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The Causes of Avian Extinction and Rarity

by

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Declaration:

I certify that this thesis results from my original investigation, except where acknowledged, and has not been submitted for a degree at any other university.

Christopher J. Lennard

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Then God said, "Let us make man in our image, in our likeness, and let them rule over the fish of the sea and the birds of the air, over all the livestock, over all the wild animals, and over all the creatures that move on the ground."

Genesis 1: 26 (New International Version of the Bible)

Abstract

Biological extinction rates have escalated by as much as 1000 times the background extinction rate over the last 1500 years, causing concern over the long-term survival of many species. Avian extinctions since 1600 have been well documented relative to other taxa, as have current levels of avian threat. This study analyses avian extinctions post-1600 and current threats in an attempt to develop some predictive capacity about which avian taxa should be awarded the highest conservation priority.

Analyses performed include examinations of the causes of avian extinction and threat, geographical location of extinct and threatened species, prehistoric and historical extinction rates, endemicity, migration, bird body size and phylogenetic diversity. An analysis dealing with historical and phylogenetic aspects of endangered and critically threatened species was performed, from which the world's most threatened species were identified. Factors which were the primary cause of historical extinctions are generally not the primary factors threatening today's extant avifauna. Whilst introduced predators and exploitation were primary causes of historical extinctions, habitat destruction poses the greatest threat to extant birds. Species predisposed to extinction typically have restricted ranges, and, compounded by habitat loss, these ranges are becoming more restricted. This has resulted in mainland-dwelling species becoming as prone to extinction as island-dwelling species have been historically. Introduced predators, however, do still threaten many of the world's most threatened species and their potential effects are highlighted in the phylogenetic analysis.

Already, many extinctions may be inevitable over the next 25 years as a result of habitat loss. The magnitude of extinctions across all animal and plant species in the next few decades could be comparable with that of previous mass extinctions unless immediate conservation action is taken. However, future conservation efforts will have to be prioritized, and this study is intended as a contribution towards such a prioritization exercise.

Chapter One: Introduction and methods.

Part 1 - Introduction

It is estimated that the 1.4 - 1.8*10^6 species of living organisms described to date may represent less than 15% of the world's biodiversity (Raven and Wilson 1992). This figure does not take into account the vast number of micro-organisms that are still to be described. The lack of knowledge of biodiversity is especially marked in the tropics, where most species occur and where the rates of extinction and form creation (*sensu* Balon 1993) appear to be the highest.

While there may be as many as 40*10^6 extant species of plants and animals, between 5 - 50*10^9 species are likely to have existed in the past, representing a 99.9% extinction rate (Raup 1992). Extinction is thus a natural and vital component of evolution. Diamond (1984a) breaks extinction into two extremes:

1. Dramatic and sudden extinction due to some clearly identifiable event, impinging on many species as a wave of extinctions.
2. "Normal" extinctions that affect populations isolated on islands or disjunct patches of habitat. This eliminates populations one by one rather than as a wave of extinctions.

Extinction can be either phyletic or terminal (Ehrlich and Ehrlich 1981, Soulé 1983). Phyletic extinction occurs when, through the process of evolution and adaptive radiation, a parental species is replaced by one or more derivative species. Terminal extinction occurs when there is no derivative species following the extinction of a unique species. These species become extinct either because they do not evolve rapidly enough to meet changing circumstances or because niches disappear and no capacity for rapid evolution could save them (Smith 1989).

Ehrlich *et al.* (1977) estimated the average species' lifespan of vertebrates at between

200 000 and 2 000 000 years, giving a background extinction rate of 0.2 to 2 species per million species per year. This rate has apparently increased by 1000 to 10 000 fold due to anthropogenic impacts (Wilson and Peter 1988), although some authors dispute this: (Budiansky 1994, Simon 1995, Simon and Wildavsky 1993). Various estimates of global extinction rates project annual losses of between 1000 and 30 000 species by the end of this century (Reid and Miller 1989, Ehrlich and Wilson 1991, Wilson 1992).

The next mass extinction?

There have been at least five mass extinctions in the past 440 million years: at the close of the Ordovician (438 mya), Devonian (360 mya), Permian (248 mya), Triassic (213 mya) and Cretaceous (65 mya) periods, when the number of families of some marine organisms declined by 12, 14, 52, 12 and 11% respectively (Wilson 1989). Wilson (*op. cit.*) states that although 90% of past species extinctions occurred at times other than these five, mass extinctions have a profound biological significance through their impact on selection regimes. Simberloff (1984, 1986a) questions if we are not at the beginning of the next mass extinction, the causes of this mass extinction being anthropogenic. Diamond (1989) and Pimm (1995) not only suggest that this is occurring, but also that it has been under way for thousands of years.

Wilson (1989) estimated that as many as 4 000 to 6 000 species per year may be being lost from tropical rain forests alone and that man-induced extinction rates may reduce current biodiversity to its lowest level since the end of the Mesozoic era, 65 million years ago. These rates of extinction are far higher than those suggested in the IUCN Red List (Groombridge 1993). Over the last decade, upwards of 20 000 species have been listed as being at risk by one or more prominent conservation organisations (McNeely *et al.* 1990, WRI 1990, Smith *et al.* 1993a).

Smith *et al.* (1993a,b) calculated that about 486 animal species have become extinct since 1600 AD. In the latest IUCN Red list of Threatened Animals (Groombridge 1993), 615 species are reported to have become extinct since 1600. This figure includes 83 mammals, 114 birds, 20 reptiles, four amphibians, 36 fishes and 358 invertebrates. Humphries and

Fisher (1994) have suggested that there was a sharp increase in the rate of animal extinctions between 1850 and 1950, which coincided with the rise of European colonial expansion and the use of natural resources to fuel the industrial revolution (Smith *et al.* 1993b); a direct correlation exists between the total amount of energy consumed by mankind and animal extinction rates (Ehrlich 1994). Ehrlich (*op.cit*) further contends that total energy consumption could be used as an index of global extinction rates, and predicts that these rates could be far higher than present estimates suggest: 30 years to the extinction of 50% of all species of mammals and birds.

Other estimates of the rate of biotic extinction over the next 50-100 years range from 15-20% of present biodiversity (Mace 1994) to 25% (Nicholson 1991) and 50% (Smith *et al.* 1993b). These rates approach that required to generate a genus-level extinction at a scale equivalent to and perhaps surpassing some of the largest mass extinctions in history (Ehrlich 1986). Although today's extinction patterns conform mainly to greatly intensified versions of background extinction rates, losses are concentrated in narrowly endemic species and subspecies (Jablonski 1994), which inhabit primarily tropical regions (Simberloff 1986a).

The loss of species is not the only consequence of extinctions. Theoretical and empirical data now exist which show that ecosystems in the tropics not only contain more species but also a richer network of interactions between species, and that they are more dynamically fragile than higher-latitude systems (reviewed by May 1981; Bruton 1989, 1990). These systems are characterised by high biotic saturation and strong interspecific interactions such as symbioses, commensalism, parasitism, hyperparasitism and communal broodcare (Ribbink *et al.* 1983, Ribbink 1994). Naeem *et al.* (1994) demonstrated that (under controlled, experimental conditions) the loss of biodiversity could alter or impair the services that ecosystems provided (Ehrlich and Wilson 1991). The stable productivity of ecosystems is dependent upon the preservation of biodiversity in these systems (Tilman and Downing 1994). An extinction of one species in a complex system could lead to an "extinction cascade" which in turn could threaten much of the biodiversity within the system (Diamond 1989, Williamson 1989).

Extinctions therefore result in the loss of both species and life-supporting interactions between species, with a resultant cascading effect on taxa that were not originally impacted. The mature successional state of tropical systems, which typically includes a high proportion of specialised, precocial species, tends to be reversed by man's perturbations, with the result that more generalised, altricial species survive (Bruton 1989). Furthermore, the precocial species that have been lost will not be replaced by other specialist species because their respective specialisations are too great to allow interchangeability (Hsu 1982). Instead, the niches of extirpated species may be adopted by altricial species that are generalists, and the complex interactions between specialist species may disappear.

Birds and extinction

A primary aim of conservation is to reduce the rate at which the world's biological diversity is being lost. *Inter alia* this requires developing predictions about which taxa are most at risk and why. Various approaches have been used, including measures of genetic variability and Minimum Viable Population analysis. An alternative approach is to analyse the reasons why species have become extinct or are facing imminent extinction.

Avian extinctions since 1600 are well documented by comparison with other taxonomic groups (Jenkins 1992) and the threats posed to extant species are well catalogued in the Red Data Books (e.g. Collar and Andrews 1988, Collar *et al.* 1994). Thus, birds lend themselves well to this type of analysis.

This thesis examines avian extinctions since 1600 and the types of threat currently faced by bird species. Specifically, the study addresses the following questions:

1. Which bird species have become extinct since 1600?
2. What were the causes of these extinctions, and did these change over time? What are the current causes of threat to avifauna?
3. How has the rate of species extinction changed over time?
4. Where did species become extinct and are there extinction "hotspots"? How do these compare with threat "hotspots"?

5. What factors or combination of factors predispose birds to extinction; e.g. range size and endemicity, body size, flight capabilities, specific threats or combinations thereof?
6. How do the attributes of species currently threatened with extinction compare to those that have already become extinct?
7. Based on the above, which avian species are potentially at greatest risk of global extinction?

Thesis structure

The thesis is divided into four chapters:

Chapter 1: The introduction and methods. Included here are a literature review, data collection procedure, and data analysis techniques.

Chapter 2: Avifaunal extinctions. The chapter is divided into a results section and a discussion section. The chronology, causes, geography and taxonomy of extinct birds are dealt with as well as migration, endemicity and body size. The discussion section considers in addition these, prehistoric extinctions.

Chapter 3: Current threats to avifauna. The chapter is divided into a results and discussion section which consider cause, geography, taxonomy, endemicity, body size and habitat of currently threatened species.

Chapter 4: This chapter draws together prehistoric and historical extinction, and current threat in terms of cause, geography and taxonomy in order to attempt to answer question seven above. A phylogenetic analysis is presented as one means of prioritising threatened species within threat categories.

Part 2 - Methods

Extinction literature

The primary sources of extinction information were six books and a list supplied via the Internet by the Worldwide Fund for Nature (Table 1).

Table 1. Sources used in gathering extinction data.

Author (s)	*Date*	*Title*	*Number of extinct species listed*
1. Clements, F. J.	1991	Birds of the World: A Check List	60
2. Collar, N.J., Crosby, M.J. and Stattersfield, A.J.	1994	Birds to Watch 2. A Checklist of Threatened Birds	14
3. Day, D.	1989	The Encyclopaedia of Vanished Species	92
4. Fuller, E.	1987	Extinct Birds	86
5. Greenway, J.C.	1967	Extinct and Vanishing Birds of the World	51
6. Mountfort, G.	1988	Rare Birds of the World	75
7. W.W.F.	1994	No Title	97

Although Fuller (1987) and Day (1989) are semi-popular publications, these were used in compiling the database of extinct species because they detailed causes of extinction more often than other sources and also listed species not listed in other sources. Fuller (1987) is reviewed by Brooke (1988).

Comparison of data from these sources revealed the following:

1. The number of sources listing any one extinction varies greatly; 32 extinctions were listed by only one of the sources. Only two extinctions were listed by all seven sources. However, Collar *et al.* (1994) listed only 14 of the most recent extinctions and, excluding this publication, 24 species are listed by all six sources.
2. Each source, except Greenway (1967) and Collar *et al.* (1994), list species that are unique to it (Table 2). These species form 23% of the dataset.

3. There was much discrepancy in allocating species and subspecies amongst the sources; this problem is discussed below. (Zink and McKitrick (1995) highlight current concepts of species and the implications of these to ornithology).

Table 2. The number of extinct avifauna unique to respective authors.

Author	*Non-passerines*	*Passerines*	*Total*
1. Clements (1991)	1	3	4
2. Day (1989)	16	1	17
3. Fuller (1988)	0	1	1
4. Mountfort (1967)	2	1	3
5.W.W.F. (1994)	5	2	7
Total	24	8	32

Threat literature

Collar *et al.* (1994) list 1111 avian species that are considered globally threatened. These are divided into four categories: extinct in the wild, critically endangered, endangered and vulnerable: there are 4, 168, 235 and 704 species in each respective category. According to the new IUCN criteria (Collar *et al.* 1994), critically endangered species stand a 50% chance of extinction in five years, endangered species a 20% chance of extinction in 20 years and vulnerable species a 10% chance of extinction in 100 years. It is thus more difficult to allocate a species to endangered or critical status as compared with vulnerable (Fig. 1).

A species listed as extinct in the wild is known to survive only in captivity or as a naturalised population (or populations) well outside the historical range. The four species falling in this category are the Alagoas Curassow *Mitu mitu*, the Guam Rail *Gallirallus owstoni*, the Socorro Dove *Zenaida graysoni* and the Kakapo *Strigops habroptilus*. I have grouped "extinct in the wild" and "critical" together to make analysis easier, thus listing 172 species as critically threatened. Alison Stattersfield (BirdLife International) supplied a dataset that was used in the threat analyses.

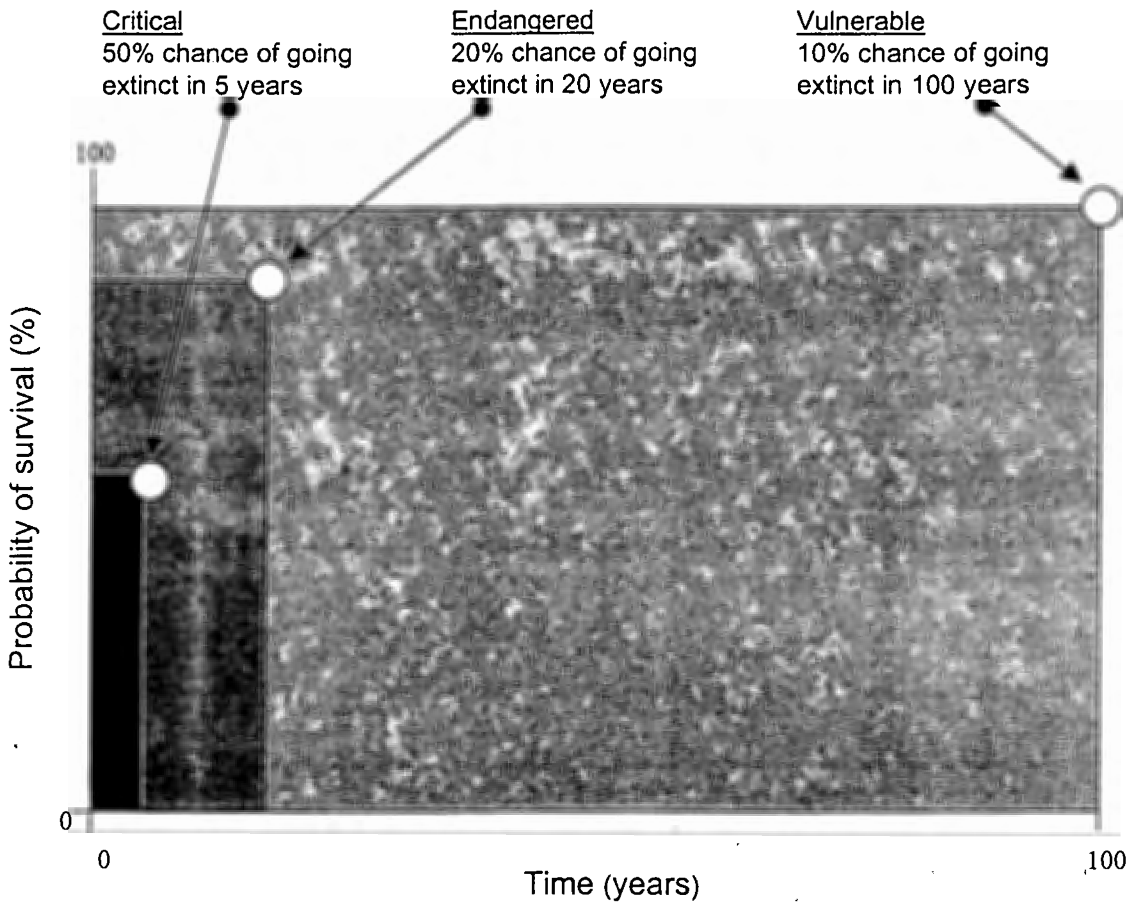


Fig. 1. Extinction probabilities and the IUCN threat categories. This representation indicates the relative difficulty (represented by the relatively small, dark rectangles enclosed by the threshold lines) of qualifying as endangered and, especially, critical, compared with vulnerable (light, pale rectangle). (From Collar *et al.* 1994).

Data analysis

i. Extinction data

Data for extinct species were extracted from the seven sources and compiled into one dataset. The compilation of this dataset took into account repetition of species by different authors and synonyms in nomenclature. There were difficulties encountered in allocating taxa to species as distinct from subspecies.

Distinguishing between species and subspecies

Initially the database contained 214 species and subspecies that the various sources listed as extinct. Three authors list subspecies: Day (1989) - 53, Greenway (1967) - 44 and Fuller (1987) - 41. Fuller also lists 29 races, resulting in his listing 70 taxa below the species level. Often, what one author called a species, another called a subspecies or race. For instance, Fuller (1987) considered the New Zealand Little Bittern *Ixobrychus minutus novaezelandiae* distinct only at the subspecies level whereas Mountfort (1988) and WWF. accorded it specific status *Ixobrychus novaezelandiae*; Greenway (1967) treated the New Zealand Quail as a subspecies *Coturnix novaezelandiae novaezelandiae* whereas Day (1989), Mountfort (1988), Fuller (1987) and the WWF. treated it specifically as *Coturnix novaezelandiae.* In these and other such cases, the following criteria were applied to determine if a taxon was included in the species list:

1. If there was a trinomial scientific name it was treated as a subspecies and not included.
2. If one source named a bird a subspecies and more than one source called the same bird a species, the classification supported by the most sources was used.
3. In the case where an equal number of sources were in disagreement, the most recent reference was used.

All scientific names are found in the appendices if not mentioned in the text.

Data compilation

All extinction data were compiled into two datasets. These datasets held information as follows:

- A dataset with information on species extinctions (Appendix 1).
- A dataset with information on subspecies extinctions (Appendix 2).

These datasets hold information on species/subspecies classification and nomenclature, bird body mass, extinction location, most recognised extinction date, extinction causes and a reference section. Sub-specific data are presented for completeness but are not included in analyses nor are body masses given for these.

Chronology of extinction

The time period from 1600 to present was divided into eight 50-year time intervals; 1600-1649, 1650-1699 etc. The year of each extinction was placed into the appropriate 50-year interval together with information concerning the causes of extinction. This enabled an analysis of the rate of extinction with time and an examination of the most important causes of extinction during a specific time period. Patterns of change in causes of extinction over time were derived from this database. Data were analysed for (1) species occurring on both islands and the mainland regions, (2) island species only and (3) mainland species only.

Causes of extinction

Temple (1978, 1986) and Simberloff (1986b) make a distinction between two types of cause of extinction, the "proximate" cause of extinction and the "ultimate" cause of extinction. Proximate causes are those which caused the death of the last remaining individuals of the species. This contrasts with the ultimate cause of extinction, which refers to events that may have occurred earlier, and led to a situation in which there would be a small, terminal population committed to extinction. In this analysis both proximate and ultimate causes are considered.

Diamond (1984b, 1989) classified known causes of extinction into four categories which he termed "the evil quartet". These were:

1. Overkill;
2. Habitat destruction and fragmentation;
3. Impact of introduced species; and
4. Chains of extinction or "extinction cascades".

I have used the first three of Diamond's categories and adapted their nomenclature in order to use them in conjunction with the threat causes listed in Collar *et al.* (1994). As a result I identified five general causes of recent avian extinctions. These were:

1. Exploitation (Ex.): Includes the hunting of birds and eggs for food; taking of birds, feathers, and eggs for trade or collection; persecution for various reasons.
2. Habitat destruction (H.D.): Includes fire, destruction of indigenous forest for logging/slash-and-burn agriculture, removal of forests for large scale crop and livestock farming, destruction of forest to make way for urban development.
3. Introduced predators (I.P.): Includes cats, rats, dogs, and a snake species. Man introduced these either accidentally or deliberately.
4. Other (O): Seven species fell into this category, the causes being:
   a. competition with man for marine invertebrates;
   b. disease introduced by alien birds; and
   c. competition with introduced alien birds for a common resource.
5. Unknown (?): The definite reasons for many extinctions are unknown, especially those occurring from 1600-1750. In here may be included the fourth of Diamond's "evil quartet".

Frequently, a combination of the above factors has caused extinctions, e.g. in the case of the Passenger Pigeon *Ectopistes migratorius* it was the combined effects of the loss of its natural habitat and severe hunting that brought this species to extinction (Bucher 1992). These were perhaps ultimate and proximate causes respectively. When there was a combination of causes it was listed as e.g. (HD/Ex.), (HD/IP) or (Ex/IP).

Geography of extinction

To investigate the geography of extinctions, islands and mainland (continental) regions were compared to determine which have experienced the most extinctions. An oceanic perspective of island extinctions was obtained by dividing the oceans of the world into the northern and southern Pacific, northern and southern Atlantic and the southern Indian Ocean (north and south being divided at the Equator). The positions and sizes of islands in these regions were assessed to determine location and size of the most affected regions and islands. A map showing global extinction density was produced. Extinctions of passerine and non-passerine species on the islands in the various regions were analysed to determine whether the different orders experienced different levels of extinction in the different regions.

Phylogeny of extinction

Avian orders and families were examined to determine if certain of these were more extinction prone than others. Orders that experienced the most extinctions were examined in greater detail. At the family level, families that experienced the most extinctions were listed and comparisons were drawn with families that have a large percentage of threatened species. Statistical analyses were performed to assess whether family diversity was linked in any way to extinction probabilities.

Body size

Gaston and Blackburn (1995) state that it seems likely that body size may be used as a pointer to recognise which species are most at risk of extinction. Body sizes of species were used, where data were available, to determine if this was true for extinct species. As no sources listed data as to bird body size, Dunning (1993) was used to extract data on bird body mass. Dunning (*op. cit.*) listed very few extinct birds and in general, body masses of extinct species had to be inferred. This was done by examining species of the same genus and comparing body sizes with data contained in Fuller (1987) on bird length. If no comparison with Fuller (1987) could be made, the body sizes of all species listed in the affected genus was averaged. In doing this all but 14 extinct species were assigned a body mass. This is a very conservative methodology. However, it was selected as being one which would tend to mask rather than exaggerate body-size effects. A chronological analysis was performed to determine if, in certain time periods, birds of particular sizes were more prone to extinction than at other times. An analysis to examine whether a relationship existed between bird body size and island size was also carried out.

ii. Threat data

Analysis of threatened taxa are based upon the data provided by Alison Stattersfield (BirdLife International) and information contained in Collar *et al.* (1994).

Data compilation

Threatened species listed by Collar *et al.* (1994) were separated into their threat categories (critically threatened [including the four "extinct in the wild" species], endangered and vulnerable). Details of extant avian orders, families and species of the world were extracted from Clements (1991) and Monroe and Sibley (1993). Clements (1991), although a popular birdwatchers' checklist, was used for the following reasons: Dunning (1993) used it as the taxonomic basis for his analysis and there was greater agreement as to taxon placement between Clements (1991) and Collar *et al.* (1994), particularly at the order and family level. Similarly, the sources from which the extinction data were obtained generally followed the older taxonomic treatment. Using both sources aided in analyses of threat to families and where there are differences, these are noted. There are taxonomic differences between Monroe and Sibley (1993) and Clements (1991) and these are summarised in Table 3.

Monroe and Sibley (1993) (hereafter M&S) list 23 orders containing 9702 species whereas Clements (1991) lists 31 orders containing 9455 species. M&S is based on Sibley and Ahlquist (1990) and Sibley and Monroe (1990), a classification derived from DNA-DNA hybridization. However, this classification is criticised by many authors; Sibley and Ahlquist (1990) by Raikow (1991), Krajewski (1991), O'Hara (1991) and Peterson (1992), and Sibley and Monroe (1990) by Siegel-Causey (1992). Siegel-Causey (1992) notes that Sibley and Monroe (1990) base their results on about 12% of avian species, inferring relationships for the other 88% in their classification, which he claims would be better termed an "arrangement". Clements (1991) bases his specific treatment on Sibley and Monroe (1990) but uses Gill (1990) for higher taxonomy, which is more conservative. Clements (1991) and M&S were used jointly in this threat analysis. Where discrepancies arose, this is noted and numbers of species in affected families compensated for.

Table 3. Summary of taxonomic nomenclature differences between Monroe and Sibley (1993) and Clements (1991)

Clements (1991)	Monroe and Sibley (1993)	Orders listed by Clements which Monroe and Sibley subsume as families in their classification	Orders listed by Monroe and Sibley which Clements subsumed as families in his classification
Orders (31)	Orders (23)		
Tinamiformes	Tinamiformes		
Struthiorniformes	Struithioniformes	Struthioniformes	
Rheiformes		Rheidae	
Casuariiformes		Casuariidae	
Dinornithiformes		Dinornithiformes as Apterygidae	
Ciconiiformes	Ciconiiformes	Ciconiiformes	
		Under sub-order Charadrii	
Charadriiformes		Charadriidae	
Pteroclidiformes		Pteroclidae	
		Under sub-order Ciconii	
Sphenisciformes		Spheniscidae	
Podicipediformes		Podicipedidae	
Procellariiformes		Procellariidae	
Pelecaniformes		Pelecanidae	
Phoenicopteriformes		Phoenicopteridae	
Falconiformes		Falconidae	
Gaviiformes		Gaviidae	
Anseriformes	Anseriformes		
Galliformes	Galliformes		
Gruiformes	Gruiformes		
Columbiformes	Columbiformes		
Psittaciformes	Psittaciformes		
Coliiformes	Coliiformes		
Musophagiformes	Musophagiformes		
Cuculiformes	Cuculiformes		
Strigiformes	Strigiformes	Strigiformes	
Caprimulgiformes		Caprimulgidae	
Apodiformes	Apodiformes		
Trochiliformes	Trochiliformes		
Trogoniformes	Trogoniformes		
Coraciiformes	Coraciiformes		
Piciformes	Piciformes		
	Turniciformes		Turnicidae under Gruiformes
	Craciformes		Cracidae under Galliformes
	Bucerotiformes		Bucerotidae under Coraciifromes
	Upupiformes		Upupidae under Coraciiformes
	Galbuliformes		Galbulidae under Piciformes
Passeriformes	Passeriformes		

Using these data, comparisons were drawn between orders and families that contained threatened species and those that did not. A comparison was also made between those orders and families that have experienced extinction of species and those that have not. In these comparisons, it was taken into account whether species were to be found on the mainland only, on islands only, or on both.

Causes of threat

Collar *et al.* (1994) list ten causes of threat to birds. These are:

0. Unknown;
1. Loss or alteration of habitat;
2. Hunting, persecution (including accidental trapping), egg collecting (subsistence);
3. Disturbance (by humans, stock);
4. Fisheries;
5. Pollution, pesticides, poisoning (accidental);
6. Introduced species (predators, competitors, herbivores, diseases);
7. Trade, egg collecting (commercial);
8. Natural causes (exacerbated by other influences); and
9. Small range or population.

I have summarised these into the same five categories as used for extinctions in order to make comparisons between the historical causes of extinction and current causes of threat: causes 1 and 3 above were included in habitat alteration, 2 and 7 were included in exploitation, 4 and 5 were included in "other" and 8 and 9 are discussed below. The threat from introduced vertebrates differs from the definition of "introduced predators" as used for extinctions in that it does not take into account only the effect of predators. For extinctions, where introduced vertebrates were not predators, they were listed as "other" in order to isolate the specific influence of predators on avian extinction.

In a number of cases, especially in the case of critical and endangered species, a main threat (habitat destruction, introduced predators or exploitation) appeared together with natural causes (exacerbated by other causes) and/or small ranges or populations (causes 8 and 9 above). In cases where natural causes and/or small range or populations accompanied the main causes; the main causes were considered as being the most important threats and are used in the analysis. Where natural causes and/or small range or populations were the only threat, the affected species were placed in the "other" category.

The number of species in each category of threat (critical, endangered and vulnerable) impacted by the above five threat types were arranged to show the following:

- the number of threatened species per family
- the number of species that fell into each of the three threat categories
- the number of species threatened by a particular threat type or combination of threats.

Using the above data, the most important threats were identified for (1) all threatened species, (2) only endangered species, and (3) only critically endangered species.

Geography of threat

A comparison between the number of threatened species found on islands, mainland areas and those inhabiting both was made. Threats were analysed to give an overview of which threats are most prevalent in the three respective range types.

The geographical distributions of endangered and critically endangered species were investigated in more detail. In these analyses the format used by Collar *et al.* (1994) was adopted in defining geographical regions. These regions were North America, Central America, South America, Africa, "Russia", Asia and Australasia.

Countries and islands in these regions supporting endangered or critically threatened birds were identified and geographical comparisons were made between species with island and mainland ranges that fell within these two threat categories. Global threat density maps for the two categories were produced. Threat to endangered and critically threatened locally endemic species was also examined because it is over these species that much concern is expressed (e.g. Balmford and Long 1994, Pimm and Askins 1995).

Taxonomy of threatened species

Family sizes were examined to test whether there is any relationship between family size and the number of threatened species. Families with 20% of their species under threat were listed. Families with only critical and/or endangered species were also examined.

Habitats of threatened birds

More taxa are under threat in forests than in other habitats (Simberloff 1984, Diamond 1989, Balmford and Long 1994, Pimm and Askins 1995, Pimm *et al.* 1995, Brooks and Balmford 1996). Consequently, special attention was paid to the number of threatened species that live exclusively or partially in forests. This was done for all threat categories together to produce an overall picture, and subsequently for each category on its own to assess what proportions of forest-dwelling species are vulnerable, endangered and critical.

Body size, endemicity, threat and extinction on ten selected islands

Ten islands of various sizes accounting for a range of endemic avifauna were selected to test whether a relationship existed between body size, endemicity, threat and extinction. Analyses were done for all endemic species and then only critical and endangered endemic avifauna. Correlations between the causes of extinction and current threat on these islands were made to determine if relationships between these existed. A coarser scale analysis was also performed to determine the distribution of extinct, extant and critical and endangered endemic avifauna on the ten islands.

iii. Prehistoric extinctions, historical extinctions and current threat

A comparison was drawn between selected families that had experienced prehistoric extinctions (before 1600), historical extinctions (1600 to present) and which currently contain threatened species to test whether or not some families are more prone to extinction than others. The data were also used to assess whether certain families had passed through an "extinction filter" (*sensu* Balmford 1996).

iv. Phylogenetic analysis

Collar *et al.* (1984) use a classification approach that treats all species as equal. They apply the same criteria on which they base their results in the same way equally to all species. They do not attempt to consider species or family history or phylogeny in their approach and are thus not able to include any element of phylogenetic uniqueness in their threat status assessment.

