

Recovery and maintenance of North Island kokako (*Callaeas cinerea wilsoni*) populations through pulsed pest control

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Abstract

Kokako (*Callaeas cinerea wilsoni*) population recovery on the North Island of New Zealand depends primarily on control of key introduced mammal pests, especially ship rats (*Rattus rattus*) and brushtail possums (*Trichosurus vulpecula*). Recovery can still occur if pest control is pulsed (x years ‘on’; y years ‘off’) because kokako sub-adults and adults are generally long-lived, although chick production is high only during ‘on’ years. Pulsing effort means that conservation resources can be extended to other sites or problems during ‘off’ years; that toxin input at any one site is reduced; and that project staff do not burn out by repeatedly working at a site. Mathematical modelling supports

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empirical evidence that pests need not be controlled every year in order to maintain or greatly increase kokako populations. It predicts that the total number of years during which there is pest control is the main factor determining population size. Three years of pest control in each ten should be sufficient to at least maintain a population with 20 females when mean parameters apply, but pulsed control should still be effective with very pessimistic parameters. In the safest strategies, control should occur in minimum pulses of 2–3 years to avoid single poor years when few breeding attempts are made. Very small populations should first be increased to at least 20 females by translocation or continuous pest control. This will greatly reduce the probability of chance extinction, and increase the efficiency of subsequent pest control. The model will apply best to closed kokako populations below carrying capacity, in which pests are controlled over the entire block. Empirical data on the effects of habitat carrying capacity on kokako dispersal, and on the importance of stoats as predators of adult females are required to further strengthen the model.

Keywords: North Island kokako; Ship rat; Brushtail possum; Pest control; Pulsed pest control; Population model

1. Introduction

North Island kokako (*Callaeas cinerea wilsoni*) is an endangered forest bird species endemic to New Zealand (Collar et al., 1994). Populations are limited by predation from introduced mammals, especially ship rats (*Rattus rattus*) and brushtail possums (*Trichosurus vulpecula*), which prey on eggs and chicks. Intensive control of these pests permits population recovery by increasing nest success (Innes et al., 1999), and

this approach is now being applied to most of the remaining (ca 14) mainland kokako populations. The Kokako Recovery Group, charged with planning actions to recover kokako populations, has a 20-year vision to restore the national population to ca 1000 pairs by the year 2020 (Innes and Flux, 1999). Urgent attention must be given to ensure pest control is sustainable in the long term, because eradication of key pests from the New Zealand mainland is unlikely in the foreseeable future.

Several factors suggest to us that, as a strategy for maximising its efficiency and effectiveness, pest management could or should be pulsed:

1. Kokako are long-lived, perhaps to 20 years, and survival of sub-adults and adults is high, so pest control may not need to be applied every year to ensure population survival (Innes et al., 1999);
2. Pulsed control is cheaper than continuous control. During ‘off’ periods at a site, pest control can be extended to new kokako populations, or pest control resources can be diverted to other conservation problems;
3. Local conservation management staff working continuously at a site can lose their enthusiasm for a project if they cannot have a break from it (P. Bradfield, pers. comm);
4. Control of small mammal pests in New Zealand currently rests heavily on using toxins, especially sodium monofluoroacetate (1080) and a range of anticoagulants (Innes and Barker, 1999). Pulsing control effort minimises the amount of toxin used at each site and may help prevent the development of bait aversion or toxin tolerance in target pests.
5. When populations approach carrying capacity (none have yet), there is clearly no point in continuing pest control to produce young that then fail to recruit. As kokako populations increase in size, shorter ‘on’ periods are likely to be required to maintain them

Mathematical modelling is a tool enabling comparisons between the many possible future pest-control strategies. Here we take a matrix modelling approach (Caswell, 1989). We counted the number of adult females in a particular year assuming that the current population size was dependent on both prior abundance and demographic processes such as adult mortality and productivity and fledgling recruitment. Such deterministic models are widely used in mathematical biology (for a thorough introduction see Edelman-Keshet (1988) or Murray (1989)) and are the underlying foundation for Population Viability Analysis (PVA) where stochasticity may be incorporated into parameter values and probabilities of extinction are calculated (Burgman et al., 1993; Hamilton and Moller, 1995). Here we also use PVA to estimate a minimum viable population size and we allow for stochasticity in parameter values by performing sensitivity analyses on key parameters.

We aimed to simulate kokako population dynamics over 10–50 years under continuous and pulsed pest control strategies to determine firstly whether pulsed pest control could at least maintain a population, and secondly to identify which of several different strategies resulted in the largest population size. We intend this paper both to advance sustainable pest control, and to boost the efficiency with which managers of kokako restore populations that are currently well below their historical densities and assumed carrying capacities. The model is generic in nature, and a similar approach can be applied to pulsed management of other species.

