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Predation and other factors currently limiting New Zealand forest birds

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Abstract: Holdaway (1989) described three phases of historical extinctions and declines in New Zealand avifauna, the last of which (Group III, declining 1780–1986) was associated with European hunting, habitat clearance, and predation and competition from introduced European mammals. Some forest bird species have continued to decline since 1986, while others have increased, usually after intensive species-specific research and management programmes. In this paper, we review what is known about major causes of current declines or population limitation, including predation, competition for food or another resource, disease, forest loss, and genetic problems such as inbreeding depression and reduced genetic variation. Much experimental and circumstantial evidence suggests or demonstrates that predation by introduced mammals remains the primary cause of declines and limitation in remaining large native forest tracts. Predation alone is generally sufficient to explain the observed declines, but complex interactions between factors that vary between species and sites are likely to be the norm and are difficult to study. Currently, the rather limited evidence for food shortage is mostly circumstantial and may be obscured by interactions with predation. Climate and food supply determine the number of breeding attempts made by herbivorous species, but predation by introduced mammals ultimately determines the outcome of those attempts. After removal of pest mammals, populations are apparently limited by other factors, including habitat area, food supply, disease or avian predators. Management of these, and of inbreeding depression in bottlenecked populations, is likely to assist the effectiveness and resilience of management programmes. At the local or regional scale, however, forest area itself may be limiting in deforested parts of New Zealand. Without predator management, the number of native forest birds on the New Zealand mainland is predicted to continue to decline.

Keywords: competition; disease; food supply; fragmentation; inbreeding depression; population limitation

Introduction

Populations decline, potentially to extinction, when the number of individuals lost through death or emigration is greater than the number recruited through birth or immigration (Caughley 1977; Caughley & Gunn 1996). However, when loss and recruitment rates are (probably temporarily) equal, the population is at equilibrium; the process determining the population size is then *limitation*, and any factor that can alter rates of birth, death, immigration or emigration and so alter the population size is potentially a *limiting factor* (Caughley & Sinclair 1994). Understanding factors that limit populations of any taxa is necessary for all population management, whether for restoring threatened species, setting harvest yields, or reducing populations of pests (Caughley 1977; Caughley & Gunn 1996). Factors limiting numbers of birds derive from generally complex interactions between evolved, intrinsic, species-specific attributes such as behaviour and demography, and external environmental factors such as food supply, competition and predation (Newton 1998).

In this context, New Zealand forest birds have much in common with those of other isolated islands, such as Hawaii, Mauritius and Madagascar (Diamond 1984; Steadman 2006; Cheke & Hume 2008). All four avifaunas evolved on an isolated land mass that lacked predatory mammals (Gibbs 2006; Tennyson 2010), and each had a unique history of environmental change resulting from human colonisation in the last 800–1000 years (Holdaway 1989; Atkinson & Milliner 1991; Bell 1991; Holdaway 1999; Worthy & Holdaway 2002). New Zealand birds have a well-known history of species loss. Nearly a third (at least 76 of 245) of bird species breeding in prehuman times in the New Zealand region (including oceanic islands) became locally or globally extinct after human arrival, including 41% of endemic birds. Extinction rates were higher

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again on the New Zealand mainland – 52% of North Island birds and 47% of South Island birds – where larger suites of mammalian predators and competitors were introduced (Holdaway et al. 2001; Worthy & Holdaway 2002).

Holdaway (1989) and Worthy and Holdaway (2002) described three phases of avian extinctions and declines, the last of which (Group III, declining 1780–present time) was associated with European hunting, habitat clearance, and predation and competition from introduced European mammals. Holdaway (1989) did not strongly apportion responsibility for declines among these possible factors or their interactions, but in later analyses concluded that predation was the most important throughout all three extinction phases, due to details of the known or inferred size, behaviour, and fecundity of prey, the predatory capabilities of introduced mammals including human hunters, and the timing of mammalian arrivals and prey declines (Holdaway 1999; Worthy & Holdaway 2002).

Ongoing declines and resultant small populations also characterise the present forest avifauna. Many species are endangered, threatened or declining (BirdLife International 2000; Hitchmough et al. 2007; Robertson et al. 2007), also threatening ecological processes such as pollination and seed dispersal (Kelly et al. 2010). Predation continues to be an obvious factor to consider as a key cause of declines inside large native forest tracts because predatory introduced mammals are still widespread there, and evidence for predation is widespread (e.g. Lovegrove 1992; Powlesland et al. 1995; McLennan et al. 1996; O'Donnell et al. 1996; Brown 1997). However, the 14 widely distributed pest mammals may also limit food supply for birds, since they include omnivores (e.g. brushtail possum *Trichosurus vulpecula* and ship rat *Rattus rattus*), and herbivores (e.g. feral goat *Capra hircus* and red deer *Cervus elaphus*), as well as carnivores (e.g. stoat *Mustela erminea* and feral cat *Felis catus*) (Brockie 1992; Innes & Barker 1999; Atkinson 2001; King 2005; Forsyth et al. 2010). While evidence of predation may be clear in the form of a bird carcase, evidence for food shortage is mostly circumstantial (Newton 1998). Further, predation and food supply may interact, so in some cases both may contribute. For example, birds trade off predation risk against the need to feed (e.g. Beck & Watts 1997; Giesbrecht & Ankney 1998; Kullberg 1998); hungry birds take more risks than satiated ones (Koivula et al. 1995), and starving birds may be more vulnerable to infection by parasites and less able to avoid predators (Rohner & Hunter 1996; Klasing 1998). In this way, deaths caused proximally by predation or parasitism may in fact be due ultimately to food shortage (Rohner & Hunter 1996; Rolstad & Rolstad 2000).

Deforestation, intensification of productive land use, and urban development have reduced a once-continuous New Zealand forest cover to scattered, small fragments (Meurk & Swaffield 2000). These changes influence bird feeding, breeding and dispersal (Newton 1998). Predation may thus also interact with habitat fragmentation, and other factors, such as disease and weather (Newton 1998). Disease itself, which has had a major impact on the Hawaiian avifauna (Warner 1968), has been raised as a possible cause of decline of New Zealand birds. Small populations themselves may have genetic problems, such as inbreeding depression (Jamieson et al. 2006). If habitat area, food supply or inbreeding limit population size or growth rate, either by themselves or with predation as an proximate factor, then implementation of predator control alone to recover the population may be less effective or even entirely ineffective. Finally, if predator control removes predation as a limiting factor, further population enhancement will be possible only if the factors that next limit the population in its new equilibrium state can be understood.

This paper reviews evidence about the relative roles of predation and other factors in current New Zealand forest bird declines and limitation. Such a review has not been attempted since King (1984). Although predation is usually assumed to be the default explanation for bird declines in New Zealand, it is important to ensure that other factors, alone or in interaction, are also carefully evaluated. A review is also required to focus future research, and to ensure the active restoration of forest birds on the New Zealand mainland that has characterised the last two decades (Clout & Saunders 1995; Craig et al. 2000) can be sustained or increased.

Forest birds

For the purposes of this paper, we define a forest bird as a species or subspecies whose individuals are found mostly in forest communities throughout their range and life cycle (Innes & Hay 1990; Table 1). We include whio or blue duck, kakapo and weka (for scientific names of included forest birds, see Table 1) among these 50 taxa, but exclude New Zealand falcon (*Falco novaeseelandiae*), kea (*Nestor notabilis*), takahe (*Notornis mantelli*), and seabirds that nest in forests but feed at sea. We include taxa from Chathams, Three Kings and Poor Knights islands.

Many of these taxa have either small or declining populations. Range contraction is potentially an important signal of population decline (Caughley & Gunn 1996). Fortunately, our review was preceded by publication of the second Atlas of New Zealand bird distribution (Robertson et al. 2007). That document's 1999–2004 field work enables comparison with the distributions revealed from the 1969–79 field work reported in the first Atlas (Bull et al. 1985). While care is required with interpreting differences (in particular, the Atlases map presence but not abundance, and invasion of new habitat may mask disappearance from an original one), the 20 to 35 year span between surveys is sufficiently large to reveal the influence of a persistent decline factor, should there be one.

Two (Three Kings and Poor Knights bellbirds) of the 50 taxa are naturally range-restricted, but 35 others (77%) are either classified with some conservation concern according to New Zealand Department of Conservation (Hitchmough et al. 2007) or have declined in distribution between the first and second Atlases. Of these, the 22 taxa whose New Zealand mainland (North, South and Stewart islands) distributions can be compared between Atlases now average only 15.3% occupancy of available grid squares in the most recent Atlas, indicating widespread reduction of historical ranges (Fig. 1). Figure 1 indicates that while some forest birds have small but apparently stable distributions, others have larger distributions but are still declining. The remaining 11 mapped mainland taxa (hollow symbols; labelled 'secure' in Fig. 1) that have no threat ranking and whose distribution has not declined between Atlases occupy 58.1% of atlas squares on average. Buff weka is in fact extinct throughout its original mainland range, but is abundant on the Chathams Islands where it was introduced (Beauchamp et al. 1999). Chathams Islands forest birds share a similar plight to mainland taxa; only one (fantail) of the six lacks a conservation concern classification.

Causes of decline or limitation

Steps to determine the cause or causes of a species' decline are:

Table 1: Common name, scientific name, New Zealand threat classification, and 1979–2004 distribution change of New Zealand forest birds. Nomenclature and sequence largely follow the Checklist of the Birds of New Zealand (OSNZ 1990), with additional taxonomy of Tennyson et al. (2003) for kiwi and Miller and Lambert (2006) for *Petroica*. The New Zealand threat classification is the 2005 listing of Hitchmough et al. (2007). Qualifiers are: CD conservation dependent; DP data poor; EF extreme fluctuations; HI human induced; OL one location; RC recovering; RF recruitment failure; ST stable. The distribution change shows changes in Atlas distribution of taxa listed in Bull et al. (1985; data collected 1969–79) and in Robertson et al. (2007; data collected 1999–2004), from Robertson et al. (2007, Appendix K). Taxa not separately listed in one or both Atlases, preventing assessment of distribution change between the time periods, are left blank. Abbreviations: NI North Island, SI South Island.

Species	Subspecies	Scientific name	NZ threat classification and qualifiers	Distribution change (1979–2004)
NI brown kiwi		*Apteryx mantelli*	Serious decline HI, RF, CD	Decrease
Southern tokoeka		*Apteryx australis*	Gradual decline HI, RF, DP	No change
Rowi		*Apteryx rowi*	Nationally critical CD, RF, OL	
Haast tokoeka		*Apteryx* 'Haast'	Nationally critical CD, RF, OL	
Little spotted kiwi		*Apteryx owenii*	Range restricted RC, HI	
Great spotted kiwi		*Apteryx haastii*	Gradual decline RF	No change
Blue duck/whio		*Hymenolaimus malacorhynchos*	Nationally endangered HI	Decrease
Weka	Western weka	*Gallirallus a. australis*	Serious decline HI, RF	Decrease
	North Island weka	*Gallirallus a. greyi*	Nationally endangered HI, EF	Decrease
	buff weka	*Gallirallus a. hectori*		
	Stewart Is weka	*Gallirallus a. scottii*	Nationally endangered HI, ST	No change
NZ pigeon/kereru	NZ pigeon	*Hemiphaga n. novaeseelandiae*	Gradual decline RF	Increase
	Chatham Is. pigeon	*Hemiphaga n. chathamensis*	Nationally critical CD, RC, HI, OL	
Kakapo		*Strigops habroptilus*	Nationally critical CD, HI	No change
Kaka	NI kaka	*Nestor meridionalis septentrionalis*	Nationally endangered HI	Decrease
	SI kaka	*Nestor m. meridionalis*	Nationally endangered HI	Decrease
Red-crowned parakeet	red-crowned parakeet	*Cyanoramphus n. novaezelandiae*		Decrease
	Chatham Is. r-c parakeet	*Cyanoramphus n. chathamensis*	Range restricted HI	
Yellow-crowned parakeet		*Cyanoramphus auriceps*	Gradual decline HI, EF	No change
Forbes' parakeet		*Cyanoramphus forbesi*	Nationally endangered CD, RC, HI, OL	
Orange-fronted parakeet		*Cyanoramphus malherbi*	Nationally critical HI, EF	
Shining cuckoo		*Chrysococcyx lucidus*		Decrease
Long-tailed cuckoo		*Eudynamys taitensis*	Gradual decline DP, HI	Decrease
Morepork		*Ninox novaeseelandiae*		No change
Rifleman	NI rifleman	*Acanthisitta chloris granti*	Gradual decline DP, HI	Decrease
	SI rifleman	*Acanthisitta c. chloris*	Gradual decline DP, HI	Decrease
Whitehead		*Mohoua albicilla*		No change
Mohua		*Mohoua ochrocephala*	Nationally endangered HI, EF	Decrease
Brown creeper		*Mohoua novaeseelandiae*		Decrease
Grey warbler		*Gerygone igata*		No change
Chatham Is. warbler		*Gerygone albofrontata*	Range restricted ST, HI	
Fantail	NI fantail	*Rhipidura fuliginosa placabilis*		No change
	SI fantail	*Rhipidura f. fuliginosa*		No change
	Chatham Is. fantail	*Rhipidura f. penita*		
Tomtit	NI tomtit	*Petroica macrocephala toitoi*		No change

