

The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective

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Abstract

The avifauna of New Zealand has been severely depleted since human colonisation and currently contains a disproportionately high number of threatened species. Of the 23 threatened shorebird species worldwide, six are endemic to New Zealand. We review the status of New Zealand's endemic shorebirds and examine the impact on them of various threats, particularly predation by introduced mammals. The conservation status of the 10 extant species (three oystercatchers, one stilt, four plovers and two snipe) is outlined and the factors that predisposed them to predation by introduced mammals are summarised. Individual species accounts are presented, including data on population trends, known or suspected impacts of predation, identification of important predator species, other threats, and conservation measures currently in place or required. One species and two subspecies are extinct, three species are confined to predator-free islands and another is found only on the Chatham Islands group. Six survive on the mainland but three have declined to varying degrees and are assigned threatened status by Collar et al. (1994). Only one plover and two oystercatchers are still relatively numerous and/or widespread. Rats, cats and mustelids have had the greatest overall impacts. Conservation measures in place to mitigate the effects of introduced predators include the formulation of recovery plans, predator control around breeding areas, captive breeding and rearing programmes and the founding of new populations by translocation. There are often substantial differences in susceptibility to predation of closely related or ecologically similar taxa, and we stress the importance of basing conservation management decisions on relevant and detailed demographic and ecological studies. The main threat to threatened shorebirds elsewhere in the world is loss or degradation of habitat; the disproportionate impact of mammalian predators on New Zealand shorebirds is unusual but not unique. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Much of the New Zealand fauna evolved in the absence of terrestrial mammals and has proved particularly susceptible to their recent introduction. The avifauna has suffered many extinctions and declines, and now contains a disproportionately high number of threatened species. Over 40% of the land bird species present before human occupation are now extinct (Clout, 1997). Excluding introductions, vagrants, migrants that breed elsewhere, and Antarctic-breeding species, the New Zealand region currently has 155 species of native or endemic birds; 45 (29%) of these are classified as threatened and a further 12 (7.7%) as near-threatened by Collar et al. (1994). A number of factors have contributed to this situation. Some habitat types, notably lowland forest and wetlands, have declined

dramatically in area since human colonisation (e.g. Stevens et al., 1988). Disease, competition and climate change have probably also played a part in some cases, but there is general agreement that the introduction of predatory mammals has had the greatest impact (Gill and Martinson, 1991; Clout, 1997). Worldwide, introduced species are a threat to 5.8% of the 1111 bird species classified as threatened; on islands this figure is usually higher, and in New Zealand introduced species are considered a threat to 25 (56%) of the 45 threatened bird species (Collar et al., 1994).

Polynesians arrived in New Zealand about 1000 years BP, bringing Pacific rats *Rattus exulans* and dogs *Canis familiaris*. Between that time and the arrival of Europeans, at least 32 species of birds became extinct (Gill and Martinson, 1991). In the past 200 years, Europeans have introduced other mammals; those that have had the greatest impact on the avifauna are ship rats *Rattus rattus*, Norway rats *R. norvegicus*, cats *Felis catus*, and two species of mustelids (ferrets *Mustela furo* and stoats

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M. erminea). During the European phase, a further nine bird species have become extinct (Gill and Martinson, 1991).

In this paper, we review the status of New Zealand's endemic shorebirds; where declines or extinctions have occurred, we attempt to determine the relative impact of predation by introduced mammals and other factors on the declines and extinctions. Except where noted, nomenclature of Australian and New Zealand birds follows Marchant and Higgins (1993) and Higgins and Davies (1996), that of birds elsewhere follows del Hoyo et al. (1996) and that of mammals follows King (1990). Major locations and island groups mentioned in the text are shown in Fig. 1.

2. Conservation status of New Zealand shorebirds

We consider members of the suborder Charadrii endemic to New Zealand. This group consists of three oystercatcher species, one stilt, four plovers and two snipe. Of the 18 species or subspecies, three have become extinct and at least eight have declined in range and/or numbers since human colonisation. The species (and their subspecies) are listed in Table 1, with data on range and population size, and two indications of conservation status: the categories assigned by Collar et al. (1994) and the New Zealand Department of Conservation's species priority ranking system (Tisdall, 1994). In the latter, category A represents highest-priority taxa (i.e. those judged most threatened and in need of conservation action). Inclusion in categories A, B, or C implies that the taxon is threatened to some degree. In Tisdall (1994), some island endemics are not considered under serious threat in the immediate future, but because of limited distribution and/or small population size, they are particularly vulnerable to predator irruptions or other catastrophes; these have (L) following the category listing in Table 1.

Because Collar et al. (1994) list species and Tisdall (1994) lists taxa (including subspecies), a precise comparison between the two systems is not possible.

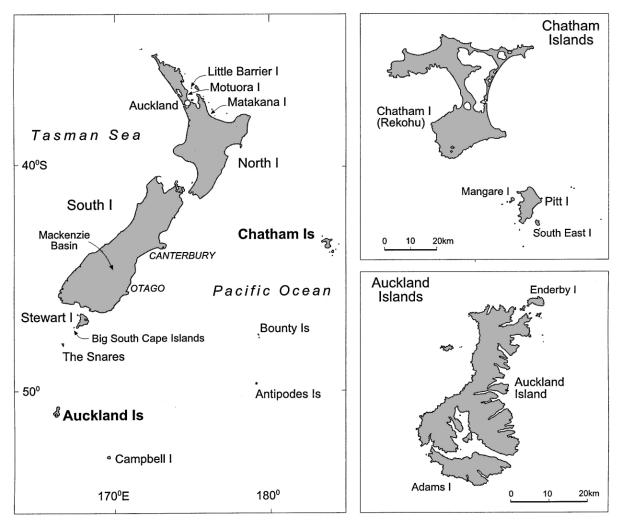


Fig. 1. Map of the New Zealand region showing outlying island groups and locations of places mentioned in the text.

However, there is generally good agreement; 7 of the ten endemic shorebird species are assigned threatened or near-threatened status by Collar et al. (1994) and they (or one or more of their subspecies) occur in categories A, B or C of Tisdall (1994).

3. Species accounts

In this section, we outline the status of each species or subspecies and consider the important threats to each taxon; where information is available, we review the impact of predation on numbers or distribution. We also consider future research and management priorities for threatened taxa.

In many cases, there is little or no direct or quantitative evidence proving that a particular predator or predators caused the decline, extirpation or extinction of a native species. However, there is often compelling circumstantial evidence. Changes in the abundance and distribution of bird species following introductions of predators to the New Zealand mainland (mainly in the nineteenth century) have been used to suggest which

predators are likely to have been responsible for particular declines (e.g. Atkinson, 1973). Local extinctions on smaller islands following predator irruptions have also provided information, as have successful re-colonisations or re-introductions after eradication of particular predators from islands. More recently, direct (and often quantitative) data have been collected during studies on the impacts of predators on extant shorebird species. These have usually focussed on the effect of predation on productivity (e.g. Pierce, 1986; Dowding, 1998; Rebergen et al., 1998).

All taxa listed in Table 1 are fully protected by law. Other conservation measures in place are outlined in the individual species accounts below and are summarised in Table 2.

