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Naïve birds and noble savages – a review of man-caused prehistoric extinctions of island birds

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Many bird species were extirpated or became extinct when prehistoric man reached oceanic islands. We list >200 species of extinct island birds only recorded as subfossils and which probably vanished due to prehistoric man. In addition, we list c. 160 cases where an extant species has been found as subfossil on islands where it no longer occurs. Several species, today considered endemic to single islands or island groups, had a much wider distribution in the past. Biogeographic analyses of insular avifaunas are almost meaningless if the extensive prehistoric extinctions are not taken into account.

Most extinct species belong to Anatidae, Rallidae and Drepanididae while local extirpations are numerous among doves and seabirds. Smaller birds are rare, mainly due to sampling bias and taphonomic factors. The bird populations were depleted mainly by overhunting, predation by introduced vertebrates and alteration of the original vegetation.

Prehistoric humans on islands, although dependent on limited animal resources, regularly failed to exploit these in a sustainable way. Several cases where human populations disappeared from islands in the Pacific may have been due to overexploitation of native animals.

Prehistoric man reached most tropical and temperate islands, and most of the few remaining island faunas have been severely depleted in historic times. The prehistoric extinctions emphasize the extreme vulnerability and value of the very few pristine island faunas that still remain.

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Introduction

The bird extinctions that followed the European expansion in the Pacific and Indian Oceans after 1600 AD are reasonably well documented and many cases are known where bird species have been lost from single islands (extirpation) or have become completely extinct (e.g. Rothschild 1907, Greenway 1967, Halliday 1978, Fuller 1987, Balouet 1990). Ninety percent of the c. 108 species thought to have become extinct since 1600 were restricted to islands (Johnson and Stattersfield 1990). Moreover, a disproportionate part of the currently threatened bird species are island endemics (Mountfort 1988, Johnson and Stattersfield 1990). Bird species endemic to single islands are particularly vulnerable. Some are flightless and most have evolved in the absence of mammalian predators and are therefore "naïve" in their attitudes towards humans and introduced predators. This is also the case for many seabirds breeding on oceanic islands without predators. In addition, insular landbird populations are small because of the limited area of suitable habitat.

Extinctions that took place during the initial Portuguese/Spanish phase of the European maritime expan-

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Table 1. The date of arrival of prehistoric people to islands after crossing sea-barriers.

Island or archipelago	Date (BP)	Reference
Lesser Sundas	100 000?	Whitten et al. 1987
Australia	>50 000	White and O'Connell 1979
New Guinea	>50 000	White and Allen 1980
New Ireland	33 000	Allen et al. 1988
Sulawesi	>30 000	Whitten et al. 1987
Solomon Islands	28 000	Wickler and Spriggs 1988
Ryukyu Islands	12 000?	Rouse 1986
Cyprus	10 000	Cherry 1990, Simmons 1991
Sardinia-Corsica	9 000?	Sondaar et al. 1986, Cherry 1990
Crete	9 000	Broodbank and Strasser 1991
Balearics	8 000	Cherry 1990
California Channel Islands	7 000	Keegan and Diamond 1987
Greater Antilles	7 000	Cruxent and Rouse 1969, Rouse 1986
Malta	6 000	Cherry 1990
Lesser Antilles	5 000	Rouse 1986
Pityuses	4 000	Cherry 1990
Central Melanesia	4 000	Rouse 1986
Micronesia	4 000	Craib 1983
Fiji	3 500	Rouse 1986, Keegan and Diamond 1987
Tonga and Samoa	3 000–3 500	Rouse 1986
New Caledonia	3 000	Roberts 1991
Tikopia	3 000	Roberts 1991
Canary Islands	2 000	J. Alcover, pers. comm.
Madagascar Islands	2 000	MacPhee and Burney 1991
Marquesas	1 500–2 000	Rouse 1986, Keegan and Diamond 1987
Cook Islands	1 600	Kirch et al. 1991
Hawaiian Islands	1 400	Keegan and Diamond 1987
Tahiti (Society Islands)	1 200	Rouse 1986, Keegan and Diamond 1987
Easter Island	1 000–1 300	Keegan and Diamond 1987, Roberts 1991
Norfolk Island	800–900	Roberts 1991
New Zealand	800	Anderson 1991
Chatham Islands	500–1 000	Cassels 1984

sion (c. 1400–1600 AD) were not recorded in contemporary literary sources and have only begun to be elucidated recently. Studies of subfossil bones have revealed a severe depletion of seabirds, several extirpated birds and several extinct species from islands in the Atlantic Ocean after European colonization (Olson 1975b, 1977b, Pieper 1985).

In prehistoric times, i.e. the time previous to the appearance of written sources, humans managed to reach many remote oceanic islands. Many voyages may have been accidental, but at least the Pacific was mainly explored through purposeful voyages by the Polynesians (Keegan and Diamond 1987, Irwin et al. 1990, McGrail 1991). The dates of arrival of humans to a number of islands are listed in Table 1. The impact of prehistoric colonizers on island birds has not been widely recognized, although e.g. J. C. Greenway (in Howland 1955) realized that many extinctions among landbirds must have followed the dispersion of *Rattus exulans* by early Polynesians in the Pacific. However, in the last few decades, studies of subfossil bones from oceanic islands have revealed numerous extinct and extirpated bird species. This has considerably altered our view of Earth's insular biota and here we review these studies and their implications for biogeography, anthropology and bird conservation.

Extinct species

The avifaunas encountered by prehistoric man were unique to each island. The exact composition of the faunas will remain unknown, but a fragmentary view of past faunas and how they were affected by the arrival of humans can be reconstructed from subfossil remains. Avian bones may be found in middens and at other archaeological sites. Bones also accumulate by natural means (often owls) in lava tubes, karst caves and calcareous dune deposits.

In Appendix 1, we list all prehistorically extinct island birds known to us, >200 species. Some of these have not yet been formally described. In other cases the remains are too scanty to permit a proper scientific description although they are definitely different from extant forms. The list is almost certainly incomplete, this being a field where new discoveries are constantly

Table 2. The number of prehistorically extinct bird species or subspecies. The species so far formally described in parenthesis. Note that numbers are only approximate due to the uncertain taxonomic status of some forms.

Family	Mediter-ranean	Atlantic Ocean	Caribbean	Indian Ocean	Pacific Ocean	Total
Aepyornithidae				7 (7)		7 (7)
Dinornithidae					13(13)	13(13)
Procellariidae	1 (0)	2 (2)			2 (1)	5 (3)
Pelecanidae					1 (1)	1 (1)
Sulidae					2 (2)	2 (2)
Ciconiidae			1 (1)			1 (1)
Threskiornithidae			1 (1)		3 (2)	4 (3)
Anatidae	2 (2)		1 (1)	2 (2)	20(15)	25(20)
Cathartidae			1 (1)			1 (1)
Accipitridae	1 (1)		4 (3)		8 (6)	13(10)
Falconidae			3 (3)			3 (3)
Megapodiidae					5 (2)	5 (2)
Phasianidae		1 (0)				1 (0)
Undescribed family *incertae sedis*					1 (1)	1 (1)
Gruidae	1 (1)		1 (1)			2 (2)
Rallidae			4 (4)	1 (1)	29(16)	34(21)
Rhynochetidae					1 (1)	1 (1)
Aptornithidae					2 (2)	2 (2)
Burhinidae			1 (1)			1 (1)
Scolopacidae			2 (1)		3 (2)	5 (3)
Laridae					1 (0)	1 (0)
Alcidae					2 (0)	2 (0)
Columbidae	1 (1)		1 (1)		11 (6)	13 (8)
Psittacidae			2 (1)		3 (2)	5 (3)
Cuculidae				1 (1)		1 (1)
Tytonidae	2 (2)		5 (5)		1 (1)	8 (8)
Strigidae	3 (2)		6 (5)		5 (5)	14(12)
Aegothelidae					1 (1)	1 (1)
Caprimulgidae			1 (1)			1 (1)
Apodidae			1 (1)			1 (1)
Xenicidae					3 (3)	3 (3)
Rhinocryptidae			1 (0)			1 (0)
Emberizidae			1 (1)			1 (1)
Muscicapidae					2 (0)	2 (0)
Meliphagidae					3 (0)	3 (0)
Drepanididae					23(14)	23(14)
Icteridae			2 (1)			2 (1)
Fringillidae	1 (0)	1 (1)				2 (1)
Estrildidae					1 (0)	1 (0)
Sturnidae					1 (1)	1 (1)
Corvidae	2 (1)		1 (1)		4 (3)	7 (5)
Total	14(10)	4 (3)	40(34)	11(11)	151(100)	220(158)