Table 1 continued

Species	Subspecies	Scientific name	NZ threat classification and qualifiers	Distribution change (1979–2004)
	SI tomtit	*Petroica m. macrocephala*		Decrease
	Chatham Is tomtit	*Petroica m. chathamensis*	Nationally endangered RC, HI	
NI robin		*Petroica longipes*		Increase
SI robin		*Petroica australis*		No change
Black robin		*Petroica traversi*	Nationally critical ST, HI	
Silvereye		*Zosterops lateralis*		No change
Hihi/stitchbird		*Notiomystis cincta*	Nationally endangered HI, OL	
Bellbird	Three Kings bellbird	*Anthornis melanura obscura*	Range restricted ST, OL	No change
	Poor Knights bellbird	*Anthornis m. oneho*	Range restricted ST, OL	No change
	bellbird	*Anthornis m. melanura*		Increase
Tui	tui	*Prosthemadera n. novaeseelandiae*		Increase
	Chatham Is tui	*Prosthemadera n. chathamensis*	Nationally endangered ST, HI, OL	
Saddleback	NI saddleback	*Philesturnus carunculatus rufusater*	Range restricted RC, HI	
	SI saddleback	*Philesturnus c. carunculatus*	Nationally endangered HI	
Kokako	NI kokako	*Callaeas cinerea wilsoni*	Nationally endangered CD, HI, RF	Decrease

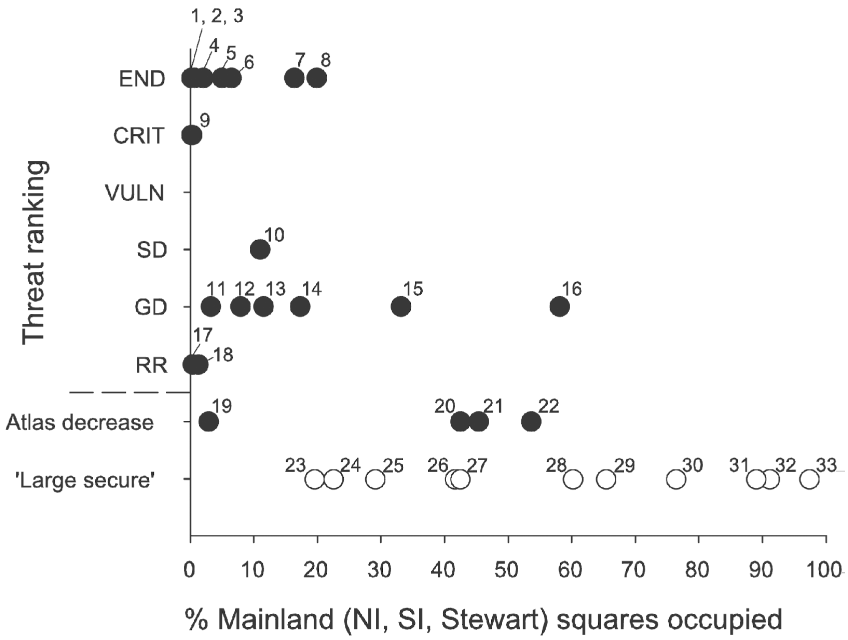

Figure 1. Threat status (Hitchmough et al. 2007) and mainland (North, South and Stewart Islands) distribution (Robertson et al. 2007) of extant forest birds. Percent squares occupied by taxa confined to either North or South Islands was calculated using the total number of squares in that Island only. Solid symbols indicate taxa with either a current threat classification (END = endangered; CRIT = critical; VULN = vulnerable; SD = serious decline; GD = gradual decline; RR = range restricted) or a known distribution decrease from the first bird distribution Atlas (Bull et al. 1985) to the second (Robertson et al. 2007) according to Robertson et al. (2007, App. K). Open symbols indicate secure taxa. Criteria for changed distribution were percent change in metric area combined with visual comparisons of ranges occupied in 1985 and 2007 (C.J.R. Robertson, *in litt*). The figure excludes taxa confined naturally to other islands including the Chathams because their distributions there were not mapped in one or both Atlases. Three mainland kiwi (southern tokoeka, Okarito brown kiwi, Haast tokoeka) are excluded because they are not mapped separately in Robertson et al. (2007). Taxa are: 1, SI saddleback; 2, kakapo; 3, hihi; 4, NI kokako; 5, blue duck; 6, mohua; 7, NI kaka; 8, SI kaka; 9, orange fronted parakeet; 10, NI brown kiwi; 11, great spotted kiwi; 12, yellow-crowned parakeet; 13, NI rifleman; 14, longtailed cuckoo; 15, SI rifleman; 16, NZ pigeon; 17, little spotted kiwi; 18, NI saddleback; 19, red-crowned parakeet; 20, brown creeper; 21, shining cuckoo; 22, SI tomtit; 23, NI robin; 24, SI robin; 25, whitehead; 26 NI, tomtit; 27, morepork; 28, tui; 29, bellbird; 30, SI fantail; 31, silvereye; 32, grey warbler; 33, NI fantail.

1. Confirm that species' abundance or distribution is actually declining.
2. Study the species' natural history to determine its ecology and the pattern of decline.
3. With adequate background knowledge, list possible agents of decline.
4. Look at the species' abundance with and without likely decline factors.
5. Challenge the hypothesised cause of decline by experiment, to show that the agent is causally associated with declines (Caughley & Gunn 1996).

However, in complex ecological systems, it is not always possible to manipulate only one factor. This is especially true in New Zealand, where many introduced mammals are both predators of birds as well as direct competitors for food. Thus, to the above list, we provide an additional step:

6. Perform manipulations accompanied by detailed research into demographic and ecological factors that link causal mechanisms to observed declines.

Similar steps can help identify what factors limit populations that are not necessarily declining. Newton (1998) reviewed potential population limitation mechanisms for birds worldwide, and noted that limiting factors are frequently complex and can vary from time to time and between sites. Furthermore, proximate causes of mortality, such as predation, may have underlying ultimate causes, such as poor habitat or food shortage that cause foraging in risky areas. He suggested that the primary limiting factor can be seen as the one that, once removed, allows the greatest increase in numbers. As with determining a cause of decline, this is best revealed by field experiments, especially those that closely examine ecological interactions that follow a manipulation. The strength of inference regarding the true cause of decline or limitation increases through these six steps.

The declines listed in Table 1 and Figure 1 are characteristically large-scaled and – on the mainland – ubiquitous across a species' range. Declining taxa have diverse life history strategies, feeding and nesting behaviours and body size. Explanatory factors must also be capable of operating on very large geographic scales and influencing diverse taxa in diverse habitats. In this paper we present evidence for predation, food supply and other factors in the following general order of increasing inference: (1) ecological and behavioural studies with no experiment, that suggest an important role for some factor; (2) bird abundance, demography or behaviour with and without the factor; and finally (3) population responses to experimental manipulation of the factor, with and without detailed research into the underlying mechanisms of change. To do this, we draw on numerous studies from the last two decades of research. This has been characterised by increased use of experimental manipulations – primarily pest mammal eradications and bird translocations – to test decline and limitation causes (Clout & Saunders 1995; Towns et al. 1997; Craig et al. 2000).

Predation

While Lack (1966) considered predation to be a negligible ultimate cause of mortality in most birds, it has since been recognised as a frequent limiting factor for populations (Newton 1998) and an important influence on the evolution of bird life-history traits and community assemblages (Martin 1988, 1992, 1995). The particular vulnerability of island avifaunas that evolved with few indigenous mammals to introduced mammal predators is now widely acknowledged (Atkinson 1989; Vitousek et al. 1997; Chapin et al. 2000; Mack et al. 2000; Steadman 2006; Cheke & Hume 2008).

Practically all birds are subject to predation, especially at the egg and chick stages, but predation can only be said to be limiting a prey population or causing its decline if the prey is not limited by another resource, such as territory space, food or nest sites; i.e. the bird population would increase if predation decreased (Cote & Sutherland 1997; Newton 1998).

Evidence that predation is affecting individual birds, and may be limiting populations, is collated in Table 2. Such evidence has frequently been detected in studies of New Zealand bird declines, as we will show below.

Table 2. Evidence consistent with limitation or decline of bird populations due to predation and food shortage, based on the reviews of Martin (1987) and Newton (1980, 1998).

	Evidence for predation	Evidence for food shortage
Individual level	Removed, killed or eaten remains of eggs, chicks or adults. Re-laying, and extended nesting season. Predator removal increases nest success, egg, chick or adult survival	Starvation of chicks or adults (low weight, no body fat, emaciated tissue). Non-laying. Small eggs. Egg desertion. Small clutches. Poor hatching success. Poor chick growth. Reduced number of nesting attempts per season. Weight loss. Reduced feeding rate and food intake. Increased proportion of time spent feeding. Fighting over food. Adding extra chicks increases brood mortality. Removing chicks reduces brood mortality. Supplemental food advances laying date or increases hatching success, chick weight, chick survival, or mean number of young fledged per attempting pair.
Population level	Poor egg, chick or adult survival, spatially or temporally correlated with high predator numbers or predator arrival. Predator removal increases population size. Excess of the non-vulnerable gender or age-class in population.	Poor egg, chick or adult survival, spatially or temporally correlated with food reduction or competitor arrival. Food addition increases population size. Excess of the gender with greater access to food.
Other evidence	Predators abundant. Prey confirmed in predator diet.	Food stock severely depleted. Confirmed deficiency (energy, nutrient, micro-nutrient) in food supply.

Detailed autecological field studies of New Zealand birds

Detailed autecological field studies frequently point to behavioural or demographic clues to a threatened species' predicament, or to the vulnerability of island species should mammalian predators arrive there. Notwithstanding that historically New Zealand birds were subject to significant predation by avian predators (Lee et al. 2010), some unfortunate attributes that increase vulnerability to mammalian predation have been known for many years, such as naivety about mammalian predators, inappropriate defence behaviours, tameness, inquisitiveness and flightlessness (McDowall 1969; Gibb & Flux 1973; Moors 1983; Holdaway 1989; Bell 1991; Lovegrove 1992; Maloney & Mclean 1995).

Nesting success of birds in mainland forests without mammal pest control is usually low, and many more nests fail from predation than desertion. Mean 'apparent nesting success' (% located nests which fledged at least one young) from 24 studies was 27 ± 15% (mean ± SD; Table 3). On average, 46 ± 18% (n = 22 studies) of all nests or eggs failed due to predation (cf. desertion 7 ± 6%, n = 21), and predation caused 61% of *known* failures. These data exclude kiwi, whose chicks rapidly leave the nest site and are nearly all killed elsewhere (McLennan et al. 1996).

Many nests fail before they are located at all, so the true failure rate would have been higher than measured in most of these studies (Brown 1997; Armstrong et al. 2002b).

Table 3. Apparent nest success of New Zealand forest birds without predator management. Apparent nest success is defined as the % of located nests or eggs fledging at least one young, over all study years. Predations in column 5 include loss of eggs, chicks, or adults so long as the nesting attempt ended. Nests in which chicks apparently starved and eggs that failed to hatch are included as desertions in column 6. Desertions caused by human nest disruption or disturbance are excluded from the table. For brown and great spotted kiwi, fledging rates given are hatching rates. An asterisk in column 1 indicates taxa with populations that have no conservation concern ranking and have not declined between the last two New Zealand bird distribution atlases, according to Figure 1.

Species	Location, date	N nests# or eggs*	N nests or eggs fledging young (%)	N failed by predation (%)	N failed by desertion (%)	N failed, other or unknown cause (%)	N with unknown fate (%)	Known failure due to predation	Reference
Bellbird	Craigieburn, 1999–2001	14 #	6 (43%)	6 (43%)	0	2 (14%)	0	75%	Kelly et al. 2005
Bellbird	Kowhai Bush, 1998–2004	42 #	9 (21%)	15 (36%)	3 (7%)	3 (7%)	12 (29%)	71%	J. Briskie, in Poirot 2004
Brown creeper	Kowhai Bush, 1975–77	11 #	1 (9%)	8 (73%)	0	0	2 (18%)	100%	Moors, 1983
Brown creeper	Kowhai Bush, 1979–82	154 *	55 (36%)	76 (49%)	Unk.	Unk.	Unk.	Unk.	Cunningham 1985
Brown kiwi	Many, 1987–1995	74 *	26 (35%)	2 (3%)	15 (20%)	31 (42%)	0	4%	McLennan et al. 1996
Great spotted kiwi	Northwest Nelson 1987–90	18 #	7 (39%)	0	0	9 (50%)	2 (11%)	0%	McLennan & McCann 1991
Grey warbler*	Kowhai Bush, 1976–79	260 *	100 (38%)	78 (30%)	21 (8%)	61 (24%)	0	49%	Gill 1982
Kereru	Pelorus Bridge, 1984–1991	45 #	10 (22%)	14 (31%)	3 (7%)	18 (40%)	0	40%	Clout et al. 1995
Kereru	Maungatapere, 1991–1993	31 #	6 (19%)	12 (39%)	1 (3%)	12 (39%)	0	48%	Pierce & Graham 1995
Kereru	Wenderholm, 1988–90	20 #	0	12 (60%)	3 (15%)	5 (25%)	0	60%	Clout et al. 1995
Kereru	Whirinaki, 1998–2002	21#	11 (52%)	4 (19%)	2 (9.5%)	4 (19%)	0	40%	R. Powlesland DOC, Pers. comm.
Kokako	Rotoehu, 1990–94	65 #	11 (17%)	32 (49%)	8 (12%)	14 (22%)	0	73%	Innes et al. 1996
Kokako	Mapara, 1997–2000	75 #	9 (12%)	39 (52%)	Unknown	27 (36%)	0	62%	Flux et al. 2006
Mohua	Eglinton Valley, 1984–88	87 #	48 (55%)	6 (7%)	0	33 (39%)	0	15%	Elliott 1996
NI kaka	Whirinaki, 1998–2002	32 #	12 (37%)	10 (31%)	5 (16%)	5 (16%)	0	50%	R. Powlesland DOC, Pers. comm.
NI robin*	Waimanoa, 1996–97	35 #	5 (14%)	25 (72%)	0	5 (14%)	0	83%	R. Powlesland DOC, Pers. comm.
NI robin*	Tahae, 1995–96	18 #	4 (22%)	10 (56%)	2 (11%)	2 (11%)	0	71%	R. Powlesland DOC, Pers. comm.
NI robin*	Tahae, 1997–98	67 #	21 (31%)	37 (55%)	2 (3%)	7 (10%)	0	80%	R. Powlesland DOC, Pers. comm.
NI robin*	Kaharoa, 1993–94	45 #	7 (15%)	26 (58%)	4 (9%)	8 (18%)	0	68%	Brown 1997
SI fantail*	Kowhai Bush, 1975–76	40 #	14 (35%)	17 (43%)	0	0	9 (22%)	100%	Moors 1983
SI fantail *	Kowhai Bush, 1976–78	546 *	252 (46%)	130 (24%)	5 (1%)	40 (7%)	119 (22%)	74%	Powlesland 1982
SI robin*	Kowhai Bush, 1975–77	46 #	6 (13%)	31 (68%)	8 (17%)	0	1 (2%)	79%	Moors 1983
SI robin *	Kowhai Bush, 1977–79	405 *	107 (27%)	212 (52%)	41 (10%)	25 (6%)	20 (5%)	76%	Powlesland 1983
NI tomtit*	Kaharoa, 1993–94	30 #	2 (7%)	21 (70%)	3 (10%)	4 (13%)	0	88%	Brown 1997
			Mean 27%:	Mean 46%:	Mean 7%:	Mean 20%		Mean 61%	