The last section of this thesis attempts to include an element of "evolutionary uniqueness" using the species listed by Collar *et al.* (1994). This analysis considers (1) the historical predisposition of a family to extinction, (2) the proportion of the family under threat and (3) the phylogenetic uniqueness of the family.

Chapter Two: The extinction of avifauna since 1600.

Part 1 - Results

Since 1600, a minimum of 214 species and subspecies of birds have become extinct. Applying the criteria for species status listed in the methods section, this list is reduced to 138 avian species. Appendix 1 lists these species by order and family. This forms 1.44% of the total number of avian species known to have existed from that time. Of these extinctions, 124 were island taxa, 12 species had exclusively mainland distributions and two extinctions were of species that had ranges spanning both islands and mainland. Appendix 2 lists the remaining 76 cases classified at the level of subspecies or race.

Chronology of extinction

From 1600 there was an escalating extinction rate until 1950 (Table 4). Since 1950 there has been a marked drop in extinction rate: 12 species having become extinct, this being the lowest extinction rate in the last 200 years. This rate is the same as in each of the two 50-year intervals between 1649 and 1749. The lowest number of extinctions occurred in the first 50-year period from 1600 - 1650 (n=6). The period with the highest rate of extinction was 1900 - 1949 when 33 species became extinct. In the preceding 50 years, 26 extinctions occurred, this being the next highest rate. Forty percent of the bird extinctions since 1600 have occurred in the 20th Century.

Chronology of mainland extinctions

Twelve species have become extinct in mainland regions since 1600 (Table 5). The first documented mainland extinction was in 1800 when the Painted Vulture *Sarcorhamphus sacra* became extinct in Florida, USA (Day 1989). The most rapid mainland extinction rate occurred between 1900 and 1949 when five species (42% of mainland extinctions) became extinct. The next 46 years saw the next highest rate having three mainland extinctions (24%). Sixty-seven percent of all mainland extinctions have occurred during the 20th Century.

Chronology of island extinctions

One hundred and twenty four species have become extinct on islands since 1600 (Table 6). It is difficult to pinpoint the first extinction accurately; the only species for which there is a relatively precise date of extinction in the years 1600 - 1649 is the Greater Broad-billed Moa *Euryapteryx gravis* (1640). The remaining five species' extinction dates are not known precisely. The insular avian extinction rate peaked in the period 1900 - 1949, with 28 extinctions. The preceding half-century with 24 extinctions followed this. This 100-year year period accounted for 42% of insular extinctions. Since 1950 there has been a sharp reduction in island extinctions, only eight species having become extinct. One recent extinction date is unknown: that of Sharpe's Rail from Indonesia.

Table 4. A chronological analysis of the causes of avian extinctions since 1600.

For habitat type:

I	Island
M	Mainland
B	Both

For reasons

Ex	Exploitation of birds and/or eggs for food, trade or feathers and includes persecution.
H.D.	Habitat destruction
I.V.	Introduced predators (rats, cats, dogs, weasels)
O	Other (see text)

Date interval	Number of extinctions	Range type			Reasons									Totals
		I	M	B	Ex	H.D.	I.V.	HD and IV	HD and Ex	Ex and IV	Unknown	Other	Percent of total	
1600-1649	6	6							1		5		4.3	6
1650-1699	12	12			3				2		7		8.7	12
1700-1749	12	12			4		1				7		8.7	12
1750-1799	16	16			4	1	4		2		5		11.6	16
1800-1849	20	17	2	1	2	2	4	2	2		8		14.5	20
1850-1899	26	25	2		3	1	5	1	2	2	8	4	18.8	26
1900-1949	33	27	5		4	6	5	6	2		8	2	23.9	33
1949-1995	12	8	3	1		4	5		1		1	1	8.7	12
Dates unknown	1	1									1		0.7	1
Causes for both	2				1				1				1.4	2
Totals	138	124	12	2	20	14	24	9	12	2	50	7	100	138
Percentages	100	90	9	1	14	10	17	7	9	1	36	5		100

Table 5. A chronological analysis of mainland avian extinctions in species since 1600.

Date interval	Ex	H.D.	Ex and H.D.	H.D. and I.V.	Unknown	Percentages	Totals
1800-1849		1			1	17	2
1850-1899					2	17	2
1900-1949	1	1	1	1	1	42	5
1950-1995		3				25	3
Totals	1	5	1	1	4		12
Percentages	6	28	6	6	22	100	67

Table 6. A chronological analysis of the causes of avian extinctions on islands since 1600.

Date interval	Number of extinctions	Range types			Reasons									
		I	M	B	Ex	H.D.	I.V.	HD and IV	HD and Ex	Ex and IV	Unknown	Other	Percent of total	Totals
1600-1649	6	6							1		5		5	6
1650-1699	12	12			3				2		7		10	12
1700-1749	12	12			4		1				7		10	12
1750-1799	16	16			4	1	4		2		5		13	16
1800-1849	20	17	2	1	1	1	4	2	2		7		14	17
1850-1899	27	25	2		3	1	5	1	2	2	6	4	19	24
1900-1949	32	27	5		3	5	5	5	1		7	2	23	28
1949-1995	12	8	3	1		1	5				1	1	6	8
Unknown cause	1	1									1		0	1
Cause for "both"	2				1				1					
Totals	138	124	12	2	18	9	24	8	10	2	46	7	100	124
Percentages	99	89	9	1	15	7	19	6	8	2	37	6	100	89

Causes of extinction

Introduced predators, exploitation, habitat destruction and combinations thereof have accounted for 58% of avian extinctions since 1600 (Table 4). The causes of 50 (36%) extinctions are unknown. These are likely, however, to include the above factors which were either not observed or recorded by explorers and biologists of the day. Single factors as sole causes of extinction have been identified for 58 species and 23 species were affected by a combination of factors. During the 20th Century, 24 extinctions were caused by one factor only (habitat destruction and introduced predators alone accounted for 10 each) and nine extinctions were a result of a combination of factors. The causes of nine 20th Century extinctions are unknown. In the last 46 years, eight extinctions were caused by one factor only and three by combinations of factors (one cause is unknown).

Introduced predators such as cats, dogs, a snake species, weasels and especially rats have been the sole cause of the extinction of 24 species, and in combination with habitat destruction and exploitation, introduced predators have accounted for the loss of a further 11 species. Exploitation of birds for food and/or feathers has caused 20 extinctions and in combination with the other factors, a further 14 species have been affected. Habitat destruction has resulted in 14 extinctions; and, in conjunction with the other two factors has contributed to a further 21 extinctions.

Seven species have become extinct for reasons that could not be incorporated into the main three categories. The extinction of the Canarian Black Oystercatcher *Haematopus meadewaldoi* was caused by competition with man for marine invertebrates (Hockey 1987). In the Hawaiian islands, introduced birds brought with them avian malaria, and this, together with competition with indigenous birds for common resources caused the extinction of six Drepanididae species (Warner 1968).

Two single causes and two combinations of causes have been responsible for the 12 mainland extinctions (Table 5). Habitat destruction has accounted for five extinctions alone, and in combination with other causes, a further two extinctions. Of the species with known extinction causes, habitat destruction features in all mainland extinctions except one, the Carolina Parakeet *Conuropsis carolinensis* that became extinct through exploitation (hunting). Introduced predators have not been the sole cause of a single extinction on the mainland and feature in only one extinction.

The causes of insular extinctions (Table 6) are broadly the same as those for all extinctions. Insular extinctions, by virtue of their prevalence, shape the trend of all extinctions.

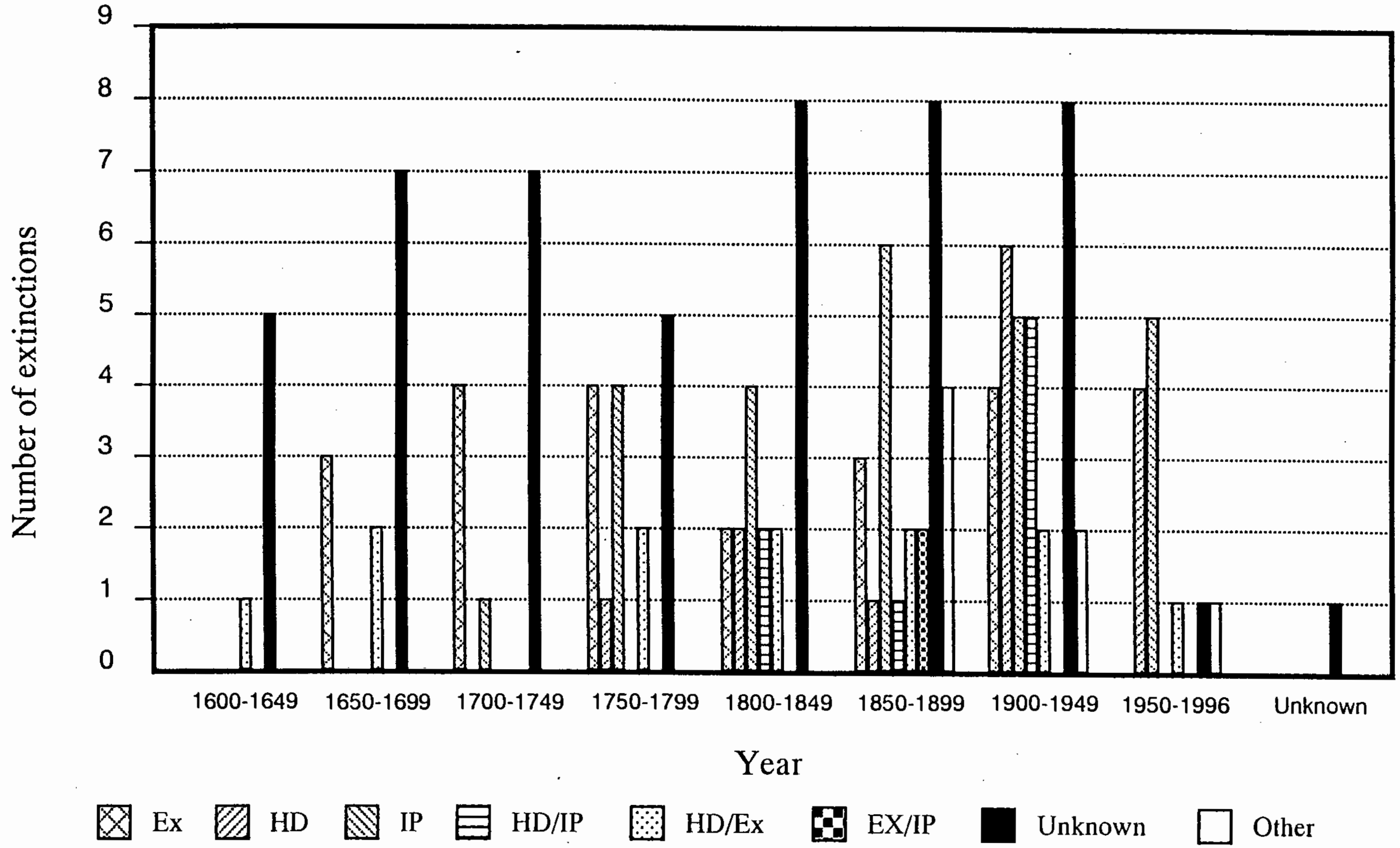
Cause and chronology

The cause and chronology of avian extinction are summarised in Fig. 2. Unknown causes dominate all the 50-year intervals except 1950-1995. During the period 1600-1800, exploitation was the most frequently identified cause of extinction. Introduced predators were first responsible for an extinction in 1700 and by 1799 had become, along with exploitation, the primary known cause of extinction. Introduced predators have remained the commonest cause of extinction until the present except in the time period 1900-1949 when habitat loss was equally serious. Only in the period 1900-1950 do recorded combinations of factors feature strongly together with single causes. In this period habitat destruction and introduced predators accounted for 16 extinctions, five being as a result of a combination of these, five being as a result of introduced predators alone and six as a result of habitat destruction alone. However, it is likely that combinations of causes also featured in extinctions prior to this but were not recognised as such.

Until 1900, there was a gradual increase in the diversity of causes that played a role in extinctions. Between 1850 and 1899 all eight of the causes and many combinations played a role. Between 1950 and 1996 five causes have been identified as causing extinction, introduced predators and habitat destruction featuring most prominently.

For mainland extinctions the period 1900-1949 had the highest number of extinctions as well as the greatest variety of causes (5). Since 1950 three mainland species have become extinct, all as a result of habitat destruction.

Fig. 2. The chronology and causes of avian extinctions since 1600



Geography of extinction

The 138 post-1600 global bird extinctions have occurred on 49 islands and in 11 mainland regions (Table 7). The Great Auk *Alca impennis* can not be attributed one island or mainland provenance as its range spanned most of the north Atlantic: this species was therefore excluded from geographic analyses. The Ivory-billed Woodpecker *Campephilus principalus*, the other species whose range included mainland and island habitat, occurred in Cuba and the USA. Both of these countries have experienced other extinctions and the species was included in the geographical analysis.

Of the 62 sites that have experienced extinctions, 41 experienced one extinction only. Thus 66% of sites experienced only 30% of the extinctions. Twenty-one sites (34%), all islands except Colombia, have experienced two or more extinctions and account for 90 extinctions (70%). Three or more extinctions were experienced at ten sites, all islands. These islands make up 16% of the total number of sites but account for 75 (54%) extinctions. Four islands experienced ten or more extinctions, affecting 49 species i.e. 6% of sites have experienced 36% of all extinctions.

Island location

New Zealand has experienced the most extinctions (16), ten of these being moa extinctions. Hawaii has suffered 12 extinctions, followed by the Mascarenes (Mauritius, Rodrigues and Réunion) with 11, 10 and nine extinctions respectively. (The only mainland country to have experienced more than one avian extinction is Colombia, with two.)

Regions that have experienced island extinctions are the northern and southern Pacific and Atlantic Oceans, and the southern Indian Ocean (Table 8). The southern Pacific region has seen the most extinctions, 43 species having been lost from 18 islands. Sixteen of these were on New Zealand. This is followed by islands in the southern Indian Ocean (39 extinctions on 6 islands) and the northern Pacific Ocean (31 extinctions on 15 islands). In the southern Indian Ocean region, 33 of the 39 extinctions were from the Mascarene Islands. In the northern Pacific, 17 of the 31 extinctions occurred on five islands in the Hawaiian Archipelago, 12 of these being on Hawaii (Fig. 3).

Island sizes

Table 9 compares the sizes of islands that have experienced extinctions. Islands of 100-200 km^2 have experienced the most extinctions (15 on six islands) followed by islands of sizes between 1 500-2 000 km^2. The number of extinctions in these two size ranges is not evenly spaced over the islands concerned. Ten of the 15 extinctions occured on Rodrigues island (in the 100-200 km^2 size category) and 11 on Mauritius (in the 1 500-2 000 km^2 range, within which there are 15 extinctions on five islands). Islands with areas smaller than 100 km^2 have experienced nine extinctions on six islands.

On a coarser island-size resolution, 32 extinctions (23%) have occurred on 17 islands which have a surface area of less than 500 km^2. In the area range 1 500-2 000 km^2, 16 extinctions have occurred on five islands, although within this island size range, 12 extinctions have occurred on two islands with areas between 1 800-1 900 km^2. (11 on Mauritius). Sixteen extinctions have also occurred on one of the larger islands, New Zealand. The next most affected island-size range are islands with areas of between 10 000-12 000 km^2, where three islands have experienced a total of 15 extinctions. Of these, Hawaii experienced 12 extinctions. Réunion and Ryukyu islands have areas between 2 000-3 000 km^2 and these have experienced the next highest number of extinctions with 11 (nine were on Réunion).

Table 7. Summary of the sites that have experienced avian extinctions since 1600 (Sources for island sizes are given in Table 8)

Place	Size (km^2)	# of extinctions
New Zealand	269000	16
Hawaii	10464	12
Mauritius	1865	11
Rodrigues Island	104	10
Réunion Island	2510	9
Chatham Island	960	4
Tahiti	238	4
Mascarene Islands	4479	3
Seychelles	404	3
Lord Howe Island	17	3
Madagascar	594180	2
Jamaica	10991	2
Ryukyu Islands	2196	2
Guadeloupe Island (West Indies)	1780	2
Molokai Island	676	2
Guadelupe Island (Mexico)	298	2
Raiatea Island	238	2
Kosrae Island	109	2
Peel and Bonin Islands	104	2
Norfolk Island	36	2
Colombia		2
Indonesia	1919445	1
Sumatra and Borneo	1219916	1
Java	130987	1
Cuba	114525	1
New Caledonia	19105	1
Fiji Islands	18330	1
Bahamas	11406	1
Canary Islands	7275	1
Kangaroo Island	4351	1
French Polynesia	3940	1
Society and Cook Islands	1880	1
Bering Island	1593	1
Oahu Island	1536	1
King Island	1098	1
Martinique Island	1079	1
Choiseul Island (Solomon Islands)	1000	1
Dominica	751	1
Aukland Island	606	1
Tanna Island	549	1
Laysan Island	500	1
Guam	450	1
Lanai Island	365	1
Grand Cayman Islands	220	1

Table 7 (cont.)

ohnpei Island	177	
Moorea	132	1
Bonin Island	93	1
Ascension Island	88	1
Wake Island	8	1
Stephen Island	2.6	1
Carolina, USA		1
Eastern Punjab, India		1
Eastern USA		1
Florida, USA		1
USA		1
New England, Canada		1
Mexico		1
Guatemala		1
Paraguay, Uruguay, Brazil, Argentina		1
Australia		1
North Atlantic islands, Canada, UK,		1
Denmark, Faeroe Islands, Greenland,		
Russia		
SE USA and Cuba		1
		138

Table 8. Regional summary of sites that have experienced avian extinctions since 1600.

The key to the symbols next to the island area column is at the end of the table and gives the source from which the island sizes were obtained.

N Pacific: (N of the Equator)	Number of extinctions	Area (km^2)	
Sumatra and Borneo	1	1219916	a,d
Hawaii Island	12	10464	e
Ryukyu Islands	2	2196	a
Bering Island	1	1593	c
Oahu Island	1	1536	e
Molokai Island	2	676	c
Laysan Island	1	500+	c
Guam	1	450	a
Lanai Island	1	365	c
Guadelupe Island (Mexico)	2	298	c
Pohnpei Island	1	177	b
Kosrae Island	2	109	c
Both Bonin and Peel islands	2	104	f
Bonin Islands	1	93	a
Wake Island	1	8	a
	31		

Passerines 21
Non-passerines 10

S Pacific: (S of Equator)			
New Zealand	16	269000	b
Java	1	130987	c
New Caledonia	1	19105	a
Fiji Islands	1	18330	a
Kangaroo Island	1	4351	c
French Polynesia	1	3940	a
Society and Cook Islands	1	1880	a
King Island	1	1098	c
Tahiti	4	1042	a
Choiseul Island (Solomon Islands)	1	1000	c
Chatham Island	4	960	b
Aukland Island	1	606	c
Tanna Island	1	549	c
Raiatea Island	2	238	a
Moorea	1	132	c
Norfolk Island	2	36	a
Lord Howe Island	3	17	c
Stephen Island	1	2.6	f
	43		

Passerines 10
Non-passerines 33

Table 8 (cont.)

N Atlantic islands:

Cuba	1	114525	a
Bahamas	1	11406	d
Jamaica	2	10991	c
Canary Islands	1	7275	a
Guadeloupe Island (West Indies)	2	1780	a
Martinique Island (WI)	1	1079	a
Dominica	1	751	a
Grand Cayman Islands	1	220	d
	10		

Passerines 1
Non-passerines 9

S Atlantic islands

Ascension Island (Non-passerine)	1	88	a

S Indian Ocean islands:

Indonesia	1	1919445	a
Madagascar	2	594180	a
All three Mascarene Islands	3	4479	a
Réunion	9	2510	a
Mauritius	11	1865	a
Seychelles	3	404	a
Rodrigues	10	104	a
	39		

Passerines 7
Non-passerines 32

Mainland

Australia	1
Eastern Punjab, India	1
Eastern USA	1
Carolina, USA	1
Florida, USA	1
USA	1
New England, Canada	1
Guatemala	1
Mexico	1
Colombia	2
Paraguay, Uruguay, Brazil, Argentina	1
	12

Passerines 3
Non-passerines 9

Table 8 (cont.)

Both mainland and island

SE USA and Cuba		1
N. Atlantic		1
		2
Passerines	0	
Non-passerines	2	

Totals:

Passerines	42
Non-passerines	96
	138

Reference key:

a	Times Atlas of the World (1975)
b	Graves (1990)
c	Goetz (1968)
d	Cook (1981)
e	Pratt *et al.* (1987)
f	Fuller (1987)

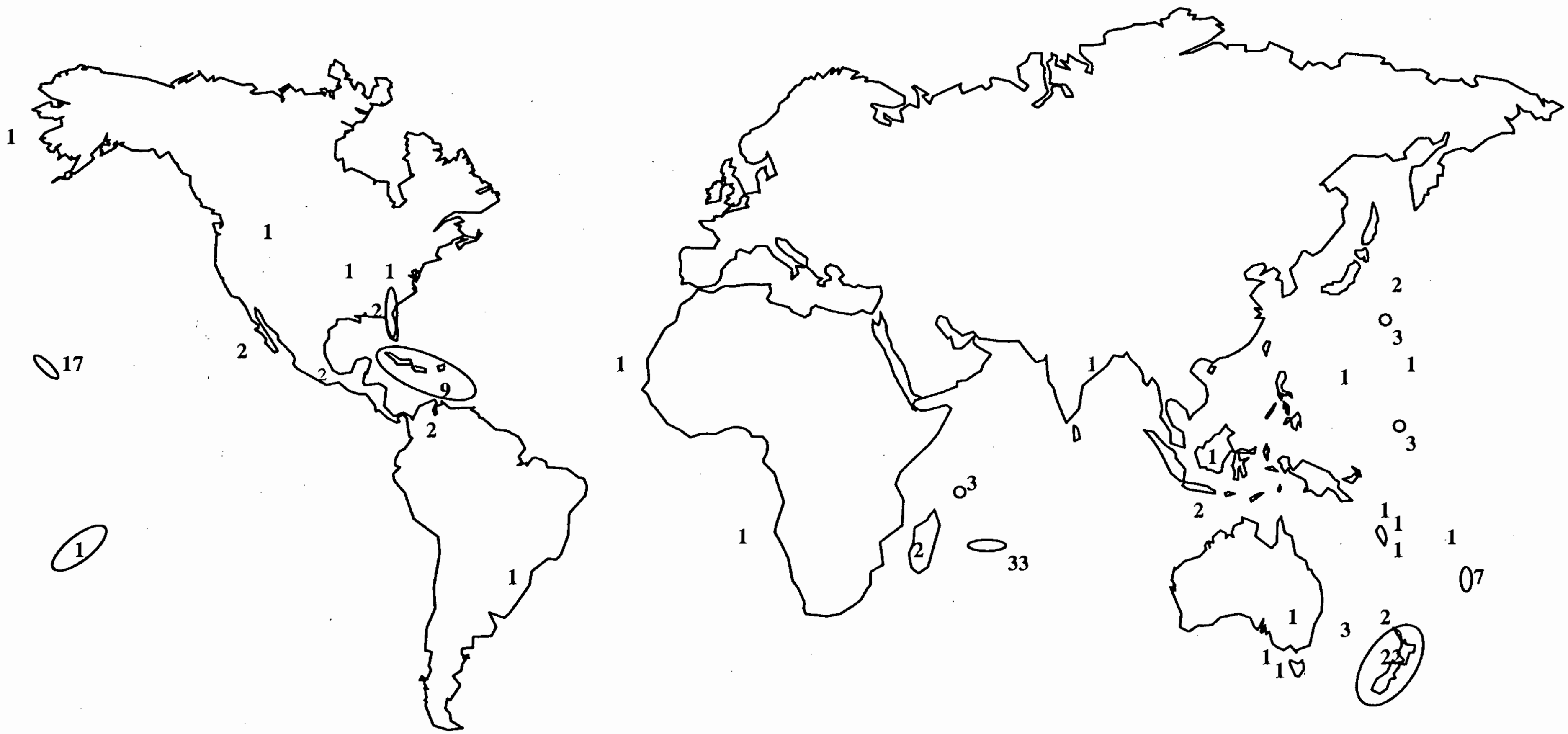


Figure 3. Global distribution of extinct avifauna represented as the number of species by locality

Table 9. Comparison between island size and extinction frequency

Island size (km^2)	Number of extinctions	Number of islands affected
0 - 100	9	6
100 - 200	15	5 (10 on Rodrigues)
200 - 300	3	3
300 - 400	1	Lanai
400 - 500	4	2
500 - 600	2	2
600 - 700	3	2
700 - 800	1	Dominica
800 - 900	0	0
900 - 1000	4	Chatham Island
1000 - 1500	7	4
1500 - 2000	16	5 (11 on Mauritius)
2000 - 3000	11	2 (9 on Réunion)
3000 - 10000	6	4
10000 - 12000	15	3 (12 on Hawaii)
18330	1	Fiji islands
19105	1	New Caledonia
114525	1	Cuba
130987	1	Java
269000	16	New Zealand
594180	2	Madagascar
1219916	1	Borneo and Sumatra
1919455	1	Indonesia

Endemicity

Of the 138 extinct species, perhaps only one was not endemic to a particular island or island group or to a localised mainland region. The Great Auk inhabited a region that stretched across the entire north Atlantic from Canada to Russia including Iceland, Greenland, Denmark, the Faeroe Islands, Funk Island and the UK (Fuller 1987). Some species inhabited an island group, amongst these being the Red-moustached Fruit Dove *Ptilinopus mercierii*, found on islands in French Polynesia and Grace's Emerald *Chlorostilbon bracei* in the Bahamas (IUCN e-mailed list). On the mainland, the Glaucous Macaw *Anodorynchus glaucus* was found in four countries in South America. In most cases, however, the species that became extinct were restricted to one island or country only. In only 24 cases did extinct species inhabit an island group, two or more islands in close proximity, or more than one country.

Migratory birds and extinction

Of the 138 extinctions, 133 species were non-migratory. Two species to have become extinct were almost certainly migratory, the Labrador Duck *Camptorhynchus labradorius* and the Passenger Pigeon (Fuller 1987). The Great Auk, the New Zealand Little Bittern *Ixobrychus novaezelandiae* and Townsend's Finch *Spiza townsendi* might have been migratory but there is little proof of this (Fuller 1987).

Phylogeny of extinction

Orders

Nineteen of the current avian orders (23 according to Monroe and Sibley (1993) and 31 according to Clements (1991)) have experienced historic extinctions. One order, the Aepyornithidae, has lost all it's species. The following section details extinction rates and causes of five orders that have experienced the highest number of extinctions. The orders examined are the Passeriformes (30% of all recent extinctions (n=42)), the Psittaciformes with (n=21), the Gruiformes (n=15), Columbiformes (n=12) and Dinornithiformes (n=10). Together, these orders account for 72% of all bird extinctions since 1600.

Passeriformes

The order Passeriformes hold the most families and species so it is not surprising that this order has experienced the most extinctions. It is best put into context when comparing all the species in the order that have become extinct since 1600 (42) with the number of species, extinct and extant, that have existed from 1600 (5781 - Monroe and Sibley 1993). These 42 extinct species thus account for only 0.73% of the Passeriformes that have existed since 1600, much less than the average of 1.44% for all bird species. Seven of the 12 extinctions that have occurred since 1950 have been passeriform and almost 50% of all passerine extinctions have occurred this century (Table 10). The highest rate of passerine extinction occurred between 1850 and 1949, however, when 25 species became extinct. The 19th Century saw 18 extinctions, only two less than the 20th Century. The period 1600-1799 saw only 4 passerine extinctions. This order contains seven of the nine most recent extinctions, all of which occurred on islands. The other two most recent extinctions are of Podicipediformes. Only three passerine species have been lost from mainland areas, one each in North, Central and South America, the two most recent being in 1910 and 1912. Of the 42 passerine extinctions, habitat loss features in 15 cases, introduced predators in 14, and the causes of 13 extinctions are unknown or uncertain. Exploitation is known to be the cause of only one extinction, the Huia *Heteralocha acutirostris* of New Zealand.

Table 10. Chronology of passeriform extinctions.

Date	'00 - '49	'50 - '99	Total
1600 - 1699	1	1	2
1700 - 1799	1	1	2
1800 - 1899	6	12	18
1900 - 1996	13	7	20

Psittaciformes

The highest extinction rate of psittaciforms occurred between 1750 and 1849 (Table 11). The 20th Century has seen only three psittaciform extinctions, all in mainland areas and each on a different continent. These are the only mainland extinctions in the order. There has not been a psittaciform extinction on an island since 1885 when the Cuban Red Macaw *Ara tricolor* became extinct. Of the 21 extinctions, exploitation and/or habitat destruction has featured in 13 cases. Introduced predators feature in four cases while the causes of seven extinctions are uncertain or unknown. Five percent of all Psittaciformes to have existed since 1600 have become extinct, almost 3.5 times the average for all bird species.

Table 11. Chronology of psittaciform extinctions.

Date	'00 - '49	'50 - '99	Total
1600 - 1699	0	1	1
1700 - 1799	1	6	7
1800 - 1899	5	5	10
1900 - 1996	2	1	3

Gruiformes

As with the passerines, the highest number of extinctions among the Gruiformes occurred between 1850 and 1949 (Table 12). The most recent extinction was in 1973 in Fiji, this also being the only gruiform extinction since 1945. All gruiform extinctions are from the rail family and all have occurred on islands. Introduced predators have featured in seven extinctions, exploitation in five and habitat destruction in three. Causes of two extinctions are uncertain or unknown. Of all the gruiform species that have existed since 1600, 7% have become extinct, almost 5 times the average for all birds. The date of one gruiform extinction (Sharpe's Rail *Rallus sharpei*) is unknown.

Table 12. Chronology of gruiform extinctions.

