Review of Holocene wildfowl extinctions

H.GLYN YOUNG, SIMON J. TONGE and JULIAN P. HUME

Brief accounts are given of 54 wildfowl taxa (Anseriformes) known to have become extinct during the Holocene Period (the last 10,000 years). Distribution, probable taxonomic affinities, and the causes of decline of these, predominantly island-living birds are discussed.

Keywords: Wildfowl, Extinction, Holocene, Flightlessness, Exploration

Wildfowl taxa possibly threatened with extinction have been reviewed in previous volumes of *Wildfowl* (Kear & Williams 1978; Green 1992; Callaghan & Green 1993) and elsewhere (Ellis-Joseph *et al.* 1992; Green 1994). Green (1992; 1994) lists eight wildfowl taxa as extinct, all presumed to have died out within the last 150 years. A species is considered extinct when there is no reasonable doubt that its last individual has died (Mace & Stuart 1994). Exact dates of extinction are difficult to confirm as many taxa were not recorded when alive, and are known only from sub-fossil remains, often from prehistoric middens. This review details wildfowl taxa that, predominately through the influence of humans, have become extinct during the Holocene Period, that is during the last 10,000 years.

Two of the taxa considered extinct by Green (1992, 1994) are not included in this review. The Pink-headed Duck *Rhodonessa caryophyllacea* is assumed extinct, and has not been seen reliably in the wild since 1935 (Ali 1960) but cannot be confirmed as extinct following reported sightings in Myanmar (Collar *et al.* 1994). The exact status in New Britain of the New Britain Wandering Whistling Duck *Dendrocygna arcuata pygmaea*, extinct in New Caledonia (where subspecies not confirmed) (Madge & Burn 1988) and Fiji (where history uncertain) (Watling 1982), is unclear. Coates (1985) records a distribution centered on Lake Dakatava and Wide Bay, New Britain, however there is no current information on numbers (S. Spanner in litt. 1995). Three taxa included by Milberg & Tyrberg (1993), *Neochen barbadiana* from Barbados (Brodkorb 1967), *Cygnus falconeri* and *Cygnus equitum* from Malta (Northcote 1992) are omitted from this review as there is no evidence that they survived beyond the Pleistocene.

It is not within the scope of this publication to discuss at length the causes of wildfowl extinction. However, it is possible to summarise the features of different regions that have led undoubtedly to many of those extinctions. The taxonomic status of many sub-fossil Anatidae is unresolved, and listing taxa by geographical region avoids confusion and further emphasises the perilous nature of several island wildfowl faunas.

The IUCN categories of extant species are from TWRG (1995).

Hawaiian Islands

The Hawaiian Islands once hosted a remarkable avifauna of which a great proportion is now extinct. These volcanic

islands offered a diverse range of habitats, available to any species able to cross the thousands of miles of Pacific Ocean to exploit them. Wildfowl underwent a dramatic adaptive radiation in the islands to take advantage of an environment free from herbivorous competitors and mammalian predators. Consequently, the need for flight diminished, resulting in gross development of size, coupled with small wings. These adaptations did not make wildfowl vulnerable in the presence of limited predator influence, the only serious predators being a large sea eagle (*Haliaeetus* sp.) and some small owls (*Grallistrix* spp.)(Olson & James 1991). Extinction, however, rapidly followed colonisation of the islands by Polynesians, approximately 1,500 years ago (Olson & James 1984), when these characteristics proved disastrously disadvantageous. Large flightless birds were easily hunted, and when James Cook 'discovered' the islands in 1778 much of the lowland forest had been destroyed and at least nine wildfowl species had become extinct through the actions of humans and/or their commensal mammals.

Goose-like ducks or moa-nalos

Large, flightless goose-like ducks, the moa-nalos have been found so far on four of the Hawaiian islands. These species, probably derived from an *Anas*-like ancestor, became the dominant herbivores in the islands, in a position analagous to the Moas of New Zealand, and to giant tortoises in Galapagos, the Mascarene Islands and Aldabra.

A remarkable feature of this group was the development of the bill from a conventional 'duck' shape to a massive tooth-lined, serrated structure used for cropping vegetation. A possible explanation for this bill size can be deduced from fossilised droppings found in association with the skeletal remains. Analysis has shown that ferns formed a substantial part of the diet (S.L.Olson & H.F.James pers. comm.). This is unusual, as fern consumption is generally avoided by herbivores as these plants are tough and unpalatable. The significance of this diet may provide the key to the extraordinary bill, particularly that of *Chelychelynechen* from Kauai. With practically all the lowland forests now gone, an adaptation to feeding on some other, once abundant plant species that has vanished, may have been equally responsible for the bill's development.

Chelychelynechen quassus Large Kauai Goose

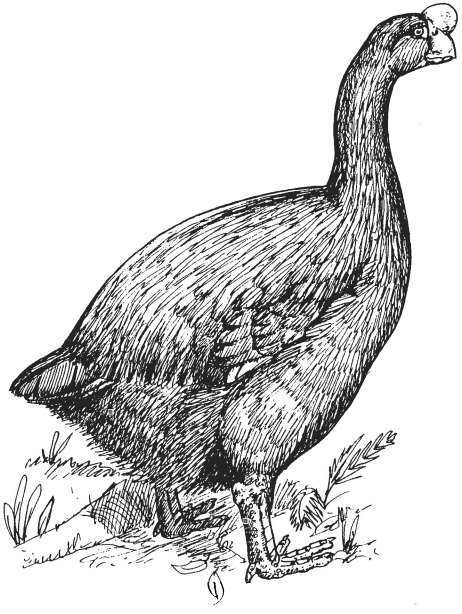

Figure 2. *Chelychelynechen quassus.* Kauai. Hawaiian Islands.

Chelychelynechen quassus Olson, S.L. & James, H.F., *Ornith. Monogr.* 45(1), 1991, pp.33-35, Figure 9. Makawehi dunes, Kauai, Hawaiian Islands.

This moa-nalo was from Kauai, and shows the most extreme divergence of any of the group. Its bill resembled the jaws of a tortoise.

Thambetochen xanion

Thambetochen xanion Olson, S.L. & James, H.F., *Ornith. Monogr.* 45(1), 1991, pp.35-37, Figure 10. Barbers Point, Oahu, Hawaiian Islands.

Found from Barbers Point and Ulupau Head, Oahu. *Thambetochen xanion* is similar to *T. chauliodous* but smaller and less robust.

