegeli*, *Coenocorypha meinhertzhagenae*, *Coenocorypha aucklandica*, *Coenocorypha* Campbell, *Charadrius exilis*, *Cyanoramphus unicolor*, *Anthus aucklandicus*, *Bowdleria caudata*, *Petroica dannefaerdi*, *Petroica marrineri*.

KERMADECS, NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, SOUTHERN OFFSHORE,
Hemiphaga novaeseelandiae.

KERMADECS, NORTH, SOUTH, STEWART, NORTHERN OFFSHORE, SOUTHERN OFFSHORE, CHATHAMS, AND SUBANTARCTIC
Prosthemadera novaeseelandiae.

Appendix 4 List of acronyms used in this paper for species in the New Zealand avifauna.

ACCH, *Acanthisitta chloris*; ACFA, *Accipiter fasciatus*; AENO, *Aegotheles novaezealandiae*; ANAC, *Anthus aucklandicus*; ANAU, *Anas aucklandica*; ANCH, *Anas chlorotis*; ANCT, *Anthus chathamensis*; ANDI, *Anomalopteryx didiformis*; ANGR, *Anas gracilis*; ANMA, *Anas* Macquarie; ANMC, *Anthornis melanocephala*; ANME, *Anthornis melanura*; ANMI, *Anous minutus*; ANNE, *Anas nesiotis*; ANNO, *Anthus novaeseelandiae*; ANST, *Anous stolidus*; ANSU, *Anas superciliosa*; APAU, *Apteryx australis*; APDE, *Aptornis defossor*; APEA, *Apteryx* Eastern South Island; APFU, *Aplonis fusca*; APHA, *Apteryx haastii*; APMA, *Apteryx mantelli*; APOT, *Aptornis otidiformis*; APOW, *Apteryx owenii*; APPA, *Aptenodytes patagonicus*; AYNO, *Aythya novaeseelandiae*; BIDE, *Biziura delautouri*; BOCA, *Bowdleria caudata*; BOPU, *Bowdleria punctata*; BORU, *Bowdleria rufescens*; CAAL, *Casmerodius alba*; CACI, *Callaeas cinerea*; CAKA, *Capellirallus karamu*; CAMO, *Cabalus modestus*; CASK, *Catharacta skua*; CAWI, *Callaeas wilsoni*; CHBI, *Charadrius bicinctus*; CHEX, *Charadrius exsul*; CHFR, *Charadrius frontalis*; CHLU, *Chrysococcyx lucidus*; CHNO, *Charadrius novaeseelandiae*; CHOB, *Charadrius obscurus*; CIEY, *Circus eylesi*; CNCA, *Cnemiornis calcitrans*; CNGR, *Cnemiornis gracilis*; COAU, *Coenocorypha aucklandica*; COBA, *Coenocorypha barrierensis*; COCA, *Coenocorypha* Campbell; COCH, *Coenocorypha chathamica*; COHU, *Coenocorypha huegeli*; COIR, *Coenocorypha iredalei*; COMA, *Corvus* Mainland; COME, *Coenocorypha meinertzhagenae*; COMO, *Corvus moriorum*; CONK, *Coenocorypha* Norfolk; CONO, *Coturnix novaezealandiae*; COPU, *Coenocorypha pusilla*; COSI, *Coenocorypha* South Island; CYAT, *Cygnus atratus*; CYAU, *Cyanoramphus auriceps*; CYFO, *Cyanoramphus forbesi*; CYMA, *Cyanoramphus malherbi*; CYNO, *Cyanoramphus novaezelandiae*; CYUN, *Cyanoramphus unicolor*; DACA, *Daption capense*; DEDE, *Dendroscansor decurvirostris*; DICH, *Diomedea chionoptera*; DIEP, *Diomedea epomophora*; DIEX, *Diomedea exulans*; DIGI, *Dinornis giganteus*; DIHA, *Diaphorapteryx hawkinsi*; DINO, *Dinornis novaezealandiae*; DISA, *Diomedea sanfordi*; DIST, *Dinornis struthoides*; DRMU, *Dryolimnas muelleri*; EGSA, *Egretta sacra*; EMCR, *Emeus crassus*; EUCH, *Eudyptes* Chathams; EUCU, *Euryapteryx curtus*; EUFI, *Euryanas finschi*; EUFL, *Eudyptes filholi*; EUGE, *Euryapteryx geranoides*; EUMI, *Eudyptula minor*; EUPA, *Eudyptes pachyrhynchus*; EURO, *Eudyptes robustus*; EUSC, *Eudyptes schlegeli*; EUSL, *Eudyptes sclateri*; EUTA, *Eudynamys taitensis*; FANO, *Falco novaeseelandiae*; FRGR, *Fregetta grallaria*; FRTR, *Fregetta tropica*; FUCH, *Fulica chathamensis*; FUPR, *Fulica prisca*; GAAU, *Gallirallus australis*; GACO, *Gallicolumba norfolciensis*; GADI, *Galllirallus dieffenbachii*; GAHO, *Gallinula hodgenorum*; GAMA, *Gallirallus macquariensis*; GANE, *Garrodia nereis*; GANO, *Gallirallus* Norfolk; GAPH, *Gallirallus philippensis*; GEAL, *Gerygone albofrontata*; GEIG, *Gerygone igata*; GEMO, *Gerygone modesta*; GYAL, *Gygis alba*; HACA, *Halobaena caerulea*; HACH, *Haematopus chathamensis*; HAFI, *Haematopus finschi*; HAMO, *Harpagornis moorei*; HAUN, *Haematopus