

REVIEW ARTICLE

Impacts of introduced mammalian predators on indigenous birds of freshwater wetlands in New Zealand

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Abstract: The impacts of introduced mammalian predators on the viability of bird populations in forest, river and coastal habitats in New Zealand are well known. However, a common understanding of their impacts in freshwater wetlands is lacking. We review evidence for impacts of introduced mammalian predators on freshwater birds, particularly specialist species restricted to wetlands, and use this information to make predictions about freshwater species likely to be vulnerable to predation. Extinctions and significant declines of freshwater species have been numerous since humans introduced mammalian predators to New Zealand. Anecdotal evidence links predation to the loss of 11 of 14 extinct birds that would have inhabited wetlands. Thirty extant species, particularly ground-nesting species, are still under threat from mammalian predators. All introduced mammalian predator species are abundant and/or widespread in New Zealand wetlands and most have been confirmed to prey upon freshwater bird species. While their precise impacts on the long-term viability of threatened bird populations have not been evaluated, evidence suggests that predation is a serious threat, warranting predator control. An evaluation using documented predation events and ecological traits suggests that six threatened wetland specialists are at high risk of predation: Australasian bittern (*Botaurus poiciloptilus*), banded rail (*Gallirallus philippensis*), brown teal (*Anas chlorotis*), fernbird (*Bowdleria punctata*), marsh crake (*Porzana pusilla*), and spotless crake (*P. tabuensis*). Research is needed on the ecology and behaviour of mammalian predators in wetlands to help understand their impacts on long-term viability of bird populations and to assist in developing and monitoring predator control programmes.

Keywords: bitterns; ecological traits; rails; swamp birds; threatened species; waterfowl

Introduction

Populations of freshwater bird species are declining globally from a range of anthropogenic threats, and numerous species are classed as threatened with extinction (Deharter & Guillemain 2008; IUCN 2014). Significant threats include habitat loss, invasive species, overexploitation and climate change (Dudgeon et al. 2006; Nebel et al. 2008; Kingsford 2011). A major challenge for conservation managers is determining precise causes of population declines so that management aimed at recovering species can be targeted appropriately. In New Zealand, threats to birds that inhabit freshwater wetlands (i.e. 'freshwater birds'; those that occupy palustrine, lacustrine and riverine swamps, marshes, bogs and fens; Johnson & Gerbeaux 2004) include the dramatic loss of >90% of wetland cover and continued modification and degradation of wetlands (Ausseil et al. 2011), but the relative impact of predation is unquantified.

Invasive species, especially predators, are one of the greatest threats to global biodiversity (Clavero & Garcia-Berthou 2005; Pimentel et al. 2005; Donlan & Wilcox 2008). The introduction of mammalian predators to New Zealand was catastrophic for the indigenous avifauna (Atkinson 1989). New Zealand had no native terrestrial mammals other than bats before humans arrived, and many bird species were poor

fliers or flightless and exhibited few behaviours for avoiding mammalian predators (Bull & Whitaker 1975). Mammalian predators were introduced by Polynesian and European settlers over the last ~ 800 years (King 2005). They included mustelids (stoat *Mustela erminea*, weasel *M. nivalis*, feral ferret *M. furo*), feral cat (*Felis catus*), rat species (Norway rat *Rattus norvegicus*, Pacific rat *R. exulans*, ship rat *R. rattus*), house mouse (*Mus musculus*), European hedgehog (*Erinaceus europaeus*), brushtail possum (*Trichosurus vulpecula*), feral pig (*Sus scrofa*), and domestic dog (*Canis familiaris*) (King 2005). All species except for the Pacific rat are now widespread throughout New Zealand (King 2005).

Impacts of these predators have been extensively documented in forest, riverine and coastal habitats and across animal groups including invertebrates (Ramsay 1978), reptiles (Townsend et al. 2007), bats (Pryde et al. 2005), freshwater fish (Baker 2006) and birds (Elliott et al. 1996a; Dowding & Murphy 2001; Sanders & Maloney 2002; Innes et al. 2010). The benefits of effective predator control programmes have also now been documented, although primarily for forest birds (e.g. O'Donnell et al. 1996; Basse et al. 2003; Dilks et al. 2003; Baber et al. 2009; Innes et al. 2010), but also see Cruz et al. (2013) for braided river birds and Reardon et al. (2012) for lizards. However, the potential impacts of these predators on freshwater birds in wetlands remain uncertain despite the

significance of this habitat type in New Zealand (Williams 2004) and the extensive declines in the range and abundance of many freshwater birds since occupation of New Zealand by humans (Travers 1868; Potts 1869; Buller 1874; Hutchinson 1900; Hope 1927; Stead 1927; Oliver 1955; Tennyson & Martinson 2006).

Scientific knowledge of predators in wetland ecosystems is poor compared with other ecosystem types in New Zealand and predator control receives little attention in contemporary texts on wetland management (Buxton 1991; Gerbeaux 2002; Peters & Clarkson 2010). There remains uncertainty about the magnitude of impacts of predators on freshwater birds, how impacts might vary among vulnerable species, how predation pressure might vary in time and space, and the impact of predators relative to the importance of other significant environmental threats (wetland drainage, degradation and fragmentation; Ausseil et al. 2011). Despite limitations in our knowledge, mammalian predator control is being conducted widely in New Zealand at and around wetlands, with a view to enhancing wildlife populations (Watts & Peters 2010).

The objectives of this review are to: (1) examine the anecdotal and published evidence for predation by introduced mammalian predators on bird species characteristic of freshwater wetlands; (2) make preliminary predictions about vulnerability of species to predation; (3) summarise information on the occurrence and behaviour of mammalian predators in wetlands; and (4) indicate future directions for research and conservation management.

In the context of our review, freshwater wetlands include places of poor drainage or where water accumulates; where seepage or flooding is frequent; and the interface where land meets streams, rivers, lakes and estuaries (Johnson & Gerbeaux 2004). These are most commonly swamps, marshes, bogs and fens, which may be associated with the riparian edges of lakes (lacustrine wetlands) or rivers (riverine) or may stand alone (palustrine).

