Making endangered species safe: the case of the kokako of North Island, New Zealand

A.R.E. Sinclair[1], John Innes[2,*] and Philip Bradfield[3]

[1]Centre for Biodiversity Research, University of British Columbia, Vancouver V6T 1Z4, Canada
[2]Landcare Research, Private Bag 3127, Hamilton, New Zealand
[3]Department of Conservation, P.O. Box 38, Te Kuiti, New Zealand
*Author for correspondence (E-mail: innesj@landcareresearch.co.nz)

Abstract: The theory of population regulation predicts that threatened species are safest at high population numbers, partly because density-dependent compensatory mechanisms counteract unpredictable disturbances. We illustrate this principle using data from the endemic kokako (*Callaeas cinerea wilsoni*) populations in the North Island, New Zealand. First we calculate the fledging rate per female (production) necessary to stabilise the population and thereby the residual numbers of nest predators, namely ship rats and possums, which have to be achieved to reach this production. Both predator species must be reduced to low densities to exceed this threshold production. At these low predator densities kokako numbers increase rapidly, and we predict that the population will at some stage experience density- dependent negative feedback producing a declining rate of increase. We review evidence for such feedback at Mapara. More research is required to verify and understand these density-dependent causes of loss at high density, particularly the role of territoriality and intra-specific and inter-specific competition, and to generalise across species. In addition to the increased resilience of a threatened species when at high numbers, the degree of predator removal can be relaxed. Consequently, the cost of management will also decline.

Keywords: kokako; *Callaeas cinerea*; density dependence; transition matrix; nest predation; emigration; mortality

Introduction

Endangered species have often declined (or are declining) as a direct or indirect result of human activities (Caughley, 1994). Causes of such declines may include reduction of habitat area or habitat quality, overexploitation by humans, and the introduction of exotic predators, competitors, parasites and diseases (Griffith *et al.*, 1989; Serena, 1994; Sinclair *et al.*, 1998; Sutherland, 1998; Chamberlain *et al.*, 2000; Kerr and Deguise, 2004). Conservation action naturally focuses first on reversing the decline in numbers by changing the underlying cause. Where predation is the cause of decline, as in many mammals in Australia (Burbidge and McKenzie, 1989; Johnson *et al.*, 1989; Short *et al.*, 1992) and birds in New Zealand and other oceanic islands (Clout and Craig, 1994; Clout and Saunders, 1995; McLennan *et al.*, 1996; Atkinson, 2001; Dowding and Murphy, 2001), there have been some successes in turning around declining populations by reducing predation. For example, the impacts of introduced mammalian predators has been removed from bird populations [e.g. kakapo *Strigops habroptilus* (Elliott *et al.* 2001); saddleback *Philesturnus carunculatus* (Hoosen and Jamieson 2003)] in New Zealand by marooning birds on safe offshore islands from which predators are naturally absent or eradicated (Towns and Broome, 2003). There is also increasing success in recovering forest bird populations at mainland sites where predation has been reduced but not eliminated [e.g. kokako *Callaeas cinerea wilsoni* (Innes *et al.*, 1999); kaka *Nestor meridionalis* (Moorhouse *et al.*, 2003); North Island brown kiwi *Apteryx mantelli* (Pierce and Westbrooke, 2003)].

However, although populations suffering from predation may not be declining they are still vulnerable to rapid collapse and even extinction from sudden unexpected perturbations if they remain at low numbers. Such vulnerability is exacerbated by the lack of compensatory mechanisms in the population. This paper explains how this compensation could operate to make endangered populations safe while simultaneously reducing the cost of predator control. We illustrate possible compensation mechanisms with data from a population of the endemic kokako in the North Island, New Zealand.

Compensatory mechanisms in changing populations

Populations at low density relative to their carrying capacity and with little or no interspecific competition have high per capita resources and so high reproduction and low mortality per capita. Thus, the population is capable of increasing near its maximum rate, r_{max}, the intrinsic rate of increase. However, as the population increases its resources are used at a faster rate and per capita food supply declines. Consequently there are declines in reproduction and increases in mortality until reproduction and mortality reach a balance, on average. The population or density where this balance occurs is called the carrying capacity (K). The change in reproduction or mortality as a proportion of the population as numbers increase is described as density dependence. Theoretically, density-dependent reproduction or mortality leads to population stability, although one may never see a stable point due to random environmental perturbations that affect numbers (Sinclair, 1989; Sinclair and Pech, 1996). Nevertheless, over the long term the population fluctuates about a mean value determined by the negative feedback mechanisms. There is now considerable evidence to suggest that this process occurs in nature (Sinclair, 1989, 1996).