unicolor*; HEAC, *Heteralocha acutirostris*; HECH, *Hemiphaga chathamensis*; HENO, *Hemiphaga novaeseelandiae*; HESP, *Hemiphaga spadicea*; HINO, *Himantopus novaezelandiae*; HYMA, *Hymenlaimus malacorhynchos*; IXNO, *Ixobrychus novaezealandiae*; LABU, *Larus bulleri*; LADO, *Larus dominicanus*; LALE, *Lalage leucopyga*; LANO, *Larus novaehollandiae*; LECA, *Leucocarbo carunculatus*; LECM, *Leucocarbo campbelli*; LECO, *Leucocarbo colensoi*; LEON, *Leucocarbo onslowi*; LEPU, *Leucocarbo purpurascens*; LERA, *Leucocarbo ranfurlyi*; MAGI, *Macronectes giganteus*; MAHA, *Macronectes halli*; MASC, *Malacorhynchus scarletti*; MEAN, *Megadyptes antipodes*; MEAU, *Mergus australis*; MEDI, *Megalapteryx didinus*; MESP, *Megapodius* sp.; MOAL, *Mohoua albicilla*; MONO, *Mohoua novaeseelandiae*; MOOC, *Mohoua ochrocephala*; MOSE, *Morus serrator*; NECH, *Nestor* Chathams; NEME, *Nestor meridionalis*; NENO, *Nestor notabilis*; NEPR, *Nestor productus*; NINO, *Ninox novaeseelandiae*; NOCI, *Notiomystis cincta*; OCMA, *Oceanites maorianus*; PAAU, *Pachyornis australis*; PACH, *Pachyanas chathamica*; PACR, *Pachyptila crassirostris*; PADE, *Pachyptila desolata*; PAEL, *Pachyornis elephantopus*; PAMA, *Pachyornis mappini*; PAPE, *Pachycephala xanthoprocta*; PATU, *Pachyptila turtur*; PAVI, *Pachyptila vittata*; PAYA, *Pachyplichas yaldwyni*; PEAL, *Pelagodroma albiclunis*; PEAU, *Petroica australis*; PEDA, *Petroica dannefaerdi*; PEEX, *Pelecanoides exsul*; PEGE, *Pelecanoides georgicus*; PEMA, *Pelagodroma marina*; PEMC, *Petroica macrocephala*; PEMR, *Petroica marrineri*; PEMU, *Petroica multicolor*; PETO, *Petroica toitoi*; PETR, *Petroica traversi*; PEUR, *Pelecanoides urinatrix*; PHCA, *Philesturnus carunculatus*; PHCR, *Phalacrocorax carbo*; PHME, *Phalacrocorax melanoleucos*; PHPA, *Phoebetria palpebrata*; PHRU, *Philesturnus rufusater*; PHVA, *Phalacrocorax varius*; POCR, *Podiceps cristatus*; POHO, *Porphyrio hochstetteri*; POMA, *Porphyrio mantelli*; POPU, *Porzana pusilla*; PORU, *Poliocephalus rufopectus*; POTA, *Porzana tabuensis*; PRAE, *Procellaria aequinoctialis*; PRCE, *Procelsterna cerulea*; PRCI, *Procellaria cinerea*; PRNO, *Prosthemadera novaeseelandiae*; PRPA, *Procellaria parkinsoni*; PRWE, *Procellaria westlandica*; PTAL, *Pterodroma alba*; PTAX, *Pterodroma axillaris*; PTCE, *Pterodroma cervicalis*; PTCO, *Pterodroma cookii*; PTIN, *Pterodroma inexpectata*; PTLE, *Pterodroma lessonii*; PTMA, *Pterodroma macroptera*; PTME, *Pterodroma magentae*; PTNE, *Pterodroma neglecta*; PTNI, *Pterodroma nigripennis*; PTPY, *Pterodroma pycrofti*; PTS1, *Pterodroma* sp. 1; PTSO, *Pterodroma solandri*; PUAS, *Puffinus assimilis*; PUBU, *Puffinus bulleri*; PUEL, *Puffinus elegans*; PUGA, *Puffinus gavia*; PUGR, *Puffinus griseus*; PUHA, *Puffinus haurakiensis*; PUHU, *Puffinus huttoni*; PUKE, *Puffinus kermadecensis*; PUPA, *Puffinus pacificus*; PUSP, *Puffinus spelaeus*; PYPA, *Pygoscelis papua*; RHFU, *Rhipidura fuliginosa*; SCAL, *Sceloglaux albifacies*; STAL, *Sterna albostriata*; STCA, *Sterna caspia*; STFE, *Stictocarbo featherstoni*; STFU, *Sterna fuscata*; STHA, *Strigops habroptilus*; STNE, *Sterna nereis*; STPU, *Stictocarbo punctatus*; STST, *Sterna striata*; STVI, *Sterna vittata*; SUDA, *Sula dactylatra*; TACH, *Tadorna* Chathams; TAVA, *Tadorna variegata*; THBU, *Thalassarche bulleri*; THCA, *Thalassarche cauta*; THCH, *Thalassarche* *chrysostoma*; THER, *Thalassarche eremita*; THIM, *Thalassarche impavida*; THSA, *Thalassarche salvini*; THSP, *Thalassarche* sp.; TOSA, *Todiramphus sanctus*; TRLY, *Traversia lyalli*; TUCA, *Turnagra capensis*; TUPO, *Turdus poliocephalus*; TUTA, *Turnagra tanagra*; XEGI, *Xenicus gilviventris*; XELO, *Xenicus longipes*; ZOAL, *Zosterops albogularis*; ZOTE, *Zosteropstenuirostris*.

