Quantifying the benefits of long-term integrated pest control for forest bird populations in a New Zealand temperate rainforest

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Abstract: The control of introduced mammalian predators has become a standard response to protecting the viability of threatened wildlife species on oceanic islands. However, examples of successful outcomes of integrated pest control in forests are few. We investigated the efficacy of a pest control programme in the Landsborough Valley, New Zealand, during 1998–2009, which used continuous trapping to control mustelids and pulsed aerial application of the toxin 1080 to control rats (Rattus spp.) and brushtail possums (Trichosurus vulpecula). We predicted recovery in the populations of mōhua (Mohoua ochrocephala) and other predator-sensitive hole-nesting birds and maintenance of numbers of South Island kaka (Nestor meridionalis meridionalis). In addition, we examined whether annual mean counts of mōhua and kaka, as potential ‘population indicator species’, could predict those of other forest bird species. Annual counts of nine species (eight indigenous: bellbird Anthornis melanura, brown creeper Mohoua novaeseelandiae, fantail Rhipidura fuliginosa, grey warbler Gerygone igata, mōhua, rifleman Acanthisitta chloris, tui Prosthemadera novaeseelandiae and yellow-crowned parakeet Cyanoramphus auriceps; one introduced: song thrush Turdus philomelos) showed significant increases during the 12-year study period. South Island kaka and redpoll (Carduelis flamméa) showed no change with time. In general, trends in the two focal threatened taxa (mōhua and kaka) were poor predictors of trends in other bird species. Lack of correlation in annual counts between bird species that share a recovery trajectory are likely due to differences in breeding biology and resource use. Our results suggest that an integrated strategy for predator management is effective at mitigating the impacts of predation by introduced mammals on forest birds, including the most vulnerable species, at a landscape scale.

Keywords: 1080; browsers; mast; Mohoua; Nestor; Nothofagus; poisoning; population indicator species; predators; trapping

Introduction

The introduction of mammalian predators to oceanic islands has resulted in declines and extinctions of numerous endemic species on these islands (Atkinson 1989; Jones et al. 2008). Therefore, the control or eradication of introduced predators has become a major conservation priority in these areas (Towns et al. 2006). Developing effective control techniques can be challenging, particularly when multiple predator species occur sympatrically, because of interspecific variability in predator cycles and the need to implement multiple control techniques (e.g. Saunders & Norton 2001; Burbidge & Morris 2002; Burrows et al. 2003; Donlan & Wilcox 2008).

Significant declines in many species of forest birds in response to predation by introduced mammalian predators have been widely documented in New Zealand (reviewed by Innes et al. 2010). Likewise, the impacts of browsing and predation by introduced brushtail possums (Trichosurus vulpecula) on forest structure and threatened species are well documented (O’Donnell 1995; Payton 2000; Sadleir 2000). Based on these impacts, attempts to control predators and browsers are now widespread in New Zealand forests, even though the benefits of control have only been documented for a limited number of bird and plant species (e.g. Sweetapple et al. 2002; Basse et al. 2003; Innes et al. 2004; Urlich & Brady 2005; Nugent et al. 2010). Pest control operations in New Zealand comprise a range of scenarios, from one-off pest specific operations (O’Donnell et al. 1996) and longer term continuous trapping (Dilks et al. 2003) or pulsed poison operations (Basse et al. 2003), to integrated and sustained control that incorporates a number of control techniques (Baber et al. 2009). While there is a growing list of examples of successful pest control operations using trapping or poisoning for single threatened species or suites of species, the benefits of longer term, integrated pest control programmes are not well understood.

