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NEW ZEALAND'S PRE-HUMAN AVIFAUNA AND ITS VULNERABILITY

Summary: In the past 1000 years New Zealand has experienced a major 'extinction event', losing 40-50% of the avifauna, at least 50% of the frog fauna, and unknown proportions of the lizard and invertebrate faunas.

During this period, bird species became extinct at different times and rates depending on the particular aspects of their ecology and life history which made them vulnerable to habitat loss, hunting, predation, and competition for food resources. Three groups of species with different levels of vulnerability are recognised within this event:

Group I, 1000-1200 AD - species susceptible to initial impact of hunting by Polynesians and dogs, and predation and competition for food after an explosive irruption of kiore (*Rattus exulans*);

Group II, 1200-1780 AD - species more resilient but gradually reduced by Polynesian hunting and continuous clearance and fragmentation of habitat;

Group III, 1780-present - species susceptible to hunting with European weapons and predation by *Rattus norvegicus*, *R. rattus*, mustelids, cats, and to competition by mammalian herbivores, and destruction of wet forest and wetland habitat.

Climatic change is seen as a negligible influence relative to these major intrusions. Discussions of the pre-human avifauna have so far concentrated almost exclusively on moas (Aves: Dinornithidae, Anomalopterygidae), partly because information on the other extinct species is sparse. The ecology of 12 species in the pre-human avifauna is inferred from their anatomy, relationships to extant species, sub-fossil evidence of diets, and analogy with related forms elsewhere.

Keywords: New Zealand; avifauna; extinction event

Introduction

The New Zealand avifauna was, when Europeans arrived, only a battered remnant of the fauna of pre-human times, surviving in a much-altered environment. This remnant, supplemented by some late immigrants is, however, the fauna used in most biogeographic and faunistic analyses. Various lists of extinct New Zealand birds are available (e.g. Kinsky, 1970), tucked away as appendices where they attract little attention. Most lists are out of date, and do not provide information on ecology. They are easily overlooked.

It is important to consider the ecology of species lost between 900 and 1800 AD in more detail, because only then can the causes and results of their extinction be better assessed. Cassels (1984) pointed out general similarities between the species which went extinct, but the present paper is the first attempt to assign a general ecology to several extinct species and to discuss faunal assemblages. As such, it may provide a framework for future work on the palaeo-ecology of the pre-human fauna, and a firmer conceptual base for studies on the relative effects of moas, ungulates, and climate on the vegetation of New Zealand.

To reconstruct the ecology of extinct species in the pre-human avifauna, some of which are only distantly related to extant species, we need to consider functional clues in their anatomy, and information on their habitat, diet, and demography. Some information can be obtained from the extensive, if uneven, literature on avian sub fossil deposits in New Zealand, but we need many more, detailed studies of sites and individual species.

Such studies as are available have concentrated on the ecology of moas, and their influence on the evolution of the New Zealand flora. Moas (Aves: Dinornithidae, Anomalopterygidae) were indeed impressive members of the diverse avifauna in pre-human New Zealand, but their effects on vegetation in the Late Holocene cannot be discussed without considering the palaeo-ecosystem as a whole. Other herbivores were present and the moas (themselves a much more diverse ecological group than is usually appreciated) were subject to the same pressures of predation and dispersion of food resources as other animals. Several of the papers in this volume treat the group as 'the moa' and assign 'it' mammal-like

characteristics. Others argue on very tenuous premises for, say, flocking behaviour, and then attempt to assess population size and grazing pressure. The results are not convincing. Although many authors have discussed the cause(s) of moa extinction (e.g. Fleming, 1953, 1962; Cumberland, 1962; Duff, 1964; Anderson, 1984; Cassels, 1984; Trotter and McCulloch, 1984), only a few aspects of moa ecology have been treated in detail (Hamel, 1979; Burrows *et al.*, 1981; Anderson, 1983). To understand the relationship between these large avian herbivores, the ecology of individual species and genera of moas must be studied more deeply, in the context of a complete avifauna: it is that avifauna which is discussed here.

Palaeo-environment

The pre-human avifauna was dominated by forest and wetland birds. Forests covered most of the land below tree-line (McGlone, this volume), but the forest fauna was radically different from that documented by European explorers 100-200 years ago. Sub fossil remains from caves and other deposits suggest that, before the arrival of Polynesians about 1000 years ago, the fauna was rich and diverse.

Declines in relict populations of *Powelliphanta* snails (Mollusca: Paryphantidae) (Meads *et al.*, 1984) and the large wetas (Insecta: Stenopelmatidae) (Watt, 1975) suggest that prehistoric populations were almost certainly far greater in numbers and more continuous. The great reductions in range, and the clear correlation between presence of introduced predators and absence or extremely low numbers of large invertebrates, lizards, and tuatara, strongly suggest that extinctions have occurred and that many mainland populations are now truly relict (Crook, 1973; Whitaker, 1973; Campbell *et al.*, 1984). Many of the disjunct distributions in the lizard fauna (e.g. *Cyclodina*) are in areas which were not greatly affected by climatic changes or physical disruption during the Pleistocene (Towns *et al.*, 1985). Conversely, one of the extreme relicts is *Leiopisma acrinasum* which presumably survived through the worst of the glaciations in Fiordland or subsequently recolonised the area within a few thousand years.

Leiopelmatid frogs were widespread on both islands. Today, *Leiopelma hamiltoni* is restricted to Stephens and Maud Islands in the Marlborough Sounds, but has been found in cave deposits as far south as Punakaiki, and at Waitomo and Hawkes Bay in the North Island (Worthy, 1987a). Worthy (1987a) describes 3 new species of *Leiopelma* from cave

deposits, including a species much larger than *L. hamiltoni*. Frogs must have been a major feature of the fauna of the pre-human forest floor, judging by the abundant remains being found in caves whose entrances were once within forest.

A variety of skinks (Scincidae) and geckos (Gekkonidae) still occurs on the main islands of New Zealand, but they are far more conspicuous and abundant on islands without mammals, particularly rats. Before humans arrived, lizards were probably as abundant on the mainland as they are now on the islands (Whitaker, 1973). Subfossil lizard material, usually not identified to species, has been found in caves and other deposits in many mainland areas (e.g. Rich *et al.*, 1979). Worthy (1987b) reports *Cyclodina alani*, *C. macgregori*, *C. whitakeri* and *Hoplodactylus duvauceli* from widespread localities in the North Island.

The tuatara (*Sphenodon punctatus*) is now confined to offshore islands, and breeds successfully only on those lacking the kiore or Polynesian rat, *Rattus exulans* and other *Rattus* species (Crook, 1973). Yet, the subfossil distribution of tuatara includes most parts of both main islands (Bull and Whitaker, 1975; Cassels, 1984). Its previous distribution indicates that it was a widespread member of the ground fauna when Polynesians arrived.

