

Protected areas for kiwi in mainland forests of New Zealand: how large should they be?

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Abstract: This paper examines, theoretically, how dispersal affects the viability of brown kiwi populations in protected areas of different size. Brown kiwi are threatened by introduced mammalian predators in mainland forests and are likely to persist only in managed forests where predators are controlled. In each protected area, the kiwi population will function as a net source, with an outflow of juveniles into the adjoining forest and minimal backflow into the reserve. Computer simulations show the minimum area of forest required for population viability increases non-linearly as the mean dispersal distance of juveniles increases. Preliminary measurements of the mean dispersal distance of brown kiwi in the wild suggest kiwi populations are unlikely to be viable in protected areas of less than 10 000 ha. Our estimate of the forest area requirement for viable populations of brown kiwi agrees with those derived by earlier workers using biogeographic techniques.

Keywords: *Apteryx* spp.; computer simulation; dispersal; kiwi; predator control; protected areas.

Introduction

North Island brown kiwi *Apteryx mantelli* are declining at about 6% per year, mainly because of predation by stoats *Mustela erminea* (McLennan *et al.*, 1996). Stoats kill about 60% of the chicks hatched each year. In closed populations with no emigration 19% of chicks must reach adulthood to maintain population stability, with higher rates of recruitment needed for population recovery (McLennan *et al.*, 1996; Basse *et al.*, 1997). Preliminary estimates indicate that brown kiwi achieve a 19% recruitment rate at a threshold stoat density of about one animal km⁻² (Basse *et al.*, 1999). Under natural conditions stoats seldom appear to dip below this threshold, except perhaps in some alpine and sub-alpine regions of the South Island. These natural kiwi refuges are relatively scarce, but may be sufficient to maintain populations of great spotted kiwi *Apteryx haastii* in parts of its current range (McLennan and McCann, 1994). There appear to be no equivalent natural refuges for kiwi in the North Island, so the birds there are likely to persist only in protected areas where stoats are controlled. Stoat control is expensive and will remain so for the foreseeable future. Inevitably then, it will be applied selectively, probably to less than 3% of the North Island brown kiwi's current range (about 21 600 km²). The immediate aim of protected areas (in relation to kiwi) is therefore to retain remnant pockets of kiwi in mainland forests until such time (if ever) that stoats can be eliminated or controlled over large areas.

Wherever its location, each protected area must be large enough to ensure that the population of kiwi within it has a reasonable chance of long-term persistence. Protected areas in mainland forests differ from those on offshore islands because of the opportunity for dispersal. Some of the kiwi hatched within a protected area will inevitably move out and settle in surrounding unmanaged areas, no matter how large the protected area is. Equally possible is movement in the other direction, though it is much less frequent because predators eliminate most of the potential immigrants. Protected areas in mainland forests will therefore function as source areas (Dias, 1996) surrounded by large sinks, with a largely one-way flow of individuals out of the reserves. The sinks will function as either 'black hole sinks' in which there is emigration from source areas but no back migration, or as 'leaky sinks' in which there is some back dispersal (Dias, 1996). Dispersal out of a protected area has both negative and positive effects for kiwi conservation. The flow of juveniles out of the protected area may be so great that the source population cannot maintain itself. Conversely, the flow may be sufficient to maintain a population in part of the surrounding sink, in the presence of an uncontrolled predator population. Intuitively, losses from dispersal will be proportionately greater from small protected areas than large ones, so outcomes will vary with reserve size.

In this paper we examine, theoretically, how different dispersal scenarios affect persistence of kiwi in protected areas of different size. Our investigation

resembles those of Skellam (1991) and Okubo (1989) who developed theoretical frameworks for determining rates of spread from a point source. We specifically addressed two questions: 1) on what scale should predator control be undertaken in a mainland forest in order to conserve a viable population of kiwi within the treated area? and 2) what proportion of a 10 000 ha block of forest should be subjected to predator control in order to maintain a viable kiwi population throughout the whole block? The second question seeks to evaluate the extent to which dispersal from a protected area can extend the zone of kiwi population viability. The analyses apply only to North Island brown kiwi, but the approach is applicable to any threatened species of animal on large land masses (McCarthy, *et al.*, 1996).

Methods

Simulations

We developed a simulation programme written in MATLAB to examine population persistence in protected areas of different size. The programme is available from the corresponding author. Both of our questions could be answered from the same simulation, described below.

We assumed that the kiwi reserve was a square patch of forest (the protected or treatment area) centred within a larger forest of 16 km x 16 km (25 600 ha). The protected area was subjected to stoat control (Fig. 1). We assumed that kiwi could move freely between the treatment and non-treatment area, but could not disperse out of the 16 km x 16 km block or enter it from the outside. In the first question, we were interested only

in what happened to the population in the treatment area. For the second question, we examined population changes in both the treatment area and in the central 10 000 ha portion of the 16 km x 16 km forest. In each simulation, the 10 km x 10 km area contained a centrally located treatment area of variable size surrounded by an untreated area of variable size. Together the treatment and non-treatment areas always totalled 10 000 ha (Fig. 1). Again, we assumed kiwi could move freely between the treated and non-treated parts of the 10 000 ha block, and between the 10 000 ha block and the remaining parts of the 16 km x 16 km forest.