True predation rates would also be higher because the many failures attributed to an 'unknown cause' would include some predations. Furthermore, interference by predators can cause desertion, egg damage and falling out of nests by eggs and chicks (e.g. Innes et al. 1999). Mean nest success of taxa deemed 'secure' in Figure 1 (25 ± 12%; n = 9) is not significantly different from mean nest success of taxa with 'small or declining' populations (28 ± 16%; n = 16; $t = -0.57$, $P = 0.57$), which suggests the different population trends of these two groups cannot be attributed to different predation rates at nests.

The predation rates at nests listed in Table 3 will have different actual impacts on populations, depending on the demography of each species. For kiwi, for example, the low predation rate of eggs does not prevent population decline, since hatching rates are low (≤31%, largely due to desertion and embryo death), and more than 90% of chicks die before reaching adulthood (McLennan et al. 1996). For mohua (yellowhead), population modelling suggests loss of adult females has far more effect on mohua population trends than does loss of eggs and young (Elliott 1996).

Behavioural factors predisposing birds to predation, such as tameness, naivety, flightlessness, ground feeding and ground and cavity nesting, vary in their importance depending on the predator species (Lovegrove 1996b; Hooson & Jamieson 2003). The vulnerability to predation of hole-nesting and hole-roosting species was noted for saddleback (tieke) (Lovegrove 1992; Hooson & Jamieson 2003), kaka (Beggs & Wilson, 1991; Moorhouse et al. 2003; Greene et al. 2004), kakariki (Taylor 1985; Elliott et al. 1996), and mohua (Elliot 1990). For all these species, only the female incubates, so predation at nests can cause an excess of males in the surviving population (e.g. kaka, Greene & Fraser 1998; Greene et al. 2004), and all are relatively long-lived (Kelly & Sullivan 2010), so the loss of females is expected to have large effects on population size.

The risks of predation by introduced mammals on some endemic birds such as mohua are increased both by long incubation periods and by nesting in late summer when predators are abundant (O'Donnell 1996). Black tits (*Petroica macrocephala dannefaerdi*) on the Snares Islands often selected nest sites close to the ground, with only one entrance, situations that would make incubating females vulnerable to any mammalian predator that managed to establish there (McLean & Miskelly 1988). Feeding on the ground is risky if predators, such as cats, are present. Frequently, radio-tracked kereru at Whirinaki Forest, central North Island, were killed by cats when going to water sources on the ground to drink (Powlesland et al. 2003). Many young kaka are killed on the ground in the first few days after fledging at sites with no pest control (Greene et al. 2004). Finally, neither cryptic colouration nor nocturnal habit (e.g. kakapo, Elliott et al. 2001; kiwi, McLennan et al. 1996) are effective protection against mammalian predators, although they are presumably effective against diurnal raptors that hunt by sight.

Kearvell et al. (2002) showed that orange-fronted parakeets forage nearer to the ground than the more widespread yellow-crowned parakeet, which may increase the predation risk to the former. Yellow-crowned parakeets in the Eglinton Valley have greatly-extended breeding when beech trees seed heavily, but the nests are very vulnerable to predation by stoats and ship rats because they are in holes from which the birds cannot escape, and because the chicks are very noisy just before feeding (Elliott et al. 1996).

Prey size itself is apparently an important determinant of predation outcomes. Brown kiwi are vulnerable to stoat predation until reaching a safe weight of about 800 g after about 110 days (McLennan et al. 2004). The smallest kiwi species (little spotted kiwi) is also the rarest, and confined to predator-free offshore islands, although recently reintroduced to a pest-free mainland sanctuary (Karori Sanctuary, Wellington; http://www.massey.ac.nz/~darmstro/nz_projects.htm accessed December 2008). McLennan et al. (2004) suggested that the extra 200 days required for this species to reach safe weight could account for its rapid and complete disappearance from the mainland in historic time. The three rat species in New Zealand (from smaller to larger: kiore *Rattus exulans*, ship rat, Norway rat *Rattus norvegicus*) have different behaviours, but also can tackle increasingly larger prey (Atkinson 1986; Holdaway 1999). Frequently, ship rats (mean weight 146g; Innes 2005) kill adults of small nesting birds such as robins (35 g), tomtits (11 g) and fantails (8 g), but they cannot kill adult kokako (230 g) (Innes et al. 1996; Brown 1997; Mudge 2002; bird weights from Heather & Robertson 1996).

Abundance, demography and behaviour on the mainland compared with islands

The persistence, increased abundance, or altered demography and behaviour of bird species on islands lacking all or most introduced mammals demonstrate interaction between birds and mammals, although the causal ecological mechanism (predation vs. competition) may be unclear without experiment.

The strongest interactions between birds and mammals are evident for those taxa formerly widespread on the mainland (little spotted kiwi, kakapo, hihi, North Island and South Island saddlebacks, plus numerous forest-nesting seabirds; OSNZ 1990), but now confined to islands (Bellingham et al. 2010) or predator-proof mainland sanctuaries. There is no evidence to suggest the symptoms of food shortage listed in Table 2 were primarily responsible for the mainland declines of any of these species, whereas the birds' vulnerability to predation has been well documented (Williams 1977; Mills & Williams 1979; Jolly & Colbourne 1991; Lovegrove 1992; Roberts 1994; Powlesland et al. 1995; Lovegrove 1996a; Armstrong et al. 1999; Hooson & Jamieson 2003).

The sequential arrival of pests on islands occasionally allows deduction of links between causes and effects. Ship rats spread rapidly on Big South Cape Island near Stewart Island after August 1962, and within 2 years had substantially reduced bird numbers at the northern end of the island. Rat numbers remained high for 3 years, after which nine landbird species had declined or disappeared, including South Island saddleback, Stead's bush wren and Stewart Island snipe (Atkinson & Bell 1973; Bell 1978). The rapid extirpation of species and the breadth of diets of the birds involved both suggest predation as the key mechanism.

Three taxa (North Island [NI] weka, buff weka, red-crowned parakeet) were formerly widespread on the mainland, but now occur mainly on islands. Red-crowned parakeets are abundant on many islands lacking all mammalian predators (Taylor 1985), but elsewhere are very susceptible to cats, stoats and ship rats because they often feed on the ground and nest in holes near the ground (Greene 1998).

Populations of some bird species still widespread on the mainland have different abundance and/or demography compared with populations on islands lacking all or most introduced mammals. Increased abundance on islands implies different limiting factors there, but does not indicate what these may be, since there are many ecological differences between any island and the mainland. Bellbird density on the Poor Knights Islands was assessed at 71 per ha, 54 times the average mainland density (Bartle & Sagar, 1987). Clues to what factors may be limiting on the mainland come from knowing *why* abundance may be greater on islands.

Low predation rates on islands are usually responsible for the greater nesting success of large natural island populations compared with the unmanaged mainland, unless established by translocation with few founders, when genetic bottlenecks may reduce hatching success (e.g. Briskie & Mackintosh 2004; see genetics section below). On Hauturu (Little Barrier Island), 75–83% of monitored kokako pairs fledged young each year, while few pairs (<30%) attempting to nest in unmanaged mainland blocks fledged young (Innes et al. 1996). Sixty-three percent of kereru nests on the Chickens Islands succeeded to late fledging stage, compared with only 19% of Northland mainland nests (Pierce & Graham 1995). Of 140 red-crowned parakeet eggs on Hauturu, 39% produced fledged young; the major cause of mortality was starvation of 71 of 117 (61%) chicks, implying that food supply rather than predation limited the population on this predator-free (except at that time for kiore) island (Greene 2003). Bellbirds on predator-free Aorangi (Poor Knights Islands) had a high breeding success: 87% of 116 eggs laid in 42 nests successfully hatched, and 83% of 21 chicks in 8 nests fledged (Sagar 1985). On Tiritiri Matangi Island, 70% of eggs in 16 nests hatched, and 68% of chicks fledged, resulting in 49% apparent nesting success overall (Anderson & Craig 2003). Overall nesting success of North Island (NI) robins on Tiritiri Matangi Island during 1992–1999 was 51% (n = 176), but varied from 25% in 1992/93 to 70% in 1996/97. The major cause of nest failure was probably predation by other birds, particularly Indian myna (*Acridotheres tristis*), moreporks (*Ninox novaeseelandiae*) or harriers (*Circus approximans*). This reproductive success was greater than in unmanaged mainland populations, but less than that of a mainland Pureora population after mammal control (Armstrong et al. 2000). Fantail nesting success in the 1981/82 breeding season on Tiritiri Matangi was 59% (n = 22 nests; McLean 1984).

Occasionally, a close correlation between the presence of a particular pest species and the absence or paucity of a bird identifies the primary predator. Nationally, kaka are scarce on all islands with stoats, but they are relatively common on offshore islands without stoats, even in the presence of other predator and competitor species (Wilson et al. 1998). This cannot be a direct food effect, since the diets of stoats and kaka do not overlap, but stoats are known kaka predators.

Many island birds show behaviour that would render them vulnerable to mammalian predation on the mainland (see previous section). In contrast, no study has described a difference in food abundance or availability that may similarly explain why these species sometimes persist only on offshore islands.

Eradication or reduction of damage agents on islands and the mainland, without detailed research on species' responses

Measuring bird responses to the removal or reduction of a pest mammal can give some indication of the strength of interactions between the species involved. However, the cause(s) of the responses may be invisible without detailed ecological research, unless the pest control is conducted as an experiment (Moller 1989; Donlan et al. 2002; Armstrong et al. 2007). Unequivocal attribution of responses is particularly problematic when the pest is an omnivore (e.g. ship rat, Norway rat, kiore, brushtail possum), since its removal may decrease predation on the protected bird species, increase available food supply, or both. Interpretation is further complicated if multiple pest species are killed (Veltman 2000), and if regard is not given to the whole-community context of the species removal (Zavaleta et al. 2001), including such possible outcomes as mesopredator release (e.g. Rayner et al. 2007). As with predator arrivals, the sequential removal of pest mammal species has the potential to clarify their impacts on remaining birds and other fauna.

Possums were controlled and eventually eradicated on Kapiti Island (1965 ha) over two periods (1960–68, 1980–86). Tui, bellbird, robin, whitehead, kereru, kaka and weka all increased markedly on at least one count transect on Kapiti during the period of control and eradication (Lovegrove 1986; Veltman 2000), although the relative roles of predation and food supply as causes of these changes are unclear. Independent counts undertaken by the Ornithological Society confirmed overall increases (H. Robertson and T. Beauchamp, unpubl. data) in tui, bellbird, robin, whitehead, and kereru on most lines, but the trends were less clear for kaka and weka (H. Robertson and T. Beauchamp, unpubl. data). The small insectivorous grey warbler (H. Robertson and T. Beauchamp, unpubl. data) and fantail (Lovegrove 1986) may have declined at the same time. Grey warbler also declined during intensive multi-species pest control programmes at three mainland sites (Te Urewera National Park, Jones 2000a; Trounson Kauri Park, Pierce 2001; Motatau, Northland, Innes et al. 2004b), perhaps (in Te Urewera) because of increased competition for food from whiteheads (Jones 2000a).

In 1996, kiore and Norway rats were both eradicated from Kapiti Island by poisoning (Empson & Miskelly 1999). Ornithological Society bird counts suggest red-crowned parakeets, robins, saddlebacks, and bellbird increased most after the eradication. Rats (like possums) are omnivores, so the role of improved food supply in the increases of these species is uncertain. Parakeets were seen more frequently feeding on the ground after the eradication, suggesting decreased competition for fallen seeds and fruit (Miskelly & Robertson 2001). However, predation is a more likely mechanism, since vulnerability to predation explains the scale of increase shown by 4 of the 15 monitored species better than does a particular food or feeding behaviour. Only two species (tui and tomtit) declined after the eradications. Miskelly and Robertson (2001) hypothesised that these were perhaps outcompeted for some resource (probably food) by bellbird and robins respectively, suggesting that second-order, resource-based bird abundance changes began after predation limitation of other species was relaxed.