3.1. Oystercatchers (Haematopodidae)

3.1.1. South Island Pied Oystercatcher Haematopus (ostralegus) finschi

This taxon is listed as an endemic subspecies of the Eurasian oystercatcher *Haematopus ostralegus* by Turbott (1990); more recently it has been considered an endemic

Table 1
Breeding range, population size and conservation status of endemic New Zealand shorebirds^a

Species subspecies	Breeding range	Population size	Status (Collar et al., 1994)	Category (Tisdall, 1994)
Oystercatchers (Haematopodidae)				
Haematopus (ostralegus) finschib	NI, SI	112,000°		
H. unicolor	NI, SI, offshore islands	3900		C
H. chathamensis	Chatham Islands	142 ^d	Endangered	A
Stilt (Recurvirostridae)				
Himantopus novaezelandiae	Mackenzie Basin (SI)	ca. 80	Critical	A
Plovers (Charadriidae)				
Charadrius obscurus			Endangered	
C. o. obscurus	Stewart Island	110e		A
C. o. aquilonius	Northern NI	1500e		В
C. bicinctus				
C. b. bicinctus	NI, SI, offshore islands	ca. 50,000		C
C. b. exilis	Auckland Is	730		C
Thinornis novaeseelandiae	Chatham Islands	150	Endangered	В
Anarhynchus frontalis	SI	5000	Vulnerable	В
Snipe (Scolopacidae)				
Coenocorypha aucklandica			Near-threatened	
C. a. aucklandica	Auckland Is	≥20,000		C (L)
C. a. huegeli	The Snares	1100		B (L)
C. a. iredalei	Is around Stewart I	extinct		
C. a. meinertzhagenae	Antipodes Is	8000		C (L)
C. a. barrierensis	Little Barrier I, ?NI	Extinct		
C. a. "Jacquemart Island"	Jacquemart I (Campbell Is)	< 150		? ^f
C. pusilla	Chatham Is	1100 pairs	Vulnerable	C (L)
C. chathamica	Chatham Is	Extinct		

^a Data on breeding ranges and population sizes are from Marchant and Higgins (1993), Heather and Robertson (1996) and Higgins and Davies (1996) except where noted. NI, North Island, SI, South Island.

^b Status unclear, treated as an endemic species.

^c Sagar, Shankar and Brown (1999).

^d Schmechel and O'Connor (1999).

^e J.E. Dowding, unpublished data.

^f Not yet classified, probably A or B (L).

species (Marchant and Higgins, 1993). Almost the entire population breeds in the South Island, but much of it now winters in the North Island, particularly in the estuaries around Auckland. Numbers over-wintering in northern New Zealand have increased dramatically since about 1940 (Sibson, 1966; Baker, 1973) when shooting of shorebirds was outlawed. It has been suggested that relief from hunting resulted in the population increase (Sibson, 1966). However, changes in breeding habitat have also occurred. Pied oystercatchers traditionally bred on braided riverbeds (e.g. Oliver, 1955) but there has been some degradation of this habitat, with the invasion of riverbeds by exotic weeds, particularly gorse *Ulex europaeus*, Spanish broom *Cyti*sus scoparium, willows (mainly Salix fragilis) and tree lupin Lupinus arborea. However, the species now also nests (and forages) extensively on agricultural land adjacent to riverbeds (Sagar and Geddes, 1999), which provides much potential breeding habitat. Productivity in one population breeding on Canterbury farmland was 0.7 chicks fledged per pair per season, and most losses that did occur were due to trampling of nests by stock (Marchant and Higgins, 1993). Agricultural activities (notably cultivation) were also considered responsible for many nest losses on farmland in Southland (Barlow et al., 1972). Other threats include flooding of riverbed nests and predation (Marchant and Higgins, 1993). Pierce (1987) recorded predation at four of 15 nests in the Tekapo River, Mackenzie Basin, and attributed it to mustelids (two nests), a cat (one) and an Australasian harrier Circus approximans gouldi (1). However, there is currently no evidence that introduced mammals have a serious impact on the survival of the South Island pied oystercatcher. By New Zealand standards it is a numerous species, which is increasing in numbers (Sagar and Geddes, 1999) and gives no cause for conservation concern.

3.1.2. Variable oystercatcher Haematopus unicolor

This species was apparently also declining in the early 1900s as a result of shooting (Heather and Robertson, 1996). Like the South Island pied oystercatcher, it has increased substantially since it was protected in 1922 (Marchant and Higgins, 1993), with the total population thought to have doubled in the past 30 years (Heather and Robertson, 1996). As with the pied oystercatcher, some new breeding habitat may have been created by human activities, such as burning and clearing of vegetation from North Island sandspits. A wide range of threats is listed by Marchant and Higgins (1993), including flooding by big tides (the species is strictly coastal), crushing of nests, disturbance during breeding, and predation of eggs, chicks and adults by a variety of native and introduced predators. However, there is limited information on the relative importance of these factors. Predation of eggs and chicks probably results in relatively low productivity in many areas, but at protected sites (i.e. those where predator control occurs) on the North Auckland east coast fledging success may be higher, e.g. an average of 0.64 chicks fledged per pair from 1987-1990 (Marchant and Higgins, 1993). Data from three Northland sites where variable oystercatchers (and other shorebirds) are protected each season has been analysed (A. Booth, personal communication). Breeding success (chicks fledged/ eggs laid) varied considerably (0-50%) between sites and years, although some of the variation may have been due to differences in monitoring effort. Causes of nesting failure included weather and flooding (29% of losses), predation (8%) and disturbance by humans and

Table 2
Conservation measures in operation in New Zealand aimed at reducing the effects of predation on endemic shorebird species^a

Species	Recovery plan published	Predator control at mainland breeding sites	Captive rearing/breeding	Translocations to predator-free islands
Haematopus (ostralegus) finschi	=	=	=	=
H. unicolor	-	(+)	_	-
H. chathamensis	+ b	+	_	-
Himantopus novaezelandiae	+ c	+	+	-
Charadrius obscurus	+d	+	+	-
C. bicinctus	-	(+)	_	-
Thinornis novaeseelandiae	+ e	-	+	+
Anarhynchus frontalis	-	(+)	_	-
Coenocorypha aucklandica	_	<u> </u>	_	-
C. pusilla	_	_	-	+

^a (+), Indicates a species which benefits (usually in a small fraction of its breeding range) from a predator-control programme primarily aimed at protecting another species.

^b Davis et al. (2000a).

c Reed et al. (1993).

^d Dowding (1993).

e Davis et al. (2000b).

vehicles (4%), but the majority of losses (53%) were to unknown causes (A. Booth, personal communication). To date, there have been no rigorous comparisons of variable oystercatcher productivity or survival at managed and unmanaged sites.

Adults are thought to have relatively few predators (Baker, 1973). Preliminary data from North Auckland suggest that average adult life expectancy is 18–19 years (J.E. Dowding and S.P Chamberlin, unpublished data), with some individuals still breeding successfully at 25–30 years (J.E. Dowding and A.J. Baker, unpublished data). The species is therefore long-lived and this may be compensating for low or variable productivity. Variable oystercatchers are large, aggressive birds and may be capable of defending themselves and their young from at least some predators (e.g. rodents and hedgehogs) more effectively than the smaller shorebirds.

3.1.3. Chatham Island oystercatcher, Haematopus chathamensis

This species is still present on the four largest islands of the Chatham group but a lack of early data makes population trends difficult to determine. Although survey methodology and coverage have varied, there may have been an increase in numbers in the past 30 years; the population was (conservatively) estimated at ca. 50 birds in 1970 (Baker, 1973), 110 were recorded by Davis (1988) and 142 in December 1998 (Schmechel and O'Connor, 1999).

Threats to the species include the small size of the population, predation by introduced mammals and native and introduced birds, disturbance, trampling of nests by stock, and flooding (Collar et al., 1994). It has also been suggested that breeding habitat may be limiting; Davis (1988) noted that most pairs bred in areas composed entirely or partly of volcanic rock platform, and suggested that availability of this habitat type explained the distribution of the species and may limit population size. However, successful breeding now occurs on sandy beaches of the northern coast of main Chatham Island, and further research on habitat requirements of the species is being undertaken (Schmechel, 1998).

The majority of the Chatham Island oystercatcher population (about 85% of breeding pairs; Schmechel and O'Connor, 1999) now breeds in the presence of cats on Chatham and Pitt Islands. In 1987–1988, productivity averaged 0.27 chicks per pair over the four main islands (Davis, 1988). There was some suggestion that breeding success was higher on South East Island (which is free of introduced predators) than on main Chatham Island; however, samples sizes were small and productivity on South East Island varied widely between 0.20 and 0.85 over a period of 12 years (Davis, 1988). Productivity was also found to vary considerably (both temporally and spatially) on main Chatham Island over a 3-year period (Schmechel, 1998). Predator control has been carried out intermittently at a few sites

on main Chatham Island; during 1998-99, intensive predator control was carried out on the northern coast and productivity there was high (1.1 chicks fledged per pair; Moore, 1999). However, productivity has also been high in some years without predator control (S. O'Connor, personal communication). To date, there appears to be no conclusive evidence on the effect of predator control on productivity. Initial results from a video-monitoring study of nests begun in 1999 have shown a cat visiting one nest, a rodent visiting another, and a third nest washed away by high seas (P. Moore, personal communication).

