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The effect of aerially applied 1080 on the nesting success and survival of kākā

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Abstract: Kākā (*Nestor meridionalis*) are vulnerable to predation by stoats (*Mustela erminea*) and possums (*Trichosurus vulpecula*), particularly when nesting. Without predator control kākā populations decline. Control of stoats and possums both by trapping and aerial application of the poison 1080 leads to increased kākā nesting success. In recent years, many 1080 poison operations have been undertaken to control ship rat (*Rattus rattus*) and stoat plagues that occur after beech mast. Kākā do not breed every year but breed in anticipation of heavy fruiting. They do not usually breed during the spring and summers following beech mast when 1080 operations are often undertaken to control rat and stoat irruptions. Using radio-tags we measured the nesting success and survival of kākā for six years in South Westland during which there were beech (Nothofagaceae) and rimu (*Dacrydium cupressinum*) masts, stoat and rodent plagues, five 1080 operations, and four seasons in which kākā bred. We then simulated varying timings and frequencies of masting and 1080 use to explore the impact of masting and predator control on kākā population growth. In the absence of pest control simulated kākā populations declined. Aerial 1080 applied a year before or just before kākā breeding resulted in increased nesting success, but 1080 applied more than two years before kākā breeding had no impact. Aerially applied 1080 also increased adult kākā survivorship for at least 18 months. Annual 1080 operations or 1080 operations at intervals less than or equal to the time it takes stoat populations to recover resulted in the most rapid simulated kākā population growth. 1080 operations in (1) kākā breeding years, (2) when following mast, and (3) during rodent and stoat plagues each resulted in progressively smaller kākā population growth rates.

Keywords: aerial 1080, beech mast, kākā, possums, stoats

Introduction

The introduction of mammalian predators into New Zealand has had a significant and often disastrous impact on many of its endemic bird species (O'Donnell 1996; Wilson et al. 1998; Brown et al. 2015). Controlling mammalian predators, particularly ship rats (*Rattus rattus*), brushtail possums (*Trichosurus vulpecula*), and stoats (*Mustela erminea*) is the main method of protecting endemic birds on mainland New Zealand (Innes et al. 2010). Trapping is the most used predator control tool in relatively small areas in New Zealand. However, traps are expensive to set up and maintain, and for large (> 5000 ha) predator control programmes the only viable method currently available is the aerial application of sodium fluoroacetate (1080) poison (Brown et al. 2015).

Aerial application of 1080 in New Zealand forests was first used to control brushtail possums during the 1950s to prevent damage to forests and reduce the transmission of bovine tuberculosis from possums to dairy cattle (Eason et al. 1993; Livingstone 1994). Aerial 1080 continued to be predominantly used for possum control until the late 1990s. An increase in knowledge and changes in methodology have seen the poison increasingly being used to target ship rats and stoats with the aim of reducing predation of native fauna (Innes

et al. 1995; Innes & Barker 1999). A significant development has been the timing of aerial operations to follow beech masts (Nothofagaceae spp.), to prevent rodents and stoats reaching plague-like proportions in response to the increased food availability (King 1983). This shift to more targeted predator control has led to an increased frequency in 1080 operations over conservation land and refinements in the method of application (Eason et al. 2006; Elliott & Kemp 2016).

Predation by introduced mammals impacts all mainland endemic New Zealand bird species but hole-nesting species are particularly vulnerable. Hole-nesting birds often cannot escape when a predator enters the hole and the incubating or brooding adult is sometimes killed along with the eggs or nestlings. In species where the female alone incubates and broods this results in a skewed sex ratio (Elliott 1996; O'Donnell 1996). Stoats are very capable tree climbers and actively hunt in holes and cavities through all forest strata (King 1990; Wilson et al. 1998). Ship rats are also arboreal predators which, because of their abundance, are the most frequent predators of the eggs, chicks and sitting adults of forest birds (Innes & Russell 2021). Possums are also known egg and nestling predators and have been recorded killing adult cavity nesting birds on the nest (Brown et al. 1993; James & Clout 1996; Moorhouse et al. 2003).

The kākā (*Nestor meridionalis*) is a large, sexually dimorphic, forest parrot endemic to New Zealand (Moorhouse et al. 1999). Kākā nest in tree cavities and the female alone incubates the eggs and broods the nestlings (Moorhouse et al. 2003). On those parts of mainland New Zealand where there is no predator control kākā are in serious decline. Possums compete with kākā for important seasonal foods such as tree fuchsia (*Fuchsia excorticata*), mistletoe (*Peraxilla* spp.; Pekelharing et al. 1998; Bockett & Knightbridge 2004), and for the use of tree cavities. Several studies have shown that nesting kākā are particularly vulnerable to predation by stoats and (to a lesser extent) possums (Wilson et al. 1998; Moorhouse et al. 2003; Taylor et al. 2009). Predation of nesting females has led to heavily skewed sex ratios of up to 6:1 of male:female adults in some kākā populations (Greene & Fraser 1998).

Kākā breeding is often synchronous with the mast seeding/fruiting of forest trees, particularly beech species (*Fuscospora* spp. and *Lophozonia menziesii*; Wilson et al. 1998) and podocarps such as rimu (*Dacrydium cupressinum*) and kahikatea (*Dacrycarpus dacrydioides*) (Greene et al. 2004). Laying most often occurs between November and March when beech trees are flowering and the seed is setting on the trees, or when podocarp fruit is ripening (Moorhouse 2013); in both cases this occurs at least six months before rodent and stoat irruptions (King 1983; Wilson et al. 1998). There is good evidence that kākā breeding productivity is improved by stoat, possum, and rodent control (Dilks et al. 2003; Moorhouse et al. 2003; Taylor et al. 2009). However, because kākā usually finish breeding 4–7 months before most beech-mast-triggered aerial

1080 operations have occurred (usually in the spring following the beech seedfall), the recent shift to beech-mast-triggered aerial 1080 operations may provide little or no benefit to kākā.

In this study we monitored the breeding success and survival of kākā in South Westland in the years of 1080 operations and in subsequent years primarily to determine whether 1080 treatment benefitted kākā and how long any benefit lasted. Since kākā productivity and survival is also likely to be affected by forest type and the fruiting and seeding of forest trees these were important covariates in our analysis. We then used simulation models to explore the timing and frequency of aerial 1080 operations that might most benefit kākā populations. In particular, we compared 1080 used at regular intervals with its use in response to mast to determine which had the greatest benefit for kākā.

Methods

Study area

The study area was centred around Lake Paringa (43°43' S, 169°25' E) in South Westland, approximately 70 km south of Fox Glacier. It comprised two blocks (Whakapohai and Paringa) that were treated two (Paringa) or three (Whakapohai) times with 1080 and one which was not (non-treatment) (Fig. 1).

The three study sites encompassed the country between the Tasman Sea and the mountain ranges. Elevation ranged from sea level to 961 m a.s.l. (above sea level) in the coastal

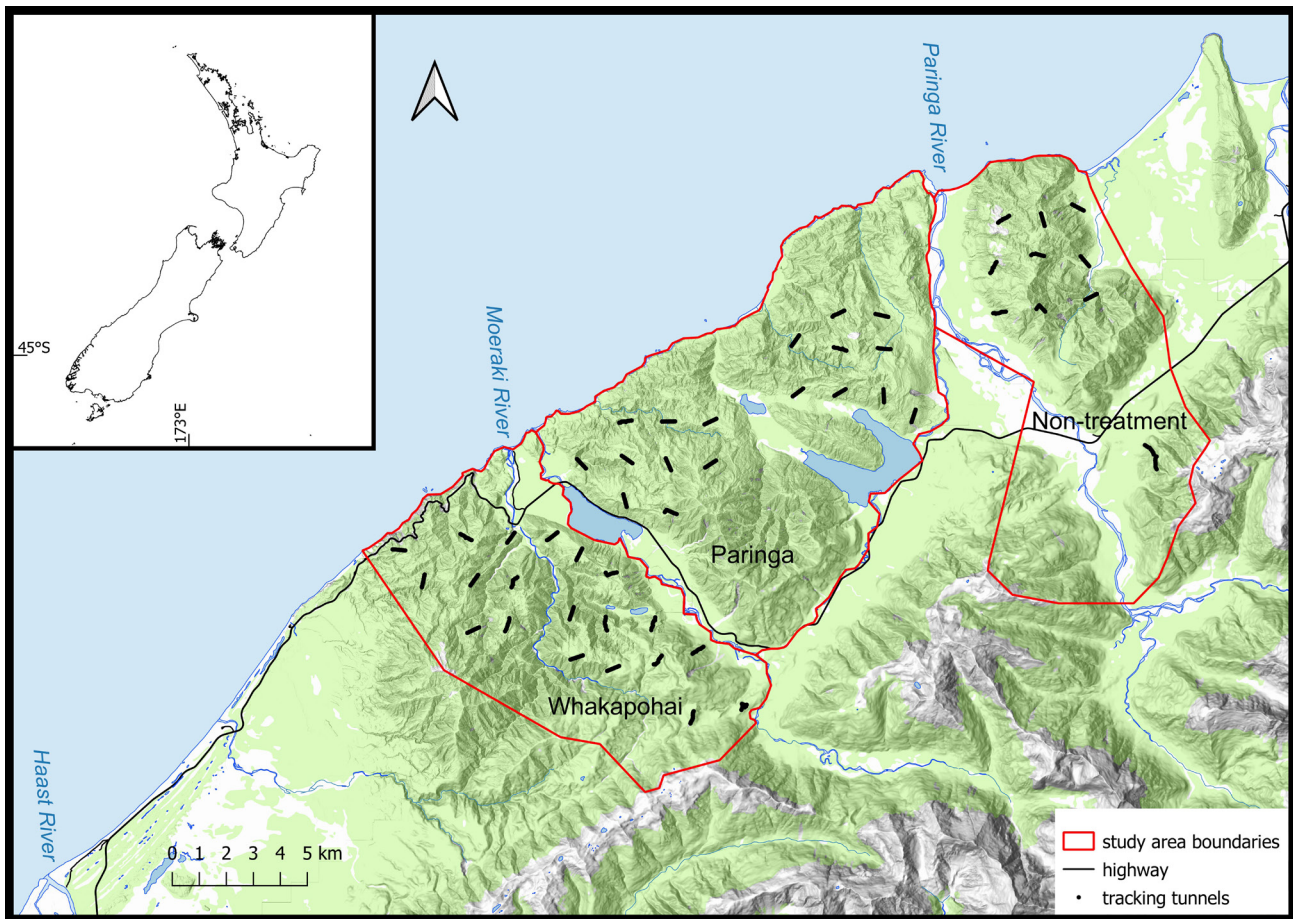


Figure 1. Map of the treatment and non-treatment areas used in the study and the locations of tracking tunnels.

hills and to a high point at 1535 m a.s.l. in the mountains. Kākā were most encountered between 250 and 800 m a.s.l. and always below the tree line. Most of the birds monitored in the non-treatment block were living on the mountain slopes east of the highway (Fig. 1).