2. Methods

2.1. Origins of field data

We studied a kokako population at Mapara in the central North Island between 1989 and 2000. Mapara is a partially logged, 1400 ha, lowland native forest remnant isolated from other forests by clearance for farming and exotic forestry in the last 100 years. Its tall forest canopy is dominated by tawa (*Beilschmiedia tawa*). Further detailed descriptions of the site are in Leathwick et al. (1983) and Innes et al. (1999).

2.2. *Pest control*

Effective pest control can be seen as a switch that creates high kokako productivity/low adult mortality when it is ‘on’ and low productivity/increased adult mortality when it is ‘off’. Control of introduced mammal pests, especially ship rats and brushtail possums, was conducted during early spring to achieve lowest possible pest densities throughout the peak kokako breeding time (November to February). Control was applied (‘on’) from the 1989–90 kokako breeding season to 1996–97 inclusive, then switched ‘off’ completely thereafter. Details of the methods and outcomes of pest control, and kokako responses to it, are in Innes et al. (1999). Ship rat populations reach pre-control abundance within 3–5 months of the cessation of effective control (Innes et al., 1995), although possums take 10–15 years (Veltman and Pinder, 2001). Kokako productivity falls dramatically on the cessation of control, but also increases immediately when it is restored (Innes et al., 1999; unpublished data).

2.3. *Kokako population parameters*

Many kokako at Mapara were individually colour-banded to improve the accuracy and efficiency of censuses and to enable verification of the disappearance of individual birds. During 1989 to 2000, 65 adults and 167 nestlings were banded. Radio

transmitters were put on some kokako each study season to improve our ability to locate nests. The gender of many adult kokako - but few juveniles - was known from breeding role, morphometrics or genetic analyses (Flux and Innes, in press).

All known kokako pairs and any newly formed pairs were noted during an annual pre-breeding census, conducted between mid-September and the end of October. We attempted to visit newly identified pairs regularly during their first breeding season to confirm whether or not they bred. We have excluded birds from our recruitment data where it was not possible to confirm whether a breeding attempt took place. Some females paired but did not breed in their first year; recruitment of banded females was taken to occur when they first bred.

During 1989–92 there were fewer than five breeding pairs; this study uses data accumulated after 1992. On average, the breeding attempts and outcomes of 16 (range 9–24) kokako females were intensively monitored each year at Mapara from 1992 to 2000 (Table 1). Productivity (number of chicks fledged per breeding female per year) was determined by climbing to nests to band young and confirming the fledging or other fate of nestlings through weekly nest visits. Due to a complex and poorly understood relationship between climate, food availability and kokako fecundity, chick output is highly variable from year to year. At Mapara, ‘good’ and ‘bad’ breeding years alternated during the past decade. For example, breeding season (defined as from first laying to final fledging) duration shows this pattern: 7 weeks in 1991–92, then in subsequent seasons 12, 7, 21, 9, 16, 7, 19 and 9 weeks respectively (I. Flux, P. Bradfield, unpublished data).

Mortality was defined as the known death or permanent disappearance of a banded kokako from annual censuses. Individuals not sighted for two years were considered dead and their date of death was recorded as the date of their first-noted absence.

2.4. *A mathematical model for the pulsed pest control of female kokako*

The comparison of pulsed pest control management strategies for North Island kokako was investigated using a simple discrete mathematical model. We used 10-, 20- or 50-year time frames where appropriate. Usually 20 years is the desired period, given the Recovery Plan's 20 year goal; however, we have sometimes considered 50-year periods in order to identify trends clearly and 10-year periods when comparing all possible strategies.

In all kokako populations studied, males have been in excess and females have been limiting, due to the vulnerability of nesting females. Kokako are monogamous and form long-term pair bonds; excess males hold exclusive territories but have no function in population terms. Thus, we have used breeding adult female number as the basic unit of modelling. The model counted breeding adult females at the beginning of the breeding season, using information from previous years such as adult abundance, adult mortality, adult productivity and fledgling recruitment. Field data suggest that female fledglings either eventually breed at age 1 or 2 years or fail to recruit. The model assumed that the number of breeding adult female kokako present at the annual pre-breeding census in year $(t+1)$ was the sum of the numbers from three different sources: those which were already breeding adults one year earlier and survived the year, those fledged one year ago and recruited at age one and those fledged two years ago and recruited at age two. A recruit was considered to be any female fledgling that subsequently paired and bred. We let $a_f(t)$ be the number of breeding adult females at time t years and the parameters in the model are: $d(t)$, the female annual mortality rate; $b(t)$, the average number of chicks fledged per year per adult female, 50% of which are presumed to be female; r_1 , the proportion of female fledglings that breed at age 1 year; r_2 the proportion of female

fledglings which breed at 2 years of age. Thus $r_1 + r_2$ equals the proportion of all fledglings recruited. There is no dispersal in the model because, although the birds may disperse up to five kilometres (unpublished data), they remain within the managed block. The equation representing this is:

$$a_f(t+1) = (1-d(t))a_f(t) + r_1 \frac{b(t)}{2} a_f(t) + r_2 \frac{b(t-1)}{2} a_f(t-1). \quad (1)$$

The first term on the right hand side of equation (1) represents adult survival, the second term counts one-year-old recruits and the third term, two-year-old recruits. It is assumed that pest control achieves predetermined control targets and occurs over the whole block hence both $d(t)$ and $b(t)$, the female annual mortality and productivity rates respectively, are each assigned one of two values, depending on whether pest control is switched ‘on’ or ‘off’.