The endemic bat *Mystacina tuberculata* has exploited an unusually diverse range of foods in the absence of mammalian competitors. Daniel (1979) reports that it feeds on the ground, foliage, and tree trunk, takes insects on the wing, and eats fruits and nectar. In some ways it was an analogue of shrews, honey possums, and other bat groups. It also builds its own galleries in fallen trees and occupies petrel burrows. Not much is known about the only other New Zealand species, *M. robusta*, and it may even be extinct (Hill and Daniel, 1985), but it used to be widespread and is frequent in cave deposits near Waitomo (T. Worthy, pers. comm.).

Remains of petrels are prominent in many cave and dune deposits throughout New Zealand. Where the deposits are inland, in hills still covered with heavy forest, they probably reflect former breeding colonies. A few mainland colonies persist in some areas (e.g. *Procellaria westlandica* at Punakaiki, *Puffinus huttoni* near Kaikoura) or at least have existed in European times (*Procellaria parkinsoni* and *Pterodroma inexpectata*). Some of the dune deposits may indicate former colonies rather than beach strandings (Millener, 1981). Mainland cave deposits contain some of the small prions (*Pachyptila* spp.) and various

example, I suggest that *Sophora* was more abundant in the forests over extensive areas in Canterbury and Otago; this would not be obvious in the pollen record because *Sophora* is pollinated by insects and birds. The lack of substantial amounts of trunk charcoal argues against forests of *Sophora* (McGlone, pers. comm.). Molloy (1971) illustrates some much-altered remnants of a *Sophora* association surviving on Great Island in the Rakaia River. McGlone (this volume) argues that *Phyllocladus alpinus*/*Halocarpus bidwillii*-shrublands and *Podocarpus hallii*-hardwood forests were formerly widespread in dry areas, yet neither association has survived in quantity.

The pre-human avifauna

A systematic list of the genera of birds in the pre-human avifauna is given in Appendix 1. The avifauna can be divided into broad ecological groups (Fig. 1) which give some insight into the previous structure and composition of avian assemblages, and palaeo-habitat.

The loss of species through time is shown in Fig. 2. The shape of the curve from the arrival of Cook (1769 AD) to the present is based on published dates for last records and is, at present, the only part which can be drawn with any sort of precision. From its

shape, I predict that the section of the curve for the first 10-50 years of occupation will also indicate an initial sudden loss of species (Group I) followed by extinctions of less vulnerable (Group II) species, and then those (Group III) which persisted as remnants into the European period or were vulnerable to further habitat destruction and the suite of predators introduced after 1769. After the immediate loss of several species when humans first arrived (circa AD 1000), the curve must, perforce, descend to the recent sudden decline commencing about AD 1800, but the exact shape will depend mainly on direct environmental influences. A steady decline over time (Curve A) implies a direct association between extinctions and loss of habitat. Conversely, a flattening in the curve followed by a steep section (or sections) (Curve B) could imply: restriction of many species to small refugia; more than one stage of habitat destruction; or that communities in different parts of the country were affected at different times.

The shape of the extinction curve therefore generates testable hypotheses about the cause(s) of the faunal collapse after 1000 BP. If it was a steady decline, as in A, then the various effects of human colonisation can be interpreted as having acted 'in concert' with species becoming extinct at random

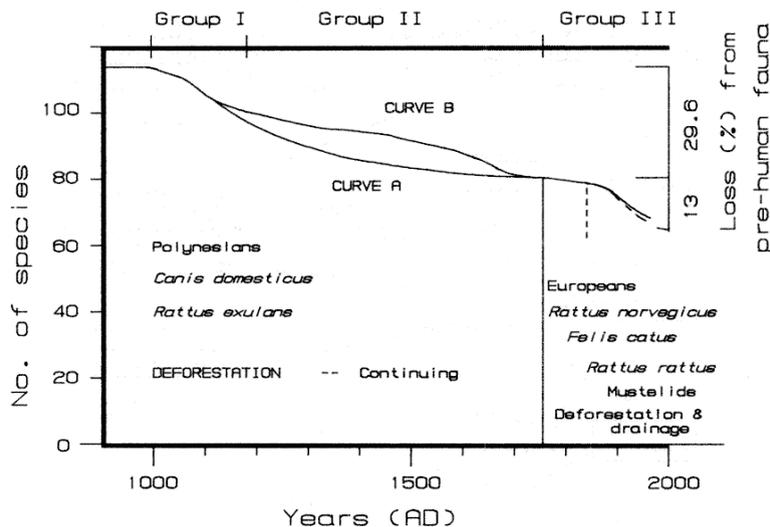


Figure 2: Loss of bird species in South Island, New Zealand through time, since 900 AD. Percentage losses before and after European contact are shown at right. Groups I to III refer to species lost in each pulse of the extinction event (see text). Approximate dates for introductions of various species of mammal are shown. The shape of the extinction curves before European contact indicates two possible courses of species loss which can be related to changes in environmental conditions.

intervals within the time span. If, however, as in B, the slope was not constant, the effects must have operated separately, or at the same rate but in different areas. The type of impact that contemporaneous environmental events may have had can be inferred from a knowledge of the ecology of the species lost in each pulse.

The Group I species would have included the pelican (*Pelecanus novaeseelandiae*) which was probably extremely vulnerable to disturbance at nesting colonies (as is the Australian pelican *P. conspicillatus* (van Tets, in Frith, 1969)). Other Group I species were: the mainland race(s) of the snipe *Coenocorypha aucklandica*; the 'Stephens Island' wren *Traversia lyalli* (and two other acanthisittids which became extinct during the Polynesian period (Millener, 1988)); and *Capellirallus*, the 'snipe-rail'. All of these were potentially very vulnerable to predation by kiore (*R. exulans*). They were all small birds, structurally or behaviourally flightless, which lived and nested on or near the ground, and had no defences against mammalian predators. *Coenocorypha*, for example, now occurs only on rat- and cat-free islands. *Xenicus longipes variabilis* died out soon after an irruption of *Rattus rattus* on Big South Cape I, off Stewart I, in the 1960s (Merton, 1975).

At present, the impact of the kiore on the smaller birds may not be fully realised, but Crook (1973) and Atkinson (1978, 1985) indicate that populations of small vertebrates, including birds, can be greatly reduced by their predation on juveniles. Kiore probably spread rapidly from local centres of high populations which developed near the original landfalls, penetrating ahead of the human colonists, entering the dense forest, and reproducing exponentially in the presence of unlimited food. A rat 'blitzkrieg' (in the sense used by Mosimann and Martin (1977) for human predators in North America) may have advanced across the landscape; a grey tide, turning everything edible into rat protein as it went. The rat irruption may well be amenable to modelling using the Mosimann and Martin algorithm.

Whereas the avian predators were double-brooded at most, kiore could raise several litters in a season and some of those young could themselves breed in the same year. The principal characteristic of the prey fauna was not high absolute numbers but high diversity, as in a tropical forest today. The original equilibrium between predators and prey would have been upset easily and catastrophically by the arrival of a new, nocturnal predator with a high reproductive

potential.

