



Declines in common, widespread native birds in a mature temperate forest

Graeme P. Elliott^a, Peter R. Wilson^b, Rowley H. Taylor^b, Jacqueline R. Beggs^{c,*}

^a Department of Conservation, Private Bag 5, Nelson, New Zealand

^b Landcare Research, Private Bag 6, Nelson, New Zealand

^c School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

ARTICLE INFO

Article history:

Received 3 December 2009

Received in revised form 29 March 2010

Accepted 27 May 2010

Available online 19 June 2010

Keywords:

Introduced species

Invasives

Predation

Population trends

Possoms

Vespula wasps

ABSTRACT

Common, widespread species are important for ecosystem structure and function. Although such species have declined in some parts of the world, for most ecosystems there is a lack of information about changes in the population status of common species. We studied the abundance of common, widespread forest birds in Nelson Lakes National Park, New Zealand using standardised 5-min bird counts, carried out over a 30-year time span. There was a significant change in the bird community structure during this period. Five native species (bellbird, rifleman, grey warbler, New Zealand tomtit and tui) declined in abundance during the 30 years. All of these declined in abundance at low but not high altitudes, and the decline was substantial for all but New Zealand tomtit and tui. Three other native species increased in abundance (silvereye, yellow-crowned parakeet and New Zealand robin). There was no change in the abundance of introduced blackbirds. We suggest that invasive alien species are the most likely cause of the ongoing declines in common native species. A peak in brushtail possum abundance and the arrival of a new species of *Vespula* wasp were two large changes in Nelson Lakes forests that occurred during this study. Both are likely to have added to the ongoing impacts of predation by introduced rats and stoats. We suggest that it is necessary to actively manage introduced species in order to maintain populations of widespread, common native bird species in New Zealand.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Human impacts have led to a global trend of biotic homogenisation. With the assistance of humans, exotic generalist species have successfully established in many places throughout the world, while many specialist species have been lost (Blackburn et al., 2009; Cagnolo et al., 2009; Masseti, 2009). Inevitably, conservation efforts tend to focus on rare and endangered species in order to reduce the loss of biodiversity. However, it is common, widespread species that are important in the structure, biomass and function of most ecosystems, so it is critical that we also consider these species when prioritising conservation management (Gaston and Fuller, 2008). There is growing concern about the status of common widespread species since initial declines may be difficult to detect, yet even relatively small proportional declines equate to large losses of individuals with a consequential alteration in ecosystem structure, function and services. Declines in common widespread species have been demonstrated for a variety of taxa and ecosystems, from common butterflies in habitat heavily modified by humans (Van Dyck et al., 2009), to common specialist woodland

birds in Europe (Gregory et al., 2006), and an appalling range of commercial fish species (Levin et al., 2006; Pauly et al., 2002). Nevertheless, there is a lack of quantitative information on the status of many common species (Gaston and Fuller, 2007).

Before human colonisation, New Zealand forests were dominated by a diverse avifauna of large, sometimes flightless birds, rather than mammals (Craig et al., 2000). At least 77 species of breeding bird have become extinct in the last 2000 years and many others have declined in range and abundance (Holdaway, 1999; Worthy and Holdaway, 1993). Much of the decline in range is attributable to loss of forest habitat, but the extinction or reduction in abundance of many species within the remaining forests is attributable to predation by introduced mammals (Atkinson, 1978; Holdaway, 1999; Towns et al., 2006). Some species have declined very rapidly on the mainland even where their forest habitat remained (e.g. kakapo (*Stripops habroptius*) (Powlesland et al., 2006), saddleback (*Philesturnus carunculatus*) (Hooson and Jamieson, 2003) and bush wren (*Xenicus longipes*) (Cooper, 1994). These species are either extinct or very vulnerable to extinction and much research and conservation effort has focussed on them. Other forest dwelling species have received much less attention either because they were still widespread and thought to have reached equilibrium with the new predators (King, 1984), or because they were declining undetectably. However, during the 1980s and 1990s it became apparent that there were some

* Corresponding author. Tel.: +64 9 3737599x86823; fax: +64 9 3737042.

E-mail addresses: gelliott@doc.govt.nz (G.P. Elliott), wilsonp@rmb.quik.co.nz (P.R. Wilson), rowley.pat@xtra.co.nz (R.H. Taylor), j.beggs@auckland.ac.nz (J.R. Beggs).

previously common, widespread bird species that had declined only slowly, but were nonetheless headed for extinction on the mainland within a few tens of years (e.g., kaka *Nestor meridionalis* (Moorhouse et al., 2003; Wilson et al., 1998); mohua *Mohoua ochrocephala* (Elliott, 1996)). There is also a suite of forest birds that have remained common, or at least widespread, but as there are no nationwide, bird monitoring programmes in New Zealand, there is little evidence on whether or not they are declining.

Between 1974 and 1984 birds were counted along an altitudinal transect through mature southern beech (*Nothofagus* spp.) forest in Nelson Lakes National Park, New Zealand. This was initially part of a comprehensive study of beech forest birds (Dawson et al., 1978), prompted by a proposal to log large areas of beech forest in the South Island (Thomson, 1971). From 2002 until 2007 birds were counted along the same transect using the same methods as a non-treatment “control” for a predator control operation being undertaken near St. Arnaud (Brow et al., 2008). Such long-term standardised counts provide an opportunity to detect sustained changes in abundance of common species.

In this paper we use data from the two sets of bird counts to test whether 11 common, native and introduced, widespread forest bird species have changed in abundance over 30 years. These species include both insectivorous and omnivorous species (Table 1). We also tested whether there were altitudinal differences in the distribution of species between 1974–1984 and 2002–2007, since other studies have shown that introduced predators can have differential effects at different elevations (Rayner et al., 2007).