An equivalent way of formulating the model is to rewrite equation (1) in terms of a projection matrix (Caswell, 1989; Burgman et al., 1993). If we consider two age classes in year t : female fledglings, $c_f(t)$, and adult breeding females, $a_f(t)$, then we can write

$$c_f(t+1) = \frac{b(t)}{2} a_f(t). \quad (2)$$

and equation (1) becomes:

$$a_f(t+1) = (1-d(t))a_f(t) + r_1 \frac{b(t)}{2} a_f(t) + r_2 c_f(t). \quad (3)$$

Equations (2) and (3) can be written in matrix form

$$\begin{bmatrix} c_f \\ a_f \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & \frac{b(t)}{2} \\ r_2 & \left(1-d(t) + r_1 \frac{b(t)}{2}\right) \end{bmatrix} \begin{bmatrix} c_f \\ a_f \end{bmatrix}_t,$$

where $\begin{bmatrix} 0 & \frac{b(t)}{2} \\ r_2 & \left(1 - d(t) + r_1 \frac{b(t)}{2}\right) \end{bmatrix}$ is called the projection matrix. For a period of n years,

the n th root of the dominant eigenvalue of the product of yearly projection matrices has been used as an ‘average’ measure of population growth (Burgman et al., 1993; Efford et al., 1998). A sensitivity analysis of parameter values can be performed by measuring the elasticity of the projection matrix (Heppell et al., 2000). In this paper we have chosen not to use this approach for a number of reasons. First, it was important for us to know how the actual population size fluctuated, with and without pest control, over a period of n years. Second, we wanted to keep the mathematics as simple as possible to present our results to as wide an audience as possible. Finally, we wanted to express our model outcomes in terms of actual population numbers rather than in terms of ‘average’ population growth rates.

2.5. *Population parameters derived at Mapara*

2.5.1. *Initial Population Size*

The initial population at Mapara in 1989 consisted of five females. Very small female populations occur also at Hunua, Tiritiri Matangi Island, Kapiti Island, Mataraua, and Manawahe. Such small populations must be intensively managed, or supplemented by introductions from other populations, until the probability of extinction due to stochastic events is minimised. Population Viability Analysis (PVA, e.g. Burgman et al., 1993) using the model and parameters described below - with stochastic variation in productivity and an initial population of 20 females - concluded that the probability of extinction within 20 years with no pest control was less than 5%. Manly and Seyb (unpublished report) reached similar conclusions using slightly less conservative parameters. We have, therefore, taken 20 females

as the starting point for our modelling. We assumed that the number of adult females at year $t=0$, $a_f(0)$, was 20 and that the number of adult females one (unmanaged) year previously was $a_f(-1)=20$.

2.5.2. Productivity

The annual productivity rate, b , is the number of chicks fledged per female per year. This averaged 1.86 in the managed seasons 92/93–96/97, and fell to 0.14 thereafter when pest management ceased (Table 1).

2.5.3. Recruitment

The mean annual survival rate of fledglings to recruitment was calculated as the total recruited during 1992/93 to 1999/00, divided by the number which fledged during 1991/92 to 1997/98; a rate of 0.63. We could not calculate separate rates for ‘on’ and ‘off’ years because many birds that fledged during pest-controlled years were not recruited until pest control had ceased. Of 17 female recruits for which we knew the year of first breeding, ten (58.8%) bred aged one year and the remaining 7 (41.2%) bred at two years of age. Recruitment between years one and two is thus given in corresponding proportions: $r_1+r_2=0.63$, where r_1 is 0.37 and r_2 is 0.26.

2.5.4. Mortality

Mortality estimates are based on a mixed-age sample of banded females. However, as there were only five adult females in the initial population, the sample is weighted toward younger females that were first banded as nestlings. Mortality rates were calculated as deaths per banded female per year. During the period when there was pest control, the sample size was 156 banded-female years (six deaths), and for the period when pest control was absent,

79 banded-female years (12 deaths), yielding estimates of 0.038 and 0.15 respectively (Table 2).