Those lost in a second pulse (Group II, e.g., most moas, the eagle *Harpagornis moorei*) probably succumbed through human hunting pressure, loss of habitat, and loss of food resources. For example, the declines in the moas, *Cnemidornis*, and swan would have been disastrous for the eagle population.

Group III species are those which were vulnerable to predation by Eurasian rats, cats, mustelids, and to habitat alteration by Europeans and introduced herbivores. It includes the shore plover (*Thinornis novaeseelandiae*), saddleback (*Philesturnus carunculatus*), and piopio (*Turnagra capensis*). Smith (1986) has shown that *Rattus rattus* is an efficient predator of nestling birds and invertebrates and that previous studies of rat diet may have underestimated the contribution of large invertebrates because rats select and consume soft flesh and thus have no identifiable hard parts in the gut. Preference for soft tissues also distorts stomach-sample estimates of predation on seeds by *R. exulans* (Campbell *et al.*, 1984).

Ecology and vulnerability

In the following list, New Zealand species have been assigned to Groups I or II on the basis of potential 'vulnerability', which predicts the period of extinction. These allocations and the hypotheses arising from possible shapes of the intermediate extinction curve can perhaps be tested when there are enough radio-isotope dates to refine the shape of that curve. Many moas have been dated but at present the only smaller bird dated directly by radio-carbon is *Euryanas finschi* at 1080 ± 70 yBP (NZ 4166) from Waikari, North Canterbury (McCulloch, 1977).

The 'field guide' style of entry is deliberate.

Where possible, the information is based on general knowledge of ecology, life history, and vulnerability of related species in their own environment, extrapolated to the New Zealand situation. To give an overall picture of the species as parts of the fauna, I have included broader conjecture: there is much opportunity for further study.

Species list

Moa *Anomalopteryx*, *Megalapteryx*, *Euryapteryx*, *Emeus*, *Pachyornis*, *Dinornis*. Though treated here as one ecological group there was undoubtedly great diversity in ecology and life history within the family, and certainly between members of the currently recognised subfamilies, Dinornithinae and Anomalopteryginae. (Group II) Large to enormous

birds (25-250 kg). Larger species browsed on twigs, leaves, fruit; and also took fallen fruit from forest floor. Smaller species more omnivorous, diet including large invertebrates. Chicks of all species insectivorous, also taking small vertebrates. Adults adapted to low quality/high volume diet; monogastric digestion, with caecal microflora breaking down hemicelluloses (as in equids) and probably cellulose and lignin; material probably returned from caeca to at least small intestine and probably gizzard where microbial protein was broken down and absorbed. (cf. emus (*Dromaius novaehollandiae*) Herd and Dawson (1984)). Diet varied, so avoiding large doses of toxins from one plant species. Large trace element requirement. Diet changed to exploit vegetation of different heights during growth. Long-lived, 'K-selected'. Solitary, or small family groups. Nests usually under fallen tree or rock overhang; clutch 1-2; chicks creched in *Dinornis*. Most abundant in drier forest/scrub mosaic on younger, nutrient-rich soils, or on limestone; *Megalapteryx* penetrating alpine grasslands. Chicks taken by goshawk; chicks and adults of all species taken by Haast's eagle. Vulnerable to hunting by humans and dogs, habitat destruction, egg collecting, disturbance of traditional breeding areas, loss of food resources for chicks (large insects). Parallel with tuatara in that juvenile life history stage is most vulnerable - in tuatara from predation by rats, and in moas because rats consumed the food supply of the young.

Pelecanus novaeseelandiae (New Zealand pelican) (Group I). Found on large lakes, rivers, and inshore waters. Food fish. Few large breeding colonies on low scrub or on the ground; very sensitive to disturbance at nest. North and South Is, both inland (Lake Waikaremoana, Lake Poukawa) and near the coast (Lake Grassmere). Hunted and disturbed at colonies by men and dogs; decline rapid because of lack of breeding success, killing of adults and removal of eggs.

Cnemiornis calcitrans (Flightless 'goose') (Group I). Large (10-15 kg, estimated from leg bone dimensions), flightless, terrestrial. Occurred in both islands. A grazer on short herbage like its presumed closest ecological counterpart, *Cereopsis novaehollandiae* (Cape Barren goose) of southern Australia; grazed herbs under open canopy and on riparian strips in forests. More abundant in the extensive areas of forest/scrub/grassland mosaic on drier eastern side of the South Island, inhabiting open seral forests of kanuka (*Kunzea ericoides*), seral grasslands, and the more extensive grasslands of Central Otago. Eggs and

adults hunted by humans and dogs; eggs and chicks vulnerable to rats. Major areas of habitat destroyed. [*Cereopsis* survived only on islands off southern Australia and proved vulnerable to habitat destruction and predation. The various flightless geese of Hawaii did not survive the early period of human settlement (Olson and James, 1982b).]

Cygnus sumnerensis (New Zealand swan) (Group I) Throughout. Up to 3.5 kg. Food predominantly aquatic plants such as *Ruppia*, and terrestrial herbs obtained by grazing. Sensitive to disturbance and predation at large breeding colonies near lakes and lagoons. Eggs collected; adults hunted during annual moult.

Euryanas finschi (Finsch's duck) (Group I) Abundant throughout in forest and scrub. Flight poor. Food: invertebrates, fallen fruit. Nests built in cavities, under logs, or in cave entrances. Eggs and chicks vulnerable to rat predation. Rats competed for food. Much habitat lost with removal of drier eastern forests.

Oxyura sp. (Blue-billed duck) (Group I) Restricted to deep, permanent lakes and ponds with dense marginal vegetation, in breeding season: flocks on open water during moult. Food: small invertebrates, obtained by diving. Never abundant because of limited habitat. Vulnerable to rat predation on eggs.

Biziura delautori (New Zealand musk duck) (Group I) As for *Oxyura*; if anything, more vulnerable to predation on nests and adults.

Mergus australis (New Zealand merganser) (Group I) Found throughout. Nests on ground, among rocks or dense vegetation. Food small fish in lakes and rivers, and on sea coast. Vulnerable to rat predation on eggs and chicks; food supply and habitat not important factors in extinction because conditions similar to those on the Auckland Is (where it survived into this century) were still present on the mainland.

Pachyanas chathamica (Chatham Is duck) (Group I) Confined to Chatham Is. Marine: a 'steamer duck' analogue, feeding on molluscs and crustaceans obtained by diving. Nests in holes among rocks and in dense vegetation. Confiding, easily caught. Extinction through direct predation by humans.