being made, and where information is widely scattered in sometimes obscure sources. Taxonomic difficulties also make it impossible to give an exact figure. E.g., there is yet no consensus about the number of moa species existing in New Zealand at the time of the Maori colonization, though a total of 11–13 species is a generally accepted figure (Anderson 1989a).

Anatidae, Rallidae and Drepanididae are most frequent among the species so far described from subfossil finds (Table 2).

In Appendix 1, we have also listed c. 160 cases where extant species have been found on islands where they no longer occur. It cannot be excluded that some of these finds might be vagrant individuals. However, we have tried not to list records of species known today as casual visitors. We have not listed extirpations for islands in the Mediterranean. There are two reasons for this. Firstly, these are not oceanic islands and many of the bird species are migrants or outliers of continental populations that can be strongly affected by conditions outside of the islands themselves. Secondly, human colonization of these islands took place in the early/middle Holocene while most of the fossil records are from the late Pleistocene. This means that some disappearances may be due to natural changes in climate and vegetation at the end of the Pleistocene. Nevertheless, it seems likely that many extirpations on the Mediterranean islands were caused, directly or indirectly, by man (Alcover et al. 1992).

Procellariidae and Columbidae are most frequent among the extirpations of island populations listed in Appendix 1.

Correlation of human arrival and extinction

In archaeological deposits, the extinct and extirpated birds are usually found only in the older strata and often disappear quite quickly after the arrival of man (e.g. Steadman 1992a). In natural assemblages, man's arrival can often be dated by the appearance of remains of introduced animals, in the Pacific often *Rattus exulans* but also other rodents, lizards and land snails (Kirch 1982). The extinct and extirpated birds are found mainly in levels below and immediately above those where introduced species begin to occur. The correlation is less clear in several cases outside the Pacific. In the Caribbean, some extinctions have been ascribed to disappearance of xeric habitats at the end of the last glaciation (e.g. Pregill and Olson 1981) and on Crete the disappearance of some Pleistocene birds may be due to climatic factors (Weesie 1987). However, the extinct forms survived earlier interglacials when conditions seem to have been similar to the present. Instead, the climatic changes at the end of the glaciation may have restricted the now extinct species to small refugia making them particularly vulnerable to human interference.

Studies of subfossil bones from islands not reached by humans in prehistory, have been unable to detect any Holocene vertebrate extinctions definitely predating human arrival (the Galapagos Islands: Steadman 1986a, Steadman and Ray 1982, Steadman et al. 1991; Lord Howe: van Tets et al. 1981, 1988).

It should be realized that the extinction of island birds can be a drawn-out process that in some cases cannot be neatly separated into "pre-European" and "European" phases. Some extinct species mentioned in Appendix 1 may well have survived until after European colonization though they were never collected or seen by competent observers. Indeed, in several cases, excavators have commented on the remarkably recent appearance of some of the bones. On the other hand, there are several cases where island birds were recorded by the first naturalist to visit an island but never seen again, e.g. *Aplonis mavornata* (Olson 1986), *Cyanoramphus ulietanus* and "*Turdus*" *ulietensis* (Fuller 1987). These extinctions might be ascribed to rats introduced by the first European ships, but it seems not unlikely that these species were already heading towards extinction when Europeans arrived.

Representativeness of the subfossil record

The subfossil record gives a biased view of past faunas because bones of species differ in their accumulation rate and capability for preservation. Large species are generally better preserved than small ones. Birds used as food by man or prey by owls are more likely to be recovered. Species that disappeared quickly after man's arrival or had small populations are less likely to be found.

The material recovered is biased toward larger bird species because large mesh sizes (e.g. 6 or 13 mm) have been used when sieving soil in most studies. Therefore, bones of larger birds e.g. seabirds, pigeons, rails and parrots are usually found but not bones of e.g. small passerines and hummingbirds. In the few cases where finer mesh screens have been used (e.g. Olson 1985b, James et al. 1987) large numbers of bones of small birds have been found.

It is often impossible to separate closely related extant species by their bones. Hence, it is likely that extinctions in some bird groups will not be detected from the fossil record.

So far, very few islands have been studied and on most of these only a single, or at most a few sites have been investigated. Therefore, only a small fraction of the island birds that existed only a few thousand years ago have been recovered to date.

Case studies

Four of the islands or island groups mentioned in Appendix 1 are briefly discussed below. We have chosen reasonably well-studied islands of different size and degree of isolation.

Henderson Island

The very isolated Henderson Island (Pitcairn Group, Pacific Ocean) was long thought to have been untouched by Polynesians and to possess a pristine fauna and flora. However, more careful studies on this limestone island revealed several archaeological sites where many bird bones were found. Today, at least 11 seabird and 4 endemic landbird species breed on the island (Graves 1992). In addition, 3 pigeons and at least 3 seabird species occurred prehistorically on Henderson (Steadman and Olson 1985, Schubel and Steadman 1989).

Ua Huka

From a single archaeological site on Ua Huka (Marquesas Islands, Pacific Ocean) bones of 36 species were identified. Ninety percent of the bones were of 20 different seabird species. Of these 8 no longer exist on the island, including one extinct subspecies (*Papasula abbotti costelloi*). The landbird fauna has been even more depleted and of 16 species identified from bones, 13 no longer occur on the island. These include 8 extinct species and 1 extinct subspecies (Steadman 1991b).

The Hawaiian Islands

Nearly 50 bird species that became extinct in pre-European time are now known from the Hawaiian archipelago (Olson and James 1991, James and Olson 1991). In addition, in c. 20 cases, extant birds have been found in a subfossil state on islands where they have not been recorded in historical times. Subfossil birds are mainly known from Kauai, Oahu, Molokai and Maui with only

a few records from Hawaii, the largest island, and none at all from Niihau, Lanai and Kahoolawe. Therefore, future investigations are likely to increase the number of recorded extinct species. Several extinct species have been found in association with archaeological remains and are thus known to have survived until after the arrival of the Polynesians. It seems that more than half the original avifauna was lost in less than a millennium.

The original avifauna contained several bizarre forms including several large flightless ibises and anatids, at least a dozen species of flightless rails, a sea eagle, four species of owls and a variety of passerines.

Cuba

The subfossil avifauna of Cuba is difficult to evaluate. The extinct species have been identified piecemeal by several workers and almost none of the finds are securely dated. Some date back to the late Pleistocene while others may be of quite recent date. It is even conceivable that some inconspicuous species e.g. the nightjar (*Siphonorhis daiquiri*) and the tapaculo (*Scytalopus* sp.) might still exist in small numbers (Olson 1985a, Olson and Kurochkin 1987).