The area has a mild climate (median annual temperature at Lake Paringa is 11 °C) and high rainfall (median annual rainfall of approximately 5500 mm; data from www.niwa.co.nz). The study area is primarily covered in native forest (Wardle 1980; Fig. 1).

Important forest trees in our study blocks include silver beech (*Lophozonia menziesii*), rimu, miro (*Prumnopitys ferruginea*), southern rātā (*Metrosideros umbellata*), kāmahi (*Pterophylla racemosa*), with kahikatea in poorly drained sites. Our study area included three main forest types (Nicholls & Herbert 2005): beech, rimu-beech, and rimu-hardwoods (Fig. 2). The distribution pattern of these forest types is primarily determined by the last glaciation and the subsequent recolonisation of glaciated areas first by rimu-hardwood forest and then by silver beech (Wardle 1980). The extent of these forest types varies between our three study blocks. The southern-most treatment block (Whakapohai) was mostly ice-free in the last glaciation and there is silver beech throughout the block while the two northern blocks (Paringa and non-treatment) were extensively glaciated and have much larger areas of rimu-hardwood forest as well as some beech (Wardle 1980).

The history of possum invasion and control has had a considerable impact on the vegetation and perhaps avifauna of

the study area. Possums invaded the area from the north after being liberated at Bruce Bay between 1925 and 1930 (Rose et al. 1990). They have been regularly controlled with 1080 south of the Paringa River, but no systematic possum control has been undertaken north of the Paringa River, though from time-to-time animals are killed by fur-trappers. Consequently, possums are more abundant north of the Paringa River than south of it and this is reflected in the low abundance of tree fuchsia (*Fuchsia excorticata*) (Pekelharing et al. 1998), and scarlet mistletoe (*Peraxilla colensoi*) (Bockett & Knightbridge 2004) north of the river. Kākā are also more common south of the Paringa River (O'Donnell & Dilks 1986), and their abundance is strongly and negatively associated with possum density (Rose et al. 1990).

1080 operations

Five 1080 operations were undertaken during our study and one a year before the study started (Table 1). The 1080 operations at the northern treatment block (Paringa) covered an area a few hundred hectares larger than the block in which we studied kākā, while the 1080 operations at the southern treatment block (Whakapohai) covered an area more than twice as large as the treatment block. The untreated block comprised the southern-most 8500 ha of an area of forest of more than 50 000 ha that has never been treated with 1080.

The 1080 operations at Whakapohai were deliberately timed to coincide with predicted kākā breeding with the aim of reducing stoat and possum densities while kākā were nesting. Kākā breeding was expected when beech and rimu seeded and

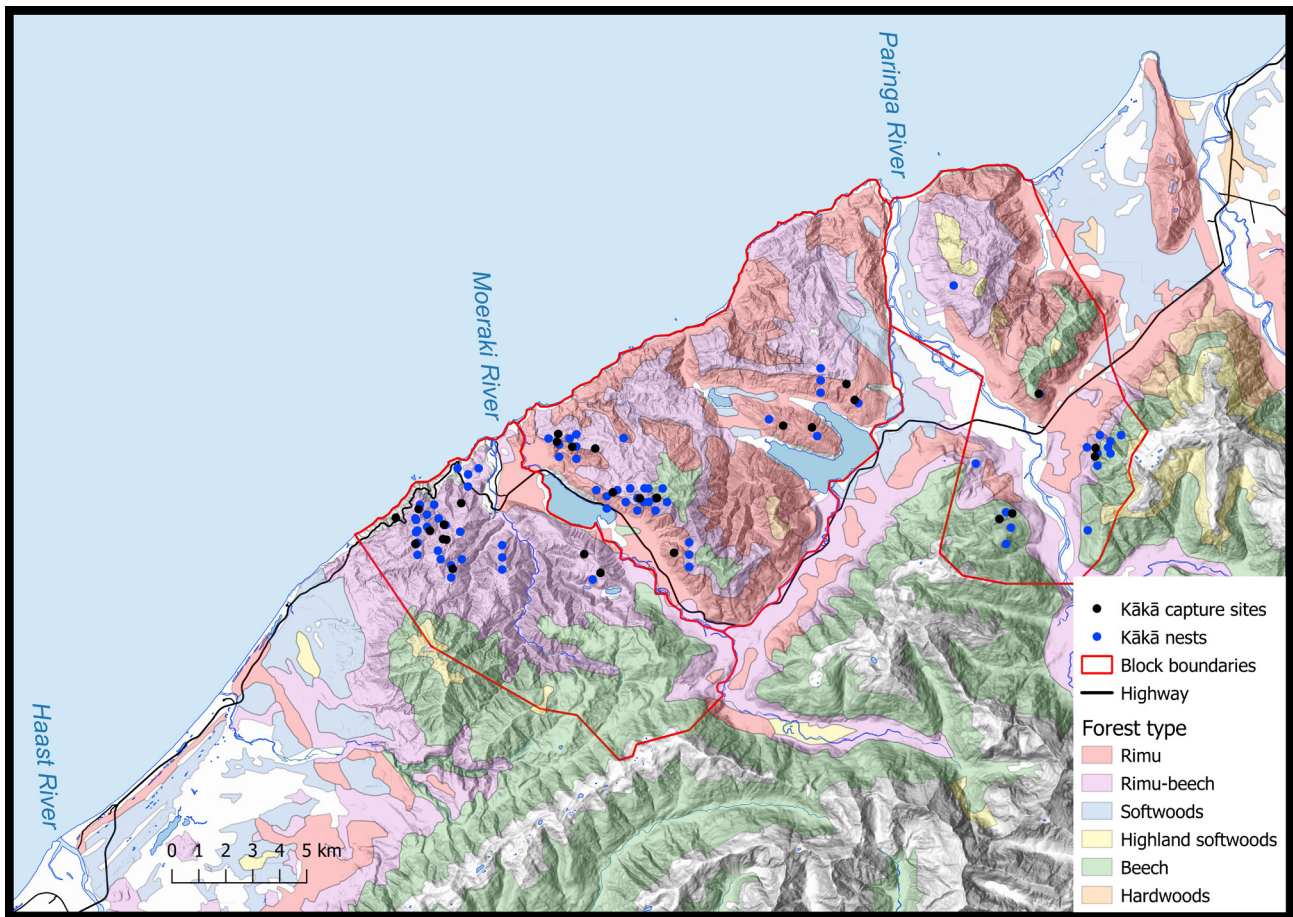


Figure 2. Forest types and Kākā nests and capture sites.

Table 1. Aerial 1080 operations undertaken in the study area since 2009. In the prefeed and toxic columns 0.15% is the concentration of 1080 in the baits, 6 g and 12 g are bait sizes, RS5 and #7 are different bait formulations, and 1 kg, 1.5 kg, 2 kg, and 3 kg refer to sowing rates of baits in kilograms per hectare.

| Block | Year | Area (ha) | Pre-feed | Date | Toxic | Date |
|------------|------|-----------|----------------|------------|-------------------------|------------|
| Paringa | 2009 | 12 050 | 6 g, #7, 2 kg | 26/5/2009 | 0.15%, 12 g, #7, 3 kg | 3/6/2009 |
| Paringa | 2011 | 14 500 | 2 g, RS5, 1 kg | 5/10/2011 | 0.15%, 6 g, RS5, 1 kg | 27/10/2011 |
| Paringa | 2014 | 15 386 | 6 g, RS5, 1 kg | 24/10/2014 | 0.15%, 6 g, RS5, 1.5 kg | 6/11/2014 |
| Whakapohai | 2010 | 26 269 | 6 g, RS5, 1 kg | 23/11/2010 | 0.15%, 6 g, RS5, 1 kg | 1/12/2010 |
| Whakapohai | 2013 | 29 733 | 6 g, RS5, 1 kg | 11/11/2013 | 0.15%, 6 g, RS5, 1 kg | 23/11/2013 |
| Whakapohai | 2015 | 27 039 | 6 g, RS5, 1 kg | 18/11/2015 | 0.15%, 6 g, RS5, 1 kg | 29/11/2015 |

these events were predicted by climate models for beech (Kelly et al. 2012), and by observations of developing rimu seeds. 1080 operations in 2011 and 2014 at Paringa were timed to occur at or about peak rat densities following beech and rimu seeding in the previous autumn with the aim of protecting small forest birds from rat and stoat predation. The timing of kākā breeding events and 1080 operations during the study enabled us to obtain nesting success data for the year of, one year after, and two years after a 1080 operation.