Circus eylesi (New Zealand hawk) [This was referred to *Circus* by Scarlett in his original description; found to be a goshawk. A paper making the necessary nomenclatural change is in preparation, but because the ecology of the two raptor groups is so different, and the presence of a large bird hawk in New Zealand has been unrecognised previously, the bird is discussed here as a goshawk, in advance of the formal name change.] (Group II) Both main islands, in forest;

North I form larger. Weight 2.5-3 kg (female). Typical bird hawk, preying on species such as kaka (*Nestor meridionalis*), kea (*N. notabilis*), kakapo (*Strigops habroptilus*), pigeon (*Hemiphaga novaeseelandiae*), Finsch's duck (*Euryanas jinschi*), weka (*Gallirallus australis*), kokako (*Callaeas cinerea*), and raven (*Corvus moriorum*). Much time spent perched on high branches; prey pursued in rapid, highly manoeuvrable flight through forest. Nest in large fork of tree, at 10-20 m; near water. Hunting range large. More abundant in drier forests east of main divides, and in areas of lower relief. Vulnerable to habitat destruction.

Haliaeetus australis (Southern sea eagle) (Group I) Chatham Is. Population small. On coast, feeding on fish, seal carrion, and marine birds (penguins and albatrosses). Highly vulnerable to disturbance at nest. Human predation on eggs and young most likely cause of extermination, although reduction of numbers of seals (by Polynesian hunters) and marine birds may have reduced food supply eventually.

Harpagornis moorei (Haast's eagle) (Group II) North and South Is. In forest, mainly east of the divide in the South I; not known north of Taupo. Immense forest eagle (male up to 10 kg, female up to 13 kg). Prey, large to very large ground birds, of up to 250 kg (e.g., *Cnemiornis*, *Aptornis*, *Megalapteryx*, *Euryapteryx*, *Pachyornis*, *Dinornis*). Prey taken by powerful strike after rapid descent from high perch. Long periods spent motionless; a 'sit-and-wait' predator. Carcase used for several days, bird(s) remaining in vicinity. Home range very large (15->30 km²). Nest enormous, in emergent tree, used by same pair for many years. Life span 15 + years. One chick per pair, nestling stage protracted (100-120 days), dependent on parents for up to 1 year. Total population small. Vulnerable to habitat destruction, human predation at the nest, and ultimately to loss of large prey species.

Capellirallus karamu (Snipe-rail) (Group I) North I only, forest. Flightless, nest on ground. Weight 250-300 g. Food: invertebrates taken from soil and litter. Highly vulnerable to rat predation on eggs and chicks. Food source drastically reduced during initial rat plague. Same habitat as kiore. (cf. surviving banded rail (*Gallirallus philippensis*), now coastal in sedges and rushes.)

Fulica chathamensis (New Zealand giant coot) (Group II) Throughout, lakes, ponds, swamps, and along streams in forest. Weight 1.5-2 kg, cf. 500-1000 g for extant *F. atra*. Food, shoots and leaves of aquatic vegetation, seeds, and invertebrates for chicks.

Susceptible to rat predation on eggs and young; dog and human predation on adults.

Gallinula hodgenorum (Hodgen's waterhen) (Group I) North and South Is, riparian swards, open forest glades, always near water. Weight 400-500 g. Food, shoots and stem bases of graminoids, seeds; food of chicks invertebrates. Short, grazed sward essential. Nest on ground, in tussock or clump of sedge. Vulnerable to rat predation of eggs and chicks.

[*Gallinula mortierii* of Tasmania is a near relative; inhabits 'marsupial lawns' and, now, short grass pastures (Ridpath, 1964); extinct on mainland but widespread there in Holocene (Olson, 1975).] *Aptornis otidiformis* (Adzebill) (Group I) North and South Is, forest. Flightless, 10-12kg. Food, large invertebrates, frogs, lizards, tuataras, petrels and petrel chicks; taken by turning over litter, tearing at rotting logs, and excavating burrows. Nest on ground, in heavy vegetation. Home range large. Vulnerable to hunting by humans, and to predation by feral dogs, rats (eggs and chicks), loss of habitat, and loss of food resources such as petrels and tuatara.

Megaegotheles novaezealandiae (Giant owl-night jar) (Group II) North and South Is, forest. Weight c. 200 g, cf. *Aegotheles*, 40-50 g. Flight weak, active on ground. Food large invertebrates, frogs, and lizards taken on ground. Nest in cavities and caves. Nocturnal. Vulnerable to rat predation, but more so to reduction of numbers and diversity of prey and perhaps loss of habitat. [May have survived into 19th Century (Potts, 1882).]

Corvus moriorum (New Zealand raven) (Group II) North, South, and Chatham Is; forest and scrub, usually near coast. Weight 900-1000 g. Omnivore, food including fruit, large insects, carrion (bird and marine mammal), lizards, tuatara, nesting petrels. Large stick nest in trees or on cliffs. Scavenger at *Harpagornis* kills. Possible predator on moa chicks. Vulnerable to human predation, habitat loss, reduction of food supply, particularly carrion.

Acanthisittidae (New Zealand wrens) (Group VII) North, South, Stewart Is. Forest, scrub, subalpine scrub, throughout. Insectivorous, some fruit taken. Nests built in cavities domed, on or near ground in most species. Four species extant at European arrival, *Traversia lyalli* (and *Xenicus longipes*?) now extinct. *Traversia* widespread on mainland recently, *Xenicus gilviventris*, now confined to alpine and other rocky areas of South I, once (last glaciation?) found in North I (T. Worthy, pers. comm.). Two genera extinct by time of European arrival; one, at least, formerly widespread, abundant (Millener, 1988).

Extinct forms at least facultatively flightless ground birds. Vulnerable to predation by rats and cats, except *X. gilviventris* which lives in and on rock piles and in heavy scrub.

Discussion

In pre-human New Zealand, the avifauna was part of a much more diverse and abundant fauna than exists today. Whole assemblages of animals have since been lost, and probably some plant assemblages as well. The extinction event in New Zealand is one of the last faunal collapses of Holocene time and is equivalent to those in Madagascar and Hawaii (Olson and James, 1982a, 1982b). It has occupied about 1000 years which is about the same length of time as it took to lose the North American megafauna (Martin and Klein, 1984). However, the New Zealand event was unlike that in North America because there were no 'pivotal megaherbivores', whose removal could result in environmental changes sufficient to precipitate the extinction of other species (Owen-Smith, 1987). In New Zealand, humans could directly affect the environment on a large scale, in a short time.

Several hypotheses on the causes of extinctions in the avifauna have been proposed, including genetic degradation (Oliver, 1949), habitat change caused by changing climate (Falla, 1955), and combinations of these (Williams, 1962). Genetic degradation is unlikely to have affected an entire fauna of diverse phylogenetic stocks. Most of the fauna survived through the great climatic fluctuations of the Pleistocene, and small relict populations of species such as the snipe (*Coenocorypha aucklandica*) and the merganser (*Mergus australis*) survived into European times on islands. Evidence for massive habitat degradation during Polynesian times is overwhelming (McGlone, 1983) and most extinctions can be dated with reasonable certainty to the period after human colonisation. Williams (1962) was wrong in assuming that "the changes in the past 160 years were greater and more sudden than those of the previous 1600 or so". The conclusion is inescapable that the extinctions resulted from the manifold effects of human colonisation (Fleming, 1953, 1962; Cumberland, 1962; Cassels, 1984).