Date	'00 - '49	'50 - '99	Total
1600 - 1699	0	3	
1700 - 1799	1	0	1
1800 - 1899	2	2	4
1900 - 1996	5	1	6

Columbiformes

The period 1850-1950 saw the highest extinction rate amongst the Columbiformes when five species became extinct (Table 13). The 18th and 20th centuries have each experienced four extinctions. The most recent columbiform extinction, the island-dwelling Ryukyu Wood Pigeon *Columba jouyi*, occurred in 1936. Only one extinction in this order has occurred on the mainland, that being the extinction of the Passenger Pigeon in the southeastern USA. This order includes perhaps the most well known avian extinction, that of the Dodo *Raphus cucullatus*. Exploitation has been a cause of five extinctions (including the Dodo and Passenger Pigeon), introduced predators and habitat destruction have featured in four and three cases respectively, and the causes of a further two extinctions are unknown. Four percent of all columbiform species that existed since 1600 have become extinct, more than double the average for all birds.

Table 13. Chronology of columbiform extinctions.

Date	'00 - '49	'50 - '99	Total
1600 - 1699	0	1	1
1700 - 1799	2	2	4
1800 - 1899	2	1	3
1900 - 1996	4	0	4

Dinornithiformes

Over half of the dinornithiform (moa) extinctions occurred in the 18th Century (Table 14). Only one species has become extinct post-1765, the Lesser Megalapteryx *Megalapteryx didinus* (by 1850). The moas were endemic to New Zealand. Habitat destruction and exploitation are the documented causes of extinction for three of the ten species, the remaining seven causes being uncertain or unknown. Of all the dinornithiform species to have existed since 1600, 77% have become extinct. All three surviving relatives of the moas, the kiwis (Apterygidae), are endangered (Collar *et al.* 1994).

Table 14. Chronology of dinornithiform extinctions.

Date	'00 - '49	'50 - '99	Total
1600 - 1699	2	1	3
1700 - 1799	5	1	6
1800 - 1899	0	1	1
1900 - 1996	0	0	0

Families

Forty-five avian families have experienced extinctions, 16 passerine and 29 non-passerine. The families that have experienced the highest number of extinctions are the Psittacidae (20), Rallidae (15), Drepanididae (11) and Dinornithidae (10) (Table 15). In the most severely impacted orders it was characteristic that the extinctions were confined to only one family. This was completely true for the Gruiformes and Dinornithiformes where all extinctions were within the Rallidae and Dinornithidae respectively. It was 95% true for the Psittaciformes (one extinction not in the family Psittacidae), and 67% true for the Columbiformes (eight species of Columbidae becoming extinct and four (all) species of Raphidae).

Three families have lost all member species, the Dinornithidae (ten extinctions), the Raphidae (four extinctions) and the Aepyornithidae (one extinction). Two-thirds of the family Dromaiidae have become extinct and 40% of the family Acanthisittidae. There are only one and three extant species in each respective family, but these are not threatened. Thirty-five percent of the family Drepanididae have become extinct and, of the 21 extant species, 16 (76%) are threatened.

Proportional extinction rates are highest in small families. Of the 12 families that have lost over 10% of their species since 1600, only the Rallidae has more than 20 extant species. Larger families tended to experience a greater number of extinctions, e.g. the Psittacidae (20 extinctions), Rallidae (15), Columbidae (8) and Sturnidae (7), but the proportional extinction rate has been lower (except for the Rallidae).

Table 15. Listing of families showing (1) the number of species within each that have become extinct since 1600 and (2) the current threat situation of extant species.

Family	Number of species extinct	Percentage of species extinct	Number of Extinctions on islands	Percentage extinctions on islands	% of all species in the family to have become extinct since 1600	# of species currently threatened	# extant species in these families	% of species currently threatened
Psittacidae	20	14	17	85	5	88	349	25
Rallidae	15	11	15	100	11	32	132	24
Drepanididae	11	8	11	100	35	16	21	76
Dinornithidae	10	7	10	100	100	0	0	0
Columbidae	8	6	7	88	3	55	310	18
Sturnidae	7	5	7	100	6	7	144	5
Anatidae*	5	4	4	80	3	25	128	20
Meliphagidae	4	3	4	100	2	11	179	6
Ardeidae	4	3	4	100	6	7	65	11
Raphidae	4	3	4	100	100	0	0	0
Turdidae	3	2	3	100	2	32	176	18
Strigidae	3	2	3	100	4	20	155	13
Dromaiidae†	2	1	2	100	67	0	1	0
Podicepididae	2	1	0	0	10	4	22	18
Falconidae	2	1	2	100	3	6	62	10
Phasianidae	2	1	1	50	1	48	175	27
Scolopacidae	2	1	2	100	2	10	88	11
Tytonidae	2	1	2	100	11	5	17	29
Acanthisittidae	2	1	2	100	40	0	3	0
Sylviidae*	2	1	2	100	0	36	261	14
Zosteropidae	2	1	2	100	2	21	93	23
Emberizidae†	2	1	0	0	0	31	612	4
Pycnonotidae	2	1	2	100	2	12	138	9
Aepyornithidae	1	0	1	100	100	0	0	0

Table 15 (cont.)

Hydrobatidae	1	0	1	100	4	1	22	5
Procellariidae	1	0	1	100	1	27	78	35
Phalacrocoracidae	1	0	1	100	2	8	37	22
Ciconiidae	1	0	1	100	5	5	26	19
Threskiornithidae	1	0	1	100	3	7	33	21
Cathartidae*	1	0	0	0	13	1	7	14
Haematopodidae†	1	0	1	100	7	1	10	10
Alcidae*	1	0	0	0	4	1	22	5
Charadriidae	1	0	1	100	2	9	78	12
Lorridae	1	0	1	100	2	0	53	0
Cuculidae	1	0	1	100	1	8	78	10
Trochilidae	1	0	1	100	0	27	322	8
Alcedinidae	1	0	1	100	1	11	86	13
Pachycephalidae	1	0	1	100	2	0	59	0
Acanthizidae	1	0	1	100	100	0	34	0
Muscicipidae*	1	0	1	100	0	20	117	17
Picidae	1	0	0	0	0	8	216	4
Icteridae	1	0	0	0	1	8	97	8
Ploceidae	1	0	1	100	0	16	118	14
Fringillidae*	1	0	1	100	0	8	170	5
Callaeidae	1	0	1	100	33	1	2	50
Totals	138	100	124	90		633	4,492	14

* Monroe and Sibley (1993) classify this as a sub-family and Clements (1991) and Collar *et al.* (1994) a family.

† Monroe and Sibley (1993) classify this as a tribe and Clements (1991) and Collar *et al.* (1994) a family.

Body size and extinction

Body masses of extinct species were inferred from data contained in Dunning (1993) and are summarised in Appendix 1. For some species it was not possible to infer body mass with any confidence (these are marked "?" in Appendix 1) resulting in 126 species being included in this analysis. Although Appendix 1 lists 127 body masses, the extinction date of one species is not known and not included here. Body masses ranged from 3 g to 500 000 g with a median of 334 g.

Birds with masses between 10-30 g experienced the most extinctions (24) followed by those with masses between 50-100 g and 100-200 g (Table 16). The fewest extinctions have occurred in the mass ranges < 10 g and 1 000-2 000 g (3), and 2 000-5 000 g and > 50 000 g (4). Birds in six of the 11 size ranges were exclusively island species; these ranges are marked with an asterix in Table 16. The very largest and very smallest species were included in these.

Table 16. Chronology of extinction of specific-sized birds on all islands

Size (g)	Time period								Totals
	1600-1650	1650-1700	1700-1750	1750-1800	1800-1850	1850-1900	1900-1950	1950-1995	
<10*						1	1	1	3
10-30		1			2	10	7	4	24
30-50	1	1		2	1	1			6
50-100*			1	2	7	4	5	1	20
100-200			2	2	3	4	8		19
200-500		2	2	2		2	2	1	11
500-1000*	2	4		3	2	3	2	2	18
1000-2000*				1		1		1	3
2000-5000	1	1		1	1				4
5000-50000*	1	2	1	8	2				14
>50000*	1	2				1			4
Totals	6	13	6	21	18	27	25	10	126

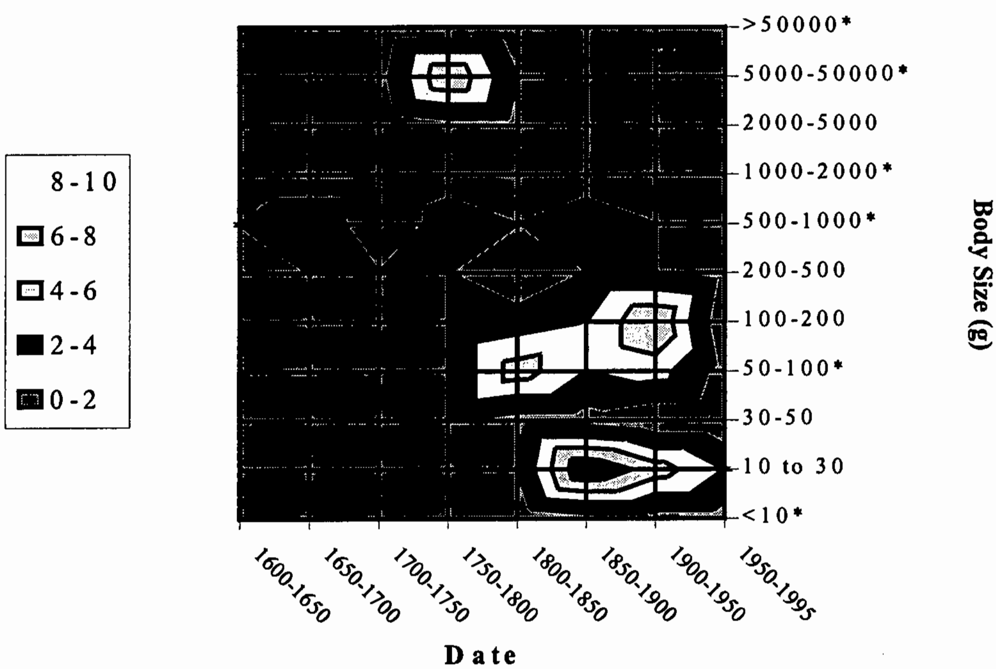
The date of the extinction of one species is unknown and not included in this table.

Table 16 also shows the time periods in which the particular size categories were affected. Birds of masses between 500-1 000 g became extinct over the greatest number of time periods (7). Only between 1700-1750 has a species in this mass range not become extinct, all of the other time periods experiencing multiple extinction. This size category has experienced the fourth highest number of extinctions. Only three birds of size >1 000 g have become extinct in the last

150 years, six in the last 200. This is less than in both the 100-year time intervals prior to 1800. There was no correlation between any one bird size going extinct over any one time period.

Figure 4 indicates a trend towards an increasing proportion of small species becoming extinct in the past 200 years. A greater number of comparatively larger birds (> 500 g) were affected between 1600-1800.

Figure 4. Distribution through time of extinct avifauna of specified body masses on islands of specified size categories

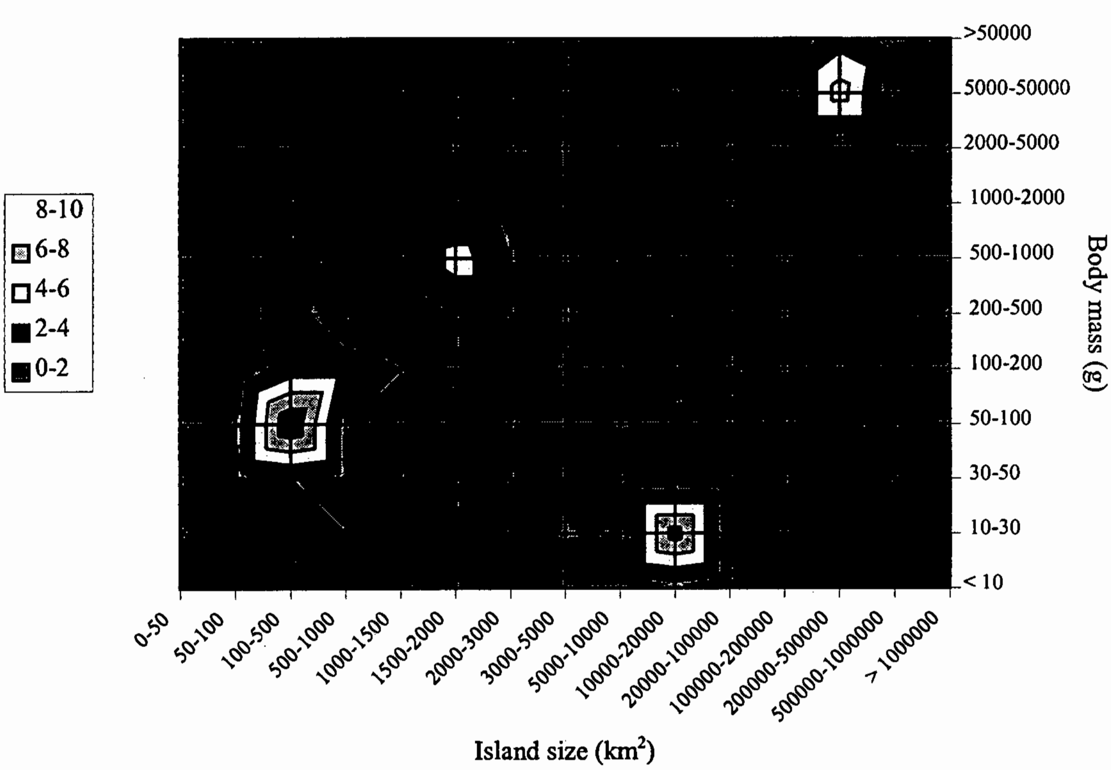


An increase in the incidence of smaller birds (<500 g) becoming extinct is especially evident in the time intervals 1800-1950 where there were 12, 21 and 29 smaller bird extinctions in each respective 50-year interval, or 67%, 84% and 88% of the extinctions in these time intervals. These numbers are higher than in any the time intervals pre-1800 for these sizes. Between 1950 and present there has been a drop in the number of extinctions in this range (7) but these nonetheless make up 70% of all post-1950 extinctions.

Body size, island size and extinction

Although there is no statistically significant correlation between the body masses of extinct birds and island size, Fig. 5 does indicate a few basic patterns which could be predicted from a positive relationship between body size and home range (and hence an inverse relationship with population density). Very large birds (> 50 000 g) are confined to (and have been lost from) the largest islands. Similarly, over 50% of the small birds (< 500g) have been lost from islands < 1 000 km^2 in area.

Figure 5. The relationship between body mass and island size for extinct avifauna on all islands



Part 2 - Discussion

Prehistoric extinctions

The total number of named species (plant and animal) stands between 1.5 and 1.8 million, of which more than 80% are animal. There is uncertainty as to how many species there may be with estimates ranging from 3 million to 80 million or more (May 1988, Stork 1988, Ehrlich 1993, Gaston 1994). Smith *et al.* (1993b) estimate the number of animal species extant today to be about 1.4 million, of which known extant avian species make up approximately 9500 (0.68%). Clements (1991) puts this figure at 9455 and Monroe and Sibley (1993) at 9702.

The average "life span" of higher vertebrate species (fish, reptiles, amphibians, birds and mammals) is estimated to be between 200 000 years and 2 million years (Ehrlich *et al.* 1977), giving a background extinction rate of between 0.2 and 2.0 species per million species per year. Raup (1988) and Wilson (1992) calculated a background extinction rate of one species per million species per year, which is used by Ehrlich (1994) and Stevens (1995a) as the best available figure; this figure is also used by Pimm (1995) for avian species.

Archaeological finds on tropical Pacific islands indicate that more recent prehistoric human activity resulted in the extinction of large numbers of land birds. (Milberg and Tyrberg (1993) define prehistoric as "times previous to the appearance of written sources" and list species from islands that were colonised between 200 and 9 000 years ago - *cf.* pg. 70). Fossil evidence from well studied islands in the Pacific suggest that prehistoric humans caused the extinction of as many as 2000 endemic landbird species across the Pacific (Olson 1989, Steadman 1995). The Polynesians first colonised Pacific islands from New Zealand in the south, to Hawaii in the north and east to Easter Island from around AD 400. They are thought to have extirpated between 500 and 1000 bird species (Pimm *et al.* 1994). Milberg and Tyrberg (1993) use these figures to refute the notion that "primitive people" were "natural conservationists" who lived in a state of ecological balance without any appreciable effect on the environment.

Pimm (1995) places the avian extinction rate in the Pacific alone over the last two thousand years at one species per ten thousand species per year and terms this rate the "conservative global rate of extinction". Comparisons with background extinction rates show that, even when using this conservative extinction rate, species are being lost 100-1000 times faster than these background rates (May *et al.* 1995, Pimm *et al.* 1995). That these extinction rates are so much higher than the background rate prompted Diamond (1989) and Pimm (1995) to suggest that we are in the midst of a mass extinction, the cause being the impact of man.

Milberg and Tyrberg (1993) state that, in some cases, the extinction of a species could not be separated into "pre-European" and "European" phases as extinction could be a long, drawn-out process. Some species mentioned in this analysis may have been approaching extinction when the first European explorers arrived, e.g. the moas (Anderson 1989), the Raiatea Parakeet *Cyanoramphus ulietanus,* Bay Thrush *Turdus ulietanus* and Mysterious Starling *Aplonis mavornata* (Olson 1986, Fuller 1987).

Historical Extinction Rates

Since 1600, there have been 251 documented higher-vertebrate extinctions (Smith *et al.* 1993b, this study). Avian extinctions account for 55% of these. This high proportion is probably an artefact of birds (and mammals) being well studied, both in intensity and geographically, when compared to other taxa (Diamond 1987, Gaston and May 1992). It does, however beg two questions: (1) are there other taxa that would be found to have experienced higher degrees of extinction if they had been studied as intensively as birds and mammals; and (2) would some taxa show more extinctions if their status was more widely studied on a global scale (all recorded fish extinctions bar one are from North America and Mexico - Gaston and May 1992)?

In 1600, it is assumed that 9840 avian species were in existence (using 138 extinct species and Monroe and Sibley's (1993) figure of 9702 extant species). Given the above background extinction rate, the extinction rate of avian species can be calculated in species per million species per year using the formula:

$$X = \frac{a \,.\, 10^6}{(9840 - b) \,.\, 10^2}$$

where: X is the extinction rate in species/million species/per year (Table 17).

a is the number of extinctions in a 100-year period.

b is the cumulative number of extinctions since 1600 until the relevant time period. This provides the number extant species at the start of that time period.

Table 17. Rates of avian extinction from 1600 until present in species per million species per year.

Period	*Extinction rate (species/million species/year)*
1600 - 1699	18.7
1700 - 1799	29.2
1800 - 1899	49.2
1900 - 1995	44.2
1600 - 1995	35.9

Myers (1979) presented two statistics: (1) the estimated extinction rate of animals between the years 1600 to 1900 was about one every four years; and (2) the estimated extinction rate for 1900 to present was about one species per year. Both these figures are clearly underestimates. Considering avian species alone, there were 93 extinctions in the years 1600 to 1900, this is an extinction rate of approximately one every three years. Between 1900 and present there have been 44 extinctions, an extinction rate of almost one every two years. As birds represent only 0,68% of known animal species, total animal extinction rates must be higher than this. King (1980) suggests the rate of avian extinction may increase to one species per six months by the end of the century.

For each 100-year time period the avian extinction rate is markedly higher than the background extinction rate. The overall avian extinction rate from 1600 until 1995 is 36 species per million species per year. There was a peak extinction rate between 1850 and 1950 of 51 species per million species per year.

An historical avian extinction rate of approximately 36 species per million species per year translates to 360 000 avian extinctions per million years, using a baseline of 10 000 extant avian species. This is very much higher than Pimm's (1995) background avian extinction rate of one extinction per million species per year. For the 400 year period covered in this study, the extinction rate was one species per 30 000 species per year. Considering only the last 200 years, this rate increases to one species per 20 000 species per year. This is approximately half the rate at which the Polynesians are estimated to have caused bird extinctions on Pacific islands (Pimm 1995).

The sharp increase in extinction rate in the 19th Century coincides with European colonial expansion, which was made partly possible by the industrial revolution (Smith *et al.* 1993b). The utilitarian attitude towards nature was one of the primary causes of extinctions in this time; directly in the form of exploitation for food as in the case of the Spectacled Cormorant *Phalacrocorax perspicillatus* or indirectly through the introduction of predators and destruction of indigenous habitats, as in the cases of the Chatham Island Fernbird *Bowdleria fufescens* and Bonin Wood Pigeon *Columba versicolor* respectively (Greenway 1967, Day 1989). The impact of the Europeans was felt throughout the world, and the elevated extinction rate probably reflects the escalating exploitation of natural resources to fuel the growth of industrial capitalism (Humphries and Fisher 1994). This is supported by Ehrlich (1994) who shows that a correlation exists between rates of extinction and total energy consumption by man.

Causes of historical extinction

Introduced predators

Introduced predators have been the most pervasive cause of extinction on islands. These alien, vertebrates were introduced accidentally or deliberately from continents by the colonising powers. The first period after the introduction of a new predator is expected to be particularly stressful to the indigenous fauna because the predator population typically increases beyond the carrying capacity of the island as easily accessible prey are over-exploited (Bell 1977, Ebenhard 1988).

Historically, oceanic islands mostly lacked mammalian predators, with the result that endemic birds, in contrast to those on continents, had lost the behavioural adaptations that would have allowed them to co-exist with the predators: for example, many taxa are flightless. Of the predators that have been introduced, rats (*Rattus rattus, R. norvegicus* and *R. exulans*) and cats (*Felis catus*) have had the most significant impacts (Moors *et al.* 1992). Birds nesting on the ground or in burrows are at greatest risk from *R. norvegicus*, whereas tree-nesting birds are at greatest risk from *R. rattus*. *Rattus rattus* has caused greater losses of forest birds on oceanic islands than any other rat in recent times, while in the same period *R. norvegicus* has caused greater losses amongst sea birds (Atkinson 1985). One cat caused the extinction of a entire species. The Stephen Island Wren *Xenicus lyalli* was exterminated by a cat named Tibbles, who belonged to the lighthouse keeper on the island, over the space of about a month (Fuller 1987).

Size and behaviour determine a species' vulnerability to rats. Larger birds and birds with aggressive behaviour towards rats (evolved as a result of native predators) are probably better able to protect nests from rats or other introduced predators (Moors and Atkinson 1984, Atkinson 1985).

Introduced birds may also have an effect on the endemic avifauna. Grant (1995) suggests that the impact of introduced mynahs on endemic birds of the Hawaiian islands may have been underestimated. The mynahs are known to eat other birds' eggs.

Exploitation

Exploitation has led to the extinction of many more island birds than mainland birds. Food and feathers were the main motivations behind the exploitation of birds. They were most often taken for food by hungry sailors, e.g. the Dodo, Spectacled Cormorant and Great Auk. In a few cases their feathers were taken for decoration, e.g. Lebat's Conure *Aratinga labati* and the Huia (Day 1991).

Exploitation is known to have been responsible for only two mainland extinctions. These were the Carolina Parakeet and the Passenger Pigeon, both hunted from super-abundance to extinction in the USA (Blockstein and Tordoff 1985, Fuller 1987). The Passenger Pigeon was hunted for food and sport and the Carolina Parakeet for sport and as a pest as it ate crops, although Day (1989) suggests this alone should not have led to its extinction.

Habitat destruction

Although responsible for more island than mainland extinctions (9 compared with 5), proportionally, habitat destruction has been a much more important factor in mainland extinctions than on islands. In mainland areas, it has alone been responsible for 42% of extinctions and, in combination with other factors, for a further 25%. All known causes of mainland avian extinctions involve habitat destruction and all of the mainland extinctions in the last 50 years were due entirely to habitat destruction.

Habitat destruction caused more insular avian extinctions during 1900-1950 than in any other time period (n=5). The Hawaiian islands experienced three of these (two on Hawaii and one on Laysan). Habitat destruction affected mainly passerines during the last century; only one of the six extinctions, the Laysan Rail *Porzana palmeri*, was non-passerine.

Unknown

The causes of fifty avian extinctions (36%) are unknown. Some of these extinctions could be assigned causes with a high degree of probability based on the knowledge of the causes of extinction in other sympatric species. For example, the seven moa extinctions of unknown cause were probably a result of exploitation and habitat destruction.

Unknown causes may also have been not-so-obvious ecological spin-offs from habitat destruction, exploitation and introduced predators. It is likely that there were other, non-avian extinctions that occurred in places that experienced avian extinctions. These extinctions may have been a food source to some avian species, which themselves subsequently became extinct. Janzen and Martin (1982) and Witmer and Cheke (1991) propose that the extinction of an important seed disperser is likely to alter the composition of the vegetation even when it is not directly affected by man. This alteration may be enough to result in the extinction of species dependent on the "old" habitat for food or nesting. The extinction or near extinction of the endemic Hawaiian plants of the genus *Hibiscadelphus* caused the secondary extinctions of several of its honeycreeper pollinators (Diamond 1989).

Islands where there have been more than one extinction may represent examples of "extinction cascades". Here, an extinction of one species in a complex system could lead to an "extinction cascade" which would affect many species in the system (Diamond 1989). For example, human removal of top predators (jaguars, pumas and harpy eagles) on Barro Colorado Island caused a population surge in medium-sized predators (monkeys and coatimundis) on which the top predators habitually preyed. A surge of medium-sized predators subsequently led to extinctions of ground-nesting birds without any further intervention by man (Terborg and Winter 1980).

Combinations of factors

It is likely that combinations of causes also featured more significantly in extinctions than recorded prior to 1900. In the 17th and 18th Centuries, factors acting in combination may have been overlooked, only later becoming apparent with improved scientific method, observation and recording. Perceptions as to the importance of combinations of factors in causing extinction may have changed over time whereas their incidence may have remained fairly constant.

As well as extinction pressures acting in combination with each other, specific attributes of the birds themselves may predispose them to the effects of such multiple pressures. Flightless or near flightless species like the Dodo, the moas and some rails would be predisposed to the pressures of both introduced predators and exploitation by man for food. On isolated islands lacking indigenous predators, the lack of an escape response towards predators and man resulted in many species succumbing to these dual threats, a case in point being the Laysan Rail (Fuller 1987).

The flocking behaviour of the Passenger Pigeon may have also predisposed it to extinction. These birds relied on communal protection (Blockstein and Tordoff 1985) and, once the great flocks had been destroyed, it may have been only a matter of time before the remaining birds became extinct. The extinction of this species was almost inconceivable in the mid-19th Century, today it stands as perhaps the most spectacular of recent extinctions.

Geography of historical extinctions

Island extinctions

Ninety percent of avian extinctions since 1600 have occurred on islands. This accords with the figure calculated by Johnson and Stattersfield (1990) and is slightly below King's (1985) estimate of 93%.

Island size

There is no clear correlation between island size and the absolute (rather than proportional) probability of extinction. Species have become extinct from islands of all sizes, ranging from very small e.g. Stephen's Island (2.6 km^2) and Wake Island (8 km^2) to very large e.g. Sumatra and Borneo, together covering an area of 1 219 916 km^2. Both small and large islands have experienced one extinction only or many extinctions: Ascension Island (88 km^2) and Java (130 987 km^2) have only experienced one extinction each, whereas Rodrigues (104 km^2) and New Zealand (269 000 km^2) have lost comparatively large numbers of species.

Oceanic regions

The most extinctions in any region have occurred in the southern Pacific (43). All the islands that have experienced three and four extinctions are situated in this region. Only two islands in this region experienced two extinctions. The highest number of affected islands (as well as the island experiencing the most extinctions - New Zealand) are situated in the southern Pacific. There were more non-passerine extinctions than passerine extinctions, which was typical of all the regions except the northern Pacific.

The northern Pacific region has experienced the third most extinctions (after the southern Pacific region and the Indian Ocean region). The island of Hawaii experienced 12 extinctions whereas other islands in the region lost only one or two species. In this region there were more passerine extinctions than non-passerine extinctions; it is the only region in which this has occurred. This is due mainly to the extinctions on the Hawaiian islands: 16 of the 21 passerine extinctions in the region occurred here.

In the northern Atlantic region, all of the extinctions except one have occurred in the Caribbean. Single extinctions per island are typical and only two islands have experienced two extinctions. Nine of the ten extinctions were non-passerine. The southern Atlantic has only one island that has experienced an extinction (Ascension Island), this being a non-passerine extinction. The Atlantic Ocean as a whole has lost relatively few species in historical times.

All of the extinctions in the Indian Ocean occurred on islands south of the Equator. With the exception the southern Atlantic, this oceanic region has the least number of affected islands (6), but has experienced the second highest number of extinctions. These six islands have experienced an average of 6.6 extinctions each, the highest of all the regions. The three Mascarene islands were most severely affected, accounting for 33 of the 39 extinctions. This island group has lost twice as many species as the Hawaiian island group. Thirty-two of the 39 Indian Ocean extinctions were of non-passerines.

Islands most severely affected

Tables 18a-e document the chronology and causes of avian extinctions on the five islands that have lost the most species. New Zealand and Hawaii each had one family that was particularly heavily impacted, the Dinornithidae and the Drepanididae respectively. These families accounted for two thirds and three quarters of the historical extinctions on these islands respectively (Table 19). The Mascarene islands experienced 33 extinctions across a comparatively large number of families. (Tables 18c-e each incorporates the extinction of the three species that inhabited all three islands.)

Table 18a. Chronology and causes of avian extinctions on New Zealand

Year	Cause Ex	IP	Ex,HD	HD,IP	Unknown	Total
1600-1649			1		1	2
1650-1699			1			1
1700-1749					5	5
1750-1799			1			1
1800-1849						0
1850-1899				1	2	3
1900-1949	1			1		2
1950-1996		2				2
	1	2	3	2	8	16

Table 18b. Chronology and causes of avian extinctions on Hawaii

Year	Cause HD	IP	Ex,HD	HD, comp disease	Unknown	Total
1600-1649						
1650-1699						
1700-1749						
1750-1799						
1800-1849						
1850-1899	1	1	1	4	1	8
1900-1949	2					2
1950-1996	1			1		2
	4	1	1	5		12

Table 18c. Chronology and causes of avian extinctions on Mauritius

Year	Cause Ex	IP	Unknown	Total
1600-1649			1	1
1650-1699	2		4	6
1700-1749	2			2
1750-1799			1	1
1800-1849		1	3	4
1850-1899				0
1900-1949				0
1950-1996				0
	4	1	9	14

Table 18d. Chronology and causes of avian extinctions on Rodrigues

Year	Cause Ex	IP	Ex,IP	Unknown	Total
1600-1649				1	1
1650-1699				1	1
1700-1749		1		3	4
1750-1799	3			1	4
1800-1849				2	2
1850-1899			1		1
1900-1949					0
1950-1996					0
	3	1	1	8	13

Table 18e. Chronology and causes of avian extinctions on Réunion

Year	Cause Ex	HD	IP	Unknown	Total
1600-1649				1	1
1650-1699				4	4
1700-1749	1				1
1750-1799	1			1	2
1800-1849		1		2	3
1850-1899			1		1
1900-1949					
1950-1996					
	2	1	1	8	12

New Zealand and Hawaii are the largest of the five islands and are also the ones most recently affected by extinction, the last Mascarene extinction being in 1876 (Table 20). New Zealand has had two historical extinction "episodes", one between 1600 and 1750 when nine species became extinct (all moas) and one between 1850 to the present when seven species have become extinct. Hawaii has had only one "episode", between 1850 to present, when 12 species became extinct. On these two islands, habitat destruction alone or in combination with some other factor (exploitation on New Zealand and competition and disease on Hawaii) was the primary cause of extinction, resulting in 15 of the 28 extinctions (Table 19).