An inventory of the forest bird population of the Landsborough Valley was conducted in 1985 as part of a wider biodiversity assessment of forests in South Westland, New Zealand (O’Donnell & Dilks 1986). The inventory noted significant bird populations in the valley, including the largest population of mōhua (yellowhead Mohoua ochrocephala) remaining in South Westland and one of the largest populations of South Island kākā (Nestor meridionalis meridionalis) in the region. The site was recommended for protection, and subsequently as part of the South Westland World Heritage Area (Department of Conservation 1989). At the time, research indicated that predation by stoats (Mustela erminea) was a major cause of decline in mōhua populations throughout the South Island, and that, for populations to be maintained or recover, predator control at those sites would be required (Elliott 1996; O’Donnell 1996a; O’Donnell et al. 1996). Research also indicated that the distribution of South Island kākā was shrinking dramatically in the region and that kākā abundance was highest at sites not yet colonised by brushtail possums and declined with increasing possum densities (O’Donnell & Dilks 1986; Rose et al. 1990). Possums were beginning to colonise...
the Landsborough Valley in the early 1980s and control of their spread was recommended to protect South Island kākā and populations of mistletoes (Peraxilla spp.) from potential decline. Mistletoes form a significant seasonal food source for South Island kākā, but they are also highly palatable to possums and therefore at risk from defoliation (O’Donnell & Dilks 1986, 1994; Sweetapple 2008).


Concerns for maintaining plant communities in the Landsborough Valley led to a control programme for possums being initiated by the Department of Conservation (DOC) in 1994. As concerns for the continued viability of the mōhua and kākā populations increased, the possum-control programme was integrated with continuous trapping of stoats and rodents in 2000. The integrated programme aimed to control sufficient numbers of stoats, rodents and possums to maintain populations of forest birds and possum-palatable species (e.g. mistletoe, fuchsia Fuchsia excorticata, Raukaua spp. and Pseudopanax spp.).

The primary objective of this study was to monitor the long-term response of forest birds to integrated pest control (a combination of ground trapping for stoats and aerial poisoning aimed at controlling brushtail possums and rats (Rattus spp.)). We predicted that if integrated pest control was effective we should detect: (1) recovery in numbers of mōhua and other hole-nesting birds; (2) maintenance of the high South Island kākā numbers in the study area (as opposed to dramatic declines documented in other parts of South Westland); and (3) a general recovery of forest bird numbers.

Because threatened species receive a disproportionate share of conservation spending and attention compared with common species, it is useful to know whether (and how) their management contributes indirectly to the preservation of other species (Bonn et al. 2002; Tognelli 2005). The presence of mōhua (Nationally Vulnerable; Miskelly et al. 2008) and South Island kākā (Nationally Endangered; Miskelly et al. 2008) in our study area provided an opportunity to examine their use as population indicator species (a species whose population trends can be used as an index of trends in other species; Hoare et al. 2010) for a range of other forest birds in a situation with a shared ecological driver (control of introduced mammalian predators). Threatened species, by definition, are the species most vulnerable to threat processes and thus can function well as indicators of trends in biodiversity generally (Lawler et al. 2003; Warman et al. 2004; Tognelli 2005; Larsen et al. 2007). However, despite many studies that target threatened and rare species to set priorities for land conservation, we found no evidence of threatened species being evaluated as population indicator species in New Zealand. As a result we also examined the degree to which annual counts of mōhua and South Island kākā could be used to predict counts of other forest birds.

Methods

Study area

The study was conducted in the mid-Landsborough Valley, South Westland, New Zealand (43°S, 169°E; Fig. 1). The study area comprised forested lower valley slopes, fans and terraces on the eastern side of the Landsborough River from McKerrow Creek in the north to Fraser Creek in the south (c. 7 km, 900 ha). The canopy forest is almost entirely silver beech (Nothofagus menziesii), with occasional subcanopy Hall’s totara (Podocarpus hallii) and rarely kāmahi (Weinmannia racemosa). Large mistletoes (Peraxilla colensoi, P. tetrapetala) are common epiphytes. The understorey is sparse and the most common shrubs include broadleaf (Griselinia littoralis), Coprosma spp., haumakaroa (Raukaua simplex), fuchsia, fivefinger (Pseudopanax arboreus) and weeping mapou (Myrsine divaricata). Ground cover is dominated by leaf litter and beds of moss.