Mammal abundance indices

Rodent and stoat abundances were monitored with tracking tunnels (Fig. 1) using a protocol modified from Gillies and Williams (2013). To save time and money we modified the protocol by simultaneously baiting tracking tunnels with both peanut butter (for rodents) and rabbit meat (for stoats) and leaving the cards in the tunnels for only one night. Tracking tunnels were run in February, May, August, and November each year. Tracking tunnel lines consisted of 10 tunnels per line spaced 50 m apart and lines were usually at least 1 km apart. There were 20 lines in the Whakapohai block, 18 in Paringa, and 11 in the non-treatment block (Fig. 1). Stoat and rodent indices at different times and places were compared using quasibinomial generalised linear models (McCullagh & Nelder 1989) using the methods of Elliott et al. (2018).

Possum abundance was monitored once in the non-treatment block and three times in each treatment block, using a 7-day wax tag protocol (National Possum Control Agencies 2008). We estimated possum abundance indices between wax tag surveys by interpolation assuming different 1080 kill rates for the two treatment blocks and a common population growth rate between 1080 operations. We assumed the population at the non-treatment site was stable and at carrying capacity.

Beech flowering and podocarp fruiting

Beech flowering and seeding was noted anecdotally each season and seed fall was measured under mature silver beech trees using circular seed fall funnels with a collecting area of 0.28 m², set 1.2 m above ground (Fitzgerald et al. 1996). Ten funnels (five in each of the two treatment blocks) ranging in elevation from 25 m a.s.l. to 700 m a.s.l. were run every year from January to July/August. Stockings mounted on the bottoms of the funnels collected the seed. Each sample was dried and then sorted with the total number of seeds and the number viable counted. To ascertain viability, seeds were either cut or, if in sufficient quantity, floated in 99% pure methanol (Ledgard & Cath 1983).

Eight mature female rimu trees (four in each of the two treatment blocks) were monitored annually to assess fruit production. The trees were climbed between March–May each year and samples of four canopy branchlets per tree were selected and a handful of growing tips on each sample were counted, aiming for between 200–300 tips in the count. Developing, ripe, and old fruits were counted and measured as a percentage of the total counted on each branchlet. An overall average proportion of developing fruit was calculated to give us a predictor for kākā breeding the following summer.

Catching and radio tagging kākā

Adult female kākā were captured each spring and radio-tagged to assess their survivorship and find nests. Kākā were attracted into canopy-height mist-nets using recorded calls of local kākā (Dilks et al. 1995). The sex of captured kākā was determined by measurement (Moorhouse et al. 1999), and males were released while females had a transmitter attached. Transmitters were attached using a weak-link flying bird harness (Karl & Clout 1987).

Mist-netting kākā has mostly been shown not to be gender selective and the sex ratio of birds caught can be used as an indicator of the status of a population (Greene & Fraser 1998; Wilson et al. 1998). However, timing of capture can affect the sex ratio of birds caught (Greene & Fraser 1998). We explored the effect of timing of capture and predator control on the sex ratio of kākā we caught in mist nets using logistic generalised linear models (Appendix S1 in Supplementary Material).

To explore possible effects of vegetation on kākā survival we assigned a forest type (as Nicholls & Herbert 2005) to each kākā capture site from NZ FSMS6 (South Island) national forest survey maps (Land Information New Zealand 2008). The location of kākā captures was primarily determined by the distribution of suitable kākā capture sites. Kākā capture sites needed to have kākā present, needed to be near the road, and needed to have vegetation and topography suitable for erecting mist nets high in trees. As a result, kākā captures were unevenly distributed amongst the treatment blocks and forest types and power to draw conclusions about possible relationships between kākā survival and vegetation is limited.

Kākā nesting success

Kākā nests were found using three methods:

- (1) Following radio-tagged females to their nests.
- (2) Following non-radio tagged birds that were showing nesting or mating behaviour.
- (3) Visiting previously used nest holes.

In the first two breeding seasons we used standard very high frequency (VHF) transmitters and found nests by regularly (weekly to fortnightly) radio tracking and observing birds to see if they were using a cavity. In the last two breeding seasons of our study we used more sophisticated transmitters which had inbuilt light and movement sensors. These transmitters logged activity and light levels (kākā nest in dark cavities) and their pulse rate was coded to broadcast a summary of the last six days which indicated whether kākā were nesting. Outputs were collected every six days and when they indicated nesting behaviour a bird was radio-tracked and observed.

When a nest was found the nest tree was climbed using single rope tree climbing techniques and the nest inspected. Movement triggered trail cameras (Ltl Acorn®-5210 series) were installed outside all active nests, usually 1–1.2 m above the nest with a view of the nest entrance and the tree trunk below it. Nests were visited weekly or fortnightly to change batteries and memory cards. The cameras recorded kākā activity, visits from predators, predation events, and fledging. Occasionally fledging was not recorded on the camera, then we would find the adults and watch and listen for fledglings (which are very conspicuous) to confirm the success of the nest.

To explore possible effects of vegetation on kākā nest success we assigned a forest type to each kākā nest in the same way we assigned forest types to kākā captures (Nicholls & Herbert 2005). Kākā capture sites and consequently kākā nest sites were not evenly distributed amongst the treatment blocks or vegetation types and samples sizes for some treatment and vegetation type combinations were small. The power of this study to draw conclusions about possible relationships between nesting success and vegetation is limited.

Nesting success was estimated using generalised linear models (GLMs) with binomial errors and complementary log-log link functions using methods from Rotella et al. (2004) and Bolker (2014). In these models the response variable is binomial, the nest having succeeded or failed in the days since it was last checked. Most often the nest was effectively checked daily by trail camera, but sometimes when cameras failed nests were checked at longer intervals. GLMs used in this way produce estimates of daily nest survival which we convert to nesting success by raising the daily survival to the power of 103 (the approximate duration of the incubation and nestling stages in days).

We estimated nesting success during each breeding season and in each block using a generalised linear model with the only explanatory variables being year and study block and the year \times study block interaction.

To determine whether time since the last 1080 operation, stoat, rat or possum abundance indices, distance to the edge of the pest controlled area, forest type, height of nest above the ground, or altitude were useful predictors of nesting success we compared a suite of generalised linear models that included all plausible combinations of these explanatory variables (but not interactions between them, nor year and study block and their interaction; Appendix S2). Models were run in R (version 3.6.3) (R Core Team 2020) and compared using AIC_c (Burnham & Anderson 2002) implemented in the package AICcmodavg (version 2.2.2) (Mazerolle 2019).

Time since 1080 and the mammal abundance indices are highly correlated and are both effectively measures of the effectiveness of pest control, so we did not include models with both mammal abundance indices and time since 1080 in our suite of plausible models. To examine the longevity of the effect of 1080 operations, four different categorisations

of time since 1080 operation were included in the plausible model set, though only one was included in any single model:

- (1) Time since 1080a (3 categories): (a) < 1 year after a 1080 operation, (b) 1–2 years after a 1080 operation, and (c) > 2 years after a 1080 operation. Nests in the non-treatment block were placed in the >2 years after 1080 category.
- (2) Time since 1080b (2 categories): (a) less or (b) more than a year since a 1080 operation. Nests in the non-treatment block were placed more than a year since 1080 category.
- (3) Time since 1080c (2 categories): (a) less or (b) more than 2 years since a 1080 operation. Nests in the non-treatment block were placed in more than 2 years since 1080 category.
- (4) Time since 1080d (2 categories): (a) treated at least once, or (b) never treated with 1080.

To examine the possibility that any apparent effect of treatment on nesting success might have been a spurious relationship caused by the uneven distribution of monitored nests amongst vegetation types, we examined the relationship between nesting success and treatment in the subset of nests we found in rimu-beech forest. We monitored nests in this forest type in all three of our study blocks.

Kākā survival

Bykill during 1080 operations

To determine whether any kākā were poisoned during the 1080 operations we regularly checked all radio-tagged birds up to two months before and two months after each 1080 operation.

Long-term survival

We used radio-tracking data from female kākā to explore a possible relationship between kākā survival and changes in mammal abundance indices associated with 1080 operations. We were able to examine female survival as a by-product of our nest success monitoring programme in which we radio-tagged females so that we could find their nests (only females incubate). Only data from birds with working transmitters were used in our analysis. Some birds were known to be alive after their transmitters failed and others disappeared either because their transmitter failed or because they moved out of our study area. These birds contributed data to the survival estimates as long as their transmitter was known to be working after which they were ‘right censored’ from the data. The transmitters we used produced a mortality signal when birds became inactive and when this happened, we closely radio-tracked the bird either to see it still alive (with a faulty transmitter), to retrieve its carcass, or to retrieve a dropped transmitter (from a broken harness).

Long-term survival was estimated using GLMs and the same methods as nesting success. The response variable in survival analysis was binomial with the bird being either alive or dead in the days since its survival was last monitored. GLMs used in this way produce estimates of daily survival which we convert to annual survival by raising it to the power of 365.

To determine whether time since the last 1080 operation, mammal abundance indices, and forest type were useful predictors of female kākā survival we compared a suite of plausible generalised linear models incorporating various combinations of these terms (Table 2; Appendix S3). To examine the longevity of the effect of 1080 operations we compared the same categorisation of time since 1080 used in modelling nest success.