We can illustrate these proportional rates in Fig. 1. For simplicity we assume reproduction rate is a constant percentage (R_1) when plotted against population density. This R_1 can represent newborn animals, or the net production after early mortality, say from nest predators. The percent non-predation mortality (M) is shown as a curve being flat at low density (little density dependence) and steep at high density (strong density dependence). In Fig. 1A where the reproduction and mortality curves cross, the percentages are equal and the potential equilibrium is indicated as K_1.

We start with some initial mortality of eggs and nestlings from predators such as possums (*Trichosurus vulpecula*) or ship rats (*Rattus rattus*) on nests, resulting in post-nesting recruitment (R_1). A sudden disturbance, such as an influx of another predator like stoats (*Mustela erminea*), a poor year for food or a bad winter, reduces the rare target species to a lower density N_1. At N_1 normal mortality from starvation is less than reproduction by a substantial amount due to the steepness of the mortality curve. This difference, c_1, is the rate at which the population can *compensate* for the disturbance. The compensation is the increase after the pulse disturbance back towards the equilibrium.

In contrast to the above events at high density, we can start at a low density equilibrium K_2 in Fig. 1B, held there by the dead weight of a much higher persistent predation on nests so that net recruitment after predation is only R_2. Again we impose an unexpected disturbance so the target population drops

by the same amount to N_2. Under these conditions the difference between net recruitment and non-predation mortality is very small (c_2) because the mortality curve is flat. Hence, there is almost no compensation: the population is already operating at its maximum rates of reproduction and survival (apart from predation) and neither can increase further after a sudden decline in numbers. These results depend on some curvilinear density dependence in either recruitment or mortality. However, there is substantial evidence for such curvilinear density dependence in nature (Fowler, 1981, 1987; Mduma *et al.*, 1999; Sinclair, 2003; Sibly *et al.*, 2005).
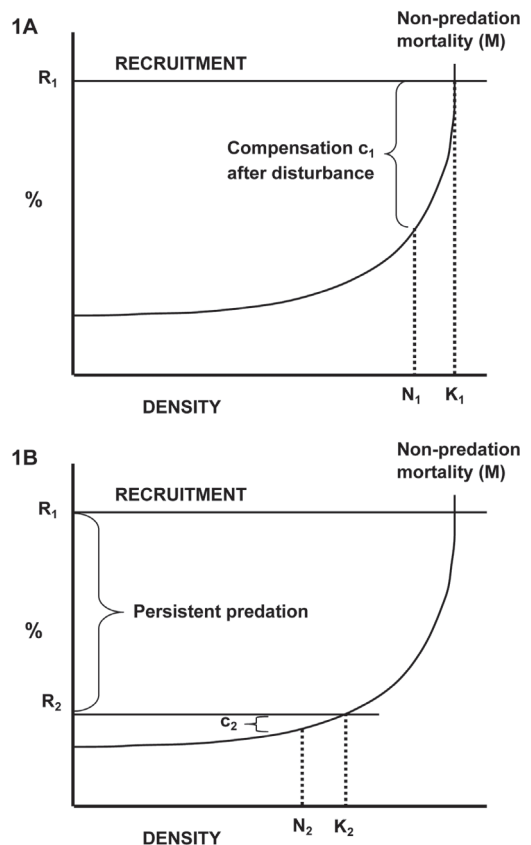

Figure 1. Theoretical relationship of a constant net recruitment (R_1) after predation of juveniles with a curvilinear density-dependent non-predation mortality. A. The population stabilises at equilibrium density K_1. **A.** Pulse disturbance reducing the population to N_1 can be compensated by the difference c_1. **B.** In the presence of severe constant predation of recruits the recruitment rate is reduced to R_2 so that a similar drop in population K_2 to N_2 can only be compensated for by a small amount (c_2).

If we allow our target population to remain at low density through persistent predation (as in Fig. 1B), there must be a high and constant effort to exclude predators because this population has almost no inherent compensation ability to withstand additional perturbations (it is already responding at its maximum r and so cannot respond further to new influxes of predators, bad winters etc.). Hence, it remains vulnerable to extinction. In contrast, let us allow the population to increase to a higher density by a period of high predator removal effort (to achieve Fig. 1A). Having reached this higher density, management effort can then be relaxed and some predators can be tolerated because their depredations merely replace mortality from lack of resources (i.e. predators are removing those that would die anyway). Furthermore, an extra perturbation can be tolerated because a decline in population is compensated by an increase in r so that the population is far less vulnerable to extinction. Thus, having reached high density, the population is doing much of the work of counteracting predation that, at low density, managers would have to do instead.