Complex food web interactions have sometimes delayed clear conclusions about whether a removed mammalian species limited other taxa. For example, contrary to expectation, the removal of cats from Hauturu during 1976–1980 was not followed by significant increases in forest bird numbers (Girardet et al. 2001), and predation on Cook's petrels actually increased (Rayner et al 2007). It was not until after the kiore were also eradicated that it became clear that kiore limited birds, especially breeding success of petrels, after the cat eradication, a case of mesopredation (Rayner et al 2007). Similarly, the 1990–97 eradications of possums and brushtailed rock wallabies (*Petrogale penicillata*) from Rangitoto Island were not followed by increases in bird populations (with the possible exception of silvereyes). The ship rats, stoats, cats and commercial honeybees that remained on the island may have sustained predation and/or food shortage, despite the removal of the two other herbivores (Spurr & Anderson 2004).

Interpretation of such cases is easier if research on mortality agents can identify likely predators beforehand. In the Tin Range, Stewart Island, in 1982, kakapo feathers were found in cat scats, and 7 of 13 radio-tagged adult kakapo were killed by cats. Mortality of adult kakapo declined sharply after cats were controlled (Powlesland et al. 1995), despite the continued presence of ship rats, Norway rats and kiore; and it stopped nearly entirely when 62 kakapo were transferred to cat-free Maud, Hauturu and Codfish Islands, despite kiore presence on the latter two (Powlesland et al. 2005).

Intensive and sustained control of several pest species simultaneously is now done at many mainland New Zealand sites, in attempts to meet species and ecosystem restoration targets (Clout & Saunders 1995; Craig et al. 2000; Atkinson 2002; Parkes & Murphy 2003; http://www.sanctuariesnz.org/projects.asp, accessed 18 January 2008). Most of these sites are unfenced, and therefore subject to constant reinvasion. The pioneering projects were initiated in 1995–96 by the Department of Conservation (DOC) and are known as 'mainland islands' (Saunders 2000; Saunders & Norton 2001). Many data have been collected, but few results published. An exception is Gillies et al. (2003), who describe significant seasonal increases in kereru abundance at Trounson Kauri Park, Northland, and high kiwi chick survival leading to increases in adult call counts.

Here, we present new analyses of five-minute bird counts (index counts that are related in an unknown way to absolute abundance; Dawson & Bull 1975) from four mainland islands that had either paired sets of counts in treatment and non-treatment (Hurunui in North Canterbury, Rotoiti in Nelson, and Boundary Stream in Hawkes Bay) or pre- and post-treatment counts (Trounson). For Trounson, the pre-treatment measurements were used in lieu of a non-treatment comparison. Species were classed as either native or exotic, and total abundance for each class was calculated for each five-minute count. For each mainland island, counts were grouped into time periods of generally one to several days, and always less than a week; and the relative difference between treatment and non-treatment were calculated for each time period. Each survey group consists of 20–50 x 5-minute bird counts. The relative difference was calculated as the treatment abundance minus the non-treatment abundance, divided by the mean abundance across all non-treatment measurements. Thus the relative difference provides a measure of the proportional increase in the abundance of birds in the treatment areas relative to the non-treatment areas. The data from the mainland islands were grouped into two categories, those with beech forest (Hurunui and St Arnaud) and those with podocarp forest (Trounson, Boundary Stream), and the relative difference was regressed against time since onset of treatment, using generalised additive models (GAMS). The package GRASP (Lehmann et al. 2002) was used to choose the degrees of freedom of the regression, using a stepwise procedure and AIC to test for significance, and cross-validation to assess model stability.

Overall, abundances of native bird species responded positively to treatment, while exotic species abundances showed no changes or weak declines. In the two DOC mainland islands in North Island podocarp-broadleaved forest (Trounson and Boundary Stream), the total abundance of native birds increased over time (proportion of deviance explained [D^2] = 41.3%, one degree of freedom, Fig. 2a) after treatment relative to nearby non-treatment sites. Conversely, the abundance of exotic birds showed no significant trend with time after treatment (Fig. 2c). In two South Island beech forest mainland islands (Hurunui and Rotoiti), the relative mean difference in total abundance of native birds between treatment and non-treatment areas showed a complex pattern of increase and subsequent variation through time (D^2 = 27.6%, six degrees of freedom, Fig. 2b). One plausible explanation is that this reflects the impacts of recurring beech masting events. However, a detailed examination of this result is beyond the scope of this paper. The abundance of exotic birds showed no significant trend with time after treatment (Fig. 2d).

The first predator-proof fence around a mainland sanctuary was completed in 1999 at 252-ha Karori Sanctuary, Wellington; since then, a further 8000 ha have been protected in a further 19 sites inside 93 km of fence (http://www.sanctuariesnz.org/projects.asp, accessed 18 January 2008). Some fences may yet be shown to sustainably stop all immigration by targeted pests, enabling permanent eradication or near-eradication inside them. The successful reintroductions of 11 species of forest birds to fenced sanctuaries (www.massey.ac.nz/~darmstro/nz; B. Burns, University of Auckland, pers. comm.) again suggests removal of pest mammals also removes the limiting factor; three species (little spotted kiwi, NI saddleback, hihi) were thereby restored to the mainland after a century of absence. Further experimental releases are required to establish the minimum residual abundance of pest mammals that can prevent reestablishment.

Detailed field study of species responses to monitored manipulations

The strongest evidence that a cause of decline has been identified has arisen from monitoring a bird's demographic response to manipulation of the hypothesised causative agent, usually by mammal pest control (Table 4). These manipulations vary greatly in the extent to which they have used strict scientific experimental procedures. Nearly all the manipulations resulted in improved life-history parameters for the study bird species, and many lessons were learned from all the trials. A review of mainly European and American predator-removal studies looking at native predators and their prey concluded that predator removal often increased bird hatching success and post-breeding populations, but rarely increased breeding populations (Cote & Sutherland 1997), but breeding populations of most New Zealand birds listed in Table 4 increased where this was measured. This is unsurprising given that these are native birds and non-native mammalian predators.

Raffaelli and Moller (2000) reviewed the design and impact of "community press" experiments in animal ecology (those involving alteration of the density of one or more animals), and concluded field experiments that produce weak inference at best should be supplemented by other research approaches, or perhaps not be carried out at all. Faced with species extinctions, New Zealand managers and scientists have invariably selected the former. Nearly all the manipulations listed in Table 4 were preceded by many years of basic ecological research exploring the demography, behaviour and pattern of decline of the species concerned. The trials themselves were then usually accompanied by detailed monitoring of outcomes. For example, mainland female kaka had greater nesting success, less predation at nests, and positive recruitment to the breeding population only in forests that received predator control. Furthermore, predation by stoats and possums was the

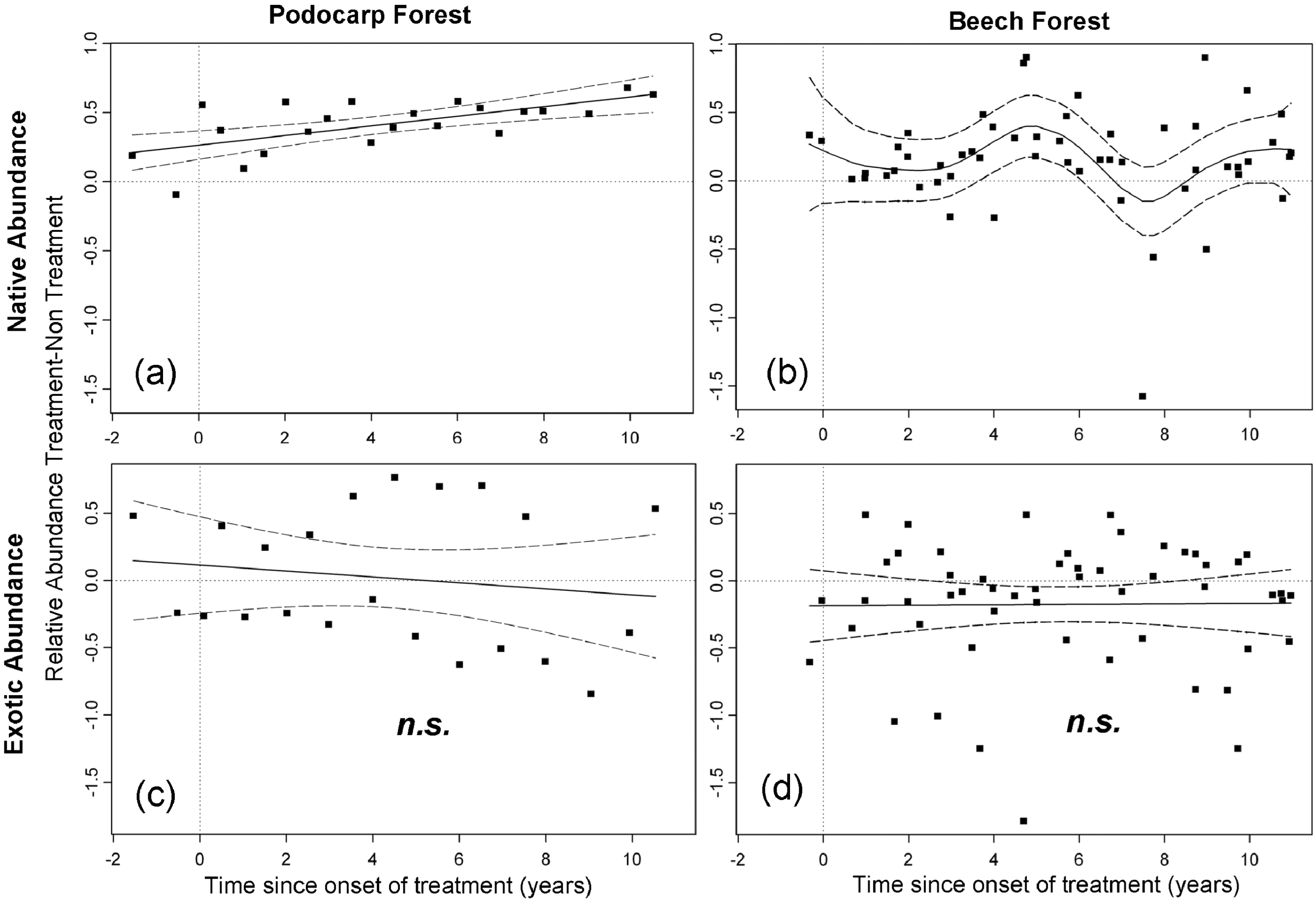

Figure 2. Overall responses of the abundance of forest birds to repeated pest mammal control in mainland islands. For all graphs, the relative abundance (treatment minus non-treatment) is graphed against time since onset of treatment. Graphs are: (a) Total native abundance in podocarp forest, (b) total native abundance in beech forest, (c) total exotic abundance in podocarp forest, and (d) total exotic abundance in beech forest. Each point on the graph represents the relative difference between a pair of survey groups in the treatment area and one or more nearby non-treatment areas. Curves are regressions with 95% confidence intervals fitted using generalised additive models (GAMs) using AIC to assess significance and choose degrees of freedom (e.g. non-linearity). Podocarp forest areas are Boundary Stream (Hawke's Bay) and Trounson Kauri Park (Northland); beech forests are Hurunui (inland Canterbury) and Rotoiti (Nelson Lakes National Park).

Table 4. Monitored manipulations undertaken to clarify causes of decline of mainland New Zealand forest bird species (subspecies aggregated), in checklist order, after Table 1.