2. Methods

2.1. Study area

Birds were counted at 20 stations 200 m apart along a transect from the shore of Lake Rotoroa at 455 m to the tree-line at about 1400 m on Mt. Misery in Nelson Lakes National Park, New Zealand (41°55'S172°39'E). The transect follows a truncated spur up the side of a glaciated valley. The study site is part of a large continuous tract of cool-temperate, southern beech rain-forest which has never been logged and is about 14 km from the nearest road-end. Rainfall at the site varies between about 2000 and 3000 mm per annum depending on altitude. The vegetation has been classified into four distinct altitudinal zones; silver (*Nothofagus menziesii*) red (*Nothofagus fusca*) beech with podocarps (455–475 m a.s.l.); red/silver beech (485–540 m a.s.l.); red/silver beech with kamahi (*Weinmannia racemosa*) or mountain beech (*Nothofagus solandri* var. *cliffortioides*) (550–1020 m a.s.l.); and mountain/silver beech (1050–1425 m a.s.l. (Beggs, 1991). Beech trees seed intermittently, but usually synchronously (termed mast seeding) with abundant seeding occurring usually 3–5 years apart (Burrows and Allen, 1991; Wilson et al., 1998). Mast seeding in turn can lead to

increases in the number of litter dwelling invertebrates and introduced predators, particularly rodents (*Mus musculus* and *Rattus* spp.) and stoats (*Mustela erminea*) (Alley et al., 2001; Murphy and Dowding, 1995; Wilson et al., 1998).

Another characteristic feature of this beech forest is high-density infestations of endemic scale insects (*Ultracoelostoma* spp.) in all but the highest altitude zone (Beggs, 1991). The scale insects exude large quantities of sugary honeydew which provides an important food resource for a range of species, including birds and introduced *Vespa* wasps (Beggs and Wardle, 2006).

The avifauna at this site is typical of a mainland New Zealand forest site that has been modified by a range of introduced animals, including rodents, stoats, red deer (*Cervus elaphus*), brushtail possums (*Trichosurus vulpecula*), and cats (*Felis catus*) (Wardle, 1984). The avifauna is dominated by a range of relatively common, widespread native forest bird species, with a few less common native species and several introduced species.

2.2. Bird counting

Birds were counted using standard “5 min bird counts” (Dawson and Bull, 1975). Observers stood quietly at a permanently marked count station and recorded all species both seen and heard within an estimated 200 m radius during a 5-min period. Birds were not knowingly counted twice. Observations were made in settled weather and observers were trained in recognising bird species. Each count station was counted an equal number of times in the morning, middle of the day and afternoon during each series of counts. Between 1974 and 1984 counts were made in May, August, November and February and on each occasion four counters were used so that each station was counted six times over a few days. Between 2002 and 2007 birds were counted in May, November and February, and two counters were used so that each station was counted three times over a period of a few days. The same counters were used whenever possible, so that most counters were used over multiple years although there were no counters in common between the 1974–1984 counts and the 2002–2006 counts.

2.3. Statistical analysis

We looked for changes in the overall bird community structure using a non-parametric approach (Clarke, 1993). Bray–Curtis similarities were computed between each pair of samples using square root transformed data and then ordinated by non-metric multidimensional scaling to display and contrast the different sources of variation in assemblage structure. The significance of differences was tested using ANOSIM (Clarke, 1993). Analyses were implemented using PRIMER 6 and PERMANOVA software (Clarke and Gorley, 2006).

Table 1
Average bird counts during February in 1974–1984 and 2002–2007, and the probability of a difference between the two sets of counts from Model 2. I – invertebrates, F – fruit, N – nectar, V – bugs, leaves and flowers.

Species	Status	Diet	1974–1984	2002–2007	p	
Bellbird	<i>Anthornis melanura</i>	Endemic	I, F, N	2.8	1.7	<0.001
NZ tomtit	<i>Petroica macrocephala</i>	Endemic	I	0.9	0.8	<0.001
Grey warbler	<i>Gerygone igata</i>	Endemic	I	0.9	0.4	<0.001
Rifleman	<i>Acanthisitta chloris</i>	Endemic	I	0.6	0.2	<0.001
Tui	<i>Prosthemadera novaeseelandiae</i>	Endemic	I, F, N	0.8	0.6	0.024
Brown creeper	<i>Mohoua novaeseelandiae</i>	Endemic	I	0.1	0.1	0.455
Yellow-crowned Parakeet	<i>Cyanoramphus auriceps</i>	Endemic	I, F, N, V	0.1	0.2	<0.001
NZ robin	<i>Petroica australis</i>	Endemic	I	0.2	0.3	0.008
NZ fantail	<i>Rhipidura fuliginosa</i>	Native	I	0.4	0.4	0.347
Silveryeye	<i>Zosterops lateralis</i>	Native	I, F, N	1.2	6.4	<0.001
Blackbird	<i>Turdus merula</i>	Introduced	I, F	0.2	0.3	0.610

We used generalised linear models (McCullagh and Nelder, 1989) to look for changes in the bird count data for individual species of the common, widespread birds (Robertson et al., 2007). We assumed that bird counts were likely to have poisson or over-dispersed poisson distributions which we modelled using negative binomial distributions (Venables and Ripley, 2002). For our analyses every species was analysed separately, and every bird count provided a single record for that species. We also added all species counts together to undertake an all species analysis. The analyses were undertaken in the program R (R Development Core Team, 2009) using the function `glm.nb` in the MASS package (Venables and Ripley, 2002) with a log link function.

We only wanted to test for relatively simple patterns in change in abundance. We therefore constructed four sets of models of plausible relationships between the number of birds counted and time, and we used Akaike's Information Criterion (AIC) to determine which model was best supported by the data for each species (Burnham and Anderson, 2002). AIC differences between models greater than 2 were taken to indicate strong support for the model with the lower AIC.

