

Can stoat (*Mustela erminea*) trapping increase bellbird (*Anthornis melanura*) populations and benefit mistletoe (*Peraxilla tetrapetala*) pollination?¹

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Abstract: There are currently many attempts in New Zealand to restore native ecosystem functioning through the intensive control of introduced mammalian predators. One system that is faltering is bird pollination of endemic mistletoes (*Peraxilla tetrapetala*) by bellbirds (*Anthornis melanura*), apparently because of stoat (*Mustela erminea*) predation. We used a paired-catchment experiment in *Nothofagus solandri* var. *cliffortioides* forest at Craigieburn, central South Island, to measure whether stoat control could restore bellbird densities and mistletoe pollination. Stoat trapping for 10–12 weeks during the 2000/01 and 2001/02 nesting seasons significantly reduced stoat abundance in the treatment area compared with the non-treatment area. As a consequence, bellbird nest survival and densities increased immediately and significantly in the treatment area. Nests in 2000/01 were four times more likely to succeed in the treatment area (66.4%) than in the non-treatment area (16.4%), where video monitoring showed stoats were the key predator. Bellbird numbers per 5-minute count increased 79%. Such a large response following a small-scale stoat control operation suggests that predators limited the Craigieburn bellbird population. Adult bellbirds seem to be less susceptible than eggs and chicks to predation, as bellbird densities were still significantly elevated 24 months after trapping ceased. However, the increase in bellbird densities did not significantly improve mistletoe pollination. Therefore, the stoat trapping was only partially successful in restoring ecosystem functioning.

Keywords: *Anthornis melanura*; bellbird; ecosystem restoration; mistletoe; *Mustela erminea*; *Peraxilla tetrapetala*; pollination; predation; stoat.

Introduction

Introduced mammalian predators have had large impacts on populations of endemic New Zealand birds (King, 1984) and on ecological processes such as pollination that depend on those birds (Robertson *et al.*, 1999). Studies of particular bird species have shown predation to be the key agent of decline (Clout *et al.*, 1995; Innes *et al.*, 1996; Elliott *et al.*, 1996; McLennan *et al.*, 1996; O'Donnell, 1996; Brown, 1997; Wilson *et al.*, 1998), and predator-control operations can be effective in protecting some of these species. More ambitious attempts to restore not just the densities of particular species but entire communities have recently become common (Saunders and Norton, 2001). Such attempts are sometimes focused on small

areas with expensive predator-proof fences (e.g. the Karori Wildlife Sanctuary) or on controlling a whole suite of carnivorous, omnivorous and herbivorous pests. In this paper, we report on an experimental attempt to restore the level of a plant-animal mutualism by trapping a single key predator in an area without predator-proof fences.

Predation has been implicated in the historical decline of many species of New Zealand birds. Field-based studies have highlighted the role of possums (*Trichosurus vulpecula*; e.g. Brown *et al.*, 1993; Pierce, 1993; Innes *et al.*, 1996), ship rats (*Rattus rattus*; e.g. Brown, 1997) and stoats (*Mustela erminea*; e.g. Elliott, 1996; Elliott *et al.*, 1996; Wilson *et al.*, 1998) as key predators. In particular, studies have shown that stoat predation may be the primary cause of decline for

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forest-dwelling birds such as kaka (*Nestor meridionalis*; Wilson *et al.*, 1998; Greene and Fraser, 1998), mohua (*Mohoua ochrocephala*; Elliott, 1996), yellow-crowned parakeets (*Cyanoramphus auriceps*; Elliott *et al.*, 1996) and brown kiwi (*Apteryx australis*; McLennan *et al.*, 1996). However, little is known about the ongoing effects of mammalian predation on bird species that are still relatively common. Predation on "common" birds may be of importance if either the bird is undergoing a yet-undetected slow decline, or the bird is at a stable density but is not sufficiently abundant to maintain ecological processes (e.g., pollination or seed dispersal; Sekercioglu *et al.*, 2004).

The bellbird or korimako (*Anthornis melanura*) is the most common endemic honeyeater (Meliphagidae) in New Zealand. It was once abundant throughout the country, but today it is very rare on mainland New Zealand north of approximately 38° S latitude (Anderson and Craig, 2003), and densities elsewhere on the mainland are lower than on predator-free islands (Murphy and Kelly, 2001). Historical records (e.g. Buller, 1877) suggest that the rapid decline in bellbirds in the North Island from 1860 and in the South Island from 1900 coincided with extensive forest clearance and the spread of ship rats (Atkinson, 1973) and stoats (King, 1984). Although bellbirds are not known to be currently declining, some evidence suggests that mammalian predation limits bellbird densities. Offshore islands with no or few introduced predators can have very high bellbird densities. For example, the Poor Knights Islands have 71 bellbirds per ha, or 54 times the average mainland density (Bartle and Sagar, 1987). Atkinson (1973) found a drop in bellbird numbers when ship rats invaded Big South Cape Island. Efford and Morrison (1991) showed that bellbird counts increased following stoat control in the Eglinton and Hollyford Valleys, and bellbird densities have increased significantly following multi-pest control in the Rotoiti Nature Recovery Project (D. Butler, *pers. comm.*; Department of Conservation, Nelson, N.Z.). Murphy and Kelly (2001, 2003) showed that the bellbird population at Craigieburn (central South Island) does not appear to be food limited, so they speculated that predation may be restricting bellbird numbers.

Although bellbirds persist on much of the mainland, their numbers may be insufficient to maintain historical ecological processes and ecosystem functioning. Recent studies have shown that a range of bird-pollinated plants, primarily dependent on bellbirds and tui (*Prosthemadera novaeseelandiae*), are frequently pollen-limited on the New Zealand mainland (Anderson *et al.*, *in press*). In particular, bellbird densities appear to be too low at several South Island sites (e.g. Craigieburn and Lake Ohau) for effective pollination of native mistletoes (*Peraxilla* spp.) that require these birds in order to reproduce (Ladley and

Kelly, 1996; Robertson *et al.*, 1999; Murphy and Kelly, 2001).