We focus our review on bird species that feed, shelter or breed in freshwater wetlands (Williams 2004), especially the specialist species that are largely restricted to wetlands. Over 80 New Zealand bird species use freshwater wetlands in some way (O'Donnell 2000; Williams 2004). Many are incidental or vagrant in wetlands, but we consider 30 extant bird species as obligate or facultative inhabitants (see Table 1 for scientific names). These include several generalists that commonly feed and breed in wetlands as well as other habitat types (western weka, Australasian harrier, spur-winged plover, pied stilt, kingfisher, NZ pipit, welcome swallow). Eighteen species (60%) are threatened or at risk as defined by Miskelly et al. (2008) (Table 1). Particular emphasis is placed on six extant threatened species that specialise in using wetlands: Australasian bittern, banded rail, brown teal, fernbird, marsh crake, and spotless crake.

Impacts of mammalian predators

Extinctions of wetland species related to predation

Eleven of 14 extinctions of species that would have inhabited wetlands in New Zealand have been attributed to the effects of predation by introduced mammals in both Polynesian and European times (Buller 1874; Oliver 1955; Tennyson & Martinson 2006; see below). These species include several pre-European extinctions and, although little is known of their habitat use patterns (Tennyson & Martinson 2006), they

belonged to families that generally use wetlands, at least to some extent (rails, Rallidae; waterfowl, Anatidae).

Introduced mammals were thought to be responsible for the extinction of the New Zealand little bittern (*Ixobrychus novaezelandiae*), with its final disappearance coinciding with the arrival of Norway rats, feral cats, ship rats and mustelids (Oliver 1955). Among the waterfowl, extinctions of Scarlett's duck (*Malacorhynchus scarletti*) and Finsch's duck (*Chenonetta finschi*) occurred in early-Polynesian times and may have been influenced by predation by Pacific rats, while the Southern merganser (*Mergus australis*) probably suffered similar predation on the mainland and its final disappearance from the subantarctic Auckland Islands coincided with introductions of dogs, cats and pigs (Tennyson & Martinson 2006). Among the rails, Pacific rats were thought to be responsible for losses of the snipe rail (*Capellirallus karamu*), New Zealand coot (*Fulica prisca*), Chatham Island coot (*F. chathamensis*), and Hodgen's waterhen (*Gallinula hodgenorum*) in Polynesian times (Tennyson & Martinson 2006). On the offshore islands, cats and possibly rats, dogs, and pigs contributed to the loss of Hutton's rail (*Cabalus modestus*), Dieffenbach's rail (*Gallirallus dieffenbachii*) and Hawkins' rail (*Diaphorapteryx hawkinsi*) on the Chatham Islands. The Auckland Islands rail (*Lewinia muelleri*) is now confined to predator-free Adams Island (Elliott et al. 1991). Its disappearance from main Auckland Island has been attributed to predation by cats and loss of habitat because of browsing by pigs (Falla 1967; Elliott et al. 1991). The extinctions of three other duck species have been attributed to over-hunting by early human inhabitants (NZ blue-billed duck *Oxyura vanetsi*, NZ musk duck *Biziura delautori*, Chatham Island duck *Pachyanas chathamica*; Tennyson & Martinson 2006).

Post-European declines attributed to predation

Freshwater bird populations declined steadily following European settlement, at a time when numerous predators were introduced but also when wetland drainage was extensive (Oliver 1955; Stidolph 1971). While much of the evidence for cause of extinctions and declines is anecdotal, species losses have occurred in many areas where wetland modification has not been extensive, but where predators are numerous. For example, on the West Coast of the South Island and Stewart Island, both areas having the highest proportions of wetlands remaining in the best condition (Ausseil et al. 2011).

Decline in the range of Australasian bittern, including disappearance from the Chatham Islands, was noted by many early authors (e.g. Hope 1927; Oliver 1955). Fernbird, brown teal, and banded rail disappeared from many areas of the East Coast of the South Island completely by the 1930s (Stead 1927; Elliott 1978, 1983). The last confirmed records we found of spotless crake from the Chatham Islands and Stewart Island were from 1949 (Bell 1955) and 1933 (Museum of New Zealand), respectively. Similarly, marsh crake have not been seen on Chatham Island since before 1950 (Oliver 1955), or on Stewart Island since 1945 (Museum of New Zealand). There were no sightings of either crake in the OSNZ atlas schemes from either island after 1969 (Robertson et al. 2007).

Predation was suspected as a major cause of decline in rails by many early authors, although the evidence was rarely recorded (e.g. Moncrieff 1937). However, it is not possible to relate these general historical reports to the timing of the arrival or spread of specific introduced predators, largely because introductions spanned over 100 years and the speed and distribution of invasions appeared variable in time and

Table 1. Indigenous bird species ($n = 30$) that characteristically feed, breed, or shelter in freshwater palustrine, riverine and lacustrine wetlands in New Zealand (based on Heather & Robertson (2000), O'Donnell (2000), and Williams (2004)). The list excludes vagrant and migratory species and species that typically use terrestrial or coastal habitats but may occur incidentally in wetlands. # threatened or † at risk species ($n = 18$), according to Miskelly et al. (2008).