The four plausible models considered were:

1. Bird abundance had not changed during the study.
2. Bird abundance had changed between the two sets of counts but was constant within both of them.
3. Bird counts decreased or increased at the same rate through the whole period of the study.
4. Bird counts changed at different rates in the two sets of counts. For example a species might decline in the first set of counts, but recover in the second.

In order to eliminate the effects of season, differences in abundance between counting stations, and seasonal movements of birds between stations, we included terms for season, station, and the interaction between season and station in all of our models. Our intention was not to examine the magnitude of these effects but to control for their possible effect.

In programming language R the four plausible models were represented by:

1. Number of birds counted $\sim 1 + \text{season} * \text{station}$.
2. Number of birds counted $\sim \text{set} + \text{season} * \text{station}$.
3. Number of birds counted $\sim 1 + \text{year} + \text{season} * \text{station}$.
4. Number of birds counted $\sim \text{set}/(1 + \text{year} + \text{season} * \text{station})$.

Where set is a factor variable with one level for each of the counting periods 1974–1984, 2002–2007. Year is a continuous variable. Season is a factor variable with one level for each time of year at which counts were carried out. Station is a factor variable with one level for each counting station.

3. Results

There was clear evidence of a change in the bird community across the years, as well as a change with altitude (Fig. 1; year $p = 0.001$, altitude $p = 0.001$). From 1974 through to 1983 the bird community was relatively similar, but in 1984 the community composition changed considerably. Although there was an 18 year gap in monitoring, the 1984 type of community was similar to that recorded in 2002–2005, followed by another change in trajectory in 2006 and 2007. Overall, the magnitude of change across years was similar to that experienced by changing in altitude from 455 m a.s.l. to 1425 m a.s.l.

Five of the common species (bellbird, New Zealand tomtit, grey warbler, rifleman and tui) were significantly more abundant in counts between 1974 and 1984 than they were after 2002 (Table 1). In contrast, three species (silveryeye, yellow-crowned parakeet and New Zealand robin) were significantly more abundant in counts after 2002 than they were between 1974 and 1984 (Table 1). The remaining three species (brown creeper, blackbird and New Zealand fantail) were equally abundant in both sets of counts (Table 1). The combined counts of all species declined throughout the study, though at a higher rate after 2002 (Table 1).

The best-supported model for each species indicated that the population trends were variable throughout the study period and often complex (Table 2, Fig. 2). The counts for bellbirds, New Zealand tomtits, grey warbler, New Zealand fantail, brown creeper and New Zealand robin all declined during the first set of counts (1974–1984), whereas rifleman, tui, yellow-crowned parakeet

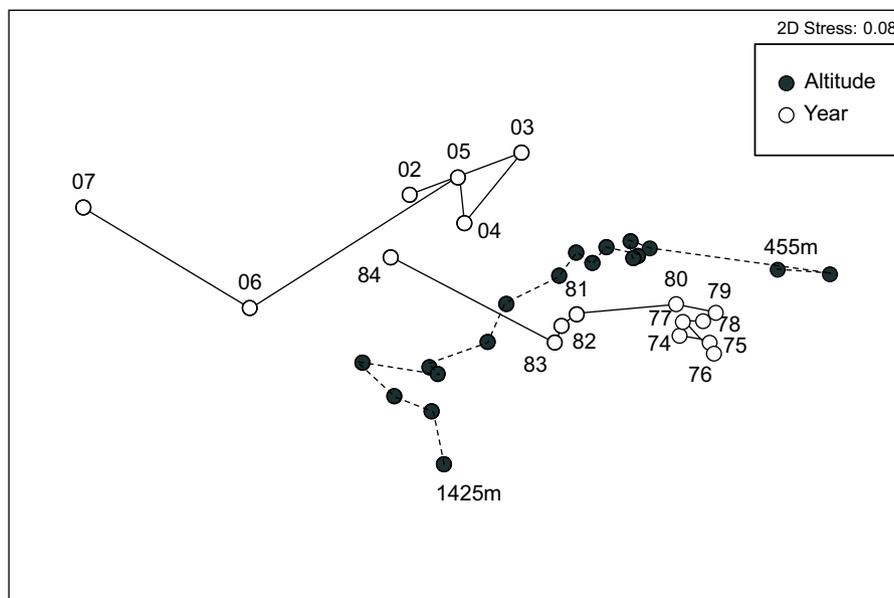


Fig. 1. Non-metric multidimensional scaling plot contrasting altitude and year as sources of variation in the forest bird community structure. All bird species were included in this analysis, including less common endemic species such as kaka (*Nestor meridionalis meridionalis*) and falcon (*Falco novaeseelandiae*) and introduced species such as chaffinch (*Fringilla coelebs*) and song thrush (*Turdus philomelos*).

Table 2
AIC values for four models of population change in 11 forest birds, and population growth rates for the best-supported models.

Species	AIC				Population growth		
	Model 1	Model 2	Model 3	Model 4	1974–2006	1974–1984	2002–2007
Bellbird	16552.1	16240.3	16131.2	15955.3*		0.95	1.11
NZ tomtit	11050.5	11037.8	11005.7	10933.1*		0.92	0.99
Grey warbler	10243.3	10116.1	10066.0*	10088.7	0.97		
Rifleman	7815.7	7652.1	7714.6	7621.3*		1.06	1.10
Tui	8920.6	8917.5	8921.2	8908.5*		1.03	0.96
Parakeet	2225.6	2194.3	2189.5*	2191.6	1.04		
NZ robin	5428.3	5423.3	5428.5	5393.5*		0.93	1.06
Brown creeper	2350.2	2351.6	2351.1	2437.0			
NZ fantail	7075.5	7076.6	7075.6	7053.8*		0.97	1.23
Silvereye	15072.5	14567.6	14547.5	14416.2*		1.05	0.93
Blackbird	4986.2	4987.9	4986.1	5031.6			
All species	26330.7	26200.6	26242.0	26162.7*		0.98	0.94