The extinct Cuban fauna contained large mammals (Morgan and Woods 1986, Woods 1990). Several extinct large raptors and owls (some probably flightless) presumably subsisted on these large insectivores, rodents and edentates. Unlike oceanic islands without mammals, the extinct avifauna on Cuba lacked large flightless herbivorous birds (e.g. ratites, large flightless swans and geese).

Besides the large raptors, the Cuban avifauna has lost a flightless crane (*Grus cubensis*), a large flightless rail (*Nesotrochis picapicensis*), a stork (*Ciconia maltha*), an icterid (*Dolichonyx kruegeri*) and the nightjar and tapaculo mentioned above. The stork is of particular interest since the same species also existed on the North American mainland where it became extinct at the end of the Pleistocene. It is not known when the stork disappeared from Cuba. It has been suggested that it might have been a "big game follower" like the Marabou stork *Leptoptilos crumeniferus* and perished together with the large mammals (Steadman and Martin 1984). As has been suggested for extinct icterids on the North American mainland (Steadman and Martin 1984), *Dolichonyx kruegeri* may also have been dependent on these mammals.

Causes of extinction

The actual causes of prehistoric extinctions cannot be determined. Even in recent extinctions, the actual cause is frequently obscure or the extinction is the result of several factors which relative importance is difficult to evaluate. Nevertheless, the historic cases enable us to guess what the important factors were in prehistory.

Overkill

Birds of uninhabited islands tend to be "naïve" and unaware of any danger posed by man or other predators. This phenomenon has been described by many travellers, e.g. Darwin (1839, Chapter 19), who wrote about the birds of the Galapagos Islands: "There is not one which will not approach sufficiently near to be killed with a switch, and sometimes, as I have myself tried, with a cap or hat." and Stetson visiting Howland Island in 1854: "... the extraordinary tameness of the birds made it necessary to scuffle through them at times as one would if walking through windrows of dead leaves in the autumn at home." (Howland 1955 p. 97). Indeed, easily accessible avian prey on uninhabited islands was probably an important reason for the long sea voyages undertaken by Polynesians (Keegan and Diamond 1987).

Larger landbirds and seabirds were probably heavily affected by hunting (Diamond 1984). In New Zealand, bones of moa species hunted by the Maori have been found in very large quantities in middens (Anderson 1984, 1989a,b, Trotter and McCulloch 1984). Other species often found in Maori middens include a swan (*Cygnus sumnerensis*) and flightless "geese" (*Cnemiornis* spp.). On Hawaii, several sites at high altitudes have been interpreted as bird hunting stations mainly used for hunting petrels, geese and possibly also passerines for ornamental feathers (Athens et al. 1991).

On islands lacking a fringing reef (e.g. Henderson Island), maritime resources were not easily accessible and the inhabitants must have been particularly dependent on birds. On atolls, birds would have been a welcome change in the fish diet. Moreover, atolls and other "low" islands lack inaccessible montane forests which might act as refuges from human hunting.

Introduced predators

Many historic bird extinctions have been attributed to introduced predators (e.g. Diamond and Veitch 1981, Savidge 1987, Ebenhard 1988, Griffin et al. 1989). Today, *Rattus rattus* and *R. norvegicus* (e.g. Atkinson 1977, 1985, Wace 1986, Campbell 1991, Seitre and Seitre 1992) and feral cats (e.g. Fitzgerald and Veitch 1985, van Rensburg and Bester 1988) are usually considered the worst devastators of native island faunas. None of these animals were spread by prehistoric man. However, the Polynesians brought the smaller *Rattus exulans* to nearly all the islands they visited (Wodzicki and Taylor 1984, Roberts 1991), and dogs and pigs to many of them (Keegan and Diamond 1987).

From many islands, there is anecdotal evidence of a "phase of superabundance" of rats some time after their introduction (e.g. Howland 1955, Cheke 1987). The first period after the introduction of a new predator can probably be very destructive because the population

tends to increase beyond the carrying-capacity of the island and easily accessible prey is severely over-exploited (Bell 1977, Ebenhard 1988).

Small birds and ground-nesting species were probably worst affected by predation by *Rattus exulans* and other introduced rodents. However, even large adult seabirds may be predated on by *R. exulans* (Kepler 1967).

An example of the catastrophic impact that an introduced predator may have on a "naïve" bird population was recently documented when a single feral dog killed c. 500 brown kiwis *Apteryx australis* over a period of six weeks (Taborsky 1988).

Habitat destruction

Habitat destruction is another important factor but is likely to have varied greatly between islands. Well documented prehistoric habitat alteration on a very large scale took place in New Zealand, where vast areas of forest were destroyed by fire and replaced by biologically impoverished grassland and scrub (Bussell 1988, Holdaway 1989, McGlone 1989). On the Hawaiian Islands, the lower drier parts had been so completely cleared before the arrival of the Europeans that there is considerable uncertainty about the composition of the natural vegetation (Olson and James 1982b, Kirch 1982). On Easter Island, the original forest was destroyed by the islanders (Flenley and King 1984). On Mangaia (Cook Islands), the original forest was largely replaced by an open pyrophytic community dominated by ferns and *Pandanus* soon after the Polynesian colonization and there is also evidence of soil erosion on a considerable scale (Kirch et al. 1991, 1992).

In the Mediterranean, the early islanders were farmers (e.g. Broodbank and Strasser 1991). Their farming activities and the introduced ovicaprines, pigs, cattle and cats should have affected the vegetation and the native fauna (Davis 1987).

It is unclear how the vegetation in the Caribbean was affected by prehistoric Indians. The agouti (*Dasyprocta*) was dispersed by the Indians (Wing et al. 1968, Morgan and Woods 1986) but it is not known what effect, if any, this rodent had on the vegetation.

Depletion of food supplies

The extinction of prey species would particularly affect raptors and owls. The very large New Zealand eagle (*Harpagornis moorei*) was probably dependent on moas and other large extinct bird species and the large eagles and owls of Cuba presumably fed on the now extinct ground-sloths and large rodents. Mourer-Chauviré and Weesie (1986) suggested that the extinction (by man) of the small lagomorph *Prolagus sardus* caused the extinction of *Bubo insularis* on Corsica and Sardinia.

Birds other than raptors and owls may also be affected by decreasing availability of food (e.g. Beggs and Wilson 1991). It has been argued that the introduction of *Rattus exulans* to New Zealand caused a great depletion of large invertebrates which may have been important in the extinction of e.g. *Aptornis* and *Megaegotheles* (Holdaway 1989).

Diseases

Introduced parasites and diseases have been considered important in some historic extinctions (Warner 1968, Cooper 1989, Steadman et al. 1990b). There is evidence that the prevalence of avian pox and avian malaria (both presumably introduced) has a considerable influence on the distribution of surviving endemic Hawaiian landbirds (van Riper et al. 1986, van Riper 1991). Since poultry (*Gallus gallus*) were brought by Polynesians to many islands (Keegan and Diamond 1987), the introduction of avian diseases cannot be ruled out as a cause of prehistoric extinctions in the Pacific. However, on many islands, the lack of a vector for the introduced diseases is likely to have prevented the spread to native birds (Warner 1968).