Table 19. Summaries of avian extinctions and their causes on the five islands that have experienced the most extinctions. (Causes from Appendix 1)

a.) New Zealand

Order	Family	Common Name	Scientific Name	Date	Cause
Dinornithiformes	Dinornithidae		*Dinornis maximus*	1850	?
		Slender Moa	*Dinornis torosis*	1670	Ex,HD
		Greater Broad-billed Moa	*Euryapteryx gravis*	1640	Ex,HD
			Euryapteryx geranoides	Before 1700	?
			Anomalopteryx parvus	Before 1800	?
			Anomalopteryx didiformes	Before 1800	?
			Anomalopteryx oweni	Before 1800	?
		Lesser Megalapteryx	*Megalapteryx didinus*	1765	Ex,HD
			Megalapteryx hectori	Before 1800	?
			Megalapteryx benhami	Before 1800	?
Ciconiiformes	Ardeidae	New Zealand Little Bittern	*Ixobrychus novaezelandiae*	1900	?
Galliformes	Phasianidae	New Zealand Quail	*Coturnix novaezelandiae*	1868	?;HD,IP
Strigiformes	Strigidae	Laughing Owl	*Sceloglaux albifacies*	1910	HD,IP
Passeriformes	Acanthasittidae	Bush Wren	*Xenicus longipes*	1965	IP
	Pachycephalinae	Popio	*Turnagra capensis*	1955	IP
	Callaeidae	Huia	*Heteralocha acutirostris*	1907	Ex

b.) Hawaii

Order	Family	Common Name	Scientific Name	Date	Cause
Gruiformes	Rallidae	Sandwich Rail	*Porzana sandwichensis*	1898	IP
Passeriformes	Meliphagidae	Kioea	*Cheatoptila augustipluma*	1860	??
		Hawaiian O'o	*Moho nobilis*	11934	HD
	Drepanididae	Great Amakihi	*Verido sagittirostris*	1900	HD
		Greater Koa Finch	*Psittirostra palmeri*	1896	HD, disease, competition or all 3
		Akiola	*Hemignathus obscurus*	1960	HD, disease, competition or all 3
		Lesser Koa Finch	*Psittirostra flaviceps*	1891	HD, disease, competition or all 3
		Kona Finch	*Psittirostra kona*	1894	HD, disease, competition or all 3
		Mamo	*Drepanis pacifica*	1899	Ex,HD
		Kona Grosbeak	*Chloridops kona*	1894	HD, disease, competition or all 3
		Kakawihie	*Paroreomyza flammea*	1963	HD
		Ula-Ai-Hawane	*Ciridops anna*	1892	?,HD

c.) Mauritius

Order	Family	Common Name	Scientific Name	Date	Cause
Ciconiiformes	Ardeidae	Mauritius Night Heron	*Nycticorax mauritianus*	By 1700	?
Anseriformes	Anatidae	Mauritian Duck	*Anas theodori*	1696	?
		Mauritian Shellduck	*Alopochen mauritianus*	1698 ?	?
Gruiformes	Rallidae	Mauritian Red Rail	*Aphanapteryx bonasia*	1693	Ex
		Mascarene Coot	*Fulicia newtoni*	1693	?
Columbiformes	Raphidae	Dodo	*Raphus cucullatus*	1655	Ex
	Columbidae	Dutch Pigeon	*Alectroenus nitidissima*	1835	?,IP
Psittaciformes	Psitticadae	Mauritius Grey Parrot	*Lophopsittacus bensoni*	1765	?
		Broad-billed Parrot	*Lophopsittacus mauritanus*	1680	?
		Mascarene Parrot	*Mascarinus mascarinus*	1834	?
Strigiformes	Tytonidae	Mauritius Barn Owl	*Tyto sauzieri*	1700	?, Ex
		Newton's Barn Owl	*Tyto newtoni*	1700	?, Ex
	Strigidae	Commerson's Scops Owl	*Scops commersoni*	1836	?
Passeriformes	Sturnidae	White Mascarene Starling	*Necropsar leguati*	1840	?

d.) Rodrigues

Order	Family	Common Name	Scientific Name	Date	Cause
Procellariiformes	Procellariidae	?	*Pterodroma sp.*	1726	?
Ciconiiformes	Ardeidae	Rodrigues Night Heron	*Nycticorax megacephalus*	1761	?
Gruiformes	Rallidae	Legaut's Rail	*Aphanapteryx leguati*	1760	Ex
		Mascarene Coot	*Fulica newtoni*	1693	?
Columbiformes	Raphidae	Rodrigues Solitaire	*Pezohaps solitarius*	1765	Ex
	Columbidae	Rodrigues Pigeon	*Columba rodericana*	1726	?, IP
Psittaciformes	Psitticadae	Rodrigues Parrot	*Necropsittacus rodericanus*	1761	Ex
		Rodrigues Ring - necked Parakeet	*Psittacula exul*	1876	?, Ex,IP
		Mascarene Parrot	*Mascarinus mascarinus*	1834	?
Strigiformes	Strigidae	Rodrigues Little Owl	*Athene murivora*	1726	?
Passeriformes	Sturnidae	Rodrigues Starling	*Necropsar rodericanus*	1726	?
		White Mascarene Starling	*Necropsar leguati*	1840	?
	Pycnonotidae	?	*Hypsipetes sp.*	1600's	?

e.) Réunion

Order	Family	Common Name	Scientific Name	Date	Cause
Ciconiiformes	Ardeidae	?	*Nycticorax sp.*	By 1700	?
	Ciconidae	?	*Ciconia sp.*	By 1674	?
	Threskiornithidae	Réunion Flightless Ibis	*Borbonibis latipes*	1773	?
Falconiformes	Falconidae	?	*Falco sp.*	1674	?
Gruiformes	Rallidae	Mascarene Coot	*Fulica newtoni*	1693	?
Columbiformes	Raphidae	Réunion Dodo / Solitiare	*Raphus solitarius*	1715	Ex
		White Dodo	*Victoriornis imperialis*	1770	Ex
Psittaciformes	Psitticadae	Réunion Ring - necked Parakeet	*Psittacula eques*	1800	HD
		Mascarene Parrot	*Mascarinus mascarinus*	1834	?
Passeriformes	Plocidae	?	*Foudia sp.*	1671	?
	Sturnidae	Réunion Crested Starling	*Fregilupus varius*	1860	IP
		White Mascarene Starling	*Necropsar leguati*	1840	?

Table 20. Chronological analysis of extinction on the five most severely affected islands

Year	N.Z.	Hawaii	Mauritius	Rodrigues	Réunion	All three Mascarene Islands	Total
1600-1649	2		1	1	1		5
1650-1699	1		5	0	3	1	10
1700-1749	5		2	4	1		12
1750-1799	1		1	4	2		8
1800-1849			2	0	1	2	5
1850-1899	2	8		1	1		12
1900-1949	3	2					5
1950-1996	2	2					4
	16	12	11	10	9	3	61

In the Mascarene islands, all extinctions occurred before 1877 (Table 19). There was a steady number of extinctions from 1650 until 1850, 11, seven, seven and nine extinctions occurring in the consecutive 50-year time periods. Unknown factors contributed to the highest number of extinctions (19 of 33). Of the known factors, exploitation was the most important, resulting in ten extinctions (one in combination with another factor). From these islands an entire family has become extinct, the Raphidae. This family contained only four species, two of which were endemic to Rodrigues. The Raphidae is one of two recently extant families which has lost all its species.

In Hawaii and the Mascarenes a single factor led to the extinction of many species. On Hawaii it was habitat destruction and on the Mascarenes it was exploitation. On Hawaii the most recent extinctions also involve habitat destruction and the most important current causes of threat to endangered and critical species are habitat destruction and introduced predators (Collar *et al.* 1994). Avian malaria is also an important threat to bird species on Hawaii and is included by Collar *et al.* (1994) with introduced species in their threat codes. New Zealand may have two prominent causes if it is assumed that the extinction of the moas was driven by exploitation and habitat destruction. Here, however, the two most recent cases of extinction are ascribed to introduced predators and these, together with habitat alteration, are the most important threats to critical and endangered species in New Zealand. On the Mascarenes there has not been an extinction for 120 years, but Collar *et al.* (1994) report that there are currently nine endemic species in the endangered and critical categories. The causes of threat on Mauritius and Rodrigues are habitat destruction and introduced predators: on Réunion, exploitation remains the greatest threat.

Islands experiencing between two and four extinctions.

Fourteen islands fell into this grouping (Table 21), more species becoming extinct in the first 50 years of this century than in any other time period. In the last 47 years, there has been only one extinction on these islands, the lowest rate since 1750. Extinctions on all but two of the 14 islands are spread over a number of time periods. Molokai and Guadeloupe Islands have only lost species in the 20th Century. Of the four extinctions on these islands, habitat destruction was responsible for three. Overall, however, of the known causes of extinction on these 14 islands, the most important has been introduced predators (Table 22). Predators have also accounted for the most recent extinction on these islands. The next most important known cause was exploitation. Introduced predators do not seem to have affected species on the two largest islands in this grouping, *viz.* Jamaica and Madagascar.

Islands experiencing one extinction

Thirty islands have experienced single avian extinctions (Table 23). The extinction rate on these islands peaked in the time period 1900-1949 when 14 species became extinct; the time period 1950-1996 saw the lowest number of extinctions since 1750, consistent with general trend in extinction rates. Island sizes ranged from very small to large and there was no correlation between island size and extinction probability. Bird body sizes ranged from large to small and no relationship was found between body size and probability of extinction on these islands. Eighteen of the 30 islands were tropical. Twelve of the birds on these tropical islands were comparatively small (< 200 g), all the passerine species (7) being <80 g. Considering all 30 islands, over two thirds of the species were non-passerine.

Of the known causes of extinction, habitat destruction alone accounted for the most extinctions. It was not, however, as over-ridingly important as were exploitation and introduced predators on islands that have experienced more than one extinction. When viewing combinations of all the factors, habitat destruction played a role in 16 extinctions, exploitation in 11 and introduced predators in ten. There were 12 extinctions from unknown causes, all between 1800 and the present.

Table 21. Chronological summary of avian extinction on islands experiencing between two and four extinctions.

Island	1600	1650	1700	1750	1800	1850	1900	1950	Total
Chatham Island		1			1	1	1		4
Tahiti				1	1		2		4
Seychelles						2		1	3
Lord Howe Island					1		2		3
Peel and Bonin Island					1	1			2
Jamaica				1	1				2
Norfolk Island						1	1		2
Raiatea Island				2					2
Ryukyu Island					1		1		2
Guadeloupe Island			1	1					2
Kosrae Island					1	1			2
Molokai Island							2		2
Guadelupe Island							2		2
Madagascar		1					1		2
	0	2	1	5	7	6	12	1	34

Table 22. A summary of the causes of extinction on islands experiencing between two and four avian extinctions.

Island	Ex	HD	IP	Ex/HD	Ex/Iv	HD/IP	Other	Unknown	Total
Chatham Island			1			2		1	4
Tahiti	1		3						4
Seychelles			1					2	3
Lord Howe Island	1		1					1	3
Peel and Bonin Island			2						2
Jamaica								2	2
Norfolk Island	1							1	2
Raiatea Island			2						2
Ryukyu Island								2	2
Guadeloupe Island	1			1					2
Kosrae Island			2						2
Molokai Island		1				1			2
Guadelupe Island	1					1			2
Madagascar				2					2
Total	5	1	12	3	0	4	0	9	34

Table 23. Cause and chronology of avian extinction on islands experiencing a single extinction.

Date	Cause								Total
	Ex	HD	IP	Ex/HD	Ex/IP	HD/IP	Other	Unknown	
1600-1649									0
1650-1699	1								1
1700-1749									0
1750-1799		1	1						2
1800-1849				2		1		3	6
1850-1899	1	1	1	1	1			1	6
1900-1949	2	3	2			1	1	2	11
1950-1996			2					1	3
Unknown								1	1
	4	5	6	3	1	2	1	8	30

Some conclusions

On the five islands that have experienced a large number of extinctions, habitat destruction was the most important known factor on the larger islands of New Zealand and Hawaii. On the smaller Mascarene islands most extinctions were a result of habitat destruction and exploitation (although here, over two-thirds of the causes are unknown). The impact of introduced predators may have been missed as a result of poor scientific observation, the majority of the extinctions of unknown cause occurring before 1800. Birds on the five islands ranged in size from very large (moas and Raphidae) to small (Bush Wren *Xenicus longipipes* and Rodrigues Starling *Necrospar rodericanus* on New Zealand and Rodrigues respectively). Many of the Hawaiian extinctions were of small birds belonging to a single family (Drepanididae).

On islands that have experienced between two and four extinctions, introduced predators were the cause in most cases. The species affected were from across the body size range. The islands affected were generally smaller than 1000 km^2. On these islands only one species has become extinct in the last 47 years, perhaps indicating that on these smaller islands, endemic species prone to extinction (through introduced predators and exploitation) had become extinct before 1900 (*cf.* Pimm *et al.* 1994).

On islands that have experienced single extinctions, there appears to be little relationship between island size and the body size of extinct species. Although habitat destruction played a role in the most extinctions in these islands, it was not significantly more important than introduced predators and exploitation as causative agents.

Mainland extinctions

Regions that human populations have expanded into and filled over the last 400 years have recorded extinctions. In parts of the world that have a long history of human occupancy, there have been relatively few extinctions recorded over the last 400 years (Europe, much of continental Asia, Africa). This suggests that extinctions in these regions took place before 1600 (Smith *et al.* 1993b). There have been no avian extinctions in Europe in the last 400 years and only one on the Asian mainland, the Himalayan Mountain Quail *Ophrysia superciliosa* in the early 1870's. There have also been no avian extinctions in Africa in the past 400 years. The advent of colonialism in Africa does not seem to have had as great an impact on African avifauna as has been the case elsewhere. There have, however, been nine mammalian extinctions in this time (Day 1989).

Since 1600, 10 bird species have become extinct in the Americas. Five of these were in North America, two in Central America and three in South America. Together these make up 83% of all mainland extinctions. Both the earliest recorded and the most recent mainland extinctions occurred here. Habitat destruction was the most important cause of extinction, being solely responsible for five extinctions and jointly responsible for five. It is likely that even in the demise of the Carolina Parakeet, habitat destruction, and not only exploitation (for food, feathers and sport), played a role. As indigenous habitat was cleared to make way for farmlands, the birds became to be regarded as pests as they fed on crops and were shot (Day 1989). The causes of extinction of three species in the Americas are unknown.

The two non-American extinctions were the Himalayan Mountain Quail in the 1870's and Australia's Paradise Parrot *Psephotus pulcherrinus* in 1927. The cause of the former's extinction is unknown and that of the latter a combination of habitat destruction and introduced predators (Fuller 1987, Day 1989).

The three most recent mainland extinctions were from central and South America (two grebes and a macaw). These extinctions form one quarter of all historical mainland extinctions and constitute the highest rate of mainland extinction since 1600. This lends support to the concern that exists over the threat to South American bird species which have restricted ranges and specialised habitat requirements (Myers 1988, Brooks and Balmford 1996).

Taxonomy of extinction

Orders

Four orders have lost 10% or more of their species, the Aepyornithiformes (100%), Dinornithiformes (77%), Casuariiformes (27%) and Podicipediformes (10%). Extinct species in the first three orders lived on islands, whereas the two extinct podicipediforms inhabited Guatemala and Colombia. One family in each order contained all the extinct species, the Aepyornithidae (one species), Dinornithidae (moas, ten species), Casuariidae (emus, two species) and the Podicipedidae (grebes, two species).

A combination of habitat destruction and exploitation were the causes of all the extinctions in these orders except the grebes, where habitat destruction alone was responsible. For the unknown causes of the moa extinctions, it is reasonable to assume that the known causes (exploitation and habitat destruction) accounted for these.

Extinctions among the Aepyornithiformes, Dinornithiformes and Casuariiformes occurred before the sharp rise in the extinction rate between 1850 - 1950; the podicipediform extinctions occurred after this.

Families

Intuitively, a greater proportion of species in small families has become extinct than in larger families. It would take only a few extinctions (in some cases only one) to affect a large proportion of the species complement of small families. The Callaeidae, for example, had only three extant species in 1600, one of which became extinct, resulting in a loss of one third of the family.

The greatest absolute numbers of extinctions have occurred in large families. The Psittacidae, with 360 extant species in 1600, have experienced the most extinctions (20), representing 6% of the extant species at the time.

Passerines make up over half the number of extant avian species. On the basis of these numbers it not surprising that 30% of post-1600 extinctions are of passerines. Of the known causes of passerine extinction, habitat destruction and introduced predators featured in all but one case, highlighting the vulnerability of this order to man's impact through these two agents.

Although non-passerines form less than half of the avifaunal compliment, they have experienced 70% of the extinctions in the last 400 years. This would indicate that the extinction pressures exerted in this time period, especially introduced predators and exploitation, affected non-passerines more severely than passerine species. The generally larger non-passerines (e.g. moas, larger parrots, dodos) were targeted for exploitation for food by colonising Europeans whereas smaller, ground-dwelling species were more at risk from introduced predators (e.g. rails).

Prehistoric extinctions

Milberg and Tyrberg (1993) have documented 41 avian families that experienced prehistoric (pre-1600) extinctions. They define prehistoric as "times previous to the appearance of written sources" and list species from islands that were colonised between 200 and 9 000 years ago. Table 24 details prehistoric extinctions of some selected families (data from Milberg and Tyrberg (1993)). One hundred and seventy seven of the 200 documented prehistoric extinctions are included. Families excluded experienced fewer than five extinctions.

The families with the greatest number of species which became extinct in prehistoric times are the Rallidae (34), Anatidae (25) and the Drepanididae (23). Species in these families were lost mostly from Pacific islands. Seven families accounted for almost two-thirds (135) of the recorded pre-historic extinctions.

Table 24. The number of prehistoric bird extinctions from selected families. (After Milberg and Tyrberg 1993).

Family	Mediterranean	Atlantic Ocean	Caribbean	Indian Ocean	Pacific Ocean	Total
Aepyornithidae				7		7
Dinornithidae					13	13
Procellariidae	1	2			2	5
Anatidae	2		1	2	20	25
Acciptiridae	1		4		8	13
Megapodiidae					5	5
Rallidae			4	1	29	34
Scolopacidae			2		3	5
Columbidae	1		1		11	13
Psittacidae			2		3	5
Tytonidae	2		5		1	8
Strigidae	3		6		5	14
Drepanididae					23	23
Corvidae	2		1		4	7
Total	12	2	26	10	127	177

The causes of prehistoric extinctions cannot be determined. As is the case for much recent extinction, the ultimate cause of extinction may be obscure or its importance difficult to evaluate. Milberg and Tyrberg (1993) list five causes that they believe were important in prehistoric extinctions: over-exploitation, introduced predators, habitat destruction, depletion of food supplies, and disease. These can be grouped into the causes listed in this study.

Large birds were probably more at risk from over-exploitation than small birds which were more at risk from introduced predators such as *Rattus exulans* (*Rattus rattus, R. norvegicus* and feral cats were not spread by prehistoric man - Milberg and Tyrberg 1993). The importance of habitat destruction is likely to have varied between islands, but New Zealand, Easter Island and islands in the Mediterranean probably were heavily impacted by habitat loss (Milberg and Tyrberg 1993).

The majority of documented prehistoric extinctions occurred on islands in the Pacific, followed by Caribbean and Mediterranean islands. Islands in the Indian and Atlantic Oceans (excluding Caribbean islands) experienced relatively few losses. This may simply be because there are fewer islands in these regions (compared to the Pacific and Caribbean regions) and therefore fewer birds. Fourteen of the 41 families listed by Milberg and Tyrberg (1993) did not experience extinctions on Pacific islands. Island size does not seem to have had an effect on the severity of extinctions; the large islands of New Zealand, Cuba and the smaller Hawaiian islands all lost a large part of their prehistoric avifauna (Milberg and Tyrberg 1993).

Extinction filters

At the end of the Pliocene (2 mya.), sea temperatures dropped dramatically with the onset of Northern-Hemisphere glaciation. In the Caribbean this resulted in the extinction of an estimated 36% of the molluscan genera and subgenera by the early Pleistocene (Jackson 1995). In subsequent and equally severe Pleistocene cycles of warming and cooling and associated sea-level changes, there was relatively little impact on the surviving Caribbean molluscs. An explanation for this is that the initial exposure to climatic changes purged marine faunas of thermally sensitive taxa, leaving behind a core of species that were relatively resilient to further temperature fluctuations (Jackson 1995). Species less resilient to climatic change are thus filtered out.

Extinction filters may be used to explain the vulnerability of biotas to modern day challenges. Introduced rats have been one of the greatest anthropogenic causes of recent avian extinctions (Milberg and Tyrberg 1993, Moors *et al.* 1992), but the vulnerability of island avifaunas to these has differed widely. Some rat introductions had catastrophic effects on the island avifauna but in other cases the introduction of rats has been followed by the co-existence of rats and native birds (Milberg and Tyrberg 1993). A possible explanation of these differences may lie in the presence or absence of indigenous predators.

Islands that have historically supported native rodents (e.g. Christmas Island and the Galapagos Islands) appear to have avifaunas that are relatively resistant to rats (Atkinson 1985). The generally lower vulnerability of birds on tropical, as opposed to temperate islands in terms of threat from predators, may be linked to the historical distribution of land crabs, potentially important predators of chicks (Atkinson 1985). In these cases, the retention of anti-predator traits may have ensured that native birds were less susceptible to introduced rats than were birds from islands that lacked land crabs.

The growing awareness of the scale of extinctions caused by prehistoric humans suggests that, as well as climatic and biotic factors, humans may have selectively purged naive biotas of particularly vulnerable species (Balmford 1996). This long-term, human-induced filtering of vulnerable taxa has probably occurred elsewhere. This may provide an additional explanation for the apparent lack of extinctions following extensive habitat modification of Europe and North America (Balmford 1996).

Table 24 indicates that, to a certain degree, there was a prehistoric filtering of species before the advent of colonialism. On islands of the Pacific ocean, the proportion of recent bird species that have become extinct or are endangered has decreased as time since colonisation increased (Pimm *et al.* 1994). The islands of the western Pacific, those occupied first by humans, have had fewer recent extinctions and have fewer currently endangered species, suggesting that species sensitive to human occupation became extinct, leaving only the more resilient species. The impact of humans appears superficially greatest in the most recently occupied areas, the implication being that places that have been occupied by humans for a long time have already lost most of their human-sensitive species.

Extinction debt

If species in a community are linked through a food web or mutualistic relationships, the extinction of one may lead to the extinction of another (Gilbert 1980). Heywood *et al.* (1994) argue that predicted extinction rates are higher than those observed because of the time lag that exists before species that are "committed to extinction" are lost. Culotta (1994) and Tilman *et al.* (1994) predict that habitat destruction causes an "extinction debt" whereby extinction occurs generations after habitat fragmentation. This represents a future ecological cost as a result of current habitat destruction.

Magsalay *et al.* (1995) support this notion from work done on Cebu Island where only 0.3% of the original dipterocarp forest remains. They consider both Cebu Island's endemic bird species (as well as five endemic sub-species) to be "committed to extinction". In Puerto Rico, less than one percent of the original forest remains but to date, no bird species has become extinct (Brash 1987). Brash (*op. cit.*) states that extinction lag (debt) is possibly a factor contributing to the depressed avian extinction rate in Puerto Rico.

Avian extinctions over the last 47 years

There have been 12 avian extinctions in the last 47 years (Table 25). This is the lowest extinction rate in the last 200 years. Of these extinctions, eight occurred on islands and three on continents. One species' range spanned both island and mainland. Habitat destruction and introduced predators were the most important causes of extinction accounting for six and five extinctions respectively.

The islands affected in the past 47 years were New Zealand (2), Hawaii (2), Fiji (1), Seychelles (1), Guam (1), and Pohnpei (1). For half these islands, these were the first avian extinctions (Fiji, Guam and Pohnpei). The most recent extinction is the Ivory-billed Woodpecker in 1991, which had a range spanning Cuba and the southeastern USA. The Seychelles has experienced the most recent island extinction (1986), followed by Guam (1985), Fiji (1973) and New Zealand (1965). Five of the eight island extinctions were caused by introduced predators.

Table 25. The chronology and cause of avian extinctions since 1950. (HD - habitat destruction, Ex - exploitation, IP - introduced predators, M - mainland, I - island, B - island and mainland.)

Species	Cause	Habitat	Date	Source
Glaucous Macaw	HD	M	1955	Mountfort (1988)
Piopio*	IP	I	1955	Fuller (1987)
Pohnpei Mountain Starling*	?	I	1956	Mountfort (1988)
Akiola*	HD/O	I	1960	Collar *et al.* (1994)
Kakawihie*	HD/O	I	1963	Collar *et al.* (1994)
Bush Wren*	IP	I	1965	Collar *et al.* (1994)
Barred-wing Rail	IP	I	1973	Collar *et al.* (1994)
Colombian Grebe	HD	M	1977	Collar *et al.* (1994)
Guam Flycatcher*	IP	I	1985	Collar *et al.* (1994)
Aldabra Warbler*	IP	I	1986	Collar *et al.* (1994)
Atitlan Grebe	HD	M	1987	Collar *et al.* (1994)
Ivory-billed Woodpecker	HD,Ex	B	1991	Collar *et al.* (1994)

(* indicates passerine species)

The three mainland extinctions occurred in countries of Central and South America, the most recent being in Guatemala (Atitlan Grebe *Podilymbus gigas*). The habitat of the

Glaucous Macaw was spread over four countries. Habitat destruction was the cause of all mainland extinctions in this time frame.

Seven extinctions were of passerines and five of non-passerines. All the passerine extinctions occurred on islands and all the mainland extinctions were non-passerine. Introduced predators were the main cause of extinction of the passerine species affected (four out of seven) and habitat destruction was responsible for all the non-passerines extinctions except one, the Barred-winged Rail *Nesoclopeus poeciloptera* of Fiji. This is the only island-dwelling non-passerine that has become extinct recently.

Body size

The mass range of extinct species in this analysis was between 3g and an estimated 500 kg with a median of 334 g. However, species with body masses less than 200 g accounted for 73 (60%) of the 126 extinct species whose mass could be inferred. This suggests that small birds are particularly at risk. However, Gaston and Blackburn (1994) report that most bird species are small-bodied, with a median mass of 37,6 g.

Only one bird weighing over 2 000 g has become extinct in the last 150 years. This is probably because large, vulnerable birds had already become extinct (before 1800). It is also thought that bigger birds will be more susceptible to extinction through habitat destruction as they need larger ranges to survive (Brown and Brown 1992). This is not reflected in the extinction record where, of causes known with certainty, the majority of larger bird extinctions were as a result of exploitation for food. Although habitat destruction is thought to have played a role in the moa, emu and Elephant Bird extinctions, its isolated effect cannot be evaluated. The effect of ongoing habitat loss and fragmentation on larger species should become evident in the next 20 years or less (Simberloff 1984, Pimm 1995).

The extinction of smaller species became more frequent post-1800, this again being coincident with the European colonial expansion and its associated extinction pressures (p. 49). All the extinction causes affected these species. Several studies concur with the hypothesis that for a given population size, small bodied species are more vulnerable than larger-bodied species (Peters and Realson 1984, Belovsky 1987, Pimm *et al.* 1988, Soulé *et al.* 1988, Gotelli and Graves 1990, Tracey and George 1992): this may be particularly true when population size is small (Pimm *et al.* 1988). However, even although more small-bodied species have become extinct than large-bodied ones, this may simply be because there are proportionally more small bird species than large ones (Gaston and Blackburn 1994).

Chapter Three: Threatened avifauna.

Part 1 - Results

Collar *et al.* (1994) identify 1111 bird species that are globally threatened. Of these, 482 species exclusively inhabit islands, 587 exclusively inhabit mainland regions and 42 inhabit both mainland and island habitats. Threatened species are placed into one of four categories: extinct in the wild, critically threatened, endangered or vulnerable. In this analysis, the four "extinct in the wild" species are grouped with those in the "critical" category, making 172 species that are critically threatened. Two hundred and thirty five species are endangered and 704 are vulnerable.

Causes of threat

All threatened species

The causes of threat as listed by Collar *et al.* (1994) have been categorized in the same way as the main causes of extinction: *viz.* habitat destruction, introduced vertebrates and exploitation. There are also "other" and "unknown" causes (Table 26). The category of introduced vertebrates differs from that of introduced predators as used in Chapter 2 for reasons discussed in the "methods" section (Part 2 of Chapter One).

Habitat destruction as a sole cause or in combination with other threat causes affects 760 species of bird. As the sole cause it affects almost half of all the threatened species in the world. Proportionally, many more mainland species (60%) than island species (37%) are threatened by habitat destruction. A combination of habitat destruction and exploitation threatens the next highest number of species, and together these two sources of threat affect almost two-thirds of the species listed by Collar *et al.* (1994).

Table 26. Distribution of threat types amongst bird species inhabiting islands and mainlands

Key:
H.D. Habitat destruction
Ex Exploitation
I.V. Introduced vertebrates

Numbers:

	Island		Mainland		Both		Total	
	(#)	(%)	(#)	(%)	(#)	(%)	(#)	(%)
HD	180	37	351	60	9	21	540	48
Ex	14	3	7	1	11	26	32	3
IV	49	10	8	1	0	0	57	6
HD/Ex	74	15	89	15	9	21	172	15
HD/IV	31	6	14	2	3	7	48	4
IV/Ex	5	1	0	0	3	7	8	1
Other	69	14	49	8	6	14	124	11
Unknown	60	12	69	12	1	2	130	12
Total	482		587		42		1111	

Habitat destruction and exploitation in conjunction threaten 172 species of which 89 are mainland species. These two factors affect 15% of threatened mainland species and 21% of the threatened species whose ranges include both mainland and islands. Species found in both mainland regions and on islands are affected most by exploitation (26%). Habitat destruction alone affects 21% of these species.