*Indicates the best supported model for each species, i.e., a model with an AIC value at least 2 less than that of the other models. The absence of a * indicates that two or more models were equally well supported.

and silvereye counts increased during this period. Similarly, there was a range of patterns during the second set of counts (2002–2006), with some species counts showing further decreases (grey warbler, brown creeper), whereas others increased (bellbird, rifleman, New Zealand fantail, yellow-crowned parakeet), remained relatively stable (New Zealand tomtit, New Zealand robin and blackbird), or fluctuated widely (silvereye). There was a gap of 16 years between the two sets of counts, during which some species apparently had a net decline (bellbird, rifleman, grey warbler), whilst others either had minimal net change (New Zealand tomtit, brown creeper, tui, New Zealand fantail, blackbird), or an increase (silvereye, New Zealand robin, yellow-crowned parakeet). There was no clear overall pattern of change for any particular period, rather species responded at different rates and in different ways throughout the study.

For most species that showed a change in counts during the study, there was apparently a greater change in abundance at lower altitudes, with a threshold at about 1000 m a.s.l. Bellbird, New Zealand tomtit, rifleman, grey warbler, and tui appeared to decrease in abundance below about 1000 m a.s.l. and increase or remain stable in abundance above 1000 m a.s.l. (Fig. 3). Indeed, rifleman almost completely disappeared from counting stations below 700 m after 2002, whereas they had been reasonably abundant at these counting stations between 1974 and 1984. Most of the increase in yellow-crowned parakeet and silvereye counts occurred at altitudes of less than about 1000 m a.s.l. (Fig. 3). New Zealand robin counts showed a different pattern as they appeared to increase in abundance at altitudes between 700 and 1000 m, but remained unchanged in abundance above and below this zone (Fig. 3). There was no change in the altitudinal distribution of brown creeper, New Zealand fantail or blackbird between 1974–1984 and 2002–2006, although brown creeper were only ever recorded above 1000 m a.s.l. (Fig. 3).

4. Discussion

There was a significant change in the bird community structure during this study. The communities were similar from 1974 to 1980, but then showed a continuous change with time. The bird community also changed with altitude which was not unexpected since we know that vegetation type and resources such as honeydew also change significantly with altitude (Beggs, 1991). The magnitude of change in bird communities was similar across time and across altitude. Since we generally consider the change in communities across one thousand meters of altitude to be substantial enough to be biologically significant, it is reasonable to argue that

the amount of change in community structure related to time is also substantial enough to be biologically significant.

There were several patterns observed in our study. There were five common and widespread endemic species (bellbird, New Zealand tomtit, rifleman, grey warbler, and tui) whose apparent abundance declined during the 30 years of this study. All of these species declined in abundance at low but not high altitudes. The decline of bellbird, rifleman and grey warbler was particularly substantial, although there was some evidence of recent recovery by both bellbird and rifleman. Similarly, New Zealand fantails initially decreased substantially, but then increased in recent years to the extent that there was no net change. Two species increased in apparent abundance between the two sets of counts but only at low altitudes (yellow-crowned parakeet and silvereye), and New Zealand robins apparently increased in abundance but only at mid-altitudes. Finally, two species did not change in apparent abundance, brown creeper which was only found at high altitude, and the introduced blackbird. Overall the total number of birds of the 11 species declined during our study.

Using counts of birds to detect population trends is confounded by changes in bird conspicuousness that is unrelated to abundance and by variability in the skills of bird counters. Statistical techniques have been developed using repeated counts that explicitly estimate both the abundance and the ability to detect birds and can thus remove the confounding effects of changing bird conspicuousness and variable observer skill (Kery et al., 2005). We initially attempted to use these techniques to analyse our bird counts but the low number of repeated counts after 2002 made this impossible. Counting birds using distance sampling techniques (Buckland et al., 2001) can specifically address problems of changing bird conspicuousness and observer variability, but distance sampling methods cannot retrospectively be applied to data collected using our counting technique, and our counts started before distance sampling techniques had been developed.

The altitude analysis we have undertaken provides some evidence that the apparent changes in bird abundance we detected were not the result of observer differences or simple changes in conspicuousness. Bellbirds, for example, appear to decrease in abundance between the two sets of counts, but the decrease only occurred at low altitudes. If observer differences were to explain the differences between the two sets of counts we would come to the conclusion that the 2002–2006 counters were worse at detecting bellbirds than the 1974–1984 counters when below 1000 m, but there was no difference between counters when above 1000 m. Similarly, if a change in bellbird conspicuousness were to explain the difference one would have to conclude that after 2002 bellbirds became less conspicuous below 1000 m but did not