Bird species		Wetland type		
Common name	Scientific name	Palustrine	Riverine	Lacustrine
Grebes				
Australasian crested grebe #	<i>Podiceps cristatus</i>	Yes	–	Yes
NZ dabchick #	<i>Poliiocephalus rufopectus</i>	Yes	–	Yes
Cormorants				
Black shag †	<i>Phalacrocorax carbo</i>	Yes	Yes	Yes
Little shag †	<i>P. melanoleucos</i>	Yes	Yes	Yes
Little black shag †	<i>P. sulcirostris</i>	–	Yes	Yes
Hérons				
White heron #	<i>Egretta alba</i>	Yes	Yes	Yes
White-faced heron	<i>Ardea novaehollandiae</i>	Yes	Yes	Yes
Royal spoonbill †	<i>Platalea regia</i>	Yes	–	Yes
Australasian bittern #	<i>Botaurus poiciloptilus</i>	Yes	Yes	Yes
Waterfowl				
Black swan	<i>Cygnus atratus</i>	Yes	Yes	Yes
Paradise shelduck	<i>Tadorna variegata</i>	Yes	Yes	Yes
Grey duck #	<i>Anas superciliosa</i>	Yes	Yes	Yes
Australasian shoveler	<i>A. rhynchotis</i>	Yes	Yes	Yes
Grey teal	<i>A. gracilis</i>	Yes	Yes	Yes
Brown teal †	<i>A. aucklandica</i>	Yes	Yes	Yes
NZ scaup	<i>Aythya novaeseelandiae</i>	Yes	Yes	Yes
Harriers				
Australasian harrier	<i>Circus approximans</i>	Yes	Yes	Yes
Rails				
Western weka †	<i>Gallirallus australis</i>	Yes	–	–
Banded rail †	<i>Rallus philippensis</i>	Yes	–	–
Spotless crake †	<i>Porzana tabuensis</i>	Yes	–	–
Marsh crake †	<i>P. pusilla</i>	Yes	–	–
Pūkeko	<i>Porphyrio porphyrio</i>	Yes	Yes	Yes
Australian coot	<i>Fulica atra</i>	Yes	–	Yes
Waders				
Spur-winged plover	<i>Vanellus miles</i>	Yes	Yes	Yes
Pied stilt †	<i>Himantopus himantopus</i>	Yes	Yes	Yes
Black stilt #	<i>H. novaeseelandiae</i>	Yes	Yes	Yes
Kingfishers				
Kingfisher	<i>Halcyon sancta</i>	Yes	Yes	Yes
Swallows				
Welcome swallow	<i>Hirundo tahitica</i>	Yes	Yes	Yes
Passerines				
Fernbird †	<i>Bowdleria punctata</i>	Yes	Yes	Yes
NZ pipit †	<i>Anthus novaeseelandiae</i>	Yes	Yes	–

space (Wodzicki 1950; Gillies & Fitzgerald 2005; Innes 2005; Clapperton & Byrom 2005).

Present-day effects of predators

We collated records of predation from Department of Conservation (DOC) wetland bird databases (~15 000 records), the Ornithological Society of New Zealand Recording Scheme, books, and searches of publication databases. Evidence for predation was generally reports of dead birds being brought into houses by pets, direct observations, interpretation of sign left in nests and, in a few cases, evidence from infrared video recordings. We found numerous records of predation events despite the cryptic nature of these species and paucity of studies investigating nest success (64 published observations,

8 personal communications; Table 2). Confirmed predators included almost the full range of species known to prey on birds in New Zealand (Table 2). The exceptions were brushtail possums, hedgehogs, feral pigs, and house mice, although all four species are known to consume eggs or chicks in other habitats (Challies 1975; Flack & Lloyd 1978; Brown et al. 1993; Sanders & Maloney 2002). Other authors commonly reported that failure of wetland bird nests resulted from predation, but the identity of the predators was unknown (e.g. Anderson & Ogdén 2003).

The most frequent predators were cats, but dogs, stoats, rats, and ferrets were also common predators (Table 2). Most reported predation attributed to dogs was a result of using them for duck shooting. The identity of rats was frequently

Table 2. Records of predators of specialist species largely restricted to wetlands in New Zealand.

Species	Cat	Stoat	Ferret	Weasel	Rat	Dog	Unidentified predator	Sources
Australasian bittern	X						X	P. C. Taylor pers. comm.; P. Langlands pers. comm.
Brown teal	X	X			X	X		Hayes & Williams 1982; Barker 1999 unpubl. report; Holdaway 1999; Williams 2001; Parrish & Williams 2001; Barker & Williams 2002; Skilton 2009
Marsh crake	X	X				X	X	Hamilton 1885; Fleming 1938; Stidolph 1949, 1950, 1955; Sibson 1957, 1960; Westerskov 1970; Edgar 1972a, 1976; Howell & Gaze 1986; Kaufmann & Lavers 1987; O'Donnell & West 1996; Taylor 2011; G. Tunnicliffe pers. comm.; S. Moore pers. comm.; P. Langlands pers. comm.
Spotless crake	X	X	X		X	X	X	Hamilton 1885; Pycroft 1898; McKenzie 1947; Stidolph 1951; Bibby 1954; Bell 1955; Sibson 1957, 1961; Howard 1962; McKenzie 1963; Kendrick 1966; Edgar 1972a; St Paul 1977; Ogle & Cheyne 1981; Kaufmann & Lavers 1987; Tennyson & Lock 2000; M. Charteris pers. comm.
Banded rail	X	X	X	X	X	X	X	Guthrie-Smith 1921, 1925; Falla 1954; Sibson 1958; Oliver 1955; Edgar 1972a, b; Elliott 1983; Howell & Gaze 1987; Marchant & Higgins 1993; Taylor & Parrish 1994; Tennyson & Lock 2000; Parker & Brunton 2004; Chau Ping Ong pers. comm.; B. Cash pers. comm.; G. Elliott pers. comm.
Fernbird	X	X			X	X	X	Guthrie-Smith 1914; Stead 1948; Oliver 1955; Bell 1978; Elliott 1978; Barlow & Moeed 1980; Fitzgerald & Veitch 1985; Kater 1999; Parker 2002; van Klink et al. 2013
'Rails'	X	X	X			X	X	Buller 1874; Moncrieff 1937; Roser & Lavers 1976; Rickard 1996

not determined, but both ship and Norway rats have caused nest losses (Elliott 1983; Pierce 1986). Mice are suspected of being nest predators, although this has not been confirmed (Parker 2002).

Among the rails there are numerous examples of predation by mammals. For pūkeko, of 91 eggs known to be lost before hatching, 38% were taken by predators (Marchant & Higgins 1993). Only rats appear to have been confirmed as mammalian predators of pūkeko eggs (Carroll 1969; Craig 1980) but stoats have been recorded preying on pūkeko adults (Fitzgerald 1964) and cats have been observed hunting them (Morgan 2002).