The kiwi population in the 16 km x 16 km forest varied in size throughout time, according to the demographic processes described below. Each year individuals 'bred' and 'died' at the same average rates as kiwi in the wild. The effect of different dispersal scenarios of sub-adults was specifically investigated, the aim being to find the minimum treatment area which ensured a high probability of adult persistence within a) the treatment area, and b) the central 10 000 ha part of the forest. By altering the dispersal characteristics of sub-adults, we changed their probability of settling in different areas.

In each of the simulations, we calculated the probability of quasi-extinction as the measure of population persistence. Quasi-extinction is a decline to a non-zero population size, rather than a population decline to zero (Burgman *et al.*, 1993). We used four different and arbitrary measures of viability, all based on the slope of the time series line for adult numbers (Table 1). Viability criterion T related specifically to viability within the treatment area, while criteria C1, C2, and C3 related to viability within the central 10 000 ha. Under criterion T, viability was achieved if adult numbers within the treatment area at Year 50 equalled or exceeded those in the treatment area at Year 1. In criterion C1, viability was achieved if adult numbers within the central 10 000 ha block increased from Year 40 to Year 50. The distribution of the birds within the central 10 000 ha block was not considered, so viability was possible even when all of the birds were clumped within the treatment area. Criteria C2 and C3 specifically considered population numbers outside the treated area. In criterion C2, viability was achieved if the adult population in the non-treated part of the 10 000 ha area in the 50th year of the simulation equalled or exceeded that in the non-treated area at the start of the simulation. Criterion C3 was less demanding; the population in the non-treated area was considered to be viable if it increased from Year 30 to Year 50. There are many other criterion we could have chosen. The four we have presented here span a wide range of possible viability thresholds.

The size of the treatment areas at the start and

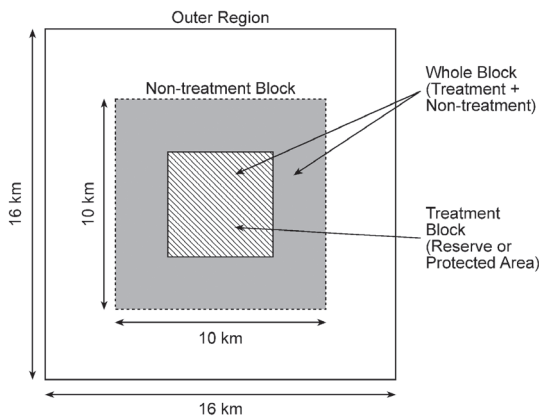


Figure 1. Schematic representation of the 10 km x 10 km kiwi reserve, with its 6 km wide forest border and centrally positioned predator control area (treatment block).

Table 1. Summary of the viability criteria used in the simulations.

Viability criteria	Area	Description
T	Treatment area	Year 50 ≥ Year 1 in treatment area
C1	10 000 ha core area	Year 50 ≥ Year 40 in 10 000 ha
C2	10 000 ha core area	Year 50 ≥ Year 1 in non-treatment area
C3	10 000 ha core area	Year 50 ≥ Year 30 in non-treatment area

finish of the simulation programme was chosen so that the probability of quasi-extinction was 1 and 0 respectively. Changes in adult numbers over 50 years were determined for a range of treatment areas of different size, with a step-size change of 0.1 km block length. The critical treatment area was defined as the smallest area that gave a 1% probability of quasi-extinction over 50 years.

Definitions and demographic parameters

The demographic parameters used in the model were derived from field measurements (McLennan *et al.*, 1996). A value for the survival rate of sub-adult kiwi (90%) was estimated from unpublished data from Lake Waikaremoana, Te Urewera National Park. For the sake of simplicity, we assumed that all of the demographic values were fixed and density independent.

Kiwi were classified into three age classes: juveniles (0–9 months); sub-adults (10–13 months); and adults (14 months–40 years). We assumed that juveniles remained in or near their natal territories during their first nine months of life, then dispersed as sub-adults. Dispersal lasted for four months, then ended with the acquisition of a territory. The birds then remained within their territory for all of their adult life.

We assumed that all adult female kiwi were paired and fledged an average of 0.85 chicks in August each year. Males and females bred for the first time when

they were two years old. The adult sex ratio was set at 1:1, reflecting equal mortality rates for males and females.

We used different recruitment rates in the treatment and non-treatment areas to reflect the impacts of stoat control. In the treatment area, 50% of juveniles reached sub-adulthood, with natural mortality and limited predation losses accounting for the remaining birds. Of those that reached sub-adulthood, 90% went on to become breeding adults, giving a juvenile to adult recruitment rate of 45%. This figure closely resembles the average recruitment rate of kiwi in a protected area at Lake Waikaremoana during three years of intensive stoat control (McLennan *et al.*, *unpubl. data*). In the non-treatment area, only 5% of juveniles survived to become sub-adults. Mortality in the sub-adult class was again assumed to be 10%, giving a recruitment rate of 4.5% in the non-treatment area.

The mortality rates for each age class were converted into monthly death rates, as shown in Table 2. We assumed that adults died when they reached an age of 40 years. In practice very few lived this long in the simulations, so the average adult mortality rate of 8.2% was applied uniformly across all adults by selecting individuals at random. This meant that the total adult mortality rate occasionally exceeded 8.2%, but was never higher than 9.5%.

At the start of each simulation, adults were distributed uniformly throughout the entire forest at a

Table 2. The multipliers used to calculate monthly losses (number of individuals) of juvenile, sub-adult, and adult kiwi in areas with (treatment) and without (non-treatment) predator control.