Table 2. Model selection table for the relationship between female kākā survival and forest type and time since 1080. “Time since 1080c” = more or less than two years since a 1080 operation. “Time since 1080b” = more or less than one year since a 1080 operation. “Time since 1080d” = treated or not treated with 1080.

| Models | K | AICc | Δ AICc | AICcWt |
|--------------------------------|---|-------|---------------|--------|
| time since 1080c | 2 | 71.18 | 0.00 | 0.38 |
| stoat | 2 | 72.60 | 1.42 | 0.19 |
| forest type + time since 1080c | 4 | 74.06 | 2.88 | 0.09 |
| stoat + possum | 3 | 74.28 | 3.10 | 0.08 |
| time since 1080d | 2 | 75.41 | 4.23 | 0.05 |
| Forest type | 3 | 75.60 | 4.42 | 0.04 |
| rat + stoat + possum | 4 | 75.96 | 4.78 | 0.03 |
| intercept only | 1 | 76.01 | 4.84 | 0.03 |
| time since 1080b | 2 | 76.08 | 4.90 | 0.03 |
| possum | 2 | 76.37 | 5.19 | 0.03 |
| forest type + time since 1080b | 4 | 76.77 | 5.59 | 0.02 |
| forest type + time since 1080d | 4 | 77.19 | 6.01 | 0.02 |

Table 3. Simulated kākā annual population growth rates (λ) for 24 pest control scenarios. Figures in bold are the mean growth rates, surround by the 2.5% and 97% percentiles.

| Scenarios | Adult nesting mortality | |
|--|----------------------------|----------------------------|
| | Low | High |
| No pest control | 0.684– 0.883 –1.152 | 0.565– 0.763 –0.967 |
| Annual pest control | 0.856– 1.161 –1.600 | 0.851– 1.134 –1.586 |
| Stoat suppression lasts 2 years | | |
| 1080 when kākā breed | 0.830– 1.142 –1.623 | 0.833– 1.122 –1.577 |
| 1080 when mast occurs | 0.740– 1.104 –1.618 | 0.681– 1.063 –1.573 |
| 1080 when rodents plague | 0.738– 1.084 –1.566 | 0.632– 1.027 –1.514 |
| 1080 at 2-year intervals | 0.855– 1.162 –1.627 | 0.851– 1.134 –1.577 |
| 1080 at 3-year intervals | 0.666– 1.058 –1.630 | 0.582– 0.998 –1.578 |
| Stoat suppression lasts 3 years | | |
| 1080 when kākā breed | 0.846– 1.152 –1.624 | 0.845– 1.130 –1.566 |
| 1080 when mast occurs | 0.783– 1.128 –1.611 | 0.720– 1.098 –1.561 |
| 1080 when rodents plague | 0.791– 1.119 –1.596 | 0.695– 1.085 –1.545 |
| 1080 at 2-year intervals | 0.854– 1.160 –1.624 | 0.850– 1.133 –1.581 |
| 1080 at 3-year intervals | 0.853– 1.160 –1.625 | 0.850– 1.133 –1.570 |

Modelling

We used matrix population models to explore the effect of varying timing and frequencies of 1080 operations on kākā population growth in rimu-beech forests; the forest type for which we have the best data in our study.

Modelling scenarios

We constructed six annual population projection matrices (Lefkovich 1965) representing all combinations of three levels of nesting success (no breeding, low nesting success, high nesting success), and two levels of adult survival while nesting (high and low). We used these matrices in various combinations to simulate 24 scenarios (Table 3) which represents plausible combinations of the following:

- (1) Mortality of adults while nesting is high or low.
- (2) Stoat suppression lasts two or three years.
- (3) Pest control either never, annual, every time kākā breed, every mast, every rodent plague, at regular intervals of two years, or at regular intervals of three years.

We compared high and low adult nesting mortality, because although we observed only one adult death on 60

nests, much higher adult nesting mortality has been recorded in other studies (Moorhouse et al. 2003; Taylor et al. 2009). We compared the effect of stoat suppression lasting two or three years because in our study the effect of stoat suppression lasted only two years, but it seems likely that stoat suppression might last longer when the area of pest control is larger (see Results section). Population parameters used in the projection matrices were derived from this study or were borrowed from earlier studies (Table 4).

Simulations all started with a population vector (N_0) representing the stable-age distribution derived from the eigenvalues of a projection matrix comprising mean values for all population parameters (Caswell 2001). We assumed kākā bred in response to mast once every two years because the average frequency of rimu masts in lanthe Forest 120 km north-east of our study area was one every 2.2 years (Norton & Kelly 1988) and kākā breed in response to beech as well as rimu in rimu-beech forests and they also occasionally breed when there is no mast, as they did in our study (Table 5).

We then repeatedly multiplied population vectors by various combinations of the 18 projection matrices to simulate each scenario. This was repeated 10 000 times

Table 4. Parameters used in kākā population simulations.

| Parameter | Estimate | SE | Distribution | Source |
|--|----------|------------------------|-------------------------|-----------------------|
| Clutch size | 2.23 | 0.17 | Normal | This study |
| Proportion breeding in a breeding year | 0.68 | 0.07 | Beta | This study |
| Juvenile survival year 1 | 0.61 | 0.06 | Beta | Moorhouse et al. 2003 |
| Juvenile survival year 2 | | Same as adult survival | | This study |
| Adult survival with pest control* | 1.00 | 0 | Normal on cloglog scale | This study |
| Adult survival without pest control* | 0.91 | 0.06 | Normal on cloglog scale | This study |
| Adult female nesting mortality | | | | |
| High mortality with pest control | 0.08 | 0.04 | Beta | Taylor et al. 2009 |
| High mortality without pest control | 0.42 | 0.08 | Beta | Taylor et al. 2009 |
| Low mortality with pest control | 0.00 | 0 | | This study |
| Low mortality without pest control | 0.08 | 0.08 | Beta | This study |
| Nesting success with pest control | 0.83 | 0.08 | Normal on cloglog scale | This study |
| Nesting success without pest control | 0.16 | 0.11 | Normal on cloglog scale | This study |
| Probability of breeding after mast | 1.00 | 0 | | This study |
| Proportion breeding in non-mast year | 0.33 | 0 | | This study |

*excludes mortality while nesting

Table 5. Seasons in which beech and rimu seeded and kākā bred showing the amount of seed produced, proportion of radio tagged birds that laid eggs and differences in clutch sizes between seasons.

| | 2010/11 | 2011/12 | 2012/13 | 2013/14 | 2014/15 | 2015/16 |
|-------------------------------|-----------|---------|----------|-----------|---------|-----------|
| Beech seeds / m ⁻² | 2699 | 0 | 0 | 1599 | 4.4 | 2003 |
| Beech seed viability % | 34 | - | - | 2 | 9 | 39 |
| % rimu tips with fruit | 18.66 | 3.91 | 2.13 | 2.64 | 1.37 | 13.03 |
| Kākā nests monitored | 10 | 0 | 8 | 15 | 0 | 27 |
| % nested (birds monitored) | 100 (6) | 0 (6) | 100 (3) | 43 (21) | 0 (7) | 85 (17) |
| Mean clutch size (clutches) | 3.40 (10) | - | 3.00 (7) | 2.87 (15) | - | 3.93 (27) |

(10 000 years) for each scenario with stochasticity simulated by randomly selecting values for each parameter from appropriate distributions (Table 4); for each simulation year, population growth rates were calculated and the mean of the logged growth rates calculated (i.e. their geometric mean) for each of the 24 scenarios (this is the time-averaged growth rate in the language of Caswell 2001).

Results

Beech and rimu fruiting and kākā breeding

Although we monitored rimu and beech seeding only in the two treatment blocks, we are confident from our anecdotal observations that the magnitude and timing of beech and rimu seeding was very similar in all three blocks.

Silver beech produced some seed in four of the six years of our study, in three of those years there were substantial seedfalls, but in only two of them were there more than a few viable seeds (Table 5). Rimu produced seed every year, but in only two seasons (2010/11 and 2015/16) was there a substantial seedfall (Table 5). Neither beech nor rimu are evenly distributed across our study blocks (Fig. 2), nor did we sample from throughout the blocks. However, it is our impression that beech and rimu flowering and seeding occurred at a similar level throughout our study blocks. Kahikatea trees in South Westland fruited exceptionally heavily in 2015 (JM pers obs.). We found some kākā nesting on four of the six seasons of our

study (Table 5; Fig. 3). Two of these seasons (2010/11 and 2015/16) were coincident with beech, rimu, and kahikatea seeding, and one season (2013/14) was coincident with beech only seeding. Some nesting occurred in 2012/13 when there was no beech seeding and very little rimu seeding.

There is no obvious relationship between the proportion of birds that bred in a year and the magnitude of beech or rimu seed, but clutch size varied significantly between years (Kruskal-Wallis chi-squared = 10.486, df = 3, p-value = 0.015) with clutch sizes largest when rimu and beech fruited and seeded heavily (Table 5).

Mammal abundance indices

The small beech seedfall in 2014 had no obvious effect on rodent and stoat populations, but the rimu and beech seedfalls in 2011 and 2016 appear to have led to increases in rodent populations, but no obvious response from stoats (Fig. 3). The pattern of changes in abundance indices of rats, mice, and stoats differed not only between the treatment and non-treatment sites, but also between the two treatment sites. Rat, mouse, and stoat abundance indices were mostly reduced following 1080 operations, but rat and mouse abundance indices rose to higher levels than in the non-treatment block in the periods between 1080 treatments.