Studies have implicated the full range of mammals as predators of banded rail (Table 2). For example, Parker and Brunton (2004) recorded video footage of a stoat consuming egg and chicks in a banded rail nest and then sleeping in the nest for ~45 min. They predicted, based on the stoat's behaviour, that returning adult birds were also at risk of predation. Graeme Elliott (1983; pers. comm.) observed a banded rail nest being preyed upon by a stoat, and two nests were preyed on by domestic cats (9 of 38 eggs monitored; 24%). He found no evidence of birds being preyed on away

from nests. Guthrie-Smith (1925) reported that eggs of 18 of 21 banded rail nests (86%) were destroyed by rats and at least one nest showed evidence of adults being killed. Banded rails have now declined and disappeared from many parts of the country including almost all of the South Island, and remaining populations continue to decline (Stead 1927; Oliver 1955; Robertson et al. 2007).

Similar high rates of nest failure were recorded in the few documented occurrences in crakes. Four of 11 spotless crake nests and one of two marsh crake nests were preyed upon at the egg stage at Pukepuke Lagoon (Kaufmann & Lavers 1987). Cats were frequent predators of both species, although there were records of mustelids, rats and dogs killing them (Table 2). A cat at Whirinaki caught the only six spotless crakes recorded for the area (St Paul 1977) and an extreme example is the report of 17 marsh crakes and 12 spotless crakes killed by a domestic cat over three years in Petane, Hawke's Bay (Hamilton 1885).

Predators take a range of waterfowl with both egg and duckling survival rates often being low. Where 'predation' was recorded, the identity of the predator was usually unknown

(Marchant & Higgins 1993), but feral cats, ferrets, and rats have been recorded as frequent predators (Williams 1975; Roser & Lavers 1976; Langham 1990; Langlands 1990; Stokes 1991; Morgan 2002).

Most evidence for predation on waterfowl comes from studies of brown teal. Brown teal have declined in numbers and range over the last 50+ years (Parrish & Williams 2001) and predation is cited as the current main agent of decline (O'Connor et al. 2007). The increase in abundance of cats on Stewart Island coincided with the decline and final disappearance of brown teal from the island (Hayes & Williams 1982). Even on Great Barrier Island, in the absence of Norway rats, mustelids, and possums, brown teal decreased exponentially between 1985 and 2001 (Ferreira & Taylor 2003) where cats and dogs were identified as predators of adult teal (Barker & Williams 2002). When brown teal were reintroduced to Travis Wetland in Christchurch in 2007, 12 of 20 were killed within the first year, largely by cats ($n=4$), harriers (*Circus approximans*) ($n=5$), and stoats ($n=1$) (Skilton 2009). Similarly, at Tawharanui (Auckland) prior to the area being protected by a predator-proof fence, seven out of eight brown teal released were thought to have been killed by mammalian predators (Rickett 2010) and at Cape Kidnappers, 19% of deaths of 26 brown teal (2008–2011) were caused by cats or mustelids (Ward-Smith & Nagakawa 2012).

A number of mammalian predators have been implicated in declines of fernbirds (Table 2). Cats exterminated fernbirds from Herekopare Island (Fitzgerald & Veitch 1985), while on Big South Cape and Solomon islands the ship rat invasion in 1964 had the same effect (Bell 1978). Fernbirds on Codfish Island have apparently increased markedly since the eradication of Pacific rats (Kater 1999; R. Cole, DOC Invercargill, pers. comm.). Elliott (1978) recorded predation on two fernbird nests at the fledgling phase, but did not verify whether predators were mammalian or avian. Predation accounted for 73% of North Island fernbird nest failures at Omaha saltmarsh and mustelids and mice were responsible for most predation (Parker 2002). Predation of adults also occurs, with one of 36 radio-tagged adults preyed upon by an unidentified animal during 27 days of monitoring (van Klink et al. 2013).

The least evidence for predation was for Australasian bittern, with one record of a cat-killed bird from near Mossburn in Southland (P. C. Taylor, pers. comm.) and a second bird from the Avon-Heathcote estuary (predator unidentified; P. A. Langlands, pers. comm.).

Predation of near relatives overseas

Predation by a wide range of mammal species is an important driver of breeding success among wetland birds elsewhere in the world (Reynolds & Tapper 1996; Drever et al. 2004; Kauhala 2004; Brook et al. 2005). Feral cats, rats, and dogs prey on marsh crakes and spotless crakes in Australia (Whitlock 1913; Bryant 1942; Sefton 1958; Sefton & Devitt 1962; de Ravin 1975). There is evidence of predation on other *Botaurus* bitterns by feral foxes (*Vulpes vulpes*), dogs, rats, mustelids, and racoons (*Procyon lotor*) (Gibbs et al. 1992; Smith et al. 1995; Puglisi & Bretagnolle 2005; Gilbert et al. 2007; Polak 2007). Although there are records of adult bitterns being preyed on in New Zealand and overseas, predation is more likely to affect eggs, chicks, and fledglings (Gilbert et al. 2007; Polak 2007) because large adult herons are relatively aggressive compared with smaller swamp-dwelling species (Teal 1965; Smith et al. 1995; Puglisi & Bretagnolle 2005). For example, in a study of Eurasian bitterns (*Botaurus stellaris*), predation accounted

for 14% of clutch, 20% of chick, and 21% of fledgling losses from 10 sites, and stoats were responsible for the deaths of 11 chicks (Gilbert et al. 2007).

Overall vulnerability of wetland bird populations

The loss of 90% of New Zealand freshwater wetland cover (up to 98% in some regions; A-G Ausseil, Landcare Research, pers. comm.) and significant declines in condition of those remaining (Ausseil et al. 2011) indicate that habitat loss would have had a major impact on birds largely restricted to wetlands. Although evidence clearly shows that individual wetland birds are commonly preyed upon by introduced mammals, evidence for significant population-scale impacts on their long-term viability in New Zealand is anecdotal, especially when considering the other major threat of wetland loss.