It has also been suggested that the establishment of introduced marram grass *Ammophila arenaria* on coastal dunes has forced birds to nest closer to the tideline, where eggs are more vulnerable to flooding (Collar et al., 1994). Dune restoration has been proposed as a management technique (Moore, 1999), although there is no guarantee that birds will nest further from the water when restored habitat is available. In 2 years, eggs threatened by flooding were removed, artificially incubated and returned to nests, but there was no evidence that fledging success was improved (F. Schmechel, personal communication).

There appears to be little information on adult survival or on survival of juveniles to breeding age. Given the small population size and uncertainty about the factors responsible for the status of the Chatham Island oystercatcher, there is an urgent need for research on productivity, recruitment and adult survival (Dowding, 1999a). There is some evidence that the population is growing, but it seems likely that this process is being slowed by predation, loss of nests to flooding and trampling, and possibly, other factors. It should also be remembered that the islands are not large and the species may never have been very numerous.

Given the widespread shooting of the two mainland oystercatchers in the past, hunting of this species probably also occurred. The recent rise in numbers appears to have been greatest on main Chatham Island (Schmechel and O'Connor, 1999), which has the bulk of the human population and is the area in which most shooting is likely to have occurred. It is, therefore, possible that the Chatham Island oystercatcher is also recovering from hunting pressure.

3.2. Stilt (Recurvirostridae)

3.2.1. Black stilt, Himantopus novaezelandiae

An early invasion of an ancestral (presumably pied) stilt from Australia is assumed to have given rise to the black stilt in New Zealand. A subsequent invasion in the early nineteenth century led to the establishment of the cosmopolitan pied (black-winged) stilt (*Himantopus himantopus*). The two species are closely related and inter-breed, producing viable, fertile hybrids. Positive

assortative mating occurs, but a black stilt unable to find a black mate will pair with a hybrid or pied bird (Pierce, 1984a). Most black stilts remain on or near their breeding grounds throughout the year, but hybrid and pied stilts usually migrate out of the area (Reed et al., 1993).

The black stilt was widespread and relatively common until the late nineteenth century, breeding in both North and South Islands. Its decline in range and numbers has been documented by Pierce (1984b), who estimated that as recently as the 1940s there were 500-1000 birds surviving in Canterbury and Otago. This population declined rapidly in the 1950s and since 1960 has numbered less than 100 individuals, with all breeding confined to the Mackenzie Basin in South Canterbury (Pierce, 1996). In 1980, the population reached a low of 23 adults and intensive management of the species began (Reed et al., 1993). This has included captive breeding, artificial incubation of wild-laid eggs, crossfostering surplus eggs (to black, hybrid and pied adults) and management of predators by trapping, poisoning and the use of exclosures. However, post-fledgling survival and recruitment of both wild- and captive-bred juveniles has been low; of 59 banded chicks fledged between 1981 and 1986, only four were recruited into the breeding population (Reed et al., 1993; Reed, 1998).

Predation, habitat modification and hybridisation are the three main factors threatening the survival of the black stilt (Reed et al., 1993; Pierce, 1996). Introduced mammalian predators are considered to be the main reason for the decline of the black stilt and the main threat today (Pierce, 1996). Pierce (1986) recorded very low productivity of unprotected black stilt pairs (chicks fledged from only 1% of eggs), and demonstrated that it could be increased substantially by control of predators. Further research has shown that predator control is effective in some years but not in others, and the reason for this is not yet clear (Saunders et al., 1996). Pierce (1986) used tracks, scats and size of shell fragments to identify predators of 40 pied stilt and black stilt nests in the Mackenzie Basin. The majority of events were attributed to Norway rats (14 nests) ferrets (13), and cats (11). Two chicks were taken, one by a ferret and one by a cat, and two adults were killed by cats. However, video-monitoring in the same area has shown that banded dotterels clean out their depredated nests quickly, suggesting that past interpretation of nest sign may not always have been reliable (Rebergen et al., 1998). Human activities have caused substantial increases in numbers of two native avian predators, the blackbacked gull Larus dominicanus and the Australasian harrier in New Zealand (Higgins and Davies, 1996) and increasing numbers of both in the Mackenzie Basin pose a growing threat to black stilts (Pierce, 1996; Saunders et al., 1996). Video-monitoring of five lethal events at black stilt nests showed that a cat ate eggs and an adult

at one nest, a harrier ate a chick and a hatching egg at another, two nests were flooded, and one nest was deserted following human disturbance (Sanders and Maloney, 1999). Saunders et al. (1996) noted that predation may have accounted for up to 77% of chick loss from 1982–1995.

Loss and modification of black stilt nesting and feeding habitat has occurred, particularly in the Mackenzie Basin, where exotic weeds have invaded river-beds and hydro-electric development has reduced river flows (Pierce, 1996). Sanders (1999) showed that black stilts were attracted to new feeding areas created when lake levels were lowered; water levels are now being manipulated in managed wetlands to attract stilts to feed (and hopefully breed) in areas where predators are controlled.

Genetic swamping resulting from hybridisation with the very numerous pied stilt *Himantopus h. leucocephalus* is also a problem for the species (Pierce, 1984a; Reed et al., 1993). The threat currently posed by hybridisation is probably a result (rather than a cause) of the severe depletion of the black stilt population by other factors (Saunders et al., 1996). Wallis (1999) noted that reduction in fitness of hybrids does reduce the effects of gene flow from pied stilts, which suggests that swamping is not inevitable; however, he also noted that information is lacking on how a larger black stilt population would behave in terms of assortative mating.

The three major threats probably also act in combination. Reduced river flows allow predators access to more nesting islands, and may also force birds to nest in drier habitat, where eggs and chicks are more vulnerable to predation (Pierce, 1996). Exotic weeds in river-beds provide more cover for ground predators (Reed et al., 1993).

Extinction of the black stilt has so far been averted, but in spite of 20 years of intensive management it is still one of the rarest shorebirds in the world. The black stilt recovery plan (Reed et al., 1993) recommended the establishment of a population on a predator-free island, but this has not so far been attempted. Black stilt chicks were cross-fostered to pied or hybrid parents during the 1980s, but this technique was abandoned when it was found that fostered juveniles migrated away from the Mackenzie Basin with their foster parents and most did not return (Reed et al., 1993). Predator-aversion training of captive-bred juveniles has been considered (Reed et al., 1993) but limited trials have so far proved unsuccessful, with no difference in post-release survival of trained and untrained juveniles (R. Maloney, personal communication). Further research on this technique remains an option. The survival of the species on the mainland currently appears to depend on intensive captive-management (particularly release of captive-bred and reared juveniles) and on predator control and exclusion around favoured nesting sites in the wild. A review of the recovery programme (Saunders et al., 1996) concluded that the species could be recovered but that substantial resources would be required "for the foreseeable future".

3.3. Plovers (Charadriidae)

3.3.1. New Zealand dotterel, Charadrius obscurus

There is relatively little reliable information on past distribution and overall numbers of the northern New Zealand dotterel Charadrius o. aquilonius. The important potential threats to the subspecies are habitat modification, disturbance during breeding, and predation (Dowding, 1993). Some degradation or destruction of breeding habitat has occurred (and continues), with coastal dunes reclaimed for housing, stabilised with marram grass Ammophila arenaria, or planted in pines *Pinus radiata* (Cumming, 1991). Disturbance by people, their vehicles, dogs and stock has increased (Dowding, 1993). Lord et al. (1997) measured the impact of disturbance on breeding birds and showed that it reduced feeding time by chicks, but it was not clear whether this had any impact on productivity. Cumming (1991) recorded greater breeding success at low-disturbance than high-disturbance sites during one season, but the difference was not significant. Over two seasons, Dowding (1998) found that nest survival was low, with 86% of all nesting attempts failing to hatch. Predation was by far the greatest cause of nest failure, accounting for 60% of all nesting attempts and 70% of those that failed. Adults of the northern subspecies are long-lived, productivity is relatively low, and the population shows little turn-over (Dowding, 1997; 1998). Important breeding sites are managed each season, with wardens roping off nesting areas, reducing disturbance and trapping predators (Dowding, 1993). About 120 (20%) of the estimated 600 breeding pairs were managed during the 1998-1999 season.