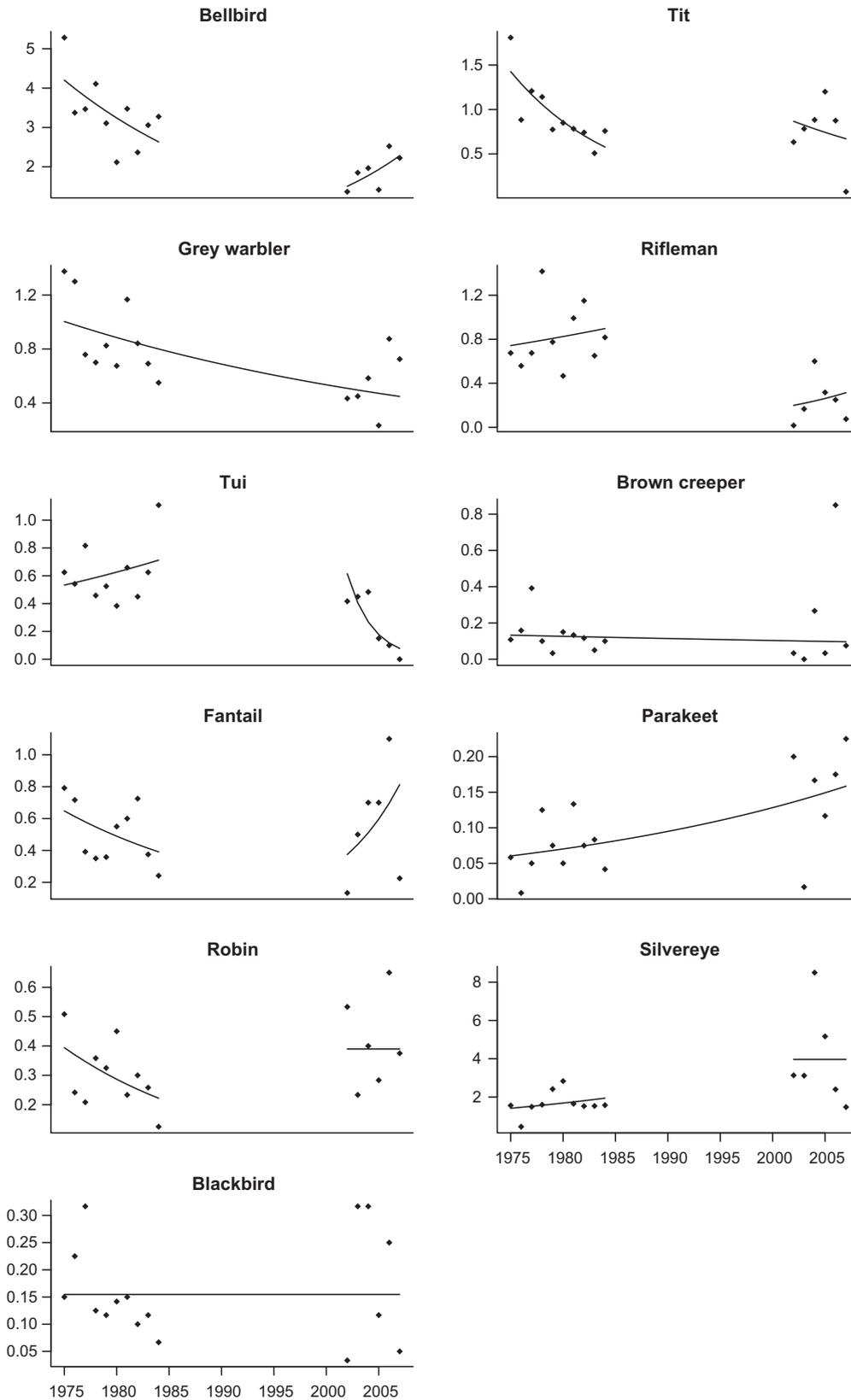


Fig. 2. Average number of each common bird species per 5-min bird count in February and the best supported trends in abundance (solid lines).

change in conspicuousness above 1000 m. The same sorts of conclusions would also have to be made for seven other species. In addition, the multivariate analysis showed that the 1984 bird counts were more similar to the 2002–2005 counts than to the

counts done in the early 1980s by the same set of counters. While it is possible that forests have changed in subtle ways at different altitudes that have resulted in bird conspicuousness changing differentially at different altitudes, we have no evidence (one way or