To further examine the likely impacts of predation in the remaining wetlands on birds, we examined the range of ecological traits that indicate the potential vulnerability of populations to predation by introduced mammals while breeding (Table 3). Because quantifiable data on the impacts of predators are not available in the literature for all wetland species (Marchant & Higgins 1990, 1993; Heather & Robertson 2000), we used a subjective assessment of vulnerable traits. We used six categories to characterise vulnerability to direct predation (Table 3). Species least resilient to predation are likely those where all breeding stages (eggs, young and adults) are vulnerable to predation and where only females incubate because of the disproportionate impact of losing adult female breeders on population viability (Table 3; Elliott 1996; O'Donnell et al. 1996; Keedwell 2004). Nest site is also important, where species that nest up trees or on floating nests are less vulnerable than those that nest on the ground (Collins 1964; O'Donnell et al. 1996; Yeh et al. 2007; Foster 2010). Rats, stoats, and cats can climb trees (Pisano & Storer 1948; O'Donnell et al. 1996), but ferrets, hedgehogs, and pigs are not likely to prey on nests or birds off the ground. Longer nest exposure times also increase predation risk (Martin 2002), with exposure times being as few as 23 days (NZ dabchick) to as long as c. 140 days (crakes). Nest defence behaviour is also likely to be important because aggressive behaviour potentially wards off predators (Fernández & Mermoz 2000). We classify species as (1) passive, (2) showing flight/weak responses, or (3) aggressive defenders. Greater fecundity, as indicated by number of eggs per clutch and median number of clutches per breeding season, is likely to increase resilience to predation. Although predators generally consume all eggs in a clutch regardless of its size, in large clutches some young may escape, and birds that lay more clutches have a higher probability of compensating for predation with subsequent clutches (Table 3).

Overall, all wetland bird species are potentially vulnerable to predation by introduced mammals. However, species predicted to be most at risk nest on the ground, or close to it, and lack predator avoidance behaviours (Table 3). Four of the wetland specialists appear particularly vulnerable: Australasian bittern, brown teal, spotless crake, and marsh crake. We predict that two other specialists, banded rail and fernbird, would be more resilient because of shorter attendance at nests and higher fecundity; Elliott (1983) suggested some rail populations may be able to cope with predation pressure

Table 3. Ecological traits predicted to signify vulnerability of indigenous bird species to predation by introduced mammals in freshwater wetlands; based on Heather & Robertson (2000). For species names see Table 1.

Species	Most vulnerable stage	Usual place of exposure	Exposure time (days)	Nest attendance strategy	Defence behaviour	Median no. eggs	Median no. clutches	Eggs per season
Crested grebe	Egg+adult	On water	31	Male+female	Flight	3	1	3
Dabchick	Egg+adult	On water	23	Male+female	Flight	2	2	4
Black shag	Egg+young	Above ground	80	Male+female	Aggressive	3	1	3
Little shag	Egg+young	Above ground	80	Male+female	Aggressive	4	1	4
Little black shag	Egg+young	Above ground	88	Male+female	Aggressive	4	1	4
White heron	Egg+young	Above ground	67	Male+female	Flight	4	1	4
White-faced heron	Egg+young	Above ground	66	Male+female	Flight	4	1	4
Royal spoonbill	Egg+young	Ground+tree	65	Male+female	Flight	3	1	3
Australasian bittern	Egg+young+adult	Ground	74	Female	Passive	4	1	4
Black swan	Egg+young	Ground	43	Male+female	Aggressive	6	1	6
Paradise shelduck	Egg+young	Ground+tree	89	Female	Aggressive	9	2	18
Grey duck	Egg	Ground+tree	77	Female	Aggressive	10	2	20
Shoveler	Egg	Ground	85	Female	Flight	11	2	22
Grey teal	Egg+young+adult	Ground+tree	86	Female	Passive	7	2	14
Brown teal	Egg+young+adult	Ground	85	Female	Passive	6	2	12
NZ scaup	Egg+young+adult	Ground	105	Female	Passive	7.5	1	8
Harrier	Egg+young	Ground	80	Female	Aggressive	4	1	4
Western weka	Egg+young+adult	Ground	101	Male+female	Aggressive	2.5	4	10
Banded rail	Egg+young+adult	Ground	85	Male+female	Passive	5.5	2	11
Spotless crane	Egg+young+adult	Ground	140	Male+female	Passive	3.5	2	7
Marsh crane	Egg+young+adult	Ground	140	Male+female	Passive	6	2	12
Pūkeko	Egg+young	Ground	112	Male+female	Aggressive	5	2	10
Australian coot	Egg+young	On water	26	Male+female	Aggressive	6	2	12
Spur-winged plover	Egg+young	Ground	87	Male+female	Aggressive	4	3	12
Pied stilt	Egg+young+adult	Ground	62	Male+female	Aggressive	4	2	8
Black stilt	Egg+young+adult	Ground	82	Male+female	Passive	4	1	4
Kingfisher	Egg+young+adult	Above ground	48	Male+female	Aggressive	5	2	10
Welcome swallow	Egg+young	Above ground	42	Female	Flight	4	3	12
Fernbird	Egg+young+adult	Ground	34	Male+female	Passive	3.5	3	10.5
NZ pipit	Egg+young+adult	Ground	31	Female	Passive	3.5	2.5	8.8

because of high productivity. The most vulnerable group also included black stilts and NZ scaup, both of which suffer high predation rates (Stokes 1991; Keedwell et al. 2002), and the NZ pipit, a species that is thought to be declining, but for which no population trend data exist (Miskelly et al. 2008). Several species currently classed as threatened were not scored in the highest category of risk on the basis of traits, largely because other factors threaten their viability (hybridisation for grey duck, aquatic predators and habitat changes for grebes; O'Donnell & Fjeldsa 1997; Miskelly et al. 2008).

Ecology of predators in wetlands

Distribution of mammalian predators in wetlands

We know of no comprehensive published studies of the distribution and abundance of mammalian predators in wetlands in New Zealand. Therefore, we sent questionnaires to DOC, Fish & Game, Biosecurity NZ, and community groups involved in wetland rehabilitation, asking whether recipients knew of predators in their wetlands or had information about their predator control. Based on the responses, we tabulated information on the predator species captured or observed at each site. Nearly the full range of mammalian predators found in New Zealand has been caught in wetlands (Table 4). Among the rats, only the Pacific rat has not been caught in any trapping programmes to date. Brushtail possums, house mice, and feral pigs all live in some wetlands, sometimes in high

densities (M. Brady, DOC Napier, pers. comm.), but possums have only been targeted in one control programme we know of (Table 4; van Klink et al. 2013).