Thambetochen chauliodous

Thambetochen chauliodous Olson,S.L. & Wetmore, *A., Proc.Biol. Soc. Washington,* 89,(18), 1976, pp.252. Moomoni dunes, Molokai, Hawaiian Islands.

This species was excavated from the Moomomi dunes and Ilio Point, Molokai and from the southern slopes of Mount Haleakala, Maui; its bill has bony tooth-like projections. *T. chauliodous* may have been more common on Maui, at lower elevations than a sympatric species, *Ptaiochen pau*. One, almost complete, egg found (121x79.5 mm) is the largest known from any anseriform (S.L.Olson & H.F.James pers.comm.).

Ptaiochen pau

Ptaiochen pau Olson,S.L. & James,H.F., *Ornith. Monogr.* 45(1), 1991, pp.39-42, Figures. 11 and 12. Auwahi Cave, Maui, Hawaiian Islands.

Ptaiochen pau was found on the southern slopes of Mount Haleakala, Maui, from 1,145 m to 1,860 m. It was apparently restricted to higher elevations on Maui than *T. chauliodous*.

True geese

Bones of the Hawaiian Goose *Branta sandvicensis* have occurred on Hawaii while further bones, considered inseparable from those, have been found on Molokai, Lanai, Kauai and Maui. Remains of other extinct *Branta* have also been found, some of which are from larger, more robust and flightless forms. It is possible that populations of *Branta* sp. in the Hawaiian islands were in the process of becoming flightless, and included flying and flightless individuals. This would be a unique scenario, where fossil remains actually capture the sequence of events prior to complete flightlessness. The inter-island mixing and merging of *B.sandvicensis* gradually decreased with these less volant forms (Olson & James 1984) which may have eventually evolved new species. The conclusion will never be known, their continued development having been curtailed by extinction.

Branta sp.

Bones of geese similar to *B. hylobadistes* have been unearthed on the Makawehi dunes, Kauai (sympatrically with *B. sandvicensis*) and at Barbers Point, Oahu (Olson & James 1991).

Branta hylobadistes

Branta hylobadistes Olson,S.L. & James,H.F., *Ornith. Monogr.* 45(1), 1991, pp.45-47, Figure 13. Auwahi Cave, Maui, Hawaiian Islands.

This species was found on the southern slopes of Mount Haleakala, Maui. Apparently abundant in formerly forested areas, the goose had reduced wings and pectoral girdle. *B. hylobadistes* and the smaller *B. sandvicensis* were sympatric.

'Large Hawaii Goose'

The 'Large Hawaii Goose' or 'Big Island Goose' was found from north Kona and north Kohala Districts, Hawaii. Fragmentary bone material has been discovered from a goose with large legs and reduced wings, considerably larger than any moa-nalo. It was thus probably the largest land animal in the archipelago. The remains of 30 individuals were uncovered in 1992 (Giffin 1993) and DNA samples taken from the remains indicate that the bird was of *Branta* rather than *Anser* origin, and closely allied to the *B. canadensis/B. bernicla* group (S.L.Olson pers.comm.).

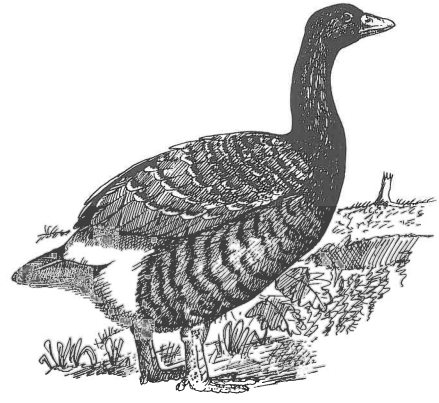

Figure 1. Big Island Goose, Hawaii.

Other goose-like birds

Goose-like wildfowl, possibly unrelated to the moa-nalos and the true geese, have been detected on several islands. Not all described, the true affinities of these birds are not yet clear.

'Supernumerary Oahu Goose'

Found from Barbers Point, Oahu, this undescribed, but apparently distinctive, species is known from only a small number of bones (Olson & James 1991).

Geochen rhuax

Geochen rhuax Wetmore, A., *Condor,* 45, 1943, pp.146-148, Figure 39. Kaumaikeohu, Hawaii, Hawaiian Islands.

This species came from the Kaui District, Hawaii, and is larger and more robust than *Branta* from the same island. *G. rhuax* was the first fossil bird described from the Hawaiian Islands in 1943.

The known distribution of geese and goose-like wildfowl from the Hawaiian Islands is shown in **Table 1.** Three endemic taxa survive in the Hawaiian Islands: the Hawaiian Goose (IUCN Endangered), Laysan Teal *Anas laysanensis* (IUCN Critical) and Hawaiian Duck *A. wyvilliana* (IUCN Low Risk: Conservation Dependent). All have a much reduced distribution having once been widespread throughout the islands (Olson & James 1991; Engilis & Pratt 1993; Cooper *et al.* 1996), within a wider habitat.

New Zealand

Like Hawaii, New Zealand's avifauna have shown a remarkable degree of diversification with a high number of flightless species. With no native land mammals, terrestial habitat was at a premium, the now extinct Moas (11 species (Bell 1991)) became the dominant herbivores, and wildfowl evolved to fill many vacant niches. The dominant predators were avian, including *Harpagornis moorei* possibly the largest eagle recorded, *Haliaeetus australis* and *Circus eylesi.* All are extinct and, being large raptors, probably preyed on wildfowl (Atkinson & Millener 1991).

Human colonisation by Polynesians, approximately 1,000-1,200 years ago led to significant changes in the avifauna, especially through forest clearance, hunting, and the introduction of exotic land mammals (Cassels 1984). Evidence for massive habitat degradation during Polynesian times is overwhelming, and most extinctions can be dated with reasonable certainty to the period after human colonisation (Holdaway 1989). The human colonists brought the first mammalian predators, Kiore *Rattus exulans* and Dog *Canis familiaris*, to New Zealand (Holdaway 1989).

The most vulnerable birds, mostly the large, terrestial and flightless taxa, had been exterminated already before James Cook's arrival in New Zealand in 1769. The second, European, period of colonisation has seen further habitat modification and

Table 1. Known distribution of geese and goose-like wildfowl in the Hawaiian Islands after Olson & James (1991). *subfossil record + subfossil and historical record

	Kauai	Oahu	Molokai	Lanai	Maui	Hawaii
Chelychelynechen	*					
T. xanion		*				
T. chauliodous			*		*	
Ptaiochen pau					*	
Branta sp.	*	*				
B. sandivcensis	*		*	*	*	+
B. hylobadistes					*	
'Very Large Hawaiian Goose'						*
'Supernumerary Oahu Goose'		*				
Geochen rhuax						*

the introduction of more mammalian carnivores, notably the rats *R. rattus* and *R. norvegicus* and Cat *Felis cattus* (Holdaway 1989). In total, 44 endemic bird species(including eight wildfowl) have become extinct during the post-colonisation period (Bell 1991), the remains of at least 30 of them have been unearthed at archaeological sites (Millener 1990).