Discussion

Biogeography

The subfossil records of extirpated birds have altered our view of the avian biogeography of the Pacific and the Caribbean (Steadman 1989d, Olson 1990). Several species with a very restricted distribution today and some which have been considered endemic to single islands, had a much larger distribution in the recent past. Such cases are known in the Pacific e.g. among pigeons (*Gallicolumba rubescens, Ducula galeata, D. aurorae, Ptilinopus rarotongensis, P. mercierii*), parrots (*Vini kuhlii, V. ultramarina*) and seabirds e.g. *Papasula abotti*, the latter today restricted to Christmas Island in the Indian Ocean (Reville et al. 1990). The scattered distribution of the genus *Megapodius* in the Pacific has been explained as the result of birds being transported by Polynesians (Lister 1911). Many finds of different species and several ignored historical records (summarized by Balouet and Olson 1989) show that *Megapodius* was earlier widespread. The most extensive changes in range and numbers have probably affected the procellariids, particularly the small *Pterodroma* petrels. The number of extinct procellariids is not very large, but extirpated species have been found on a large number of islands. Subfossil finds on the "mainland" of islands like Hawaii and New Zealand show that the restriction of the breeding sites of many species to offshore islets is a recent phenomenon (e.g. Millener 1991). Many disjunct bird distributions are likely to be the results of prehistoric extinctions on intervening islands.

One striking feature of the subfossil avifaunas is the occurrence of flightless rails (*Porzana, Gallirallus, Porphyrio*) on most oceanic islands studied outside the Mediterranean. At least on the larger islands, two or three species of different size coexisted. Apart from a few cases where islands were divided by rising sea-levels at the end of the last glaciation, such flightless rails were restricted to single islands. Considering the number of islands in the Pacific, 2000 species of rails may have been lost in this ocean alone (Steadman 1991b). Even assuming the total number of prehistorically lost species to be 2000, this would mean the prehistoric loss of 20% of *all* Holocene bird species.

Most biogeographic analyses of island avifaunas do not take the extensive prehistoric extinctions into account (e.g. Mayr 1965, Greenslade 1968, Power 1972, Ricklefs and Cox 1972, Terborgh 1973, Lack 1976, Abbott and Grant 1976, Diamond and Mayr 1976, Diamond et al. 1976, Gilpin and Diamond 1976, Diamond 1977, Holyoak and Thibault 1978, Juvik and Austring 1979, Abbott 1980, Williamson 1981, Adler 1992). Immigration rates and species turnover on oceanic islands are probably larger today than in pre-human times and it is possible that a student of pristine island avifaunas would put more emphasize on evolution and speciation on islands than on species turnover. Conclusion drawn from present-day avifaunas on e.g. competitive exclusion, niche-width and species-"poorness" of island birds might not be valid on an evolutionary time-scale.

During the last century, some 10 species of Australian landbirds have colonized New Zealand (Fleming 1962, Falla et al. 1978), a rate of colonization that must be much higher than the long-term average. Furthermore, in the Caribbean several bird species have colonized new islands in the last century (Ricklefs and Cox 1972). Many of these colonizations have probably been facilitated by habitat alteration and the extinction of native island birds (Diamond and Veitch 1981, Jehl and Parkes 1983). Similar processes must have started on islands already after the first prehistoric human contact. Hence, insular birds that show little or no differentiation from mainland forms may be recent colonizers. This might be the case for e.g. *Podiceps cristatus, Platalea regia, Circus approximans, Porphyrio porphyrio, Gallirallus philippensis, Ninox novaeseelandiae* and *Halcyon sancta* in New Zealand (Cassels 1984, Millener 1991) and for *Asio flammeus* and several waterbirds in the Hawaiian Islands (Olson and James 1982b) since all these species are very rare or completely absent as subfossils.

The size of the islands seems to have had little effect on the severity of the extinctions. New Zealand, of nearly continental size, and Cuba and the Hawaiian Islands, also of considerable size, have lost a large part of their fauna. This has some bearing on the much debated question whether "overhunting" caused the extensive late Pleistocene extinctions of continental megafaunas ("Pleistocene overkill"; Martin and Klein 1984, Webster and Webster 1984, Owen-Smith 1987, Stuart 1991). That the descendants of a few canoe-loads of people, without any previous experience in hunting large animals, could exterminate every large bird in New Zealand (c. 270 000 km^2) within about half a millennium, supports the view that late palaeolithic hunters, expert big game hunters, might well have done the same on a continental landmass given a few thousand years.

It should be noted that not only birds but also molluscs (Kirch 1982), insects (Worthy 1984), amphibians (Alcover et al. 1981, Worthy 1984), turtles (Balouet 1991), reptiles (Watters et al. 1984, Pregill et al. 1988, Pregill and Dye 1989, Dye and Steadman 1990, Balouet 1991), crocodiles (Balouet and Buffetaut 1987, Balouet 1991), rodents (Wing 1973, Steadman et al. 1984b, Watters et al. 1984, Pregill et al. 1988), bats (Pregill et al. 1988) and other mammals (Caloi et al. 1986, Dewar 1984, Morgan and Woods 1986, Sondaar 1987, Woods 1990) became extinct following island colonization by prehistoric people. In addition, extirpations have been recorded for land-crabs (Pregill et al. 1988).

The extinct large browsing birds may have influenced the evolution of several species traits of plants, e.g. the occurrence of spines, stinging hairs and secondary chemical compounds (Atkinson and Greenwood 1989, Greenwood 1992). Many widespread Pacific plants have fruits adapted for dispersal by birds and Guppy (1906) postulated extinct pigeons or megapodes to account for the wide distribution of some of these plants, a remarkably perceptive speculation. The former wide distribution of several species of fruit-eating pigeons in the Pacific implicates at least some inter-island exchange of birds and presumably seed dispersal. The extinction of important seed dispersers is likely to alter the composition of vegetation even when it is not directly affected by man (e.g. Janzen and Martin 1982, Witmer and Cheke 1991).

Anthropology

There is a widespread myth that "primitive" people are "natural conservationists" and live in a state of "ecological balance" without any appreciable effect on the environment (e.g. Kirch 1982, Chapman 1985, Diamond 1986, Woodley 1991). The impact of prehistoric people on island biota is a convincing rebuttal of this myth. The effect has invariably been highly destructive, not only to birds but to most types of organisms. Even on isolated Pacific islands, where the likely consequences of overexploitation should have been obvious, humans regularly failed to exploit wildlife or forest resources in a sustainable way. At least 14 Polynesian islands provide evidence for local extinction (or emigration) of human populations (Pitcairn, Anuta, Christmas, Fanning, Henderson, Howland, Malden, Necker, Nihoa, Norfolk, Palmerston, Raoul, Suwarrow and Washington; Keegan

and Diamond 1987). Over-exploitation of resources may well have been the cause of the disappearance of these human populations. By the time of European contact, the Polynesian population on the Hawaiian Islands was decreasing, possibly due to environmental degradation (Kirch 1982) and on Mangaia (Cook Islands) the local society was under severe strain because of resource shortages (Kirch et al. 1992).

In traditional societies in the South Pacific, a complex system of resource-use taboos helped preventing over-exploitation (Pernetta and Hill 1984, Chapman 1985). However, taboos, if used in the early phase of Polynesian expansion, did not prevent the extensive prehistoric extinctions. Maybe the use of taboos started as a result of these extinctions and the misuse of other resources.

Apparently the "ecological balance" between pre-industrial societies and their environment only applies to biota that cannot be profitably over-exploited with the available technology and that can survive habitat destruction and the introduction of new organisms.

Conservation

Prehistoric extinctions on islands demonstrate the extreme vulnerability of island environments. Few of Earth's numerous islands were never reached by prehistoric people and most of these have been severely affected by Europeans. Hence, very few reasonably pristine island faunas remain, a notable exception being the Galapagos Islands. The value of these few reasonably intact island biotas can hardly be over-estimated.