Catch rates from recent trapping programmes provide some information on occurrence of different predators in wetlands. For example, in Whangamarino wetland, Waikato, 466 mammalian predators were caught in 14 months from February 2008 in 69 traps of various designs (M. Brady, pers. comm.). Of these, 160 (34%) were ship rats, 85 (18%) were hedgehogs, 71 (15%) ferrets, 62 (13%) Norway rats, 37 (8%) weasels, 25 (5%) stoats, 17 (4%) possums and 10 (2%) cats. In comparison, predator trapping around coastal wetlands at Whananaki in Northland between December 2006 and 2009 resulted in 1158 predator captures using 112 trap sites. Captures were 635 (55%) Norway rats, 142 (12%) hedgehogs, 140 (12%) stoats, 103 (9%) possums, 55 (5%) cats, 52 (5%) ship rats, 30 (3%) weasels, and 1 (<0.1%) ferret (unpublished DOC files). Similarly, at Mimiwhangata in Northland over the same period, captures comprised 1014 (53%) Norway rats, 260 (22%) hedgehogs, 249 (21%) stoats, 206 (17%) possums, 89 (5%) ship rats, 89 (5%) cats, 18 (2%) weasels, and no ferrets ($n = 1925$ captures) using 244 traps of various designs (unpublished DOC files.). Low captures of ferrets in Northland reflects their low density and patchy distribution (Clapperton & Byrom 2005).

The percentages of different predators caught at these three sites varied considerably. For example, 34% of captures were ship rats at Whangamarino, but only 5% of captures at Whananaki. Likewise, such variability was seen in smaller

Table 4. Records of known or suspected mammalian predators known to kill wetland bird species in selected New Zealand freshwater wetlands (* indicates data come from trapping programmes).

Wetland site	Type	Dog	Cat	Mustelids	Ferret	Stoat	Weasel	Ship rat	Norway rat	Rat species	Hedgehog	Source
Mimiwhangata, Northland*	Swamps and farm Restoration	–	Yes	–	–	Yes	Yes	Yes	Yes	–	Yes	J. Altham pers. comm. (DOC File No. DOCDM-103656)
Mimiwhangata, Northland*	Shallow marsh, streams, ponds & drains	–	Yes	Yes	–	Yes	–	–	–	–	–	N. Miller, DOC Northland pers. comm.
Whananaki, Northland*	Coastal swamp	–	Yes	–	Yes	Yes	–	Yes	Yes	–	Yes	J. Altham pers. comm. (DOC File No. DOCDM-103656)
Jackie Bisset, Northland	Human-made swamp	–	Yes	Yes	–	–	–	–	–	Yes	–	G. White, Northland Fish & Game Council, pers. comm.
Great Barrier Island	Coastal swamps	Yes	Yes	–	–	–	–	Yes	–	–	–	Anderson & Ogden 2003; J. Sim pers. comm.
Moehau, Coromandel	Coastal streamside	–	Yes	–	–	Yes	Yes	–	–	Yes	Yes	Brown teal. com/moehau (accessed 23 September 2013)
Whangamarino	Inland bog, swamp, fen	–	–	–	Yes	Yes	–	–	–	Yes	–	Ogle & Cheyne 1981
Whangamarino*	Inland bog, swamp, fen	–	Yes	–	Yes	Yes	Yes	Yes	Yes	–	Yes	M. Brady pers. comm. (DOC File No. DOCDM-2259562)
Hawke's Bay	Lowland swamps	Yes	Yes	–	Yes	Yes	Yes	Yes	Yes	–	Yes	J. Cheyne, Fish & Game, pers. comm.
Pukepuke Lagoon*	Coastal swamp	–	–	–	Yes	Yes	Yes	–	–	Yes	Yes	Lavers 1973; Roser & Lavers 1976; Moors & Lavers 1981; Clapperton et al. 1989, BKC unpubl. data
Western Wellington	Swamps and marshes	Yes	Yes	–	Yes	Yes	Yes	Yes	Yes	–	Yes	G. Falcon, Greater Wellington Regional Council, pers. comm.
Wairarapa	Small lakes, coastal swamps	–	Yes	–	Yes	Yes	Yes	–	–	Yes	Yes	S. Playle, Greater Wellington Regional Council, pers. comm.
Rotoiti Nature Recovery Project	Lateral moraine kettle holes	–	–	–	–	–	Yes	Yes	Yes	–	–	M. Maitland, Auckland Regional Council, pers. comm.
Styx River wetlands	Coastal swamp	–	Yes	Yes	–	–	–	–	–	Yes	Yes	Langlands 1990
Travis Swamp*	Coastal swamp	–	Yes	–	–	Yes	–	–	Yes	–	–	Morgan 2002
Lake Ellesmere	Coastal swamp and brackish reedbeds	–	–	–	Yes	Yes	–	–	–	–	Yes	Fitzgerald 1964
Lake Ellesmere	Coastal swamp and brackish reedbeds	–	Yes	–	–	–	Yes	–	–	–	Yes	Lettink 2007
Waitangitoana	Swamp forest	–	–	–	–	Yes	–	–	–	–	–	Miller 2001

Table 4 continued

Wetland site	Type	Dog	Cat	Mustelids	Ferret	Stoat	Weasel	Ship rat	Norway rat	Rat species	Hedgehog	Source
Ruataniwha wetlands*	Inland swamp and ponds	–	Yes	–	Yes	Yes	–	–	Yes	–	Yes	Anderson 2007
Cooks	Swamp, marsh	–	–	–	–	Yes	Yes	–	Yes	–	Yes	T. Riding, Environment Southland, pers. comm.

scale studies. For example, at Pukepuke Lagoon, more weasels than stoats were caught during live-trapping experiments on ferrets (Clapperton et al. 1989; BKC, unpubl. data), while at Nukuhou wetland, Ohiwa Harbour, the opposite was true in kill traps every year from 2005 to 2012 – in total 184 stoats to 86 weasels in a ferret-free area (S. Slade, unpubl. data). It is important to note that predators might not be caught in numbers proportional to their own abundance because trapping techniques may favour one species over another and their relative importance as predators of different bird species is unknown.