Plant phenology

The amount of beech seedfall in a year is a clear indicator of predator levels and predation risk over the subsequent year (King 1983; O’Donnell & Phillipson 1996) and beech seedling indicates that food resources are sufficient for kākā to breed (O’Donnell & Dilks 1994; Moorhouse 1997). Therefore, because the flowering intensity of silver beech (and the resultant seedfall) varies considerably from year to year, the phenology of silver beech was monitored over the duration of

Figure 1. Location of the Landsborough Valley, South Island, New Zealand.
the study at Patsy Creek in the lower Landsborough Valley. Beech seedfall typically occurs in autumn (February–March) through to early spring, with the majority of seed falling in March–May (Wardle 1984). Seedfall was monitored from March to May each year using the standardised New Zealand protocols (sensu Wardle 1984). Seeds were collected in standard funnels (plastic funnels 0.28 m in diameter, Gyro Plastics, Lower Hutt) placed along a random line-transect (8 funnels, 1.25 m off the ground, 50 m apart, > 50 m away from a forest edge or 20 m away from a canopy gap). Seeds that fell into funnels were collected in stockings fitted over the narrow ends of the funnels. Funnels were opened on 1 March and closed on 31 May each year. At the end of the collecting period, all seeds were counted and the number of seeds per square metre was calculated. Wardle (1984) defined masting events as: full (or heavy) = >4000 seeds m–2, partial = 500–4000 seeds m–2, poor = <500 seeds m–2.

**Pest control**

Three techniques for controlling mammalian pests have been used at the study site: standard Fenn trapping (King et al. 1994) aimed at stoats; ground control (trapping and poisoning) aimed at brushtail possums; and aerial bait application using baits impregnated with the toxin sodium fluoroacetate (compound 1080) aimed primarily at possums and rats.

The first operation (8585 ha) to control possums in the study area involved ground trapping (using baited Victor traps set along bush edges) and poison baiting (using cyanide baits on ridges), and was carried out in January–March 1994. Since then, possum control has been by periodic aerial application of 1080-laced baits (8-g cereal pellets, 0.15% w/w 1080 RS5 bait) sown at 2 kg ha–1 after a prefeed drop of non-toxic 6-g 1080-laced baits (8-g cereal pellets, 0.15% w/w 1080 RS5) aimed at stoats; ground control (trapping and poisoning) aimed at brushtail possums; and aerial bait application using baits impregnated with the toxin sodium fluoroacetate (compound 1080) aimed primarily at possums and rats.

Counts were undertaken over three consecutive days by a team of three expert bird counters. All bird species seen and heard within 5-min periods were counted at 122 count stations. Counts were carried out in standardised fine conditions between 0900 and 1500 hours to avoid times of the day when conspicuousness of birds is most variable (dawn and dusk). To ensure independence, stations were spaced at 200-m intervals along a transect through habitats representative of the study area (Dawson 1975). The transect followed the forest edge from McKerrow Creek down the valley to Fraser Creek, then turned inland and ran back up the valley, parallel with the edge but 200–500 m into the forest. One count per station was conducted, except for the central 65 stations, which were counted twice on each occasion (n = 177 counts).

**Data analysis**

We used generalised linear mixed-effects models to investigate whether trends in bird counts were explained by time (year) and amount of beech seedfall (seeds m−2 year−1) for each bird species counted. Models contained counts as the response variable, year and seedfall as predictor variables, and count station as a random effect to account for the repeated measures nature of the study. Individual models for each species were fitted using a Poisson distribution. We used the statistical programme R (version 2.12.1; R Development Core Team 2010) for all analyses. Predator captures from Fenn-trapping were not included in the model because seedfall is the best predictor of likely predation pressure during the following bird breeding season (King 1983; O’Donnell & Philippson 1996) and an unknown number of predators (likely the majority) would have been killed following toxin applications.