Essentially there are three ways a population can compensate for a drop in density, say from a poor food season: it can increase its reproduction, decrease its mortality or decrease its dispersal of juveniles. As mentioned above these factors respond most rapidly at higher numbers, and not at all once they are at maximum values at low density. In reality, there is little known about the nature of these compensation mechanisms in endangered New Zealand birds and reptiles because we have not seen them at high density on the mainland for a century or more. However, increasing populations of endemic birds when predator numbers have been reduced could supply important clues to these mechanisms. We analyse data for the North Island kokako obtained from three small populations at Mapara, Rotoehu and Kaharoa, with the great majority of data coming from the first area (Innes *et al.*, 1999; Basse *et al.*, 2003).

Determining threshold demographic parameters of kokako under predation

The number of fledglings produced per female per season (production) at Mapara was calculated by visiting all known pairs throughout the breeding season to find nests. Productivity was confirmed by climbing to nests to band young and by following pairs after nesting to confirm fledging. Survival of juveniles in their first two years was measured by finding birds as adults after they had been individually banded as nestlings; 65 adults and 167 nestlings were banded during 1989–2000. Adult survival was also measured by the re-location of banded birds; individuals not seen for 2 years were considered to have died and their date of death was recorded as the date of their first-noted absence (Basse *et al.*, 2003).

We used mean values for juvenile (years 1–3) and adult survival because it was apparent that most changes in demographic values took place during nesting when nestlings and females were vulnerable to nest predation by ship rats and possums. Production was measured annually as fledglings per adult. Adults suffered a low degree of predation by stoats and possums. Thus, we used two mean values for the probability of adult survival, 0.96/year when predators were removed from the system, and 0.85/year when predators were present. These mean values are given in Table 1 with further details presented in Basse *et al.* (2003).

We used a Leslie transition matrix (POPTOOLS 2.4, www.cse.csiro.au/CDG/poptools) to calculate the instantaneous rate of change in these populations (r) when at low density with little density dependence in the system. First, in the absence of all predation, i.e. with the observed number of 0.95 fledged young adult and an adult survival of 0.95, then the kokako population shows a robust instantaneous rate of increase of 0.149 (Table 1). Second, with the same production rate of 0.95 (i.e. no nest predation) but with adult mortality from stoats reducing adult survival to 0.86, the population could still increase fast at an r of 0.096.

Table 1. Demographic values for kokako populations used in the transition matrix. Values in bold are those estimated from the matrix.

	Without predators	With stoats alone	Threshold production with stoats
Fledged per adult	0.95	0.95	**0.495**
1st year breeding proportion	0.59	0.59	0.59
Post-fledgling survival	0.63	0.63	0.63
1st year survival	0.63	0.63	0.63
2nd year survival	0.63	0.63	0.63
Adult survival	0.95	0.86	0.86
Rate of increase	**0.149**	**0.096**	0.0

Third, the population is held constant ($r = 0$) in the presence of stoat predation of adults when the fledgling rate is 0.495 young per adult, or effectively l young per female per year.

Determining threshold level of predation for kokako population stability

In order to achieve a kokako production threshold of 0.495 young per adult, we need to calculate the equivalent nest predation levels by possums and rats, and hence their associated densities. Most of the field data on production are in the form of an index, namely the percentage of nests that hatched young. At the three kokako study sites the percentage of nests that successfully hatched young can be related to an index of possum and rat density, measured separately. A range of predator densities was achieved by comparing periods when both predators were present in high density [i.e. ship rats > 10% mean tracking rates during October to February, and possums > 6% trap-catch at 1 November, using standard techniques (Innes *et al.*,