Swans

Cygnus sumnerensis New Zealand Swan

Chenopsis sumnerensis Forbes,H.O., *Nature*, 41, 1890, pp.209. Monck's Cave, Sumner, New Zealand.

This swan was common throughout New Zealand including Stewart and the Chatham Islands. *C. sumnerensis* is considered to be related closely to, although larger than, the Black Swan *C. atratus* (Howard 1964; Livezey 1989a). An apparently abundant species, it was exploited widely for food (Williams 1964). Possibly a colonial nester, the swan would have been vulnerable to predation hunting at colonies and during the wing and moult.

Extinct Geese *Genus Cnemiornis*

This genus consists of two large, flightless, goose-like wildfowl. Once considered relatives of the Cape Barren Goose *Cereopsis novaehollandiae*, Livezey (1989a) has shown that the genus is very primitive, having branched in evolution shortly after the Magpie Goose *Anseranas* and, represents a sister group to the Anatidae.

Cnemiornis calcitrans South Island Goose

Cnemiornis calcitrans Owen,R., *Trans. Zool. Soc. Lond.*, 5, 1865, pp.395-404, pls.63-68. Timaru, South Island, New Zealand.

This South Island species has been found from the east, Marlborough to Southland, and in the northwest. *C. calcitrans* was most abundant in the east, in areas of forest/scrub/grassland mosaic (Holdaway 1989). Large, with reduced wing and pectoral bones, the goose stood up to 1 m tall and may have weighed between 10 and 15 kg (Gill & Martinson 1991). Being flightless, it was probably very vulnerable to hunting (Holdaway 1989).

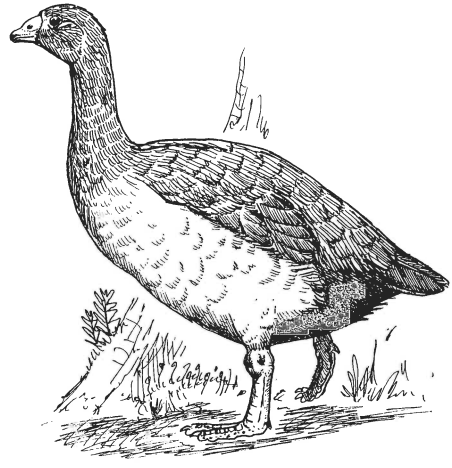

Figure 4. *Cnemiornis*. South Island, New Zealand.

Cnemiornis gracilis North Island Goose

Cnemiornis gracilis Forbes, H.O., *Trans. New Zealand Inst.*, 24, 1892, pp.187-188. North Island, New Zealand. Synonymy: *C. minor* and *C. septetrionalis*.

This species has been excavated throughout the North Island. Fossilised bones (Pleistocene) have been found, with the possibility of others in middens. *C. gracilis* was probably 25% smaller than *C. calcitrans* (Gill & Martinson 1991).

Other primitive ducks

Pachyanas chathamica Chatham Islands Duck

Pachyanas chathamica Oliver,W.R.B., *New Zealand Birds*, second edition, revised, 1955, pp.599-600, 2 figures Chatham Islands, New Zealand.

This large, probably flightless, duck is from the Chatham Islands, where bones have been unearthed from prehistoric

middens. *P. chathamica* is a stoutly-built duck with a robust skull, weight up to 2 kg (Gill & Martinson 1991). The exact affinities of the genus are unclear. In common with other terrestial birds of mammal-free small islands, *P. chathamica* may have been confiding and caught easily by humans.

Euryanas finschi Finsch's Duck

Anas finschi Van Beneden, P.J., *Bull. Soc. Geol. Belgique*, 2, 1875, pp.123-130, pl.3. Earnsclough Cave, Otago, South Island, New Zealand.

Common throughout the North and South Islands, bones have been found in prehistoric middens of this 2.2-2.3 kg, short-billed duck which probably fed in terrestial vegetation and forest, occasionally dabbling in streams, and may have nested in caves (Atkinson & Millener 1991). Millener (1991) states '..neither *Pachyanas* nor *Euryanas* (contra Worthy, 1988) would seem to have been capable of powered flight'. Livezey (1989a) places *Euryanas* in a separate sub-family, Euryanatinae.

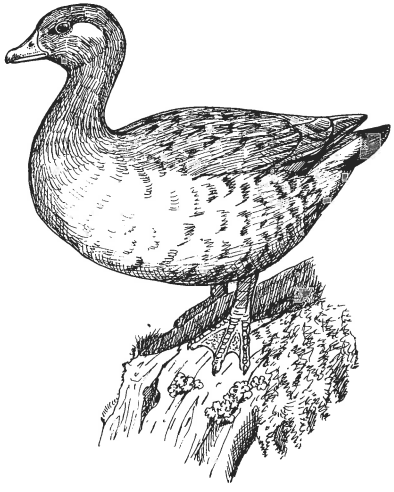

Figure 3. *Euryanus*. New Zealand.

Ducks

Malacorhynchus scarletti Scarlett's Duck

Malacorhynchus scarletti Olson, S.L., *Emu*, 77, 1977, pp.132-133. Pyramid Valley Swamp, Waikari, North Canterbury, South Island, New Zealand

This duck has been found from Pyramid Valley, Lake Grassmere and Hastings, South Island. *M. scarletti* is similar to, but larger than, the Australian Pink-eared Duck *M. membranaceus*. Described in 1977 from bill fragments approximately 3,500 years old (Olson 1977), a subsequent analysis of more complete skeletons has confirmed the identification (Worthy 1995). This species may never have been abundant in a limited habitat, and thus very vulnerable to predation and hunting (Holdaway 1989).

Biziura delautouri de Lautour's Duck

Biziura delautouri Forbes, H.O., *Nature*, 45,(1166), 1892, pp.417. Enfield Swamp, Oamaru, South Island, New Zealand.

This species was found in the North and South Islands, where bones have indicated a duck slightly larger than the Australian Musk Duck *B. lobata*; however, there is much variation in size due to dramatic sexual dimorphism in *B. lobata* (Olson 1977). Whether *B. delatouri* and *B. lobata* are conspecific is not clear.