We then used Bayesian techniques to evaluate the two threatened species (mōhua and South Island kākā) as potential indicators of population trends for every other species, by fitting a multivariate linear regression model with an AR1 autoregressive structure. For these analyses we used only the continuous data series from 2002 to 2009 (i.e. counts from 1998 were excluded). Bayesian inference via Markov chain Monte Carlo (MCMC) methods allows greater flexibility in model fitting compared with maximum-likelihood analyses (Link et al. 2002; Gelman et al. 2004; Royle & Dorazio 2006), including the ability to model temporal dependence. Specifically, we assumed that the observations were drawn from a multivariate normal distribution with mean of the indicator species counts $X_j$ and variance-covariance matrix $\Sigma$ given by $T$. The $\mu_j$ were related to the indicator species counts $X_j$ according to the linear model $\mu_j = \beta_0 + \beta_jX_j$.

We assumed non-informative normal priors for the $\beta$ terms ($\beta_{0} \sim N(0,10^6)$ and $\beta_{j} \sim N(0,10^6)$) for all indicator species. The variance-covariance matrix $\Sigma$ was structured to reflect an AR1
autoregressive power correlation structure. The covariance of successive observations over time was described by \( \text{cov}(y_{ij}, y_{i(j+1)}) = \rho/\tau \) where \( \rho \) is the correlation coefficient and \( \tau \) is the inverse of the sample variance. We assumed a uniform prior on \( \rho \) from 0 to 1, and a uniform distribution for the prior on \( \tau \) from 0 to 100.

We fitted the models in the software WinBUGS (version 1.4.3; Imperial College and MRC, UK). After convergence, a further 10 000 iterations were used for inference. Positive and negative correlations between species were identified using 95% credible intervals on the slope (\( \beta_{ij} \)) terms for which the limits excluded zero. Positive trends are defined as those in which interannual changes are in the same direction and negative trends are those that are divergent.

## Results

### Seedfall and predator trap catch

Silver beech seedfall was recorded in all years, with partial mast or full mast occurring in five of the 11 years (Fig. 2). There were 118 rounds of trap checking in the study area during the 10 years (2000–2010) of the study period, resulting in the trapping of 806 predators representing three species. The majority were stoats (\( n = 608, 75.4\% \)), with most of the remainder being ship rats (\( Rattus rattus \); \( n = 189, 23.5\% \)) and a few mice (\( Mus musculus \); \( n = 9, 1.1\% \)). There was marked variation in annual captures of predators. Stoats were caught in relatively high numbers in four of the 10 years (Fig. 3). Three of these years coincided with partial or full beech mast (2000, 2006, 2008; Fig. 2), but captures were low after the partial mast of 2003.
Trends in bird counts
Between 168 and 177 bird counts were undertaken annually, except in 2006 when counting was curtailed by poor weather (n = 113 counts). We analysed counts for 15 bird species (see Table 1 for scientific names) that were counted >100 times during all counts at all stations (Fig. 4). Eight indigenous species (bellbird, brown creeper, fantail, grey warbler, mōhua, rifleman, tūī and yellow-crowned parakeet) and one introduced species (song thrush) showed significant (P < 0.05) increases between 1998 and 2009 (Fig. 4, Table 1). South Island kākā and redpoll showed no change with time. Two indigenous species (silvereye, tomtit) and two introduced species (blackbird, chaffinch) showed a significant decline (Table 1).

Counts for seven bird species (blackbird, mōhua, redpoll, rifleman, silvereye, tomtit and yellow-crowned parakeet) were higher in years when seedfall was also high (Table 1). Fewer bellbird and South Island kākā were recorded in years with high seedfall (Table 1).