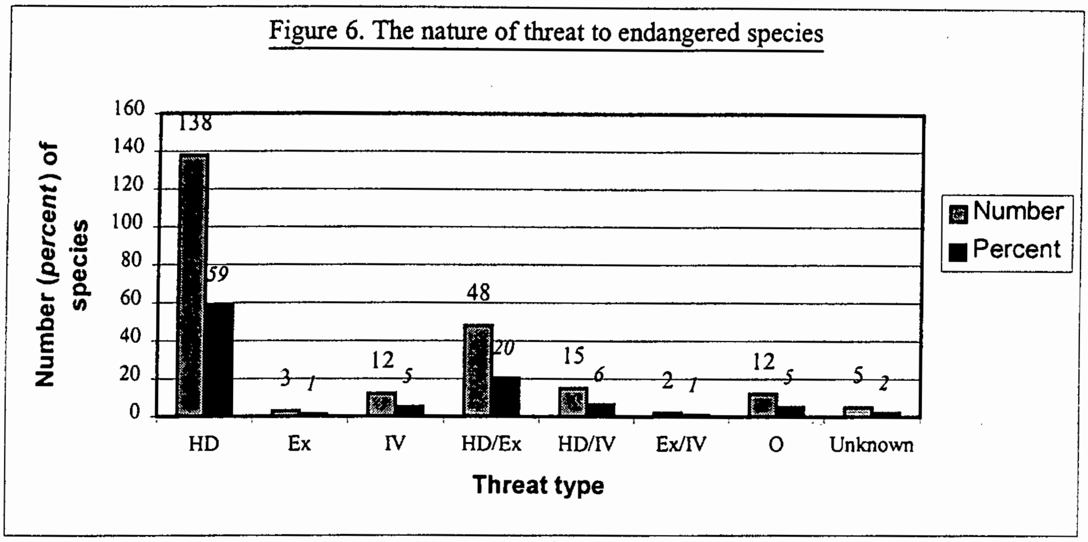
"Other" causes threaten 124 species. These vary from drowning on tuna longlines (Wandering Albatross *Diomedea exulans*) to genetic swamping and fire (Black-eared Miner *Manorina melanotis*). Of the remaining known threat factors, introduced vertebrates threaten 6% of threatened species, habitat destruction and introduced vertebrates 4%, exploitation 3% and introduced vertebrates and exploitation 1%. Unknown causes threaten 130 species; 60 of these species live exclusively on islands and 69 exclusively in mainland regions and one species inhabits both.

Endangered species

A detailed analysis of the 403 endangered and critically threatened species was carried out. In 271 cases, the major threat factor (habitat destruction, introduced vertebrates, exploitation, other or unknown) appeared together with one or both of two other threats listed by Collar *et al.* (1994) *viz.* natural causes (exacerbated by other causes) and small ranges or populations. One hundred and eighteen of the 235 endangered species and 153 of the 168 critical species were affected in this way. Excluding those affected by natural causes, 233 species are affected: 96 endangered species and 137 critically threatened species. Balmford and Long (1994) showed that of all threatened bird species, nearly 80% have breeding ranges less than 50 000 km^2 in extent.

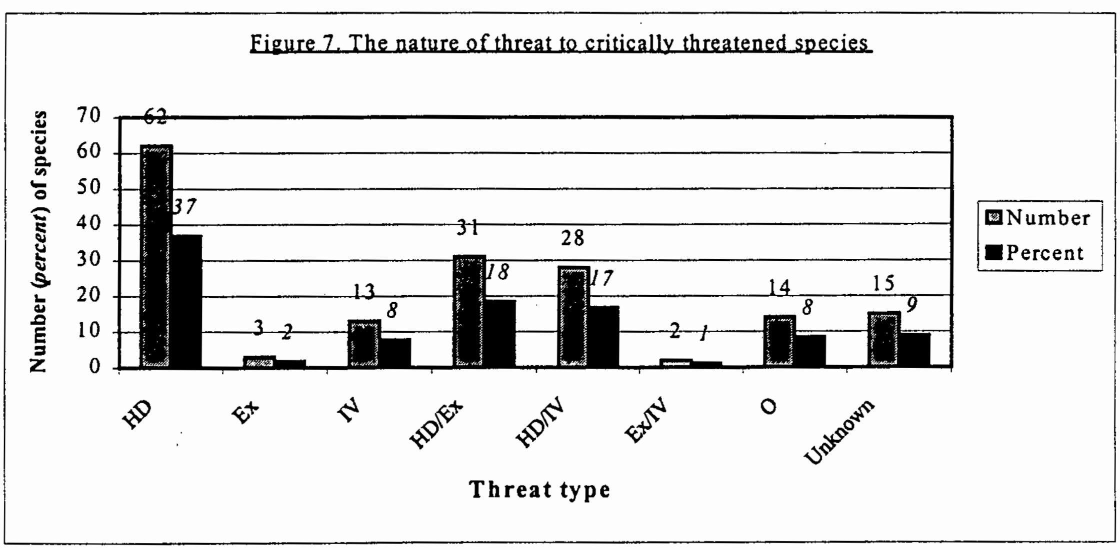
Only the main threat factors are discussed below but cognizance needs to be taken in considering the proportion of species that are also affected by natural causes and/or have small ranges or populations.

Habitat destruction alone affects 138 (59%) endangered species (Fig. 6); habitat destruction and exploitation combined affect a further 48 species (20%). These two threat types account for 79% of threat to endangered birds. Habitat destruction coupled with introduced vertebrates affects 15 species. Habitat destruction is therefore implicated in the poor conservation status of 86% of all endangered species. Introduced vertebrates alone, and causes classified as "other" each threaten 12 species. There are five species for which the threat is unknown.



Critical species

Sixty-two critical species (37%) are threatened primarily or exclusively by habitat destruction (Fig. 7). Combinations of habitat destruction and exploitation, and habitat destruction and introduced vertebrates are the next major sources of threat, affecting 31 (18%) and 28 (17%) species respectively. Thus, habitat destruction contributes to the critical status of 72% of critically threatened species worldwide. Fourteen species are threatened by the "other" causes mentioned earlier. Introduced vertebrates affect 13 species. Eighty-two percent of critical species have small ranges and/or populations. The threats to 15 species (9%) are unknown.



Geography of threat

All threatened species

Figures 8a+b compare the numbers and percentages of extinct and threatened species as a function of their distribution (mainland, island or both). Forty-nine percent of critically threatened species are found exclusively in mainland habitats. Forty-eight percent occur on islands only, and 2% inhabit both. In each threat category there are more species threatened in mainland habitats than on islands with the exception of critical species.

A summary of threat in the 25 most affected countries is presented by Collar *et al.* (1994). Asian countries contain the most threatened species (600) followed by South American countries (376). Specifically, Indonesia and Brazil have the greatest number of threatened species, 104 and 103 respectively, followed by the Philippines and China, both with 86.

Figure 8a. Distribution of extinct and threatened bird species amongst islands and mainlands (number)

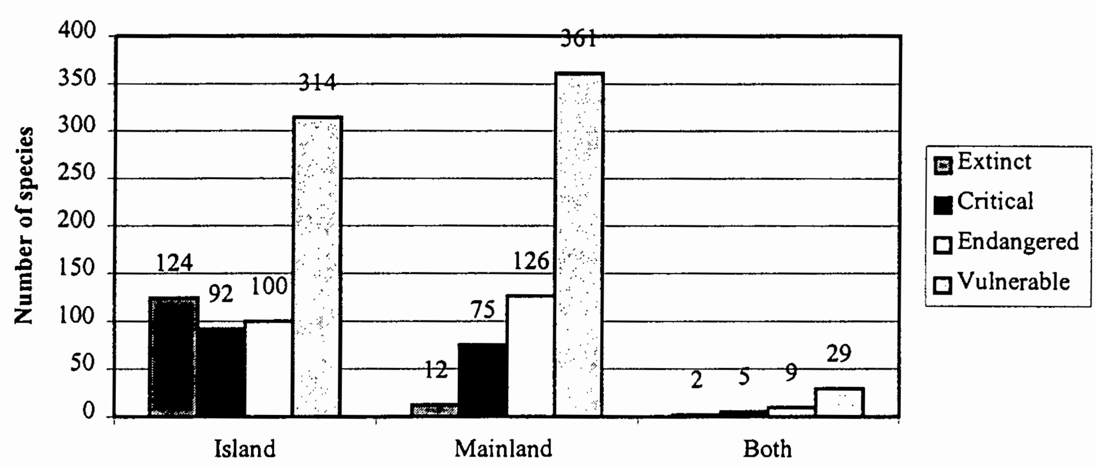
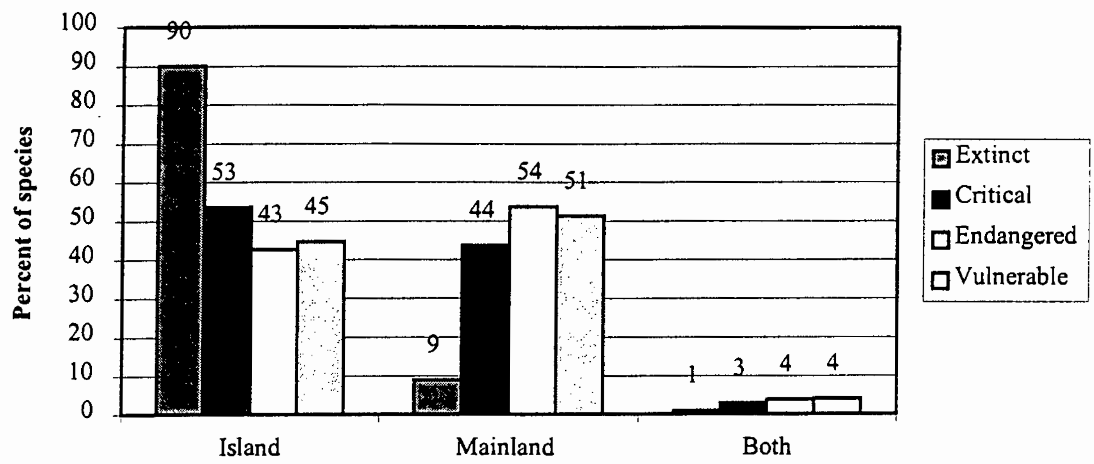


Figure 8b. Distribution of extinct and threatened bird species amongst islands and mainlands (percent)



Of endangered and critically threatened species, 264 (64%) occur on the mainland and 146 on islands (Table 27). South America has 159 species and Asia 145. (A larger proportion of species are vulnerable in the Asian region (86%) than in South America (48%) - Collar *et al.* (1994)). Forty-seven endangered and critically threatened species occur in Brazil and 45 in the Philippines. Colombia follows with 31 species; Mexico and Indonesia each have 20 species in these threat categories.

Table 27. Geographical distribution of threat in the 25 countries with the largest number of threatened species (not divided into regions).

All categories (vulnerable, endangered and critical)	Number of threatened species	*Endangered and Critical species* Country	Number of threatened species	*Threatened endemics* Country	Number of threatened species	Percentage of threatened species that are endemic
Indonesia	104	Brazil	47	Philippines	40	89
Brazil	103	Philippines	45	Brazil	32	68
Philippines	86	Colombia	31	Colombia	24	77
China	86	USA	25	USA	17	68
India	71	Indonesia	20	Indonesia	12	60
Colombia	62	Mexico	20	New Zealand	12	92
Peru	60	Peru	18	Australia	11	92
Ecuador	50	Ecuador	16	Madagascar	10	100
USA	46	Argentina	16	Peru	9	50
New Zealand	45	Vietnam	16	Venezuela	7	64
Vietnam	45	China	13	Ecuador	6	38
Australia	44	India	13	Cuba	6	60
Thailand	44	New Zealand	13	Angola	5	83
Myanmar	43	Australia	12	Kenya	5	100
Argentina	40	Venezuela	11	Somalia	5	100
Russia	35	Thailand	11	Vietnam	5	31
Mexico	34	Japan	11	Ethiopia	4	100
Japan	31	Madagascar	10	India	4	31
Malaysia	31	Paraguay	10	Seychelles	4	100
Papau New Guinea	31	Cuba	10	New Caledonia	4	100
Tanzania	30	Solomon Islands	9	Micronesia	4	100
Bangladesh	28	French Polynesia	9	Comoros	4	100
Madagascar	28	Malaysia	8	Mexico	3	16
Bolivia	27	Myanmar	8			
Zaire	26	Bolivia	8			

Endangered species

Nine South American countries contain a total of 73 endangered species (Table 28, Fig. 9). These species are spread over most of South America except for the southern part of the continent. Brazil and Colombia are most affected with 19 and 17 species respectively. Forty-nine of the 79 species are endemic to one country. Twenty-three species are found in two countries and 10 species in three countries.

There are 70 endangered species in Asia, 15 of which are mainland species. The Philippines has the highest number of endangered species with 26, more than one third of the endangered species in the region. Indonesia has the next most endangered species (10).

Africa has 31 endangered species, the country with the most endangered species being Angola with 6. There are nine endangered species on "African" islands, five of which are on Madagascar. There are two regions where there are a disproportionally large number of endangered species, east central Africa and the western parts of southern Africa. This is seen in Figure 10, which shows the global density of endangered birds.

Central American countries and islands contain the next highest number of endangered species (26), 14 of these occurring in Mexico. Eleven species inhabit islands, six being found on Cuba.

Australia and New Zealand have 19 endangered species, ten in Australia, eight in New Zealand and one that is found in both countries. There are a further five species that are threatened on islands in the south Pacific around Australia and New Zealand. In this region there are more species endangered on islands than in mainland regions, Asia being the only other region where the bias is skewed toward island species.

Europe is the only continental region that has no globally endangered species.

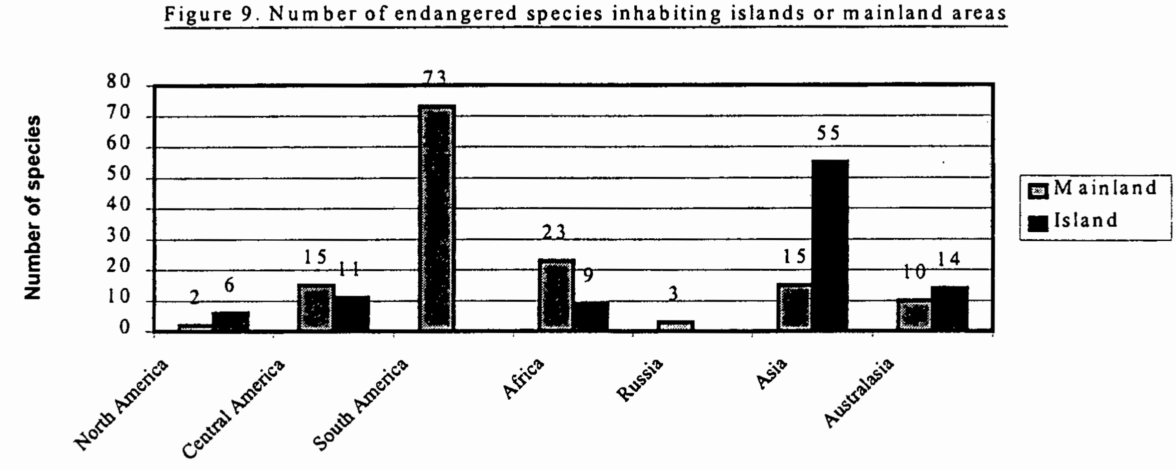
Table 28. Geographical distribution of endangered species

Region		Country	Number of endangered bird species	Totals
South America		Bolivia (BO)	3	73
Key: AR - Argentina		Brazil (BR)	19	
PY - Paraguay		Colombia (CO)	17	
CL - Chile		Ecuador (EC)	3	
		Peru (PE)	4	
		Venezuela (VE)	3	
		AR,BR,PY	9	
		AR,BR	1	
		BO,BR	1	
		BO,PE	2	
		CO,EC	2	
		CO,VE	2	
		EC,PE	5	
		PE,CL	1	
		CO,EC,VE	1	
Central America	Mainland	Mexico	14	26
		Guatemala	1	
	Islands	Bermuda	1	
		Cuba	6	
		Dominican Rep. and Haiti	1	
		Martinique	1	
		St. Lucia and Martinique	1	
		Puerto Rico	1	
North America		Canada	1	8
		U.S.A. (Mainland)	1	
		(Hawaii)	6	
Asia	Mainland	China	2	70
		Vietnam	2	
		India (and Bangladesh)	4	
		More than one country	7	
	Islands	French Polynesia	6	
		Indonesia	10	
		Japan	2	
		Micronesia	3	
		Philippines	26	
		Solomon Islands	1	
		Papua New Guinea and Solomon Islands	5	
		Sri Lanka	2	

Table 28 (cont.)

Russia		Russia	2	3
		Russia and China	1	
Africa	Mainland	Algeria	1	31
Key: CI - Ivory Coast		Angola	6	
GH - Ghana		Ethiopia (ET)	4	
ZA - South Africa		Kenya (KE)	1	
ZM - Zambia		Tanzania	1	
MW - Malawi		Somalia	4	
SD - Sudan		Zimbabwe (ZW)	1	
		CI,GH,GN	2	
		ET,ZA,ZM	1	
		MW,ZA,KE,SD	1	
	Islands	Cape Verde	1	
		Madagascar	5	
		Mauritius	1	
		Réunion	1	
		St. Helena	1	
Australia			10	10
Australia and N.Z			1	1
New Zealand and surrounding islands		New Zealand	8	13
		New Caledonia	3	
		Fiji	1	
		Togo	1	
			235	235

Figure 9. Number of endangered species inhabiting islands or mainland areas



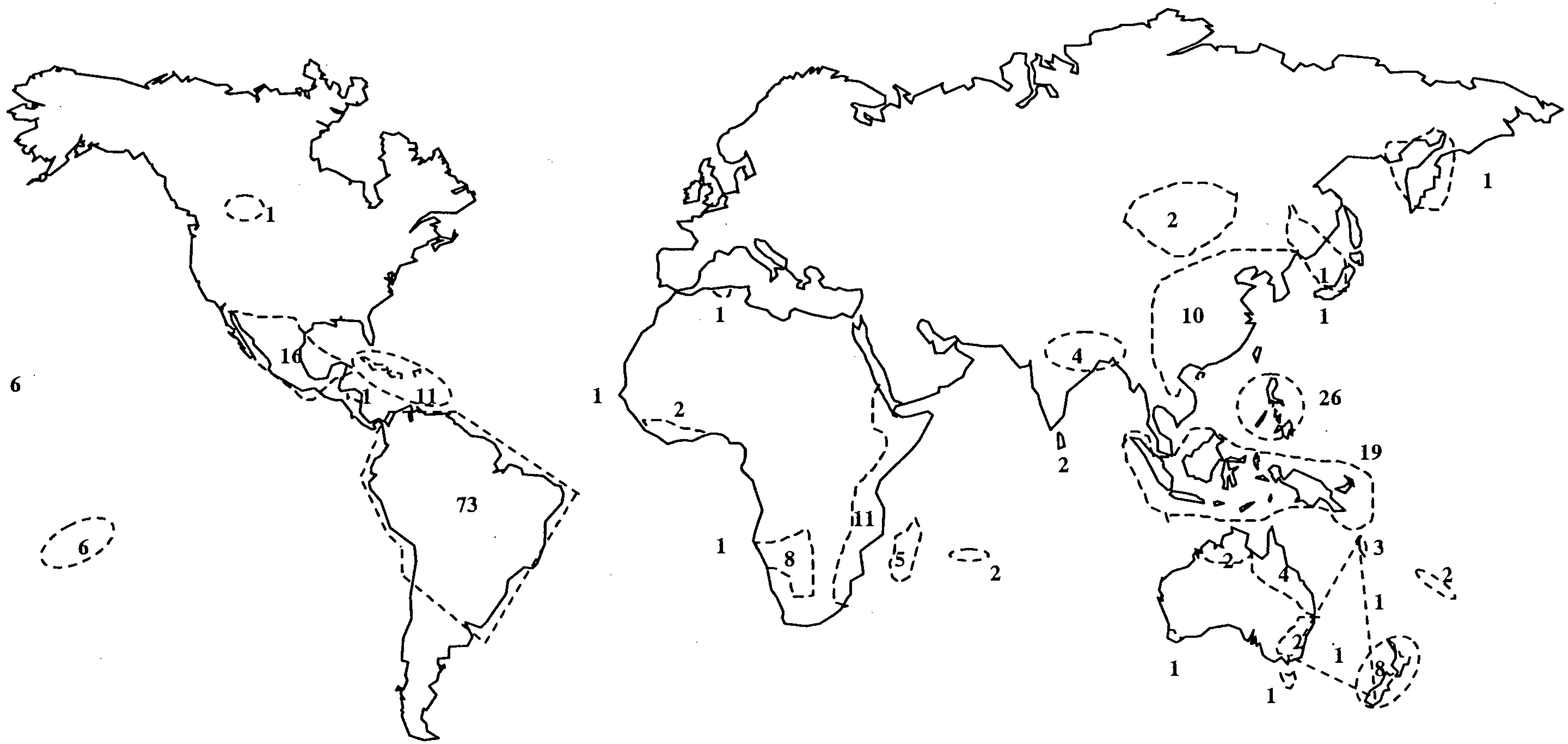


Figure 10. Distribution of endangered avifauna

Critically threatened species

South America has the highest number of critically threatened species with 42 (Table 29, Fig. 11). Asia and Africa are the next two most affected regions, with 41 and 37 critically threatened species respectively.

In South America, the 42 critical species are distributed in 11 countries and all are mainland species (Fig. 11). Brazil has 14 critical species, followed by Colombia with eight. Four species inhabit more than one country. There are 38 species endemic to eight respective countries.

Asia has 18 countries and islands that collectively hold 41 critical species. Mainland countries hold 14 species, of which China and Vietnam have four each. India and Nepal together share three critical species. Three species inhabit several countries; these are included as "other" in Table 31. Eight islands or island chains hold 27 critical species, 14 being found in the Philippines (Figure 12).

The 37 critically threatened African species are distributed amongst ten mainland countries and eight islands. Islands hold 68% of these species. There are 12 species that are critical in the ten mainland countries. Of the mainland countries, only Kenya has more than one species, with four. Some species' ranges extend over more than one country. The most affected region of mainland Africa is along the east coast where there are seven critical species. There are 25 critical species on eight islands/island groups. Madagascar and Mauritius each have five species and the Seychelles four.

Central American countries and islands have 15 critically threatened species. Mexico has the highest number with five followed by Jamaica with three. There are nine species that inhabit islands and six with mainland ranges.

Table 29. Geographical distribution of critically threatened species

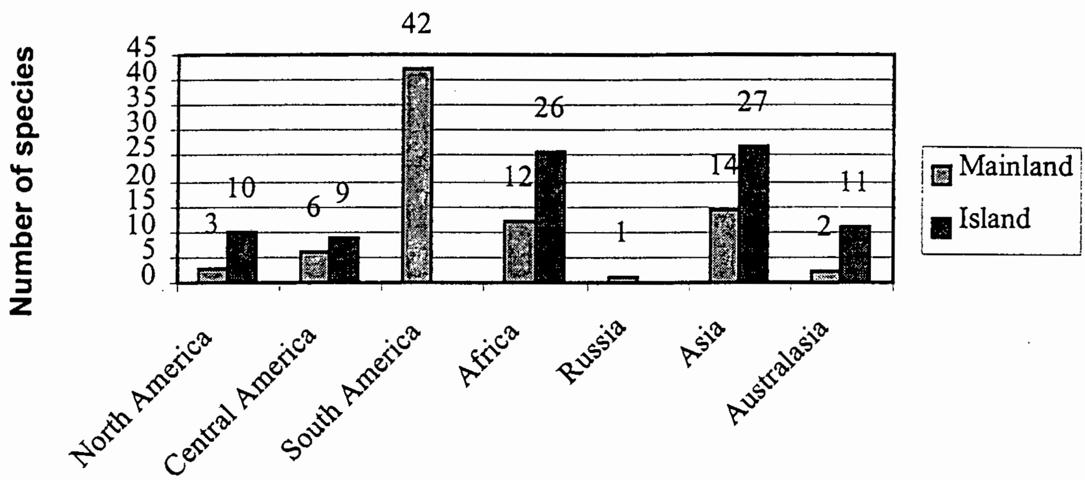
Region		Country	Numbers	Totals
South America		Argentina	1	42
(Codes for South American countries are as in		Bolivia	1	
Table 28).		Brazil	14	
		Chile	1	
		Colombia	8	
		Ecuador	4	
		Paraguay	0	
		Peru	5	
		Venezuela	4	
		AR,BR,PY	2	
		AR,CL	1	
		CO,EC	1	
Central America	Mainland	Mexico	5	16
		Honduras	1	
	Islands	Cuba	2	
		Jamaica	3	
		St. Lucia	1	
		Puerto Rico	2	
		Trinidad and Tobago	1	
		Granada	1	
North America		Canada and U.S.A.	1	13
		U.S.A. (Mainland)	2	
		(Hawaii)	10	
Asia	Mainland	China	4	45
		Vietnam	4	
		Other	4	
		India	3	
	Islands	Guam and N'rn Marianas	4	
		Indonesia	2	
		Japan	2	
		Micronesia	1	
		Philippines	14	
		Solomon Islands	2	
		Papau New Guinea and Solomon Islands	2	
		French Polynesia	2	
Russia			1	1

Table 29 (cont.)

Africa	Continent	Algeria	1	38
		Cameroon	1	
		Djibouti	1	
		Kenya	4	
		Liberia	1	
		Mozambique and Tanzania	1	
		Nigeria	1	
		Somalia	1	
		South Africa	1	
	Islands	Comoros	4	
		Madagascar	5	
		Mauritius	5	
		Mayotte	1	
		Réunion	2	
		Sao Tome and Principé	3	
		Seychelles	4	
		St. Helena	1	
		Madeira	1	
		Amsterdam Island	1	
Australia			2	2
New Zealand and surrounding islands		New Zealand	4	11
		Fiji	2	
		Norfolk Island	2	
		Cook Island	1	
		Western Samoa	2	
			168	168

Extinct in the wild		
NE Brazil	(Alagoas Curassow)	1
Guam	(Guam Rail)	1
Revillagigedo Is. (Mexico)	(Socorro Dove)	1
New Zealand	(Kakapo)	1
		4

Figure 11. The number of critically threatened species inhabiting islands or mainland areas



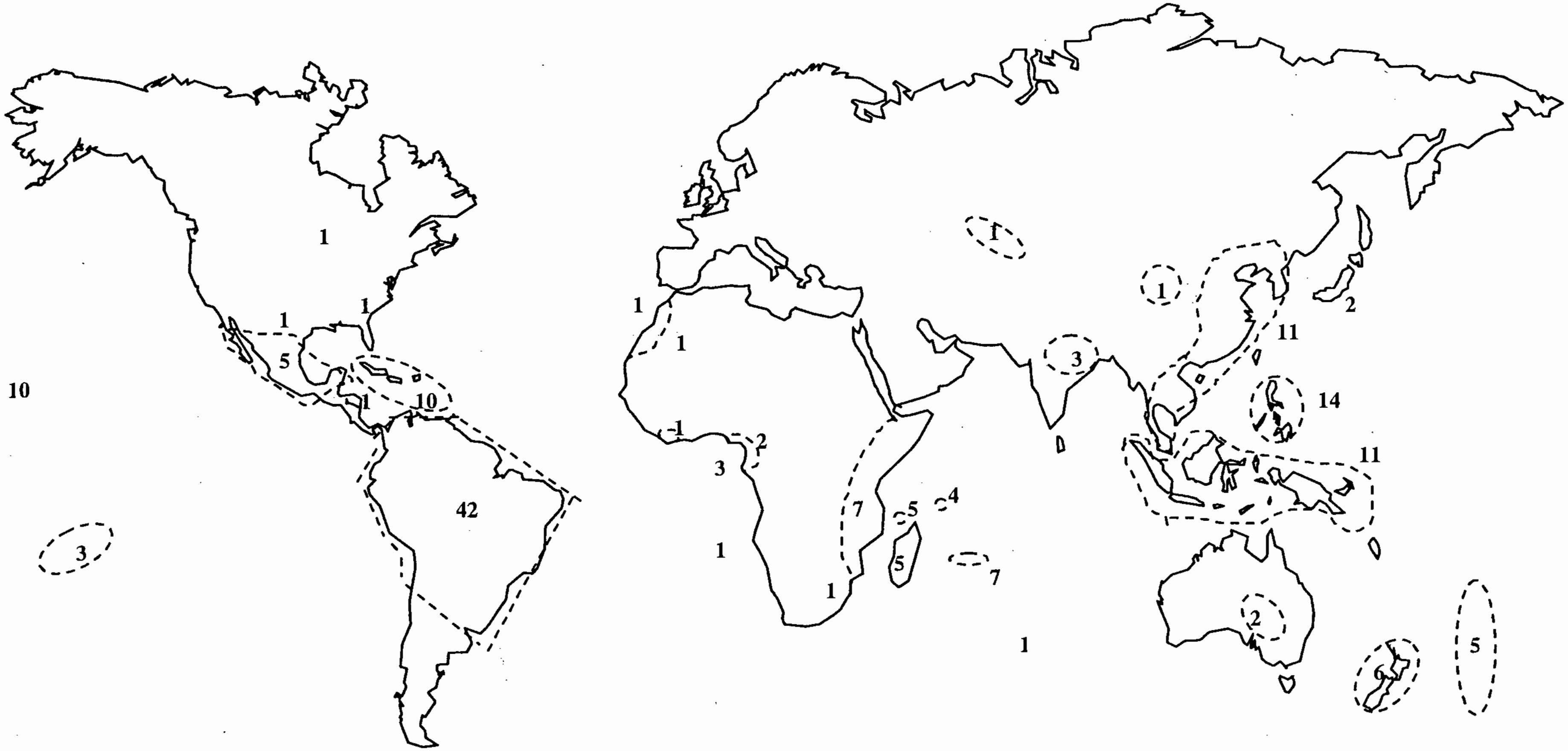


Figure 12. Global distribution of critically threatened avifauna

North American countries have 13 critical species: one species inhabits both Canada and the USA, the remainder being restricted to the USA. The North American continent, however, contains only three critical species as the remaining ten occur on the Hawaiian islands.

In the Australian region, there are 11 species critically threatened on islands and two on the Australian mainland. New Zealand and the immediate area around it, including Norfolk Island, contains six critically threatened bird species.