In summarising the decline of species in the European period, Williams (1962) overlooked the possibility that different groups in the avifauna could be vulnerable to different environmental stresses. The view that all species react in the same way to habitat loss and mammalian predation is implicit in most of

the literature on extinctions in New Zealand. Each species has, of course, its own 'Achilles heel', but groups of species can be discerned which have similar vulnerability to environmental disturbances. The most vulnerable species group had been exterminated by 1769 AD; and forms lost since then were those which had been able to cope with the environmental disturbances associated with Polynesian culture, but not those brought by Europeans. The present avifauna consists largely of the most resilient species, usually the most recent colonists from Australia and elsewhere.

Event structure

This view requires that the extinction event involved two or more 'pulses' as different groups of species became extinct at different times in response to different environmental stresses. By tracking the extinctions through time, the vulnerability of each species and group to various contemporary factors can be inferred. The first pulse coincided with the introduction of three mammalian predators; *Rattus exulans*, *Canis domesticus*, and humans. These arrived in a land in which the birds were not used to mammalian predation, and depended for food on a ground fauna which was itself highly susceptible to predation. The second extinction pulse involved birds which were less immediately affected by mammalian predators, but more vulnerable to habitat destruction. The fauna was already depauperate when Europeans arrived, but there was yet another pulse of extinctions under the onslaught of cats (*Felis catus*), two more rats (*R. norvegicus* and *R. rat/us*), and mammalian herbivores (bovids, marsupials) and omnivores (*Sus*). The combined effects of habitat loss and predation would probably have driven some species, such as takahe (*Porphyrio mantelli*) and kakapo (*Strigops habroptilus*), to extinction even if Europeans had not arrived.

Until many more dates of last occurrence are available, the species comprising the groups associated with each extinction pulse can only be inferred. I suggest that Group I includes species vulnerable to predation by kiore (snipe, wrens, rails); large, meaty species of open habitats (swan, *Cnemiornis*); and those of the more open eastern forests (moas, adzebill, *Cnemiornis*) whose behaviour and generally low population densities made them particularly susceptible to human hunting. Similarly, Group II includes species (e.g. moas) susceptible to continued human and dog predation, and gross loss of habitat, and those which depended

on the diminishing supply of large and small prey (the raptors, raven, and perhaps moa chicks).

Group III species - saddleback (*Philesturnus carunculatus*), kokako (*Callaeas cinerea*), piopio (*Turnagra capensis*), and bush wren (*Xenicus longipes*) – appear to have been susceptible to predation by the two Eurasian rats, cats, mustelids, and perhaps to competition from mammalian herbivores. Although the moas constituted a guild of terrestrial browsers, there were no terrestrial grazers to compete with takahe as do cervids today (Mills and Mark, 1977), so takahe were vulnerable to competition as well as mammalian predation. Hunting pressure was probably responsible for their original decline. R.J. Rowe (pers. comm.) has suggested that Group III species lived in denser, wet forests, and were comparatively safe until the Polynesians, who were reluctant to enter dense forest, began to clear it in the later stages of occupation (e.g., Best, 1942; McGlone, 1983). When metal axes became available, the Polynesians cleared dense forest to cultivate potato (*Solanum tuberosum*) (McGlone, 1983). Later, Europeans cleared much of the remaining lowland forest for livestock farming and introduced new predators, and the extinction rate accelerated again.

The laughing owl (*Sceloglaux albifacies*) was also lost in European times, although its numbers had been declining before then, at least in the North Island (Williams and Harrison, 1972). Large beetles could have been important in its diet, and perhaps bats and small birds. The rats reported from castings in the 19th Century were a relatively new item in the diet. Bats were probably important before they too declined.

Predators and the avifauna

The laughing owl survived into the 20th Century, but three other avian predators had gone extinct before Europeans arrived. The absence of two of these from the present fauna has led to fundamental misconceptions about the environment under which the flightless birds of New Zealand evolved. Haast's eagle and the goshawk were the largest of their kinds anywhere in the world. With the falcon, they constituted a guild of predators capable of exploiting the whole size range of prey, from wrens to the largest moa. New Zealand's avifauna did *not* evolve in the absence of predators, but only in the absence of mammalian predators. There was ample selection pressure for traits such as cryptic colouration and nocturnal habits (kiwi (*Apteryx* spp.), kakapo, kea, and kaka).

For example, the kakapo, is a large, terrestrial herbivore which exploits higher quality parts of the plant, such as shoots and young leaves. It has a lek breeding system (Merton *et al.*, 1984) because preferred food plants are dispersed, and carrying capacity of the habitat limited. It was probably constrained to being a nocturnal lek species by predation from the goshawk. Lek birds elsewhere, such as grouse in North America, are diurnal, but they are exposed to mammalian predators at night as well as diurnal raptors. Kakapo were abundant in areas subjected to little predation pressure from dense human populations in 'Classic' Polynesian times (post 1600 AD) but they declined dramatically after nocturnal mammalian predators such as cats were introduced.

Faunistics and biogeography

There were gains as well as losses in the avifauna during the Polynesian period, as well as since Europeans arrived. New niches resulting from changes in vegetation during the Polynesian period allowed new species to colonise from Australia. Several species, such as the morepork (*Ninox novaeseelandiae*) and harrier (*Circus approximans*), are rare or absent in pre-human deposits. Others, such as the grey teal (*Anas gibberifrons*) have been assumed to be recent colonists, although their remains have been found in deposits dating from pre-Polynesian times. Still others (pied stilt *Himantopus leucocephalus*, black-backed gull *Larus dominicanus*) have increased in abundance since Europeans arrived. Clearly, not all the members of the present fauna have been here since at least the end of the last (Otiran) glaciation. That misconception has led to the use of *current* species lists in biogeographical studies. It is not surprising that the extinct species are ignored when the 1970 checklist relegates species known only as sub fossils to an appendix (Kinsky, 1970).

The most frequent application of island biogeographic theory in New Zealand has been in reserve design (e.g., Hackwell, 1982; East and Williams, 1984). This use is now being questioned (Williams, 1984; Boecklen, 1986; Zimmerman and Bierregaard, 1986). Species-area relationships based on drastically altered and incomplete lists provide a poor basis for management decisions, and the ecology of a threatened species is perhaps a better measure of the suitability of a projected reserve. A knowledge of the environment and assemblage in which the species evolved is fundamental to any study of its ecology. Ecological and biogeographical studies of the common

species in the present avifaunas are not very useful bases for management of the endemic forms endangered now. Similarly, discussions on the comparative effects of moas, ungulates, and climate on the evolution of New Zealand vegetation must be based on an understanding of the palaeo-environment and the ecology of the species living at that time.