2.5.5. Carrying Capacity

Because populations never increase indefinitely, a carrying capacity parameter was included in the model. No kokako population has been free of pest-mammals for long enough to reach a new carrying capacity; all managed populations are still slowly increasing. Thus we know nothing of the population regulating mechanisms that might come into play as densities become higher. However, as the smallest known Mapara kokako pair territory is four hectares, we have assigned a crude pest-mammal-free carrying capacity as 0.25 female kokako per hectare. Carrying capacity at Mapara (1400 ha) is therefore estimated as 350 females. In the model, the net number of birds entering the adult cohort is scaled by a factor that tends to zero as the population approaches carrying capacity. The scaling factor used here is $(1-a_f(t)/K)$, where K is the carrying capacity. The model with carrying capacity included is:

$$a_f(t+1) = a_f(t) + \left(r_1 \frac{b(t)}{2} a_f(t) + r_2 \frac{b(t-1)}{2} a_f(t-1) - da_f(t) \right) \left(1 - \frac{a_f(t)}{K} \right). \quad (4)$$

This simple approach may be unrealistic in some aspects. For example, mortality is virtually scaled to zero at K , but mortality may in fact increase as the population increases because of competition for territories. This is irrelevant to this paper, which focuses primarily on population changes well below K . Difficult long-term research is required to recognise K in the field, and a more sophisticated model will be needed to represent the resultant demography.

3. Results

Without carrying capacity, modelled populations increased indefinitely under continuous management and two pulsed management strategies, but an unmanaged population declined (Fig. 1). When carrying capacity is incorporated (Fig. 2), all three pest control strategies still increase populations over 20 years.

3.1. *Modelled versus measured Mapara populations*

The actual number of breeding females at Mapara was taken to be the number of pairs counted each season minus the number that were never known to breed (assumed or known to be male/male). In 1996, two females were removed to Kapiti Island. In late 1997 and early 1998, seven further females were translocated (two to Pikiariki, one to Tiritiri Matangi Island, and four to Hunua). Fig. 3 shows a reasonably good fit between modelled populations with and without allowance for the translocated females, compared with the number of breeding females actually counted at Mapara.

3.2. *Possible management strategies*

If biennial pest control is compared with 3 years 'on', 5 years 'off', biennial control results in a larger population size at year ten despite both strategies having had five years of pest control (Fig. 2).

It is not practical to model and compare all possible pulsed pest control strategies. For example, if we want to apply pest control for a total of 10 years allocated over a time frame of 20 years, there are 184,756 possible strategies! The maximum number of possible strategies (252) over 10 years occurs when there are five total years of pest control. All the strategies yield comparable populations by year 10 (Table 3), although there are major differences in the population trajectories. Modelling with mean Mapara parameters suggests that any 3 years

of pest control out of 10 will always maintain the population, irrespective of the management strategy chosen (Fig. 4).

The model suggests that if 5 or fewer years of pest control are planned during a 10-year period, largest populations are achieved with biennial pest control until the required number of controlled years is reached. This strategy ensures that the population never dwindles below 20 birds. When there were more than 5 years of total pest control, the strategy that resulted in the highest population size at year ten was continuous pest control followed by biennial. However, biennial pest control should be undertaken with caution because it may coincide with several poor breeding years (see discussion), resulting in less than optimal densities at year ten.

Equal 'on'-'off' periods may be useful to managers hoping to alternate effort between two kokako populations. Fig. 5 depicts the results of modelling 50 years of biennial pest control plus four other alternating strategies of increasing duration. Overall trends are the same for each, although longer 'off' periods result in bigger oscillations. All strategies reached carrying capacity at approximately the same time.

Fig. 6 considers four strategies that may be useful to managers of three blocks, with x years of pest control followed by $2x$ years of no pest control in each block. As with Fig. 5, the trends of all strategies are the same over 50 years. In any strategy, it is the number, not the order, of pest control years that most strongly influences the final population.

3.3. *Sensitivity analysis: Varying population parameter values*

We undertook a sensitivity analysis to identify which parameters have the greatest effect on model outcomes. We used Mapara parameter values (Table 2), and varied each parameter over its estimated range while keeping all others fixed.

Figs 7 to 13 graph the adult female population at year ten against a range of values for a particular parameter, after 4, 6 or 8 years of pest control during the 10 years. The actual strategy for 4 years of total pest control was biennial pest control followed by no pest control. For 6 and 8 years of pest control in total, the simulated strategy was continuous followed by biennial.

First, consider annual productivity, b , in years when pest control is present (in 'on' years; Fig. 7) and absent (in 'off' years; Fig. 8). We have used parameter values of 1.86 (SD 1.02) and 0.14 (SD 0.15) for these two situations respectively. The large standard deviation of productivity in pest-controlled years is caused by annual variation in numbers of breeding attempts and yields a wide range of possible parameter values. In Fig. 7 the vertical lines show the value 1.86 plus and minus one standard deviation. For example, if there are 8 years of pest control in total, a difference of plus or minus one standard deviation from the mean productivity in 'on' years can result in a population at year ten of between 70 and 340 birds. However, extreme outcomes are unlikely provided that pest control occurs over several consecutive years. As already noted, field data currently show a biennial pattern of fluctuating 'good' and 'bad' years. Biennial pest control might, by chance, coincide with either good or bad years, and could produce extreme outcomes. The same analysis for productivity in the absence of pest control (Fig. 8) gives a much smaller range of possible densities at year ten because the severe predation impacts of pests override and obscure good and bad year effects.