Based on tracks at nests monitored over a 6-year period, Wills (1998) attributed most predation by mammals at New Zealand dotterel nests on Matakana Island to cats (17 nests), stoats (10) and Norway rats (9). Discovery of stoat dens containing remains of northern New Zealand dotterel adults, eggs and chicks indicated that stoats can be important local predators of this subspecies (Dowding and Murphy, 1996). Videomonitoring of northern New Zealand dotterel nests on the North Auckland east coast showed eggs eaten by hedgehogs (two nests) and a cat (one). In the same study, tracks around recently depredated nests suggested egg predation by cats (five nests), a hedgehog (one) and a stoat (one) (Dowding, 1998). Large colonies of black-backed gulls (some sustained by urban rubbish dumps) at North Island coastal sites can have a major local impact. Before a colony of over 4000 black-backed gulls was controlled on Matakana Island, Wills (1996) attributed 75% of dotterel nest predations over a 3-year period to the gulls.

The southern New Zealand dotterel Charadrius o. obscurus was once widespread in the South Island (and probably the southern North Island) but there are no recent records of breeding there (Dowding, 1994). The initial decline in the South Island during the mid-nineteenth century was attributed to shooting and predation by cats and possibly Norway rats; following the introduction of mustelids in the mid-1880s, the decline became rapid (Dowding, 1999b). A population estimated at about 350 birds survived on Stewart Island (which is free of mustelids) until the early 1950s, but subsequently declined and reached a low of 62 in 1992 (Dowding and Murphy, 1993). As there is very little disturbance, and no flooding and loss of habitat on the remote hill-top breeding grounds, cats (and possibly rats) are thought to be the main reason for this decline (Dowding and Murphy, 1993); both have been controlled around important breeding sites since 1995 (Dowding, 1998). Before predator control, adult mortality was almost three times higher on Stewart Island than in the northern subspecies; mortality of males was almost twice as high as that of females, probably because males incubate at night when cats are most active (Dowding, 1997). However, productivity is higher than in the North Island and the population shows rapid turnover (Dowding, 1997). With a population of 108 individuals in 1998 (Dowding, 1998) and 150 in 1999 (J.E. Dowding, unpublished data), the taxon is increasing slowly but is still highly endangered. Its survival and growth appear to depend very largely on continuing predator control.

Trials are being undertaken with birds of the northern subspecies to establish captive-rearing techniques for the species, in case this form of management is required to boost numbers of the southern subspecies (Dowding, 1998).

There are very large differences in demographics between the subspecies and predation has very different impacts on them (Dowding, 1997). There is little doubt that predation has been the main reason for the decline of *Charadrius o. obscurus*. The northern subspecies appears stable at present but about 20% of the breeding population is protected from predation and disturbance each season. The recovery plan (Dowding, 1993) has now expired and the compilation of an updated plan for the species is a priority.

3.3.2. Banded dotterel, Charadrius bicinctus

The nominate race of the banded dotterel is still numerous and widespread on the New Zealand mainland, and is by far the most abundant of the endemic plovers. Banded dotterels tend to breed and feed in open habitat and have benefited from human activities in some areas (Marchant and Higgins, 1993) but not in others (e.g. Owen and Sell, 1985).

Bomford (1988) studied breeding of the species on the Cass River, Mackenzie Basin and recorded 56% of eggs

lost before hatching, attributing these losses to predation. Rebergen et al. (1998) studied breeding success on three Mackenzie Basin riverbeds; overall, 50% of nests lost eggs due to predation and 22% of nests fledged at least one chick. In one season, hatching success differed significantly between the three sites (within 25 km of each other), varying between 32 and 74%. Nests on islands were significantly more successful than nests on the mainland, possibly because access by mammalian predators was reduced (Rebergen et al., 1998). Also in the Mackenzie Basin, Norbury and Barlow (1998) showed that predator control reduced banded dotterel nest loss; in untrapped areas, nest loss averaged 49% and in trapped areas 22%.

In 1984–1986, Pierce (1987) used egg-shell remains to identify nest predators in the Cass and Tekapo Rivers and considered that mustelids (50 nests), cats (eight), hedgehogs (six), stoats (four), birds (three) and a ferret (one) were responsible. As noted above however, interpretation of nest sign may not always be reliable. Stoats also killed adult banded dotterels (Pierce, 1987). Videomonitoring of banded dotterel nests in the Mackenzie Basin between 1994 and 1998 (Sanders and Maloney, 1999) showed eggs being eaten by ferrets (13 nests), cats (12), hedgehogs (11) and stoats (three). Nests were also lost to trampling by sheep (two) and flooding (one). Cats were recorded killing two adults and three chicks, and an Australian magpie *Gymnorhina tibicen* killed one chick.

Predation of eggs, chicks and adults by a range of introduced mammals occurs and almost certainly reduces survival and productivity; however, the fact that the species is widespread and numerous suggests that it may be able to cope with current predation rates. Recent research by Norbury and Barlow (1998) suggests that rates of change in dotterel numbers are density-dependent, "such that the population may be able to compensate for increased predation pressure".

The Auckland Island subspecies Charadrius b. exilis breeds on Enderby and Adams Islands, both of which are free of predatory mammals. Numbers on Enderby Island appear to have risen in recent years, probably because changes in vegetation caused by grazing mammals have increased the area of nesting habitat (Walker et al., 1991). Cats were introduced to the main Auckland Island between 1806 and 1840 (Fitzgerald, 1990). Falla (1978) noted that "There is no evidence that they [banded dotterels] are subject to any adverse predation pressures either on nesting grounds or coastal habitat". He apparently based this suggestion on the assumption that the birds' upland breeding areas were beyond the range of cats, an assumption that appears incorrect (Taylor, 1975). Banded dotterels formerly bred on the main island (Marchant and Higgins, 1993) and few pairs (if any) now breed there (Walker et al., 1991). The little evidence available suggests that predation by cats (and possibly pigs) has caused a decline in numbers and breeding range of this taxon. Grazing mammals have now been removed from Enderby Island, and it seems inevitable that there will be a reduction in suitable breeding habitat as re-growth of vegetation occurs. Ideally, numbers should be monitored during this change, but the islands are uninhabited and isolated and only occasional counts are likely.

3.3.3. Shore plover, Thinornis novaeseelandiae

Originally widespread in the South Island at least, this species had disappeared from mainland New Zealand by the 1870s (Davis, 1994), after which it was found only on the Chatham Islands. It appears sensitive to cats and Norway rats, being extirpated from the mainland before the spread of ship rats in the South Island or the introduction of mustelids. There are subfossil and midden remains from the main Chatham Island (Turbott, 1990), but Norway rats and cats were present by 1840 (Moors, 1990; Fitzgerald, 1990) and the species was apparently not recorded alive there by European observers. Cats were present on Pitt Island by 1868 (Fitzgerald, 1990) and the shore plover was probably extirpated in the 1880s (Davis, 1994), although stragglers are still occasionally reported (Marchant and Higgins, 1993). Cats were introduced to Mangere Island shortly before 1893, and shore plover disappeared quickly; with the exception of rare stragglers, the last record was a single bird seen in 1898 (Fleming, 1939). By 1900, the shore plover was believed confined to the predator-free 220-ha South East Island. Large-scale collecting of specimens occurred there until 1910, and numbers became very low (Fleming, 1939). In recent years, productivity on South East Island has been high, and Davis (1994) calculated that the population has the potential to grow by 12% per annum. However, breeding habitat is now limiting on the island and this potential is not realised. In the early 1970s, adult and juvenile shore plover were transferred from South East Island to Mangere Island (11 km away) in an attempt to establish a population there. The attempts failed when the birds quickly returned to South East Island (Bell, 1974).