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References

- Anderson, A.J. 1983. Habitat preferences of moa in central Otago, A.D. 1000-1500, according to palaeobotanical and archaeological evidence. *Journal of the Royal Society of New Zealand* 12: 321-336.
- Anderson, A.J. 1984. The extinction of moa in southern New Zealand. In: Martin, P.S.; Klein, R.G. (Editors). pp 741-67. *Quaternary extinctions: a prehistoric revolution*. Tucson, University of Arizona Press.
- Atkinson, I.A.E. 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. In: Dingwall, P.R.; Atkinson, I.A.E. (Editors) pp. 7-31. The ecology and control of rodents in New Zealand Nature Reserves. *New Zealand Department of Lands and Survey Information Series No.4*. 237 p.
- Atkinson, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, In: Moors, P.J. (Editor). pp. 35-81. *Conservation of island birds*. International Council for Bird Preservation Technical Publication No.3.
- Best, E. 1942. *Forest lore of the Maori*. Dominion Museum Bulletin No. 14.
- Boecklen, W. J. 1986. Effects of habitat heterogeneity on the species-area relationships of forest birds. *Journal of Biogeography* 13: 59-68.
- Bull, P.C.; Whitaker, A.H. 1975. The amphibians, reptiles, birds, and mammals. In: *Biogeography and ecology in New Zealand*. Kuschel, G. (Editor). pp. 231-76. The Hague, Dr W. Junk.
- Burrows, C.J.; McCulloch, B.; Trotter, M.M. 1981. The diet of moas based on gizzard contents samples from Pyramid Valley, North Canterbury, and Scaifes Lagoon, Lake Wanaka, Otago. *Records of the Canterbury Museum* 9: 309-336.
- Campbell, D.J.; Moller, H.; Ramsay, G.W.; Watt, J.C. 1984. Observations on foods of Kiore (*Rattus exulans*) found in husking stations on northern offshore islands of New Zealand. *New Zealand Journal of Ecology* 7: 131-8.
- Cassels, R. 1984. The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific Islands. In: Martin, P.S.; Klein, R.G. (Editors). pp. 741-67. *Quaternary extinctions: a prehistoric revolution*. Tucson, University of Arizona Press.
- Crook, I.G. 1973. The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale). *Proceedings of the New Zealand Ecological Society* 20: 115-20.
- Cumberland, K.B. 1962. 'Climatic change' or cultural interference? In: McCaskill, M. (Editor) pp. 88-142. *Land and livelihood*. Christchurch, New Zealand Geographical Society.
- Daniel, M.J. 1979. The New Zealand short-tailed bat, *Mystacina tuberculata*; a review of present knowledge. *New Zealand Journal of Zoology* 6: 357-70.
- Duff, R. 1964. Thomas Cawthron Memorial Lecture No. 38: The problem of moa extinction. Nelson, Cawthron Institute. 27 p.
- East, R.; Williams, G.R. 1984. Island biogeography and the conservation of New Zealand's indigenous forest-dwelling avifauna. *New Zealand Journal of Ecology* 7: 27-35.
- Falla, R.A. 1955. Cawthron Lecture: Past and present changes in New Zealand bird life. In: Cawthron Institute, Nelson, New Zealand, Annual Report 1953-54. pp. 30-1.
- Fleming, C.A. 1953. Materials for a Recent geochronology of New Zealand. In: Black, M.A. (Editor) pp. 114-123. Report of the Seventh

- Science Congress, Christchurch, May 15-21, 1951. Christchurch, Royal Society of New Zealand.
- Fleming, C.A. 1962. The extinction of moas and other animals during the Holocene period. *Notornis* 10: 113-17.
- Hackwell, K.R. 1982. The island biogeography of native forest birds and reserve design. In: Owen, J.M. (Editor). pp. 28-41. *Proceedings of a workshop on a biogeographic framework for planning an extended national parks and reserves system*. Department of Lands and Survey, Reserves Series No. 10.
- Hamel, G. 1979. The breeding ecology of moas. In: Anderson, A. (Editor). pp. 25-52. *Birds of a feather: osteological and archaeological papers from the South Pacific in honour of R.J. Scarlett*. New Zealand Archaeological Monograph 11, BAR International Series 62.
- Herd, R.M.; Dawson, T.J. 1984. Fiber digestion in the emu, *Dromaius novaehollandiae*, a large bird with a simple gut and high rates of passage. *Physiological Zoology* 57: 70-84.
- Hill, J.E.; Daniel, M.J. 1985. Systematics of the New Zealand short-tailed bat *Mystacina* Gray, 1843 (Chiroptera: Mystacinidae). *Bulletin of the British Museum Natural History (Zoology)* 48: 279-300.
- Holdaway, R.N. 1988. The New Zealand passerine checklist: what if Sibley and Ahlquist are right? *Notornis* 35: 63-70.
- Kinsky, F.C. 1970. *Annotated checklist of the birds of New Zealand*. Wellington, Ornithological Society of New Zealand, A.H. & A. W. Reed.
- McCulloch, B. 1977 (unpublished). Faunal remains from a cave at Waikari, North Canterbury. BSc Honours project, Department of Zoology, University of Canterbury, Christchurch. New Zealand.
- McGlone, M.S. 1983. Polynesian deforestation of New Zealand: a preliminary synthesis. *Archaeology in Oceania* 18: 11-25.
- Martin, P.S.; Klein, R.G. (Editors) 1984. *Quaternary extinctions: a prehistoric revolution*. Tucson, University of Arizona Press. 892 p.
- Meads, M.J.; Walker, K.J.; Elliott, G.P. 1984. Status, conservation, and management of the land snails of the genus *Powelliphanta* (Mollusca: Pulmonata). *New Zealand Journal of Zoology* 11: 277-306.
- Merton, D.V. 1975. The saddleback: its status and conservation. In: Martin, R.D. (Editor). pp. 61-74. *Breeding endangered species in captivity*. London, Academic Press. 420 p.
- Merton, D.V.; Morris, R.B.; Atkinson, I.A.E. 1984. Lek behaviour in a parrot: the Kakapo *Strigops habroptilus* of New Zealand. *Ibis* 126: 277-83.
- Millener, P.R. 1981 (unpublished). The Quaternary avifauna of the North Island, New Zealand. PhD thesis, Department of Geology, University of Auckland, Auckland, New Zealand. 897 p.
- Millener, P.R. 1981 (unpublished). The Quaternary avifauna of the North Island, New Zealand. PhD thesis, Department of Geology, University of Auckland, Auckland, New Zealand. 897 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.
- Mills, J.A.; Williams, G.R. 1979. The status of endangered New Zealand birds. In: Tyler, M. (Editor) pp. 147-68. *The status of endangered Australasian wildlife*. Adelaide, Royal Society of South Australia.
- Molloy, B.P.J. 1971. Possibilities and problems for nature conservation in a closely settled area. *Proceedings of the New Zealand Ecological Society* 18: 25-37.
- Mosimann, J.E.; Martin, P.S. 1977. Simulating overkill by Paleoindians. *American Scientist* 63: 304-13.
- Oliver, W.R.B. 1949. The moas of New Zealand and Australia. *New Zealand Dominion Museum Bulletin No. 15*: 206 p.
- Olson, S.L. 1975. The fossil rails of C.W. De Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland. *Emu* 75: 49-54.
- Olson, S.L.; James, H.F. 1982a. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by Man before Western contact. *Science* 217: 633-35.
- Olson, S.L.; James, H.F. 1982b. Prodrum of the fossil avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology No. 365*.
- Owen-Smith, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* 13: 351-62.
- Potts, T.R. 1882. *Out in the open: a budget of scraps of natural history gathered in New Zealand*. Christchurch, Lyttelton Times. Reprinted by Capper Press, Christchurch, 1976.
- Rich, T.H.V.; Rich, P.V.; Fordyce, R.E.; Gatehouse, P.; Scarlett, R.J. 1979. A deceptive terrestrial vertebrate site on the Waipara River, North Canterbury, New Zealand. In: Anderson,