Species	Year and site	Manipulation	Outcome for species	Reference
NI brown kiwi	1993–2002 Waikaremoana	Pest control	Juvenile survival increased	J. McLennan, Landcare Research, pers. comm.
	1994–1998 Northland	Rat and possum control – mustelids and cats secondarily	Juvenile survival increased	Robertson et al. 1999
	2000–2006 Whangarei	Mustelid control	Juvenile survival increased	Gardiner 2004, 2005, 2006; DOC 2006
	1996–2006 Trounson Kauri Park	Mustelid, cat, rat and possum control	Juvenile survival increased	Gillies et al. 2003, Anon. 2006
	2000–2005 Moehau	Stoat control	Juvenile survival increased	De Monchy & Forbes 2006
	2000 & 2006 Tongariro Forest	Aerial 1080	Juvenile survival increased	DOC 2006; Hood et al. 2007
	1996–2000 Northern te Urewera	Mustelid, rat and possum control	Juvenile survival increased	Burns et al. 2000
	1999–2007 Boundary Stream	Mustelid, cat, rat and possum control	Juvenile survival increased	Ward-Smith et al. 2006; Nakagawa 2007
Okarito brown kiwi	2001–2006 Okarito	Mustelid control, Operation Nest Egg (ONE) & Operation Chick Rescue	Juvenile survival increased for ONE birds only	Wickes 2006
Haast tokoeka	2001–2007 Haast	Mustelid control & Operation Nest Egg	Juvenile survival increased	Liddy 2007

Table 4 continued

Species	Year and site	Manipulation	Outcome for species	Reference
Blue duck	2004–2007 Manganui-o-te-Ao	Mustelid control	Nest success and adult number increased	Bristol et al. 2005, 2006, 2007
	2003–2005 Egmont National Park	Mustelid control	Adult survival increased	Caskey & Peet 2005
	1999–2007 Te Waiiti	Mustelid and possum control	Nest success and adult number increased	Glaser 2007; Moorcroft et al. 2007
	2002–2007 Takaputahi	Mustelid and cat control	Apparent nest success and adult number increased	Glaser 2007
	2002–2007 Oparara-Ugly	Mustelid control	Nest success and adult number increased	Elliott & Suggate 2007
	2003–2007 Wangapeka/Fyfe	Mustelid control	Adult survival increased	Anon. 2007c; Elliott & Suggate 2007
	2000–2006 Clinton, Arthur, Cleddau	Mustelid control	Juvenile survival increased	Whitehead et al. 2008
Weka	1992–94 Gisborne	Pest control	Uncertain	Bramley 1996
	1999–2007 Motu/Whitikau	Mustelid and cat control	Juvenile survival increased	Kemp 2007
NZ pigeon	1993–95 Wenderholm	Pest control	Increased nest success	James & Clout 1996
	1997–2000 Motatau	Pest control	Nest success and adult number increased	Innes et al. 2004b
Kakapo	1983–2007	Pest control, translocation, supplementary feeding	Nest success, adult survival and adult number increased	Powlesland et al. 2006
Kaka	1989–96 Nelson	Supplementary feeding	Uncertain	Wilson et al. 1998
	1994–2000 & 2004–2006 Waipapa	Rat and possum control – mustelids and cats secondarily	Increased adult survival, nest success and juvenile survival	Moorhouse et al. 2003; Dennis 2005, 2006
	1997–2005 Rotoiti	Mustelid, rat and possum control	Increased adult survival, nest success and juvenile survival	Moorhouse et al. 2003; Paton et al. 2007
	1998–2001 Eglinton	Mustelid control	Increased nest success and juvenile survival	Dilks et al. 2003; Moorhouse et al. 2003
Yellow-crowned parakeet	1990–93 Eglinton	Stoat control	No increase in nest success	Elliott et al. 1996
Orange-fronted parakeet	2003–2007 Hawden & Poulter	Mustelid, rat and possum control + nest protection	Increased nest success	Anon. 2007a; Elliott & Suggate 2007
	2006–2007 Hurunui South Branch	Mustelid, rat and possum control + nest protection	Increased nest success	Anon. 2007b; Elliott & Suggate 2007
Mohua	1990–93 Eglinton	Stoat control	Nest success and female survival increased	O'Donnell et al. 1996
	1999–2000 Eglinton	Stoat control	Increased nest success but year-round predation by ship rats	P. Dilks, DOC, pers. comm.
	1997–2007 Hurunui South Branch	Mustelid, rat and possum control	Increased nest success except in 1999–2000 rat plague year	Grant et al. 1998 ; Anon. 2007b ; Elliott & Suggate 2007
	2004–2007 Dart	Mustelid, rat and possum control	Increased nest success and adult survival	Elliott & Suggate 2007; Lawrence 2007
	2006–2007 Catlins	Mustelid, rat and possum control	Increased nest success	Elliott & Suggate 2007
Tomtit	1993–94 Kaharoa	Nest exposure	No change in predation rates	Brown 1997
NI robin	1993–94 Kaharoa	Nest exposure	No change in predation rates	Brown 1997
Bellbird	1999–2001 Craigieburn	Stoat control	Increased nest success	Kelly et al. 2005
Kokako	1989–97 Central NI	Pest control	Nest success and adult number increased	Innes et al. 1999

most common cause of nesting failure at all sites (Moorhouse et al. 2003).

Only one mainland manipulation (South Island (SI) kaka, Wilson et al. 1998) aimed to increase food quantity or quality, although supplementary feeding has been used more frequently on offshore islands when predators cease to be a limiting factor (see Food supply section below). Supplementary feeding of SI kaka failed to show whether shortage of high energy food limited breeding because most nesting attempts were ended by stoat predation (Wilson et al. 1998).

Projects that have increased kiwi, mohua, kaka and kakariki numbers through stoat, cat or ferret control strongly suggest the primary mechanism is predation rather than food supply because the mammal pests are carnivores whose diets barely overlap with those of their prey. However, frugivorous, herbivorous, insectivorous and nectivorous birds, such as kokako, kereru, tui or bellbird, may increase after control of the omnivorous ship rats and brushtail possums due to reduced predation, or increased food, or both. Detailed research of particular demographic parameters can tease these two mechanisms apart (e.g. Innes et al. 1999; Wilson et al. 1998).

The manipulations in Table 4 have usually proceeded through the first three logical components of a falsifications test (observation, explanation, prediction), but are weak on the final stage, a critical test capable of rejecting the hypothesis (Medawar 1969; Underwood 1990). This is frequently because the manipulations are of a whole ecological community, not just one component, and many complex interactions between community members may obscure the association between the manipulated pest and the featured threatened species (Yodzis 1988). Stoats – predators of NI kokako – ate more birds (all species) when ship rats were killed to protect kokako (Murphy & Bradfield 1992). This could have meant that stoats might substitute for rats as important predators of kokako, with the results that kokako numbers remained steady or even declined despite the removal of ship rats. However, detailed monitoring of the survival of colour-banded kokako suggested this did not in fact occur (Innes et al. 1999).

Ongoing research and management has sometimes revised the conclusions of earlier work. Research on mohua in the Eglinton valley, Fiordland, in the early 1990s concluded that "Mohua suffer periodic population crashes due to severe predation by the introduced stoat" (O'Donnell et al. 1996: 279) and stoat control has assisted mohua populations (Dilks 1999). Subsequent mortality monitoring indicates a greater role for ship rats than previously assumed (Dilks et al. 2003). At present, it is not possible to tell whether the high ship rat numbers observed since the mid-late 1990s were the consequence of (1) more than 4 years of low-intensity stoat control, or (2) three mild winters and two consecutive beech mast years 1999 and 2000 (P. Dilks, unpubl. data).

Likewise, in a 1989–97 study, ship rats and possums were key predators at nests of NI kokako (Innes et al. 1999). Ship rat and possum control ceased at Mapara Wildlife Reserve after 1997, and 12 of 31 banded kokako females were killed in nests during the 1998/99 and 1999/2000 breeding seasons, probably by stoats, despite high numbers of ship rats, their preferred prey in that habitat (Murphy & Bradfield 1992). Three possible explanations cannot be distinguished: (1) stoats became more abundant after ship rat and possum poisoning stopped; (2) resident stoats changed behaviourally to eat more kokako; (3) stoats were simply more abundant in these two seasons than previously (Basse et al. 2003). Ongoing experimentation and monitoring are needed to strengthen weak, single experiments in the long term; and benefits will be increased considerably if such work is accompanied by ongoing revision of quantitative models (Armstrong et al. 2007).

Predation by introduced mammals maintains mainland and some island bird populations below the density at which competition for food and other resources is an important influence on bird community structure, as first suggested by McCallum (1982). For example, grey warblers are the most widespread native bird on the New Zealand mainland (Bull et al. 1985), and among the most frequently detected in bird counts (e.g. Gill 1980; Harrison & Saunders 1981; Moffat & Minot 1994). They feed mainly by gleaning invertebrates from forest understoreys (O'Donnell & Dilks 1994). However, they are rare on Kapiti Island and Hauturu, which both lack predatory mammals (Diamond & Veitch 1981; Lovegrove 1986; Girardet et al. 2001; Miskelly & Robertson 2001; J. Innes et al. unpubl. data). Bellbird and whitehead are extremely common on both islands and, along with robins, may out-compete grey warblers. Grey warblers declined significantly when intensive mammal pest control was undertaken at three mainland sites (see previous section), despite predation by ship rats (one of the targeted pests) being the likely major source of grey warbler nest failure (Gill 1982). They also declined (and bellbirds increased) on Tiritiri Matangi Island after the 1993 eradication of kiore there (Graham & Veitch 2002). These outcomes indicate some strong interaction – perhaps food competition – between grey warblers and probably bellbird and whiteheads.

Similar interactions have been reported for other species at different locations. Four introduced bird species, plus fantails and silvereyes, disappeared or declined on Cuvier Island after the eradication of cats and goats and exclusion of domestic stock (Diamond & Veitch 1981; Lovegrove 1986). Silvereyes declined along with grey warblers on Tiritiri Matangi Island after kiore eradication (Graham & Veitch 2002). On Big South Cape Island, where ship rats irrupted in 1962–64, tui and tits increased after robins and saddlebacks disappeared, and bellbirds greatly declined. Introduced birds, especially blackbird, chaffinch and hedge sparrow, also increased markedly after rats arrived (Bell 1978).

Monitored translocations can become powerful experiments (Armstrong & McLean 1995; Seddon et al. 2007), particularly if accompanied by analysis or a manipulation of a possible limitation or decline factor (e.g. Lovegrove 1996a; Castro et al. 2003; Hooson & Jamieson 2003; Armstrong et al. 2006a, b, 2007). Twenty seven of the 50 forest birds listed in Table 1 have been subjected to some translocation in New Zealand (http://www.massey.ac.nz/~darmstro/nz_projects.htm, accessed February 2008), gradually refining habitat and management requirements for successful population establishment (Armstrong et al. 2002a, 2006a).

Non-predation factors

Food supply

The effects of food supply on birds can be difficult to measure when food shortage results in emigration, reduced breeding rates, or mortality via another cause, such as predation or disease, rather than from obvious starvation. The term 'food shortage' may apply to food of inadequate quantity, quality or availability (Newton 1998). The nutritional needs of birds change in time and space, being highest when they hatch, decreasing continuously as they grow, but increasing again for females when they breed. All birds must invest heavily in time and energy to obtain adequate nutrition (Klasing 1998). Food supply is therefore always a potential contributor to bird declines and limitation.

In comparison with the abundant experimental data on predation, it is remarkable how little direct experimentation has been done on the food supplies of birds in New Zealand. Nearly all evidence about food limitation in New Zealand forest birds is circumstantial, and its contribution to mainland declines and population limitation remains little understood. Basic field studies of forest birds on the New Zealand mainland (and therefore in the presence of many pest mammal species) have rarely established field evidence consistent with food limitation (Table 2), although there has been only one food addition experiment in the presence of a mainland predator guild (Wilson et al. 1998; see below). Desertion of eggs and chicks by incubating adults is typically rare, causing only 7.2 ± 6% of nest or egg failures on average (n = 21; Table 3), consistent with the assumption that food supply is generally adequate for breeding. The failure of some kokako pairs to attempt breeding in a season, combined with the apparent impact of geographically expanding possums on kokako populations, was initially thought to be a food problem (Hay 1981), but later analysis showed that (1) these were male-male pairs; (2) possums are important nest predators; and (3) neither the body weight nor the diet of breeding kokako differed from those of non-breeders (Innes et al. 1999). Male-male pairing is now known to be a reversible outcome of predation causing an excess of males, because predator control returns the sex ratio to near 50:50 (Innes et al. 1999).

Food competition has been most frequently raised as a hypothesis to explain declines when there was demonstrated overlap between the diets of a declining bird and a pest (e.g. NI kokako and possums, Leathwick et al. 1983; Fitzgerald 1984; kereru and ship rats and possums, Clout et al. 1995). In each case, predation was a viable alternative hypothesis, and food was never demonstrated to be in short supply, although this was not experimentally tested.

The abundance and richness of invertebrate food did not explain why blue ducks (whio) were present in some river sections and not others (Collier et al. 1993), nor did the diet of blue ducks seem so specialised that food shortage seemed a viable mechanism of decline (Veltman et al. 1995). Predation by stoats is likely to be the most widespread and important single factor limiting whio populations today (Whitehead et al. 2008; A. Glaser, DOC, pers. comm.).

However, food shortage may have been an additional component of past declines of forest birds caused primarily by predation, and may still contribute to current limitation. In the latter case, this seems most likely when a bird is known to greatly reduce or even stop breeding attempts when food is scarce, combined with a competitor being known to drive food supplies to low levels.

Taxa whose breeding is known to be variable depending on food supply include parrots and frugivores, including kakapo (Cockrem 2006; Harper et al. 2006; Wilson et al. 2006), kaka (Moorhouse 1991; Wilson et al. 1998; Moorhouse et al. 2003; R. Powlesland et al. unpubl. data), kea (Elliott & Kemp 1999), yellow-crowned parakeets (Elliott et al. 1996), red-crowned parakeets (Higgins 1999), kereru (Clout et al. 1995; Powlesland et al. 2003), Chatham Island pigeon (parea) (Powlesland et al. 1997) and kokako (Innes et al. 1999; Flux et al. 2006), reflecting the intrinsically variable abundance of annual fruit crops on many New Zealand tree species (Ogden 1985). In contrast, arboreal insectivores seem to have more regular breeding seasons, less affected by food supply. For example, the number of mohua breeding attempts is unaffected by masting seed and associated fluctuations in invertebrates (Alley et al. 2001) in South Island *Nothofagus* forest (C. O'Donnell, Department of Conservation, pers. comm.).

Brushtail possums are the most likely agent of food limitation for mainland frugivores in podocarp-broadleaved forest, because they are large, ubiquitous, arboreal, and can consume large quantities of flowers and fruits, suppressing fruit production (hinau *Elaeocarpus dentatus*, Cowan & Waddington 1990; nikau *Rhopalostylis sapida*, Cowan 1991; many species, Atkinson 1992; Table 5). Suppression of possums and ship rats in Auckland forests has permitted more fruit production, less fruit damage, more fruits maturing and more fruits consumed by birds that subsequently excreted the seed unharmed (Dijkgraaf 2002). In the Otamatuna 'mainland island', Te Urewera National Park, possums consumed 85–89% of green tawa (*Beilschmiedia tawa*) fruit in 1997 and 1999 (Barraclough 2006). Conversely, Nugent et al. (2001) suggested that possums are probably unable to utilise "much of the ephemeral flower and fruit crops during the few weeks that such foods are typically available".