Mergus australis Auckland Islands Merganser

Mergus australis Hombron, J.B. & Jacquinot, H., *Annls. Sci. Nat., Zool., Paris*, ser.2, (16), 1841, pp.320. Auckland Islands, New Zealand.

M. australis has been found from Auckland, Stewart, North and South Islands (possibly also Campbell Islands, where recently discovered bones may represent a distinct *Mergus* species). Discovered in 1840 in the Auckland Islands, *M. australis* was extinct around 1902. This small, long-billed, and possibly sedentary seaduck was probably approaching flightlessness (Livezey 1989b). Populations may never have been high, with the Auckland Islands unable to sustain many pairs. Since it has been found in prehistoric middens, extinction was probably caused by excessive hunting, habitat modification, and the actions of introduced mammals. The last

few birds were collected for museums (Kear & Scarlett 1970).

Bones of the Australian Blue-billed Duck *Oxyura australis* have been found at Hawke's Bay and may represent a resident population of a duck not recorded in New Zealand during historic times (Horn 1983). Sub-fossil remains of two further ducks, an unidentified brown teal *Anas* sp. with reduced wings (Bell 1991), and a shelduck *Tadorna* sp.(Tennyson & Millener 1994) have been obtained from the the Chatham Islands.

New Zealand has eight surviving endemic taxa (one in an endemic genus) of which the Blue Duck *Hymenolaimus malacorhynchus* (IUCN Endangered), Grey Duck *Anas s. superciliosa* (IUCN Critical), Brown Teal *A. chlorotis* (IUCN Endangered), Auckland Islands Teal *A. aucklandica* (IUCN Vulnerable) and Campbell Island Teal *A. nesiotis* (IUCN Critical) still face possible extinction.

Madagascar and the islands of the western Indian Ocean

Madagascar, the Mascarene Islands (Réunion, Mauritius and Rodrigues), Seychelles, Aldabra and the Comores represent a distinct faunal region, the Malagasy Region (Benson 1985). Wildfowl are also recorded from the sub-antarctic islands of St. Paul, Amsterdam, Crozet and Kerguelen that lie outside of the faunal region.

The Malagasy Region is characterised by a very high degree of plant and animal endemism. Madagascar has many native mammals, including viverrid carnivores, but no terrestial mammals are native to the other islands. The guild of predators in Madagascar also included large, now extinct, eagles *Aquila* sp. and *Stephanoaetus mahery* (Goodman 1994a; 1994b).

In Madagascar, elephant birds (6-12 species), Giant Lemurs and Pygmy Hippopotami became the dominant herbivores, a role filled on other islands by giant pigeons, e.g. Dodo *Raphus cucullatus* and Solitaire *Pezophaps solitarius*, and giant tortoises.

Madagascar was colonised by humans approximately 1,500 years ago (Dewar 1984) and the Mascarenes in the 16th century (Cheke 1987). Extinction of all the large bird, mammal and reptile herbivores (except for the Giant Tortoise *Geochelone elephantina* in Aldabra) followed shortly after colonisation. Habitat modification including burning, marsh reclamation and rice cultivation have had serious effects on the wetland birds of Madagascar (Langrand & Goodman 1995). In the Mascarenes, deforestation, hunting and the introduction of terrestial mammals have brought about the extinction of many endemic birds, reptiles and bats. Five wildfowl taxa have been lost from the Malagasy Region, plus at least one other from the southern Indian Ocean islands of Amsterdam and St. Paul.

Sheldgeese

Four sheldgeese, similar to the Egyptian Goose *Alopochen aegyptiacus* have been described from the region. The exact relationships between these taxa is unclear, and four full species may not be involved. There are no recent records of any sheldgeese from the region (Young in press), although the remains of many wetland birds have been discovered in Madagascar, extinct sheldgeese have not been found in association with the bones of the widespread and common Comb Duck *Sarkidiornis melanotos* (S.M.Goodman pers.comm.). The exact causes of extinction, particularly in Madagascar, are unclear. Bones of *Centrornis majori* and *Alopochen sirabensis* have been found in the arid areas of western and southwestern Madagascar amid evidence of a gradual aridification that pre-dated the arrival of humans (Goodman & Rakotozafy in prep.); this may suggest that the decline occurred, in part, through natural processes. There is no evidence of flightlessness in any of these species.

Centrornis majori

Centrornis majori Andrews, C.W., *Ibis*, ser 7,(3), 1897, pp.344-350, pl.8. Sirabe, Central Madagascar.

Found from central and western Madagascar, this sheldgoose is larger than the Egyptian Goose with longer legs (Andrews 1897).

Alopochen sirabensis

Chenalopex sirabensis Andrews,C.W., Ibis, ser. 7,(3), 1897, pp. 350-355, pl.9, figures 1-3. Sirabe, Central Madagascar.

This sheldgoose has been found in central and western Madagascar. A species very similar, but a little larger in all dimensions, to the Egyptian Goose (Andrews 1897), *A. sirabensis* has been the most commonly recorded aquatic bird at many sites investigated. It was, however, probably extinct when European naturalists arrived in Madagascar in the mid-17th century (Goodman & Rakotozafy in prep.).

Alopochen mauritiana

Sarcidiornis mauritiana Newton,E. & Gadow,H., *Trans. Zool. Soc. London*, 13, 1893, pp. 290-301, pl.34, figures 9-10. Mare aux Songes, Mauritius.

Endemic to Mauritius, this sheldgoose was observed in 'woods or dry ponds' and considered plentiful in 1681, declining rapidly until assumed extinct in 1698 (Cheke 1987).

Mascarenachen kervazoi

Mascarenechen kervazoi Cowles, G.S., *Geobios*, 27, (1), 1994, pp. 87-93, fig.1. Grotte des Premiers Franáais, St. Paul, Réunion.

Endemic to Réunion, this species which was smaller than *A. sirabensis*, possibly resembled the Kelp Goose *Chloephaga hybrida* in size (Cowles 1994). Geese, described as smaller than those of Europe and with red feet and beaks, were common in freshwater ponds in 1619 but were rapidly exterminated, and certainly extinct by about 1700 (Cheke 1987; Cowles 1987; 1994). **(see colour plate 3).**

Ducks

Anas theodori

Anas theodori Newton, E.T. & Gadow, H., Trans. Zool. Soc. London, 13, 1893, pp. 282 & 291-292, pl.34, figures 11-17. Mare aux Songes, Mauritius. **(see colour plate 3).**

Described from Mauritius, bones from *A. theodori* have been recently dug up on Réunion (C. Mourer-Chauviré in litt.1996). Ducks described as 'grey teal' were common in 1681 in Mauritius on lakes and ponds in the woods, but extinct by at least 1700 (Cheke 1987). In Réunion ducks were recorded in 1613, and in 1671-2 described as common, but they too were extinct by 1700 (Cheke 1987). The exact relationship between *A. theodori* and any extant species is unclear. It was smaller than the Madagascan species Meller's Duck *A. melleri* but larger than the Madagascar Teal *A. bernieri* (Hachisuka 1953). It may be very similar to the Grey Teal *A. gracilis* and *A. gibberifrons*, close relatives of *A. bernieri* (C.Mourer-Chauviré in litt.1996). The cranium is unlike that of any other duck (Cowles 1987).