Age class	Treatment ¹	Non-treatment
Juveniles 0–9 months	1-(1-0.5) ^{1/9} = 0.0741 50% over 9 months	1-(1-0.95) ^{1/9} = 0.2831 95% over 9 months
Sub-adults 10–13 months	1-(1-0.1) ^{1/4} = 0.0260 10% over 4 months	1-(1-0.1) ^{1/4} = 0.0260 10% over 4 months
Adults 14 months–40 years	1-(1-0.082) ^{1/12} = 0.0071 8.2% per annum	1-(1-0.082) ^{1/12} = 0.0071 8.2% per annum

¹ The multipliers used to calculate monthly losses within each age class were derived from field measurements of mortality rates listed in McLennan *et al.*, 1996.

density of 20 km⁻². Densities as high as this are now uncommon in today's mainland forests, but are still encountered in parts of Northland (Robertson *et al.*, 1999). The ages of the adults were distributed uniformly between 14 and 480 months. The initial population contained no sub-adults or juveniles. Figure 2 shows the flowchart used to determine the changes in the composition and size of the population over time. We did not impose a carrying-capacity on the forest, and thus did not limit the extent to which a population could rise during a simulation.

Sub-adult dispersal scenarios

We measured the effect of three different dispersal scenarios on population viability. Each of the scenarios approximate the dispersal patterns of three sub-adult kiwi at Lake Waikaremoana, Te Urewera National Park. None of them, however, may approximate the average movements of dispersing sub-adult kiwi in extensive forest tracts.

Scenario 1: This scenario was chosen to represent directional dispersal. The sub-adult makes four successive movements distributed uniformly between

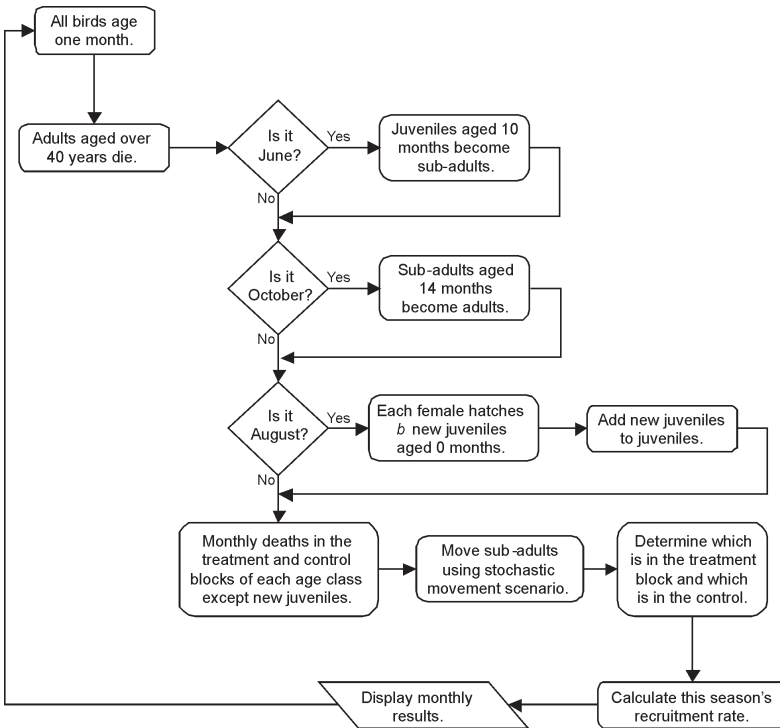


Figure 2. Schematic representation of the population changes occurring during each simulation. Dispersal distances and the size of treatment areas were altered systematically to determine the combinations that resulted in population persistence.

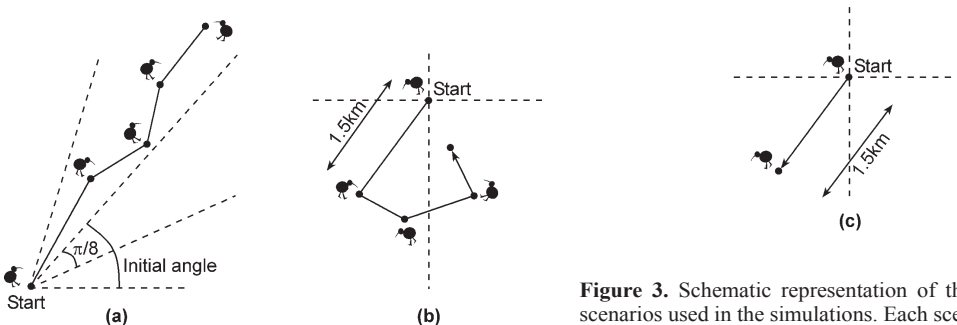


Figure 3. Schematic representation of the three dispersal scenarios used in the simulations. Each scenario combined a different mix of directional and random movements.

0 and 1.5 km. The direction of each movement is a bearing uniformly distributed between $\sigma \pm \pi/8$, where σ is set randomly at the beginning of the four movements (Fig. 3a).

Scenario 2: This scenario is a mix of directional and random dispersal. The first jump is 1.5 km, but the remaining three jumps are at a random bearing, uniformly distributed between 0 and 2π , with the length uniformly distributed between 0 and 1.5 km (Fig. 3b). Under this scenario, dispersing juveniles can reverse direction and return to natal areas.

Scenario 3: This scenario represents limited dispersal. The sub-adult makes one directional jump of 1.5 km at a bearing uniformly distributed between 0 and 2π , then settles (Fig. 3c).