Average tracking rates for stoats were higher in the non-treatment block (18%) than in the two treatment blocks (Whakapohai 6%, Paringa 5%) and the difference was statistically significant (quasi binomial ANOVA $F = 41.6$, df

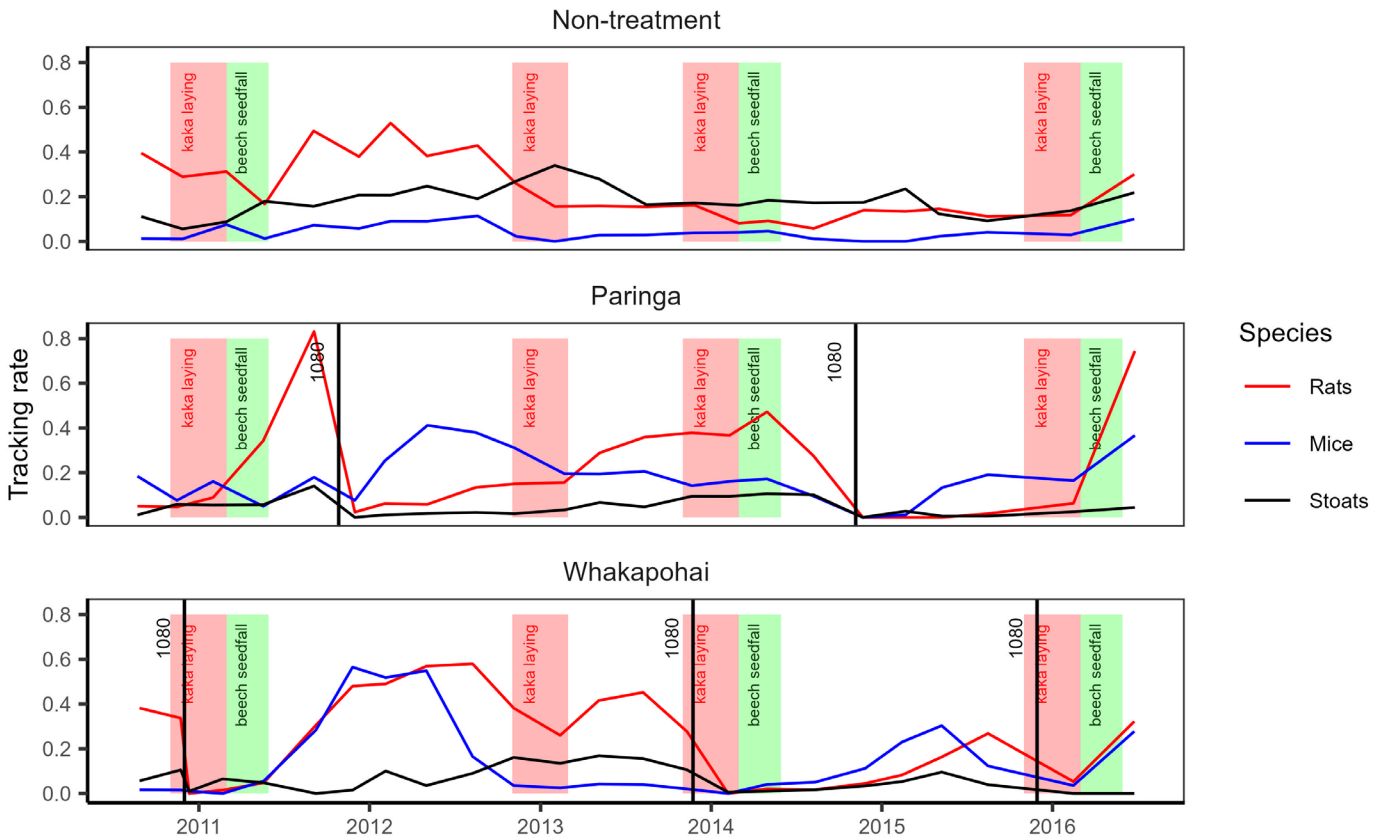


Figure 3. Tracking tunnel indices for rats, mice and stoats between May 2010 and November 2016 and the timing of beech seedfall, kākā laying, and 1080 operations.

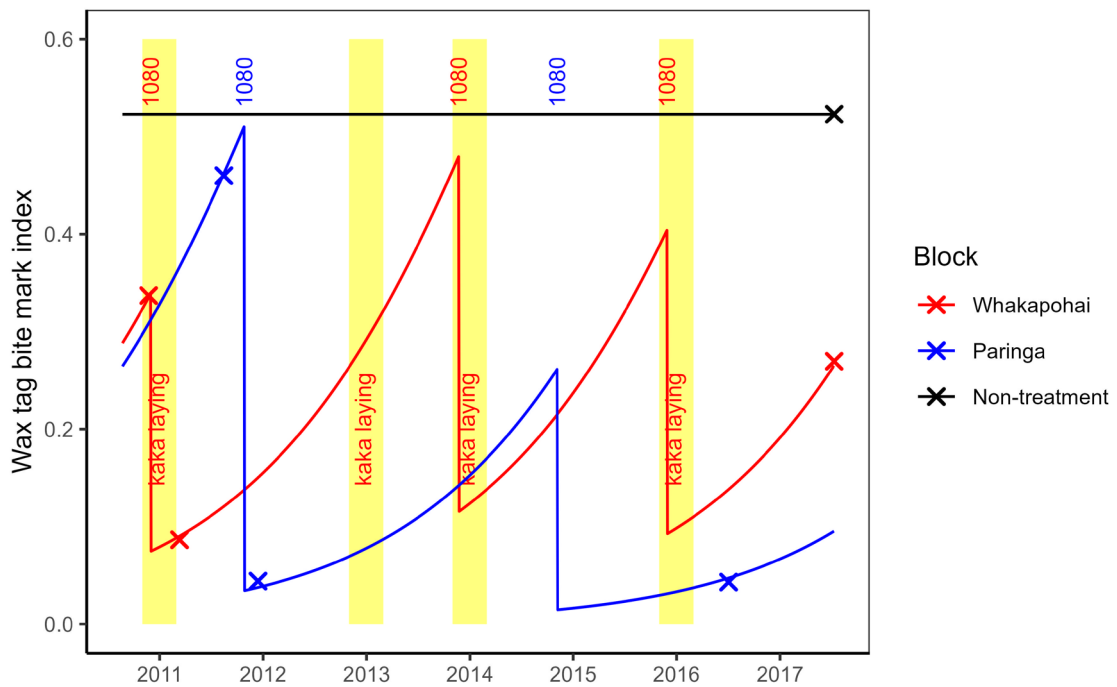


Figure 4. Waxtag possum bite mark indices and estimated bite mark indices for the three study blocks between 2011 and 2017. Crosses are actual data and lines are interpolated assuming a constant kill rate in each block and a common growth rate between 1080 operations. Kākā laying occurred in the periods indicated by yellow rectangles and 1080 operations occurred at dates indicated by “1080” in blue at Paringa and “1080” in red at Whakapohai.

= 2, $p < 0.001$). Average tracking rates for rats were highest in the Whakapohai block (25%), intermediate in the non-treatment block (23%) and lowest in the Paringa block (20%) and these differences were significant (quasi binomial ANOVA $F = 3.36$, $df = 2$, $p = 0.035$). Mouse abundance indices were on average higher in the two treatment blocks (Whakapohai 14%, Paringa 18%) than in the non-treatment block (4%) and the differences were significant (quasi binomial ANOVA $F = 38.8$, $df = 2$, $p < 0.001$).

Possum abundance indices were higher in the non-treatment block than the two treatment blocks (Fig. 4). Kill rates in the 1080 operations at Whakapohai in 2010 and Paringa in 2011 were 81% and 95% respectively and assuming that subsequent 1080 operations in the two blocks achieved the same kill rates the population growth rate between operations must have been 200% per annum (i.e. it doubled every year). This population growth rate is higher than recorded elsewhere (Hickling & Pekelharing 1989) and suggests that much of the population growth was driven by immigration from neighbouring untreated forests.

Kākā sex ratio

The sex ratio of captured kākā varied between years (Table 6) with the male bias greater in the treatment sites during the first season of catching than in later seasons, and greater at

Table 6. Sex ratio of captured birds from each season. No catching was attempted in the non-treatment site in 2010.

| Sites | Year | No. caught | | Sex ratio (Male:Female) |
|---------------|------|------------|--------|----------------------------|
| | | Male | Female | |
| Whakapohai | 2010 | 23 | 5 | 4.6:1 |
| | 2013 | 7 | 9 | 1:1.28 |
| | 2015 | 13 | 7 | 1.8:1 |
| Paringa | 2010 | 12 | 4 | 3:1 |
| | 2013 | 8 | 7 | 1.14:1 |
| | 2015 | 11 | 8 | 1.38:1 |
| Non-treatment | 2013 | 18 | 6 | 3:1 |
| | 2015 | 13 | 1 | 13:1 |

Table 7. Model selection table of generalised linear models of the relationship between the sex ratio of kākā caught in mist nets and time of year, year and treatment with 1080.

| Model | df | AIC _c | ΔAIC _c | logLik |
|-----------------------------------|----|------------------|-------------------|---------|
| ~ time of year + year | 3 | 174.7 | 0.00 | -84.244 |
| ~ time of year | 2 | 175.2 | 0.57 | -85.573 |
| ~ time of year + year + treatment | 4 | 176.6 | 1.93 | -84.149 |
| ~ time of year + treatment | 3 | 177.3 | 2.61 | -85.548 |
| ~ year + treatment | 3 | 179.7 | 5.00 | -86.741 |
| ~ treatment | 2 | 180.8 | 6.14 | -88.356 |
| ~ . | 1 | 183.1 | 8.47 | -90.552 |
| ~ year | 2 | 183.5 | 8.89 | -89.731 |

Table 8. Kākā nests monitored in three blocks and three forest types in South Westland. Days monitored in brackets.

| Blocks | 2010/11 | 2012/13 | 2013/14 | 2015/16 | Total | Beech | Rimu-beech | Rimu-hardwoods |
|---------------|----------|---------|----------|-----------|-----------|-------|------------|----------------|
| Non-treatment | 1 (7) | 3 (90) | 4 (171) | 5 (329) | 13 (597) | 10 | 2 | 1 |
| Paringa | 4 (176) | 3 (228) | 8 (271) | 11 (788) | 26 (1449) | 0 | 15 | 11 |
| Whakapohai | 5 (261) | 2 (86) | 3(81) | 11 (815) | 21 (1243) | 0 | 21 | 0 |
| Total | 10 (444) | 8 (404) | 15 (509) | 27 (1932) | 60 (3289) | 10 | 38 | 12 |

the non-treatment site than at the treatment sites. However, analysis using generalised linear models (Table 7) shows that while time of year is an important predictor of sex ratio, and year probably a useful predictor, the addition of a treatment effect to the models made them worse and there is thus no evidence that treatment had any effect on sex ratio.