1999; Fig. 2A, B)], and when both were held experimentally at low density (i.e. less than above) by repeated removals (Fig. 2C, D). After the removals ceased, rat populations rebounded within a few weeks while possum numbers remained low for 1 or 2 years, so that we could observe the effect of high rat numbers and low possum numbers (Fig. 2C). There was only one occasion when the reverse situation held, namely high possum numbers with low rat numbers (Fig. 2D). These figures show that nest success was very low, around 15%, when both predators were at high density (Fig. 2A, B). In contrast, nest success was high, about 70%, when both predators were at low density (Fig. 2C, D). When possum numbers were low there was a strong negative relationship between nest success and rat density, and the highest densities resulted in very low nest success (5–15%) (Fig. 2C). Similarly, when rats were at low density there appears to be a decline in nest success from 60–90% at low possum density to 30% at the one value when possums were in high numbers (Fig. 2d).
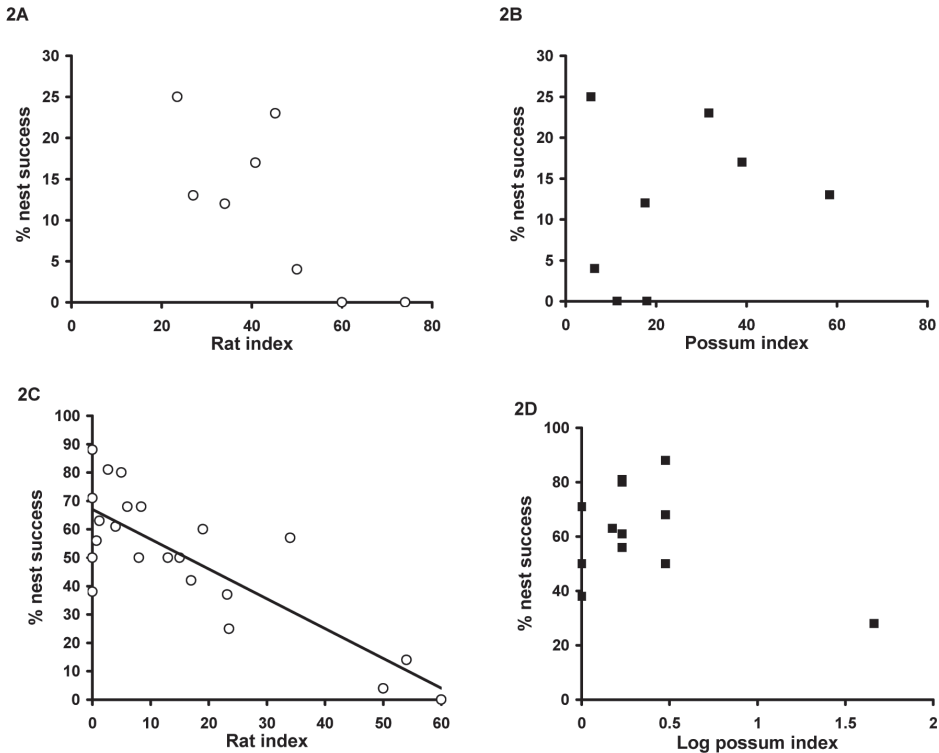

Figure 2. Percent nest success of kokako at different levels of nest predator densities. A. Rats at high indices of density (> 10% mean tracking in Oct. to Feb.). B. Possums at high density (>6% trap-catch at 1 Nov., using standard techniques). C. When possum density is low there is a negative relationship between % nest success (NS) and rat density (RD). NS = 67.054 – 1.0507RD, r^2 = 0.668. D. The relationship between % nest success and log (possum density +1) when rat density is low.
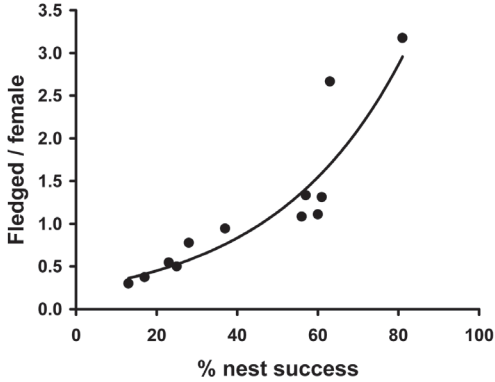
Figure 3. Relationship between per capita production rate (fledged/female, F) and the % nest success (NS). $F = 0.2428e^{0.0309NS}$, $r^2 = 0.894$.
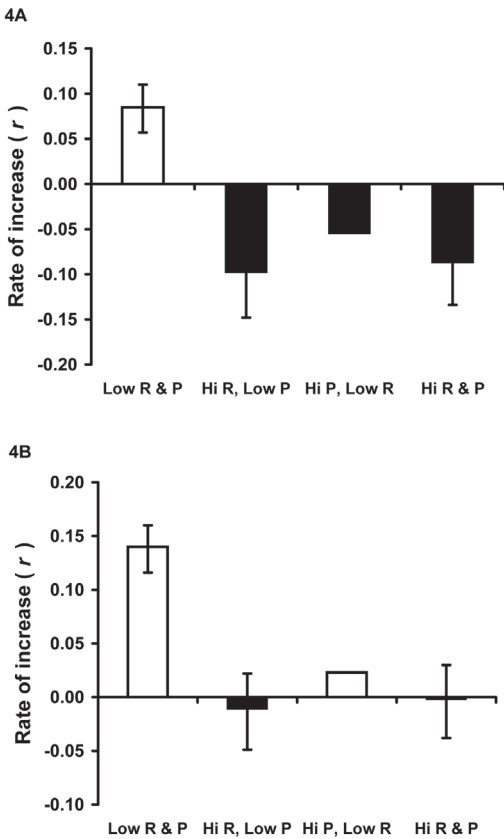