In each simulation, we calculated the distance travelled by each sub-adult, defined as the straight-line distance between its locations at the beginning and end of dispersal. We also calculated the critical recruitment rate for the population for each dispersal scenario, by determining the proportion of juveniles that must settle within a population in order to maintain its viability.

Results

Average distance travelled by dispersing sub-adults

The mean distance travelled (between start and finish positions) by sub-adult kiwi during their four month dispersal phase was 2.95 km in scenario 1, 1.94 km in scenario 2 and 1.5 km in scenario 3. In all scenarios, the total distance travelled during dispersal was linearly related to the maximum length of each monthly movement (Fig. 4).

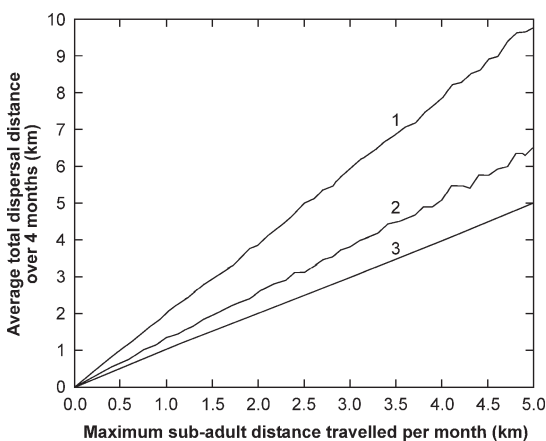


Figure 4. The relationship between monthly jump distance and total distance travelled by sub-adults over four months for each dispersal scenario.

Population viability in the treatment area in relation to dispersal distance

We used dispersal scenario 1 in this analysis (any of them would have been suitable) and varied the average total distance travelled by sub-adults during their dispersal phase by varying maximum jump length. The population in the protected area was considered to be viable if, in all 50 simulations, it remained stable or increased in size over 50 years (viability criteria T, Table 1).

The size of protected area required for population viability increased non-linearly as average dispersal distance increased (Fig. 5). In the event of limited dispersal, or no dispersal at all, kiwi populations (at least theoretically) maintain viability in all protected areas, irrespective of their size. With mean dispersal distances of 1km, viability was achieved only in protected areas of ≥ 700 ha. At 2km, 2000 ha was required for viability, and at 5km, 10 000 ha was insufficient to maintain a kiwi population over the long term. When protected areas were too small relative to mean dispersal distance, leakage of sub-adults eventually caused population failure, despite the lack of predators in the protected area.

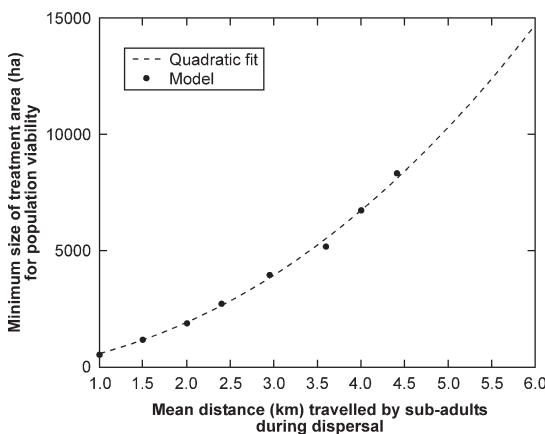


Figure 5. The relationship between the minimum area required for population viability (criterion T) and mean total distance travelled by sub-adults during dispersal. In the area below the line, recruitment rates fall below mortality rates and the population eventually fails.

Maintaining a kiwi population in a 10 000 ha forest

In the absence of physical barriers, there will always be some emigration of sub-adults out of a protected area and a small flow of immigrants back into the reserve. In this analysis, we examined how leakage from a protected area contributes to the maintenance of kiwi

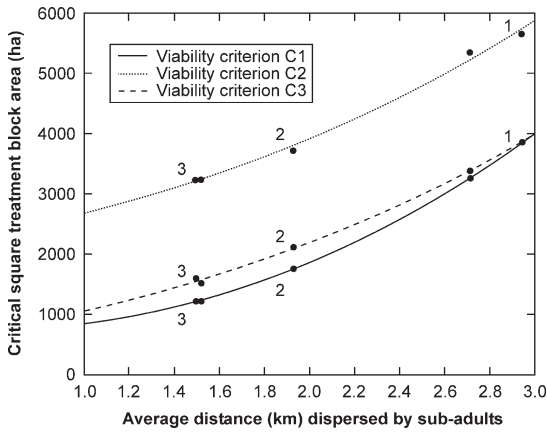


Figure 6. Minimum treatment block area required to maintain a viable population of kiwi in a 10 000 ha block of forest in relation to sub-adult dispersal distance. In viability criterion C1, the population in the whole 10 000 ha block increases from Year 40 to Year 50. In criterion C2, the population in the non-treated part of the block at Year 50 is \geq that at Year 1; and in criterion C3, the population in the non-treated part of the block increases from Year 30 to Year 50.

populations in the surrounding sink area. We specifically determined how large a centrally-located treatment area should be in order to maintain a viable population of kiwi in a 10 000 ha area of forest.

The minimum size of treatment area required for population viability throughout the 10 000 ha forest increased as the mean dispersal distance of sub-adult kiwi increased (Fig. 6.). It also changed according to which criterion was used to evaluate population viability. Minimum treatment area estimates ranged from 1225 ha (dispersal scenario 3 and viability criterion C3) to 5625 ha (dispersal scenario 1 and viability criterion C1). The mean value for all 9 combinations was 2995 ± 361 (S.E.) ha.