Behaviour of predators in wetlands

The presence of predator species in wetlands per se provides little information with which to assess the relative importance of impacts or to design effective control programmes. Studies of the ecology and behaviour of predators in New Zealand wetlands have been limited, short term, and usually single species focused. Few systematic studies of habitat use by predators have been undertaken (Recio & Seddon 2013; Recio et al. 2013); our limited understanding often relies on anecdotes, such as Pierce's (1986) observation that fewer ferrets, cats, and Norway rats were trapped in swamp than by ponds or side streams around the Cass River, South Canterbury. How such observations really reflect distribution patterns is unknown and alternative explanations, such as differential ability to trap species in swamps, need to be explored. However, ecological studies are needed if predator control is to be undertaken because knowledge of factors such as spacing behaviour, movements and dispersal is fundamental to designing effective management strategies.

It is well known that all the predators can swim (Pierce 1987; Pascoe 1995; Veale 2013) and stoats can colonise islands possibly up to 5 km from the mainland (King et al. 2014). However, the extent to which different species cross water is uncertain. On rivers, channels limit the extent to which some species, particularly ferrets and hedgehogs, disperse to islands that may support nesting birds (Pascoe 1995). Radio-tracking studies in predominantly terrestrial systems indicate that predators stray into wetlands and prey on wetland species. For example, in Hawke's Bay, cats in farmland also made use of swamps and were recorded preying on paradise ducklings and mallard ducks at a willow-fringed small pond (Langham & Porter 1991; Langham 1992). At Travis Wetland in Christchurch, Morgan (2002) found that domestic cats mainly used the periphery of the wetland, but could travel 200 m into it. They appeared to prefer habitat that provided shelter including tall grass, rushes, sedges and trees and used walking tracks and crossed drains, ditches and swales by either jumping or moving around them (Morgan 2002). Thus, the

notion that fluctuation in prey abundances in the surrounding habitat matrix influences how often predators enter wetlands and hunt alternative prey needs to be investigated.

There is also little information on density and spacing behaviour of predators in wetlands. At Pukepuke Lagoon, a swampland within the dune country of coastal Manawatu, male and female ferrets maintained territories in the wetland, at least in the non-breeding season, but female home ranges were smaller and overlapped more (Lavers 1973; Moors & Lavers 1981). At Pukepuke, home ranges of ferrets were smaller and overlapped less than those of ferrets in the semi-arid rabbit-prone zones of the South Island (Norbury et al. 1998a). Information on spatial behaviour and its temporal variability is needed to determine how predation risk varies, to indicate optimal timing of predator control and to design trap or bait station layouts that maximise the probability of predators being killed.

Compared with cats and ferrets, even less is known about stoats, weasels, hedgehogs, and rats in wetlands. Although Norway rats tend to favour wetland habitats (Innes 2005), ship rats may be more of a problem in some areas because they can dominate in some wetlands (see above). Hedgehogs have been tracked crossing marshy areas and patches of standing water that would have required them to swim (Jones & Norbury 2006; Shanahan et al. 2007) and were frequently captured in the traps set for ferrets around the swamp lands of Pukepuke Lagoon (Clapperton et al. 1989).

The diets of predators in wetlands appear to be diverse and the relative proportion of the diet that consists of birds variable (Fitzgerald 1964). For example, the diet of ferrets at Pukepuke Lagoon consisted of rabbits, rodents, and birds supplemented by frogs, carrion, fish, and invertebrates. Birds included Passeriformes, rails, ducks, and unidentified eggs (Roser & Lavers 1976). While domestic cats visiting Travis Wetland mainly ate rodents, 20% of food items were birds, which were mostly exotic species including mallard (*Anas platyrhynchos*) ducklings, but included fantail (*Rhipidura fuliginosa*), kingfisher, and welcome swallow (Morgan 2002).

Some understanding of the risks that brushtail possums, roaming dogs, mice and feral pigs pose to wetland birds is also needed. Possums take adult birds and eggs, at least in terrestrial environments (Cowan 2005); roaming dogs can be very destructive to ground-dwelling wildlife (Taborsky 1988; Van't Woudt 1990) as can free-ranging wild pigs (Challies 1975; Meads et al. 1984; Onley 1982). The potential impacts of feral mice on birds have only recently been recognised (Cuthbert & Hilton 2004) and there has been no research done on the predatory impact of these pests in New Zealand wetlands.

Managing predators in wetlands

Lessons from coastal and riverine habitats

The same predators as prey on wetland bird species have a considerable impact on water bird populations in river and coastal habitats in New Zealand (e.g. Fitzgerald 1964; Pierce 1986; Dowding & Murphy 2001; Sanders & Maloney 2002; Keedwell 2005). For example, as a consequence of predation only 11–42% of banded dotterel nests fledged young on the Tekapo, Ohau and Ahuriri rivers (Rebergen et al. 1998). Thus lessons learnt from investigating the impacts of predators on braided rivers and their control are likely to be relevant to managing mammalian predators in wetlands.

Research on braided rivers indicates how varied mammalian predator density, and thus predation pressures, can be. The impacts of predation seem to depend not only on the numbers of each predator species at a site, but also on the prey present and their population fluctuations (Brown & Keedwell 1998; Cruz et al. 2013). Similarly, many predators are cryptic and detection probabilities depend partly on which detection devices are used (Pickerell et al. 2014). On braided rivers, ferret captures showed a strong bias towards certain microsites, whereas cat and hedgehog captures were relatively evenly spread over the Tasman Valley (Leseberg et al. 2006). At bird colonies, the presence of one predator may cause localised predation pressure. Sanders (1997) noted that ferrets make return trips to the same nest, and a single predator can destroy entire colonies of black-fronted terns (O'Donnell et al. 2010). Episodic pulses in predation pressure seem to be typical in other habitats (e.g. O'Donnell et al. 1996; Reardon et al. 2012).