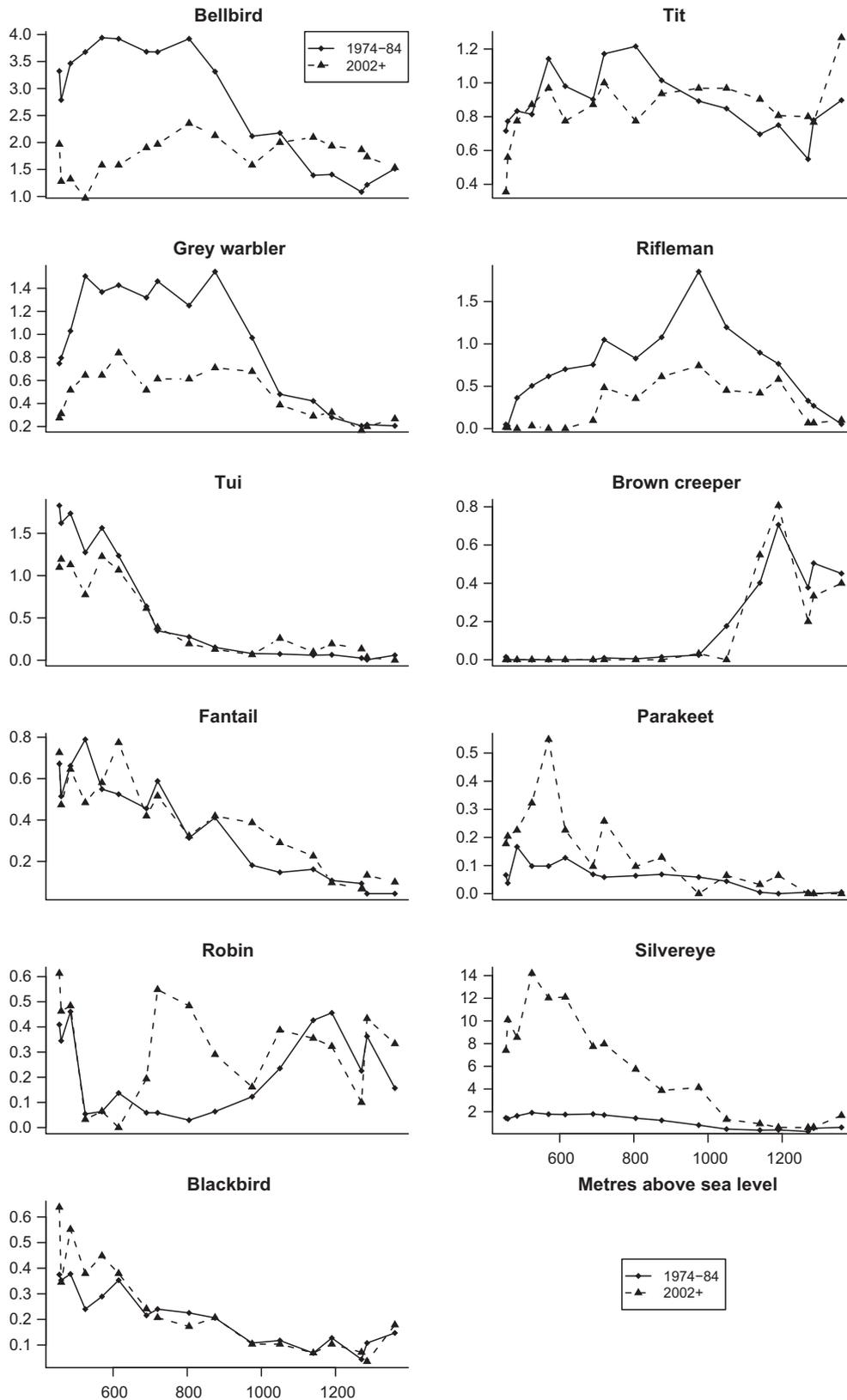


Fig. 3. The altitudinal distribution of common bird species in February 1974–1984 and 2002–2007. The Y axis is the mean number of birds counted at each counting station in February.

the other) for such change and it is clearly more parsimonious to conclude that the abundance of bellbirds and the seven other species have really changed.

There are two possible conclusions to account for these changes. Firstly, that there has been some change in the forest environment at low altitudes at Nelson Lakes that has led to

changes in the abundance of birds, but that this change has been less pronounced at high altitudes. Secondly, that the biota at low altitudes was more susceptible to a change in the forest environment than the biota at high altitudes.

The human-induced decline or extinction of most species is usually attributed to four major drivers; habitat loss or change, overexploitation, the introduction of alien species, and extinction cascades (Diamond, 1984). Mt. Misery is in the midst of an extensive National Park (>100,000 ha) that has not experienced habitat loss or overexploitation of species for many decades. Nor is climate change a likely driver, since New Zealand's climate has not changed substantially (Withers et al., 2009) and in any case the geographic distribution of all of the species that declined includes areas both cooler and warmer than experienced at Mt. Misery (Robertson et al., 2007). A similarly long-term study at Hubbard Brook concluded that natural forest succession was the most important local factor affecting bird abundance (Holmes and Sherry, 2001), but our study site is mature forest that has undergone minimal successional change over the 30 years of our study. Furthermore, all of the species studied are non-migratory, so were not susceptible to changes in other habitats. It is possible that there are complex, interacting drivers of population decline (Didham et al., 2007), but we think that the most likely explanation for the altitude-related changes in bird abundance we observed is the effect of introduced animals through their predation, competition for food, and vegetation modification. As elsewhere in New Zealand, periodic plagues of rodents and stoats are likely to have caused reductions in many species of forest birds through predation, but this is probably not sufficient to explain the patterns of change in abundance that we observed. We suggest that introduced possums and wasps are two large changes in the biology of Nelson Lakes forests that occurred during this study and are likely to have added to the ongoing impact of rat and stoat predation.

Brushtail possums were introduced into New Zealand from Australia in the mid 19th century and have subsequently spread throughout North and South Islands from coast to tree-line (Clout, 2006). They reached the Nelson Lakes region in about 1960 (Pracy, 1974) and their peak densities are likely to have occurred 20–30 years later, during the first set of our bird counts. Possums are known to prey on nesting birds (Brown et al., 1993; Moorhouse et al., 2003) and through their browsing can change the structure and composition of forests (Payton, 2000). Both predation and browsing could lead to changes in the abundance of forest birds. Furthermore, at Nelson Lakes their abundance declines with altitude (Clout and Gaze, 1984) and this could explain why we found that changes in some species abundances was greatest at low altitudes.

Common wasps also arrived in the Nelson Lakes area during the course of our study (in the mid 1980s) and quickly became very abundant. They are known to prey on nestling birds (Moller, 1990), and by eating insects, honeydew and nectar they compete with insectivorous and nectar feeding birds (Beggs, 2001; Beggs and Wardle, 2006). Common wasps are generalist insect predators and in these *Nothofagus* forests their predation rate is so high that some species of insects have virtually no chance of surviving the peak wasp season (Beggs and Rees, 1999; Toft and Rees, 1998). Interestingly, the five endemic bird species that declined in abundance over the study period are all either insectivorous, or rely heavily on invertebrates during the breeding season. Common wasps are most abundant in the vegetation zones below about 1000 m a.s.l., particularly in the mid-altitude red/silver beech zone (Beggs, 1991), so their altitudinal distribution directly aligns with the 1000 m a.s.l. threshold we detected for change in abundance of seven bird species.

The increase in abundance of yellow-crowned parakeets is of note, since parakeets are generally considered to be in decline throughout mainland New Zealand (Elliott et al., 1996; Kearvell et al., 2002). It is possible that the impact of invasive animals on parakeets has been counteracted by an increase in reproductive rate caused by an increase in the frequency of mast beech seed fall years. Parakeets rely heavily on beech seed to feed their young (Kearvell et al., 2002), and there has been an increase in the frequency of major seedfall events in this region over the period of our study (Schauber et al., 2002; Wilson et al., 1998).