Sensitivity analyses for mortality and recruitment are based on predicted realistic ranges of each variable because of unavoidable problems with their direct measurement in the field (Figs 9 to 13). These ranges are large, and correspondingly there is a wide range of possible population size at year ten. As with productivity, small changes in individual parameter values do not have a major effect on population size at year ten. It seems (Fig. 13) that changes in total recruitment, r_1+r_2 , have a greater effect on model outcomes than changes in the individual recruitment parameters, r_1 and r_2 (Figs 11 and 12).

Even with particularly pessimistic parameters, the model still predicts that pulsed pest control is effective (Fig. 14). With these data, 8 years of management (irrespective of strategy) in total over a period of 10 years is enough at least to maintain the population starting at 20 adult females.

4. Discussion

4.1. *Implications for kokako management*

The model supports empirical evidence (Innes et al., 1999) that kokako populations do not need continuous pest control to maintain or greatly increase them. It suggests that 3 years of pest control out of each 10 will be sufficient to at least maintain a kokako population at 20 adult females (i.e. well below carrying capacity), provided population parameters approximate those measured at Mapara. The number of years of pest control appears to be the main factor determining population size, but some strategies totalling the same number of years are safer than others and may result in higher numbers. Managers of kokako populations should at least verify, using standard census techniques (Flux and Innes, 2001), that their population is following a similar recovery trajectory to that described here before developing any long-term management plan. Safe strategies which result in higher numbers than others may or may not be the cheapest, which deserves further research (see below), but pulsed regimes offer large cost-efficiencies over annual pest control, and they demand forward thinking about pest management.

We see three benefits of initially rapidly increasing a small managed population to total at least 20 females. This can be seen as a ‘salvage’ phase of recovery, which is then followed

by a 'restoration' or 'maintenance' phase. First, population viability modelling suggests that whereas a population of five females has a high probability of extinction (>75%) when no pest control occurs over 20 years, one of 20 females has only a small (<5%) probability of extinction. Second, if pest control is applied to an entire forest-block (such as by aerial poisoning), it becomes more cost-effective as the number of pairs increases; that is, many more chicks fledge for the same pest control effort. Third, an initial rapid population increase will maximise the effective population size, thus reducing the possibility of detrimental genetic bottleneck effects.

In 1999, eight of the remaining ca 14 managed North Island kokako populations had ten or fewer females, and all had more males than females (Innes and Flux, 1999). Continuous pest-control should first be implemented to boost female numbers rapidly in these populations to at least 20. Where current populations are of five or fewer females, we also recommend further trial translocations of pairs from other secure populations to get the recovery curve rapidly onto a higher trajectory, and to provide the possible additional benefits of genetic variability.

The model is intended to compare population trends between a number of management options. Such modelling cannot predict the exact population size in a particular year as parameter variability, particularly of productivity, between years was very high. Clearly, managers should focus on variables they can actually control, especially the number of years in which they plan pest control, and whether the required low residual pest density targets are achieved (Innes et al., 1999).

We recommend that pest control occurs in minimum pulses of 2–3 years, particularly when populations are low. This will benefit populations by ensuring that pest control operations coincide with at least some years when kokako make multiple breeding attempts. Single-year or biennial pest control strategies risk lesser rewards because these may coincide with one or several consecutive 'poor' years.

4.2. *Limitations to the model*

The model is a simple one, and yet its parameter values took many years of intensive field work to obtain. Most kokako at Mapara were individually colour banded, but some uncertainties or errors in the estimation of parameters were unavoidable. Dead kokako were rarely recovered, thus disappearances for 2 years were assumed to be deaths. During this research, emigration was not possible as kokako are weak fliers and the forest was isolated by pastoral land. Recruitment was taken to be when an individual first bred rather than when it first became territorial. It was sometimes difficult to confirm nesting if nests failed quickly, in which case age of recruitment may have been overestimated. Estimates of the fledging rate based on nest visits could have been artificially high if some chicks were preyed on between the final nest check and fledging, or artificially low if nests could not be visited before fledging, and some fledglings remain undetected. Finally, kokako are monomorphic and can be gendered only by DNA analysis or by breeding behaviour (Flux and Innes, in press). However, they also form male-male pairings in which one member may even build a nest. As separating a rapid failure of a fertile nesting by a male-female pair from an eggless nesting of a male-male pair is frequently very difficult in the field, verifying the actual number of females in a population will always be difficult. We have assumed all these potential problems apply equally to both 'on' and 'off' years. If so, they may impair quantitative predictions for particular years and sites but not medium to long-term comparisons between treatments.