The introduction of predators and habitat destruction are accelerating in the Pacific and elsewhere (e.g. Wodzicki 1981, Moors 1985, Gade 1985, Loope et al. 1988, Carew-Reid 1990, Nunn 1990). Many island birds are severely threatened and can survive only through preservation of the remaining natural vegetation, by preventing the introduction of new predators and, if possible, by eradicating those already introduced. An additional conservation method is to translocate threatened landbirds to predator-free and/or uninhabited islands (Griffith et al. 1989, Franklin and Steadman 1991). Considering the many extirpations and range reductions in the Pacific, there should be few objections to this from a biogeographic viewpoint. In many cases, translocation would mean a reintroduction to an island where the species or a close relative existed in the recent past.

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Appendix 1. Island bird species extinct or extirpated in prehistoric time. We have used English names and family names according to Howard and Moore (1984), although their treatment of passerine families in the Australasian/Pacific area is unsatisfactory.

Extinct Extirpated	Family	Human association
MEDITERRANNEAN		
ARMATHIA (Pieper 1984)		
Athene cretensis	Strigidae	o
CORSICA & SARDINIA (Mourer-Chauviré and Weesie 1986, Alcover et al. 1992)		
Bubo insularis	Strigidae	o
CRETE (Weesie 1982, 1987)		
Aquila chrysaetos simurgh (extinct subspecies)	Accipitridae	o
Athene cretensis	Strigidae	o
IBIZA & FORMENTERA (Florit et al. 1989, Alcover et al. 1992)		
Undescribed Procellariid	Procellariidae	o
Undescribed small owl	Tytonidae/Strigidae	o
Corvus antecorax	Corvidae	o
MALLORCA & MENORCA (Mourer-Chauviré et al. 1980, Alcover et al. 1981, 1992, Florit and Alcover 1987, Mourer-Chauviré and Sanchez-Marco 1988)		
Tyto balearica	Tytonidae	o
Undescribed Corvid	Corvidae	
Undescribed large Fringillid	Fringillidae	
MALTA (Lydekker 1891, Bate 1916, Northcote 1982a,b, 1983, 1984, 1985, 1988a,b, 1992)		
Cygnus equitum	Anatidae	o
Cygnus falconeri	Anatidae	o
Grus melitensis	Gruidae	o
Columba melitensis	Columbidae	o
Tyto melitensis	Tytonidae	o
ATLANTIC OCEAN		
CANARY ISLANDS (Alcover and Florit 1987, McMinn et al. 1990, Walker et al. 1990, Baez 1992, J. Alcover pers. comm.)		
Puffinus holei	Procellariidae	o
Puffinus olsoni	Procellariidae	
Coturnix undescribed sp.	Phasianidae	
Carduelis triasi	Fringillidae	
CARIBBEAN		
ANTIGUA (Wing et al. 1968, Steadman et al. 1984a, Pregill et al. 1988)		
Puffinus lherminieri, Audubon's shearwater	Procellariidae	**
Puffinus puffinus, Manx shearwater	Procellariidae	**
Phoenicopterus ruber, greater flamingo	Phoenicopteridae	**
Porzana flaviventer, yellow-breasted crake	Rallidae	*
Porphyrio martinica, purple gallinule	Rallidae	**
Amazona? undescribed sp.	Psittacidae	**
Cinclocerthia ruficauda, brown trembler	Mimidae	*
BAHAMAS (Wetmore 1937b, 1938, Brodkorb 1959, Olson and Hilgartner 1982)		
Puffinus puffinus, Manx shearwater	Procellariidae	**
Pterodroma cahow, cahow	Procellariidae	**
Pterodroma hasitata, black-capped petrel	Procellariidae	o
Buteo »quadratus«	Accipitridae	o
Titanohierax gloveralleni	Accipitridae	o
Polyborus creightoni	Falconidae	o
Burhinus [bistriatus] nanus	Burhinidae	o
Gallinago undescribed sp.	Scolopacidae	o
Columba squamosa, red-necked pigeon	Columbidae	o
Tyto pollens	Tytonidae	o
Colaptes sp.	Picidae	o
Sturnella undescribed sp.	Icteridae	o
Corvus nasicus, Cuban crow	Corvidae	**
Corvus palmarum, palm crow	Corvidae	o

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
Barbados (Brodkorb 1965, 1967, Olson 1974)		
Neochen barbadiana	Anatidae	
"Fulica" podagrica	Rallidae	
Barbuda (Watters et al. 1984)		
Puffinus lherminieri, Audubon's shearwater	Procellariidae	**
Cuba (Arredondo 1958, 1970, 1971, 1972a,b, 1976, 1982, Brodkorb 1961, 1968, 1971, Fischer and Stephan 1971a,b, Olson 1974, 1985a, Pregill and Olson 1981, Olson and Hilgartner 1982, Olson and Kurochkin 1987)		
Ciconia maltha	Ciconiidae	
Antillovultur varonai	Cathartidae	o
Titaniohierax borrasi	Accipitridae	o
Grus cubensis	Gruidae	o
Nesotrochis picapicensis	Rallidae	o
Burhinus sp., stone-curlew	Burhinidae	
Tyto noeli	Tytonidae	o
Tyto riveroi	Tytonidae	o
Ornimegalonyx acevedoi	Strigidae	
Ornimegalonyx gigas	Strigidae	
Ornimegalonyx minor	Strigidae	
Ornimegalonyx oteroi	Strigidae	
Pulsatrix arredondoi	Strigidae	o
Siphonorhis daiquiri	Caprimulgidae	o
Scytalopus undescribed sp.	Rhinocryptidae	
Dolichonyx kruegeri	Icteridae	o
Haiti (Wetmore 1922b, Bernstein 1965, Olson 1974, 1976a, Olson and Hilgartner 1982)		
Titanohierax undescribed sp.	Accipitridae	
Milvago alexandri	Falconidae	o
Nesotrochis steganinos	Rallidae	o
Tyto ostologa	Tytonidae	o
Jamaica (Olson and Steadman 1977, 1979)		
Xenicibis xympithecus	Threskiornithidae	
Accipitridae, large species	Accipitridae	
Athene cf. *cunicularia*, burrowing owl	Strigidae	
Martinique (Wetmore 1952)		
Pterodroma cf. *hasitata,* black-capped petrel	Procellariidae	**
Mona Island (Pregill and Olson 1981)		
Athene cunicularia, burrowing owl	Strigidae	
Puerto Rico (Wetmore 1920, 1922a, 1923, 1938, Brodkorb 1978, Olson 1976b, 1982, 1985b, Olson and McKittrick 1981		
Polyborus latebrosus	Falconidae	
Nesotrochis debooyi	Rallidae	**
Scolopax anthonyi	Scolopacidae	
Geotrygon larva	Columbidae	**
Tyto cavatica	Tytonidae	
Athene undescribed sp.	Strigidae	
Tachornis uranoceles	Apodidae	o
Mimus gundlachii, Bahama mockingbird	Mimidae	o
Pedinorhis stirpsarcana	Emberizidae	o
Carduelis dominicensis, Antillean siskin	Fringillidae	o
Corvus pumilis	Corvidae	
Virgin Islands (Wetmore 1918, 1937a, Brodkorb 1972, 1978, Olson and Hilgartner 1982)		
Pterodroma cf. *hasitata,* black-capped petrel	Procellariidae	
Sula dactylatra, blue-faced booby	Sulidae	**
Nesotrochis debooyi	Rallidae	**
Ara autocthones	Psittacidae	**
Corvus leucognaphalus, white-necked crow	Corvidae	**
Corvus pumilis	Corvidae	**