Kākā nesting success

During our study kākā nested in four summer seasons and 68 active nests were found of which 60 were monitored and produced some useable data (Table 8). Five of the eight unmonitored nests failed before we found them; at one the camera failed, at another there were bees in the nesting tree, and another nest was too deep for us to see inside.

There was considerable spatial and temporal variation in nesting success and the estimates had large standard errors (Fig. 5).

Preliminary analysis of the relationship between nest success and nest age indicated that there was a curvilinear relationship between them with nest success declining with nest age. We included a quadratic term for nest age in all our plausible models.

The best models of kākā nesting success (Table 9) indicated a strong association between kākā nesting success and time since 1080. The best categorisation of time since 1080 suggested that 1080 results in improved nesting success for two breeding seasons following a 1080 operation (Fig. 6). Of the other possible explanatory variables forest type, altitude, nest height, and distance to edge of the 1080 block were decreasingly important explainers of nesting success. The apparent effect of forest type on nest success needs to be treated with caution as the forest types were not distributed evenly amongst the treatment blocks nor amongst the time since treatment classes. In particular, we monitored a small number of ($n = 10$) nests in beech forests in the non-treatment block but no nests in beech forest in the two treatment blocks. The models predicted the highest nesting success in beech forest, then in beech-rimu and rimu-hardwood forest (Fig. 6), but since nesting success in beech forest is confounded with non-treatment, we cannot confidently estimate nesting success in beech forest except in the non-treatment block nor

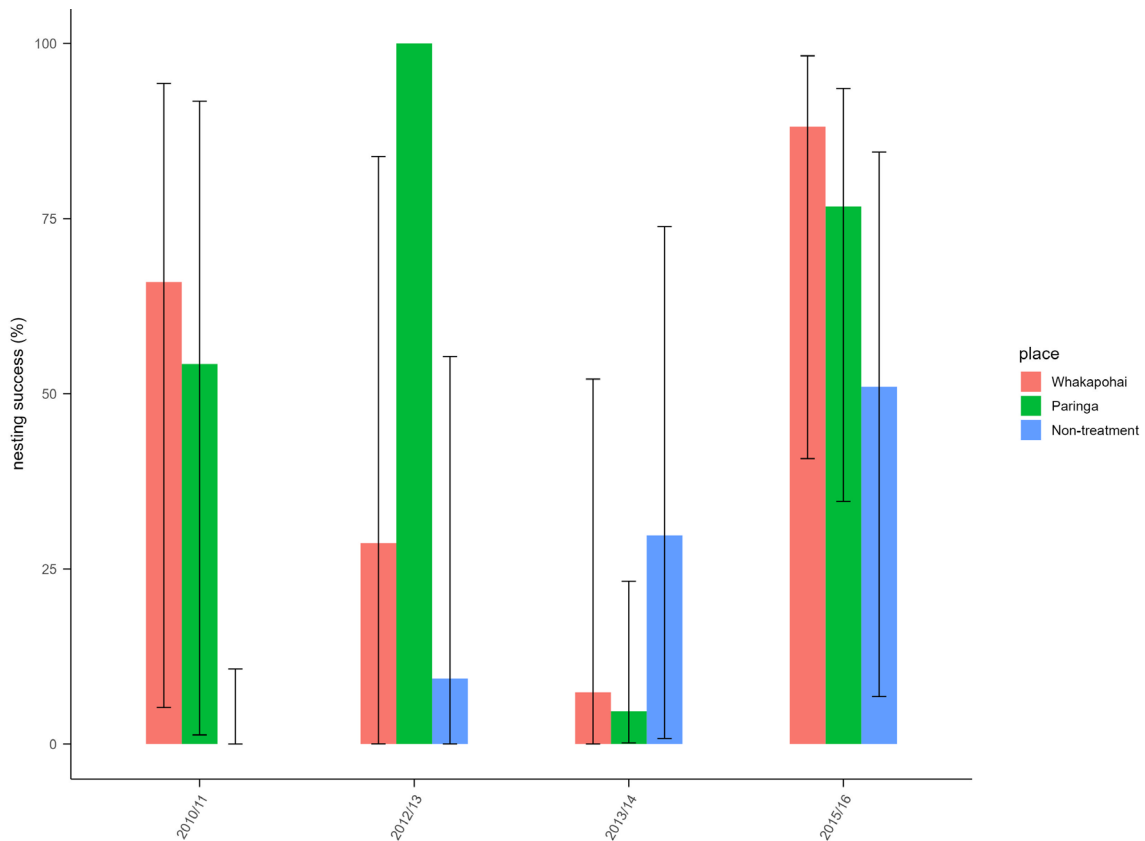


Figure 5. Kākā nesting success in three study blocks during four breeding seasons. Nesting success was estimated from GLMs of daily nest survival. Error bars are 95% confidence intervals.

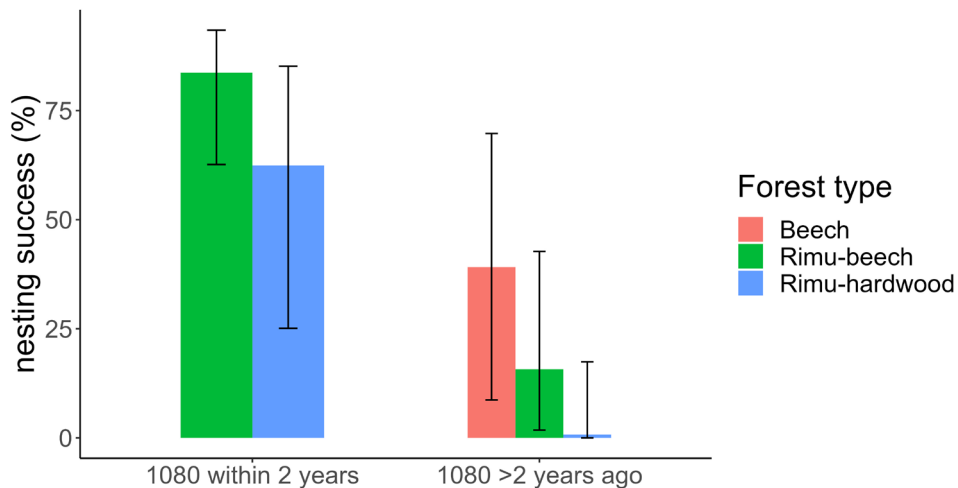


Figure 6. The relationship between kākā nesting success, the timing of 1080 operations, and forest type. Error bars are 95% confidence intervals.

can we usefully examine possible interactions between forest type and treatment. Nesting success was greater at higher altitudes, greater in nests high off the ground, and greater when nests were further into treatment blocks. Models including treatment with 1080 were clearly better predictors of kākā nesting success than models including the abundance indices of rats, stoats, and possums, as the best models with mammal abundance indices had delta AICc scores greater than 5.68.

Amongst models with no 1080 treatment effect, the order of

importance of small mammals as predictors of nest success was stoat, then rat, then possum, with nests being more successful when mammals were less abundant.

When the nest survival modelling exercise was repeated with only those nests that occurred in rimu-beech forest, the results were very similar with time since 1080 being clearly the best predictor of nest survival. It is unlikely that the most important relationships revealed by the GLMs are spurious ones caused by the uneven distribution of nests amongst forest types.

Table 9. Model selection table of the 10 best plausible generalised linear models of the relationship between kākā nesting success and possible explanatory variables. Time since 1080c = time since 1080 categorised as less or more than two years since a 1080 operation. Time since 1080a = time since 1080 categorised as < 1 year after a 1080 operation, 1–2 years after a 1080 operation, and > 2 years after a 1080 operation.

| Models | npar | AIC _c | ΔAIC _c | weight |
|---|------|------------------|-------------------|--------|
| ~ time since 1080c + forest type | 6 | 250.1 | 0.00 | 0.184 |
| ~ time since 1080c + altitude | 5 | 250.8 | 0.64 | 0.134 |
| ~ time since 1080a + forest type | 8 | 251.0 | 0.85 | 0.121 |
| ~ time since 1080c + altitude + nest height | 6 | 251.0 | 0.86 | 0.120 |
| ~ time since 1080c + nest height + forest type | 7 | 251.4 | 1.29 | 0.097 |
| ~ time since 1080c + forest type + distance to edge | 7 | 251.6 | 1.51 | 0.086 |
| ~ time since 1080c + forest type + altitude | 7 | 251.8 | 1.70 | 0.079 |
| ~ time since 1080c | 4 | 252.2 | 2.08 | 0.065 |
| ~ time since 1080c + distance to edge + forest type | 8 | 252.4 | 2.25 | 0.060 |
| ~ time since 1080a + forest type + distance to edge | 9 | 252.6 | 2.46 | 0.054 |

Causes of kākā nest failure

Of the 60 monitored nests used for data analysis 22 failed and the cause of failure was identified for 21 of them using trail cameras (Table 10). Predation was the main (82%) cause of nest failure and stoats accounted for 83% of nests that were preyed upon. Sixty percent of stoat predations occurred in the 2013 season. Two nests (11.1%), both at incubation stage were preyed upon by possums. One of these nests subsequently became a possum den. A single nest was preyed upon by a kea; this is the first recorded instance of kea eating kākā eggs. We found no direct evidence of eggs or nestlings being preyed on by rats. The two nests which failed due to natural causes were two successive infertile clutches laid by one female in a single season. One bird deserted her nest after we modified the entrance to enable a clearer view for the motion sensor camera; we almost certainly caused her to desert.

Stoats were photographed outside the nest entrances at a total of 20 nests. Of those nests, five (25%) were not preyed upon and subsequently fledged. No nests were preyed upon after nestlings reached 16 days old (range 0–16 days, median 11 days, SD = 5.477, $n = 10$) and an incubating female kākā which successfully raised nestlings was photographed confronting a stoat which did not return to the nest.