With a total wild population of about 130 birds in one location, the shore plover would be very susceptible to extinction in the event of a predator irruption on South East Island (Dowding and Kennedy, 1993). In February 1999, a second population of 21 birds (including four or five pairs) was discovered on a small, low-lying reef in the Chatham Islands (S. O'Connor, personal communication); the long-term viability of this population is unclear and the need to establish another larger wild population is obvious. A captive breeding programme was begun in 1994 and captive-bred birds are currently being used in attempts to establish new populations on predator-free islands near mainland New Zealand.

These translocations have encountered the problems of juvenile dispersal and predation. Between 1994 and 1998, 75 captive-bred birds were released on Motuora Island, near Auckland. The majority of these left the island at some stage; many of them were seen on the nearby mainland and most did not return (Taylor et al., 1998; Aikman, 1999). Historical information indicates that shore plover are particularly susceptible to cats and rats (and thus, almost certainly to mustelids too), making it likely that many of the birds dispersing from Motuora were killed on the mainland. Predation of translocated birds by a native owl (the morepork Ninox novaeseelandiae) also occurred on Motuora Island (Aikman, 1999). By the 1998-1999 season, two pairs of birds were resident on Motuora Island and both attempted to breed. Unfortunately it seems likely that any juveniles produced on Motuora will also disperse; it may, therefore, prove difficult or impossible to establish a self-sustaining population there.

3.3.4. Wrybill, Anarhynchus frontalis

There is relatively little historical information on breeding range or numbers of this species (Hay, 1984). In historic times, it has apparently bred only on the braided river-beds of the central South Island; it appears to be adapted in plumage, egg colour (and probably in bill morphology) to breeding and feeding on the greywacke shingle in these rivers (Hay, 1984). The breeding range has changed somewhat since the late nineteenth century and may have decreased. There has been a substantial reduction in range in Marlborough and North Canterbury, where the species once bred on five rivers (Handly, 1895; Stead, 1932) on which it is no longer found (O'Donnell and Moore, 1983). In the south, there has been an apparent expansion of breeding range into Central Otago (Child, 1973), although O'Donnell and Moore (1983) suggested that this may have been a result of increased observer awareness of the species. Almost the entire population migrates to the North Island and over-winters on harbours and estuaries, particularly around Auckland (Heather and Robertson, 1996). Numbers have fluctuated over the past 40 years and trends are difficult to determine, but Veitch and Habraken (1999) suggest that the population appears to be declining slowly.

Three major factors are likely to have an impact on wrybills, namely flooding during breeding, degradation of breeding habitat, and predation (Marchant and Higgins, 1993; Collar et al., 1994). Flooding had little impact in Hay's (1984) study but caused very low productivity in one year of Hughey's (1985) study. As a specialist riverbed breeder, the wrybill has presumably evolved in the presence of regular floods; it lays replacement clutches after loss and can double-brood (Hay, 1984) and it seems unlikely that flooding alone would threaten the survival of the species.

Growth of exotic weeds in riverbeds (see Section 3.1.1) has reduced breeding habitat, particularly on the lower reaches of braided rivers. Modifications to prevent flooding have also stabilised riverbeds and assisted the spread of weeds. Water abstraction for crop irrigation and pollution of rivers by agricultural industries have reduced habitat further (Cromarty and Scott, 1996).

Predation had little impact on nest or chick survival in Hay's (1984) study on the Upper Rakaia River, and productivity was high, averaging 0.79 young fledged per pair per season over three years. Hughey (1985) also recorded low rates of nest loss in the Lower Rakaia and Ashley Rivers, with seven (12.1%) of 58 nests being lost to predation. However, provisional results from a study in the Mackenzie Basin (E.C. Murphy and J.E. Dowding, unpublished data) indicate that productivity is much lower than in Hay's study, varying between 0.15 and 0.60 chicks fledged per pair in four study sites in 1998–1999. Temporal and spatial differences between the two studies may be important (rabbit densities are higher in the Mackenzie Basin and recent rabbit control there may have induced prey-switching — see Section 5.3 below). This study has also shown that survival of adults was significantly higher in areas with predator control and that there is a gender bias in survival adult males have lower survival than females, probably because males incubate and brood at night when many mammalian predators are active.

The relative importance to the wrybill population of flooding, habitat degradation and predation is not yet clear. As with black stilts, there is probably some interaction between these threats — weeds in riverbeds provide cover for predators, reductions in water flow may allow predators easier access to nesting islands, and flooding forces birds to re-nest and makes them vulnerable for longer. Determining the long-term impact of introduced predators on the species will require further research; collection of demographic data to allow modelling of population trends is under way. Other potential threats include increased levels of disturbance caused by anglers, powerboats, off-road vehicles and other recreational activities, and the possibility of further hydro-electric development.

3.4. Snipe (Scolopacidae)

3.4.1. New Zealand snipe, Coenocorypha aucklandica

Relationships within this species are unclear; five subspecies are recognised by the New Zealand checklist (Turbott, 1990), but Higgins and Davies (1996) propose at least three (and possibly four) "recent" species. Miskelly (1989) has noted, however, that the various island populations probably separated no more than 10,000 years ago, following the end of the Otiran Glaciation. A population discovered in November 1997 on 19-ha Jac-

quemart Island (near Campbell Island) is undescribed and is provisionally included in the species here (Table 1); based on the density of the Snares Islands population (Miskelly, 1989), this population is likely to number less than 150 birds. Following Turbott (1990), three subspecies and the Jacquemart Island population are still extant and each is confined to an isolated subantarctic island or group.

The Little Barrier snipe Coenocorypha a. barrierensis became extinct on Little Barrier Island in the 1870s, coinciding with the time cats became established; however, the population had probably been reduced by Polynesian rats before the introduction of cats (Miskelly, 1988). Sub-fossil remains of snipe, probably subspecies of Coenocorypha aucklandica, are known from the North and South Islands; Miskelly (1987a) proposed that these be referred to Coenocorypha a. barrierensis and Coenocorypha a. iredalei, respectively, but further research is required before the identities of mainland forms are clear (Worthy, 1987). The extinction of these populations appears to have followed human colonisation; no direct evidence is available, but it has been suggested that Pacific rats were responsible (Atkinson, 1978; Holdaway, 1989).

Other examples provide more convincing evidence for the role of individual predator species in extirpations and extinctions of snipe populations.

The Stewart Island snipe Coenocorypha a. iredalei survived into the twentieth century on a number of islands around Stewart Island, and its progressive disappearance from these islands was attributed by Miskelly (1987a) to the arrival of rats, cats or weka Gallirallus australis (an endemic predatory rail introduced to these islands by humans). By 1960, the subspecies was probably confined to the Big South Cape Islands, south-west of Stewart Island. The irruption of ship rats on these islands and the subsequent extirpation or extinction of five bird taxa, a bat and a large flightless weevil is a well-known example of a 'rat-induced catastrophe' (Atkinson, 1985). Ship rats arrived on the islands in 1962 or early 1963 (Bell, 1978). Snipe were still present in August 1964 (Miskelly, 1987a), but an attempt to transfer them to another island failed and they could not be found on Big South Cape Island in February–March 1965 (Blackburn, 1965). New Zealand snipe are long-lived (Miskelly, 1989) and the rapidity of the extinction of Coenocorypha a. iredalei on Big South Cape Island suggests that even adults are highly vulnerable to rats.

The Auckland Island snipe Coenocorypha a. aucklandica was apparently present on the larger islands of the group, but disappeared from main Auckland Island and Masked Island after cats were introduced in the 1840s (Veitch, 1985). It still breeds on three smaller islands of the group and has been recorded from five others (Higgins and Davies, 1996).