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
INDIAN OCEAN		
MADAGASCAR (Brodkorb 1963, 1964, 1967, 1971, Olson 1977a)		
Mullerornis agilis	Aepyornithidae	
Mullerornis betsilei	Aepyornithidae	
Mullerornis rudis	Aepyornithidae	
Aepyornis gracilis	Aepyornithidae	
Aepyornis hildebrandti	Aepyornithidae	
Aepyornis maximus	Aepyornithidae	
Aepyornis medius	Aepyornithidae	
Alopochen sirabensis	Anatidae	
Centrornis majori	Anatidae	
"Hovacrex" roberti	Rallidae	*
Coua primaeva	Cuculidae	
PACIFIC OCEAN		
BONIN ISLANDS (Rich et al. 1986)		
Aogashima		
Diomedea sp., albatross	Diomedeidae	
Hahajima		
Calonectris leucomelas, streaked shearwater	Procellariidae	
Pterodroma leucoptera, Gould's petrel	Procellariidae	
CALIFORNIA CHANNEL ISLANDS (Howard 1964, Jefferson 1991, Guthrie 1992)		
Chendytes lawi	Anatidae	*
Fratercula undescribed sp.	Alcidae	
Mancalla? undescribed sp.	Alcidae	
Asio priscus	Strigidae	
CHATHAM ISLANDS (Kear and Scarlett 1970, Harrison and Walker 1973, Olson 1975a, 1984, Cassels 1984, Fordyce 1991, Millener 1991)		
Aptenodytes patagonicus, king penguin	Spheniscidae	**
Eudyptes pachyrhynchus, Victoria penguin	Spheniscidae	**
Megadyptes antipodes, yellow-eyed penguin	Spheniscidae	o
Phoebetria palpebrata, light-mantled sooty albatross	Diomedeidae	o
Pterodroma cf. *externa,* Juan Fernandez petrel	Procellariidae	o
Pterodroma inexpectata, mottled petrel	Procellariidae	**
Pterodroma lessonii, white-headed petrel	Procelariidae	o
Pterodroma macroptera, great-winged petrel	Procellariidae	o
Pterodroma magentae, Chatham Island taiko	Procellariidae	**
Pterodroma neglecta, Kermadec petrel	Procellariidae	o
Pterodroma cf. *ultima,* Murphy's petrel	Procellariidae	o
Sula sp.	Sulidae	o
Anas gibberifrons, grey teal	Anatidae	
Aythya novaeseelandiae, New Zealand scaup	Anatidae	
Cygnus sumnerensis	Anatidae	**
Mergus australis	Anatidae	**
Pachyanas chathamica	Anatidae	**
Circus eylesi	Accipitridae	o
Haliaeetus australis	Accipitridae	o
Falco novaezeelandiae, New Zealand falcon	Falconidae	**
Diaphorapteryx hawkinsii	Rallidae	**
Fulica chathamensis	Rallidae	**
Gallirallus minor?	Rallidae	**
Coenocorypha chathamica	Scolopacidae	**
Chlidonias hybridus, whiskered tern	Laridae	**
Sterna nereis, fairy tern	Laridae	**
Nestor meridionalis, kaka	Psittacidae	**
Sceloglaux albifacies, white-faced owl	Strigidae	o
Corvus moriorum antipodum	Corvidae	**

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
Cook Islands		
Mangaia (Steadman 1985, 1986b, 1989b, d, 1992a, Steadman and Kirch 1990, Kirch et al. 1992)		
Pterodroma nigripennis, black-winged petrel	Procellariidae	**
Nesofregetta fuliginosa, white-throates storm petrel	Hydrobatidae	**
Gallirallus ripleyi	Rallidae	**
Porzana rua	Rallidae	**
Gygis microrhyncha, white tern	Laridae	**
Ducula aurorae, Society Islands pigeon	Columbidae	**
Ducula galeata, Marquesas pigeon	Columbidae	**
Gallicolumba erythroptera, Society Islands ground dove	Columbidae	**
Gallicolumba nui	Columbidae	**
Ptilinopus rarotongensis, Rarotongan fruit dove	Columbidae	**
Vini kuhlii, Kuhl's lory	Psittacidae	**
Vini vidivici	Psittacidae	**
Aitutaki (Allen and Steadman 1990, Steadman 1991a)		
Pterodroma rostrata, Tahiti petrel	Procellariidae	**
Sula sula, red-footed booby	Sulidae	**
cf. *Dendrocygna* undescribed sp.	Anatidae	**
Porzana tabuensis, sooty crake	Rallidae	**
Vini kuhlii, Kuhl's lory	Psittacidae	**
Atiu (Steadman 1991a)		
Ducula aurorae, Society Islands pigeon	Columbidae	o
Gallicolumba erythroptera, Society Islands Ground Dove	Columbidae	o
Moturakau (Allen and Steadman 1990)		
Porzana tabuensis, sooty crake	Rallidae	
Easter Island (Carr 1980)		
Diomedea cauta, shy albatross	Diomedeidae	**
Fiji (Gibbons 1985, Steadman 1989b)		
Lakeba		
Megapodius undescribed sp.	Megapodiidae	**
Ducula undescribed sp.	Columbidae	**
Naigani		
Megapodius undescribed sp.	Megapodiidae	**
Hawaiian Islands (Olson and James 1982a,b, 1984, 1991, James et al. 1987, James and Olson 1991, Athens et al. 1991)		
Kauai		
Pterodroma phaeopygia, Hawaiian petrel	Procellariidae	o
Branta undescribed sp. aff. *hylobadistes*	Anatidae	o
Branta sandvicensis, Hawaiian goose	Anatidae	o
Chelychelynechen quassus	Anatidae	o
Porzana undescribed sp. 1	Rallidae	o
Porzana undescribed sp. 2	Rallidae	o
Grallistrix auceps	Strigidae	o
Chloridops undescribed sp.	Drepanididae	o
Ciridops tenax	Drepanididae	o
Hemignathus upupirostris	Drepanididae	o
Himatione undescribed sp. aff. *sanguinea*	Drepanididae	o
Telespiza persecutrix	Drepanididae	o
Xestospiza conica	Drepanididae	o
"Various unidentified finches"	–	
Oahu		
Pterodroma jugabilis	Procellariidae	**
Pterodroma phaeopygia, Hawaiian petrel	Procellariidae	**
Pterodroma hypoleuca, Bonin petrel	Procellariidae	**