Anas marecula Amsterdam Island Flightless Duck

Anas marecula Olson, S.L. & Jouventin, P., Condor 98, (1), 1996, pp.1-9, figures 1-8. Amsterdam Island, Indian Ocean.

Small brown ducks were recorded on St. Paul Island in 1793 and subfossil bones of a small *Anas* duck were found on Amsterdam Island in 1955-56 (Bourne *et al.* 1983; Olson & Jouventin 1996). Further material from Amsterdam Island was examined by Martinez (1987). These sub-antarctic islands are outside of the Malagasy Region.

Olson & Jouventin (1996) considered that the Amsterdam Island form was a small, flightless and strongly terrestial duck derived from a wigeon, possibly European Wigeon *A. penelope* or Chiloe Wigeon *A. sibilatrix*. This species was exterminated by humans through direct hunting, or through the actions of introduced mammals, 100-200 years ago (Bourne *et al.* 1983).

The duck from St. Paul Island remains unidentified. Even with a common ancestor, this taxon would have been morphologically different to *A. marecula*, and can not be considered conspecific with the Amsterdam Island species (Olson

& Jouventin 1996).

Bones of small duck, considered as *Aythya* sp. have recently been found in Réunion (C.Mourer-Chauviré in litt.1996), and could be similar to the Madagascar Pochard *A. innotata*.

There are five surviving endemic taxa in the western Indian Ocean: the Madagascar White-backed Duck *Thalassornis leuconotus insularis* (IUCN Vulnerable), Meller's Duck (IUCN Vulnerable), Madagascar Teal (IUCN Endangered), Eaton's Pintail *A. eatoni drygalskii* (IUCN Endangered) from Crozet, *A. e. eatoni* (IUCN Vulnerable) from Kerguelen, and Madagascar Pochard (IUCN Critical). All face possible extinction.

Other Pacific Ocean islands

Away from Hawaii and New Zealand, there are very few distinct wildfowl taxa in the Pacific Ocean, and most are isolated representatives of migratory, continental species. Of six taxa recognised here, two are doubtfully distinct. The reasons for their extinction were varied but include hunting, habitat modification, and the release of exotic mammals.

True Geese

Branta canadensis asiatica Bering Canada Goose

Branta hutchinsi asiatica Aldrich, J.W., *Wilson Bull.*, 58, 1946, pp.95. Bering Island, Siberia.

Recorded breeding on Bering and Komandorskiye Islands until 1900, and the Kuril Islands in 1892, *B. c. asiatica* wintered in Japan (Delacour 1964). This poorly defined taxon was probably a pale form of the Aleutian Canada Goose *B.c. leucopareia* (IUCN Vulnerable). The last bird known was a specimen collected in 1914 (Delacour 1964). Populations of both subspecies declined through hunting pressures at migration stop-overs and in the wintering areas, plus the release of foxes *Alopex* and *Vulpes* onto previously predator-free islands (Palmer 1976).

Ducks

Anas gracilis remissa Rennell Island Teal

Anas castanea remissa Ripley, S.D., Auk, 59, 1942, pp.94-95. Rennell Island, Solomon Islands.

Found from only Rennell Island, Solomon Islands, this poorly defined taxon was restricted to a single island which had only one freshwater lake. The island has been mined for bauxite, and this disturbance coupled with the introduction of the fish *Tilapia*, appears to have extirpated the population (Kear & Williams 1978). Teal on Rennell Island, however, may have been simply a temporary population of the highly dispersive Australian Grey Teal *A.g. gracilis*.

Anas strepera couesi Coues' Gadwall

Chaulelasmus couesi Streets, T.H., *Bull. Nuttall Ornith. Club*, 1, 1876, p.46. Washington Island, Fanning Group.

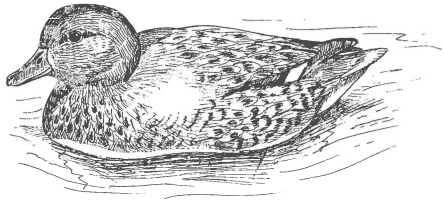

Figure 6. Coue's Gadwall. Washington Island.

This duck was found on Washington and New York Islands (Teraina), Kiribati (Line Islands). A sedentary population of the Holarctic, migratory Gadwall *A. strepera*, this subspecies resembled the nominate form in eclipse plumage and was discovered in 1874 when two specimens were collected (Phillips 1923). Coues' Gadwall has not been seen since its discovery, and probably became extinct shortly after the first people landed on the islands. Gadwall have been recorded in the Hawaiian, Mariana and Marshall Islands (Pratt *et al.* 1987).

Anas oustaleti Marianas Mallard or Oustalet's Grey Duck

Anas oustaleti Salvadori, T., *Bull. Brit. Ornith. Club*, 20, 1894, p.i. Mariana Islands.

Traced from Guam, Saipan and Tinian, Mariana Islands, this enigmatic duck is considered generally to be a subspecies of the Northern Mallard *A. platyrhynchos* or a hybrid swarm (Livezey 1991). Two 'types' of *A. oustaleti* have been described, birds that resemble *A. platyrhynchos* and those that resemble Grey Duck *A. superciliosa* (Yamashina 1948; Reichel & Lemke 1994). There are only two records of Northern Mallard, and none of Grey Duck from the Marianas (Reichel & Lemke 1994).

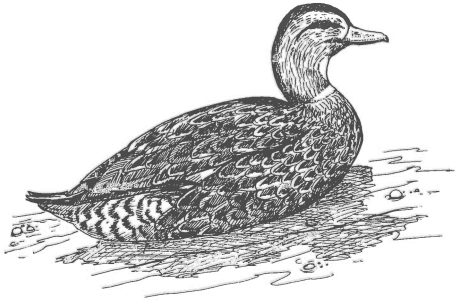

Figure 5. Marianas Mallard.