Russia has one critically threatened species, the Slender-billed Curlew *Numenius tenuirostris*.

Table 29 also lists the names of those birds classified as "extinct in the wild" and the country in which they are found. Three islands and one mainland country are affected.

Taxonomy

Monroe and Sibley (1993) and Collar *et al.* (1994) do not follow identical classifications. Adopting a particular classification influences measures of degrees of threat at the family level. For threatened species I have adopted Collar *et al.*'s (1994) classification and indicate where these classifications differ at the family level (Table 32). For numbers of extant species in families I follow Monroe and Sibley (1993). Where Monroe and Sibley (1993) and Collar *et al.* (1994) differ on the family/sub-family level this is indicated in Table 30 and is explained.

All threatened species

One hundred and forty five avian families hold the approximately 9700 bird species in the world (Monroe and Sibley 1993). The sizes of these families range from 1 species (Struthionidae) to 824 species (Emberizidae). Collar *et al.* (1994) list 102 families and 14 sub-families that contain threatened species. Numbers of threatened species within families range from a single species (e.g. Hydrobatidae and Sulidae) to the Psittacidae where 88 (24%) of the 349 species are threatened.

A correlation between family size and the number of threatened species in them, using all the extant families, including those which did not have threatened species in them, indicated no relationship between family size and the number of threatened species in it. ($r_{204} = -0.06$).

Table 30 lists families in which 20% or more of species are threatened. Three hundred and sixty three species are contained in these families. Five families have all of their species threatened; all of these are families containing between one and three species. The Drepanididae, a larger family, has almost 80% of its species threatened. This is followed by the (smaller families) Casuariidae, Picarthartidae, Callaeidae and Orthonychidae, each with 50% of the family threatened. These families have only two or four extant species in them.

Among families with threatened taxa, 16 (40%) contain having fewer than ten species: these include 26 threatened species. Eight of the 39 families in Table 30 are relatively large, having more than 50 extant species. These eight families together account for 257 of the threatened species, almost one quarter of the global total.

Table 30. Status of families which have over 20% of their species threatened

Family	Number of species threatened	Number of extant species	Percent threatened	Percent extinct
Casuariidae	2	4	50	0
Apterygidae	3	3	100	0
Spheniscidae	5	17	29	0
Diomedeidae	3	14	21	0
Procellariidae	23	79	29	1
Pelecanoididae	1	4	25	0
Pelecanidae	2	9	22	0
Phalacrocoracidae	8	36	22	2
Fregatidae	2	5	40	0
Ciconiidae	5	26	20	4
Threskiornithidae	7	33	21	5
Phoenicopteridae	2	5	40	0
Cracidae	15	50	30	0
Phasianidae	48	175	27	1
Megapodiidae	8	19	42	0
Mesitornithidae	3	3	100	0
Turnicidae	5	16	31	0
Rallidae	32	132	24	10
Heliornithidae	1	4	25	0
Pedionomidae	1	1	100	0
Gruidae	7	15	47	0
Rhynochetidae	1	1	100	0
Psittacidae	88	349	25	5
Tytonidae	5	17	29	6
Coraciidae	4	12	33	0
Capitonidae	3	14	21	0
Pittidae	7	31	23	0
Philepittidae	1	4	25	0
Cotingidae†	15	69	22	0
Atrichornithidae†	2	2	100	0
Picathartidae	2	4	50	0
Zosteropidae	21	93	22	2
Drepanididae†	16	21	76	33
Callaeidae	1	2	50	33
Orthonychidae	1	2	50	0
Laniidae	1	30	35	0
Cinclidae	1	5	20	0
Totals	363	1332		

† Monroe and Sibley (1993) classify these below the family level whereas Clements (1991) and Collar *et al.* (1994) list them as families. Column three uses figures for sub-families or tribes as listed by Monroe and Sibley (1993) that best reflect the grouping used by Collar *et al.* (1994).

Endangered and critical species

Eighty-three families contain one or more endangered or critically threatened species. Of these, 25 families have five or more endangered and critical species in them (Table 31). One hundred and fourteen of the 168 critical species (68%) and 155 of the 235 endangered species (66%) are contained in these families. Thus, approximately one-third of all families with endangered and critical species in them hold 67% of the total endangered and critical species complement.

Table 31. Status of families with five or more endangered and critical species

Family	Critical	Endangered	Number of extant species	Percent endangered and critical species
Procellariidae	9	4	78	16
Ciconiidae	5	1	26	23
Anatidae	4	2	129	4
Accipitridae	3	6	251	4
Cracidae	5	3	50	16
Phasianidae	8	6	175	8
Rallidae	6	10	132	12
Columbidae	13	9	310	7
Psittacidae	10	26	349	10
Strigidae	4	4	155	5
Trochilidae	8	7	322	4
Furnariidae†	3	4	279	3
Formicariidae	2	8	244	4
Tyrannidae†		6	539	1
Alaudidae	1	4	91	5
Turdidae†	6	6	176	6
Timaliidae†	1	5	236	2
Muscicapidae†	1	6	117	6
Monarchidae†	4	6	138	10
Zosteropidae	7	1	93	8
Emberizidae*	4	14	612	3
Drepanididae†	4	6	21	48
Icteridae†	1	6	97	7
Fringillidae†	1	4	170	3
Parulidae†	4	1	116	4
Totals	114	155	4906	

† These taxa are listed at a sub-family level by Monroe and Sibley (1993) but at the family level by Collar *et al.* (1994) and Clements (1991).

* Monroe and Sibley (1993) include in this family what Clements (1991) and Collar *et al.* (1994) consider families (Emberizidae, Icteridae and Parulidae) and list 824 species. This table follows the latter's classification.

The Psittacidae have the highest number of species in these categories (36) followed by the Columbidae (22) and the Emberizidae (18). These families contain a relatively large number of species; 360, 313 and 612 respectively. Families with the highest proportion of endangered and critical species are the Drepanididae (48%), Ciconiidae (23%) and Cracidae (16%). These families contain fewer taxa: 21, 26 and 50 species respectively.

There is a negative correlation between the size of a family and the proportion of endangered or critical species within it ($r_{25} = -0.36$, $p < 0.05$). Families that are smaller tend to face a higher degree of threat.

Endemicity

There are 81 endemic species in six South American countries, 61 in four Asian countries, 23 in Australasia and 19 in Africa (Collar *et al.* 1994). Of the 86 endangered and critical species endemic to islands, 40 are endemic to the Philippines and 12 each to Indonesia and New Zealand.

The country with the greatest number of endangered and critical endemic species is the Philippines with 40, accounting for two-thirds of the endangered endemics in the Asian region. The next two most affected countries are Brazil (32) and Colombia (24).

Seven countries have only endemic birds that are endangered or critical, the number of species affected being either four or five. Of these countries four are islands. Ninety-two percent of New Zealand's and Australia's endangered and critical species are endemics. In the Philippines this figure stands at 89% and in Brazil and Colombia it is 68% and 77% respectively.

Habitat of threatened birds

Avian species that live in forests are under greater threat than species that live in other habitats. Over half of the threatened birds of the world (632 species, 56.9%) live exclusively in forests. When considering birds that inhabit forests as well as some other habitat, 74.6% of all threatened birds are affected (709 species) (Collar *et al.* 1994).

Comparing the habitat requirements of vulnerable, endangered and critically threatened species shows that the same percentage of birds that are vulnerable and endangered inhabit forests (55.7%). Almost 80% of endangered species live in forests or both forests and some other habitat. Of the critically threatened species 63.4% inhabit forests only and over three quarters inhabit forest or both forest and some other habitat.

Of the other habitats that hold a higher proportion of the remaining threatened birds, scrub, wetlands and grasslands are most important. Scrub holds 9.3% of threatened species, wetlands 8.8% and grassland 6.3%.

Body size, endemicity, threat and extinction on ten selected islands

Ten islands of various sizes accounting for a range in the diversity of endemic avifauna were selected to test whether a relationship existed between body size, endemicity, threat and extinction. This excluded island groups and archipelagos but did include individual islands found within these. Dunning (1993) does not list body masses for all the endemics on these islands so only endemics for which a body mass was available or could be reasonably inferred were used.

Within the selected subset of islands, Madagascar and Jamaica hold the most diverse endemic avifaunas and are also the two largest islands, although Jamaica is only marginally larger than the island of Hawaii (which has fewer endemics - Table 32).

Molokai has no endemics. No other island has more than ten endemics and, of these, no particular sized island has suffered a disproportionately large number of endemic extinctions.

Table 32. Body mass of endemic species on ten selected islands

Island	Island size (km^2)	Number of endemics	Body mass (g)					Total
			< 50	50 - 100	100 - 300	300 - 700	> 700	
Lord Howe	17	2	1			1		2
Rodrigues	104	2	2					2
Molokai	676	0						0
Chatham	960	6	2		2		1	5
Tahiti	1042	2	1			1		2
Mauritius	1865	7	4		2	1		7
Réunion	2510	6	2	2	1	1		6
Hawaii	10464	5	3			1		4
Jamaica	10991	25	13	2	5	2	1	23
Madagascar	594180	104	38	6	22	7	6	79
Total			66	10	32	14	7	130

Most endemics for which there was information on body size had masses of <50 g (51%) or between 100-300 g (26%). Body masses of critical and endangered endemics on the ten islands are found in Table 33. The island with the most critical and endangered species is Madagascar (9), followed by Mauritius (5) and the island of Hawaii (3). Two islands have no critical or endangered species, and three islands one such species.

Overall, twenty percent of the endemics on these islands are critical or endangered. Although the largest fall within the weight ranges <50 g and 100-300 g, the largest proportion of critical and endangered species have body masses >700 g (63%). Four of these birds are on Madagascar and one on Chatham Island.

Table 33. Critical and endangered endemics on ten selected islands

The "%" in the Total column indicates the percentage of all endemic avifauna on the island that are critical or endangered (for which body masses were available).

Island	Island size (km^2)	Primary threat cause	Body size (g)					Total	
			< 50	50 - 100	100 - 300	300 - 700	> 700	#	%
Lord Howe	17	IP				1		1	50
Rodrigues	104	HD	1					1	50
Molokai	676	?						0	
Chatham	960	IP	1		1		1	3	60
Tahiti	1042	?						0	0
Mauritius	1865	HD	2		2	1		5	71
Réunion	2510	HD,Ex		1	1			2	33
Hawaii	10464	HD,O	2			1		3	75
Jamaica	10991	HD,Ex,IP			2			2	8
Madagascar	594180	HD	3		2		4	9	11
Total			9	1	8	3	5	26	20
Percent under threat			16	9	26	23	63	20	

Habitat destruction features as the primary threat on six islands affecting 22 endemics. Introduced predators feature on three islands and affect six species; exploitation on two islands, in combination with other factors, affects four species. Combinations of primary threats occur on only three islands, these being two large islands (Jamaica and Hawaii) and one smaller island (Réunion).

Three of the islands have experienced ten or more extinctions - Rodrigues, Mauritius and Hawaii (Table 34), but there is no correlation between the number of extinct species and island size. The other islands, with the exception of Réunion, have experienced four or less extinctions. Madagascar, Mauritius and Hawaii have the most critical and endangered species (Table 34). Hawaii and Mauritius are islands that have experienced a large number of extinctions and also have a high proportion of their endemic avifauna endangered or critically threatened.

Table 34. Numbers of extinct, extant endemic, threatened and resident bird species on selected islands

Island	Island size (km^2)	Number of extant endemic species	Extinct species		Number of extant and extinct endemics	Critical and endangered endemics		Total number of resident species	Human population
			Cause	Number		Cause	Number		
Lord Howe	17	2	Ex,IP	3	5	IP	1	27	371
Rodrigues	104	2	Ex	10	12	HD	1	14	36115
Molokai	676	0	HD	2	2		0	37	6587
Chatham	960	6	HD,IP	4	10	IP	3	16	760
Tahiti	1042	2	IV	4	6		0	21	131309
Mauritius	1865	7	Ex	11	18	HD	5	25	1116923
Réunion	2510	6	Ex	9	15	HD,Ex	2	26	652857
Hawaii	10464	5	HD,O	12	17	HD,O	4	62	120317
Jamaica	10991	25	?	2	27	All 3	3		2555064
Madagascar	594180	105	HD,Ex	2	107	HD,Ex	9	201	13427758
Totals		140		59	219		28	429	

In analyses that excluded Madagascar (which is an order of magnitude larger and has an order of magnitude more endemics than any other island in Table 34), there are significant correlations between island size and the number of extinct and extant endemic species ($r=0.86$, $p<0.05$) and between island size and the number of resident species ($r=0.89$, $p<0.05$). These correlations are perhaps intuitive, as one would expect larger islands to have more endemics and more residents. There is also a statistically significant correlation between the proportion of extinct and critical and endangered endemic birds (of all extant and extinct endemics since 1600) and human population density ($r=0.77$, $p<0.05$). This lends support to the idea that anthropogenic effects may be the cause of many more extinctions (Diamond 1989, Milberg and Tyrberg 1993, Simberloff 1984, 1986a).

Extinction and primary threat causes have changed over time on six of the islands in Table 34. On two islands there has been a complete switch between extinction and threat cause, and on four islands a threat cause has been added or removed (however this may only be an artifact of changed perception of threat cause based on improved scientific observation). Two islands have no critical or endangered endemic birds. On Hawaii and Madagascar the historical extinction and current threat causes affecting endemic species are the same.

Small islands are characterized by single threat causes, and larger islands by multiple threat causes. Extinction was caused on the smaller islands by both multiple and single factors and on larger islands by multiple factors. For critical and endangered endemics, habitat destruction threatens 19 species, exploitation four and introduced predators four. A swing from exploitation as the primary extinction factor to habitat destruction as the primary threat factor on these islands is evident.

Considering bird body size, 30 and three extinct species fell into the size ranges <50 g and 100-300 g respectively (27% and 3%). Nineteen extinct species fell into the 50-100 g range (17%) and 11 into the 300-700 g range (10%) with 12 (11%) being >700 g. The highest proportion of extinct species were placed in the <50 g size range, different to critical and endangered species that had the highest proportion in the >700 g range. In terms of numbers of endemic species, however, both had a maximum in the <50 g range.

The ten islands were placed into size categories of <1 000 km^2, 1 000-10 000 km^2 and >10 000 km^2 and bird body sizes of the endemic species into mass categories of <100 g and >100 g (Table 35). This was done for extinct, extant, critical and endangered avifauna for which masses were available or could be inferred.

Table 35. Numbers and proportions of extinct, extant and critical and endangered endemic species on the ten selected islands in relation to their body masses. Proportions are of numbers in the column headings.

	Extant and extinct species (192 *spp.*)				Extinct species (56 *spp.*)				Critical and endangered species (26 *spp.*)			
Body mass (g)	< 100		> 100		< 100		> 100		< 100		> 100	
Island size (km^2)	#	%	#	%	#	%	#	%	#	%	#	%
< 1 000	19	10	15	8	7	13	11	19	2	7	3	12
1 000 - 10 000	13	7	25	13	4	7	19	34	3	12	4	15
> 10 000	73	38	47	24	11	20	4	7	5	19	9	35
Totals	105	55	87	45	22	40	34	60	10	38	16	62

The largest proportion of critical and endangered endemic bird species are those with a body mass >100 g found on islands whose area is >10 000 km^2. The largest proportions of extinct birds had body mass in the same range and were found on islands with a size range of 1 000 - 10 000 km^2. The largest proportions of extinct and extant endemics in both size ranges was on islands >10 000 km^2; this result is due largely to the higher number of endemics found on Madagascar. On Hawaii and Madagascar (islands of >10 000 km^2 which support endemic avian species in both mass ranges - Table 33), the proportion of critical and endangered endemics is lower by almost half the proportion of species that has become extinct since 1600.

The number of critical and endangered endemic species in Table 35 is very much less than the number of species that have become extinct since 1600. There are two exceptions: endemic birds on islands with areas between 1 000 and 10 000 km^2 whose mass is <100 g, and endemic birds on islands > 10 000 km^2 with body masses of > 100 g. In the former category, although numbers are similar, the proportion of endemic species which are critical and endangered is almost double that of species that have become extinct. In the latter category, the number of critical and endangered endemic species affected is double that of extinct avifauna. The proportion of critical and endangered endemic bird species is five times that of avifauna that have become extinct on these islands since 1600.

In terms of extinct and extant species, the three islands in the size range >10 000 km^2 had more small birds become extinct since 1600 than are currently threatened: of birds <100 g, 11% became extinct whereas currently 4% are critical or endangered. There is, however, a higher proportion of large birds currently threatened on these islands than became extinct since 1600: 9% of birds >100 g are critical or endangered whereas 3% of birds in this range have become extinct since 1600. Perhaps this is an indication of the effect of habitat destruction (a threat on all three islands) on larger species, which need larger habitat ranges to survive.

On islands of <10 000 km^2, the lower proportions of critical and endangered species compared with those of islands of area > 10 000km^2 (Table 36) are as a result of the large proportion of extinct species making up the total extinct/extant endemic avifauna compliment (41 of 72 species - 57%).

The proportion of extinct and extant endemic bird species on these ten islands that are critical and endangered is generally much lower than the proportions of birds that have become extinct (Table 36). Extinct species (in both mass categories) made up 30% of 192 species that formed the historical species compliment and critical and endangered species 12%. The largest proportions of the historical endemic species compliment to become extinct were birds with body masses of >100 g (18%), primarily from islands whose size was <10 000 km^2. Relatively few threatened birds fall in these categories.

Table 36. Proportions of the total historical endemic avifauna (of the ten islands) that have become extinct or are classified as critical and endangered.

Body mass (g) / Island size (km^2)	Extinct species < 100 g	> 100 g	Critical and endangered species < 100 g	> 100 g
< 1 000	4	6	1	1
1 000-10 000	2	10	1	2
> 10 000	6	2	2	5
Totals	12	18	4	8

The majority of critical and endangered species have masses >100 g, and inhabit islands >10 000 km^2: more than twice as many species in this category are threatened or have already become extinct. This suggests, that on these islands, where extinct species form a very low proportion of all birds inhabiting them since 1600, larger species are more at risk of extinction today. Islands that have experienced a comparatively high proportion of extinction of birds of a certain size have a low proportion of critical or endangered species of that same size category. However, considering all islands, the proportion of large birds at risk of extinction is approximately double the proportion of small birds, despite the fact that proportionally more large birds are already extinct. This is perhaps the result of a new extinction pressure being applied, that of habitat destruction i.e. those birds which survived the early threats of exploitation and predators may be unable to survive the more recent threat of habitat loss.

Part 2 - Discussion

Causes of threat

Habitat destruction

The most important factor affecting currently threatened avifauna is habitat destruction. This threat is not unique to birds and impacts most other taxa (Smith *et al.* 1993b). Of the threatened birds, almost two-thirds (65%) live all or part of their lives in forest (Collar *et al.* 1994 - Fig. 5). Other habitats that have endangered or critical species inhabiting them include scrub, wetlands and savannah and grasslands. Between them, these habitats support the majority of the remaining threatened species (Collar *et al.* 1994).

In addition to forest-dwelling birds, approximately two-thirds of the world's land and fresh water animal species are found in tropical forests (Raven 1988, Stevens 1995b). Overall annual losses of open and closed forests averaged 15.4 million hectares during 1981-1990, or 0.8% per annum, with 40% of their original area already lost (Wilson 1988, Myers 1992, Grainger 1993). This rate appears to be accelerating (Sayer and Whitmore 1991, Whitmore and Sayer 1992, Brooks *et al.* 1997). Balmford and Long (1994) show a positive association between the rate at which tropical forests are being cleared and their biological importance. On average, countries with large numbers of range-restricted forest endemics are losing their forests faster than countries with lower levels of endemism. The reasons underlying this relationship are unclear (Balmford and Long 1994), but it should be noted that these countries are tropical, mostly third-world and therefore poor. Logging plays a vital role in foreign exchange earnings for these countries, which are needed to meet their debts. The economies of these countries are placed before their ecologies, with potentially disastrous effects on endemic (as well as other) species.

1. Predation, competition and introduced disease

Introduced vertebrates affect 6% of threatened bird species and all of these are island species. Although this is a small percentage of the total number of threatened species, extinction risk seems to be particularly high for these species: five of the nine most recent extinctions were as a result of introduced predators. Savidge (1987) documents the extinction of the Guam Flycatcher as a result of the introduction of the Brown Tree Snake *Boiga irregularis* and Pimm *et al.* (1995) allude to the disastrous impact the introduction of this snake might have on Hawaiian avifauna. Of the four species that are classified "extinct in the wild", two (the Guam Rail and Socorro Dove) were driven to this state by introduced vertebrates and for a third (the Kakapo), this has become the primary threat (Collar *et al.* 1994). The original habitats of these three species are islands.

2. Hybridization

Another threat stemming from introduced vertebrates is that of hybridization. In New Zealand, hybrids between the endemic Grey Duck *Hymenolaimus malachorynchus* and the introduced Mallard *Anas platyrhynchos* are common throughout both the main islands and on Chatham Island (Rhymer *et al.* 1994). In some areas, hybrids greatly outnumber "pure" Grey Ducks and there is strong reason to think that only a hybrid form will remain (Rhymer *et al.* 1994). In the Hawaiian islands, where the Mallard breeds with the endangered Hawaiian Duck *Anas wyvilliana*, hybridization appears to be rampant on Hawaii and Oahu (Simberloff 1994). Owen *et al.* (1986) expressed concern that the North American Ruddy Duck *Oxyura jamaicensis*, feral in Britain, would, as it spread to continental Europe hybridize with the rare White-headed Duck *O. leucocephala* of Spain. This has indeed happened in southern Spain and the offspring are viable (del Hoyo *et al.* 1992, Urdiales and Pereira 1993).

Inbreeding

Another potential factor that may play a role in the extinction proneness of island avifauna is that of inbreeding depression. Frankham (1998) showed that island populations were significantly inbred, with breeding co-efficients significantly higher in endemic than non-endemic island populations. Threatened island avifauna may therefore be more difficult to conserve than threatened mainland species. Habitat destruction is likely to increase the effect of inbreeding as small, isolated populations will become inbred over time.

Endangered and critical species

Habitat destruction is the main threat to species in these two categories, affecting 86% of all endangered species and 72% of critical species. Over half the species in this list are found in South America and Asia, and it is in these regions and for this reason that greatest concern is expressed over the next mass extinction (Balmford and Long 1996, Brooks *et al.* 1997).

<u>Geography of threat</u>

There are more threatened species in mainland areas than on islands. However, the proportion of species under threat on islands is greater than those on the mainland. Approximately 23% of all birds that inhabit islands are under threat (calculated from Monroe and Sibley 1993). Of species that inhabit mainland areas, less than 10% are under threat. The global average of birds under threat, as listed by Collar *et al.* (1994), is 12 %. In terms of avian biodiversity, islands therefore have proportionally a lot more to lose than mainland regions (and have already lost proportionally considerably more). Island species face threat primarily from habitat destruction and introduced vertebrates.

Hot Spots

Myers (1988) identified ten tropical areas that (a) are characterised by exceptional concentrations of species with high levels of endemism and (b) are experiencing unusually rapid rates of habitat depletion. These "hotspots" comprise less than 3.5% of remaining primary forests but harbour over 34 000 endemic plant species and 700 000 endemic animal species. Should these areas lose 90% of their forest cover, 7% of the Earth's plant species and a similar proportion of animal species would become extinct. Myers (1988) estimated that in the next 25 years, the extinction rate in these ten hotspot areas could be as much as 20 000 times the background extinction rate.

The ten "hotspots" are Madagascar, the Atlantic coast of Brazil, western Ecuador, the Colombian Choco, the uplands of western Amazonia, the eastern Himalayas, Peninsular Malaysia, northern Borneo, the Philippines and New Caledonia. Hawaii and Queensland are also identified as hotspots, but here conservation resources are much more plentiful than in the developing world (in which the ten other hotspots are found), so extinction threats can (at least in theory) be readily reduced.

Geography of endangered and critical species

South America currently holds 73 endangered and 42 critical species, the highest number for any region in this analysis. This has resulted primarily from forest loss in the region. Although there are so many species in these two categories, there have been only three avian extinctions here in recent history. The most recent extinction was in 1977 as a result of habitat destruction (Colombian Grebe *Podiceps andinus* - Table 26). The causes of the other two losses (the Tumaco Seedeater *Sporophila insulata* and the Glaucous Macaw *Anodorynchus glaucus*) were also habitat destruction, these being in 1912 and 1955. Taking into account the effects of a time lag between deforestation and extinction (Heywood *et al.* 1994), many of the endangered and critical species in this region are likely to be in imminent (and perhaps irreversible) danger of extinction.

There are more endangered and critical species in mainland regions than on islands. This is in contrast to the extinction trend, where island extinctions have out numbered mainland ones. This pattern is largely a result of the large number of endangered species on the South American mainland. Of critical species world-wide, however, just under half are found on islands (83 of 168 species). In geographical areas which incorporate both mainland and island areas, islands support the greatest numbers of critical species (Table 37).

Table 37. The number of critical species found on islands and the mainland in regions where islands are present.

Region	Number of species on islands	Number of species on the mainland
Asia	27	14
Africa	26	12
North and Central America (including Hawaii)	19	10

The fate of Hawaii's endemic avifauna is sobering testimony to man's impact on biodiversity. Should the ten critically threatened birds become extinct within the next ten years, this will raise the total number of extinctions on these islands since the arrival of the Polynesians to 111, leaving only 25 of the estimated 136 original species (Pimm 1995) extant by the year 2008. In historical times, the islands will have experienced 27 extinctions, at an extinction rate of 496 species per million species per year, a rate 500 times the background extinction rate.

Mainland Africa has not experienced any avian extinctions since 1600 but currently holds 22 endangered species and 12 critical species. On African islands there are 9 endangered and 26 critical species. The islands with threatened taxa have generally more than one critical species on them, only three having a single species. Four of the nine islands holding critically threatened species have experienced extinctions in recent history (Madagascar, Mauritius, Réunion and the Seychelles) and these currently hold 16 of the 25 critical species. The primary causes of threat on these islands are habitat destruction and introduced vertebrates. All but one of the extinctions on these islands occurred before this century, the exception being the recent extinction of the Aldabra Warbler *Nesillas aldabrana* in 1986 as a result of introduced vertebrates from the Seychelles. On the Mascarene Islands, there are fewer species currently threatened than have become extinct historically, suggesting that the species most prone to extinction have already been lost. However, seven of the 12 threatened species are critically threatened. This may indicate an imminent effect of a new extinction filter on these islands as the last extinction was in 1876, the new filter being habitat destruction and introduced vertebrates. Historically, exploitation has been the major cause of bird extinctions in the Mascarenes. Two species in Madagascar are on the brink of extinction, if not already extinct (O. L. Langrand, pers. comm.). These are the Madagascar Pochard *Aythya innotata* and Alaotra Grebe *Tachybaptus rufolavatus*.

Endangered and critical endemic species in the 25 most affected countries

The greatest numbers of endemic species in the endangered and critical categories are found in central and South America (81). It is also here where some of the most severe deforestation is taking place (Sisk *et al.* 1994). Brooks and Balmford (1996) predict that 88 species will be lost from the South American Atlantic forests over some (unspecified) time lag. As this figure includes birds from one small region only, South America as a whole may well be facing a major extinction event.

The Philippines and Indonesia hold the highest number of endangered and critical endemics in the Asian region. Birds in both countries are under threat primarily from habitat destruction. Dinnerstein and Wikramanayake (1993) identify the Philippines as one of the areas with the lowest percentage of protected forest in the Indo-Pacific region, and, if current deforestation rates continue, very little indigenous forest will remain in ten years. Indonesia is ranked as the region with the highest overall level of endemism (all species, including birds) in the world (Sisk *et al.* 1994). Brooks *et al.* (1997) showed that deforestation affects species with small ranges most severely and that these ranges generally overlap to form "hotspots" (ICBP 1992). Deforestation is often concentrated in these hotspots (Balmford and Long 1996).

The number of species listed as threatened in insular south-east Asia by Collar *et al.* (1994) is very similar to the number of bird species that Brooks *et al.* (1997) predict will become extinct in this region using the species-area curve. They separated island endemics into single-island endemics and intra-archipelago endemics and found that single-island endemics are more at risk than the more widespread species. Small populations of single-island endemics are at greatest risk of extinction here (Pimm *et al.* 1993).

In the Afrotropics, Madagascar has the highest number of endangered and critical avian endemics. Habitat destruction is a pervasive threat to all endemics here with eight of the ten threatened endemics having small ranges or populations. Considering all animal species, Madagascar is ranked 5th in endemic species richness by Sisk *et al.* (1994). The last proven avian extinction here (Snail Eating Coua *Coua delalandei*), some time between 1920 and 1930, was a result of habitat destruction and exploitation. Madagascar is considered by Myers (1988) to be a "hotspot" for extinction. There have been no documented mainland bird extinctions in Africa in recent history although several species have not been seen for many years. Today, however, there are five mainland countries that contain 19 endangered and critical avian endemics. Kenya has four critical species and Somalia one. Sisk *et al.* (1994) list Kenya and Angola as areas of critical global concern and rank the Ivory Coast as the country in the world with the highest forest-loss index.

Of the 17 "North American" endangered and critical endemics, 16 are on the Hawaiian islands. The threats faced by the Hawaiian birds are habitat destruction and introduced vertebrates, the same threats that caused most of the extinctions on these islands (Olson and James 1984). All the species listed as critical have small ranges or populations. Myers (1988) considers Hawaii a "hot spot", but adds that because conservation resources are more plentiful here (compared to developing countries), extinction threats can be reduced.

New Zealand has the same number of endangered and critical endemics as Indonesia, only the Philippines having more species in these categories. The New Zealand birds are threatened by habitat destruction and introduced vertebrates and all but three have small ranges or populations. These are the same factors that resulted in the post-moa extinctions, the two most recent of which, in 1955 (the Piopio *Turnagra capensis*) and 1965 (Bush Wren *Xenicus lyalli*), were caused by introduced vertebrates.

Taxonomy

Family size

When considering the three threat categories of vulnerable, endangered and critical, family size cannot be used as a good predictor of risk. Although families with the highest number of threatened species tend to be large, not all large families have a high proportion of threatened taxa.

Families with all their species under threat

The five families with 100% of their species threatened include 10 species that are endemic to a certain region or island group. New Zealand and Madagascar hold three species each, the other four species being found in south-western Australia (3) and New Caledonia. The Australasian species are all classified as vulnerable with the exception of the Kagu *Rhynochetos jubatus*, which is endangered on New Caledonia. Introduced predators, especially dogs, are the main threat to this species. Introduced predators also threaten the three New Zealand species and affect one Madagascan species, whereas habitat destruction affects the Australian and remaining Madagascan species.