- A. (Editor). pp. 25-52. *Birds of a feather: osteological and archaeological papers from the South Pacific in honour of R.J. Scarlett*. New Zealand Archaeological Monograph II, BAR International Series 62.
- Ridpath, M.G. 1964. The Tasmanian native hen. *Australian Natural History* 14: 346-50.
- Sibley, C.G.; Ahlquist, J.E. 1985. The phylogeny and classification of the Australo-Papuan passerine birds. *Emu* 85: 1-14.
- Smith, K.M. 1986 (unpublished). The diet of the ship rat, *Rattus rattus* L., in a kauri forest in Northland, New Zealand. MSc thesis, Department of Zoology, University of Canterbury. Christchurch, New Zealand. 152 p.
- Towns, D.R.; Daugherty, C.H.; Newman, D.G. 1985. An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). In: Grigg, G.; Shine, R.; Ehmann, H. (Editors). pp. 107-15. *Biology of Australasian frogs and reptiles*. Chipping Norton, New South Wales, Surrey Beatty and The Royal Zoological Society of New South Wales.
- Trotter, M.M.; McCulloch, B. 1984. Moas, men, and middens. In: Martin, P.S.; Klein, R.G. (Editors). pp. 741-67. *Quaternary extinctions: a prehistoric revolution*. Tucson, University of Arizona Press.
- van Tets, G.F. 1969. Pelican. In: Frith, H.J. (Editor) pp. 44-5. *Birds of the Australian high country*. Sydney, A.H. & A.W. Reed.
- Watt, J.e. 1975. XIII. The terrestrial insects. In: Kuschel, G. (Editor) pp. 507-35. *Biogeography and ecology in New Zealand*. The Hague, Dr W. Junk.
- Whitaker, A.H. 1973. Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). *Proceedings of the New Zealand Ecological Society* 20: 115-20.
- Williams, G.R. 1962. Extinction and the land and freshwater-inhabiting birds of New Zealand. *Notornis* 10: 15-32.
- 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, G.R.; Harrison, M. 1972. The Laughing Owl *Sceloglaux alhilacies* (Gray, 1844): a general survey of a near-extinct species. *Notornis* 19: 4-19.
- Worthy, T.H., 1987a. Osteology of *Leiopelma* (Amphibia: Leiopelmatidae) and descriptions of three new subfossil species. *Journal of the Royal Society of New Zealand* 17: 201-51.
- Worthy, T.H. 1978b. Osteological observations on the larger species of the skink *Cyclodina* and the subfossil occurrence of these and the gecko *Hoplodactylus duvaucelii* in the North Island, New Zealand. *New Zealand Journal of Zoology* 14: 219-29.
- Zimmerman, B.L.; Bieeregaard, R.O. 1986. Relevance of the equilibrium theory of island biogeography and species-area relationships to conservation with a case from Amazonia. *Journal of Biogeography* 13: 133-43.

Appendix 1: Systematic list of genera of birds breeding in New Zealand, excluding Antarctica and the Kermadecs, before 900 AD, with losses pre- and post-European contact.

	No. of genera	No. of species	Extant (%) 'Cook'	Extant (%) today
Dinomithiformes				
Dinomithidae	1/0/0	3	0 (0)	0 (0)
<i>Dinornis</i>		3	0	0
Anomalopterygidae	5/0/0	8	0 (0)	0 (0)
<i>Anomalopteryx</i>		1	0	0
<i>Megalopteryx</i>		1	0	0
<i>Emeus</i>		1	0	0
<i>Pachyornis</i>		3	0	0
<i>Euryapteryx</i>		2	0	0
TOTAL	6/0/0	11	0 (0)	0 (0)
Apterygiformes				
Apterygidae	1/1/1	3	3 (100)	3 (100)
<i>Apteryx</i>		3	3	3
TOTAL	1/1/1	3	3 (100)	3 (100)

Sphenisciformes					
Spheniscidae	3/3/3	6	6 (100)	6 (100)	
<i>Megadyptes</i>		1	1	1	
<i>Eudyptula</i>		1	1	1	
<i>Eudyptes</i>		4	4	4	
TOTAL	3/3/3	6	6 (100)	6 (100)	
Podicipediformes					
Podicipedidae	1/1/1	2	2 (100)	2 (100)	
<i>Podiceps</i>		2	2	2	
TOTAL	1/1/1	2	2 (100)	2 (100)	
Procellariiformes					
Diomedeidae	2/2/2	8	8 (100)	8 (100)	
<i>Diomedea</i>		7	7	7	
<i>Phoebastria</i>		1	1	1	
Procellariidae	6/6/6	24	24 (100)	24 (100)	
<i>Macronectes</i>		1	1	1	
<i>Daption</i>		1	1	1	
<i>Pterodroma</i>		8	8	8	
<i>Pachyptila</i>		4	4	4	
<i>Procellaria</i>		4	4	4	
<i>Puffinus</i>		6	6	6	
Hydrobatidae	3/3/3	3	3 (100)	3 (100)	
<i>Garrodia</i>		1	1	1	
<i>Pelagodroma</i>		1	1	1	
<i>Fregatta</i>		1	1	1	
Pelecanoididae	1/1/1	2	2 (100)	2 (100)	
<i>Pelecanoides</i>		2	2	2	
TOTAL	12/12/12	37	37 (100)	37 (100)	
Pelecaniformes					
Pelecanidae	1/0/0	1	0 (0)	0 (0)	
<i>Pelecanus</i>		1	0	0	
Sulidae	1/1/1	1	1 (100)	1 (100)	
<i>Sula</i>		1	1	1	
Phalacrocoracidae	3/3/3	6	6 (100)	6 (100)	
<i>Phalacrocorax</i>		3	3	3	
<i>Leucocarbo</i>		2	2	2	
<i>Stictocarbo</i>		1	1	1	
TOTAL	5/4/4	8	7 (88)	7 (88)	
Ciconiiformes					
Ardeidae	3/3/2	4	4 (100)	4 (100)	
<i>Egretta</i>		2	2	2	
<i>Botaurus</i>		1	1	1	
<i>Ixobrychus</i>		1	1	0	
TOTAL	3/3/2	4	4 (100)	3 (75)	
Anseriformes					
Anatidae	12/5/4	16	8 (50)	7 (44)	
<i>Cygnus</i>		1	0	0	
<i>Cnemiornis</i>		2	0	0	
<i>Tadorna</i>		1	1	1	
<i>Anas</i>		4	4	4	
<i>Hymenolaimus</i>		1	1	1	
<i>Aythya</i>		1	1	1	
<i>Euryanas</i>		1	0	0	
<i>Pachyanas</i>		1	0	0	
<i>Mergus</i>		1	1	0	
<i>Malacorhynchus</i>		1	0	0	
<i>Biziura</i>		1	0	0	
<i>Oxyura</i>		1	0	0	
TOTAL	12/5/4	16	8 (50)	7 (44)	