Results of this model will apply best to comparisons between management options in closed populations (no emigration or immigration) in which pests are controlled in the entire block during 'on' years, as was the case at our study populations. Such sites include offshore islands. Preliminary indications are that, even in open populations, the majority of fledglings

are recruited within managed areas; perhaps due to the improved vegetation quality of those areas.

We have estimates of the annual variation inherent in chick output (calculated for each ‘on’ year with large sample sizes) but not in mortality or recruitment, which had to be calculated from several years’ accumulated data. Female mortality rates, for instance, were meaningless on an annual basis, as from a sample of 20 to 30 individuals we recorded no deaths during most ‘on’ years. The upper and lower limits of the error bars to the population estimates in Fig. 3, could only be achieved if pest control always coincided with either excellent or poor breeding years respectively. This is unlikely to occur in practice and its likelihood is further reduced if pulses of pest control operations are at least of 2 or 3 years duration.

Kokako population parameters have been measured robustly at few populations besides Mapara. The annual productivity rate, b , measured at Rotoehu Forest, Bay of Plenty, during the ‘off’ seasons 1990–91 to 1993–94 inclusive, was 0.54 (SD 0.16) chicks fledged per adult female per annum (unpub. data), somewhat higher than the 0.14 (SD 0.15) measured in ‘off’ seasons at Mapara. However the female mortality rate was the same, at 0.15 per year. Too few juveniles of known gender were available at Rotoehu to obtain a second estimate of recruitment rates (r_1 and r_2).

The greatest uncertainty in our understanding of the ecology underlying the model probably concerns the role of stoats (*Mustela erminea*) as predators of adult females. Large-scale poisoning of ship rats and mice (*Mus musculus*) with either 1080 or brodifacoum can kill stoats by secondary poisoning (Alterio, 1996; Alterio et al., 1997; Gillies and Pierce, 1999; Murphy et al., 1999), so this may have killed stoats at Mapara in ‘on’ years, in addition to those killed in traps. Stoat trapping there during years of low and localised pest-control effort (1989/90) and of extensive pest-control, using 1080 (1990–1993) and brodifacoum (1993–1995), revealed a moderate and near constant stoat capture rate (Innes et al., 1999),

although the number of stoats actually present is unknown. During these ‘on’ years we detected no female kokako loss attributable to stoats. Similarly, during the first season without pest control (1997/98) no females were lost. However, during the two subsequent (1998/99 and 1999/2000) breeding seasons 12 of the 31 banded adult females were killed in nests, probably by stoats. This greatly increased the mortality rate in ‘off’ years (Table 2). This outcome suggests either that stoats became more abundant after trapping and poisoning stopped (in 1995 and 1997 respectively), or that the behaviour of resident stoats then turned more to killing kokako at nests. Perhaps mature resident stoats or breeding stoats pose greater risk to breeding birds. Stoats were, however, much more abundant throughout the North Island in 1999–2000 than in previous years (C. Gillies, pers. comm.), so it is possible that increased predation by them at Mapara was unrelated to the cessation of pest control. Further, during ‘off’ years at Rotoehu, we recorded only possums as predators of nesting adult kokako, but stoats were being trapped on an adjacent property at that time to protect gamebirds, and this may have given Rotoehu kokako some reprieve from stoat predation. If managers in future apply control techniques that effectively control rats and possums but not stoats, then we might expect that female kokako would be vulnerable to stoat predation for a greatly extended period. Managers should be aware that such a strategy could result in major female losses not predicted in our modelling.

4.3. Community perceptions of pulsed pest control

In our experience, some individuals in both local communities and in conservation management agencies did not understand or approve of periodically switching pest control efforts ‘off’ in managed kokako areas. This reaction was strongest from residents who perceived that ‘their’ local kokako might disappear rapidly once pest control stopped. Some conservation managers felt their agency looked foolish to the public when, after investing

heavily in pest control at a site for several years, the agency ‘simply walked away’ allowing pests to re-invade gradually. We found these concerns were allayed when the empirical and modelled data presented in this paper were explained. Pest management on the New Zealand mainland is for the foreseeable future, and many restoration projects are now emerging from the honeymoon period of triumphant success to face the harder issue of how such success can be sustained, for decades, and then centuries.

Managers in our study blocks did not stop controlling browsing mammal pests such as goats during ‘off’ periods. If left unchecked, ungulate browsers may induce long-term changes to forest composition and successional pathways but their maintenance at low densities requires only low intensity effort. Intensive pre-breeding season control of possums and ship rats did stop for the entire ‘off’ period. There may be less criticism of pulsed pest control if a reduced predator control effort in the ‘off’ periods can be found that cost-effectively assists kokako or other elements in their ecosystem. We did not pursue this option during this research because of strong empirical evidence that to be effective, predator control must be intensive.