In all of the simulations, kiwi numbers in the non-treated part of the 10 000 ha forest generally declined over the first 10 to 30 years, then began to increase only when densities in the treatment area reached high levels (Fig. 7). This general pattern was expected because the population in the treatment area had to reach a certain size before it could produce enough young to maintain itself and offset the decline in the surrounding untreated area. In Fig 7a, for example, the 5625 ha treatment area contained 1125 adults at the start of the simulation. Numbers declined to about 1000 over the first four years, due to the absence of juveniles in the population at the onset of predator control. However, by Year 5, the population had begun to increase, and by Year 15 it had recovered to its initial

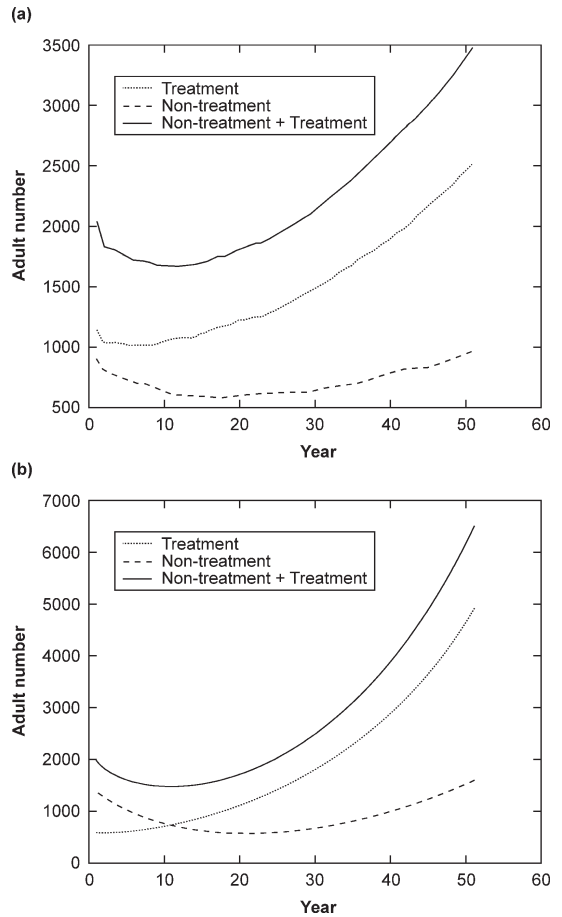


Figure 7. Changes in the number of adult kiwi in a 10 000 ha block of forest over 50 years. In (a) sub-adults disperse 2.95 km and the critical treatment area is 5625 ha. In (b) sub-adults disperse 1.5 km. The critical treatment area for population viability is 3249 ha. In both examples, the population in the non-treated part of the block takes 50 years to recover to its starting size.

starting size. From Year 25 to Year 50, it produced sufficient dispersers to offset the decline in the non-treatment area, eventually allowing the population there to recover to its starting size. By the end of the simulation, the treatment area contained 2450 kiwi, equivalent to 43 birds km^{-2} , and the entire population in the 10 000 ha forest had increased over the 50 years from 2000 to 3325.

The same general pattern is evident in Fig 7b, with a recovery in the non-treatment area from Year 25 to Year 50. In this case though, kiwi densities in the 3249 ha treatment area reach 45 km^{-2} at Year 25, then continue to increase to about 148 km^{-2} at Year 50. In

the wild, adult densities occasionally reach 100 km⁻² in isolated forest patches in farmland in Northland, but seldom if ever exceed 40 km⁻² in large tracts of continuous forest (H. Robertson, Department of Conservation, Wellington, New Zealand, *pers. comm.*). It is therefore highly unlikely that the results of this simulation are meaningful; the population in the non-treated area can never recover unless densities in the treatment area exceed carrying capacity. This problem occurred whenever treatment areas were smaller than 5000 ha, implying that this is about the minimum size of treatment area needed to maintain kiwi in a 10 000 tract of forest. Smaller treatment areas might be acceptable if an increasing proportion of juveniles dispersed out of the treatment area when densities approached carrying capacity. We did not attempt to model this possibility, or the alternative one of increasing sub-adult mortality (i.e., fewer dispersers) with increasing adult density.

Figure 7a also shows that the population in the non-treatment area always lagged behind the one in the treatment area. This is a consequence of the assumptions of our model, and would not necessarily happen in the wild if dispersal was density dependent. Furthermore, despite effective predator control and relatively high rates of chick survival, kiwi numbers in the treatment area remained almost static for the first 15 years of the simulation. Over the same period, numbers in the surrounding non-treatment area declined, and total numbers in the whole 10 000 ha forest declined. Most managers would expect a quicker response to predator

control; and indeed it would be a truly remarkable manager who persisted with a predator control programme that failed to deliver any measurable benefits for 15 years.

In summary, treatment areas of at least 5000 ha are probably required to maintain kiwi in 10 000 ha tracts of forest. This conclusion is critically dependent on the demographic values and viability criteria used in the model, as well as the assumption that the mean dispersal distance of sub-adult kiwi is 2.95 km regardless of density.