Endangered and critical species

The families that hold the largest number of endangered and critical species are all relatively large. The Psittacidae have 36 of these species, the Columbidae 22 and the Emberizidae 18. The number of extant species in these families are 349, 313 and 612 respectively (Monroe and Sibley 1993). However, not all the large families have a large number of endangered or critical species; the Furnariidae have seven of 279 species endangered or critical and the Muscicapidae, seven of 255 species.

Body size

Blackburn and Gaston (1994) documented the frequency distribution of bird body masses based on data for two-thirds of extant species. Bird body masses are highly skewed to the left, even on a logarithmically transformed body-mass axis, meaning that most bird species are small-bodied. Although bird masses range from 2 g to 80 kg, the median mass is 37.6 g.

Gaston and Blackburn (1995) used data from Collar and Andrew (1988) to show that threatened birds are, on average, larger-bodied than non-threatened species. Size differences between island endemics and species with a continental distribution do not account for this difference. Within taxa there is still a relationship between body size and extinction threat. They also show that the degree of threat faced by threatened species may be related to body size and that there is a genuine tendency for large-bodied birds to be more at risk from extinction than small-bodies species.

It is likely that large-bodied birds have larger home ranges and hence spatial requirements than small-bodied species (Gaston and Blackburn 1995), resulting in an inverse relation between body size and species density. Thus, as habitat area decreases, large birds will become rarer than small birds at a much faster rate. Although it seems possible that body size may be used as an indicator of the degree of threat amongst threatened taxa, there is not as yet an understanding of the mechanisms by which body size and extinction risk interact.

Island biogeography theory and extinction rates

The number of species present in an area is a function of its size. Arrhenius (1921) proposed this to be a power function. The derivation of the power function from first principles by Preston (1962) has led to the form $S = cA^z$ where S = species, A = area, and c and z are constants (Simberloff 1992). This function is reasonably consistent across different well known taxa in different areas (Rosenzweig 1995).

Rosenzweig (1995) summarised the work of Williams (1943) on z-values into four patterns, of which three are mentioned here:

1. Nested subsets of habitat - In nested areas with continuous forest $z < 0.25$, typically ranging from 0.12 - 0.18 (Johnson *et al.* 1968).
2. Real islands - For islands within an archipelago $z \sim 0.25$ (Preston 1962), typically ranging from 0.25 - 0.35 (Johnson *et al.* 1968), but decreasing for particularly isolated archipelagos (Diamond and Mayr 1976).
3. Tiny fragments - In small, isolated forest patches $z \sim 0.6$ - 1. These contain few individuals of each species so z-values will be high (Blake and Karr 1984, Pimm and Askins 1995).

The value of z is traditionally expected to be approximately 0.25 (Preston 1962). This value is used by, amongst others, Brooks and Balmford (1996), Brooks *et al.* (1997) and Pimm and Askins (1995). In effect this relationship predicts that if 90% of a particular habitat is lost, 50% of the species that live in that habitat will become extinct with time.

Pimm and Askins (1995) show that this relationship is true for the endemic species of the forests of eastern North America. These endemics are the species most at risk through the clearing of forest and, at times, local extinction rates exceed the species-area relationship predictions. Brookes and Balmford (1996) show that in forests in the South American Atlantic region, where nearly 90% of the rainforest has been cleared, more endemics restricted to a single Endemic Bird Area (*sensu* Brown and Brown 1992, Stattersfield *et al.* 1998) are threatened with extinction than those found more widely. They predict the number of avian extinctions in the region, through forest loss, will reach 88 and that these will become extinct after some unspecified time lag. This is equivalent to two-thirds of the global extinctions over the last 400 years in one relatively small region. Brooks *et al.* (1997) have shown the number of bird species in south-east Asia predicted to become extinct using the species-area relationship is very similar to the number currently listed as threatened by Collar *et al.* (1994). It should be noted, however, that Boechlen and Simberloff (1986) warned that the species-area model, as well as their faunal collapse and relaxation model, though useful, are not very good indicators of extinction and that care should be taken when working with them. The results from these should not be absolutized and blindly applied to all situations.

Endemicity, body size, threat and extinction on ten selected islands

Madagascar has, by a factor of ten, the greatest number of endemic bird species of islands considered in the analysis. Madagascar is also the only "hotspot" (*sensu* Meyers 1988) in this particular analysis and has the highest number of critical and endangered species. Habitat destruction is the main threat to critical and endangered species here. In addition to this, the endemic Alaoltra Grebe may have been driven to extinction through genetic swamping by the Little Grebe *Tachybaptus ruficollis*, which first colonised Madagascar in the 1930's (Langrand 1990). Birds of all sizes are threatened, no species of a certain size being more vulnerable.

Jamaica has 25 endemic bird species, but only two of these are critical or endangered. Jamaica is of similar size to Hawaii but has many more endemics. This ratio is perhaps an artefact of past extinction rates: since 1600, Hawaii has experienced 12 extinctions and Jamaica only two. The causes of extinction and threat to birds on Jamaica and Hawaii include habitat destruction but each site also has unique threats. Avian malaria still threatens the Hawaiian avifauna and introduced vertebrates and exploitation are impacting the Jamaican endemics.

The islands of Hawaii and Mauritius have the highest proportion of endemic avifauna in the endangered or critical categories - 75% and 71% respectively (three and five species). The major factor threatening the Mauritian species is habitat destruction in all instances. This is different to the primary extinction cause (exploitation), indicating perhaps that another set of extinctions is imminent, this time however through a different extinction factor.

The extinction and primary threat causes affecting endemic species on six of the ten islands considered have changed (two islands do not have critical or endangered endemics and on Hawaii and Madagascar the causes have remained the same). On two islands there has been a complete change between extinction and threat causes and on the other four a threat cause has been added or lost. The absence of a current threat that had been rated as an extinction cause probably indicates that all the endemic avifauna on the island prone to that specific factor have been lost. The addition of new threat factors may indicate either improved observation techniques in identifying threat or that the endemic avifauna on these islands face new extinction pressures. In the case of the latter, and where threat factors are new, it may be that further extinctions are imminent.

On these islands, birds with body sizes of >50 g and between 100-300 g are most threatened. Only 3% of extinct species fall in the size range 100-300 g; more extinct, critical and endangered species fall in the <50 g category than any other. This is not unexpected, as the median bird body size is 37.6 g for all species. Small birds may be particularly susceptible to extinction as a result of introduced predators. The effect of habitat alteration on small birds is less than on larger species as the former need smaller ranges in which to live; these species may be able to survive even extreme habitat loss. The greatest threat to smaller birds could be the combined effects of habitat alteration and introduced predators. On islands which have supported birds of <50 g, introduction of predators was the most frequent sole cause of extinction of these birds (n=8) and, in combination with habitat alteration, led to the extinction of a further two species. As habitat patches become smaller, the greater will be the effects of predators, again highlighting the effect of combinations of threat pressures.

The high proportion of larger species under threat, especially on Madagascar and Mauritius, is reason for concern as all these are affected by habitat alteration, and larger birds require large ranges. Although there is no significant correlation between body size, extinction and threat among the endemic species on the selected islands, I suggest that a greater number of relatively large birds will become extinct in the next two decades than smaller birds, failing any conservation action. This is largely due to the extinction debt that is being built up by habitat alteration and its more severe impact on larger-bodied species. This is probably also true for species on the mainland that are critical and endangered and whose habitat is being fragmented.

Chapter Four: Summary and conclusions.

Prehistoric extinction, historical extinction and current threat

Extinctions

There have been 138 avian extinctions since 1600 (Table 38) and between 500-2 000 prehistoric ones (Milberg and Tyrberg 1993). At least 41 families experienced prehistoric extinctions and 45 historical extinctions. Fourteen families that experienced prehistoric extinctions have not lost additional species since 1600; 20 families that have experienced recent extinctions are not represented in the prehistoric extinction record.

In most families that experienced both prehistoric and historic extinctions, there were more than twice as many prehistoric extinctions as historical ones. This is expected as the time spanned in Milberg and Tyrberg's (1993) analysis is almost four times that considered in this analysis. The Rallidae (mostly flightless forms) had the highest number of prehistoric extinctions and the second highest number of historical extinctions. Of families that experienced prehistoric extinctions, only the Psittacidae have experienced more historical extinctions than prehistoric ones. They also account for the greatest absolute number of historical extinctions (20).

Three families have lost all their species in the last ±1400 years. There are at present possibly ten families in which all the species are listed as threatened (the uncertainty arises as a result of different classifications used by Clements (1991), Monroe and Sibley (1993) and Collar *et al.* (1994)). These families typically have between one and three species in them. Family-level extinctions are thus set to increase by perhaps three times the historical rate within the next 100 years. Intuitively, families with a smaller number of species face a greater risk of family-level extinction than those with a larger number of species. These small families are phylogenetically more unique and their loss, though small in numbers of species, represents a large evolutionary loss in terms of biodiversity. These species should thus be accorded a high conservation status because their phylogenetic uniqueness.

Table 38. Summary of extinct (post-1600), threatened and non-threatened extant bird species.

- I - Island, M - Mainland, B - Both
- The first row of figures indicates the number of species in each category; the bottom row expresses them in values as percentages
- Extant figures from Monroe and Sibley (1993)

Number of extinct species			Number of extant species				Number of critical species			Number of endangered species			Number of vulnerable species			Total number of threatened species				Percentage of all species threatened			
I	M	B	I	M	B	Total	I	M	B	I	M	B	I	M	B	I	M	B	Total	I	M	B	Total
124	12	2	2328	6113	1261	9702	83	85	4	85	141	9	314	361	29	482	587	42	1111				
90	9	1	24	63	13		48	49	2	36	60	4	45	51	4	43	53	4		21	9	4	12

Within the families listed by Milberg and Tyrberg (1993) that experienced prehistoric extinctions but have not experienced historical extinctions, 29 were non-passerine and 12 were passerine. The Accipitridae (13), Corvidae (7) and Megapodiidae (5) together account for more than half of these. Among families that lack evidence of prehistoric extinctions but have experienced historical ones, 11 were non-passerine and nine passerine. These 20 families have experienced 49 extinctions, the Sturnidae (7), Ardeidae (4) and Raphidae (4) having experienced more than other families. Recent extinctions in families "new" to extinction have generally affected non-passerines and passerines equally. This contrasts with families that experienced prehistoric extinctions but have not experienced historical ones: within these families non-passerines experienced more than twice as many extinctions as passerines. This may simply be because bones of (generally larger) non-passerines are more likely to be preserved than those of the smaller passerine species in the fossil/sub-fossil record. However, if Gaston and Blackburn's (1995) predictions about body size and extinction are correct (larger birds are more likely to become extinct than smaller birds), coupled with the fact that large birds are more likely to be impacted by exploitation than small birds, then the pattern may well be real.

Extinction and threat

Collar *et al.* (1994) consider 12% of all avifauna to be threatened. Only three families that have experienced prehistoric and historical extinction, and have currently threatened species, have fewer than 12% of their extant species threatened. In the 25 families that have experienced prehistoric and historical extinctions, an average of 25% of the remaining species are threatened.

One-third of all the currently threatened species are found in 14 families that have experienced both prehistoric and historical extinctions. Table 39 presents a comparison, using some of the more severely impacted families, between prehistoric extinction, historical extinction and current threat. The Drepanididae have been particularly heavily impacted in both extinction periods and also have a number of species that are currently threatened. The long-term survival of most species in this family is doubtful if the pressures currently being applied through habitat destruction are not alleviated through conservation action. Other families that feature prominently in all three time periods are the Rallidae and Columbidae which, respectively, have experienced 49 and 21 extinctions and have 25% and 18% of the remaining species currently threatened.

Table 39. Comparison, using selected families, between prehistoric extinction, historical extinction and current threat.

Family	Prehistoric extinctions	Historical extinctions (#)	(%)	Species threatened (#)	(%)	% extinct and threatened since 1600
Aepyornithidae	7	1	(100)			100
Dinornithidae	13	10	(100)			100
Procellariidae	5	1	(1)	27	(35)	35
Anatidae	25	5	(3)	25	(17)	19
Acciptridae	13	0	(0)	24	(8)	8
Megapodiidae	5	0	(0)	8	(44)	44
Rallidae	34	15	(11)	32	(25)	34
Scolopacidae	5	2	(2)	10	(11)	13
Columbidae	13	8	(3)	55	(18)	20
Psittacidae	5	20	(5)	88	(24)	28
Tytonidae	8	2	(11)	5	(29)	37
Strigidae	14	3	(4)	20	(27)	30
Drepanididae	23	11	(35)	16	(80)	87
Corvidae	7			13	(11)	11
Sturnidae		7	(6)	7	(7)	13
Ardeidae		4	(6)	7	(11)	16
Raphidae		4	(100)			100
Turdidae		3	(2)	32	(18)	19
Total	177	99	(71)			

The Megapodiidae experienced five prehistoric extinctions and no historical extinctions, but almost half the remaining species are threatened. This may indicate the beginning of a new extinction event for this family. It is possible that extinction filters may have removed a number of "weaker" species before the arrival of Europeans, the remaining species being able to adapt to pressures introduced by the Europeans. Today, however, threats faced by the megapodes include egg harvesting, introduced predators and declining ranges as a result of human development (Collar *et al.* 1994). Although the first two threats may not be new, they may be exacerbated by the emergence of development and subsequent range restriction as a new threat. This combination of threats may act as a new filter through which the family will pass, with the consequent loss of some species. This trend, where there were a large number of prehistoric extinctions, comparatively few historical extinctions, but a high current threat rating, is evident to varying degrees in several families in Table 39, including the Procellariidae, Anatidae, Rallidae, Tytonidae, Strigidae and Drepanididae.

Islands of the Pacific Ocean have been similarly affected by extinction in prehistoric and historical times (Tables 8, 25). Currently there are 74 endangered species and 51 critical species inhabiting these islands. This constitutes 77% and 57% of all island-dwelling endangered and critical species respectively. The Philippines and Indonesia hold the highest number of endangered and critical island-dwelling species but have experienced few historical extinctions (only one in Indonesia). There are only two island groups that have experienced a large number of extinctions but also have a relatively large number of endangered and critical species - New Zealand and Hawaii.

The Caribbean had more extinctions across more families in prehistoric times (26) than historical times (9). This region also has a relatively high number of endangered and critical species. The Mediterranean region has not experienced any historical extinctions although it experienced 12 prehistoric ones. There is only one endangered bird species in the region.

In the Indian Ocean there have been over three times more historical extinctions than prehistoric ones. Currently, there are nine endangered and 21 critical species in this region, of which ten inhabit Madagascar and nine the Mascarene Islands (see Figs 9 and 11). In the Mascarene Islands, there have been 33 historical extinctions (there is no mention of prehistoric extinctions by Milberg and Tyrberg (1993)), all of which occurred before 1900. This means there are fewer remaining endemic species on these islands (20 - Horne 1987, Staub 1976) than have already become extinct. Twelve of the remaining 20 endemics are threatened.

Regions at risk

The Philippines and Indonesia, and Central America and northern South America are regions that are likely to experience many extinctions in the near future. Both regions have a high level of endemism and are severely impacted by habitat loss. Importantly, in neither of these regions is there evidence that species have passed through any significant historical or prehistoric extinction filter.

Mainland Africa, which has not experienced any historical extinctions, is a region that may experience its first avian extinction within the next decade or two. Kenya and Angola are countries identified as areas of global concern (Sisk *et al.* 1994). African extinctions, however, will not be on the same scale as South American or insular Asian extinctions.

Families at risk

The number of species in a family is important in determining the vulnerability of the entire family to extinction. There are 44 extant families (33 non-passerine, 11 passerine) that contain five or less species (Monroe and Sibley 1993); 12 (27%) of these families have species under threat. Species in ten of these small families inhabit islands only and of these, four have threatened species. Madagascar holds four of the ten island families (one family with threatened species) and New Zealand three (two families with threatened species). Two of the New Zealand families and one from Madagascar are passerine, these being the only threatened, island-dwelling passerine families. Body masses of the New Zealand species range between 6 g and 2 500 g and on Madagascar between 34 g and 220 g. These species inhabit a range of environments from rainforest to scrub and subdesert.

The thirty-two families that do not include threatened species typically comprise taxa with a low level of regional endemism (only five families are endemic to a certain region) that are not highly habitat specific. The body sizes of the birds in these families varies from large (Struthionidae) to small (Hypocoliidae).

Table 40 lists families that have the highest percentage of their species at risk of extinction and compares it with the number of extant species in the family. All but two of the families are small, holding five or less species.

Table 40. Families most at risk of extinction.

Family	Number of extinct species	Number of extant species	Percentage of species threatened	Endemic to one island group or country?	Principal threat habitat destruction?
Casuariidae	0	4	50	Y	N
Apterygidae	0	3	100	Y	N
Fregatidae	0	5	40	N	N
Phoenicopteridae	0	5	40	(S.Am.)	N
Megapodiidae	0	19	42	N	N
Mesitornithidae	0	3	100	Y	N
Pedionomidae	0	1	100	Y	Y
Rhynochetidae	0	1	100	Y	N
Rynchopidae†	0	3	33	N	N
Atrichornithidae†	0	2	100	Y	Y
Picathartidae	0	4	50	(Afr.)	Y
Drepanididae†	22	21	76	Y	N
Callaeidae	2	2	50	Y	N
Orthonychidae	0	2	50	(Australia)	Y

† These taxa are listed at a sub-family level by Monroe and Sibley (1993) but at the family level by Collar *et al.* (1994) and Clements (1991).

Habitat loss as the sole threat affects only four of the 14 families listed in Table 40. The only other sole cause of threat here is an introduced predator affecting the Rhynochetidae species. Combinations of causes threaten more species in these families than sole causes, confirming Bibby's (1994) idea that factors acting in combination with each other are likely to cause more extinctions than are exclusive factors.

In five families, the full species compliment is threatened. These families are small, containing between one and three species. They are all local endemics and are threatened by a variety of factors. The Apterygidae and Mesitornithidae are threatened by both habitat alteration and introduced predators whereas the Rhynochetidae species is threatened by introduced predators. The remaining two families are threatened by habitat alteration.

The long-term future of the Drepanididae must be uncertain, having lost a third of its species since 1600 and having only four of the remaining 20 apparently free of threat. The main threat is a combination of habitat alteration and avian malaria. However, this family has been heavily affected by extinction historically and prehistorically, so the four non-threatened species may have a very good chance of long-term survival when seen in the context of extinction filters.

One other family (Megapodidae) has a relatively larger number of species threatened. Species in this family are threatened by a diversity of factors and especially combinations thereof. They are not endemic to any one area, being found in Australia and at a number of south Pacific islands.

Body sizes of species in the families included in Table 40 vary from large (Casuariidae, mean = 4 400 g) to small (Pedionomidae, mean = 43 g). The passerine species are generally smaller than the non-passerines with masses between 7 g (a drepanid species) and 250 g species in the Callaeidae family. In small families with threatened species, body size is not correlated with extinction likelihood.

Species at risk: a phylogenetic approach

All (403) species listed by Collar *et al.* (1994) as critical and endangered were used in an analysis which considered (1) the historical predisposition of a family to extinction, (2) the proportion of the family under threat and (3) the phylogenetic uniqueness of the family. A score of one to four was assigned to each critical and endangered species for each of the three above criteria. Determination of a score is shown in the key to Table 41. These three scores were summed to give a 'phylogenetic threat rating'. This was then compared with the conservation status of each species as defined by Collar *et al.* (1994).

Table 41 lists the 21 species with the highest ratings. Using a χ^2 test it was determined that the species listed in this table were a random subset of species from Collar *et al.* (1994). (Of the species with ratings of four and less (those not recorded in Table 41), 31 scored zero, 78 scored one, 77 scored two, 133 scored three and 62 scored four.) There are seven critical species and 14 endangered species that were given a rating of five or more. These species represent 11 families, the family with the most species being the Drepanididae (10). Only three of these families have experienced historical extinction.

The primary causes of threat to these 21 species are habitat alteration and introduced vertebrates: habitat alteration features in 16 (76%) cases and is the sole threat to two species; introduced vertebrates feature in 13 (62%) cases and are the sole threat to two species. According to Collar *et al.* (1994), habitat loss plays a role in the threat to 80% of all endangered and critical species and introduced vertebrates 20%. The proportion of species in Table 41 threatened by habitat loss (76%) is similar to the global average (80% - Collar *et al.* 1994). However, the proportion threatened by introduced predators (62%) is much higher than the global average (20%).

Seventeen species in Table 41 inhabit islands and four inhabit mainland regions. All except two are forest dwellers, the two exceptions inhabiting marine or coastal cliffs. Of the island-dwelling species, ten are found on Hawaii (the Drepanididae) and two on Madagascar.

Table 41. Analysis of species which have high conservation priority on the basis of the probability of family-level extinction as a function of past extinctions and present threats

Key:

Proportion of family under threat:
- 4 - above 40% of family under threat
- 3 - 25 - 40% of family under threat
- 2 -15 - 25% of family under threat
- 1 - 5 - 15% of family under threat
- 0 - 0 - 5% of family under threat

Historical predisposition of family to extinction:
- 4 - above 40% of family extinct
- 3 - 20 - 40% of family extinct
- 2 - 10 - 20% of family extinct
- 1 - 1 - 10% of family extinct
- 0 - 0% of family extinct

Phylogenetic uniqueness
- 4 - 1 species represents over 20 % of the family
- 3 - 1 species represents between 16-20% of the family
- 2 - 1 species represents between 11-15 % of the family
- 1 - 1 species represents between 6-10% of the family
- 0 - 1 species represents between 1-5% of the family

Habitat type: (from Collar *et al.* (1994))
- F - Forest
- S - Scrub
- R - Rocky areas, including cliffs
- M - Marine
- G - Grassland
- W - Wetlands

(Threat codes are as listed in the Introduction)

Species name	Proportion of family under threat	Historical predisposition to extinction within family	Phylogenetic uniqueness	Phylogenetic threat rating	BirdLife threat status	Habitat type	Threat codes
Rhynochetos jubatus	4	0	4	8	EN	FS	169
Phytotoma raimondii	4	0	4	8	CR	S	19
Psittirostra psittacea	4	3	1	8	CR	F	1689
Loxioides bailleui	4	3	1	8	EN	F	168
Hemignathus lucidus	4	3	1	8	CR	F	169
Hemignathus wilsoni	4	3	1	8	EN	F	1
Oreomystis bairdi	4	3	1	8	EN	F	1689
Oreomystis mana	4	3	1	8	EN	F	6
Paroreomyza maculata	4	3	1	8	CR	F	19
Loxops caeruleirostris	4	3	1	8	EN	F	1689
Loxops coccineus	4	3	1	8	EN	F	16
Melamprosops phaeosoma	4	3	1	8	CR	F	1689
Callaeas cinerea	4	0	4	8	EN	F	6
Fregata aquila	4	0	3	7	CR	RM	369
Pelecanoides garnotii	2	0	4	6	EN	RM	1246
Tyto soumagnei	3	2	1	6	EN	F	19
Neodrepanis hypoxanthus	2	0	4	6	EN	F	1
Gymnogyps californianus	1	2	2	5	CR	SGR	2589
Megapodius pritchardii	4	0	1	5	EN	F	12689
Grus leucogeranus	4	0	1	5	EN	W	129
Grus americana	4	0	1	5	EN	W	59

The historical/phylogenetic analysis presented here prompts some conclusions that differ from those of Collar *et al.* (1994). Firstly, not all the "top 21" species are listed by Collar *et al.* (1994) as critically threatened. Secondly, it gives much greater emphasis to the importance of introduced predators in threatening island bird species (and families) with extinction. The classification approach used by Collar *et al.* (1994) treats all species as equal; i.e. the same criteria are applied in the same way to all species. However, by ignoring history, and especially phylogeny, they are not able to include an element of "evolutionary uniqueness" in their status assessments.

However, this analysis also some short-comings. It fails to place some species which are on the verge of extinction or possibly already extinct such as the Writhed-billed Hornbill *Aceros waldeni* of the Philippines or Madagascar Pochard and Alaotra Grebe in the "top 21" listing. It also lists species which do not represent those most at risk of extinction (e.g. the Ascension Frigatebird *Fregata aquila* and Madagascar Red Owl *Tyto soumagnei*). In terms of ensuring family-level survival, it is perhaps also not realistic that four of the top five priorities should fall within one family.

Although the analysis presented here does not include all of the species included by Collar *et al.* (1994) as being in imminent danger of extinction, Collar *et al.*'s (*op. cit.*) approach does fail to incorporate an evolutionary element in species prioritization. The global loss of a major (family-level) evolutionary pathway potentially has a greater impact on future evolutionary potential than does the loss of a single species from within a diverse family. Given recent molecular advances in knowledge of avian evolution, future listings of the world's threatened bird taxa may benefit by introducing a phylogenetic component to threat rating.

It is unlikely that national or international conservation efforts can be directed equally at all species of equal status in the future. Future conservation efforts will have to effect some form of prioritization exercise. I suggest that those species identified by Collar *et al.* (1994) as critical, which also appear in Table 41, must currently rate as the world's highest bird conservation priorities. On this basis, the five species of greatest concern are: Peruvian Plantcutter *Phytotoma raimondii*, Ou *Psittirostra* *psittacea*, Nukupuu *Hemignathus lucidus*, Oahu Alauahio *Paroreomyza maculata* and Po'o-uli *Melamprosops phaeosoma*. Four of these five species are Hawaiian Honeycreepers (family Drepanididae).

Conclusions

Evidence from prehistoric and historical extinctions indicates an avian extinction rate that is between 100 and 1 000 times the background avian extinction rate. The known causes of these extinctions have remained essentially the same over time (exploitation, introduced predators and habitat destruction) but the relative importance of the causes has changed from introduced predators to habitat alteration. Island and mainland endemic birds with small ranges face the greatest risk of extinction over the next few decades, ultimately through habitat loss. A time lag between habitat loss and extinction has resulted in fewer than expected extinctions in some regions, but it is likely that further extinctions are already inevitable and that a greater proportion of large species will become extinct than smaller species. An increasing number of mainland species are likely to become extinct with time as it is here, especially in tropical forests, that very high rates of habitat loss are being experienced.

This study has examined only avian species, which form a very small part of global biodiversity. When considering total global biodiversity, it is likely that the number of species facing imminent extinction is very large. It is probable that the magnitude of these extinctions, considered together with extinctions over the last 1 500 years, will be similar to that of previous mass extinctions, justifying fears of some conservationists that an extinction event, unprecedented in human history, is looming.

Appendix 1. List of species that have become extinct since 1600

Author key:

1. Day (1989) * indicates rumours of survival; incorporates the period 1680-1980
2. Clements (1991) * indicates on the verge of extinction
3. Greenway (1967) [p] indicates probably extinct
4. Mountfort (1988) [m] indicates there may be survivors
5. Fuller (1987) [S] indicates subspecies; [r] indicates race ;*[s] indicates probably extinct* and subspecies[s], Uses Archey (1941) for recognition of Moa species
6. Collar *et al.* (1994)
7. Thorstrum *et al.* (1995).
8. IUCN emailed list of extinct birds

Masses are estimated from Dunning (1993).