Preliminary analysis of invertebrate take by mammals (Table 6) suggests that hedgehogs at mean density consume most invertebrates compared with other mammals, and could be competitors for ground insectivores, such as kiwi, as suggested by Berry (1999). While food limitation is undoubtedly a much smaller problem for kiwi than is predation by stoats (McLennan et al. 1996), faster growth rates of chicks in areas rich in invertebrates may reduce the time taken for kiwi to reach safe weight (P. de Monchy unpubl. data).

Introduced *Vespula* wasps may also be important consumers of food (honeydew and invertebrates) previously eaten by native forest birds in South Island *Nothofagus* forests (Harris 1991; Beggs & Rees 1999; Beggs 2001). Honeydew produced by an endemic scale insect in New Zealand beech forests is an important food for native birds, but is monopolised by wasps for up to 4 months of the year. South Island kaka spend about 30% of their foraging time collecting honeydew when it is available, but are strong fliers and can leave to

Table 5. Estimated weights of flowers and fruits consumed per hectare per night by arboreal pest mammals in North Island podocarp-broadleaved forest. Mean weight consumed by possums is expressed with mean, minimum and maximum because fruit may be 4–86% of possum diet, mean 35% (Nugent et al. 2000; King 2005).

Species	Mean body weight (g)	Weight flowers & fruit eaten (g animal^{-1} night^{-1})	Mean density (animals ha^{-1})	Weight flowers & fruit eaten (g ha^{-1} night^{-1})
Ship rat	143	10	3.9	39
Possum	2450	76	8	212 (24–522)
TOTAL				251 (63–561)

Table 6. Likely mean weights of invertebrates consumed per hectare per night by introduced pest mammals in North Island podocarp-broadleaved forest (Fitzgerald & Karl 1979; Berry 1999; Efford 2000; King 2005; C. Gillies unpubl. data). The mean hedgehog density figure is the only available estimate, from a single site.

Species	Mean body weight (g)	Weight invertebrates eaten (g animal^{-1} night^{-1})	Mean density (animals ha^{-1})	Weight invertebrates eaten (g ha^{-1} night^{-1})
Mouse	17	2	4.5	9
Ship rat	143	10	3.9	39
Stoat	259	1.4	0.03	0.04
Hedgehog	685	120	5.5	660
Possum	2450	4	8	32
Feral cat	3500	1.7	0.2	0.34
TOTAL				740.38

forage elsewhere when wasps are numerous. Tui also left the study sites or reduced the time feeding on honeydew when little was available. Bellbirds remained in the forest but ate less honeydew, or reduced their non-foraging activities, such as singing, flying, social interactions and grooming (Beggs 2001). The effects of these responses on breeding outcomes or demography are unknown. However, it should be noted that kaka are limited primarily by stoat predation rather than by food supply (Wilson et al. 1998).

Kearvell et al. (2002) suggested that both orange-fronted and yellow-crowned parakeet might suffer from shortage of invertebrate food due to competition from vespulid wasps and mammals, and shortage of beech-seed food caused by competition from introduced finches and rodents. They based their opinion on a demonstrated substantial diet overlap between orange-fronted and yellow-crowned parakeets, implying competition was possible, but they did not determine any other evidence for food shortage.

Few studies have examined the time New Zealand birds spend feeding compared with other activities, although this can point directly to food shortage as a problem. New Zealand robins on the Outer Chetwode Islands had smaller territories, shorter breeding and less productivity than South Island mainland robins, and Powlesland (1981) hypothesised that food on the island might be in short supply. For example, male Chetwode robins in April–June foraged significantly more (85–95% of observation time) than mainland robins (72–87%). By way of contrast, three other time-budget studies agreed that food was not apparently in short supply for mainland bird populations. Less than a third (32%) of observations of North Island kokako at Puketi forest were of feeding (Powlesland 1987). Bellbirds in mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest at Craigieburn spent less than 20% of their time feeding, and their foraging time did not change significantly from winter to summer as food resources became more plentiful (Murphy & Kelly 2001). Male blue ducks foraged for less than 20% of their time throughout the year, although females spent more than half their day feeding before laying (Veltman & Williams 1990).

Only one food supplementation experiment has been undrtaken in the presence of mainland predators. Wilson et al. (1998) gave supplementary food to kaka to test whether food supply was limiting breeding, but the outcome was unclear because most nesting attempts were ended by stoat predation and because the researchers could not establish a non-treatment area. However, kaka initiated nesting in anticipation of heavy beech seeding, perhaps by detecting hormonal or other nutrient differences in beech sap, and did not even attempt to breed during the post-seedfall year (Wilson et al. 1998).

On New Zealand islands, several food supplementation experiments have examined the role of food supplies on populations of forest birds free of mainland limitations. Mackintosh and Briskie (2005) fed mealworms to a translocated population of robins on Motuara Island (59 ha) to test whether high hatching failure was caused by food shortage, and concluded that inbreeding depression was a more likely explanation. Food supplementation increased productivity of hihi on both Mokoia Island, Lake Rotorua and on Tiritiri Matangi Island by increasing female egg production and by increasing the number of fledglings produced and the recruitment of young into the population (Armstrong & Ewen 2001; Castro et al. 2003). The hihi were taken from Hauturu, so food supplementation was likely to be beneficial to both groups of translocated birds, but for different reasons: Mokoia Island has only secondary vegetation compared with Hauturu (Perrott & Armstrong 2000), and bellbirds displace hihi from nectar sources when nectar is scarce on Tiritiri (Armstrong & Ewen 2001). Food supplementation and other management practices developed on Mokoia Island are now applied also to manage three other translocated hihi populations on island and mainland sanctuaries (Armstrong et al. 2007), but predators still primarily limit the free return of hihi to the New Zealand mainland (Taylor et al. 2005). Supplementary feeding of kakapo failed to increase the frequency of breeding and hatching success has remained poor, perhaps because of inbreeding (Elliott et al. 2006).

Other kinds of competition

Criteria required to detect interspecific competition with varying degrees of certainty are listed by Newton (1998: 320). Weak evidence includes overlap between species in use of common resources; stronger evidence includes negative effects of one species on the other, apparent at both individual and population levels.

No case has been made for interspecific competition for food or any other resource, such as nest sites, being the primary cause of decline or current limitation of any New Zealand forest bird. Forsyth et al. (2002) reviewed the impacts of introduced birds as conservation pests in New Zealand, and noted that: information was sparse; bird communities were poorly studied; only one manipulative experiment had been undertaken (with magpies, in rural habitat; Innes et al. 2004a), and that introduced birds may compete with natives for nesting and roosting sites. Two introduced parrots, the sulphur-crested cockatoo (*Cacatua galerita*; Watts et al. 2000) and eastern rosella (*Platycercus eximius*; Wright & Clout 2001) might compete with native parrots for nest sites if all species were abundant and overlapping, but they do not live in the same habitats. Predation has been shown to maintain native parrots well below the levels at which nest sites are likely to be limiting (Elliott et al. 1996; Wilson et al. 1998; Moorhouse et al. 2003).

Kaka abundance in South Westland is greatest at sites not yet colonised by possums and those with the shortest history of possum occupation, and declines with increasing possum density (Veltman 2000). However, possums are known kaka predators (Moorhouse et al. 2003) and the relative contribution to kaka decline of disturbance at nest sites or competition for sites by possums remains little understood (R. Powlesland, DOC, pers. comm.).

Habitat area

The persistence and restoration of threatened forest bird species on small pest-free islands of 2817 ha (Hauturu) or less suggest that forest loss on the mainland – where much larger tracts remain – has not directly caused the extinction of any species. The 15 National Parks in New Zealand average 235 855 ha, the largest of which (1 260 742 ha Fiordland) is mostly native forest, and total areas of continuous forest tracts of all tenures are much larger again, yet many forest birds have become extinct or are threatened in these huge areas. The recent establishment of mainland populations of little spotted kiwi, hihi and saddlebacks in the partially-forested 220 ha pest-fenced Karori Sanctuary in urban Wellington shows these sensitive species can persist in very small sites, in the short term at least. The declines of all forest birds inside the largest remaining forest tracts are a significant clue to their causes, explicable when the past and present distributions of pest mammals are understood (Holdaway 1999; Basse & McLennan 2003; King 2005).

In some regions, near-complete forest loss has clearly caused local or even regional extirpation of forest-dependant taxa, and thus contributed to total extinctions. National distributions of extant forest birds show clear gaps where most forest is missing – in the Waikato, southern Hawke's Bay, Manawatu, Canterbury, Otago and Southland (Robertson et al. 2007: 350). Recent studies show that urban properties (Day 1995), farms and rural landscapes (Blackwell et al. 2005; Stevens 2006) with more native vegetation have more native bird species. Restoration of many forest birds in urban and rural landscapes first demands adequate area of forest habitat of the right type (Clarkson & McQueen 2004; van Heezik et al. 2008), although a few species (e.g. fantail, grey warbler, kereru, morepork, silvereye, tui) have already adapted to exotic-dominated habitats for at least some of the year (Robertson et al. 2007; van Heezik et al. 2008). Despite these exceptions, the return of more obligate native forest taxa, such as kokako, saddlebacks, and hihi, to urban and rural sanctuaries depends both on the supply of adequate areas of suitable food species (extant or restored), and on intensive or complete control of predatory mammals. In deforested urban and rural landscapes *at local and regional scales*, therefore, habitat area is frequently a primary limiting factor for all but the most pest-resistant and habitat-generalist forest birds (these latter being primarily the "large secure" species in Fig. 1).

Research to determine minimum habitat and area requirements of forest birds is a clear current priority, stimulated by the rapidly growing interest in mainland sanctuaries of various kinds (Clout & Saunders 1995; Saunders & Norton 2001). There are two important research avenues: (1) how small can a forest be to sustain a genetically viable population of a bird species, at various residual pest abundances? (2) what spatial arrangement of sanctuaries could best maximise both abundance and diversity of birds at a landscape or regional scale? The questions are relevant to wild landscapes such as large National Parks, as well as to urban and farmed landscapes, because the current limitations of annual pest control permit intensive pest management in only small parts of large native forests.

Projects targeting stoats alone, such as for some kiwi restoration, are larger (e.g. the mean area of the four Department of Conservation kiwi zones targeting stoats alone is 11 000 ha, max. 12 000 ha, DOC 2006) than those targeting ship rats (e.g. mean area of unfenced mainland sites managed for NI kokako is 1008 ha, max. 3000 ha, n = 18, J. Innes et al. unpubl. data). This is partly to accommodate kiwi dispersal (see below) and because stoats range further (mean home range area in non-beech forest, both genders, 84 ha, King & Murphy 2005, their table 55) than ship rats (0.28 ha, data from Daniel 1972; Innes & Skipworth 1983; Dowding & Murphy 1994; Hooker & Innes 1995). The 18 sites managed for kokako are only 2.3% of the suitable contiguous habitat that is actually available (J. Innes et al. unpubl. data). Fenced mainland sanctuaries are even smaller, with mean size 438 ± 905 ha (n = 18, B. Burns unpubl. data), although this mean is greatly influenced by the two largest sanctuaries at Maungatautari (3300 ha) and Cape Kidnappers (2200 ha). Evidence to date is that small sites (<200 ha) will be used by common insectivores such as grey warbler and fantail, and (perhaps seasonally) by mobile, adaptable frugivores such as tui and kereru (Stevens 2006). Translocated SI saddlebacks have persisted on islands as small as 6 ha, despite inbreeding depression (Hooson & Jamieson 2003), although it is not yet known if emigration from fenced sanctuaries on the mainland, often described as "virtual islands" would be as restricted as is emigration from real islands by sensitive taxa reluctant to cross water. Numerous experimental translocations of many taxa to sites of varying size, habitat quality, and predator threat will slowly clarify what is possible (e.g. Armstrong & McLean 1995; Armstrong et al. 2007). At present, it appears that the taxa least able to benefit from small mainland sanctuaries are those that, although highly sensitive to pests, are also most mobile and with large territories.

Long-term population maintenance demands management areas that accommodate natal dispersal distances, although these have been measured for few species. NI brown kiwi disperse at least 5 km (n = 11), necessitating managed areas of 9–11 000 ha (Basse & McLennan 2003; Westbrooke 2007). NI kokako dispersed on average 1616 m (data from Mapara, Te Urewera, Kapiti Island and Rotoehu, n = 174, J. Innes et al. unpubl. data), and modelling suggests that the minimum area required to sustain a population is 500 ha (B. Basse et al. unpubl. data). NI robins breed successfully in the 80-ha Wenderholm Regional Park, Auckland, but of 186 banded juveniles produced during 1999–2006, only 8 females (4%) and 3 males (1.6%) have remained within the park. Others dispersed up to 13.5 km away, eventually establishing satellite populations (still requiring pest management) up to 8.5 km from Wenderholm via a vegetated corridor through which robins were known to disperse (Andrews 2007; T. Lovegrove unpubl. data). Juvenile dispersal may limit the establishment of viable robin populations at small pest-managed sites like Wenderholm (Lovegrove et al. 2002). Virtually all young kaka fledged within the 1100-ha Waipapa Ecological Area remained there, but most fledglings from the 825-ha Rotoiti Nature Recovery Project and the 13 000-ha Eglinton Valley dispersed into surrounding unmanaged habitat (Moorhouse et al. 2003) where the females are at grave risk once they begin to breed. Leech et al. (2008) estimated that at least 500 square kilometres of South Island beech (*Nothofagus*) forest would be need to maintain a minimum viable kaka population size of 258 kaka (155 adults).