Sensitivity analyses

The relationships shown in Figs. 5 and 6 are sensitive to changes in the demographic values used in the simulations, so do not have application to any other species of forest bird, or indeed, to any of the other three species of kiwi. For example, the estimate of the size of treatment area needed to sustain kiwi in a 10 000 ha tract of forest is influenced substantially by changes in the annual productivity rate of females (Fig. 8). Larger variation is produced by changing survival rates, with higher rates of recruitment resulting in smaller treatment areas for population viability. Our results are probably conservative; with current methods of stoat control, the survival values that we used in the simulations are unlikely to be exceeded in the field.

Discussion

Dispersal behaviour of kiwi

The simulations suggest that protected areas for kiwi have to be sufficiently large to accommodate sub-adult dispersal. Intensive predator control will fail to restore populations unless it is conducted on a scale which allows ≥ 20% of each annual crop of juveniles (or about half of the annual crop of sub-adults) to settle within the treatment area. This prediction hinges critically on the assumption that dispersal is density independent, i.e. that young kiwi will always disperse the same average distance from natal areas, even when they are raised in sparse populations, unrestrained by food supply or some other critical resource.

Preliminary field studies at Lake Waikaremoana, Te Urewera National Park, show that most sub-adult kiwi disperse from natal areas in large forest tracts, sometimes travelling five or more kilometres in a few weeks. The minimum mean dispersal distance of 11 sub-adults was 5.24 ± 0.97 (S.E.) kilometres. The actual mean could have been considerably larger because four individuals walked out of the catchment and their final destinations were not established. The salient point is that this dispersal occurred within what is now a declining and low-density kiwi population,

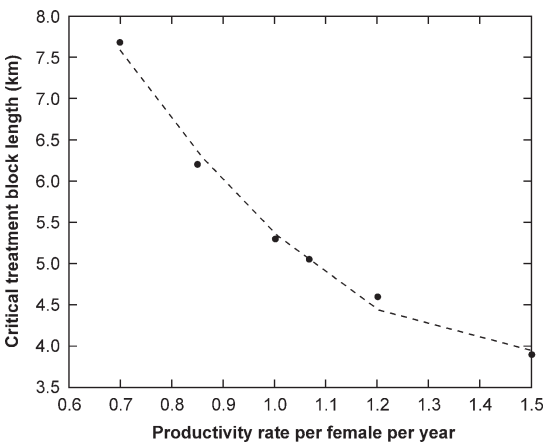


Figure 8. Sensitivity analysis of the relationship between female reproductive rate and the size of treatment block required to maintain kiwi in 10 000 ha blocks of forest. Dispersal scenario 1 was used in this analysis.

with an average density of adults (3.3 km^{-2}) about one-thirtieth of that on stoat-free offshore islands (H. Robertson, *pers. comm.*). Long-distance movements by sub-adults have also been observed in a sparse remnant population of kiwi in Tongariro Forest Park (C. Speedy, Department of Conservation, Turangi, New Zealand, *pers. comm.*). The preliminary findings also suggest that females disperse further than males though samples are still too small for a rigorous comparison.

These unpublished field observations do not necessarily support our assumption of density independent dispersal, but they do show dispersal occurs within populations that appear to be unrestrained by environmental resources. The possibility still remains that dispersal distances increase with density, especially in populations near carrying capacity. Low density dispersal may in part be driven by crowding because adults in remnant populations expand their territories and actively defend them against intruders (McLennan, *et al.*, 1987). At Waikaremoana, sub-adults generally settle on or near territorial boundaries, and progressively expand their ranges from there. Low density dispersal may also be partly driven by innate behaviour, since sub-adults often travel through unoccupied habitat, even though it appears suitable and may have formerly supported resident adults as little as a few years previously. Young females in particular often disperse beyond territories occupied by solitary males, forgoing the opportunity to settle.

The field observations therefore suggest that the predictions of the simulations are biologically reasonable, at least for low-density populations. Despite their honorary mammal status (Calder, 1978), kiwi appear to have dispersal characteristics typical of birds rather than mammals (Greenwood, 1980; Pusey, 1987), with variable movements by males (depending on the availability of local opportunities for settlement) and density independent movement by females. Given that territorial adults often travel one or two kilometres in a single night (McLennan *et al.* 1987) it is not surprising that sub-adult kiwi sometimes disperse tens of kilometres in a few weeks.

Area requirements of kiwi

Figure 5 shows that treatment areas for kiwi should be at least 11 000 ha when the mean dispersal distance of sub-adults is 5.24 km. This estimate is tentative because our preliminary estimate of mean dispersal distance at Lake Waikaremoana could differ substantially from the long-term average, and (less likely) sub-adults in this locality may behave differently from those elsewhere in the North Island. If it is close to the mark, then our second lot of simulations probably do nothing more than demonstrate a principle; the concept (that spill-over from a treatment area will sustain a viable

kiwi population in part of the surrounding, unmanaged area) is still relevant, but only in forest blocks exceeding 11 000 ha in size.

The important point is that kiwi appear to have large area requirements: Protected areas for them in continuous tracts of forest probably need to be in order of hundreds rather than tens of square kilometres. This finding is consistent with those of earlier workers using completely different techniques to determine minimum areas for population viability, as discussed below.