The Antipodes Island snipe *Coenocorypha a. meinertzhagenae* breeds on the main Antipodes Island and probably on at least three smaller islands nearby (Higgins and Davies, 1996). The only introduced mammal in the group is the house mouse *Mus musculus*, which is present on the main island (Murphy and Pickard, 1990).

The Jacquemart Island snipe is currently known to exist on one small predator-free island. It seems likely that it was previously also on Campbell Island, before the establishment of Norway rats (before 1867; Atkinson, 1985) and cats (about 1908; Veitch, 1985).

3.4.2. Chatham Island Snipe, Coenocorypha pusilla

This species was formerly present on Chatham, Pitt and Mangere Islands, but by 1970 was confined to South East Island and Star Keys. Norway rats and cats were both introduced to Chatham Island before 1840 and cats to Pitt Island before 1868 (Moors, 1990; Fitzgerald, 1990); the Chatham Island snipe is no longer present on either island. Cats were introduced to Mangere Island shortly before 1893, and *Coenocorypha pusilla* died out soon after (Higgins and Davies, 1996). The cats declined and were hunted (I.A.E. Atkinson, personal communication) and had disappeared by the 1950s (Veitch, 1985). Chatham Island snipe were reintroduced successfully to Mangere Island in 1970 (Bell, 1974) and subsequently colonised nearby Little Mangere Island, which is also predator-free.

3.4.3. Extinct (Giant) Chatham Island Snipe, Coenocorypha chathamica

Bones of this large, extinct species are known from sub-fossil deposits. Almost nothing is known of its ecology and the reasons for its extinction can only be speculative. Midden remains from two islands indicate that it survived until colonisation of the Chatham Islands by humans (and Pacific rats) about 400–450 years ago (McFadgen, 1994). Given the extreme susceptibility of other *Coenocorypha* species to rats, it is possible that predation by humans and Pacific rats may have been partly or wholly responsible for the extinction.

Current distributions and the history of island invasions suggest that all extant snipe taxa are highly susceptible to introduced mammalian predators and even adult birds are unable to co-exist with anything larger than the house mouse. Reduced flying ability and naivety probably increased their susceptibility. Miskelly (1987b) commented that "Their present distribution symbolises the vulnerability of New Zealand's ecosystems to modification by man and his camp-followers". The Chatham Island snipe and the Auckland Islands, Antipodes Islands and Snares Islands populations of the New Zealand snipe appear secure, but their survival depends entirely on keeping those islands free of mammalian predators. Priorities for the Jacquemart Island

snipe include the formulation of a recovery plan and the establishment of a second population. Once nearby main Campbell Island (11,300 ha) is free of cats and rats, it should be possible to re-establish the snipe there; cats may already have died out (I. McFadden, personal communication) and eradication of Norway rats is planned within 5 years.

4. Susceptibility of New Zealand birds to predation

Introduced predators are or were a major threat to (or restrict the distribution of) at least 12 of the 18 taxa considered above. Like other island fauna that evolved in the absence of terrestrial mammals, New Zealand's birds (including shorebirds) display a number of ecological and behavioural features that rendered them vulnerable to introduced predators (e.g. King, 1984; Gill and Martinson, 1991; Newton, 1998).

- 1. Many New Zealand birds are flightless or show reduced flying ability. Among the shorebirds, none is flightless and only the New Zealand snipe shows a noticeable reduction in flying ability (Higgins and Davies, 1996).
- Island bird species often evolve large size, a feature which may make them particularly attractive as food to humans and other introduced predators (Newton, 1998). The New Zealand dotterel is the largest member of its genus and its decline in the South Island was probably partly caused by shooting for food (Dowding, 1999b).
- 3. Many species show lowered reproductive rates; in particular, clutch size is often reduced and reproductive maturity delayed. Breeding systems of New Zealand shorebirds are summarised in Table 3 and compared with those of related or similar species elsewhere.
- 4. Like most shorebirds, all New Zealand species are ground-nesting. Many have extended incubation and fledging times, resulting in eggs and chicks (and the adults incubating or defending them) being vulnerable for long periods. In particular, fledging times of New Zealand shorebird species are especially protracted (Table 3).
- 5. Some species, particularly those displaying a higher degree of endemism, may be behaviourally naive towards mammalian predators. The ease with which adult New Zealand snipe can be captured by hand-net (Miskelly, 1989) is consistent with extreme naivety towards predators. Less-obvious behavioural traits may also have an effect; Pierce (1986) suggested that differences in timing of nesting, nest-site selection, and in distraction displays of the pied stilt and black stilt resulted in marked differences in nest predation rates.

Although terrestrial mammals were absent, endemic New Zealand birds evolved in the presence of a range of avian predators, including raptors, owls, gulls, skuas, rails and a crow (Gill and Martinson, 1991). Most of these probably hunt (or hunted) almost entirely by sight and the majority are usually diurnal. Predation by birds has apparently been countered by shorebirds in New Zealand (and elsewhere) in a number of ways.

- Eggs and chicks of all species are cryptic and small chicks crouch and remain motionless when danger hreatens.
- Some species, such as shore plover and Chatham Island snipe, nest out of sight in holes or under vegetation.
- 3. Most species have well-developed distraction and injury-feigning displays.

It seems likely that these responses are less effective against introduced mammals such as rodents, cats and mustelids, which may hunt by a combination of sight, hearing and olfactory cues (King, 1989; Kitchener, 1991). Video-monitoring of charadriiform nests in the Mackenzie Basin indicated that cats appeared to hunt visually or aurally, whereas ferrets and hedgehogs approached nests with their noses close to the ground, presumably using olfactory cues (Sanders and Maloney, 1999). The small size, agility and slim body shape of rodents and mustelids also allows them to prey on species that nest or roost under cover or in restricted spaces. Most of the carnivores introduced to New Zealand are also partly or largely nocturnal.

5. Discussion

5.1. Mammalian predators

Overall, rats, cats and mustelids appear to be the introduced mammals that have had the greatest impacts on New Zealand shorebirds. This is broadly in agreement with the analysis of King (1985), which shows that the greatest numbers of extinctions of island birds worldwide due to predators have been caused by rats (54%) and cats (26%). At present, cats, ferrets and stoats appear to be the introduced species posing the greatest threats to remaining mainland shorebird species, although hedgehogs are probably an under-rated egg predator of ground-nesting birds, including shorebirds. The introduced brushtail possum Trichosurus vulpecula is also a predator of birds' eggs and chicks (Brown et al., 1993); it occurs at highest densities in forested areas and nearby grassland (Cowan, 1990) but is also found in coastal dunes, where it has been recorded taking eggs of northern New Zealand dotterels (Wills, 1998).

Because shorebird chicks are nidifugous and highly mobile, recording the identity of predators of chicks is notoriously difficult (e.g. Pierce, 1986; Rebergen et al., 1998). Little information is available on chick predators, but there may be differences in the relative importance of individual predator species during the egg and chick phases; hedgehogs, for example, take eggs but probably kill few chicks.

5.2. Avian predators

Survival and productivity of shorebirds are also affected by native avian predators. Two of these, the southern black-backed gull and Australasian harrier, are now at much higher densities because of human activities (Heather and Robertson, 1996); their impacts are therefore likely to be considerably greater than in the past and are now additional to those of introduced mammals and other recent threats. Both species are increasingly common on inland riverbeds and in coastal areas, so most endemic shorebird species are likely to be affected. The self-introduced spur-winged plover *Vanellus miles* has spread rapidly throughout New Zealand during the twentieth century; it has been recorded breaking eggs in New Zealand dotterel nests (Dowding,

1998; Wills, 1998), but it is not yet clear how common this behaviour is or whether it is likely to pose a threat in the future. On the Chatham Islands, brown skuas *Catharacta skua* occasionally prey on Chatham Island oystercatcher and shore plover eggs and chicks (Higgins and Davies, 1996). Red-billed gulls *Larus novae-hollandiae scopulinus* are known predators of New Zealand dotterel eggs (Dowding, 1993) and shore plover chicks (Fleming, 1939). Two introduced species, the myna *Acridotheres tristis* and the Australian magpie, are known to eat birds' eggs and chicks; they are, therefore, potential predators of native shorebirds, but little information is available on their impact.