The purpose of this study was to determine whether bellbird numbers at Craigieburn would increase if mammalian predators were controlled; and whether controlling predators could also indirectly benefit *Peraxilla tetrapetala* mistletoes by improving bellbird pollination rates, thereby restoring this mutualism closer to its pre-pest state.

Methods

This study used a paired-catchment design in Craigieburn Conservation Area, inland Canterbury (171°42.5'E, 43°9.1'S). During two summers (1999/2000 and 2000/01), stoats were controlled in 400 ha of the Broken River catchment, while the adjacent Cheeseman site (c. 300 ha) was left unmanipulated. The two areas are separated by approximately 3.5 km of forest and tussock grassland and by the Broken River watercourse. Both sites have similar climate, elevation (900 m a.s.l.) and aspect (see Shanks *et al.*, 1990). At both sites, mountain beech (*Nothofagus solandri* var. *cliffortioides*) is the main canopy species. The mistletoe species *Peraxilla tetrapetala* and *Alepis flavida* are common, and the key mistletoe pollinators are bellbirds (Ladley and Kelly, 1996; Ladley *et al.*, 1997). Tui are absent at this site, and probably always have been rare there due to the very low abundance of nectar-producing plants (Murphy and Kelly, 2001; 2003).

Possum control

The original experimental design called for the control of both stoats and possums, since possums prey on a range of bird species (Brown *et al.*, 1993). Possums also eat mistletoes, although for unknown reasons there was little herbivory on mistletoes at Craigieburn even without possum control (Sessions and Kelly, 2001). However for the reasons outlined in the Results section, possum control was abandoned after the first year, and we believe that stoats were the key predator of bellbirds at Craigieburn.

A single possum trapping operation was conducted at the treatment site (Broken River) using Victor leg-hold traps for ten nights in August 2000. Pre- and post-trapping indices of possum abundance were obtained using lines of scented wax blocks (called WaxTags®) following Thomas *et al.* (1999). Each line consisted of ten WaxTags placed at 10-m intervals. Seventeen WaxTag lines were used to monitor the treatment site and 16 lines were used in the non-treatment site. The lines were placed >100 m apart to maintain their independence. The WaxTags were left out for three fine nights and then collected to check for possum bite

marks. The same lines were used for both pre- and post-control monitoring.

Analysis of the WaxTag data used a repeated measures generalised linear model with binomial error distribution (run in S-plus version 4.5, Mathsoft Inc.). Site (i.e. differences overall between the two sites) was tested using lines as the error term, and in this "BACI" (before/after, control/intervention) design we tested for a significant effect of the intervention using the site \times census interaction (which was tested over residuals as the error term).

Stoat control

Late in the first summer of our study (1999/2000), the Department of Conservation carried out a small experimental programme of stoat control in the treatment area using cholecalciferol-poisoned eggs from 20 January until 10 March 2000, at the end of the bellbird breeding season. This poisoning resulted in nine confirmed stoat kills (C. Gillies, *pers. comm.*; Department of Conservation, Wellington, N.Z.). The following two summers (2000/01 and 2001/02), we trapped stoats in the treatment area during the bellbird nesting season for 10–12 weeks (late October to early January) using a grid of 45 Mark IV Fenn traps spaced >200 m apart. The traps were placed under wire mesh cages to exclude non-target species, and they were pre-baited for two weeks with broken hen eggs, following Dilks *et al.* (1996). Traps were checked approximately every four days and rebaited when necessary.

From May 1999 until January 2002, indices of stoat and rodent numbers were obtained using lines of baited tracking tunnels as described by King *et al.* (1994). From May 2002 until November 2003, monitoring was continued in only the treatment area by the Department of Conservation. Each line consisted of five confluence plastic tunnels spaced 100 m apart. Each tunnel was baited with rabbit meat on a central sponge soaked in blue food dye, between two papers that collected animal footprints. There were seven tunnel lines in the treatment area, and six lines within the non-treatment area (spread across two subsites in the Cheeseman and adjacent Thomas Bush catchments to maintain a spacing of 1 km between lines). The proportion of tracking tunnel lines that contained rodent or mustelid footprints was used to calculate an index of abundance for each species (King, 1994). The graphs illustrate the percentage of tunnels with footprints, but following Brown and Miller (1998), statistical tests were based on the percentage of lines with footprints. As for possums, the analysis for both stoats and mice used a repeated measures binomial GLM. If the site \times census interaction was significant, we used a series of contrasts to subdivide the series of dates and explore which contrasts had significant interactions with site (i.e., showed a change from

trapping). The orthogonal contrasts were: contrast 1, before vs. after the first trapping; contrast 2, after first trapping vs. after second trapping; contrast 3, among censuses between first and second trapping; contrast 4, among censuses before first trapping. Each site \times contrast term was tested against the residual (error) deviance. For ease of presentation in Figure 1, where the site \times census interaction was significant, post-hoc means comparisons were also run by comparing the two sites in separate GLMs for each date.

Bellbird nest success

Bellbird breeding activity was monitored intensively in the non-treatment area from November 1999 to mid-February 2000, and in both the treatment and non-treatment areas from October 2000 to mid-January 2001. Although no birds were banded, bellbirds are highly territorial (Anderson and Craig, 2003), so re-nesting attempts could be identified by following breeding pairs within a territory. We found nests by following adults as they built or returned to nests and by listening for chick vocalisations.