Trends in the mean annual counts of South Island kākā in the Landsborough Valley were negatively correlated with trends in mōhua, tomtits and yellow-crowned parakeets (Fig. 5). Trends in the mean annual counts of mōhua were positively correlated with riflemen and yellow-crowned parakeets (Fig. 6). Mean annual counts in other taxa were not correlated with either South Island kākā or mōhua counts (Figs 5 & 6).

Figure 4. Annual mean counts of birds per five-minute count in the mid-Landsborough Valley, 1998–2009. Trends were significant (P < 0.05) for all bird species except South Island kākā and redpoll. See Table 1 for scientific names of birds.

Table 1. Influence of year and seedfall on trends in bird counts in the Landsborough Valley, 1998–2009. Generalised linear mixed-effects models contained counts as the response variable, year and seedfall as predictor variables, and count station as a random effect (* = significant at P < 0.05).

<table>
<thead>
<tr>
<th>Species</th>
<th>Scientific name</th>
<th>Year</th>
<th>Z-value</th>
<th>P-value</th>
<th>Seeds</th>
<th>Z-value</th>
<th>P-value</th>
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<tr>
<td>Bellbird</td>
<td>Anthornis melanura</td>
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<td>10.924</td>
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<td>−1.241</td>
<td>0.022*</td>
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<td>Blackbird</td>
<td>Turdus merula</td>
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<td>−8.378</td>
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<td>5.124</td>
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<tr>
<td>Brown creeper</td>
<td>Mohoua novaeseelandiae</td>
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<tr>
<td>Chaffinch</td>
<td>Fringilla coelebs</td>
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<td>−7.805</td>
<td>&lt;0.001*</td>
<td></td>
<td>1.205</td>
<td>0.228</td>
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<td>0.023*</td>
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<td>0.388</td>
<td>0.698</td>
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<td>Gerygone igata</td>
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<td>2.289</td>
<td>0.022*</td>
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<td>0.548</td>
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<td>Kākā (South Island)</td>
<td>Nestor m. meridionalis</td>
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<td>0.539</td>
<td>0.590</td>
<td></td>
<td>−7.126</td>
<td>&lt;0.001*</td>
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<td>15.331</td>
<td>&lt;0.001*</td>
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<td>4.875</td>
<td>&lt;0.001*</td>
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<tr>
<td>Redpoll</td>
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<td>−0.833</td>
<td>0.404</td>
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<td>3.333</td>
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</tr>
<tr>
<td>Rifleman</td>
<td>Acanthisitta chloris</td>
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<td>6.018</td>
<td>&lt;0.001*</td>
<td></td>
<td>2.044</td>
<td>0.041*</td>
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<td>Silvereye</td>
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<td></td>
<td>2.898</td>
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Discussion

Response of birds to management

Relative abundance of the majority of forest birds in the Landsborough Valley changed following the implementation of integrated pest control, with increases in nine species and no decreases in abundance in another two species during the period of study. The increase in the relative abundance of mōhua, one of the two species most vulnerable to predator impacts, was particularly notable. Dramatic declines in mōhua have occurred over the last 40 years in most South Island forests as a result of predation by introduced rats and stoats (Gaze 1985; O’Donnell & Dilks 1986; Elliott 1996; Dilks et al. 2003). Declines have been reversed at a local scale (<100 ha) through intensive trapping of stoats (O’Donnell et al. 1996; Dilks 1999). However, when these techniques were applied at a landscape scale (13,000 ha), but did not include specific rat control, declines continued (Dilks et al. 2003). In contrast, the translocation of mōhua to predator-free offshore islands has been highly successful, with large populations now established on eight islands (R. Cole, DOC, Invercargill, pers. comm.). Mōhua counts in the Landsborough Valley increased...
from a low of 14 birds encountered when the count stations were established in 1992 (O'Donnell et al. 1996b) to a cumulative sum of >300 birds recorded on the five-minute counts during 2007–2009.