Inbreeding depression and genetic impoverishment

Ian Jamieson argues persuasively that inbreeding depression has been overwhelmed by intense predation pressure and habitat clearance as causes of declines of island endemics in places such as New Zealand (Jamieson et al. 2006; Jamieson 2007). However, very small populations are also vulnerable to inbreeding depression and perhaps long-term genetic impoverishment, regardless of the original cause of population decline (Jamieson 2007), especially when there are recurrent bottlenecks such as with repeated translocation (Lambert et al. 2005). Recent research on the consequences of known population bottlenecks in New Zealand birds has demonstrated both decreased genetic diversity (Robertson 2006; Sainsbury et al. 2006; Boessenkool et al. 2007) and increased hatching failure (Jamieson & Ryan 2000; Briskie & Mackintosh 2004; Mackintosh & Briskie 2005; Boessenkool et al. 2007), although the former does not always result in the latter (Ardern & Lambert 1997).

Lowered genetic diversity may threaten the viability of populations in the long term if it reduces their ability to adapt to threats such as new diseases or competitors. For example, one study has demonstrated reduced immune response in a severely bottlenecked New Zealand robin population (Hale & Briskie 2007). Low hatching success or reduced juvenile survival (Jamieson et al. 2007) may slow population recovery in the short term, although case studies in New Zealand so far show that such inbred populations do still grow (Briskie & Mackintosh 2004; Hooson & Jamieson 2004; Boessenkool et al. 2007; Jamieson 2007). Therefore, managing inbreeding depression may materially assist population recovery rates, and maintaining genetic diversity for any taxa may assist long-term survival of a species against unforeseen stresses in the future (Jamieson et al. 2008). Fortunately, prospects for management of inbreeding by regular exchanges of birds between sites are good, except in the most severely bottlenecked species.

Parasites and diseases

Newton (1998) suggested parasites and diseases were much less frequent major limiting factors for birds worldwide compared with predation and food shortage. The importance of parasites and diseases may increase with recent greater human impacts on habitats and landscapes, combined with increased translocations of birds between populations (Deem et al. 2001). A strongly documented example is from Hawaii, where avian malaria (*Plasmodium relictum capistranae*) has reduced the range and numbers of many native birds in Hawaiian forests below 1500 m elevation (van Riper et al. 1986).

Documented accounts of the effects of avian diseases in New Zealand are rarer than speculation about them, and data on free-living birds rarer than on captives (Alley 2002). Cases have been noted among non-captive individuals of weka on Kawau Island (Beauchamp 1997), of black robins on Little Mangere (Tisdall & Merton 1988), and of hihi on Mokoia Island. Aspergillosus and nest mites killed hihi adults and broods respectively on Mokoia Island, contributing finally to the decision to translocate the remaining birds to Kapiti Island (Alley et al. 1999; Armstrong et al. 2007). Saddlebacks on Motuara Island declined by 50% after 2002, perhaps because of an unknown disease (Hooson & Jamieson 2004).

The role of disease in the rapid disappearance of Northland bellbirds in the 1860s is discussed by Bartle and Sagar (1987), who concluded the cause remained a mystery. However, predation by irrupting ship rats is a stronger alternative explanation, for two reasons: (1) the disease hypothesis does not explain the persistence of bellbirds on near-shore islands such as Motuihe and Tiritiri Matangi, which a possible disease must have reached but ship rats did not (Lee 2005); (2) 500–1000 bellbirds now inhabit Tawharanui Regional Park, which is subject to intensive ship rat control, and bellbirds are now spreading across the Hunua Ranges from the 1000-ha Kokako Management Area, where there is similar intensive rat control (T. Lovegrove, unpubl. data).

Both native and non-native New Zealand birds are susceptible to avian malaria, although evidence for its effect on populations of native bird populations in the wild is still only suggestive (Tompkins 2007). The mosquito vector responsible for malaria outbreaks is widespread, and non-native birds, such as blackbirds with generally high infection rates, may act as reservoirs of infection to native species (Tompkins & Gleeson 2006).

There is no documented case where disease has been the primary driver of a forest bird decline in New Zealand, but it is difficult to make observations and retrieve fresh corpses from remote and rugged field locations (Tisdall & Merton 1988). Methodical surveys for parasites and diseases in wild birds have only recently started, and interpreting the significance of findings is difficult. Some parasite and microorganism investigations are obligatory before translocations of forest birds, but there is limited understanding of which organisms are natural and the circumstances in which they may be seriously threatening to populations (D. Tompkins, Landcare Research, Dunedin, pers. comm.).

Discussion

The six necessary steps to determining the cause of a species' decline listed here confirm pest mammals as the primary cause of current declines and limitation of birds in remaining large New Zealand forest tracts (Table 7), even though complex interactions between 'proximate' (usually predation) and other 'ultimate' causes (Newton 1998) may be the norm.

Interactions between predation and food supply

In the New Zealand setting, disentangling predation and food supply as potential limiting factors is difficult, because they can have identical demographic outcomes (Table 2), and because they frequently interact. Interactions include:

1. Some key predators, especially ship rats and brushtail possums, are omnivores that eat birds as a minor diet component. Removing these predators is likely both to reduce predation on birds and increase birds' food supply (flowers, fruit, invertebrates and leaves). Birds may immigrate to pest-controlled sites, such as mainland islands. because there is more food there, thus confusing increases due to increased reproduction or reduced mortality with those due to immigration; the relative contribution of these three mechanisms to bird recovery in mainland islands is presently unknown.
2. The timing and frequency of pest control also influences the outcome. Intermittent control of possums and ship

Table 7. Perceived main causes of original declines and current limitation of populations of New Zealand forest bird taxa that have either a current New Zealand Threat Classification (Hitchmough et al. 2007) or whose distribution has declined from the first Atlas (Bull et al. (1985; data collected 1969–70) to the second (Robertson et al. 2007; data collected 1999–2004), as listed in Robertson et al. (2007, Appendix K). Taxa are listed by common name in checklist order (OSNZ 1990); scientific names are in Table 1. Subspecies are merged if they have the same causes of decline. Major predators are listed in capitals where evidence permits.

Common name Species	Subspecies	Original decline	Current limitation	Reference
NI brown kiwi		Predation, forest clearance	Predation by STOATS, cats and dogs	Robertson 2003
Southern tokoeka		Predation, forest clearance	Predation by STOATS	Robertson 2003
Okarito brown kiwi		Predation, forest clearance	Predation by STOATS	Robertson 2003
Haast tokoeka		Predation, forest clearance	Predation by STOATS	Robertson 2003
Little spotted kiwi		Predation, forest clearance	Food, intraspecific competition on islands. Predation by STOATS on the mainland	Robertson 2003
Great spotted kiwi		Predation, forest clearance	Predation by STOATS	Robertson 2003
Blue duck		Lowland forest clearance, predation, river damming	Predation by STOATS, plus floods, dams, forest clearance	A. Glaser, DOC, pers. comm.; Whitehead et al. 2008
Weka	Western weka	Predation, food supply, land clearance, disease, droughts and floods	Predation, competition, land clearance, disease and parasites, motor vehicles, pest control by-kill	Beauchamp et al. 1999
	North Island weka	Predation, food supply, land clearance, disease, droughts and floods	Predation, competition, land clearance, disease and parasites, motor vehicles, pest control by-kill	Beauchamp et al. 1999
	Stewart Is weka	Predation	Food supply on islands other than Stewart. Predation on Stewart Island	Beauchamp et al. 1999
NZ pigeon		Forest clearance, predation, hunting, food competition	Predation by SHIP RATS and POSSUMS, food competition, illegal hunting, motor vehicles	Mander et al. 1998
	Chatham Is. pigeon	Forest clearance, predation, hunting, food competition	Predation by SHIP RATS and POSSUMS, food competition, small habitats	Powlesland et al. 1997
Kakapo		Predation by people, kuri, kiore, stoats, ship rats, cats, forest clearance	Food supply (infrequent podocarp fruiting) and hatching failure due to inbreeding depression, on pest-free islands. Predation by STOATS and FERAL CATS on the mainland	Powlesland et al. 2005
Kaka		Forest clearance, predation	Predation by STOATS	Wilson et al. 1998; Moorhouse et al. 2003
Red-crowned parakeet	red-crowned parakeet	Forest clearance, predation	Predation by STOATS and SHIP RATS on the mainland, by KIORE on some islands	Taylor 1985; Higgins 1999
	Chatham Is. r-c parakeet	Forest clearance, predation, grazing	Predation by SHIP RATS?, grazing	Taylor 1985
Yellow-crowned parakeet		Forest clearance, shooting, predation	Predation by STOATS, and SHIP RATS	Elliott et al. 1996
Forbes' parakeet		Forest clearance, predation, hybridisation	Hybridsation on Mangere, L. Mangere Islands.	Taylor 1985, Boon et al. 2000
Orange-fronted parakeet		Predation, forest clearance	Predation by STOATS and SHIP RATS	Boon et al. 2000
Shining cuckoo			Unknown	
Long-tailed cuckoo			Unknown	
Rifleman	NI rifleman		Unknown	
	SI rifleman		Unknown	
Mohua		Predation, forest clearance	Predation by STOATS and SHIP RATS	O'Donnell et al. 2002
Brown creeper		Predation, forest clearance	Predation by STOATS and SHIP RATS	Higgins & Peter 2002
Chatham Is. warbler		Habitat change by stock grazing, predation	Habitat change by stock grazing, predation	Higgins & Peter 2002
Tomtit	SI tomtit	Forest clearance, predation	Unknown	Higgins & Peter 2002
	Chatham Is tomtit	Forest clearance, predation	Grazing and predation	Higgins & Peter 2002
Black robin		Habitat loss, predation	Food supply, inbreeding on pest-free island	Higgins & Peter 2002
Hihi		Forest clearance, predation	Food supply and *Aspergillus* fungus on islands, predation by SHIP RATS and STOATS prevents mainland return	Taylor et al. 2005

Table 7 continued

Common name Species		Subspecies Original decline	Current limitation	Reference
Bellbird	Three Kings bellbird	No original decline	Unknown	
	Poor Knights bellbird	No original decline	Island area, food supply	Sagar 1985; Sagar & Scofield 2006
Chatham Is tui		Forest clearance, predation and grazing	Cat predation on Pitt Is., food supply	Dilks 2004
Saddleback	NI saddleback	Forest clearance, predation	Food supply on islands, Predation by SHIP RATS and STOATS prevents mainland return	Lovegrove 1992
	SI saddleback	Forest clearance, predation	Food supply on islands, Predation by SHIP RATS and STOATS prevents mainland return	Hooson & Jamieson 2003
NI kokako		Forest clearance, predation	Predation by SHIP RATS and POSSUMS	Innes et al. 1999 ; Innes & Flux 1999

rats may have the nett effect of increasing ship rats for most of the time (Sweetapple & Nugent 2007); removing stoats may also increase ship rats (I. Flux, C. Gillies, unpubl. data), altering both predation and food supply scenarios in complex ways. The relative effect of variation in pest densities (e.g. the difference between stable numbers, versus low numbers with occasional peaks which give the same mean density) is also largely unknown, but will depend on the shape of the density/damage relationship and the longevity of individual birds relative to the timescale of pest fluctuations.

3. Changes in food supply controlled by climate can initiate bird breeding attempts, but predators may determine the success of those attempts (e.g. Wilson et al. 1998; Innes et al. 1999; Moorhouse et al. 2003).
4. The climatic or food events that initiate or promote bird nesting also may increase predator abundance, via complex community linkages (King 1983; King & Moller 1997; Wilson et al. 1998). This is especially well known for beech forest systems (Ruscoe et al. 2006; Tompkins & Veltman 2006; Kelly et al. 2008), although in podocarp-broadleaf forests, mast events also can be important triggers (e.g. podocarp seed instigating kakapo breeding; Cockrem 2006), and lesser mast events of fleshy-fruited species can greatly lengthen breeding seasons for kereru and kokako. The inter-annual variability of fruit crops in plants of diverse North Island forests, and the degree of synchrony among the component plant species, are little known (Dijkgraaf 2002), but are important areas for future research.
5. Abundant food can reduce fledging time and, presumably, vulnerability to predation in the nest, e.g. in kereru from seven weeks to four (Mander et al. 1998).

Acknowledging these interactions does not change the general conclusion, from several strands of evidence, that predation is the major decline and limitation factor. First, predation is known to be the main cause of nesting attempt failure, while desertion is much less common (Table 3). Mortality of sitting adults (usually females) through predation at nests is also common (e.g. Brown 1997; Wilson et al. 1998; Innes et al. 1999), and the excess of the non-incubating gender (usually males) in predation-vulnerable taxa on the mainland is evidence of severe predation impact. While food supply can also induce male excess in particular situations other than predation-driven declines (e.g. bellbird males outcompete females when food is scarce, Sagar & Scofield 2006; supplementary feeding promotes more male kakapo chicks, Clout et al. 2002), predator control has routinely restored gender ratios in experimental studies published so far (Innes et al. 1999; Moorhouse et al. 2003; Armstrong et al. 2006a). Much less is known about the causes of subadult and adult mortality away from nests.