Previous studies on area requirements

In the late 1970s and early 1980s conservation biologists evaluated the area requirements of New Zealand forest birds, based on species persistence on real and virtual islands (Hackwell and Dawson, 1980; Hackwell, 1982; Dawson, 1984; Diamond, 1984a; East and Williams, 1984). Twelve species (yellowhead *Mohoua ochrocephala*, whitehead *M. albicilla*, kokako *Callaeas cinerea*, robin *Petroica australis*, red-crowned parakeet *Cyanoramphus novaeseelandiae*, yellow-crowned parakeet *C. auriceps*, kaka *Nestor meridionalis*, kea *N. notabilis*, weka *Gallirallus australis*, brown kiwi, great spotted kiwi, brown creeper *Mohoua novaeseelandiae*) were shown to persist mainly in large forest patches, suggesting their main threats were habitat destruction and forest fragmentation (Diamond, 1984a).

Nineteen years later, this conclusion must be questioned. At least seven of the 12 species identified by Diamond have continued to decline, largely because of predation by introduced mammals (Wilson *et al.*, 1998; O'Donnell, 1996; McLennan *et al.*, 1996; Innes *et al.*, 1999). Indeed, it is now clear that the continuing impacts of introduced predators in New Zealand ecosystems were grossly under-estimated in the early 1980s. The biogeographic studies undertaken then are a snapshot in time, undertaken in the presence of predator-driven declines. They undoubtedly show that certain species of birds persist for longer in large forest patches than in small patches, but do not reveal much about the underlying processes or the area requirements of individual species. In the presence of unsustainable predation losses, the apparent area requirements of vulnerable species inevitably increase with time. Today's estimate of area requirement may bear little resemblance to one obtained in the absence of predators, or to another one obtained in a 100 years time. Indeed, it is highly likely that some species now restricted to large forest patches would become abundant enough to re-colonise smaller forest patches if predators were removed.

The same concerns do not apply to the data set of East and Williams (1984) based on species persistence on land-bridge islands. Their analyses show that only

D'Urville Island (162 km²) retained a population of kiwi following its isolation from greater New Zealand some 10 000 years ago. Little Barrier Island (30 km²) should probably also be added to their list, given that it has its own endemic species of feather louse (*Apterygon rodericki*) specific to brown kiwi (Palma, 1991). Kiwi were thought to be extinct on the island in the early 1900s (Oliver, 1955). Either way, their conclusion that reserves of tens and perhaps hundreds of square kilometres are necessary for the long-term preservation of kiwi in mainland forests remains unaltered.

East and Williams (1984) used area requirements as an indirect method of evaluating how large isolated populations have to be in order to survive the combined threats of inbreeding, genetic drift, demographic stochasticity, disease outbreaks, and adverse climatic events. Our central question was identical to theirs, but our timescale was much shorter (50 years *v.* thousands of years) and our focus was restricted entirely to dispersal-induced population failure, a threat unique to populations on the mainland. The common thread in both studies is population size, the dominant factor influencing the rate of local extinction of isolated populations (Diamond, 1984b). Are populations which are large enough to survive the threats of isolation also large enough to survive dispersal losses?

East and Williams (1984) used Frankel and Soule's (1981) estimate of 500–1000 individuals as their estimate of minimum population size for long-term persistence. On this basis, Little Barrier Island just meets the area requirements of brown kiwi, assuming (as East and Williams did) a maximum adult density of 30 km⁻². More recent estimates of minimum viable population size (5500 individuals; Thomas, 1990) suggest Little Barrier is much too small for long-term persistence, but D'Urville Island qualifies (5346 individuals) if all of it is suitable for habitation. Given a mean dispersal distance of 5.24 km, our estimated minimum treatment area (11 000 ha) would contain 3300 adults at carrying capacity, a population which falls neatly between the two estimates suggested for long-term persistence. Dispersal behaviour in kiwi may well have evolved to avoid inbreeding depression (Pusey and Wolf, 1996), so it is probably not coincidental that a population which is large enough to survive the threats of isolation is also large enough to survive dispersal losses.

As East and Williams (1984) noted, there is clearly a general tendency for the species in greatest need of conservation to have large area requirements. Currently, effective, on-going predator control over hundreds of square kilometres is beyond the reach of existing technology. On the other hand, all of the six (official) 'mainland-islands' currently managed by the Department of Conservation are too small to protect

the species that are most in need of help. Paradoxically, at least half of the nine species most likely to respond to small-scale initiatives (pigeon *Hemiphaga novaeseelandiae*, bellbird *Anthornis melanura*, tui *Prothemadera novaeseelandiae*, fantail *Rhipidura fuliginosa*, robin, greywarbler *Gerygone igata*, silvereye *Zosterops lateralis*, tomtit *Petroica macrocephala*, and morepork *Ninox novaeseelandiae*) require no protective measures at all to maintain viable populations.

The problem of preserving species with large area requirements may not, however, be as intractable as it first appears. The mismatch between what is achievable now and what is required will narrow over coming decades as predator control techniques improve. In the meantime, dispersal in kiwi and other flightless species can be prevented by erecting low fences, or by choosing treatment areas bounded by natural barriers. If necessary, individuals can be swapped between treatment areas to increase effective population size (Frankham, 1995; Lynch and Lande, 1998; Franklin and Frankham, 1998). For flighted species, a network of small, manageable treatment areas (< 5000 ha) could be just as effective as one large one, provided they are sufficiently close to each other to allow dispersers to move between them.