4.4. *Restoring biological communities*

Pulsed pest control will succeed for kokako because fledged juveniles and adults survive ‘off’ periods well, although eggs and chicks do not, and because adults are generally long-lived. We suggest that pulsed pest control may also be a valuable initial approach to sustaining restoration of biological communities, despite most species having very different attributes from kokako, since such control should reduce staff burnout and minimise toxin input and development of bait aversion by pests at any site. Any species that survives in mainland forests today, but is limited by introduced predators, is likely to benefit from the periodic intensive control of those predators. Plant species limited by seed destruction by rats

or possums are also likely to benefit from periodically increased germination. The converse is also true: it is conceivable that some parts of the ecosystem are harmed, directly or indirectly, by such management. Mice, for example, appear to increase their populations following intensive control of rats and possums (Innes et al., 1995). Thus any organism limited by mice may suffer during 'on' years. Pulsing pest control offers the ecosystem respite from any such unrecognised impacts.

4.5. *Future modelling*

Future modelling will focus on incorporating dispersal to increase the relevance of the model to open populations, and on national multi-population recovery, carrying capacity and management costs. We are currently measuring kokako dispersal from managed sites within a very large forest area. We also intend to model all remaining managed populations to see how the overall Recovery Group goal (20 populations averaging 50 females each, by 2020) can be achieved most cost-effectively. Carrying capacity has never been measured in any kokako population. Only Little Barrier Island may already be near carrying capacity, because kokako were first translocated there more than 20 years ago and the only mammalian predator present is *Rattus exulans*. Several key aspects of demography (for example juvenile recruitment rates) may change greatly as a population becomes limited by density dependent influences. The nature of any density dependent limitation may differ between different communities. Finally, it would be valuable to cost different management strategies that look biologically favourable, to see which are likely to be most cost effective. Kokako management must be cost-efficient as well as biologically effective, so that pest control can be applied systematically to as many populations as possible, securing and increasing each according to its urgency.

Acknowledgements

We thank the many field staff who braved pre-dawn starts to collect the kokako field data that make this model possible, especially Philip Bradfield, Kerry Brown, Suzanne Clegg, Paul Jansen, Rachel Lander, Denise Fastier, Simon Clearwater, Catherine Rufaut, Nigel Miller, Mike North, Lloyd Robbins, Rachel Shorten, Hazel Speed, Tertia Thurley and Dale Williams. Thanks to John McLennan, Murray Efford and Graham Nugent who commented helpfully on the manuscript, and to Anne Austin for valuable editing. The research was funded partly by the Foundation for Research, Science and Technology (under Contracts CO9X0009 and CO9X0004) and the NZ Department of Conservation.

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Figure Captions

Figure 1.

Time series of adult female kokako abundance under four different pulsed pest management strategies over 20 years, using Mapara data with unlimited carrying capacity. Parameter values are given in Table 2. Starting number of females, $a_f(0)$ and $a_f(-1)$, is 20.

Figure 2.

Adult female abundance under the same pulsed strategies as in Figure 1, but with fixed carrying capacity (set at 350).

Figure 3.

Time series for the model and actual Mapara data of female adult kokako for the annual pre-breeding census (September) 1994 to 2000. The seasons during which there was pest control were 94/95–96/97. The model parameter values are given in Table 2 with $K=350$. Starting number of females, $a_f(t=0)=23$ (1995) and $a_f(t=-1)=18$ (1994). Error bars were superimposed on the model (without translocations) using average values for productivity plus and minus one standard deviation thus, $b=0.84, 2.88$ (pest controlled years), $b=0, 0.29$ (no pest control).

Figure 4.

All 240 scenarios in which there are 3 years of pest control in total over a time frame of ten years. Thus, modelling with Mapara parameters suggests that any 3 years of pest control out of ten will always at least maintain the population, irrespective of the management strategy chosen. Parameters are those given in previous figures and Table 2.

Figure 5.

Strategies which have even 'on'/'off' periods of pulsed pest control over 50 years. Parameter values are given in Table 2. Here $K=350$ and the starting number of females, $a_f(0)$ and $a_f(-1)$, is 20.

Figure 6.

If three blocks are managed in strict rotation, at each block there will be x years of pest control followed by $2x$ years off. Thus, this figure plots the time series of adult female kokako over a period of 50 years for the strategies 2 on 4 off, 3 on 6 off, 4 on 8 off, and 5 on 10 off. Parameter values are given in Table 2 with $K=350$. Starting number of females, $a_f(0)$ and $a_f(-1)$, is 20.

Figure 7.

Sensitivity analysis for b , productivity in pest controlled years. The number of females at year ten is plotted against the annual managed productivity rate (young fledged per female per annum).