Falconiformes				
Accipitridae	4/1/1	5	1 (20)	1 (20)
<i>Circus</i>		1	1	1
<i>Harpagornis</i>	1	1	0	0
<i>Accipiter</i>		2	0	0
<i>Haliaeetus</i>		1	0	0
Falconidae	1/1/1	1	1 (100)	1 (100)
<i>Falco</i>		1	1	1
TOTAL	5/2/2	6	2 (33)	2 (33)
Galliformes				
Phasianidae	1/1/0	1	1 (100)	0 (0)
<i>Coturnix</i>		1	1	0
TOTAL	1/1/0	1	1 (100)	0 (0)
Gruiformes				
Rallidae	8/4/4	12	8 (67)	7 (58)
<i>Rallus</i>		1	1	1
<i>Gallirallus</i>		3	3	2
<i>Porzana</i>		2	2	2
<i>Porphyrio</i>		2	2	2
<i>Gallinula</i>		1	0	0
<i>Fulica</i>		1	0	0
<i>Capellirallus</i>		1	0	0
<i>Diaphorapteryx</i>	1	1	0	0
Aptornithidae	1/0/0	1	0 (0)	0 (0)
<i>Aptornis</i>		1	0	0
TOTAL	9/4/4	13	8 (62)	7 (54)
Charadriiformes				
Haematopodidae	1/1/1	3	3 (100)	3 (100)
<i>Haematopus</i>		3	3	3
Charadriidae	3/3/3	4	4 (100)	4 (100)
<i>Charadrius</i>		2	2	
<i>Thinornis</i>		1	1	1
<i>Anarhynchus</i>		1	1	1
Scolopacidae	1/1/1	2	1 (50)	1 (50)
<i>Coenocorypha</i>		2	1	1
Recurvirostridae	1/1/1	2	2 (100)	2 (100)
<i>Himantopus</i>		2	2	2
Stercorariidae	1/1/1	1	1 (100)	1 (100)
<i>Catharacta</i>		1	1	1
Laridae	1/1/1	3	3 (100)	3 (100)
<i>Larus</i>		3	3	3
Sternidae	1/1/1	5	5 (100)	5 (100)
<i>Sterna</i>		5	5	5
TOTAL	9/9/9	20	19 (95)	19 (95)
Columbiformes				
Columbidae	1/1/1	1	1 (100)	1 (100)
<i>Hemiphaga</i>		1	1	1
TOTAL	1/1/1	1	1 (100)	1 (100)
Psittaciformes				
Cacatuidae	1/1/1	1	1 (100)	1 (100)
<i>Strigops</i>		1	1	1
Nestoridae	1/1/1	2	2 (100)	2 (100)
<i>Nestor</i>		2	2	2
Platycercidae	1/1/1	3	3 (100)	1 (100)
<i>Cyanoramphus</i>		3	3	3
TOTAL	3/3/3	6	6 (100)	6 (100)

Cuculiformes				
Cuculidae	2/2/2	2	2 (100)	2 (100)
<i>Chrysococcyx</i>		1	1	1
<i>Eudynamys</i>		1	1	1
TOTAL	2/2/2	2	2 (100)	2 (100)
Strigiformes				
Strigidae	2/2/1	2	2 (100)	1 (50)
<i>Ninox</i>		1	1	1
<i>Sceloglaux</i>		1	1	0
TOTAL	2/2/1	2	2 (100)	1 (50)
Caprimulgiformes				
Aegothelidae	1/0/0	1	0 (0)	0 (0)
<i>Megaegotheles</i>		1	0	0
TOTAL	1/0/0	1	0 (0)	0 (0)
Coraciiformes				
Alcedinidae	1/1/1	1	1 (100)	1 (100)
<i>Halcyon</i>		1	1	1
TOTAL	1/1/1	1	1 (100)	1 (100)
Passeriformes				
Acanthisittidae	5/3/2	7	4 (57)	2 (29)
<i>Acanthisitta</i>		1	1	1
<i>Xenicus</i>		2	2	1
<i>Traversia</i>		1	1	0
<i>Pachyplichas</i>		2	0	0
N. gen. 1		1	0	0
Meliphagidae	3/3/3	3	3 (100)	3 (100)
<i>Notiomystis</i>		1	1	1
<i>Anthornis</i>		1	1	1
<i>Prothemadera</i>		1	1	1
Acanthizidae	1/1/1	2	2 (100)	2 (100)
<i>Gerygone</i>		2	2	2
Eopsaltriidae	1/1/1	3	3 (100)	3 (100)
<i>Petroica</i>		3	3	3
Corvidae	7/6/4	10	9 (90)	6 (60)
<i>Turnagra</i>		2	2	0
<i>Mohoua</i>		3	3	3
<i>Rhipidura</i>		1	1	1
<i>Corvus</i>		1	0	0
<i>Philesturnus</i>		1	1	1
<i>Heteralocha</i>		1	1	0
<i>Callaeas</i>		1	1	1
Sylviidae	1/1/1	1	1 (100)	1 (100)
<i>Megalurus</i>		1	1	1
Ploceidae	1/1/1	1	1 (100)	1 (100)
<i>Anthus</i>		1	1	1
TOTAL	19/16/13	27	23 (85)	18 (69)
GRAND TOTAL	97/69/65	168	132 (78)	124 (74)
(without seabirds)	82/54/50	125	89 (71)	81 (65)

Notes: 'No. of genera' is given as number in pre-human fauna/number at time of Captain Cook's first voyage/number in present fauna. Extant 'Cook' is the number of species in fauna at time of Cook's first voyage.

2. Extinct: 6 families, 32 genera, 44 species. Evidence is lacking for early occurrence of *Gerygone*, *Halcyon*, and *Porphyrio melanotus* (T. Worthy, pers. comm. They are treated here as having been present).

3. Passerine classification is after Sibley and Ahlquist (1985) and Holdaway (1988).