During the first season (1999/2000), 11 active nests within the non-treatment area were monitored using infrared video equipment to identify the causes of nest failures. We filmed nests only in the non-treatment area because these were believed to be more likely to suffer predation. During the second season (2000/01) more effort was put into direct observation of nests and less into video monitoring; a total of 75 nests were found across both sites, of which 36% were second or third re-nests. Fifteen nests either were not used by the birds once constructed, or their success or failure could not be ascertained. The remaining 60 nests (29 at the treatment site and 31 at the non-treatment site) were observed until fledging or failure. Four of the nests in the non-treatment area were videoed, and all nests at both sites were monitored visually every two days for up to 40 minutes to record their progress (e.g. construction, incubation, feeding chicks). The 40-minute period was chosen because incubating females typically left the nest to feed for 3–5 minutes every 20–25 minutes, and nestlings were rarely left for more than 30 minutes between feeding visits.

The contents of nests were determined where possible by climbing with a nest mirror mounted on a 3-m pole. Where nests were too high to reach with the pole, their stage was inferred from the behaviour of the adults. A nest was considered to have failed if it had previously contained eggs or young nestlings and then no activity was observed in it for three consecutive visits (over six days). Where possible, failed nests were collected using climbing ropes to search for evidence of causes of failure including eggshell damage, chick remains, mammal hairs and obvious disturbance of the nest lining.

The data from the two seasons of bellbird nest monitoring were analysed following the methods of Stanley (2000) to calculate the corrected daily nest survival probabilities. This method provides a more accurate estimate of nesting success than simply counting the proportion of discovered nests that fledged young, because nests that fail early on are less likely to be found. Corrected daily nest survival probabilities raised to the power of the number of days gives the overall nest survival probability. The incubation period for bellbirds was taken to be 17 days (3 days for laying and 14 days for incubation) and the nestling stage 14 days, following Heather and Robertson (1996).

We statistically tested the survival data using Akaike's Information Criterion (AIC), following Armstrong *et al.* (2002). The best model had the lowest AIC, signifying the best combination of simplicity and fit. The data we collected allowed us to use two models: (1) a comparison of the two seasons (1999/2000 and 2000/01) at the non-treatment site only, and (2) a comparison of the non-treatment and treatment sites in the 2000/01 season. Within each model, we also tested for the effects of timing within each season (nests begun before or after mid-November of each year) and stage (incubation versus nestlings).

Bellbird densities

Five-minute bird counts (Dawson and Bull, 1975) were used as a relative index of bellbird densities in the treatment and non-treatment areas from May 1999 until January 2004. Each session lasting 3–4 days used the same 15 counting stations per area at 200-m intervals along roads and tracks. Each station was visited twice per day between 0900 and 1630, and observers swapped sites on alternate days. The recorder noted all birds that were either seen or heard within a 100-m radius of the counting point during a five-minute period. Tests for a treatment effect used repeated measures GLMs as for stoats, except that a poisson rather than binomial error distribution was appropriate for the data, and the site \times contrast tests used the station \times day interaction as the error term. The longer run of data than for tracking tunnels also allowed us to add another contrast, contrast 5: among dates after the second trapping.

Mistletoe flowering and pollination

To measure the effectiveness of pollination of *P. tetrapetala* mistletoes, we recorded visitation rates to flowers by birds, fruit set on mistletoe plants, and the density of mistletoe flowers per hectare in the two catchments.

Bird visitation rates to mistletoe flowers were measured by direct observation of groups of mistletoe plants (usually six stations per site in each year). Each station was observed, usually for 90–110 minutes

(range 50–150) in 10-minute periods over 3–5 days. For each avian flower visitor, the bird species and duration of visit in seconds were recorded. Most visits (>90%) were by bellbirds, with occasional silvereyes (*Zosterops lateralis*) and chaffinches (*Fringilla coelebs*). The total number of available flowers at each station was counted, or for large plants estimated independently by two observers and the mean taken. The visitation rate was expressed as seconds of bird visit per mistletoe flower per hour.

Fruit set by *P. tetrapetala* is largely determined by level of pollination (Ladley and Kelly, 1995; Kelly *et al.*, 1996; Ladley *et al.*, 1997; Robertson *et al.*, 1999; Montgomery *et al.*, 2003). We measured the natural fruit set rate (the percentage of unmanipulated flowers which ripened their single-seeded fruit) on permanently tagged plants ($n = 20$ to 45 at the treatment site, $n = 11$ to 21 at the non-treatment site) by counting flowers on tagged branches in January, and then counting ripening fruits on the same branches in April.

The relative abundance of mistletoe flowers in the two catchments over the three years was estimated using permanently tagged plants and randomly located transects. Flowering effort was recorded each year on permanently tagged plants near the ground in all years ($n = 75$ at the treatment site, $n = 35$ at the non-treatment site). For each plant, its size in three dimensions was measured, the number of flowers counted, and its flowering intensity calculated in flowers/m³ of mistletoe volume. This flowering intensity was averaged across all plants at a site to get a mean flowering effort per unit of mistletoe for that year.

To allow for variation between sites in the number of mistletoes per unit area of ground, we randomly placed 18 transects at each site running off roads through the forests. Each transect was 100 \times 5 m, and the size and flowering intensity (on a 6-point scale) was estimated for all flowering mistletoes therein. For the permanently tagged mistletoes described above, flowering intensity was estimated on the same scale and compared to the measured flowers/m³. This allowed us to calculate a conversion factor from flowering intensity score to flowers per m³ of mistletoe, which was used to calculate the total number of mistletoe flowers per m² of transect. Transects were measured in both catchments in 2000/01 and at Cheeseman in 2001/02. For other years, changes in the numbers of flowers/m² of ground was estimated from changes in flowers/m³ of mistletoe plant on the tagged plants, since few mistletoe plants at Craigieburn die from one year to the next, and variation in flowering effort across years is significantly synchronised among plants (unpublished data).