Cameras were left operating at 41 nests after they had fledged or failed. At one nest the camera continued working for 11 months after the nestlings fledged. At this nest, a stoat was photographed outside the entrance at night while the female was inside when the nestlings were 39 days old, but it did not prey upon the nest and the nestlings subsequently fledged. A stoat was photographed visiting the empty nest in May, June, September, December, and February but it was

Table 10. Causes of nest failure amongst 60 kākā nests monitored in South Westland.

| Cause of failure | <i>n</i> |
|------------------|-----------|
| Natural | 2 |
| Human induced | 1 |
| Unknown | 1 |
| Predator | |
| Stoat | 15 |
| Possum | 2 |
| Kea | 1 |
| Total | 22 |

not possible to determine whether a single, or multiple stoats visited the nest cavity.

Trail cameras mounted at nests showed that the number of nests visited by possums was much higher than the number preyed upon by them. Possum visitation was also much higher in the non-treatment block with its corresponding higher possum abundance indices. Of nests which had trail cameras installed, possum visits were recorded at 58.3% ($n = 12$ nests) in the non-treatment block, 25% ($n = 24$ nests) in the Paringa block, and 21.05% ($n = 19$ nests) in the Whakapohai block. It should be noted that some kākā nest trees appeared to be favoured possum trees and recorded possum visits on multiple nights and in some cases multiple seasons. Possum visitation behaviour ranged from the animal climbing the tree trunk outside the nest entrance but showing no interest in the nest (44% of visits); to the possum forcibly trying to enter the nest multiple times (11% of visits). There were possum/kākā interactions at six (33%) nests, and in most cases the female kākā was seen coming to the entrance and vocalising at the possum. There were some instances where the kākā chased the possum away.

Distinctive signs of rat predation of eggs (Moor 1978) were observed in two nests, though it is not possible to definitively attribute the causes of failure to rats. One nest failed during laying and before cameras were installed and the other nest appeared to have been deserted in early incubation and the eggs subsequently scavenged. Rats were photographed visiting seven active nests, but they continued successfully without being preyed upon. In all cases the rats appeared to be ship rats. During the study, only ship rats were positively identified in the study area.

Adult survival

Bykill during 1080 operations

A total of 42 radio tagged kākā were monitored through the six aerial 1080 operations which occurred during our study. There were no deaths or disappearances within two months after any of the 1080 operations.

Long-term survival

Of the 68 adult kākā (53 females and 15 males) we radio-tagged and monitored, only four females died. This included 2 out of 41 monitored females in the treatment blocks and 2 out of 12 in the non-treatment block. All appeared to have been preyed upon by stoats and all died between January and April 2014.

One of the birds was nesting at the time it was killed. A fifth, cached, male kākā was found in the Whakapohai block during October 2013. This record has not been used in the analysis.

The best GLM model of the relationship between female kākā survival, time since 1080, mammal abundance indices, and forest type (Table 2) included only a term for time since 1080, in which the time since 1080 effect was classified as either more or less than two years since the last 1080 operation. All female kākā survived when there had been a 1080 operation less than two years previously, but survival was only 86% per annum (95% confidence intervals 67–95%) when the most recent 1080 operation was more than two years previously or when 1080 had never been used. The second-best model included only a term for stoat abundance which indicates that the suppression of stoats was the main reason why kākā survival improved following 1080 operations. The inclusion of forest type in the models increased the AICc by more than two. We conclude that its inclusion in the models is not justified (Burnham & Anderson 2002).

Modelling

All the pest control regimes had simulated kākā population growth rates substantially higher than populations without pest control – any of these pest control regimes increase kākā population growth rates (Table 3). Kākā populations performed better when the effect of pest control lasted more than two years and when nesting mortality was low. The best (and essentially identical) pest control regimes were annual pest control, or pest control repeated at intervals equal to or less than the time that stoats stayed suppressed. These represent the likely population growth rates of kākā in the absence of stoat and possum predation. The next best pest control regimes were those where pest control was undertaken every time kākā bred, but such pest control regimes would be almost impossible to implement because it is currently not possible to accurately predict when kākā breed. Pest control undertaken in response to mast invariably performed better than pest control undertaken during a rodent plague, but the differences were small. Pest control undertaken at regular intervals performed better than pest control undertaken at the same frequency in response to beech mast or rodent plagues.

Discussion

Kākā breeding frequency

Kākā breeding is most often synchronous with the mast fruiting of forest trees (Wilson et al. 1998; Greene et al. 2004), but in our study at least some kākā bred in one year when there was almost no fruit on silver beech and rimu, the dominant masting tree species in the study area. Moorhouse (1997) observed that kākā, kākāpō (*Strigops habroptila*), and yellow-crowned parakeets (*Cyanoramphus auriceps*) all apparently breed in response to mast seeding, but that all three species also start breeding before the seed is available. Our study indicates that kākā may sometimes be stimulated to breed when the beech trees flower, even if the trees subsequently produce little viable seed (see Table 5).

Kākā predators

Stoats were the main predator of kākā nests and adults in our study as they were in Wilson et al.'s (1998) and Taylor et al.'s (2009) studies near Nelson Lakes National Park, and

Moorhouse et al.'s (2003) study at four sites in both the North and South Islands. However, the proportion of preyed on nests at which the female was also killed (1 female killed in 18 nests that were preyed on) was significantly smaller (χ^2 (Yate's correction) = 8.4, df = 1, p = 0.004) in South Westland than at Nelson Lakes National Park (Taylor et al. 2009) (14 females killed in 27 preyed-on nests, χ^2 (Yate's correction) = 8.4, df = 1, p = 0.004) and the central North Island (unpublished data from Moorhouse et al. 2003) (9 females killed in 17 preyed on nests, χ^2 (Yate's correction) = 7.4, df = 1, p = 0.006). We expect nest predation rates to vary with the abundance of predators, but it seems surprising that the proportion of females that are killed when a nest is preyed upon should differ as it suggests a behavioural difference between the predators at different places. Other possible explanations include differences in nest hole characteristics and differences in stoat and rodent abundances. Kākā in South Westland nested mostly in silver beech trees while most kākā in Nelson Lakes nested in red beech (*Fuscospora fusca*) trees and silver beech is not present at the North Island sites. Differences in cavities in different tree species might make kākā more or less likely to be killed when the nest is visited by a predator. When stoats are more abundant, kākā nests will on average be discovered by stoats more quickly and at an earlier stage than when stoats are rare. Female kākā are more likely to be killed on nests found early during incubation than they are on nests found with chicks, when the female kākā is less likely to be present. Rat abundances vary and when they are abundant the ready availability of attractive alternative prey might make large kākā nestlings or adults less attractive to stoats.

Of perhaps greater significance in our study was the loss of three non-nesting radio-tagged females probably to stoats during the 2013 breeding season and the discovery of a recently cached dead male early in the same season. More of our radio-tagged kākā were killed when they were not nesting than were killed while nesting, an unexpected result for a species we have supposed to be mostly vulnerable to predators while nesting in holes. Kākā spend some time on the ground (Best 1942), and during our study they were occasionally seen on the ground digging for grubs in rotten logs. These behaviours may make kākā more vulnerable to predation by stoats than we had previously supposed. Regardless of the circumstances in which these birds were killed, it suggests that in a stoat plague year all adults are at risk, not just nesting females.

Possoms were infrequent nest predators in this study: they preyed on 3% of our nests. At Nelson Lakes possums preyed on 9% of 55 nests (Taylor et al. 2009) and in Whirinaki Forest Park they preyed on 18% of 33 nests (Powlesland et al. 2003) and a simple contingency table analysis suggests these differences are significant (χ^2 (Yate's correction) = 8.4, df = 1, p = 0.004). These differences are likely to reflect the abundance of possums at the three sites. Podocarp/broadleaf forests, like those at Whirinaki, support higher densities of possums than do the beech forests (Efford 2000) at Nelson Lakes. The beech/podocarp forests of our 1080 treated study area in South Westland probably support even lower numbers of possums because of the long history of aerial 1080 operations there. In our study possums found many more kākā nests than they preyed on and it is clear that possums are not focused on preying on kākā nests. One of the nests that was preyed upon by a possum subsequently became its den and it is possible that some apparent possum predation events are possums taking over kākā nests to use as dens.

Although possums were relatively infrequent kākā nest

predators, they may also have indirect impacts on kākā abundance. The forest in the non-treatment area had much less tree fuchsia and scarlet mistletoe than the treatment blocks. Both species are important sources of nectar for kākā, both are preferentially browsed by possums, and both become much less abundant when possums are not controlled (Pekelharing et al. 1998; Bockett & Knightbridge 2004).

Our observations indicate that kākā eggs might occasionally be eaten by rats though there are no other records of rats preying upon kākā nests on the mainland. On Kāpiti Island Moorhouse (1991) attributed 23% of kākā nest predations to Norway rats (*Rattus norvegicus*) and all but one of these nests had entrances less than 20 cm above the ground, making them particularly accessible to the predominantly ground dwelling Norway rats that occurred on Kāpiti Island. Our observations indicate that kākā do not start incubating properly until at least the second egg has been laid. Until then nests are unattended for long periods and eggs may be vulnerable to rat predation, which would not be detected in a study such as ours in which nests were mostly found after incubation had started. Incubating females also routinely leave their nests at night for short periods and an opportunistic rat could potentially prey upon eggs in the female's absence. We may have failed to detect some rat predation of nests that we monitored; kākā breeding at times and places when rat numbers are high, might suffer even higher rates of rat predation.

Kākā and 1080

None of the radio-tagged kākā in this study were killed by 1080 and a total of 140 radio-tagged kākā have been monitored through 1080 operations without any having been killed (this study and Greene et al. 2013). Evidence to date indicates that kākā are rarely, if ever, killed by aerially applied 1080. Kākā nesting success was better when kākā bred within 18 months of an aerial 1080 operation. 1080 operations substantially reduced the abundance indices of stoats, possums, and rats, but it is likely that the increase in kākā nesting success associated with 1080 operations is caused mostly by a decrease in stoats as in our study these were the main nest predators.