In the Landsborough Valley, the forecast decline in numbers of South Island kākā (Rose et al. 1990; Veltman 2000) did not eventuate, and we suggest this may in part be due to the protection from predation provided by the pest control operation in the valley. We did not necessarily expect South Island kākā numbers to increase dramatically in the Landsborough Valley over the study period, firstly, because a proportion of the population was likely to spend some time outside of the valley and, secondly, because they have a relatively low reproductive rate making them slow to respond to benefits of pest control. Kākā in South Westland are sequential specialist foragers, moving extensively across the landscape, exploiting seasonal food sources (O'Donnell & Dilks 1989, 1994). Thus, although South Island kākā are particularly prone to predation on the nest by stoats, their abundance and survival reflects the distribution of threats in the wider landscape.

We cannot account for declines in four bird species. Blackbirds, chaffinches and tomtits tend to feed on or close to the ground (O'Donnell & Dilks 1994) so may be more vulnerable to predation compared with the other species monitored (e.g. Brown et al. 1998). It is also possible that factors such as competition influence the persistence of species when overall bird numbers increase (Innes et al. 2010). In this case, the dramatic increases in the two aggressive honeyeater species (bellbird and tūī) may influence persistence of the third species that consumes similar nectar foods (silvereye) (O'Donnell & Dilks 1994).

Many bird species appeared to benefit from beech seed production, as evidenced by higher bird counts in years with high seedfall. These responses are likely to relate to increases in productivity or survival, which reflect increased availability of invertebrate foods (e.g. Alley et al. 2001). The effect appeared greatest in yellow-crowned parakeet, which breeds prolifically following beech masting in response to the abundance of seed (Elliott et al. 1996).

**Efficacy of the integrated pest management strategy**

We could not practically replicate monitoring in a comparable non-treatment area in this study, nor was pre-treatment monitoring undertaken using five-minute bird counts. In future monitoring studies it would be prudent to adopt a ‘Before-after Control-impact (BACI)’ experimental design to strengthen the potential inference of studies such as this one. Nonetheless, we suggest that the overall increases in bird abundance were likely to be a result of successful implementation of integrated pest control. Declines in the Landsborough Valley before control started, as well as declines in some forest bird species reported in similar forest types elsewhere in New Zealand where pest management has not been implemented (e.g. Elliott 1996; McLennan et al. 1996; Dilks et al. 2003; Elliott et al. 2010), contrast with results from this study. For example, Elliott et al. (2010) analysed a 30-year point-count monitoring dataset of forest birds in an unmanaged beech forest at Nelson Lakes, New Zealand, and found a significant change in the bird community structure, with five common native species (bellbird, rifleman, grey warbler, tomtit, tūī) declining in abundance. Declines were attributed to ongoing impacts of predation.

Mōhua and South Island kākā, as the two threatened taxa in the Landsborough Valley, were likely to be the most sensitive species in their response to the integrated pest management strategy. Based on the increased abundance of mōhua and the absence of any decline in South Island kākā in the Landsborough Valley (contrasting with ongoing declines elsewhere), the pest control strategy deployed appeared to be sufficient to mitigate the impacts of predation on populations of both species. However, we are unable to apportion increased abundance of mōhua to a particular component of the pest control programme, largely because stoats and rats are either killed directly by trapping or indirectly through secondary poisoning, and rats are also killed by directly-targeted poison operations (Murphy et al. 1998, 1999).