Second, there is no coherent, food-centred argument that may explain why the threat of extinction is concentrated on certain types of taxa or life stages, whereas predation is self-explanatory. Many threatened species are ground-feeding, hole-nesting or roosting, tame, or vulnerable when nesting (Table 1). The diets of such taxa are very broad, including litter and soil invertebrates (kiwi), aquatic invertebrates (whio), leaves and fruit (kakapo and kakariki), and forest invertebrates (mohua), and diet breadth varies also from just invertebrates (kiwi, whio) to invertebrates, leaves, fruit, and nectar (kaka, kokako). Brown kiwi chicks and adults both eat litter and soil invertebrates, but these taxa decline primarily because predation-vulnerable chicks are eaten by stoats, whereas the larger adults are comparatively safe.

The clearest experimental demonstration of successful predator control that does not interact with food supply is for seabirds, such as petrels that nest on land but feed at sea. Like forest birds, seabirds nesting where pest mammals are present have been decimated by them (Holdaway 1999) and can be protected by predator control (e.g. Imber 1987; Imber et al. 2003; Bellingham et al. 2010), which clearly cannot interact with their marine food source.

Third, threatened forest birds persist on predator-free islands like Hauturu and mainland sanctuaries like Karori Wildlife Sanctuary (Wellington), despite possibly greater intra- and inter-specific competition resulting from the extra diversity and abundance of birds in such locations. The counter-hypothesis, that they persist at such places because introduced mammals have driven mainland food supplies below survival levels, could be tested by measuring food abundance with the same techniques at sites with pest mammals and with abundant, diverse native birds and other fauna, to see which community drives food supply lowest.

For managers, the steps required to reduce predation (kill predators, either all species together, or provided the ones removed are the ones doing the damage) are the same as those to increase food supply when the key predators are ship rats and possums. Stoat control may actually decrease food for birds if ship rats increase when stoats are reduced (I. Flux, C. Gillies, unpubl. data). Robust experimental exploration of this dilemma should be a very high priority for future research.

The conclusion that predation alone is a sufficient explanation to account for recent and current declines of forest birds on the New Zealand mainland was applied also to the historical extinctions by Holdaway (1999) and Worthy and Holdaway (2002), even though these were perhaps due to different combinations of predator species. While reduced food supply may make birds more vulnerable to predation, there is no strong evidence that food shortage per se has had a primary role in the extinction of any forest species. However, these alternatives have rarely been explored rigorously with experiments, such as supplementary feeding or artificial brood reduction. In New Zealand, predation is an easier factor to experiment with than food supply because predator numbers can usually be reduced experimentally and will recover rapidly afterwards, often within months, whereas vegetation recovery may take many years. Furthermore, the frugivorous taxa whose breeding efforts respond most to food supply are generally much harder to deliver supplementary food to than are insectivores, such as robins, that will eat commercially available mealworms. Having said that, experiments involving supplementary feeding can be quite straightforward for birds that will take artificial food such as sugar water, commercially grown fruit, fat, nuts, and seeds, provided the complex influence of nutrition on breeding condition is clearly understood (Elliott et al 2001). More such experiments would be very revealing.

Limitation in the absence of predation

Island populations free of predation by introduced mammals exhibit demographic evidence of other limiting factors, including disease (hihi, Armstrong & Perrott 2000), food shortage (kaka, Moorhouse 1991; kakapo, Elliott et al. 2001; kakariki, Greene 2003), low hatching success and infertility (Briskie & Mackintosh 2004; SI saddlebacks, Hooson & Jamieson 2004; SI robin, Mackintosh & Briskie 2005; Boessenkool et al. 2007), habitat availability and territory acquisition (NI robins, Armstrong et al. 2000), and predation by native (harriers and perhaps long-tailed cuckoos on kokako on Kapiti and Tiritiri Matangi (I. Flux unpubl. data; Jones 2000b) and introduced birds (Indian mynas as well as harriers and moreporks on NI robins on Tiritiri Matangi Island, Armstrong et al. 2000). However, whether any of these factors truly limit the populations has rarely been tested by experiment. Exceptions are a series of supplementary feeding trials with hihi that demonstrated increased productivity and helped population persistence on both Mokoia and Tiritiri Matangi Islands, despite aspergillosis on Mokoia (Armstrong & Ewen 2001; Castro et al. 2003); and another 2-year trial exploring the effects of food supply on hatching failure in an already high-density robin population on Motuara Island (Mackintosh & Briskie 2005)

Forest birds on islands free of pest mammals typically reach higher densities than on the mainland (bellbirds, Sagar 1985; tits, McLean & Miskelly 1988; robins, Mackintosh & Briskie 2005). Low per-pair chick productivity and high parental investment in chicks are characteristic of high-density island populations of small forest passerines, including tits, fantails, robins and bellbirds (Powlesland 1981; McLean & Miskelly 1988; Sagar 1985). Bellbirds at high density on 66-ha Aorangi Is (Poor Knights) displayed density-dependent delayed plumage maturation, so that 33% of the population was subadult (Sagar & Scofield 2006). McLean and Miskelly (1988) suggested low per-pair chick production by island tits was an outcome of high intra-specific competition, leading to the production of fewer, more competitive offspring. Density-dependent population effects can arise within 5 years of initial population establishment on islands (Armstrong & Ewen 2002; Armstrong et al. 2002a). The proportion of juvenile robins surviving to breeding age declined on mammal-free Tiritiri Matangi Island as the population increased after initial translocation (Armstrong et al. 2000). Armstrong et al. suggested the Tiritiri Matangi population was limited by available breeding habitat, rather than by mammalian predation on nests and nesting females as on the mainland.

Mammal eradications on offshore islands and inside predator-proof fence enclosures on the mainland provide experimental opportunities to explore ecosystem function (Zavaleta et al. 2001; Donlan et al. 2002; Sekercioglu et al. 2004), especially (in a New Zealand setting) which and whether predators might limit bird populations. Such experiments are particularly instructive when predators can be removed one at a time. Designs of published manipulative field experiments in animal ecology were reviewed by Raffaelli & Moller (2000). Yodzis (1988) suggested as a rough guide 'press perturbations' (e.g. predator control) should be sustained for twice the summation of generation times of species in the longest trophic path being studied, e.g. for NI kokako, 2 x 2 years = 4 years. Similarly, species translocations may result in population *establishment*, but long-term monitoring is required to demonstrate population *persistence* (Armstrong & Seddon 2007).

In the absence of introduced mammals, fauna densities and behaviours may become more like those of some past time (a 'restoration'). Individual birds may eventually have less food when introduced mammals are removed, since the densities of many species are likely to increase after predation by mammals ceases. This will increase intra-specific competition, as suggested for 'equilibrium populations' (Caughley 1977) of SI robin on Outer Chetwode Island (Powlesland 1981) and black tit on the Snares Islands (McLean & Miskelly 1988). Bellbirds may reach extremely high densities on offshore islands because male and female bellbirds have greater differences in diet, foraging, and habitat use than other species, thus reducing intra-specific competition (Bartle & Sagar 1987). Inter-specific competition between birds is also important on islands lacking introduced mammals. For example, bellbird densities are extremely high on islands (Three Kings, Poor Knights) where they lack competition from tui and hihi (Bartle & Sagar 1987). The lower densities of bellbirds and tui which persist on the North and South Islands appear to be insufficient at many sites for the maintenance of ecosystem functions like pollination and fruit-dispersal of native plants (Kelly et al. 2010), which are still, in some cases, functioning well on the islands with high bird densities.

Bird community responses to pest mammal arrivals, eradications and control on islands and the mainland suggest that endemic birds can outcompete non-endemic species in intact native forest when mammal predators are absent. Diamond and Veitch (1981) first noted the apparent exclusion of exotic (e.g. blackbird *Turdus merula*, chaffinch *Fringilla coelebs*) and common native passerines (e.g. grey warbler, silvereye) from native forest that lacked mammal browsers and predators and structural change due to disturbances such as logging. They indicated the relative importance of the two possible causes of this exclusion – intact vegetation, and the high abundance of endemic birds – was unknown. Bird community changes on Kapiti Island after the 1996 eradication of rats (Miskelly & Robertson 2001) may have been due either to release from rat predation or perhaps to ongoing vegetation change after the earlier (ended 1986) eradication of possums. However, increases in blackbirds, chaffinches and hedge sparrow (*Prunella modularis*) on Big South Cape Island after ship rats arrived in 1962 and eradicated saddleback, wren and snipe definitely suggest a greater role for competition than for forest structure change, since there were no browsing mammals or logging activities on those islands. The demographic mechanisms (Table 2) of these declines deserve study. These changes in relative abundance suggest that competition, probably for food, can powerfully influence bird demography when predation is reduced as a limiting factor. Resource partitioning among closely-related species such as honeyeaters (Gravatt 1971) suggests that food competition has been an important evolutionary influence on New Zealand bird communities, despite the relative lack of food specialisation that characterises the New Zealand forest avifauna (O'Donnell & Dilks 1994).

Preliminary model of limitation

We conclude that:

1. Predation by introduced pest mammals continues to be primarily responsible for current declines and limitation of New Zealand forest birds at the national level, the same conclusion derived by Holdaway (1999), Worthy and Holdaway (2002) and Tennyson (2010) for historic declines (Fig. 3).
2. There is an unknown, but probably small, additional role for both food availability and habitat clearance, although neither factor by itself can explain the loss of any taxon.
3. The resultant small populations are then vulnerable to stochastic events, such as disease, extreme weather or arrival of a new predator species, and may become extinct.
4. Predator control may restore the abundance of small populations, but cannot (without translocation or managed immigration) recover lost genetic variation if the population becomes severely bottlenecked. The likely impacts of such genetic losses on long-term population survival in the face of new threats, such as climate change, are poorly understood.
5. Both inbreeding depression and food shortage may slow recovery rates when limitation by predation is alleviated.
6. Forest loss is clearly primarily responsible for forest bird decline or extinction in some regions or localities where no or little forest is left, and habitat restoration is a necessary precursor to forest bird re-establishment there.

Future research

Research on declining populations of New Zealand birds in the last 20 years has greatly advanced our understanding of the extinction process in our particular ecological and behavioural setting. We are dealing with previously successful endemic birds that have inappropriate behavioural and demographic responses to introduced mammalian predators.

We predict that few of the current indigenous New Zealand forest birds will persist on the mainland without predator control on a vastly larger scale than currently undertaken. Five species (SI saddleback, kakapo, hihi, little spotted kiwi, NI saddleback; Taxa 1–3, 17–18 in Fig. 1) are already extinct on the mainland, although hihi, NI saddlebacks and little spotted kiwi were recently returned to the pest-free Karori Sanctuary. The 17 remaining birds, shown with black symbols in Figure 1, are in known or perceived declines attributed primarily to mammalian predation. Recovery of populations of the most threatened of these – NI kokako, blue duck, mohua, NI kaka, SI kaka, orange-fronted parakeet, and NI brown kiwi – already focuses primarily on predator control. Identifying which predatory species present the most imminent threat, and disentangling the complex interactions between declining species and possible agents of decline, will inevitably require more "case-by-case ecological investigations and recovery operations" (Caughley 1994: 217) in future studies, in which experimental manipulation of perceived damage agents and

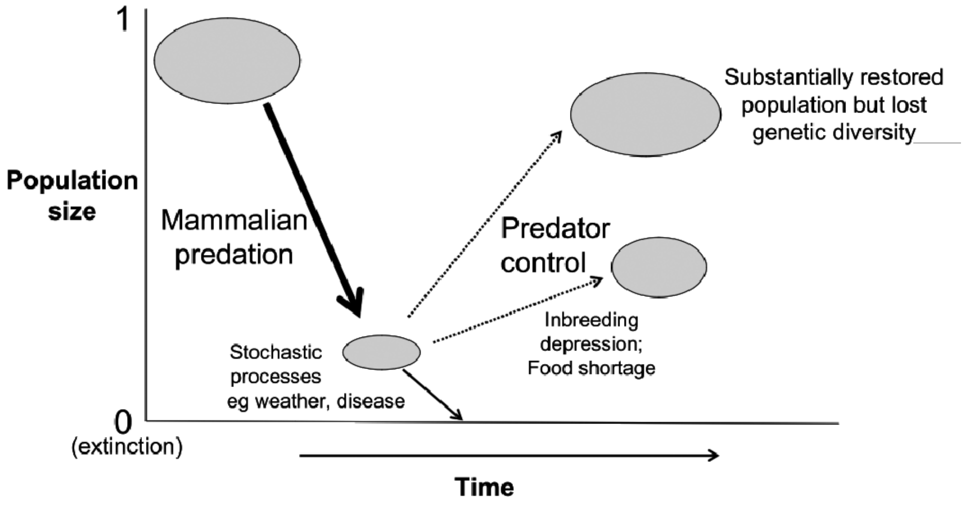

Figure 3. Schematic model of relationships between factors currently limiting New Zealand forest birds. Introduced pest mammals primarily drive population declines by predation of eggs, chicks and adults. Small populations are then vulnerable to disease, extreme weather and other stochastic processes, and may become extinct. Predator control may substantially restore population size but cannot recover lost genetic diversity, although translocation or mutation may do so in the short and long terms respectively. Both inbreeding depression and food shortage may slow recovery rates, and food limitation and other kinds of competition may reduce population size (carrying capacity). Based on initial draft of Ian Jamieson, Otago University, pers. comm.

detailed monitoring of bird demographic responses are the most likely options for teasing predation and food shortage apart.

Studying the effects of food shortage, competition, inbreeding and density-dependence is becoming more important in New Zealand as forest restoration projects become more ambitious and successful. The increasing area of pest-free habitat, both on islands and the mainland, challenges current knowledge of how birds interact with each other and what limits their numbers when introduced predators no longer drive abundances of some species downwards.

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