Results

Possum control

The possum trapping in August 2000 caught 98 possums, but WaxTag monitoring showed that the trapping did not result in significantly lowered possum densities in the treatment area compared to the non-treatment area (Fig. 1c; Appendix 1, treatment×census interaction, $P = 0.43$). Since the video monitoring in the untreated catchment showed no evidence of possum interference with bellbird nests, we did not conduct any further possum control.

Stoats and mice

Stoat tracking rates were lower in the treatment area than in the non-treatment area following the Department of Conservation stoat poisoning operation in January 2000, and after our two periods of stoat trapping (Fig. 1a). The GLM showed that the overall treatment×census interaction was significant ($P = 0.0017$, Appendix 1), with the post-hoc means testing showing that the two sites differed widely immediately after each trapping event (Fig. 1a) but that the differences caused by the first trapping had disappeared by the following spring. The trapping during summer

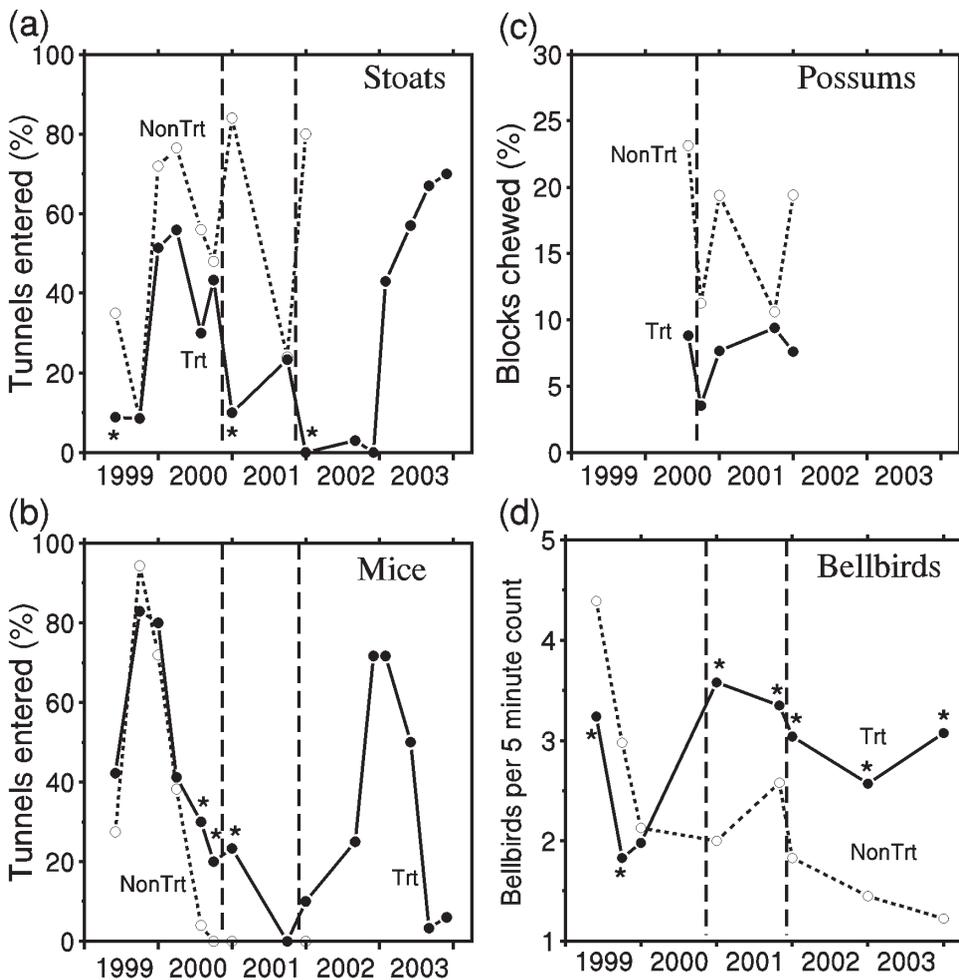


Figure 1: Changes in animal density indices over time in treated (filled symbols, Broken River) and untreated (hollow symbols, Cheeseman) catchments at Craigieburn. (a) Stoats in tracking tunnels; (b) mice in tracking tunnels; (c) possum bites on wax blocks; (d) bellbirds heard or seen per five-minute count. The two periods of stoat trapping are shown on (a), (b) and (d) with dashed lines, and the single period of possum trapping on (c) with a dashed line. Where the treatment mean was significantly different from the non-treatment mean ($P < 0.05$ using post-hoc tests), it is marked with an asterisk.

Table 1. Bellbird nest survival at Craigieburn [daily % survival rate, and overall % of nests surviving each stage, which lasts 17 days for incubation (including laying) and 14 days for nestlings].

(a) In non-treatment areas over two seasons. $n = 11$ in 1999/2000 and $n = 31$ in 2000/01.

Stage	Year			
	1999/00 % survival		2000/01 % survival	
	Daily	Overall	Daily	Overall
Incubation	99.27	88.3	96.66	56.1
Nestling	95.77	54.6	91.59	29.2
Overall		48.2		16.4

(b) Comparison of the treatment (Broken River) and non-treatment (Cheeseman) areas in the early and late parts of the 2000/01 season. Early nests were built before mid-November, while late nests were built anytime after this point. $n = 29$ in the treatment area (15 early, 14 late) and $n = 31$ in the non-treatment area (15 early, 16 late). The "overall" line uses the model excluding early vs. late to calculate a season-long mean success rate.

Timing	Treatment site		Non-treatment site	
	Daily	Overall	Daily	Overall
Early	96.42	32.3	95.45	23.6
Late	100	100	93.73	13.4
Overall		66.4		16.4

Table 2. Models used to test bellbird nest survival data. AIC values indicate which model best explains the data without introducing redundant parameters.