5.3. Indirect effect of rabbit control

Rabbits *Oryctolagus cuniculus* are a significant agricultural pest in parts of New Zealand and their control may indirectly have affected predation rates on some shorebirds. Rabbits are a major prey item of a number of introduced predators, particularly cats, ferrets and stoats (King, 1990). Where rabbit densities are high and are subsequently reduced, prey-switching by these predators may occur and predation rates on native fauna, including birds, may increase.

Table 3
Breeding systems of New Zealand shorebirds compared to those of similar and related taxa elsewhere ^a

Species	Usual age at first breeding (years)	Typical clutch size	Incubation time (days)	Fledgling time (days)
Oystercatchers				
Haematopus (ostralegus) finschi	4–5	2–3	24–28	ca. 42
H. unicolor	4–5	2–3	25–33	42-49
H. chathamensis	4–6	2–3	25	46-49
H. ostralegus ^b	4	3	24–27	28-32
H. moquini ^b	3–4	2	26-31	35–40
Stilts				
Himantopus novaezelandiae ^c	2–3	4	24.5–26	41-55
H. himantopus leucocephalus ^c	2	4	23–26	28-38
H. h. himantopus ^b	2	4	22–25	28-32
Plovers				
Charadrius obscurus	2	3	28–32	40-50
C. leschenaultii ^b	2	3	≥24	≥30
C. bicinctus	1	3	25	35-42
C. alexandrinus ^b	1–2	3	24–27	27-31
Thinornis novaeseelandiae ^d	2–3	3	26-31	31–63
T. rubricollis ^b	Unknown	2–3	27–31	32-36
Anarhynchus frontalis ^e	2–3	2	30–36	35–37
Snipe				
Coenocorypha aucklandica	1–3	2	22	ca. 30
C. pusilla	Unknown	2	Unknown	ca. 21
Gallinago gallinago ^b	1–2	4	18-20	19-20
Lymnocryptes minimus ^b	Unknown	4	21–24	Unknown

^a Data for New Zealand and Australian birds are mostly from Marchant and Higgins (1993), Heather and Robertson (1996) and Higgins and Davies (1996), with other sources as noted. Data for other species are from Cramp and Simmons (1983) and del Hoyo et al. (1996).

^b Similar and related taxa elsewhere.

^c Additional data from Pierce (1982).

^d Additional data from Davis (1987).

^e Additional data from Hay (1984).

In the mid-1940s, World War II interrupted control and rabbit densities became very high. In the 1950s control was intensified and dense populations were successfully and rapidly reduced (Gibb and Williams, 1990). Pierce (1996) has suggested that the sudden decline of black stilts in the 1950s may have resulted from prey-switching following intensive rabbit control in Central Otago and the Mackenzie Basin at that time. Pierce (1987) recorded numerical and functional responses of ferrets, cats and harriers to autumn/winter poisoning of rabbits in the Mackenzie Basin, and noted increased predation pressure on nesting charadriiforms during the following spring. Rebergen et al. (1998) reviewed studies of banded dotterel breeding success undertaken on South Island rivers between 1977 and 1995, and also concluded that nest predation rates were higher in seasons following rabbit-poisoning operations.

In 1997, rabbit haemorrhagic disease (RHD) was introduced to New Zealand and prey-switching became a potential threat to a number of shorebird species. Rabbits are very numerous in some inland South Island areas (including the Mackenzie Basin) where South Island pied oystercatchers, black stilts, banded dotterels and wrybills breed, and are common in many North Island coastal dune areas where variable oystercatchers and New Zealand dotterels breed. The Department of Conservation's RHD response plan (Aikman, 1997) considered six bird taxa to be particularly vulnerable to prey-switching, of which three are shorebirds (black stilt, northern New Zealand dotterel and wrybill).

Where RHD significantly reduced dense rabbit populations in the Mackenzie Basin, predation rates on banded dotterel nests were higher than those normally found during breeding seasons in which rabbit control did not occur, and similar to those reported immediately after rabbit poisoning (Norbury and Barlow, 1998). Intensive predator control undertaken at some of the breeding sites increased both breeding success of banded dotterels (Norbury and Barlow, 1998) and breeding success and adult survival of wrybills (E. Murphy and J. Dowding, unpublished data). However, it is still not clear what the medium- or long-term effects of RHD will be on rabbit populations, and continued research is required to gauge future impacts on threatened shorebirds.

5.4. Differences in vulnerability

There may be substantial differences in sensitivity to predation among closely related or ecologically similar taxa. As noted above, Pierce (1986) demonstrated that differences in behaviour of the closely-related pied and black stilts resulted in markedly different predation rates. The northern and southern subspecies of the New Zealand dotterel differ very markedly in demographics and *Charadrius o. obscurus* appears to have a greater

inherent susceptibility to predation (Dowding, 1997). A further comparison is provided by the four plovers which bred in the South Island in the mid-nineteenth century; all were ground-nesting, and three were similar in size (50–70 g). Although related (some authorities place them all in the genus Charadrius) and ecologically similar in some respects, their populations have responded in quite different ways to the introduction of mammalian predators. The shore plover was extirpated by about 1872, apparently by cats and/or Norway rats, and before the introduction of mustelids (Davis, 1994). The southern New Zealand dotterel was declining during this period but declined more rapidly following the introduction of mustelids in the 1880s (Dowding, 1999b). The wrybill persists, but its range has changed and the population is probably declining slowly. The banded dotterel remains common and widespread; it may be a more recent arrival in New Zealand than the other species, and may have retained more effective anti-predator behaviours. Consistent with the suggestion of shorter isolation is the fertile pairing of a banded dotterel with an Australian species, the red-capped plover Charadrius ruficapillus (Oliver, 1955).

5.5. Demographic studies

These wide differences in sensitivity to predation suggest that it is potentially dangerous to extrapolate from findings on one species to another; even intra-specific comparisons between populations that differ temporally or spatially may be misleading. While research on species or subspecies that are numerous is simpler logistically, statistically and ethically, it may not result in appropriate management decisions for similar or related threatened taxa. When demographic data are required to assist management decisions, we therefore advocate specific, targeted research for different species, subspecies, or even populations. A similar conclusion has emerged from a study of Buller's albatross Diomedia bulleri; Sagar et al. (1999) showed large differences in population trends (within a subspecies) between two island groups 180 km apart and noted that their results "illustrate the necessity for conservation measures to be based on appropriately detailed data".

A number of studies of New Zealand shorebirds have measured the impact of predation on productivity (e.g. Pierce, 1986; Dowding, 1998; Rebergen et al., 1998), but without accurate measures of recruitment and adult survival, the influence of changes in productivity on overall population trends are difficult to assess accurately. However, if productivity is demonstrably lower in the presence of introduced predators than in their absence, there is cause for concern, as adult survival and recruitment are unlikely to have increased to compensate. Survival and productivity are likely to vary between seasons and areas, so data may need to be col-

lected over a number of years and possibly in different areas. Collection of adequate data on recruitment may be time-consuming, particularly where productivity is low and natal site fidelity is not high.

In both the southern New Zealand dotterel and the wrybill, mortality of adult males is higher than that of females (Dowding, 1998; E. Murphy and J. Dowding, unpublished data); the possibility of a similar gender bias in other species should be considered in future studies (e.g. Dowding, 1999a).