The Marianas Mallard was extirpated from Guam in the 1960s and became extinct on Tinian during the mid 1970s (Reichel & Lemke 1994). A pair was captured on Saipan in 1979 to initiate a captive breeding programme; however, these died without breeding in 1981. *A. oustaleti* has not been seen on Saipan since the early 1980s. Extinction of this taxa followed excessive hunting and habitat degradation in the Mariana Islands (Reichel & Lemke 1994).

Bones from unidentified wildfowl have been found on several Pacific islands, including a large, possibly arboreal and non-aquatic whistling-duck *Dendrocygna* from Aitutaki, Cook Islands (Steadman 1989; 1991), an *Anas* duck from Rota, Mariana Islands, the 'Rota duck' (Steadman 1992) and possibly a small subspecies of *A. gracilis* from New Caledonia (Balouet & Olson 1989).

Three further, extant, endemic taxa are known from the Pacific: the Grey Duck *A. superciliosa pelewensis* (IUCN Near Threatened) from much of the Pacific, Galapagos Pintail *A. bahamensis galapagensis* and Hardhead *Aythya australis extima* (IUCN Vulnerable) from Banks Island, Vanuata.

Continental areas

In contrast to the plight of island wildfowl, only four taxa from continental areas have become extinct during the Holocene (for a review of fossil wildfowl see Howard (1964)). Overhunting and habitat modification, however, have increasingly threatened many continental wildfowl and the future of several taxa appears bleak.

Ducks

Anas georgica niceforoi Niceforo's Pintail

Anas georgica niceforoi Wetmore, A. & Borrero, J.I., *Caldesia*, IV,(16), 1946, p.68. Laguna de Tota, Boyaca, Columbia.

This pintail was found in the eastern Andes of Colombia, in the modern Departments of Cundinamarca and Boyaca. A darker, longer-billed race of the Brown Pintail it was hunted in pre-Columbian times by the Chibchas and Muiscas tribes. *A. g. niceforoi* was described only in 1946, when it was already difficult to observe in the highlands. Its continued contraction of range and final extermination can be chronicled by the last reported sightings. It was considered extinct in Cundinamarca in 1948, and everywhere else after disappearing from its last stronghold at Lake Tota, Boyaca in the mid-1950s (A.J.Negret in litt. 1995). The most likely causes of extinction were overhunting and wetland drainage. Pollution and the introduction of trout *Salmo* sp., often cited as causes, have probably only affected wetlands since extinction (A.J.Negret in litt. 1995).

Camptorhynchus labradorius Labrador Duck

Anas labradoria Gmelin, J., *Linne's Systema Naturae*, ed.13, 1,(2), 1789, p.537. Arctic America, Labrador to Connecticut.

Once established along the bays, coasts, and inlets, with occasional inland records, from Labrador to Chesapeake Bay, this small, dimorphic, seaduck is considered to represent a sister group to the scoters *Melanitta* (Livezey, 1995). Described in 1789, the last confirmed bird was shot near Long Island in 1875, although another was reported shot at Elmira, New York in 1878 (Phillips 1926). Great numbers of Labrador Ducks were shot, but it is unlikely that this alone exterminated the species. It is more probable that over-exploitation of the mollusc diet of this highly specialised feeder, by developing coastal town communities, pushed it toward extinction (Phillips 1926).

Chendytes

This seaduck genus, related to the eiders *Polysticta* and *Somateria*, and scoters *Melanitta*, comprises two species from the Pleistocene and early Holocene of California. Both species were large, flightless, foot-propelled divers that fed primarily on benthic invertebrates (Livezey 1993). Apparently sedentary and restricted to islands off the Pacific coast of California and Oregon, over-harvesting by aboriginal hunters was probably important in the extinction of both species (Moorejohn 1976).

Chendytes lawi

Chendytes lawi Miller, L., *Condor*, 27, 1925, pp.145-147, figure 40. Santa Monica, California, USA,

This duck probably inhabited shores of coastal islands but may have ranged at least 720 km north of the Channel Islands, California to Oregon (Moorejohn 1976). Adult weight estimated at 2.5-3.7 kg (Livezey 1993). Skeletal remains have been found at California Indian midden sites and have been Carbon 14 dated, suggesting extinction less than 3780 years ago (Moorejohn 1976).

Chendytes milleri

Chendytes milleri Howard, H., *Condor*, 57, 1955, pp.137-143, figures 1 (a,d-i) and 2 (b&c). San Nicholas Island, California, USA.

This species is smaller than *C. lawi*, the adult weight being estimated at 1.8-2.6 kg, with better developed wings (Livezey 1993). The exact period of extinction is not clear.

Of several continental wildfowl threatened with extinction, the Crested Shelduck *Tadorna cristata*, from Korea, Borrero's Cinnamon Teal *Anas cyanoptera borreroi*, from upland Colombia, Pink-headed Duck, from India and Myanmar, and Brazilian Merganser *Mergus octocetaceus* from Brazil and Argentina (all IUCN Critical) appear most in danger.

Conclusion

It is apparent from this review that wildfowl have been successful in exploiting isolated island groups, and have undergone spectacular radiations in environments that are free from significant competitors and mammalian predators. More than 200 species of island birds are, however, only recorded as sub-fossils, and were probably exterminated through the actions of prehistoric human colonists (Milberg & Tyrberg 1993). The number of species lost when man colonised the Pacific is possibly double the number so far recorded and may represent half the species present (Pimm *et al.* 1995).

The processes of extinction are varied, complex, and may differ between areas. The importance of introduced mammals in wildfowl extinctions is obvious (see e.g King (1985); Atkinson (1985); Steadman (1989); and Atkinson & Millener (1991). Over-hunting and habitat change have also played a major part in the extinctions of island wildfowl, and will continue to affect populations of the remaining island forms and, increasingly, their continental relatives.

The catastrophic plight of the endemic wildfowl fauna of Hawaii, New Zealand and the western Indian Ocean islands is shown in **Table 2**.

Table 2. Conservation status of wildfowl from Hawaii, New Zealand and western Indian Ocean islands. * taxa, for this Review, includes wildfowl not yet described.