(a) Comparison of survival at the non-treatment site in 1999/2000 and 2000/01.

Model	AIC
Year×Stage	203.40
Stage	204.70
Timing×Stage	208.05
Year	208.38
Year×Timing×Stage	208.72
Constant	210.60
Year×Timing	211.62
Timing	212.38

(b) Comparison of the treatment and non-treatment sites in 2000/2001.

Model	AIC
Site×Timing	198.03
Site×Timing×Stage	198.74
Site×Stage	204.63
Site	206.77
Stage	214.95
Constant	215.62
Timing	216.57
Timing×Stage	217.72

Table 3. Fates of observed bellbird nests (numbers of nests in each category) where outcome was known from video observation in untreated areas at Craigieburn in 1999/2000 and 2000/01.

Fate	1999/2000	2000/2001
Fledged	6*	
Preyed on by stoat (chick stage)	1*	3
Preyed on by unknown predator	1 (eggs)	1 (chicks)
Preyed on by bird (harrier or kea)	1	
Nest tipped over in high wind	1	
Nest abandoned (chainsawing nearby)	1	
Failed (chicks), reasons unknown	1	
TOTAL	11	4

* One nest had one chick preyed on by a stoat and the other escaped to fledge, so is counted twice.

2000/01 killed 20 stoats (8 non-lactating adult females, 4 lactating females and 8 adult males) and one ship rat. Stoat tracking rates at the non-treatment site were very high in January 2001 (Fig. 1a). Trapping in 2001/02 killed 13 stoats (4 non-lactating adult females, 3 lactating females and 6 adult males). As a result, by January 2002 none of the tracking tunnels in the treatment area were visited by stoats, compared to 80% stoat visitation of the tracking tunnels on all lines in the non-treatment area.

Mouse tracking rates (Fig. 1b) did not differ strongly with trapping (treatment \times census interaction $P=0.07$, Appendix 1), but did differ between treatments before and after the first stoat trapping period ($P=0.047$, and Fig 1b). Essentially, mouse tracking rates were similar in the two areas before July 2000, the winter following the stoat poisoning operation, but rates were lower in the non-treatment area thereafter. From September 2000 until the end of the monitoring in January 2002, no mice were recorded at the non-treatment site. Subsequent monitoring at only the treatment site showed an irruption of mice in late 2002 to levels similar to 1999/2000, followed by a matching increase in stoats through 2003 (Fig. 1).

Bellbird nest survival

Bellbird nests were typically located in a fork between the trunk and a sturdy lateral branch of a mountain beech tree, or among fine branches high in the tree's canopy. The average nest height was 8.5 m. Eleven nests at Broken River (30% of nests at this site) were built in the upper branches of mature conifers adjacent to the beech forest.

Many of the monitored nests in the non-treatment area did not survive long enough to produce fledglings, particularly in the 2000/1 season (Table 1a). Analysis of the nest survival data showed that the best model for comparing the two summers included both year (1999/2000 or 2000/01) and stage (incubation or nestling; Table 2a). Survival of nests in the non-treatment area fell from 48.2% in 1999/2000 to only 16.4% in 2000/01, and was higher during incubation than during the nestling stage in both years despite the extra days in the incubation period (17 compared to 14; Table 1a).

The best model for comparing the treatment and non-treatment areas in 2000/01 included site and timing (early or late), although the model with site, timing and stage was almost as good (Table 2b). Nests built early in the season at both sites had a relatively low chance of surviving, but survival at the treatment site improved later in the season so that all of the nests built at this site after mid-November fledged at least one chick (Table 1b). In contrast, the low survival early in the season at the non-treatment site worsened later in the season, so that only 13.4% of late nests fledged chicks. At both sites, nestlings were more vulnerable than eggs,

particularly later in the season (means not shown).

Data on the 15 nests in the non-treatment area whose fate was verified from videos are summarised in Table 3. Predation events were recorded at five nests: four involving stoats and the fifth involving either a harrier (*Circus approximans*) or a kea (*Nestor notabilis*). In all five cases, predation occurred at the nestling stage. All four of the nests filmed during 2000/01 failed. Stoats caused three failures, and the cause of the fourth failure is unknown due to a video recorder fault when all three nestlings disappeared. Examination of failed nests generally gave little forensic information (no obvious eggshell or chick remains or hair).

Bellbird density

Bellbird numbers per 5-minute count were initially lower in the treatment site, but after the first season of stoat trapping, counts were 79% higher at the treatment site (Fig. 1d). These higher densities persisted in the treatment area through October 2001 (30% higher), January 2002 (66% higher), January 2003 (77% higher), and January 2004 (151% higher). GLM analyses showed a highly significant treatment \times census effect, with all the subdividing orthogonal contrasts also showing significant interactions with treatment (Appendix 1). This can be summarised by the post-hoc means testing (Fig. 1c) to show that bellbirds were significantly less abundant at the treatment site before the treatment began, but thereafter were consistently significantly more abundant at the treatment site.

The fact that counts remained elevated even two years after stoat trapping ceased, despite another period of high stoat numbers (Fig. 1a), suggests that adult bellbirds remain in their natal areas, and are relatively insensitive to stoat predation. Even after pest control bellbird densities were apparently below the long-term carrying capacity of the habitat.

Mistletoe pollination

Despite the increase in bellbird numbers following stoat trapping, there was no evidence of higher bellbird visitation rates to *P. tetrapetala* flowers at the treatment site than at the non-treatment site following either stoat trapping operation (Fig. 2a). In fact, the bellbird visitation changed in the opposite direction. Similarly, we found no evidence that mistletoe fruit set was higher in the treatment than the non-treatment site in years with elevated bellbird numbers (Fig. 2b).