Appendix 5 Bird species added to the New Zealand fauna since first human contact. (Heather & Robertson 1996; this study)

A. Bird species that have successfully colonised (established permanent breeding populations in) New Zealand unaided since human contact.

Order Podicipediformes	
Tachybaptus novaehollandiae	Australian little grebe
Order Procellariiformes	
Thalassarche melanophris	Black-browed albatross
Pterodroma mollis	Soft-plumaged petrel
Order Pelecaniformes	
Phalacrocorax sulcirostris	Little black shag
Order Ciconiiformes	
Ardea novaehollandiae	White-faced heron
Botaurus poiciloptilus	Australasian bittern
Platalea regia	Royal spoonbill
Order Anatiformes	
Anas rhynchotis	Shoveler
Order Accipitriformes	
Circus approximans	Australasian harrier
Order Gruiformes	
Porphyrio melanotos	Pukeko
Fulica atra	Australian coot
Order Charadriiformes	
Himantopus leucocephalus	Pied stilt
Charadrius melanops	Black-fronted dotterel
Vanellus miles	Spur-winged plover
Order Passeriformes	
Hirundo tahitica	Welcome swallow
Zosterops lateralis	Silvereye

B. Bird species that have been successfully introduced by humans (established permanent breeding populations) in New Zealand.