	No. of endemic taxa	Extinctions	IUCN category of surviving endemics				'safe'endemic taxa
			CR	EN	VU	LR	
Hawaiian Islands	12*	9	1	1	1	1	–
New Zealand	16	8	1	3	1	–	3
W. Indian Ocean	12	6	1	2	3	–	–

We are grateful to David Burney, Graham Cowles, Steve Goodman, Andy Green, Helen James, Olivier Langrand, David Lorence, Cécile Mourer-Chauviré, Alvaro Jose Negret, Storrs Olson, Steve Spanner, Alan Tennyson and Cyril Walker for their knowledge of extinct wildfowl and encouragement during the preparation of this review. Pamela Barker and Anna Feistner helped with the manuscript, Des Callaghan, Jo Cooper, Nigel Collar, Robert Prŷs-Jones, Pam Rasmussen and Michael Walters read through the earlier drafts and made invaluable comments.

References

Ali, S. 1960. The Pink-headed Duck *Rhodonessa caryophyllacea* (Latham). *Wildfowl Trust Ann. Rep.*11:55-60.

Andrews, C.W. 1897. On some fossil remains of carinate birds from central Madagascar. *Ibis ser.*7(3):343-359.

Atkinson, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on avifaunas. In: Moors, P.J. (Ed.), *Conservation of Island Birds: Case Studies for the Management of Threatened Island Species*. ICBP Technical Pub.No.3, Cambridge.

Atkinson, I.A.E. & Millener, P.R. 1991. An ornithological glimpse into New Zealand's pre-human past. *Proc.20th Int. Orn. Congr. Wellington, New Zealand*, Vol.1:129-192.

Balouet, J.C. & Olson, S.L. 1989. Fossil birds from the Late Quaternary deposits in New Caledonia. *Smithsonian Contri. Zool.* 469:1-38.

Bell, B.D. 1991. Recent avifaunal changes and the history of ornithology in New Zealand. *Proc.20th Int. Orn. Congr. Wellington, New Zealand*, Vol.1:195-230.

Benson, C.W. 1985. Malagasy Region. In: Campbell, B. & Lack, E. (Eds.). *A Dictionary of Birds*. T. & A.D.Poyser, Calton. Pp. 335-336.

Bourne, W.R.P., David, A.C.F. & Jouanin, C. 1983. Probable Garganey on St. Paul and Amsterdam Islands, Indian Ocean. *Wildfowl* 34:127-129.

Brodkorb, P. 1967. Catalogue of fossil birds: Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). *Bull. Florida State Mus., Biol. Sci.* 11(3):99-220.

Callaghan, D.A. & Green,A.J. 1993. Wildfowl at risk, 1993. *Wildfowl* 44:149-169.

Cassels, R. 1984. The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific islands. In: Martin, P.S. & Klein, R.G.(Eds.). *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press Tucson. Pp.741-767.

Cheke, A.S. 1987. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. In: Diamond, A.W.(Ed.). *Studies of Mascarene Island Birds*. Cambridge University Press, Cambridge. Pp.5-89.

Coates, B.J. 1985. *The Birds of Papua New Guinea*, Vol.1. Dove Publications, Queensland.

Collar, N.J., Crosby, M.J. & Stattersfield, A.J. 1994. Birds to Watch 2. *The World List of Threatened Birds*. BirdLife International, Cambridge.

Cooper, A.,Rhymer, J., James, H.F., Olson, S.L., McIntosh, C.E., Sorenson, M.D. & Fleischer, R.C. 1996. Ancient DNA and island endemics. *Nature* 381:484.

Cowles, G.S. 1987. The fossil record. In: Diamond, A.W. (Ed.), *Studies of Mascarene Island Birds*. Cambridge University Press, Cambridge. Pp.90-100.

Cowles, G.S. 1994. A new genus, three new species and two new records of extinct Holocene birds from Réunion Island, Indian Ocean. *Geobios* 27(1):87-93.

Delacour, J. 1964. *The Waterfowl of the World*, Vol.1. Country Life, London.

Dewar, R.E. 1984 Extinctions in Madagascar: the loss of the subfossil fauna. In: Martin, P.S. & Klein, R.G. (Eds.). *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona, Tucson. Pp.574-593.

Ellis-Joseph, S., Hewston, N. & Green, A. 1992. *Global Waterfowl Conservation Assessment and Management Plan*. IUCN Captive Breeding Specialist Group and The Wildfowl & Wetlands Trust.

Engilis, A. & Pratt, T.K. 1993. Status and population trends of Hawaii's native waterbirds, 1977-1987. *Wilson Bull.*105(1):142-158.

Giffin, J.G. 1993. New species of fossil birds found at Pu'u Wa'awa'a. *Elepaio* 53(1):1-3.

Gill, B. & Martinson, P. 1991. *New Zealand's extinct birds*. Random Century, New Zealand.

Goodman, S.M. 1994a. The enigma of antipredator behaviour in lemurs: evidence of a large extinct eagle on Madagascar. *Int.J. Primatol.* 15(1):129-134.

Goodman, S.M. 1994b. Description of a new species of subfossil eagle from Madagascar: *Stephanoaetus* (Aves: Falconiformes) from the deposits of Ampasambazimba. *Proc.Biol.Soc.Wash.* 107(3):421- 428.

Goodman, S.M. & Rakotozafy, L.M.A. (In prep). *Subfossil birds from coastal sites in western and southwestern Madagascar: A paleoenvironmental reconstruction.*

Green, A.J. 1992. Wildfowl at risk, 1992. *Wildfowl* 43:160-184.

Green, A.J. 1994. Globally threatened Anatidae. *Unpubl. Rep. to Anatidae 2000, Strasbourg, France 5-9 Dec.*, 1994. 2 pp.

Hachisuka, M. 1953. *The Dodo and kindred birds, or extinct birds of the Mascarene Islands*. H.F & G. Witherby, London.

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

Horn, P.L. 1983. Subfossil avian deposits from Poukawa, Hawkes Bay, and the first record of *Oxyura australis* (Blue-billed Duck) from New Zealand. *J.Royal Soc. New Zealand* 13:67-78.

Howard, H. 1964. Fossil Anseriformes. In: Delacour, J. *The Waterfowl of the World*, Vol.4. Country Life, London. Pp.233-326.

Kear, J. & Scarlett, R.J. 1970. The Auckland Islands Merganser. *Wildfowl* 21:78-86.

Kear, J. & Williams, G. 1978. Waterfowl at risk. *Wildfowl* 29:5-21.

King, W.B. 1985. Island birds: will the future repeat the past? In: Moors, P.J (Ed.), *Conservation of Island Birds: Case Studies for the Management of Threatened Island Species*:3-15. ICBP Technical Pub.No.3, Cambridge.