Improving the model

Models are never a perfect description of reality (McCarthy *et al.*, 2001) and our one is no exception. However, empirical tests on reserve sufficiency would take decades to complete, by which time kiwi could well be extinct in mainland forests. We believe that both of our main conclusions (increasing dispersal is bad for viability, and kiwi require large reserves) are reasonable. But the detail of the predictions is suspect, due largely to the almost total absence of information on dispersal behaviour of kiwi in the wild. The predictive performance of our model (with its reliance on the statistic, *mean dispersal distance*) is likely to be poor if dispersal distances do prove to be sex related with an underlying bimodal distribution, and/or if dispersal is density dependent. Modelling is an iterative process involving development, testing, subsequent modification and re-testing (McCarthy *et al.*, 2001). We have just completed the first step; the next phase will begin when better information becomes available.

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References

- Basse, B.; Wake, G.C.; McLennan, J.A. 1997. Predation thresholds for survival of endangered species. *IMA Journal of Mathematics Applied in Medicine and Biology* 14: 241-250.
- Basse, B.; McLennan, J.A.; Wake, G.C. 1999. Analysis of the impact of stoats, *Mustela erminea*, on northern brown kiwi, *Apteryx mantelli*, in New Zealand. *Wildlife Research* 26: 227-237.
- Burgman, R.L.; Ferson, S.; Arcakaya, H.R. 1993. *Risk assessment in conservation biology*. Chapman and Hall, London, U.K.
- Calder, W.A. 1978. The kiwi. *Scientific American* 239: 102-110.
- Dawson, D.G. 1984. Principles of ecological biogeography and criteria for reserve design. *Journal of the Royal Society of New Zealand* 14: 11-25.
- Diamond, J.M. 1984a. Distributions of New Zealand birds on real and virtual islands. *New Zealand Journal of Ecology* 7: 37-55.
- Diamond, J.M. 1984b. "Normal" extinction of isolated populations. In: Nitechi, M.H. (Editor), *Extinctions*, pp. 191-246. Chicago University Press, Chicago, U.S.A.
- Dias, P.C. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* 11: 326-330.
- East, R.; Williams, G.R. 1984. Island biogeography and the conservation of New Zealand's indigenous forest-dwelling avifauna. *New Zealand Journal of Ecology* 7: 27-35.
- Frankel, O.H.; Soule, M.E. 1981. *Conservation and evolution*. Cambridge University Press, Cambridge, U.K.
- Frankham, R. 1995. Effective population size / adult population size ratios in wildlife: a review. *Genetic Research* 66: 95-107.
- Franklin, I.R.; Frankham, R. 1998. How large must populations be to retain evolutionary potential? *Animal Conservation* 1: 69-70.
- Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140-1162.
- Hackwell, K.R.; Dawson, D.G. 1980. Designing forest reserves. *Forest and Bird* 13: 8-15.
- Hackwell, K.R. 1982. The island biogeography of native forest birds and reserve design. In: Owen, J.M. (Editor), *Proceedings of a workshop on a biogeographical framework for planning and extending national parks and reserves system*, pp 28-41. Department of Lands and Survey, Wellington, N.Z.
- Innes, J.; Hay, R.; Flux, I.; Bradfield, P.; Speed, H.; Jansen, P. 1999. Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. *Biological Conservation* 87: 201-214.
- Lynch, M.; Lande, R. 1998. The critically effective size for a genetically secure population. *Biological Conservation* 1: 70-72.
- McCarthy, M.A. 1996. Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and spatial structure. *Ecological Modelling* 85: 151-163.
- McLennan, J.A.; Rudge, M.R.; Potter, M.A. 1987. Range size and denning behaviour of brown kiwi, *Apteryx australis mantelli*, in Hawke's Bay, New Zealand. *New Zealand Journal of Ecology* 10: 97-107.
- McLennan, J.A.; McCann, A.J. 1994. *Genetic variability, distribution, and abundance of great spotted kiwi, Apteryx haastii*. Landcare Research, Havelock North, N.Z.
- McLennan, J.A.; Potter, M.A.; Robertson, H.A.; Wake, G.C.; Colbourne, R.; Dew, L.; Joyce, L.; McCann, A.J.; Miles, J.; Miller, P.J.; Reid, J. 1996. Role of predation in the decline of kiwi, *Apteryx* spp., in New Zealand. *New Zealand Journal of Ecology* 20: 27-35.
- O'Donnell, C.F.J. 1996. Predators and the decline of New Zealand forest birds: an introduction to the hole-nesting bird and predator programme. *New Zealand Journal of Zoology* 23: 213-219.
- Okubo, A. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70: 329-338.
- Oliver, W.R.B. 1955. *New Zealand birds*, Second edition. A.H. and A.W. Reed, Wellington, N.Z.
- Palma, R. L. 1991. A new species of Rallicola (Insecta: Phthiraptera: Philopteridae) from the North Island brown kiwi. *Journal of the Royal Society of New Zealand* 21: 313-322.
- Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution* 2: 295-299.
- Robertson, H.A.; Colbourne, R.M.; Graham, P.; Miller,

- P.J.; Pierce, R.J. 1999. Survival of brown kiwi exposed to 1080 poison used for control of brushtail possums in Northland, New Zealand. *Wildlife Research* 26: 209-214.
- Skellam, J.G. 1991. Random dispersal in theoretical populations. *Bulletin of Mathematical Biology* 53: 135-165.
- Thomas, C.D. 1990. What do real population dynamics tell us about minimum viable population sizes? *Conservation Biology* 4: 324-327.
- Wilson, P.R.; Karl, B.J.; Toft, R.J.; Beggs, J.R.; Taylor, R.H. 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological Conservation* 83: 175-185.

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