There is no obvious explanation for the apparent increases in abundance of silvereyes and New Zealand robins. However, since these two species appear not to be susceptible to the changes caused by increasing possum and wasp abundance, they might well benefit from the declines in abundance of competing forest bird species.

Declines in some rare native forest-dwelling birds have been well documented (Hooson and Jamieson, 2003; Powlesland et al., 2006) and this study shows that there have also been declines in some more common species. Clearly commonness is not a good indicator of the resistance of species to further change. Furthermore, we speculate that some of the declines and increases that we observed might not be caused solely by long-established agents of decline such as rats and stoats, but by more recent changes such as peak possum abundance and the arrival of a new species of wasp.

It seems likely that invasive species are primarily responsible for the ongoing decline in native biodiversity and that in the New Zealand context invasive species remain a major conservation issue. Whatever the explanation, it is apparent that the abundance of even the common and widespread forest birds has undergone significant change in the last 30 years and there is no evidence of a new equilibrium in forest bird community structure having been reached.

Clearly it is not enough just to reserve large tracts of native ecosystem, but active management of invasive species and monitoring of common as well as rare native species may be required if we want to maintain the diversity of native forest birds in New Zealand.

Acknowledgments

Thanks to all the people who undertook bird counts over the 30 years of this study including Peter Dilks, Bruce Thomas, Matt Maitland, Genevieve Taylor, David Butler and Peter Gaze. Marti Anderson advised on multivariate statistics. We thank Mick Clout, Mark Hauber and two anonymous reviewers for comments on the manuscript. Financial support was provided by Ecology Division, Department of Scientific and Industrial Research, Department of Conservation, and the University of Auckland.

References

- Alley, J.C., Berben, P.H., Dugdale, J.S., Fitzgerald, B.M., Knightbridge, P.I., Meads, M.J., Webster, R.A., 2001. Responses of litter-dwelling arthropods and house mice to beech seeding in the Orongorongo Valley, New Zealand. *Journal of the Royal Society of New Zealand* 31, 425–452.
- Atkinson, I.A.E., 1978. Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. In: Dingwall, P.R., Atkinson, I.A.E., Hay, C. (Eds.), *The Ecology and Control of Rodents in New Zealand Nature Reserves*. Department of Lands and Survey, Wellington, pp. 7–25.
- Beggs, J.R., 1991. Altitudinal variation in abundance of common wasps *Vespula vulgaris*. *New Zealand Journal of Zoology* 18, 155–158.
- Beggs, J.R., 2001. The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biological Conservation* 99, 17–28.
- Beggs, J.R., Rees, J.S., 1999. Restructuring of Lepidoptera communities by introduced *Vespula* wasps in a New Zealand beech forest. *Oecologia* 119, 565–571.