Langrand, O & Goodman, S.M. 1995. Monitoring Madagascar's ecosystems: a look at the past, present, and future of its wetlands. In: Herman, T.B., Bondrup-Nielsen, S., Martin Wilson, J.H. & Munro, N.W.P.(Eds.), *Ecosystem Monitoring and Protected Areas. Proc.2nd Int. Conf. Sci. and Manage. of Protected Areas, Dalhousie Univ., Halifax, Nova Scotia 16-20 May, 1994*. Pp.204-214.

Livezey, B.C. 1989a. Phylogenetic relationships of several subfossil Anseriformes of New Zealand. *Occ. Paper 128. Mus. Nat. Hist. Kansas.*

Livezey, B.C. 1989b. Phylogenetic relationships and incipient flightlessness of the extinct Auckland Islands Merganser. *Wilson Bull.*101(3):410-435.

Livezey, B.C. 1991. A phylogenetic analysis and classification of recent dabbling ducks (tribe Anatini) based on comparative morphology. *Auk* 108:471-507.

Livezey, B.C. 1993. Morphology of flightlessness in *Chendytes*, fossil seaducks (Anatidae: Mergini) of coastal California. *J.Vert. Paleontol.*13:185-199.

Livezey, B.C. 1995 Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). *Condor* 97:233-255.

Mace, G. & Stuart, S. 1994. Draft IUCN Red List categories, version 2.2. *Species* 21-22:13-24.

Madge, S. & Burn, H. 1988. *Waterfowl: An Identification Guide to the Waterfowl of the World.* Helm, London.

Martinez, J. 1987. Un nouveau cas probable d'éndemisme insulaire: le canard de L'ile Amsterdam. *Table Ronde Int. du CNRS sur l'Evolution des Oiseaux d'après le Témoignage des Fossiles, Lyon-Villeurbanne, 18-21 September 1985*: 211-218.

Milberg, P. & Tyrberg, T. 1993. Naive birds and noble savages - a review of man-caused prehistoric extinctions of island birds. *Ecography* 16:229-250.

Millener, P.R. 1990. Evolution, extinction and the subfossil record of New Zealand's avifauna. In: Gill, B.J. & Heather, B.D. (Eds.). *A Flying Start: Commemorating Fifty Years of the OSNZ 1940-1990.* Random Century, New Zealand. Pp.93-100.

Millener, P.R. 1991. The Quarternary avifauna of New Zealand. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F. & Rich, T.H. (Eds). *Vertebrate Palaeontology of Australasia.* Monash University Publications, Australia. Pp.1317-1344.

Moorejohn, G.V. 1976. Evidence of survival to recent times of the extinct flightless duck *Chendytes lawi* Miller. In: Olson, S.L. (Ed.), *Collected Papers in Avian Paleontology Honoring the 90th Birthday of Alexander Wetmore. Smithsonian Contr. Paleobiol.* 27:207-211.

Northcote, E.M. 1992. Swans (*Grus*) and cranes (*Cygnus*) from the Maltese Pleistocene. *Los Angeles County Mus. Nat. Hist. Sci. Ser.* 36:285-291.

Olson, S.L. 1977. Notes on subfossil Anatidae from New Zealand, including a new species of Pink-eared Duck *Malacorhynchus. Emu* 77:132-135.

Olson, S.L. & James, H.F. 1982. Prodromus of the fossil avifauna of the of the Hawaiian Islands. *Smithsonian Contr. Zool.* 365:1-59.

Olson, S.L. & James, H.F. 1984. The role of Polynesians in the extinction of the avifauna of the Hawaiian Islands. In: Martin, P.S. & Klein, R.G.(Eds.). *Quaternary Extinctions: A Prehistoric Revolution.* University of Arizona Press,Tucson. Pp.768-780.

Olson, S.L. & James, H.F. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands: part 1, Non-passeriforms. *Orn. Mono.No 45.* AOU, Washington D.C.

Olson, S.L. & Jouventin, P. 1996. A new species of small flightless duck from Amsterdam Island, southern Indian Ocean (Anatidae: *Anas*). *Condor* 98(1):1-9.

Palmer, R.S. 1976. *Handbook of North American Birds*, Vol. 2. Yale University Press, New Haven.

Phillips, J.C. 1923. *A Natural History of the Ducks*, Vol. 2. Houghton Mifflin, Boston.

Phillips, J.C. 1926. *A Natural History of the Ducks*, Vol. 4. Houghton Mifflin, Boston.

Pimm, S.L., Moulton, M.P. & Justice, L.J. 1995. Bird extinctions in the central Pacific. In: Lawton, J.H. & May, R.M. (Eds.), *Extinction Rates.* Oxford University Press, Oxford. Pp.75-87.

Pratt.H.D., Bruner, P.L. & Berrett, D.G. 1987. *A Field Guide to the Birds of Hawaii and the Tropical Pacific*. Princeton University, New Jersey.

Reichel, J.D. & Lemke, T.O. 1994. Ecology and extinction of the Mariana Mallard. *J.Wildl. Manage*. 58(2):199-205.

Steadman, D.W. 1989. Extinction of birds in Eastern Polynesia: a review of the record and comparisons with other Pacific island groups. *J.Archaeological Sci*. 16:177-205.

Steadman, D.W. 1991. Extinct and extirpated birds from Aitutaki and Aitu, Southern Cook Islands. *Pacific Sci*. 45(4):325-347.

Steadman, D.W. 1992. Extinct and extirpated birds from Rota, Mariana Islands. *Micronesia* 25(1):71-84.

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

TWRG. 1995. Taxa considered by the Threatened Waterfowl Research Group. *TWRG Newsl*.8:3-4.

Watling, D. 1982. *Birds of Fiji, Tonga and Samoa*. Millwood Press, Wellington.

Williams, G.R. 1964. Extinction and the Anatidae of New Zealand. *Wildfowl Trust Ann. Rep*. 15:140-146.

Worthy, T.H. 1988. Loss of flight ability in the extinct New Zealand duck *Euryanas finschi*. *J.Zool.(London)* 215:619-628.

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

Yamashina, Y. 1948. Notes on the Marianas Mallard. *Pac. Sci*.2:121-124.

Young, H.G. (in press). The distribution and origins of wildfowl (Anatidae) of western Indian Ocean islands. In: Lourenço, W.R. (Ed.). *Biogéographie de Madagascar*. Editions de l'Orstom, Paris.

H.Glyn Young, Jersey Wildlife Preservation Trust, Les Augrés Manor, Trinity, Jersey, JE3 5BP, Channel Islands.
Simon J. Tonge, Zoological Society of London, Regent's Park, London NW1 4RY, UK.
Julian P. Hume, 3, The Circle, Wickham, Hampshire PO17 5HW, UK.