Strategies are 4, 6 and 8 years of total pest control over a time frame of 10 years. The particular 'on'/'off' regimes chosen for each strategy were those that resulted in the largest number of females at year ten as described in the text. Parameter values are given in Table 2, except that productivity in pest controlled years, b , ranges in value from 0 to 3. Here $K=350$ and the starting number of females, $a_i(0)$ and $a_i(-1)$, is 20. The vertical lines show the value of $b = 1.86$ from Table 2 plus and minus one standard deviation (1.02).

Figure 8.

Sensitivity analysis for b , productivity in years with no pest control. It is essentially the same as Figure 7, except b ranges in value from 0 to 1 while all other parameters are fixed at the values given in Table 2. The vertical lines show the value of $b = 0.14$ from Table 2 plus and minus one standard deviation (0.15).

Figure 9.

Sensitivity analysis for d , mortality in pest-controlled years. It is essentially the same as Figure 7 except d ranges in value from 0 to 0.5 while all other parameters are fixed at the values given in Table 2. The vertical line shows the value of $d = 0.038$ from Table 2.

Figure 10.

Sensitivity analysis for d , mortality in years with no pest control. It is essentially the same as Figure 7 except d ranges in value from 0 to 0.5 while all other parameters are fixed at the values given in Table 2. The vertical line shows the value of $d = 0.15$ from Table 2.

Figure 11.

Sensitivity analysis for r_1 , the proportion of fledglings that breed at age 1 year. It is essentially the same as Figure 7, except r_1 ranges in value from 0 to 0.74 while all other parameters are fixed at the values given in Table 2. The vertical line shows the value of $r_1 = 0.37$ from Table 2.

Figure 12.

Sensitivity analysis for r_2 , the proportion of fledglings that breed at age 2 years. It is essentially the same as Figure 7, except r_2 ranges in value from 0 to 0.63 while all other parameters are fixed at the values given in Table 2. The vertical line shows the value of $r_2 = 0.26$ from Table 2.

Figure 13.

Sensitivity analysis for $r_1 + r_2$, the proportion of fledgling females that breed at 1 or 2 years of age. The number of females at year ten is plotted against $r_1 + r_2$, the proportion of fledgling females that breed at 1 or 2 years of age. The strategy chosen was continuous followed by biennial pest control where there are 6 years of total management over ten years. Ratios of $r_1 : r_2$ plotted are 0.25:0.75, 0.5:0.5 and 0.75:0.25. Parameter values are given in Table 2 except $r_1 + r_2$ ranges in value between 0 and 1. The vertical line shows the value of $r_1 + r_2 = 0.63$ from Table 2. Starting number of females, $a_f(0)$ and $a_f(-1)$, is 20.

Figure 14.

Number of females at year ten versus the total number of years of pest control out of ten. Parameter values are $b=0.84$ (pest controlled productivity), $b=0$ (productivity in years with no pest control), $d=0.1$ (pest controlled mortality), $d=0.2$ (mortality in years with no pest control), $r_1=0.2$, $r_2=0.2$ and $K=350$. Starting number of females, $a_j(0)$ and $a_j(-1)$, is 20.

Season	Pest control	Number of females monitored	Productivity rate, b (average number chicks fledged per female per annum)
92/93	on	9	1.34
93/94	on	9	1.12
94/95	on	17	3.23
95/96	on	18	0.94
96/97	on	24	2.67
			$\bar{x}=1.86$ SD=1.02
97/98	off	14	0.29
98/99	off	24	0.13
99/00	off	15	0
			$\bar{x}=0.14$ SD=0.15

Table 1. Annual Mapara female productivity rate, b , 1992–2000, in relation to presence and absence of pest control.

Parameter	Description	Pest control 'on' (1992-1997) (5yrs)	Pest control 'off' (1997-2000) (3yrs)
b	Annual productivity rate (average number of chicks fledged per female per year)	$\bar{x}=1.86$, SD=1.02	$\bar{x}=0.14$, SD=0.15
d	Female annual mortality rate	0.038	0.15
r_1	Proportion of female fledglings that breed at age 1 year	0.37	0.37
r_2	Proportion of female fledglings that breed at age 2 years	0.26	0.26

Table 2. Annual productivity, mortality and recruitment rates for Mapara female kokako

Total number of pest-controlled years out of 10	Number of possible strategies	Predicted population at year ten
0	1	6
1	10	10—12
2	45	16—20
3	120	26—35
4	210	42—57
5	252	66—91
6	210	100—128
7	120	145—174
8	45	199—223
9	10	253—269
10	1	297

Table 3. Number of possible strategies and approximate populations at year ten where there are n years of pest control during the 10 years and starting with 20 females. Throughout the 10 years there is a wide variation in predicted population between strategies, but by year ten densities are similar.