The decline in nesting success two years and more after 1080 operations is probably mostly caused by a recovery in stoat abundance, once again because these were the main nest predators. If the recovery of stoat numbers following 1080 operations is caused by breeding of surviving stoats, then the size of the 1080 block will have little impact on the rate of stoat recovery. However, if recovery of stoats is mainly through immigration, then low stoat abundance might persist much longer in large 1080 operations. There have recently been many 1080 operations much larger than the 14 000–28 000 ha operations in this study and close monitoring of stoat

abundance during and after these operations will indicate whether stoat recovery post-1080 is driven by breeding or immigration.

Nesting success rates of kākā nesting within two years of a 1080 operation were within the range of nesting success rates recorded at other sites using traps and/or poisons in bait stations (Table 11). Similarly, the rates of nest success recorded when kākā nest more than two years after a 1080 operation are within the range of rates recorded at sites with no pest control (Table 11). The different methods of estimating nesting success used in previous studies preclude rigorous statistical comparison.

Adult female survival, as well as nesting success, was greater within 18 months of a 1080 operation than it was thereafter and once again this is most likely attributable to reduced stoat abundance. In this study all recorded adult deaths occurred in one season (2013) either in the non-treatment block or in Paringa which had not been treated with 1080 for two years and stoats had recovered to pre-treatment levels.

Kākā and forest type

Forest type appeared to have a considerable effect on kākā nesting success, but a weak if any effect on female survival. Our analysis suggests that in the absence of pest control, nesting success was highest in forest types with the greatest beech component though this conclusion is weakened by the unbalanced distribution of nests amongst treatments and forest types. Since most nest failures were caused by predators it is reasonable to suppose that differences in nest success rates are likely to be associated with different predator abundances. Walker et al. (2019) showed strong relationships between rodent abundances and latitude, altitude, and forest type and while there is no similar information for stoats their abundance often tracks that of rodents. Efford (2000) has shown similar relationships between possum abundance and forest type. Our study provided no explanation for the different nesting successes we detected in three forest types, but it did show that aerial 1080 was associated with improved nesting success in all of them.

Sex Ratio

A skewed sex ratio (more males than females) was first noted amongst wild kākā by Greene and Fraser (1998) who attributed the skew to high rates of predation of nesting females. Since then, the sex ratio of mist-netted samples of kākā has been used as a rough index of the health of kākā populations and a measure of the success of pest control to protect kākā (Terry Greene, DOC, pers. comm.).

The sex ratio of captured kākā in our study varied between years but the differences were mostly associated with time of

Table 11. Kākā nesting success under different pest control regimes.

| Site | Nest success (%) | Pest control | Reference |
|-------------------------|------------------|--|-----------------------|
| Waipapa Ecological Area | 87 | Poison in bait stations | Moorhouse et al. 2003 |
| Eglinton Valley | 80 | Poison in bait stations and stoat trapping | Moorhouse et al. 2003 |
| South Westland | 73 | Within 2 years of an aerial 1080 operation | This study |
| Nelson Lakes | 63 | Poison in bait stations and stoat trapping | Taylor et al. 2009 |
| Whirinaki | 38 | None | Moorhouse et al. 2003 |
| South Westland | 18 | > 2 years after a 1080 operation | This study |
| Nelson Lakes | 5 | None | Taylor et al. 2009 |

year rather than pest control. It was already known that the sex ratio of mist-netted kākā varied seasonally, with the number of females captured declining as they started nesting, so the fact that our catching sessions were not carried out at the same time of year means that we cannot reasonably expect sex ratio to indicate the success or otherwise of our predator control. Mawson (2000) examined the sex ratios of some Australian parrots sampled using three techniques and found that mist-netted samples often did not accurately reflect the sex ratio of the population. Our results combined with Mawson's (2000) suggest that a change in sex ratio rather than an absolute sex ratio might indicate the effectiveness of predator control at protecting kākā, but only if samples are collected at the same time of year.

Simulation model

Although simulation models such as ours, can be useful tools for exploring “what-if” scenarios, they are not necessarily good predictors of the trajectories of real populations (Caswell 2001). They cannot predict, for example, what will happen if conditions change dramatically. Furthermore, our accounting for uncertainty is of necessity simplistic as our dataset was too small to usefully partition the variation we encountered between process and sampling variation (White 2000). For some parameters about which we are uncertain (such as breeding frequency, the rate of nest predation of adult females, and the duration of stoat suppression following pest control) we have effectively conducted a crude sensitivity analysis and we conclude that these factors are of considerable significance in our predictions. We have also ignored density dependent effects, but this seems justifiable given the obviously low current kākā densities compared with earlier times when they were “exceedingly abundant” (Oliver 1955). Given these short-comings and uncertainties it seems prudent to regard our simulation models only as tools for examining the relative efficacy of different predator control regimes.

Simulated timing and frequency of pest control

There are two questions that we hoped to answer using simulation modelling of the timing and frequency of pest control for kākā:

- (1) What factors affect kākā population growth and the effectiveness of pest control to protect kākā?
- (2) What is the best pest control prescription to protect kākā?

(1) What factors affect kākā population growth and the effectiveness of pest control for kākā?

The highest simulated population growth rates occurred either when pest control was annual or when it was undertaken so frequently that stoat populations did not recover between successive pest control operations. If the time taken for stoat populations to recover is related to the size of the pest control operation (which seems likely) then it follows that at small sites pest control will best be undertaken annually or continuously with traps. At our 14 000–28 000 ha sites the effect of stoat suppression lasted through two breeding seasons, and in even larger blocks it is likely that stoat suppression will last longer. At large sites pest control undertaken once every three or four years might be the most-cost effective pest control regime.

Pest control undertaken every time kākā breed initially seems an effective pest control strategy to protect kākā. However, while kākā breed predictably when beech masts, they also breed at other unpredictable times. Furthermore,

most of the advantage of pest control every time kākā breed, comes not from the synchrony between breeding and pest control, but rather from the high frequency of pest control. In many cases kākā will perform as well with lower frequency, but regularly spaced pest control.

Our finding that pest control undertaken during masts is less effective than pest control undertaken at the same average frequency but at regular intervals seems at odds with earlier observations that kākā are particularly vulnerable while nesting (Moorhouse et al. 2003; Taylor et al. 2009). In our study in South Westland, kākā proved not to be particularly vulnerable to predation while nesting and the finding that regular rather than mast-timed pest control was best, is not surprising. However, even amongst our simulation models with high kākā nesting mortality, population growth was better when pest control was regular rather than mast timed. We attribute this to some mast-timed pest control operations being unnecessary for kākā protection because they are undertaken two years in a row and the second operation happens before stoat populations have recovered. This never happens when pest control operations occur at regular intervals.

Our finding that mast-timed pest control was more effective than pest control timed to coincide with rodent and stoat plagues was not surprising. Kākā nesting success is higher when they nest soon after pest control operations, and this is more likely to occur when pest control is mast-timed than it is when pest control is plague-timed. At sites where there are species that decline dramatically during rodent and stoat plagues it might be worth undertaking plague-timed pest control operations (Elliott & Kemp 2016), and kākā might still benefit, but if kākā are the main intended beneficiary of pest control then it is best undertaken at regular intervals.

(2) What is the best pest control prescription to protect kākā?

The simulated pest control regimes that gave rise to the fastest kākā population growth were those where 1080 was applied biennially or annually. Obviously 1080 applied every second year is more cost-effective than annual application of 1080, and our simulation suggests it will be no less effective. These regimes were best regardless of female mortality on the nest, mast frequency, or the duration of stoat suppression. The next best simulated regimes were those where 1080 operations were undertaken at regular intervals less than or equal to the length of time that stoat suppression lasted: two years in treatment areas the size of those in our study area (14 000–28 000ha) and probably longer in larger blocks. These regimes were also effective regardless of female mortality on the nest or mast frequency. The next best simulated regimes were those where 1080 operations were undertaken every time kākā bred. These regimes also worked regardless of female mortality on the nest, mast frequency, or the duration of stoat suppression, but they are impractical to implement because kākā breeding is not reliably predictable. The next best regimes are those where 1080 operations were undertaken every time masting occurs, but we can only be confident of the success of such regimes when there is low adult nesting mortality. The worst regimes we simulated were those where aerial 1080 was applied in response to rodent plagues. We can be confident of the success of these regimes for kākā only in large forest blocks where stoat suppression is likely to last more than two years, and where the rate of adult kākā mortality on the nest is low.

The most cost-effective pest control regime to protect kākā will vary from site to site and depend on the adult mortality rate and the size of the treatment area. At sites, like our study area,

where female nesting mortality is low and stoat suppression lasts for only two breeding seasons, the most cost-effective pest control regime will be 1080 operations every two years. This regime may not however protect other native wildlife that is vulnerable to beech mast induced rat plagues. At similar but larger treatment areas 1080 operations every three years will be the most cost-effective regime, but 1080 operations every rodent plague will also work and will protect rat-sensitive native animals as well as kākā. At sites with high nesting mortality and sites where we have no information about the likely rate of mortality on the nest, we can be confident only that regular 1080 operations every two years in blocks like ours, and every three years in larger blocks, will produce kākā population growth but will not protect other rat sensitive species during rat plagues. The best pest control regime at many sites where protection of rat sensitive species as well as kākā is required might be a combination of rat-plague timed 1080 operations in combination with continuous stoat trapping.

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Ethics: No permits required as the research was carried out by Department of Conservation staff. Ethics approval for radio tagging kākā comes from the Department of Conservation's ethics committee's blanket approval for techniques covered by a best practice document.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. GLM for sex ratio

Appendix S2. GLM for nest success

Appendix S3. GLM for survival

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