5.6. Translocation

Where small populations of sensitive taxa exist on a single island, the risk of extinction in the event of a predator irruption is obviously high. The priority for such taxa must be the prevention of access by predators and the establishment of one or more 'insurance' populations. Translocations of shorebird species are currently being attempted in New Zealand, but techniques for establishing new populations of shorebirds are not as well developed as they are for forest birds. Much of the research and management undertaken on threatened avian species in New Zealand has centred on forest birds, such as black robin Petroica traversi, saddleback Philesturnus carunculatus, and kakapo Strigops habroptilus. In many cases, the use of island refuges free of introduced predators has been important or essential to the survival of the species. The fact that many of these forest birds have reduced powers of flight or are 'psychologically flightless' (Diamond, 1981) has obviously assisted these programmes. With the exception of snipe, which have been transferred successfully, extant New Zealand shorebirds can fly strongly. In addition, shorebirds often disperse widely, particularly during the juvenile stage, and translocations of young birds may fail as a result. As adults, many species show high site fidelity and, if transferred, may attempt to return to their previous site (e.g. Bell, 1974). The use of captivereared birds, which are likely to be more naive towards predators than wild-bred birds, may compound these problems.

5.7. Future research and management

Long-term predator control will be required to stop the declines and possible extinctions of some endemic shorebirds, such as the black stilt and southern New Zealand dotterel. For technical and legal reasons, it is unlikely that any form of widespread biological control of predators (such as immuno-contraception) will be available for many years (e.g. Bomford and O'Brien, 1997; Guynn, 1997; Rodger, 1999). There are also ethical considerations; biological control (particularly of cats) may prove unacceptable to the general public. Existing techniques of poisoning and trapping, there-

fore, need to be refined and made more cost-effective (Murphy, 1999). Research is currently under way on the development of species-specific toxins and lures, so that poisoning can be more targeted.

Predator exclosures around individual nests are a possible management technique, although very labour-intensive. Wire mesh exclosures have been shown to result in greatly increased hatching success of piping plover *Charadrius melodus* nests (Deblinger et al., 1992). However, the main mammalian predators of piping plovers are relatively large animals, such as fox *Vulpes vulpes*, raccoon *Procyon lotor*, and skunk *Mephitis mephitis*, and are excluded even by large-sized mesh. Important predators in New Zealand are much smaller (rats, cat and mustelids) and Dowding (1997) found that mesh large enough to allow New Zealand dotterels through did not exclude rats, mustelids or small cats.

Research on the use of decoys may provide a technique to attract translocated, released or wild shorebirds to safe feeding or breeding areas, or to increase densities of birds in managed areas, making management more cost-effective. Recent experiments show that New Zeal-and fairy terns are strongly attracted to decoys (D. Jeffries, personal communication), and that breeding Chatham Island oystercatchers attack decoys in their territory (F. Schmechel, personal communication). However, the use of decoys as a management tool has not been tested on any of the shorebird species reviewed here.

5.8. Comparisons with threats to shorebirds elsewhere

Of the 23 threatened shorebird species worldwide, no fewer than six are endemic to New Zealand (Collar et al., 1994). How do the threats to these New Zealand species compare with threats to shorebirds in other parts of the world? Table 4 lists 17 threatened and three recently extinct shorebirds (excluding New Zealand species) and summarises the known or likely reasons for their decline or extinction. Overall, it is clear that degradation or loss of habitat is the single largest threat to shorebird species worldwide, as it is for all bird species (Collar et al., 1994). Using the threat codes assigned by Collar et al. (1994), loss or alteration of habitat is listed for 13 of the 17 threatened species in Table 4 and for three of the six threatened New Zealand species. Small range or population (in most cases a direct result of other threats) is listed for seven of 17 species elsewhere and four of six in New Zealand. Hunting (listed for four of the 17 species, none in New Zealand) was a widespread threat to shorebirds in the past; although prohibited in some countries now, it continues in others and poses an ongoing threat. It has been estimated that in Asia for example, up to 1.5 million shorebirds are trapped or shot each year during migration (Lane, 1987). Introduced species are listed as a definite threat to four (and possible threat to one) species of the 17 in

Table 4
Causes of recent extinctions and threats to extant threatened shorebird species outside New Zealand^a

Species		Main threats or causes of extinction
Canarian black oystercatcher Haematopus meadewaldoi	X	Habitat loss; competition with humans for food
Jerdon's courser Rhinoptilus bitorquatus	E	Habitat under grazing pressure; very sensitive to disturbance
Javanese wattled lapwing Vanellus macropterus	X	Habitat modification; hunting
Sociable lapwing V. gregarius	V	Habitat changes; grazing and other agricultural activities
Piping plover Charadrius melodus	V	Habitat modification, disturbance, increase in predation in some areas
Black-banded plover C. thoracicus	V	Possibly competition with recently-arrived C. pecuarius and/or C. marginatus
St Helena plover C. sanctaehelenae	E	Expansion of urban areas; habitat changes
Mountain plover C. montanus	V	Habitat changes
Hooded plover Thinornis rubricollis	V	Crushing of nests; disturbance; predation
Amami woodcock Scolopax mira	V	Habitat loss through deforestation; hunting; predation by mongooses
Moluccan woodcock S. rochussenii	V	Unknown
Wood snipe Gallinago nemoricola	V	Possibly loss of habitat in wintering range
Eskimo curlew Numenius borealis	C	Habitat loss; hunting
Bristle-thighed curlew N. tahitiensis	V	Unclear; possible threats include hunting and other human activities, predation
Slender-billed curlew N. tenuirostris	C	Loss of habitat; hunting; drainage of staging areas
Nordmann's greenshank Tringa guttifer	E	Urbanisation; increasing crow predation; disturbance; hunting
White-winged sandpiper Prosobonia leucoptera	X	Probably introduction of mammalian predators
Tuamotu sandpiper P. cancellata	E	Introduction of mammalian predators
Spoon-billed sandpiper Eurynorhynchus pygmeus	V	Small population; specialised breeding habitat requirements, risk of nest predation
Plains-wanderer Pedionomus torquatus	V	Alteration of habitat; possibly also hunting, predation, and pesticides

^a Data are from Collar and Andrew (1988), Collar et al. (1994) and del Hoyo et al. (1996). X, extinct; C, critically endangered; E, endangered, V, vulnerable.

Table 4 (Collar et al., 1994); they currently threaten four of the six New Zealand species and effectively threaten the remaining two, which are confined to predator-free islands.

Predation, therefore, poses an unusually high degree of threat to shorebirds in New Zealand, but this situation is not unique. Species endemic to other oceanic islands have also declined (*Prosobonia cancellata*) or become extinct (*P. leucoptera*) following the introduction of mammalian predators. In most cases however, few shorebird species have been involved. Hawaii for example, another of the larger isolated island systems dramatically affected by introduced species, has no endemic shorebirds extant or extinct (Pratt et al., 1987). The impact has been more obvious in New Zealand, probably because of the relatively larger land area of the archipelago and the greater number of shorebird species present.

6. Conclusions

Many of the best-known conservation programmes in New Zealand have involved forest birds. With the possible exception of the black stilt, threats to shorebirds have, until recently, been less widely recognised. However, based on the proportion of species under some degree of threat, shorebirds appear to have suffered at least as much as other groups of birds in New Zealand. Collar et al. (1994) listed as threatened six (46%) of 13 native and endemic shorebird species and 39 (27%) of 142 species other than shorebirds. Considering endemic species only, six (60%) of 10 shorebirds and 34 (57%) of 60 other species are threatened. During the past 10–20 years, awareness of the status of (and threats to) shorebirds has increased and recovery programmes are now in place for a number of threatened taxa.

There can be little doubt that most of New Zealand's endemic shorebirds have declined in range and numbers since human colonisation. In some cases, disturbance and destruction or modification of habitat have played a part, but predation by introduced mammals has been the main agent of most of the declines. Of New Zealand's 10 extant endemic shorebird species, three are confined to predator-free islands, and a fourth is found only on the Chatham Islands group. Three of the six species that survive on the mainland have declined to varying degrees and are threatened. Only one plover and two oystercatchers are still relatively numerous or widespread. New Zealand currently has no fewer than five of the world's rarest shorebird taxa (three species, one subspecies and one probable subspecies), all with populations of 150 individuals or less. Future efforts to save these taxa from extinction will rely on detailed demographic and ecological research, strict quarantine procedures to ensure that predators do not reach refuge islands, improvements in predatorcontrol techniques on the mainland, and development of shorebird translocation protocols.

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