Order Anseriformes	
Cygnus olor	Mute swan
Branta canadensis	Canada goose
Anser anser	Feral goose
Anas platyrhynchos	Mallard
Order Galliformes	
Callipepla californica	California quail
Alectoris rufa	Red-legged partridge
Alectoris chukar	Chukor
Synoicus ypsilophorus	Brown quail
Phasianus colchicus	Pheasant
Pavo cristatus	Peafowl
Meleagris gallopavo	Turkey
Numida meleagris	Tufted guineafowl
Order Columbiformes	
Columba livia	Rock dove
Streptopelia roseogrisea	Barbary dove
Streptopelia chinensis	Spotted dove

Order Psittaciformes	
Cacatua galerita	Sulphur-crested cockatoo
Cacatua roseicapilla	Galah
Platycercus eximius	Eastern rosella
Platycercus elegans	Crimson rosella
Order Strigiformes	
Athene noctua	Little owl
Order Coraciiformes	
Dacelo novaeguinae	Kookaburra
Order Passeriformes	
Alauda arvensis	Skylark
Pycnonotus cafer	Red-vented bulbul
Prunella modularis	Dunnock
Turdus merula	Blackbird
Turdus philomelos	Song thrush
Emberiza citrinella	Yellowhammer
Emberiza cirlus	Cirl bunting
Fringilla coelebs	Chaffinch
Chloris chloris	Greenfinch
Carduelis carduelis	European goldfinch
Carduelis flammea	Redpoll
Passer domesticus	House sparrow
Sturnus vulgaris	European starling
Acridotheres tristis	Common myna
Gymnorhina tibicen	Australian magpie
Corvus frugilegus	Rook

Appendix 6 Comparison of Williams's (1981: Appendix 1) list and list of species of terrestrial and freshwater species in this paper. Note: all groups of terrestrial and freshwater taxa omitted by Williams (1981) are omitted here, except for *Casmerodius albus*, *Ixobrychus novaezelandiae*, and *Coenocorypha* snipe, which are unequivocally non-marine. List of species of terrestrial and freshwater birds used by Williams (1981) in his biogeographical analysis in comparison with those recognised in the present paper as being part of the late Holocene fauna. Species omitted here from Williams's list are mostly now regarded as having colonised since the start of Polynesian settlement (Appendix 5). Species added here have been recognised as distinct in this paper, or their presence was discovered after 1981. Norfolk Island taxa were not fully covered by Williams (1981).

In Williams	In this paper	In Williams (1981), not in this paper	Not in Williams (1981)	In Williams but name changed	In both papers
	Anomalopteryx didiformis		1		
	Megalapteryx didinus		1		
	Pachyornis mappini		1		
	Pachyornis elephantopus		1		
	Pachyornis australis		1		
	Euryapteryx curtus		1		
	Euryapteryx geranoides		1		
	Emeus crassus		1		
	Dinornis struthoides		1		
	Dinornis novaezealandiae		1		
	Dinornis giganteus		1		
Apteryx australis	*Apteryx australis*				1
	Apteryx mantelli		1		
	Apteryx (Eastern South Island)		1		
Apteryx owenii	*Apteryx owenii*				1
Apteryx haastii	*Apteryx haastii*				1
Podiceps cristatus	*Podiceps cristatus*				1
Podiceps rufopectus	*Poliocephalus rufopectus*			1	1
	Casmerodius albus		1		
	Ixobrychus novaezelandiae		1		

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Appendix 6 continued

In Williams	In this paper	In Williams (1981), not in this paper	Not in Williams (1981)	In Williams but name changed	In both papers
	Cygnus atratus		1		
	Cnemiornis gracilis		1		
	Cnemiornis calcitrans		1		
Tadorna variegata	*Tadorna variegata*				1
	Tadorna (Chathams)		1		
Anas superciliosa	*Anas superciliosa*				1
Anas gibberifrons	*Anas gracilis*			1	1
	Anas aucklandica		1		
Anas aucklandica	*Anas chlorotis*			1	1
	Anas nesiotis		1		
Anas rhynchotis		1			
	Euryanas finschi		1		
	Biziura delautouri		1		
	Mergus australis		1		
	Malacorhynchus scarletti		1		
Hymenolaimus malacorhynchos	*Hymenolaimus malacorhynchos*				1
Aythya novaeseelandiae	*Aythya novaeseelandiae*				1
Circus approximans		1			
	Circus eylesi		1		
	Harpagornis moorei		1		
Falco novaeseelandiae	*Falco novaeseelandiae*				1
Coturnix novaezelandiae	*Coturnix novaezelandiae*				1
	Megapodius sp.		1		
Rallus philippensis	*Gallirallus philippensis*			1	1
Gallirallus australis	*Gallirallus australis*				1
Rallus dieffenbachii	*Gallirallus dieffenbachii*			1	1
Rallus modestus	*Cabalus modestus*			1	1
Rallus pectoralis	*Dryolimnas muelleri*			1	1
	Diaphorapteryx hawkinsi		1		
	Capellirallus karamu		1		
Porzana pusilla	*Porzana pusilla*				1
Porzana tabuensis	*Porzana tabuensis*				1
	Gallinula hodgenorum		1		
Porphyrio melanotos		1			
Porphyrio mantelli	*Porphyrio hochstetteri*			1	1
	Porphyrio mantelli		1		
	Fulica prisca		1		
	Fulica chathamensis		1		
	Himantopus novaezelandiae		1		
	Coenocorypha barrierensis		1		
	Coenocorypha iredalei		1		
	Coenocorypha huegeli		1		
	Coenocorypha meinertzhagenae		1		
	Coenocorypha aucklandica		1		
	Coenocorypha chathamica		1		
	Coenocorypha pusilla		1		
Hemiphaga novaeseelandiae	*Hemiphaga novaeseelandiae*				1
	Hemiphaga chathamensis		1		
Strigops habroptilus	*Strigops habroptilus*				1
Nestor meridionalis	*Nestor meridionalis*				1
	Nestor (Chathams)		1		
Nestor notabilis	*Nestor notabilis*				1