- Beggs, J.R., Wardle, D.A., 2006. Keystone species: competition for honeydew among exotic and indigenous species. In: Allen, R.B., Lee, W.G. (Eds.), *Biological Invasions in New Zealand*. Springer-Verlag, Berlin, Heidelberg, pp. 281–294.
- Blackburn, T.M., Lockwood, J.L., Cassey, P., 2009. *Avian Invasions: The Ecology and Evolution of Exotic Birds*. Oxford University Press, Oxford.
- Brow, A.K., Bruce, T.A., Chisnall, D.T., Gasson, P.A., Leggett, S.A., Paton, B.R., Hawes, M., 2008. Rotoiti Nature Recovery Project Annual Report 2006–2007, Occasional Publication 73, Department of Conservation, Nelson.
- Brown, K., Innes, J., Shorten, R., 1993. Evidence that possums prey on and scavenge birds' eggs, birds and mammals. *Notornis* 40, 169–177.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Burrows, L.E., Allen, R.B., 1991. Silver beech (*Nothofagus menziesii* (Hook. f.) Oerst) seedfall patterns in the Takitimu Range, South Island, New Zealand. *New Zealand Journal of Botany* 29, 361–365.
- Cagnolo, L., Valladares, G., Salvo, A., Cabido, M., Zak, M., 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conservation Biology* 23, 1167–1175.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143.
- Clarke, K.R., Gorley, R.N., 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- Clout, M.N., 2006. Keystone aliens? The multiple impacts of brushtail possums. In: Allen, R.B., Lee, W.G. (Eds.), *Biological Invasions in New Zealand*. Springer, Berlin.
- Clout, M.N., Gaze, P.D., 1984. Brushtail possums (*Trichosurus vulpecula* Kerr) in a New Zealand beech (*Nothofagus*) forest. *New Zealand Journal of Ecology* 7, 147–155.
- Cooper, A., 1994. Ancient DNA sequences reveal unsuspected phylogenetic relationships within New Zealand wrens (Acanthistidae). *Experientia* 50, 558–563.
- Craig, J., Anderson, S., Clout, M., Creese, B., Mitchell, N., Ogden, J., Roberts, M., Ussher, G., 2000. Conservation issues in New Zealand. *Annual Review of Ecology and Systematics* 31, 61–78.
- Dawson, D.G., Bull, P.C., 1975. Counting birds in New Zealand forests. *Notornis* 22, 101–109.
- Dawson, D.G., Dilks, P.J., Gaze, P.D., McBurney, J.G., Wilson, P.R., 1978. Seasonal differences in bird counts in forests near Reefton, South Island, New Zealand. *Notornis* 25, 417–427.
- Diamond, J.M., 1984. 'Normal' extinctions of isolated populations. In: Nitecki, M.H. (Ed.), *Extinctions*. University of Chicago Press, Chicago, pp. 191–246.
- Didham, R.K., Tylianakis, J.M., Gemmill, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution* 22, 489–496.
- Elliott, G.P., 1996. Mohua and stoats: a population viability analysis. *New Zealand Journal of Zoology* 23, 239–247.
- Elliott, G.P., Dilks, P.J., O'Donnell, C.F.J., 1996. The ecology of yellow-crowned parakeets (*Cyanoramphus auriceps*) in Nothofagus forest in Fiordland, New Zealand. *New Zealand Journal of Zoology* 23, 249–265.
- Gaston, K.J., Fuller, R.A., 2007. Biodiversity and extinction: losing the common and the widespread. *Progress in Physical Geography* 31, 213–225.
- Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution* 23, 14–19.
- Gregory, R.D., Vorisek, P., Van Strien, A., Meyling, A.W.G., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P., Burfield, I.J., 2006. Population trends of widespread woodland birds in Europe. In: *Conference on Woodland Birds – Their Ecology and Management*. Blackwell Publishing, Leicester, England, pp. 78–97.
- Holdaway, R.J., 1999. Introduced predators and avifaunal extinction in New Zealand. In: MacPhee, R.D.E. (Ed.), *Extinctions in Near Time: Causes, Contexts, and Consequences*. Kluwer Academic/Plenum Publishers, New York.
- Holmes, R.T., Sherry, T.W., 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk* 118, 589–609.
- Hooson, S., Jamieson, I.G., 2003. The distribution and current status of New Zealand Saddleback *Philesturnus carunculatus*. *Bird Conservation International* 13, 79–95.
- Kearvell, J.C., Young, J.R., Grant, A.D., 2002. Comparative ecology of sympatric orange-fronted parakeets (*Cyanoramphus malherbi*) and yellow-crowned parakeets (*C. auriceps*), South Island, New Zealand. *New Zealand Journal of Ecology* 26, 139–148.
- Kery, M., Royle, J.A., Schmid, H., 2005. Modeling avian abundance from replicated counts using binomial mixture models. *Ecological Applications* 15, 1450–1461.
- King, C.M., 1984. *Immigrant Killers: Introduced Predators and the Conservation of Birds in New Zealand*. Oxford University Press, Auckland.
- Levin, P.S., Holmes, E.E., Piner, K.R., Harvey, C.J., 2006. Shifts in a Pacific ocean fish assemblage: the potential influence of exploitation. *Conservation Biology* 20, 1181–1190.
- Masseti, M., 2009. Mammals of the Mediterranean islands: homogenisation and the loss of biodiversity. *Mammalia* 73, 169–202.
- McCullagh, P., Nelder, J.A., 1989. *Generalised linear models*, second ed. Chapman and Hall, London.
- Moller, H., 1990. Wasps kill nestling birds. *Notornis* 37, 76–77.
- Moorhouse, R., Greene, T., Dilks, P., Powlesland, R., Moran, L., Taylor, G., Jones, A., Knegtman, J., Wills, D., Pryde, M., Fraser, I., August, A., August, C., 2003. Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: reversing the decline of a threatened New Zealand parrot. *Biological Conservation* 110, 33–44.
- Murphy, E.C., Dowding, J.E., 1995. Ecology of the stoat in *Nothofagus* forest: home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology* 19, 97–109.
- Pauly, D., Christensen, V., Guenette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. *Nature* 418, 689–695.
- Payton, I.J., 2000. Damage to native forests. In: Montague, T.L. (Ed.), *The Brushtail Possum: Biology, Impact and Management of an Introduced Marsupial*. Landcare Research, Lincoln, New Zealand, pp. 111–125.
- Powlesland, R.G., Merton, D.V., Cockrem, J.F., 2006. A parrot apart: the natural history of the kakapo (*Strigops habroptilus*), and the context of its conservation management. *Notornis* 53, 3–26.
- Pracy, L.T., 1974. *Opossums (1)*. *New Zealand Nature Heritage* 3, 873–882.
- R Development Core Team, 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <<http://www.R-project.org>>.
- Rayner, M.J., Hauber, M.E., Imber, M.J., Stamp, R.K., Clout, M.N., 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences of the United States of America* 104, 20862–20865.
- Robertson, C.J.R., Hyvönen, P., Fraser, M.J., Pickard, C.R., 2007. *Atlas of Bird Distribution in New Zealand 1999–2004*. The Ornithological Society of New Zealand, Inc., Wellington.
- Schauber, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B., Payton, I.J., Wilson, P.R., Cowan, P.E., Brockie, R.E., 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* 83, 1214–1225.
- Thomson, A.P., 1971. *Utilisation of South Island Beech Forest*. Government Printer, Wellington, p. 29.
- Toft, R.J., Rees, J.S., 1998. Reducing predation of orb-web spiders by controlling common wasps (*Vespula vulgaris*) in a New Zealand beech forest. *Ecological Entomology* 23, 90–95.
- Towns, D.R., Atkinson, I.A.E., Daugherty, C.H., 2006. Have the harmful effects of introduced rats on islands been exaggerated. *Biological Invasions* 8, 863–891.
- Van Dyck, H., Van Strien, A.J., Maes, D., Van Swaay, C.A.M., 2009. Declines in common, widespread butterflies in a landscape under intense human use. *Conservation Biology* 23, 957–965.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth ed. Springer-Verlag, New York.
- Wardle, J., 1984. *The New Zealand Beeches: Ecology, Utilisation and Management*. New Zealand Forest Service, Wellington.
- Wilson, P.R., Karl, B.J., Toft, R.J., Beggs, J.R., Taylor, R.H., 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological Conservation* 83, 175–185.
- Withers, C.S., Krouse, D.P., Pearson, C.P., Nadarajah, S., 2009. Modelling temperature trends in New Zealand. *Environmental Modeling and Assessment* 14, 231–249.
- Worthy, T.H., Holdaway, R.N., 1993. Quaternary fossil faunas from caves in the Punakaiki area, West Coast, South Island, New Zealand. *Journal of the Royal Society of New Zealand* 23, 147–254.