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
Puffinus lherminieri, Audubon's shearwater	Procellariidae	
Puffinus puffinus, Manx shearwater	Procellariidae	**
Oceanodroma castro, Madeiran storm petrel	Hydrobatidae	**
Anatidae, "supernumerary Ohau goose"	Anatidae	**
Branta undescribed sp. aff. *hylobadistes*	Anatidae	**
Thambetochen xanion	Anatidae	**
Buteo undescribed sp.	Accipitridae	o
Circus dossensus	Accipitridae	o
Haliaeetus undescribed sp.	Accipitridae	o
Fulica undescribed sp.	Rallidae	o
Porzana ralphorum	Rallidae	**
Porzana ziegleri	Rallidae	**
Grallistrix orion	Strigidae	o
Chaetoptila undescribed sp. aff. *angustipluma*	Meliphagidae	**
Aidemedia chascax	Drepanididae	o
Aidemedia zanclops	Drepanididae	o
Chloridops regiskongi	Drepanididae	*
Chloridops wahi	Drepanididae	o
Ciridops undescribed sp.	Drepanididae	o
Hemignathus upupirostris	Drepanididae	o
Rhodacanthis undescribed sp. aff. *flaviceps*	Drepanididae	o
Telespiza bailleui, palila	Drepanididae	o
Telespiza cantans, yellow Laysan finch	Drepanididae	o
Telespiza persecutrix	Drepanididae	o
Xestospiza fastigialis	Drepanididae	o
"Various unidentified finches"	–	
Corvus impluviatus	Corvidae	
Corvus viriosus	Corvidae	
Molokai		
Pterodroma hypoleuca, Bonin petrel	Procellariidae	**
Pterodroma phaeopygia, Hawaiian petrel	Procellariidae	
Puffinus lherminieri, Audubon's shearwater	Procellariidae	
Oceanodroma castro, Madeiran storm petrel	Hydrobatidae	
Apteribis glenos	Threskiornithidae	**
Branta sandvicensis, Hawaiian goose	Anatidae	**
Thambetochen chauliodous	Anatidae	**
Buteo solitarius, Hawaiian hawk	Accipitridae	o
Circus dossenus	Accipitridae	o
Haliaeetus undescribed sp.	Accipitridae	*
Porzana menehune	Rallidae	*
Grallistrix geleches	Strigidae	**
Aidemedia lutetiae	Drepanididae	o
Ciridops cf. *anna*	Drepanididae	o
Hemignathus undescribed sp. aff. *lanaiensis*	Drepanididae	o
Hemignathus lucidus, nukupuu	Drepanididae	o
Himatione undescribed sp. aff. *sanguinea*	Drepanididae	o
Pseudonestor xanthophrys, Maui parrotbill	Drepanididae	o
Telespiza cantans, yellow Laysan finch	Drepanididae	o
Telespiza ultima, Nihoa finch	Drepanididae	o
Telespiza ypsilon	Drepanididae	o
Xestospiza fastigialis	Drepanididae	o
Corvus viriosus	Corvidae	**
Maui		
Apteribis brevis	Threskiornithidae	o
Apteribis undescribed sp.	Threskiornithidae	o
Branta hylobadistes	Anatidae	
Branta sandvicensis, Hawaiian goose	Anatidae	
Ptaiochen pau	Anatidae	o
Thambetochen chauliodous	Anatidae	o
Haliaeetus undescribeded sp.	Accipitridae	o
Porzana keplerorum	Rallidae	o
Porzana severnsi	Rallidae	o
Porzana undescribed sp.	Rallidae	o
Grallistrix erdmani	Strigidae	o
Myadestes undescribed sp. aff. *lanaiensis*	Muscicapidae	o

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
Chaetoptila undescribed sp. aff. *angustipluma*	Meliphagidae	o
cf. *Chaetoptila* undescribed sp.	Meliphagidae	o
Moho undescribed sp.	Meliphagidae	o
Aidemedia lutetiae	Drepanididae	o
Chloridops wahi	Drepanididae	o
Chloridops undescribed sp.	Drepanididae	o
Drepanis funerea, black mamo	Drepanididae	o
Hemignathus undescribed sp. aff. *lanaiensis*	Drepanididae	o
Orthiospiza howarthi	Drepanididae	o
Rhodacanthis undescribed sp. aff. *flaviceps*	Drepanididae	o
Rhodacanthis undescribed sp. aff. *palmeri*	Drepanididae	o
Telespiza ypsilon	Drepanididae	o
Telespiza undescribed sp. aff. *ypsilon*	Drepanididae	o
Vangulifer mirandus	Drepanididae	o
Vangulifer neophasis	Drepanididae	o
Xestospiza fastigialis	Drepanididae	o
"Various unidentified finches"	–	
Corvus undescribed sp. aff. *hawaiiensis*	Corvidae	o
Hawaii		
Pterodroma cf. *hypoleuca,* Bonin petrel	Procellariidae	**
Pterodroma jugabilis	Procellariidae	
Anatidae, very large Hawaii goose	Anatidae	*
Geochen rhuax	Anatidae	
Porzana undescribed sp. small Hawaii rail	Rallidae	
Porzana undescribed sp. large Hawaii rail	Rallidae	**
Corvus undescribed sp. aff. *hawaiiensis*	Corvidae	
Henderson Island, Pitcairn Group (Steadman and Olson 1985, Schubel and Steadman 1989)		
Pterodroma externa, white-necked petrel	Procellariidae	**
Pterodroma sp., small unknown petrel	Procellariidae	**
Puffinus nativitatis, Christmas Island shearwater	Procellariidae	**
Nesofregetta fuliginosa, white-throated storm petrel	Hydrobatidae	**
Ducula cf. *aurorae,* Society Islands pigeon	Columbidae	**
Ducula cf. *galeata,* Marquesas pigeon	Columbidae	**
Gallicolumba sp., ground dove	Columbidae	**
Huahine, Society Islands (Steadman 1989a,b,d, 1992a, Steadman and Pahlavan 1992)		
Pterodroma alba, Phoenix petrel	Procellariidae	**
Pterodroma arminjoniana, Trinidade petrel	Procellariidae	**
Pterodroma rostrata, Tahiti petrel	Procellariidae	**
Puffinus lherminieri, Audubon's shearwater	Procellariidae	**
Puffinus nativitatis, Christmas Island shearwater	Procellariidae	**
Puffinus pacificus, wedge-tailed shearwater	Procellariidae	**
Sula leucogaster, brown booby	Sulidae	**
Sula sula, red-footed booby	Sulidae	**
Fregata ariel, lesser frigate bird	Fregatidae	**
Fregata minor, great frigate bird	Fregatidae	**
Ardeola striata, striated heron	Ardeidae	**
Gallirallus undescribed sp.	Rallidae	**
Porzana tabuensis, sooty crake	Rallidae	**
Anous minutus, white-capped noddy	Laridae	**
Larus undescribed sp.	Laridae	**
Ducula aurorae, Society Islands pigeon	Columbidae	**
Ducula galeata, Marquesas pigeon	Columbidae	**
Gallicolumba erythroptera, Society Islands ground dove	Columbidae	**
Gallicolumba nui	Columbidae	**
Macropygia arevarevauupa	Columbidae	**
Vini sinotoi	Psittacidae	**
Vini vidivici	Psittacidae	**
Aplonis diluvialis	Sturnidae	**

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
MARQUESAS ISLANDS (Steadman and Zarriello 1987, Steadman et al. 1988, Steadman 1988, 1989b,d, 1991b, 1992a)		
Ua Huka		
Pterodroma cf. *alba*, Phoenix petrel	Procellariidae	**
Pterodroma rostrata, Tahiti petrel	Procellariidae	**
Pterodroma sp., small unknown petrel	Procellariidae	**
Puffinus lherminieri, Audubon's shearwater	Procellariidae	**
Puffinus nativitatis, Christmas Island shearwater	Procellariidae	**
Fregetta grallaria, white-bellied storm petrel	Hydrobatidae	**
Papasula abbotti costelloi (extinct subspecies)	Sulidae	**
Sula dactylatra, blue-faced booby	Sulidae	**
Gallirallus undescribed sp.	Rallidae	**
Porzana undescribed sp.	Rallidae	**
Prosobonia cf. *cancellata* (extinct subspecies)	Scolopacidae	**
Ducula galeata, Marquesas pigeon	Columbidae	**
Gallicolumba nui	Columbidae	**
Gallicolumba rubescens, Marquesas ground dove	Columbidae	**
Macropygia heana	Columbidae	**
Ptilinopus mercierii, red-moustached fruit dove	Columbidae	**
Vini sinotoi	Psittacidae	**
Vini ultramarina, ultramarine lory	Psittacidae	**
Vini vidivici	Psittacidae	**
Halcyon godeffroyi, Marquesas kingfisher	Alcedinidae	**
cf. *Myiagra* undescribed sp.	Muscicapidae	**
Hiva Oa		
Papasula abbotti costelloi (extinct subspecies)	Sulidae	**
Gallirallus undescribed sp.	Rallidae	**
Porphyrio paepae	Rallidae	**
Ducula galeata, Marquesas pigeon	Columbidae	**
Gallicolumba nui	Columbidae	**
Gallicolumba rubescens, Marquesas ground dove	Columbidae	**
Vini sinotoi	Psittacidae	**
Vini vidivici	Psittacidae	**
Tahuata		
Papasula abbotti costelloi (extinct subspecies)	Sulidae	**
Gallirallus undescribed sp.	Rallidae	**
Porphyrio paepae	Rallidae	**
Ducula galeata, Marquesas pigeon	Columbidae	**
Gallicolumba nui	Columbidae	**
Gallicolumba rubescens, Marquesas ground dove	Columbidae	**
Vini sinotoi	Psittacidae	**
Vini ultramarina, ultramarine lory	Psittacidae	**
Vini vidivici	Psittacidae	**
Nuku Hiva		
Gallirallus undescribed sp.	Rallidae	**
Vini sinotoi	Psittacidae	**
Halcyon godeffroyi, Marquesas kingfisher	Alcedinidae	**
NEW CALEDONIA (Poplin 1980, Poplin et al. 1983, Poplin and Mourer-Chauviré 1985, Balouet and Olson 1989, Balouet 1991)		
Accipiter efficax	Accipitridae	o
Accipiter quartus	Accipitridae	o
Megapodius molistructor	Megapodiidae	o
Sylviornis neocaledoniae	Undescribed family	**
Porphyrio kukwiedei	Rallidae	o
Rhynochetos orarius	Rhynochetidae	o
Coenocorypha? undescribed sp.	Scolopacidae	o
Caloenas canacorum	Columbidae	o
Gallicolumba longitarsus	Columbidae	o
Tyto? letocarti	Tytonidae	o
Ninox cf. *novaeseelandiae*, boobook owl	Strigidae	o