Appendix 6 continued

In Williams	In this paper	In Williams (1981), not in this paper	Not in Williams (1981)	In Williams but name changed	In both papers
Cyanoramphus unicolor	*Cyanoramphus unicolor*				1
Cyanoramphus novaezelandiae	*Cyanoramphus novaezelandiae*				1
Cyanoramphus auriceps	*Cyanoramphus auriceps*				1
Cyanoramphus malherbi	*Cyanoramphus malherbi*				1
	Cyanoramphus forbesi		1		
	Cyanoramphus erythrotis		1		
Chalcites lucidus	*Chrysococcyx lucidus*			1	1
Eudynamys taitensis	*Eudynamys taitensis*				1
Ninox novaeseelandiae	*Ninox novaeseelandiae*				1
Sceloglaux albifacies	*Sceloglaux albifacies*				1
	Aegotheles novaezealandiae		1		
Halcyon sanctus	*Todiramphus sanctus*			1	1
Acanthisitta chloris	*Acanthisitta chloris*				1
Xenicus longipes	*Xenicus longipes*				1
Xenicus gilviventris	*Xenicus gilviventris*				1
Xenicus lyalli	*Traversia lyalli*			1	1
	Pachyplichas yaldwyni		1		
	Dendroscansor decurvirostris		1		
Anthus novaeseelandiae	*Anthus novaeseelandiae*				1
	Anthus chathamensis		1		
	Anthus aucklandicus		1		
Bowdleria punctata	*Bowdleria punctata*				1
	Bowdleria caudata		1		
	Bowdleria rufescens		1		
Finschia novaeseelandiae	*Mohoua novaeseelandiae*			1	1
Mohoua albicilla	*Mohoua albicilla*				1
Mohoua ochrocephala	*Mohoua ochrocephala*				1
Gerygone igata	*Gerygone igata*				1
Gerygone albofrontata	*Gerygone albofrontata*				1
Rhipidura fuliginosa	*Rhipidura fuliginosa*				1
Petroica macrocephala	*Petroica macrocephala*				1
	Petroica toitoi		1		
	Petroica dannefaerdi		1		
	Petroica marrineri		1		
Petroica australis	*Petroica australis*				1
	Petroica longipes		1		
Petroica traversi	*Petroica traversi*				1
Zosterops lateralis		1			
Notiomystis cincta	*Notiomystis cincta*				1
Anthornis melanura	*Anthornis melanura*				1
	Anthornis melanocephala		1		
Prosthemadera novaeseelandiae	*Prosthemadera novaeseelandiae*				1
Philesturnus carunculatus	*Philesturnus carunculatus*				1
	Philesturnus rufusater		1		
Heteralocha acutirostris	*Heteralocha acutirostris*				1
Callaeas cinerea	*Callaeas cinerea*				1
	Callaeas wilsoni		1		
Turnagra capensis	*Turnagra capensis*				1
	Turnagra tanagra		1		
	Corvus moriorum		1		
	Corvus (Mainland)		1		
60	119	4	63	12	56