The predictive framework using beech seedfall as an indicator for determining when different forms of pest control were required was useful in the Landsborough Valley. Generally, though not exclusively, there was a strong positive relationship between heavy beech seedfall and the occurrence of peaks in predator captures, as has been found in other studies (King 1983; O'Donnell & Philipson 1996). Heavy seedfall also coincided with intensive flowering of *Peraxilla mistletoes* in the summers of 1999/2000, 2005/06 and 2008/09 and there was moderate flowering in 2002/03 (P. Knightbridge, DOC, Hokitika, pers. comm.). Pulses in trap-catch rates of stoats associated with full beech mast (>4000 seeds m⁻²; Wardle 1984) are usually associated with real irruptions in populations, but there is uncertainty as to whether partial masts have the same effect (O'Donnell & Philipson 1996). In the Landsborough Valley, the partial mast in 2006 did not result in increased stoat captures; a similar outcome to that observed in the Eglinton Valley (O'Donnell & Phillipson 1996). However, the partial mast in 2008 did. There was a high capture rate for stoats in 2007 when there was virtually no seedfall, but there was no increase in captures following the mast seeding in 2009. Based on the low capture rate in 2009, we infer that the 1080 control operation in 2009 fulfilled its objective; this was the first season in which the application of aerial 1080 control in the study area was timed specifically to maximise control of predators, particularly rats.

Two risks to non-target indigenous species have been identified when using toxins to control introduced pests: killing non-target species directly if they consume baits, or indirectly through secondary poisoning (Spurr 1979; Notman 1989; Lloyd & McQueen 2002; Powlesland et al. 2003; Westbrooke & Powlesland 2005). The majority of bird species in the Landsborough Valley were unlikely to encounter either toxic baits or invertebrates that may have fed on baits because they primarily forage in the upper strata of the forest, particularly the canopy (O’Donnell & Dilks 1994). We conclude that on the four occasions where 1080 was used in the study area, there were no significant negative impacts on indigenous birds at the population level, largely because indices for most indigenous species increased following the operations.

**Population indicator species**

Annual mōhua counts were positively correlated with two species, rifleman and yellow-crowned parakeet, despite sharing positive linear trends with a further six species over the duration of the study. We suggest that correlations between mōhua, rifleman and yellow-crowned parakeet may have resulted from peak breeding in both species occurring simultaneously following heavy seedfall (Elliott et al. 1996). Furthermore, breeding success is likely to have been enhanced by controlling predator irruptions that usually coincide with peak breeding. Mōhua and yellow-crowned parakeets are
known to suffer significant predation on incubating females, eggs and chicks by introduced mammals during the summers following heavy seedfall where predators are not controlled (Elliott et al. 1996; O’Donnell et al. 1996; Dilks et al. 2003) and this is also likely to be true for riflemen, based on recent declines (Miskelly et al. 2008; Elliott et al. 2010).

Counts of South Island kākā were negatively correlated with counts of mōhua, tomtit and yellow-crowned parakeet, which may be attributable either to their asynchrony in how each species responds to food availability and use or to their relatively slow reproductive rates. Increases in the productivity of kākā associated with increased food supplies occur in the season prior to heavy seedfall (Moorhouse et al. 2003), whereas productivity of yellow-crowned parakeet increases significantly in the breeding season following masting (Elliott et al. 1996). Positive relationships between high seedfall and counts of both mōhua and tomtits (Table 1) suggest that productivity in these species also follows beech masting.

The inability of the two threatened taxa (mōhua and South Island kākā) to predict trends in the more common bird species is likely to be a result of their particular behavioural and breeding strategies. Compared with other forest birds, mōhua are among the most susceptible species to predation, because their peak in breeding overlaps precisely with peak abundance of stoats and rats, and female mōhua demonstrate no predator avoidance behaviours when incubating (Elliott 1996; O’Donnell et al. 1996). Kākā, however, appear to anticipate masting events and breed prior to the peak in seedfall (Moorhouse et al. 2003). Thus, the extent to which annual changes in abundance of these two threatened taxa should be expected to vary in synchrony with a range of other taxa is debatable. Common species, selected on the basis of shared traits, may be better indicators of a more widespread response to management. Annual variations in abundance of birds are likely to be more extreme in beech forests because heavy seedfall results in extreme variability in both food supplies and predator densities. Our results demonstrate that multiple species can benefit from integrated pest control, but that the pattern of response varies among species. This raises the issue of the scale at which population indicator relationships should be evaluated and applied to outcome monitoring programmes.

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