The differences in visitation rates and fruit set between the sites may partly reflect differences in mistletoe density, as measured by mistletoe flowers/m² of ground (Fig 2c). Mistletoe flower density increased over time at both sites, but the densities were always 15–18 times greater in the treatment site.

To allow for changes in both bellbird density and mistletoe flower density, we divided the number of

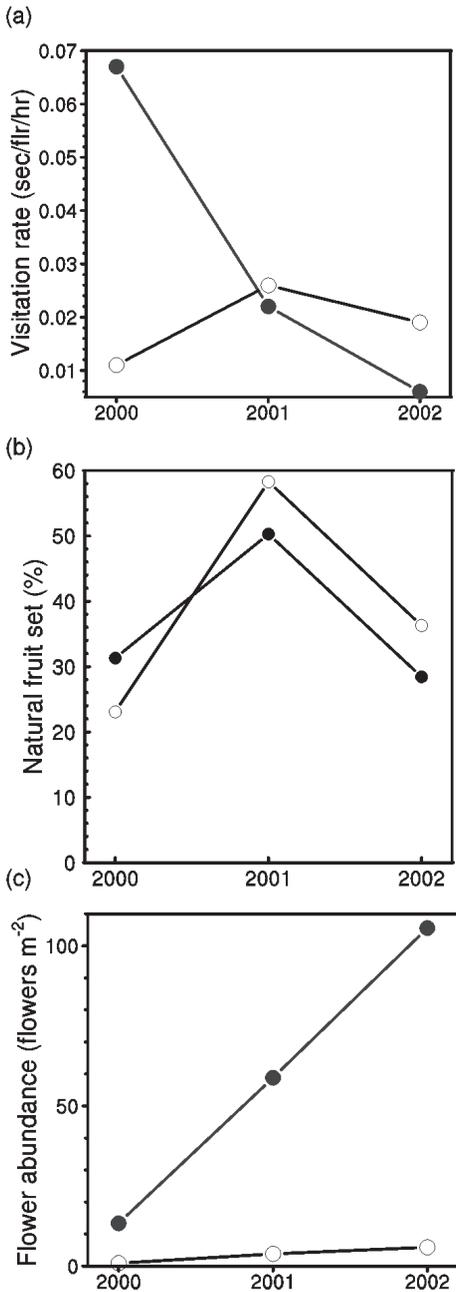


Figure 2. Mistletoe flowering and pollination at Craigieburn, in treated (filled symbols, Broken River) and untreated (hollow symbols, Cheeseman) catchments. (a) Visitation rate of birds to mistletoe flowers (seconds of bird visit per flower per hour). (b) Fruit set rate (% of flowers) for unmanipulated flowers. (c) Total flowering intensity per unit ground area (flowers per m²).

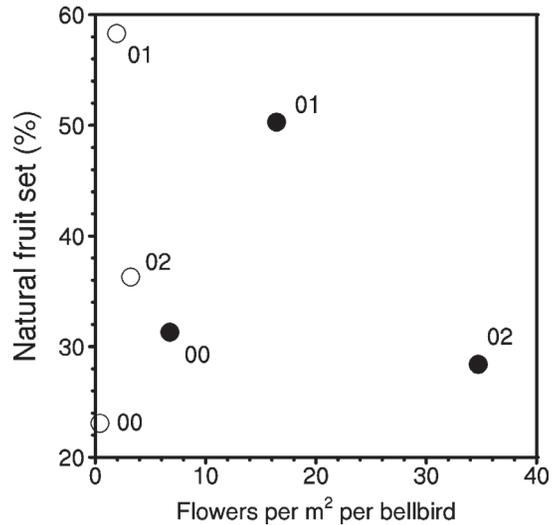


Figure 3. Fruit set on unmanipulated flowers of *P. tetrapetala* at Craigieburn, in relation to bird/flower ratio (number of flowers/m² of ground divided by mean bellbirds per 5-minute count in January) in the treated (filled symbols, Broken River) and untreated (hollow symbols, Cheeseman) catchments. Numbers indicate the last two digits of the season (e.g. 00 indicates 1999/2000). There was no relationship between the variables ($R^2 = -0.16$, NS).

mistletoe flowers/m² of ground (Fig 2c) by the bellbird index (bellbirds per five-minute count in January; Fig. 1d) and compared this index to the natural fruit set rate. There was no clear relationship between flowers per bellbird and fruit set rates (Fig. 3), which suggests either that there is too much noise in our various estimates of density, or that other unmeasured variables have an effect on the pollination rate.

Discussion

This study shows that trapping stoats can have a significant effect on bellbird density by decreasing the rate of nest predation, but that such trapping was not enough to improve mistletoe pollination. Stoat trapping during the summers of 2000/01 and 2001/02 significantly reduced stoat numbers in the treatment area compared to the non-treatment area, and as a consequence, nest survival increased four-fold and bellbird numbers increased 79% in the treatment area. Such a significant difference following a small scale, short-term pest control operation suggests that the Craigieburn bellbird population is limited by predators, at least when stoat numbers are high.

Since we did not replicate treatment sites or switch treatment areas, our trapping experiment alone cannot

prove that stoat trapping caused the increase in bellbird densities. However, the inference is greatly strengthened by the data from video monitoring and nest survival rates. Of the 15 nests that we videoed, at least four were preyed on by stoats, including all of the confirmed predation events from 2000/01 when stoat numbers were high and mice numbers were low.