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
New Zealand (Scarlett 1957, 1968, 1969, 1970a,b, 1976, Olson 1975a, 1977c, Cracraft 1976, Millener 1981, 1988, 1991, Holdaway 1989, Anderson 1989a, Worthy 1989, Millener and Worthy 1991, Fordyce 1991)		
Anomalopteryx didiformis	Dinornithidae	**
Dinornis giganteus	Dinornithidae	**
Dinornis novaezealandiae	Dinornithidae	**
Dinornis struthoides	Dinornithidae	**
Dinornis torosus?	Dinornithidae	**
Emeus crassus	Dinornithidae	**
Euryapteryx curtus	Dinornithidae	**
Euryapteryx geranoides	Dinornithidae	**
Euryapteryx gravis?	Dinornithidae	**
Megalapteryx didinus	Dinornithidae	**
Pachyornis australis	Dinornithidae	o
Pachyornis elephantopus	Dinornithidae	**
Pachyornis mappini	Dinornithidae	**
Pelecanus [conspicillatus] novaezeelandiae	Pelecanidae	**
Biziura delautori	Anatidae	**
Cnemiornis calcitrans	Anatidae	**
Cnemiornis gracilis	Anatidae	**
Cygnus sumnerensis	Anatidae	**
Euryanas finschi	Anatidae	**
Malacorhynchus scarletti	Anatidae	o
Mergus australis	Anatidae	**
Circus eylesi	Accipitridae	**
Harpagornis moorei	Accipitridae	**
Capellirallus karamu	Rallidae	**
Fulica prisca	Rallidae	**
Gallinula hodgenorum	Rallidae	**
Gallirallus insignis?	Rallidae	
Aptornis defossor	Aptornithidae	**
Aptornis otidiformis	Aptornithidae	**
Megaegotheles novaezealandiae	Aegothelidae	o
Dendroscansor recurvirostris	Xenicidae	
Pachyplichas jagmi	Xenicidae	o
Pachyplichas yaldwyni	Xenicidae	o
Corvus moriorum	Corvidae	**
Norfolk Island (van Tets et al. 1981, 1988, Schodde et al. 1983, Meredith 1991)		
Pachyptila sp., prion	Procellariidae	o
Pterodroma [longirostris] pycrofti, Pycroft's petrel	Procellariidae	o
Pterodroma undescribed sp.	Procellariidae	o
Pelagodroma marina, white-faced storm petrel	Hydrobatidae	o
Sula tasmani	Sulidae	o
Gallirallus undescribed sp.	Rallidae	o
Coenocorypha cf. *aucklandica*, sub-Antarctic snipe	Scolopacidae	
Ofu, American Samoa (Steadman 1990, 1991c)		
Pterodroma rostrata, Tahiti petrel	Procellariidae	**
Puffinus griseus, sooty shearwater	Procellariidae	**
Puffinus pacificus, wedge-tailed shearwater	Procellariidae	**
Megapodius sp., scrub hen	Megapodiidae	
Raoul Island, Kermadec Islands (Anderson 1980, Meredith 1991)		
Pterodroma inexpectata, Peale's petrel	Procellariidae	**
Pterodroma magentae, Chatham Island taiko	Procellariidae	**
Pelecanoides urinatrix, common diving petrel	Pelecanoididae	**
Rota, Mariana Islands (Steadman 1992b)		
Anatidae undescribed sp.	Anatidae	o
Gallinula chloropus, moorhen	Rallidae	*
Poliolimnas cinereus, white-browed rail	Rallidae	o
cf. *Porphyrio* sp.	Rallidae	o
Procelsterna caerulea, blue-grey noddy	Laridae	o
Ducula oceanica, Micronesian pigeon	Columbidae	o
Gallicolumba undescribed sp.	Columbidae	o

Appendix 1 (cont.)

Extinct Extirpated	Family	Human association
Psittacidae undescribed sp.	Psittacidae	○
Myiagra cf. *freycineti*, Guam myiagra flycatcher	Muscicapidae	○
Erythrura undescribed sp.	Estrildidae	○
RYUKYU ISLANDS (Rich et al. 1986)		
Okinawa		
Scolopax mira, Amami woodcock	Scolopacidae	
Garrulus cf. *lidthi*, purple jay	Corvidae	
Miyake		
Haliaeetus cf. *albicilla*, white-tailed sea eagle	Accipitridae	
Grus sp.	Gruidae	
Gallirallus cf. *okinawae*, Okinawa rail	Rallidae	
SOLOMON ISLANDS (Steadman et al. 1988, 1990a)		
Tikopia		
Puffinus lherminieri, Audubon's shearwater	Procellariidae	**
Papasula abbotti abbotti, Abbott's booby	Sulidae	**
Sula sula, red-footed booby	Sulidae	**
Megapodius freycinet, common scrub hen	Megapodiidae	**
Gallirallus philippensis, banded rail	Rallidae	**
Sterna fuscata, sooty tern	Laridae	**
Anuta		
Puffinus lherminieri, Audubon's shearwater	Procellariidae	**
Puffinus pacificus, wedge-tailed shearwater	Procellariidae	**
Sula sula, red-footed booby	Sulidae	**
Fregata ariel, lesser frigate bird	Fregatidae	**
Sterna fuscata, sooty tern	Laridae	**
TONGA		
Lifuka (Steadman 1989c)		
Megapodius alimentum	Megapodiidae	**
Megapodius cf. *molistructor*	Megapodiidae	**
Caloenas cf. *canacorum*	Columbidae	**
Ducula cf. *david*	Columbidae	**
Ducula undescribed sp.	Columbidae	**
Eua (Steadman 1989b, 1991c)		
Puffinus lherminieri, Audubon's shearwater	Procellariidae	*
Gallicolumba cf. *stairi*, friendly quail dove	Columbidae	*
Megapodius pritchardii, Polynesian scrub hen	Megapodiidae	
WALLIS (Balouet and Olson 1987)		
Ducula david	Columbidae	**

? = systematics uncertain
undescribed sp. = not formally described
○ = not associated with man
* = radiocarbon-dated as contemporary with man or associated with artefacts or introduced animals
** = in middens