Control techniques

There is a lack of information on how to mitigate the effects of introduced mammalian predators in wetlands. Authoritative texts on wetland management internationally have virtually no information on pest mammals (Streever 1999; Weller 1999; Falk et al. 2006), despite predation being considered a major factor affecting the breeding success of water birds, with mammalian predators often considered to be the most important (e.g. Kauhala 2004; Brook et al. 2005). Similarly, there is little specific guidance on predator control in wetlands in New Zealand (Watts & Peters 2010), probably because best practices have yet to be developed.

Direct control of predators in New Zealand wetlands using trapping and poisoning strategies is feasible, using best-practice techniques developed in forest and open habitats (e.g. O'Donnell et al. 1996; Alterio et al. 1997; Keedwell et al. 2002; Table 4) and applying new predator control technologies (such as new toxins and application methods; Dilks et al. 2011; Blackie et al. 2014) should also be considered and trialled in wetlands. However, application of best practice or new methods in wetlands needs to be trialled in conjunction with studies of productivity and survival of birds to properly gauge the effectiveness of different techniques.

In designing any pest control programme it is important to remember that predators can show behavioural responses to sudden declines in their primary prey (Pierce 1987; Rebergen 1993; Norbury et al. 1998b), with prey-switching causing serious pulses of predation on birds (Sanders 1997; Brown & Keedwell 1998; Murphy et al. 1998; White & King 2006). While there have been no studies of prey-switching by mammals in wetland habitats, Haselmayer and Jamieson

(2001) thought that the increased predation on pūkeko eggs in a raupō (*Typha orientalis*) swamp observed after rabbit haemorrhagic disease reduced the rabbit population most likely resulted from a shift in diet by Australian harrier. However, cats on the Freshwater wetlands, Stewart Island, did not eat more birds when rat abundance was low even though birds were the main alternative prey (Harper 2005). It is also important to remember that controlling predators can produce unforeseen effects, such as mesopredator release following control of top predators, or subsequent vegetation changes after the control of browsers (Norbury et al. 2013).

Indirect techniques of mediating predator numbers, such as water level management and safe habitat creation, may also have potential. Studies show that fewer mammalian predators are present on islands compared with the nearby mainland (Zoellick et al. 2005) and that smaller or more isolated islands are visited less frequently than larger or less-isolated ones (Heikkilä et al. 1994; Nordström & Korpimäki 2004; Zoellick et al. 2004). Man-made pontoons provide brown teal with safe roosting sites (BKC pers. obs.) but it is not known whether such devices enhance survival. Seasonal and human-induced-seasonal variations in water levels are likely to affect access and impact of predators on wetland birds (Duncan et al. 2008). Water level fluctuations in wetlands influence breeding success of birds directly via frequency of nest flooding (Desgranges et al. 2006), but water level fluctuations and drying of wetlands also influence potential access by ground-based predators (Anderson et al. 2000; Jobin et al. 2009). Polak (2007) found a significant positive relationship between water depth around the nest and breeding success in Eurasian bitterns (*Botaurus stellaris*). In this case, lower water levels allowed greater access by ground predators, but there may also have been a confounding relationship between depth of water and food availability (Gilbert et al. 2007).

There have also been few investigations of how the development of structures, such as roads or stopbanks, influences predation risk. It is known that predators use vehicle and walking tracks and bridges to move around, and cats, mustelids and rats will all nest in buildings (Fitzgerald 1964; Kristiansen 1998; Foresman 2001), so designing structures in certain ways may reduce potential invasions of wetlands.

It is likely that specific ecological processes within and around wetlands affect predation rates on wetland birds. These include fluctuations in prey abundances in the surrounding habitat matrix influencing how often predators enter wetlands and hunt alternative prey. Similarly, there may be impacts on wetland predators of predator control operations in adjacent habitat types. For example, predator control to protect kiwi (*Apteryx rowi*) in Okarito forest (Murphy et al. 2008) and white heron (*Ardea modesta*) at Waitangitōana (Miller 2001) may affect predator densities around nearby Three Mile, Five Mile and Okarito lagoons. Thus, to achieve protection of wetland communities it is likely that control should include adjacent ecosystem types and ultimately realise biodiversity benefits and efficiencies across the broader landscape (Bryce et al. 2011; Reardon et al. 2012).

Conclusions

Although predation on specialist wetland birds has been recorded frequently, predators appear numerous and diverse in wetlands, and they are responsible for a relatively high proportion of nest failures in similar species overseas, the

impacts of predators on long-term viability of these bird populations in New Zealand is uncertain. This review highlights an important gap in our knowledge of the impacts of introduced mammalian predators on biodiversity in New Zealand. Impacts occur through predation of adults, eggs and fledglings. Although these impacts on the long-term viability of populations of these species have not been quantified, we suggest the results of this review imply that impacts are likely to be considerable. Our examination of traits making freshwater wetland birds vulnerable to predation provides a broad framework for predicting which species are most likely to be affected. Autecological studies and adaptive pest management experiments would also provide data to construct population models, which could then be used to simulate population trajectories with and without management and expose the most vulnerable life history stages through sensitivity analysis (Keedwell 2004; Hegg et al. 2013).

If control of predators in wetlands is to be effective, knowledge of the behaviour, detection probabilities, and ecology of different predator species is also needed. Information on the relative distribution and densities of the various predator species, their diurnal and seasonal activity patterns, habitat use, and trappability is needed to guide the development of management techniques. It is likely that specific ecological processes within and around wetlands and predator control programmes in adjacent habitats affect rates of predation on wetland birds.

The review clearly shows that all predators known to impact on indigenous birds are widespread and abundant in wetlands, just as they are in other habitats. Monitoring methods for cryptic swamp birds have yet to be developed in New Zealand and are needed urgently if we are to begin assessing population trends. Although techniques are available for monitoring predators, these have yet to be tested in wetland situations, where behaviour of predators might differ from other habitats, or where terrestrial monitoring methods are simply not suitable.

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