ORDER	FAMILY NAME	COMMON NAME(S)	SPECIES NAME	MASS (g)	PLACE	DATE	CAUSE	AUTHOR
1. Casuariiformes (2)	Dromaiidae (2)	Dwarf Emu / Kangaroo Island Emu	*Dromaius baudinianus*	10 000	Kangaroo Island[1]	1830[1]	Ex,HD	1[s],3[s],4,5[r],8
		King Island Emu	*Dromaius ater*	40 000	King Island[5]	1822[5]	Ex,HD	5[r],8
2. Dinornithiformes (10)	Dinornithidae (10)		*Dinornis maximus*	275 000	All New Zealand	1850[1]	?	1,5
		Slender Moa	*Dinornis torosis*	100 000		1670[4,8]	Ex,HD	4,5,8
		Greater Broad-Billed Moa	*Euryapteryx gravis*	100 000		1640[5,8]	Ex,HD	1,5,8
			Euryapteryx geranoides	40 000		Before 1700[1]	?	1,5
			Anomalopteryx parvus	40 000		Before 1800[1]	?	1
			Anomalopteryx didiformes	40 000		Before 1800[1]	?	1,5
			Anomalopteryx oweni	40 000		Before 1800[1]	?	1
		Lesser Megalapteryx	*Megalapteryx didinus*	40 000		1765[5,8]	Ex,HD	1,5,8
			Megalapteryx hectori	40 000		Before 1800[1]	?	1
			Megalapteryx benhami	40 000		Before 1800[1]	?	1,5

3. Aepyornitheformes (1)	Aepyornithidae (1)	Elephant Bird	*Aepyornis maximus*	500 000	Madagascar	1650[4,8]	Ex,HD	1,4,8
4. Podicipediformes (2)	Podicipedidae (2) (Grebes)	Atitlan Grebe	*Podilymbus gigas*	500	Guatemala	1980[4]1987[8]	HD	2,4,6,8
		Colombian Grebe	*Podiceps andinus*	400	Colombia	1977[4,8], 1980[2]	HD	2,4,6,8
5. Procellariiformes (2)	Hydrobatidae (1)	Guadelupe Storm Petrel	*Oceanodroma macrodactyla*	50	Guadelupe (Mexico)	1912[4]	IV,HD	1,2,3,4,5
	Procellariidae (1)	?	*Pterodroma sp.*	400	Rodrigues Island	1726	?	8
6. Pelecaniformes (1)	Phalacrocoracidae (1)	Spectacled Cormorant	*Phalacrocorax perspicillatus*	1 900	Bering Island and satellites	1852[4]	Ex	1,2,3,5,8
7. Ciconiiformes (6)	Ardeidae (4)	New Zealand Little Bittern	*Ixobrychus novaezelandaie*	150	New Zealand	1900[4]	?	4,5[5],8
		Mauritius Night Heron	*Nycticorax mauritianus*	900	Mauritius	By 1700[4]	?	4,8
		Rodrigues Night Heron	*Nycticorax megacephalus*	900	Rodrigues Is.	1761[4]	?	4,5,8
		?	*Nycticorax sp.*	900	Réunion Is	By 1700	?	8
	Ciconiidae (1)	?	*Ciconia sp.*	3 700	Réunion Is.	By 1674	?	8
	Threskiornithidae (1)	Réunion Flightless Ibis	*Borbonibis latipes*	1 200	Réunion Is.	1773[4,8]	?	3,4,8
8. Anseriformes (5)	Anatidae (5)	Mauritian Duck	*Anas theodori*	700	Mauritius	1696[4,8]	?	4,8
		Labrador Duck	*Camptorhynchus labradorius*	?	New England, Canadian maritime provinces[1]	1875[4]1878[8]	?	1,2,3,4,5,8
		Aukland Island Merganser	*Mergus australis*	1000	Aukland Is.	1905[4,8], 1910[1]	IV	1,2,3,4,5,8
		Mauritian Shelduck	*Sarkidiornis mauritianus*	2600	Mauritius	1698[4]	?	1,3,5,8
		Chatham Island Swan	*Cygnus sumnerensis*	7000	Chatham Is.	1590-1690[4,8]	?	4

9. Falconiformes (3)	Cathartidae (1)	Painted Vulture	*Sarcorhamphus sacra*	3400	Florida USA	1800[1]	HD,?	1
	Falconidae (2)	Guadelupe Caracara	*Polyborus lutosis*	900	Guadelupe Is.	1900[4]	Ex	1,2,3,4,5,8
		????	*Falco sp.*	250	Réunion	1674	?	8
10. Galliformes (2)	Phasianidae (2)	New Zealand Quail	*Coturnix novaezelandiae*	100	New Zealand	1868[1], 1875[4]	?,HD,IV	1,3[s],4,5,8
		Himalayan Mountain Quail	*Ophrysia superciliosa*	700	Eastern Punjab, India[1]	1868[4], 1870[1], 1876[5]	?	1,2,4,5
11. Gruiformes (15)	Rallidae (15)	Wake Island Rail	*Rallus wakensis*	150	Wake Is.	1945[1]	Ex	1,2,3,4,5,8
		Tahiti Rail	*Rallus ecaudata*	150	Tahiti	1900[1]	?,IV	1
		Modest Rail	*Rallus modestus*	150	Chatham Is.[1]	1900[4]	IV,HD	1,2,3,4,5,8
		Dieffenbach's Rail	*Rallus dieffenbachii*	150	Chatham Is[1]	1840[4]	IV,HD	1,2,3,4,5[r],8
		Tahitian Red-Billed Rail	*Rallus pacificus*	150	Tahiti Is	Early 1900's[5]	IV	2,3,5,8
		Sharpe's Rail	*Rallus sharpei*	150	Indonesia?[2]	?	?	2
		Ascension Island Flightless Crake	*Atlantisia elpenor*	38	Ascension Is.	1656[4]	Ex	5,8
		Mauritian Red Rail	*Aphanapteryx bonasia*	?	Mauritius	1693[4]	Ex	1,5,8
		Leguat's Rail	*Aphanapteryx leguati*	?	Rodrigues Is.[5]	1700[1], 1760[4,5]	Ex	1,5,8
		Laysan Rail	*Porzana palmeri*	60	Laysan Is.[1,5]	1944[4]	HD	1,5,8
		Sandwich Rail	*Porzana sandwichensis*	60	Hawaii[1,5]	1884[4], 1898[8]	IV	1,5,8
		Kittlitz's Rail / Kosrae Island Crake	*Porzana monasa*	60	Kosrae Is.	1827[4], 1850[1]	IV	1,2,4,5,8
		Barred-winged Rail	*Nesoclopeus poeciloptera*	?	Fiji Islands[6]	1965[1] ,1973?[8]	IV	1*,6,8
		White Gallinule/Lord Howe Swamphen	*Phorphyrio albus*	800	Lord Howe Is.	1834[4]	Ex	1,2,3[s] ,5,8
		Mascarene Coot	*Fulica newtoni*	700	Mascarene islands	1693[4]	?	4,8

12. Charadriiformes (5)	Scolopacidae (2)	White-winged Sandpiper	*Prosobonia leucoptera*	36	Tahiti	1773[4]	?,IV	1,2,3,4,5,8
		Moorean Sandpiper	*Prosobonia ellisi*	36	Moorea	1773[4]	?,IV	1
	Heamatopodidae (1)	Canarian Black Oystercatcher	*Haematopus meadewaldoi*	600	Canary Is.[???]	1913[4,8]	O	2,4,5[r],6
	Alcidae (1)	Great Auk	*Alca impennis*	2 000	N Atlantic islands[1] Canada,Denmark,Faeroe Islands, Greenland, Iceland, Russia,UK	1844[4,8]	Ex	1,4,5,8
	Charadriidae (1)	Javanese Wattled Lapwing	*Vanellus macropterus*	200	Java	1920[2]	?	6,8
13. Columbiformes (12)	Raphidae (4)	Dodo	*Raphus cucullatus*	25 000	Mauritius[4]	1655[4]	Ex	1,2,3,4,5,8
		Rodrigues Solitaire	*Pezophaps solitarius*	20 000	Rodrigues Is.	1765[4]	Ex	1,2,4,5,8
		Réunion Dodo or Réunion Solitaire	*Raphus solitarius*	25 000	Réunion Is.	1710-1715[4]	Ex	1,4,8
		White Dodo	*Victoriornis imperialis*	20 000	Réunion Is.[1]	1770[1]	Ex	1
	Columbidae (8)	Bonin Wood Pigeon	*Columba versicolor*	350	Bonin Islands	1889[4]	HD	1,3,4,5,8
		Ryukyu Wood Pigeon	*Columba jouyi*	350	Ryukyu Island	1936[4]	?	2,4,8
		Rodrigues Pigeon	*Columba rodericana*	350	Rodrigues Is.	1726[4]	?,IV	4,5,8
		Dutch Pigeon	*Alectroenus nitidissima*	150	Mauritius[5]	1826, 1835[4,5,8]	?,IV	1,3,4,5,8
		Passenger Pigeon	*Ectopistes migratorius*	200	E'rn USA[5]	13:00, Sept 1 1914[5]	Ex,HD	1,2,3,4,5,8
		Tanna Dove	*Gallicolumba ferruginea*	130	Tanna Island	Post 1774[5], 1800[1]	?	1,2,5
		Choiseul Crested Pigeon	*Microgoura meeki*	?	Choiseul Is. in Solomon Island group	1904[4]	IV[6],HD	1,2,3,4,5,6,8
		Red-moustached Fruit Dove	*Ptilinopus mercierii*	130	French Polynesia[4,8]	1922[4]	IV[6]	2,4,5[r],6,8

14. Psittaciformes (21)	Psittacidae (20)	Norfolk Island Kaka	*Nestor meridionalis*	450	Norfolk Island	1851[4,5]	Ex	1,2,3[s],4,5[r],8
		Yellow-headed Macaw	*Ara gossei*	800	Jamaica[1]	1765[1]	?	1
		Green and Yellow Macaw	*Ara erythrocephala*	800	Jamaica[1]	1842[1]	?	1
		Dominican Macaw	*Ara atwoodi*	800	Dominica, WI	1800[1]	?	1
		Cuban Red Macaw	*Ara tricolor*	800	Cuba	1885[4,5]	Ex,IV	1,3,4,5,8
		Labat's Conure	*Aratinga labati*	120	Guadeloupe, WI	1722[1]	Ex,Trade	1
		Carolina Parakeet	*Conuropsis carolinensis*	?	Carolina, USA	1914[4]	Ex	1,2,3,4,5
		Guadeloupe Amazon	*Amazona violacea*	?	Guadeloupe, WI	1750[1]	Ex.,HD	1
		Martinique Amazon	*Amazona martinica*	?	Martinique Is., WI	1750[1]	HD	1
		Mauritius Grey Parrot	*Lophopsittacus bensoni*	250	Mauritius	1765[4,8]	?	4,8
		Broad-billed Parrot	*Lophopsittacus mauritanus*	250	Mauritius[4]	1680[4,5]1675[8]	?	1,5,8
		Rodriguez Parrot	*Necropsittacus rodericanus*	250	Rodrigues Is.	1761[4,5,8], 1800[1]	Ex	1,4,5,8
		Mascarene Parrot	*Mascarinus mascarenus*	?	Mascarene Islands	1834[4,5,8], 1840[1]	?	1,2,3,4,5,8
		Seychelles Parrot	*Psitticla wardi*	120	Seychelles	1870[4,8], 1881[1],	?	1,2,3[s],4,5[r],8
		Réunion Ring-necked Parakeet	*Psittacula eques*	120	Réunion Is.	1800[1]	HD	1
		Rodriguez Ring-necked Parakeet	*Psittacula exsul*	120	Rodrigues Is.	1876[4,5,8], 1880[1]	?,Ex,IV	1,2,3[m],4,5,8
		Black-fronted Parakeet	*Cyanoramphus zealandicus*	70	Tahiti[4]	1844[4,5,8], 1850[1]	Ex	1,2,3,4,5,8
		Raiatea Parakeet	*Cyanoramphus ulietanus*	70	Raiatea Is.	1773[4,5,8]	?,IV	2,3,4,5,8
		Glaucous Macaw	*Anodorynchus glaucus*	1 200	Paraguay, Uruguay, Brazil, Argentina[4,6]	1955[4]	HD	2,4,6,8
		Paradise Parrot	*Psephotus pulcherrinus*	60	Australia[6]	1927[4]	IV,HD	2,5,6,8
	Lorridae (1)	New Caledonian Lorikeet	*Charmosyna diadema*	50	New Caledonia	1860[4]	Hd,Ex	1*,4
15. Cuculiformes	Cuculidae	Snail-eating Coua	*Coua delalandei*	160	Madagascar[6]	1920[1], 1930[4,5,8]	Ex,HD	1,2,3[p],4,5,6,8

16. Strigiformes (5)	Tytonidea (2)	Mauritian Barn Owl Newton's Barn Owl	*Tyto sauzieri* *Tyto newtoni*	550 550	Mauritius Mauritius[1]	1700[1] 1700[1]	?,Ex ?,Ex	1 1
	Strigidae (3)	Commerson's Scops Owl Laughing Owl Rodrigues Little Owl	*Scops commersoni* *Sceloglaux albifacies* *Athene murivora*	120 ? 160	Mauritius[1] New Zealand Rodrigues Is.	1850[1],1836[8] 1900[1], 1910[4,5] 1726[4,5,8]	? HD,IV ?	1,8 2,5,8 1,4,5,8
17. Apodiformes	Trochilidae	Grace's Emerald	*Chlorostilbon bracei*	3	Bahamas	1887	?	8
18. Coraciiformes	Alcedinidae	Ryukyu Kingfisher	*Halcyon miyakoensis*	80	Ryukyu Is.	1841[4,5], 1887[1]	?	1,3,4,5
19. Piciformes	Picidae	Ivory-billed Woodpecker	*Campephilus principalus*	511	SE USA, Cuba[6]	1991[6]	HD,Ex	1[s] *,2*,6,8

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20. Passeriformes (42)	Acanthisittidae (2)	Stephen Island Wren	*Xenicus lyalli*	16	Stephen Is.	1874[4,8], 1894[1]	IV	1,2,3,4,5,8
		Bush Wren	*Xenicus longipipes*	16	New Zealand	1965[1]	IV	4,6,8
	Turdidae (3)	Bonin/Klittlitz's Thrush	*Zoothera terristris*	80	Bonin and Peel islands	1828[4,5,8]	IV	1,2,3,4,5,8
		Bay Thrush	*Turdus ulietensis*	80	Raiatea Is.	1780[1]	IV	1,3,5
		Grand Cayman Thrush	*Turdus ravidus*	80	Grand Cayman Is.	1938[5,8]	HD	2,4,5
	Pachycephalinae (1)	Piopio or New Zealand Thrush	*Turnagra capensis*	?	New Zealand	1963[4],1955[8], 1906[5]	IV	4,5,8
	Sylviidae (2)	Chatham Island Fernbird	*Megalurus fufescens*	35	Chatham Is.	1895[1,5]	IV	1,3,5*[s]
		Aldabra Warbler	*Nesillas aldabrana*	<10	Seychelles[6]	1986[6]	IV (rats)	6,8
	Acanthizidae (1)	Lord Howe Island Island Flycatcher	*Gerygone insularis*	<10	Lord Howe Is.	1920[1]	?	1[s],2,3[s],5[s],8
	Muscicapidae (1)	Guam Flycatcher	*Myiagra freyceniti*	13	Guam	1985[6]	IV (snake)	6,8
	Zosteropidae (2)	Lord Howe Island/ Robust White-eye	*Zosterops strenua*	10	Lord Howe Is.	1928[4,5,8]	IV	1,3,5,8
		Marianne Seychelles White-eye	*Zosterops semiflava*	10	Seychelles	1880's[5]	?	1,3,5*[s]
	Meliphagidae (4)	Kioea	*Chaetoptila angustipluma*	30	Hawaii Is.	1860[4,5,8]	?	1,2,4,5
		Hawaiian O'o	*Moho nobilis*	30	Hawaii Is.	1934[1,4,5,8]	HD	1,2,3[P],4,5
		Oahu O'o	*Moho apicalis*	30	Oahu Is.	1837[1,4,5,8]	HD,IV	1,2,4,5,8
		Molokai O'o	*Moho bishopi*	30	Molokai Is.	1904[1]	HD,IV	1,2*,3[P],5
	Emberizidae (2)	Townsend's Finch	*Spiza townsendi*	15	USA[4]	1833[4,8]	?	4,8
		Tumaco Seedeater	*Sporophila insulata*	10	SW Colombia	1912[6]	HD[6]	2
	Drepanididae (11)	Great Amakihi	*Hemignathus sagittirostris*	10	Hawaii Is.[1,2,5]	1900[4,5]	HD	1,2,3[P],4,5,8
		Akiola	*Hemignathus obscurus*	10	Hawaiian islands	1960[6,8]	HD,disease,comp, or all 3	1,2,3,4,8
		Greater Koa Finch	*Psittirostra palmeri*	20	Hawaii Is.[1]	1896[1,4,5,8]		1,2,3,4,8
		Lesser Koa Finch	*Psittirostra flaviceps*	20	Hawaii Is.[1]	1891[4,8]	HD etc.	1,3[P],
		Kona Finch	*Psittirostra kona*	20	Hawaii Is.[1]	1894[5]	HD etc.	2
		Lanai Finch	*Dysmorodrepanis munroi*	20	Lanai Is.	Post 1913??[2]	?	1,2,3,4,5,8
		Mamo	*Drepanis pacifica*	20	Hawaii Is.[1]	1899[1,4,5,8]	Ex,HD	1,2,3,4,5,8
		Black Mamo	*Drepanis funerea*	20	Molokai[1]	1907[1,4,5,8]	HD etc.	4,5,8
		Kona Grosbeak	*Chloridops kona*	?	Hawaii Is.[5]	1894[5,8]	HD etc.	4,5,8

		Kakawihie	*Paroreomyza flammea*	11	Hawaii Is.[5]	1963[4,8]	HD	4,6,8
		Ula-Ai-Hawane	*Ciridops anna*	20	Hawaii Is.[5]	1892[1,4,5,8]	?	1,2,3,4,5,8
	Fringillidae (1)	Bonin Grosbeak	*Chaunoproctus ferreorostris*	56	Peel Is. And Bonin islands[1]	1890[4,5,8]	IV	2,4,5,8
	Icteridae (1)	Slender-billed Grackle	*Quiscalus palustris*	130	Mexico[5]	1910[4,5]	?	2,4,5*[s],8
	Ploceidae (1)	?	*Foudia sp.*	17	Reunion	1671[8]	?	8
	Sturnidae (7)	Pohnpei Mountain Starling	*Aplonis pelzelni*	60	Pohnpei Is.	1956[4]	?	4
		Kusaie Mountain Starling	*Aplonis corvina*	60	Kusaie/Kosrae Is.	1828[4,5,8]	IV	1,2,3,4,5,8
		Mysterious Starling	*Aplonis mavornata*	60	Society Islands?	1825[5,8]	?	1,2,3,4,5,8
		Norfolk Island Starling	*Aplonis fusca*	60	Norfolk Is.	1925[4,5]	?	4,5,8
		Bourbon /Reunion Crested Starling	*Fregilupus varius*	80	Reunion Is.	1850-1860[4,5,8] 1868[1]	IV	1,2,3,4,5,8
		White Mascarene Starling	*Necropsar leguati*	80	Mascarene Islands	1840[1]	?	1
		Rodrigues Starling	*Necropsar rodericanus*	80	Rodrigues Is.	1726[4,5,8]	?	1,2,4,5,8
		Blue-Wattled Bulbul	*Pycnonotus nieuwenhuisii*	25	Sumatra and Borneo	Post 1939	HD	2
	Pycnonotidae (2)	?	*Hypsipetes sp.*	40	Rodrigues Is.	1600's?	?	8
	Callaeidae (1)	Huia	*Heteralocha acutirostris*	225	North Is., NZ	1907[4,5,8]	Ex	1*,3[P],4,5,8

Appendix 2. List of subspecies that have become extinct since 1600

Author key:

1. Day (1989) * indicates rumours of survival; incorporates the period 1680-1980
2. Clements (1991) * indicates on the verge of extinction
3. Greenway (1967) [p] indicates probably extinct
4. Mountfort (1988) [m] indicates there may be survivors
5. Fuller (1987) [S] indicates subspecies; [r] indicates race ; *[s] indicates probably extinct* and subspecies[s].
   Uses Archey (1941) for recognition of Moa species
6. Collar *et al.* (1994)

ORDER(S)	FAMILY NAME	COMMON NAME(S)	SUBSPECIES / RACE NAMES	PLACE	DATE	CAUSE	SOURCE
1. Struthiorniformes (1)	Struthiornidae (1)	Arabian Ostrich	*Struthio camelus syriacus*	Syria and Arabia	1941[1], 1966[5]	Ex	1[s],5[r]
2. Casuariiformes (1)	Dromaiidae (1) (Emus)	Tasmanian Emu	*Dromaius novaehollandiae diemenensis*	Tasmania	1850[1]	Ex,HD	1[s],3[s],5[r]
3. Ciconiiformes (2)	Ardeidae (1)	Bonin Night Heron	*Nycticorax caledonicus crassirostris*	Peel Island	?	Ex,HD	1[s],3[s],5[s]
	Threskiornithidae (1)	Principe Olive Ibis	*Lambrihis olivacea rothschildi*	Principé, Gulf of New Guinea	1st half of this century	?	5[s]
4. Anseriformes (4)	Anatidae (4)	Coue's Gadwall	*Anas strepera couesi*	Terania Island, Pacific[1]	1874[1]	?	1[s],3[s],5[r]
		Rennel Island Grey Teal	*Anas gibberifrons remissa*	Rennel Island (In Solomon Islands)	1959[5]	Intro of alien fish	5[r]
		Niceforo Brown Pintail	*Anas georgia niceforoi*	Colombia[5]	1952[5]	?	5[r]
		Bering Canada Goose	*Branta canadensis asiatica*	Kurile and Commander Islands[5]	1914[5]	?	3[s], 5[r]

5. Galliformes (1)	Tetraonidae (1)	Heath hen	*Tympanuchus cupido cupido*	New England States, USA[1]	11 March 1932[5]	Ex,HD	1[s],3[s],5[s]
6. Gruiformes (3)	Rallidae (3)	Macquarie Island Banded Rail	*Rallus philippensis macquariensis*	Macquarie Is.	1880[1]	?	1[s], 5[r]
		Jamaican Wood Rail	*Aramides concolor concolor*	Jamaica	1881[1]	IV	1[s],3[s],4
		Iwo Jima Rail	*Porzana cinereus brevipes*	Iwo Jima	1924[1]	IV,HD	1[s],3[s],5[r]
7. Charadriiformes (2)	Scolopacidae (2)	Barrier sub-Antarctic Snipe	*Coenocorypha auklandica barrierensis*	Little Barrier Island	1870[5]	?	3[s],5[r]
		Stewart Island sub-Antarctic Snipe	*Coenocorypha auklandica iredalei*	Stewart Is.	?	?	5[r]
8. Columbiformes (5)	Columbidae (5)	Lord Howe Island Pigeon	*Columba vitiensis godmanae*	Lord Howe Is.	1853[1]	?	1[s],5[r]
		Madeiran Wood Pigeon	*Columba palumbus maderensis*	Madeira	Early 1900's[5]	?	5[r]
		Cebu Amethyst Fruit Dove	*Phapitreron amethystina frontalis*	Cebu Is.land	Before 1900[5]	IV[6],HD	5[r]
		Seychelles Turtle Dove	*Streptopelia picturata rostrata*	Seychelles	1975[5]	O	5[r]
		Norfolk Island Pigeon	*Hemiphaga novaeseelandiae spadicea*	Norfolk Island	1801[1]	IV,HD	1[s],3[s],5[r]
9. Psittaciformes (8)	Psittacidae (8)	Puerto Rican Conure	*Aratinga choloptera maugei*	Mona Island, Puerto Rico	1892[1]	Ex,O	1[s],3[s],5[r]
		Western Carolina Parakeet	*Conuropsis carolinensis ludovciana*	W Carolina, USA	1914[4]	Ex	1[s],2,3[s]
		Eastern Carolina Parakeet	*Conuropsis carolinensis carolinensis*	E Carolina, USA	1914[4]	Ex	1[s],2,3[s],4,5
		Culebra Island Amazon	*Amazona vittata graciliceps*	Culebra Is.	1899[1]	?	1[s],3[s], 5[r]
		Siquijor Hanging Parrot	*Loriculus phillipensis siquijorensis*	Siquijor Is.	This century[5]	?	5[r]
		Cebu Hanging Parrot	*Loriculus phillipensis chrysonotis*	Cebu Is.	This century[5]	?	5[r]
		Macquarie Island Parakeet	*Cyanoramphus novaezelandaie erythrotis*	Macquarie Is.	1890[1], early 1900's[5]	Ex,Iv	1[s],3[s], 5[r]
		Red-fronted Parakeet	*Cyanoramphus novaezelandaie subflavescens*	Lord Howe Is.	1869[1,5]	Ex,HD	1[s],3[s], 5[r]

10. Strigiformes (6)	Strigidae (6)	Comoro Scops Owl	*Otus ritilus capnodes*	Anjouan, Comoro Is.[1]	1890[1]	?	1[s]
		South Island Laughing Owl	*Sceloglaux albifacies albifacies*	New Zealand	1900[1], 1910[4,5] 1914[8]	HD,IV	1[s] *,4
		North Island Laughing Owl	*Sceloglaux albifacies rubifacies*	New Zealand	1900[1], 1910[4,5] 1914[8]	HD,IV	1[s],3[s]
		Antigua Burrowing Owl	*Speotyto cunicularia amaura*	Antigua, Nevis and St Kitts in WI[1]	1900[1,5]	IV	1[s],3[s],5[r]
		Guadeloupe Burrowing Owl	*Speotyto cunicularia guadeloupensis*	Marie Galante, WI[1]	1900[1]	IV	1[s],3[r]
		Lord Howe Island Morepork	*Nonox novaeselandiae albaria*	Lord Howe Island	1940[5]	?	5[r]
11. Piciformes (1)	Picidae (1)	Guadelupe Flicker	*Colaptes cafer rufipileus*	Guadelupe Is., Mexico[1]	1906[1]	HD,IV	1[s],3[s]

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12. Passeriformes (61)	Acanthisittidae (2)	North Island Wren	*Xenicus longipipes stokesi*	North Island	1900[1] } 1972[4,8]	IV	1[s],4
		Stead's Bush Wren	*Xenicus longipipes variabilis*	Stewart Is[1]	1965[1] }	IV	1[s],4
	Troglodytidae (3)	Guadelupe Bewick's Wren	*Thryomanes bewikii brevicauda*	Guadelupe Is.	1897[5], 1892[1]	IV,HD	1[s],3[s]
		Martinique House Wren	*Troglodytes aedon martinicensis*	Martinique Is.	1900[1]	IV,HD	1[s],3[s]
		St Lucia House Wren	*Troglodytes aedon mesoleucus*	St. Lucia, WI	1971[1]	IV,HD	1[s]
	Turdidae (12)	Lord Howe Island Blackbird	*Turdus poliocephalus vivitinctus*	Lord Howe Is.	1920[1,5]	IV	1,3[s], 5*[s]
		Mare Island Thrush	*Turdus poliocephalus mareensis*	Mare Is.	During WW2	?	3,5*[s]
		Lifu Island Thrush	*Turdus poliocephalus pritzbueri*	Lifu Is.	During WW2	?	5*[s]
		Yakushima Seven Islands Thrush	*Turdus celaenops yakushimensis*	Yakushima Seven islands	1904[5]	?	5*[s]
		Lanai Omao	*Myadestes obscurus lanaiensis*	Lanai Is.	1931[1]	HD,O	1[s],3[s]
		Oahu Omao	*Myadestes obscurus oahensis*	Oahu Is.	1825[1]	HD	1[s],3[s]
		Molokai Omao	*Myadestes obscurus rutha*	Molokai Is	1963[5]	?,IV,HD	1[s],3[s]
		Cebu Black Shama	*Copsychus niger cebuensis*	Cebu Is.	1956[5]	IV	5*[s]
		Lanai Thrush	*Myadestes obscurus lanaiesiss*	Lanai Is.	1931[5]	IV,?HD	1[s],3[s],5*[s]
		Oahu Thrush	*Myadestes obscurus oahensis*	Oahu Is.	First half of 19th century[5]	IV,HD	1[s],2,5*[s]
		Burma Jerdon's Babbler	*Moupinia altirostris altirostris*	S'rn Burma	During WW2[5]	?	5*[s]
		Muriel's Chat	*Saxicola dacotiae murielae*	Allegranzo Is.	Post 1913[5]	?	5*[s]
	Dicaeidae (1)	Cebu Orange-bellied Flowerpecker	*Dicaeum trigonostigma pallida*	Cebu Is.	1963	HD	5*[s]
	Sylviidae (6)	Laysan Millerbird	*Acrocephalus familiaris familiaris*	Laysan Is.	1920[1], 1912-1923[4,5]	HD	1[s],3[s],5*[s]
		Lord Howe Island Grey Warbler or Lord Howe	*Grygone igata insularis*	Lord Howe Is.	Post 1918[5], 1920[1]	?	1[s],2,3[s],5*[s]

		Gerygone					
		Hautrine Island Long-billed Reed Warbler	*Acrocephalus caffra garretti*	Hautrine Is.	?	?	5*[s]
		Raiatea Long-billed Reed Warbler	*Acrocephalus caffra musae*	Raiatea Is.	?	?	5*[s]
		Astrolabe Nightingale Reed Warbler	*Acrocephelus luscinia astrolabii*	Pacific somwhere	?	?	5*[s]
		Diato Japanese Bush Warbler	*Cettia diphone restricta*	Borodino (Diato) islands	?	?	5*[s]
	Paridae (1)	Daito Varied Tit	*Parus varius orii*	Borodino Is.	1923[5]	?	5*[s]
	Muscicapidae (3)	Tonga Tabu Tahiti Flycatcher	*Pomarea nigra atra*	Tahiti	1800[1]	?	1
		Maupiti Flycatcher	*Pomarea nigra pomarea*	Maupiti, Solomon islands	1823[5]	?	5*[s]
		Lord Howe Island Fantail	*Rhipidura fuliginosa cervina*	Lord Howe Is.	1924	IV	1,3
	Zosteropidae (2)	Cebu Everett's White-eye	*Zosterops everitti everitti*	Cebu Is.	Early 19th century	?	5*[s]
		Lord Howe Island Grey-backed White Eye	*Zosterops lateralis tephropleura*	Lord Howe Is.	?	?	5*[s]
	Meliphagidae (1)	Chatham Island Bell Bird	*Anthornis melanura melanocephalus*	Chatham Is.	1906[1,5]	HD,IV	1,3[s],5*[s]
	Emberizidae (3)	St Kitts Puerto Rican Bullfinch	*Loxigilla portoricensis grundis*	St. Kitts Is.	1880[5], 1900[1]	?	1[s],3[s],5*[s]
		Guadelupe Rufous-sided Towhee	*Pipilo erythrophthalmus consobrinus*	Guadelupe Is.	1897[5], 1900[1]	IV monkeys	1[s],3[s], 5*[s]
		Santa Barbara Song Sparrow	*Melospiza melodia graminea*	California[5]	1960's[5]	?	5*[s]
	Drepanididae (12)	Molokai Alauwahio	*Loxops maculata flammea*	Molokai Is	1970[1]		1[s],3[s],
		Lanai Alauwahio	*Loxops maculata montana*	Lanai Is.	1937[1]	HD, competion and avian malaria	1[s],3[s]
		Oahu Akepa	*Loxops caccinea rufa*	Oahu Is.	1900[1]		1[s],3[s]
		Hawaiian Akioloa	*Hemignathus obscurus obscurus*	Hawaii Is.	1940[1]		1[s],3[s],5*[s],6

		Lanai Akioloa	*Hemignathus obscurus lanaiensis*	Lanai Is.	1894[1]	or combination	1[s],2,3[s],5*[s],6
		Oahu Akioloa	*Hemignathus obscurus ellisianus*	Oahu Is.	1840[1,5]	of all	1[s],2,3,5*[s],6
		Kauai Akioloa	*Hemignathus obscurus procerus*	Kauai Is.	1965[1]	"	1[s],2,6
		Oahu Nukupuu	*Hemignathus lucidus licidus*	Oahu Is.	1890[1,5]	"	1[s],3[s],5*[s]
		Kauai Nukupuu	*Hemignathus lucidus hanapepe*	Kauai Is.	1905[1]	"	1[s]
		Maui Nukupuu	*Hemignathus lucidus affinis*	Maui Is.	1896[1]	"	1[s],3[s],
		Lanai Creeper	*Paroreomyza montana montana*	Lanai Is.	1930's[5]	HD	5*[s]
		Laysan Apapane	*Himatione sanguinea freethii*	Laysan Is.	1925	HD	1
	Fringillidae (1)	McGregor's House Finch	*Carpodacus mexicanus mcgregori*	San Benito Islands, USA	1838[5]	?	5*[s]
	Icteridae (2)	Slender-billed Grackle	*Quiscalus palustris mexicanus*	Mexico[5]	1910[4,5]	?	4,5*[s]
		Grand Cayman Jamaican Oriole	*Icterus leucopteryx bairdi*	Grand Cayman Is.	Post WW2[5] Pre-1950	?	5*[s]
	Ploceidae (1)	Réunion Fody	*Foudia madagascariensis bruante*	Réunion Is.	1776[1]	?	1[s]
	Sturnidae (1)	Lord Howe Island Starling	*Aplonis fuscus hullianus*	Lord Howe Is.	1925[1]	IV	1[s],3[s]
	Oriolidae (1)	Cebu Dark-throated Oriole	*Oriolus xanthonotus assimilis*	Cebu Is.	1906[5]	?	5*[s]
	Callaeidae (1)	South Island Kokako	*Callaeas cinerea cinerea*	South Is., NZ	1961[5].	?	5*[s]

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