In contrast, we found no evidence of rats or possums visiting bellbird nests during this study, even though both species are known to prey upon birds such as North Island kokako (*Callaeas cinerea wilsoni*), kaka (*Nestor meridionalis*) and kereru (*Hemiphaga novaeseelandiae*; Brown *et al.*, 1993; Pierce, 1993; Brown *et al.*, 1996; Innes *et al.*, 1996; Moorhouse *et al.*, 2003). We cannot completely rule out a role for possum predation on bellbirds. Our single possum-trapping operation at the treatment site in August 2000 did not result in significantly lower possum densities (Fig 1c), possibly because possums rapidly move into newly vacated areas (Efford, Warburton and Spencer, 2000). However, at some other monitoring dates possum sign on the WaxTags was significantly more common in the non-treatment site. Sessions and Kelly (2001) found that possum densities at Craigieburn are relatively high (19.9 catches per 100 trap-nights) compared to other mountain beech forest sites. Despite these high densities, we found no evidence that possums interfered with bellbird nests. In c. 5000 hours of nest monitoring videos from the untreated site, we observed only one possum encounter, during which the possum paused 25 cm from a nest containing an incubating female, then stepped over it without disturbing either the nest or the adult female. We conclude that possums were not a major predator of bellbirds during this study, but we cannot say that possums do not prey upon bellbird nests.

Ship rats are recorded at Craigieburn at extremely low densities: during our study only one ship rat was trapped and no rat prints were found in tracking tunnels. In an earlier study, King (1983) also found very low densities of ship rats at Craigieburn. Thus, while rats were not common enough to cause serious harm to bellbirds at Craigieburn, rats could reduce bellbird populations at other sites. As a result, stoat control may have different effects in areas with high ship rat numbers.

The effect of beech masting on stoat predator pressure

Stoat trapping may have had a particularly marked effect on bellbird nest success in 2000/01, because it coincided with a period of high stoat numbers and low mouse numbers. Stoat and rodent populations have been shown to cycle in response to the irregular flowering and seeding of beech forests in New Zealand, known as beech masting (Wardle, 1984; Schaubert

et al., 2002). As a result of the increase in food supply during the beech mast, rodent numbers increase (King, 1983), and in response to this rodent irruption, stoats breed prolifically (King, 1989; Murphy and Dowding, 1995; Dilks *et al.*, 2003).

Our tracking tunnel data indicate that the heavy beech seeding in autumn 1999 (Schauber *et al.*, 2002) led to high mouse densities in the Craigieburn area by the following spring, followed by an increase in stoat numbers in 2000. By mid-2000, stoats continued to increase in abundance, but mouse numbers began to decline, probably because of declining food and increasing predation. The abundance of predators and lack of mice in 2000/01 may thus have caused stoats to prey more heavily on birds, even though the stoat tracking tunnel rates were similar in the two years. Previous work on mouse/stoat cycles in New Zealand has generally shown that there is no effect of mouse density on stoat predation rates on native birds (King, 1983). However, satiation of predators and consequent reduced predation rates on birds is now thought to occasionally occur when mice reach extremely high densities (C. M. King, *pers. comm.*, Waikato University, Hamilton, N.Z.). The Craigieburn data for 1999/2000 are consistent with this. Stoat population irruptions have been shown to increase nest predation on several other native bird species including mohua (Elliott, 1996; O'Donnell and Phillipson, 1996), yellow-crowned parakeets (Elliott *et al.*, 1996) and kaka (Dilks *et al.*, 2003; Moorhouse *et al.*, 2003). Another heavy beech seed crop at Craigieburn in early 2002 (Rob Allen, *pers. comm.*; Landcare Research, Lincoln, N.Z.) resulted in another mouse/stoat cycle from late 2002.

An increase in predation pressure during 2000/01 would explain both why the trapping operation resulted in high bellbird nest survival, and also why nest success was so much lower in 2000/01 than in 2001/02 at the non-treatment area. These results suggest that stoat control may be particularly important for bellbirds during stoat irruptions. Several studies on other forest birds have found that trapping can reduce the high predation pressure during stoat irruptions. O'Donnell *et al.* (1996) found that a very intensive trapping programme significantly reduced stoat predation on breeding mohua during a stoat irruption. Similarly, Dilks *et al.* (2003) and Moorhouse *et al.* (2003) both showed that stoat control apparently improves kaka breeding success. However, Elliott *et al.* (1996) found that trapping during a stoat irruption did not improve parakeet breeding success.

Implications for restoration of a pollination mutualism

Bellbirds remain abundant throughout much of New Zealand's fragmented native forest (Heather and

Robertson, 1996), but both previous evidence (Atkinson, 1973; Bartle and Sagar, 1987; Efford and Morrison, 1991; Graham and Veitch, 2002) and our experimental data show that mammalian predators reduce bellbird densities.

Given that native mistletoes require honeyeaters such as bellbirds to reproduce (tui are not present at Craigieburn), we expected that an increase in bellbird numbers would improve mistletoe pollination. However, no such pattern was detected during our study. These results highlight the complexity of multi-trophic interactions. Irregular flowering during the study period may have partially affected these results, but accounting for the density of mistletoe flowers at each site did not improve the relationship between bellbird density and pollination. Other factors such as the timing and extent of floral rewards and variations in the birds' diet may also have been important. Also, *Peraxilla tetrapetala* is not entirely reliant on birds for pollination, as two species of solitary native bees can also open flowers and effect some pollination (Kelly *et al.*, 1996; Robertson *et al.*, 2005). Bees are more sensitive than birds to inclement weather, so their contribution may vary more widely among years.

It is also possible that predator control did not increase bellbird numbers enough to have an impact on mistletoe pollination. Five-minute bird counts indicate that bellbird numbers are generally lower at Craigieburn than at other eastern South Island sites, which in turn have lower bellbird counts than the western South Island and offshore islands (Murphy and Kelly, 2001). Perhaps bellbird densities must be much higher than recorded at Craigieburn during this study for mistletoe pollination to improve. If this is the case, even moderate densities of bellbirds may not be enough to repair the faltering mutualism between mistletoes and their bird pollinators (Ladley *et al.*, 1997; Robertson *et al.*, 1999; Murphy and Kelly, 2001) and to restore maximal mistletoe reproduction.

Nonetheless, it is noteworthy that bellbird numbers can be increased so readily in an unfenced area of 400 ha with only 45 Fenn traps in place for c. 12 weeks over the breeding season, at least in habitats where ship rats are absent. Moreover, the bellbirds appeared to be faithful to their natal area, so that bellbirds raised within intensively managed areas may remain within the protected area. Adult bellbird densities remained high for at least 24 months after stoat trapping ceased, despite high stoat numbers during that time. All of this means that local enhancement of bellbird numbers appears to be practical, even if we cannot show that this fully restores bird/plant interactions.

Bellbirds as indicators of predator control success

The large response of bellbird density to our stoat trapping suggests that bellbirds may be a very good

species to use as an indicator of the effectiveness of predator control. Bellbirds are present throughout much of mainland New Zealand, and are conspicuous enough to readily show up in counts. Several other studies have shown bellbirds to give one of the largest responses of any native forest bird to predator control. In the Eglinton Valley, bellbirds and blackbirds were the species which responded most to changes in stoat control (Efford and Morrison, 1991). On Tiritiri Matangi Island, bellbirds were the only bird to show a significant increase after the eradication of kiore (Graham and Veitch, 2002). The responses of bellbirds may vary depending on what predators are present, but they seem to have many of the attributes which would be useful in an indicator of pest control effectiveness – especially as high densities of bellbirds are also important in ensuring pollination and dispersal services to native plants.

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Appendix 1: Repeated measures GLM analyses of BACI data on animal density indices. Significant effects are in bold text. The key test for a treatment effect is a significant site \times census interaction. For details of analysis methods and contrasts see Methods section.

(a) Possums

Model	df	Deviance	<i>F</i>	<i>P</i>
Site	1	34.75	20.42	0.0001
Line	31	52.75		
Census	4	15.29	2.49	0.0466
Site \times Census	4	5.84	0.97	0.4275
Residual	124	210.31		
Total	164	319.04		

(b) Stoats

Model	df	Deviance	<i>F</i>	<i>P</i>
Site	1	41.26	9.82	0.0121
Subsite	1	14.15	3.37	0.0997
Error(Line)	9	37.82		
Census	6	35.08	2.89	0.0171
Contrast 1: Before vs. after first treatment date	1	17.08	8.45	0.0055
Contrast 2: Before vs. after second treatment date	1	0.15	0.08	0.7833
Contrast 3: Within period between treatments 1 and 2	1	6.42	3.18	0.0809
Contrast 4: Within period before treatment 1	3	11.43	1.88	0.1446
Site \times Census	6	51.11	4.21	0.0017
Site \times Contrast 1	1	16.61	8.21	0.0061
Site \times Contrast 2	1	13.47	6.66	0.0129
Site \times Contrast 3	1	17.02	8.42	0.0055
Site \times Contrast 4	3	3.03	0.50	0.6839
Subsite \times Census	6	22.89	1.89	0.1020
Subsite \times Contrast 1	1	13.50	6.68	0.0128
Subsite \times Contrast 2	1	1.48	0.73	0.3965
Subsite \times Contrast 3	1	1.60	0.79	0.3788
Subsite \times Contrast 4	3	7.29	1.20	0.3190
Residual	49	109.15		
Total	78	311.46		

(c) Mice

Model	df	Deviance	<i>F</i>	<i>P</i>
Site	1	20.82	11.20	0.0086
Subsite	1	3.08	1.66	0.2299
Error(Line)	9	16.73		
Census	6	140.47		0.0000
Contrast 1: Before vs after first treatment date	1	54.75		0.0000
Contrast 2: Before vs after second treatment date	1	0.057		0.8116
Contrast 3: Within period between treatments 1 and 2	1	10.58		0.0011
Contrast 4: Within period before treatment 1	3	75.09		0.0000
Site \times Census	6	11.66		0.0700
Site \times Contrast 1	1	3.95		0.0470
Site \times Contrast 2	1	0.00		0.9991
Site \times Contrast 3	1	<0.01		0.9726
Site \times Contrast 4	3	7.72		0.0522
Subsite \times Census	6	3.00		0.8083
Subsite \times Contrast 1	1	0.00		0.9916
Subsite \times Contrast 2	1	0.00		1.0000

Appendix 1 contd.

Subsite × Contrast 3	1	0.00	1.0000
Subsite × Contrast 4	3	3.00	0.3910
Residual	49	46.97	
Total	78	242.75	

(d) Bellbirds

Model	df	Deviance	<i>F</i>	<i>P</i>
Site	1	71.37	6.86	0.0140
Error(station)	28	291.11		
Census	7	185.35	35.41	0.0000
Contrast 1: Before vs after first treatment date	1	12.08	11.29	0.0008
Contrast 2: Before vs after second treatment date	1	52.56	49.12	<0.0001
Contrast 3: Within period between treatments 1 and 2	1	1.28	1.19	0.2747
Contrast 4: Within period after treatment 2	2	10.35	4.83	0.0082
Contrast 5: Within period before treatment 1	2	109.08	50.97	0.0000
Site × Census	7	208.49	39.83	0.0000
Site × Contrast 1	1	170.62	159.46	0.0000
Site × Contrast 2	1	9.96	9.31	0.0023
Site × Contrast 3	1	8.29	7.75	0.0055
Site × Contrast 4	2	11.45	5.35	0.0049
Site × Contrast 5	2	8.17	3.82	0.0224
Error(station:day)	886	948.05	1.94	0.0000
Residual	810	536.84		
Total	1739	2241.42		