Figure 4. Mean and standard error values for calculated instantaneous rates of increase (r) at different levels of rat (R) and possum (P) densities. **A.** With stoat predation on adult kokako. **B**. Without stoat predation.

To interpret these effects of nest predators it is necessary to transform the percent nest success into fledged young per female. For a subset of nests both pieces of information were obtained, and they provide a reasonably tight positive relationship (Fig. 3). Using the equation from Fig. 3, the production rate was calculated for each observation of high and low rat or possum density presented in Fig. 2. These production values were then used in the transition matrix to calculate a value of r for each observation of the kokako population. The mean and standard error of the r-values of kokako for each combination of high and low rats and possums are presented in Fig. 4A where stoats also reduced adult survival. This figure confirms that the high nest success when both rats and possums were low in number resulted in a high positive rate of increase of 0.08 in the presence of stoats. In contrast, a negative rate of increase occurred at any combination where at least one of the nest predators was in high density. The negative values of r were similar whether it was rats or possums that were high in the absence of the other, suggesting that the two species compensated for each other and their effects were not additive.

Figure 4B shows the rates of increase when there was no stoat predation of adult kokako. The absence of stoats does not alter the main conclusion from Fig. 4A, namely that it is only when *both* rats and possums are at low numbers does the kokako population show a significantly positive rate of increase. With the other combinations of high nest predators the kokako population cannot increase even in the absence of stoats. These conclusions are not changed even when the two highest points in Fig. 3, produced in years of multiple broods, are omitted.
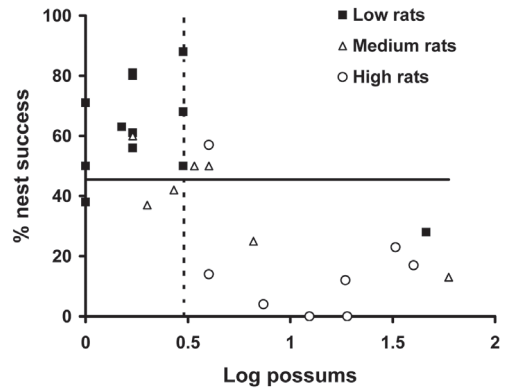

Figure 5. Relationship between kokako nest success and log (possum density +1) in the presence of low, medium, and high rat numbers. There is a positive rate of increase of kokako when nest success reaches 45.5% (from Fig. 3) (solid line) and this level is achieved when the index of log (possum density +1) is 0.48 (approximately 2.0) or lower (broken line).

Determining threshold densities of predators for kokako population stability

Table 1 shows that to avoid a negative rate of increase for the kokako population production should be 0.495 fledglings per adult, i.e. 0.99 fledglings per female. The equation from Fig. 3 predicts that this production is equivalent to a 45.5% nest success.

The equation in Fig. 2C predicts that a 45.5% nest success is reached when the index of rat density is 20.5 or less. Possum density at three levels of rat density is plotted against nest success in Fig. 5. The 45.5% nest success at low rat density is achieved when the index of possum density is approximately 2.0 or lower. Therefore, these are the levels below which nest predator density has to be kept for a positive rate of increase for kokako populations, based on Mapara parameters. Predator (especially ship rat) indices need to be even lower to *maximise* kokako population growth, however, so the figures presented here are not intended to replace those in Innes *et al.* (1999) as management targets.

Density dependence and compensation at high population levels of kokako

It can be seen from Fig. 1 that at high population numbers there are likely to be density-dependent feedbacks acting on the population from causes such as undernutrition and emigration. For long-lived species, such as kokako, these density-dependent effects should be stronger at high density compared to those at low density. The prediction is that r should eventually decline with population numbers. This prediction is based on both theory and empirical data (Fowler, 1987; Sinclair, 1996). Is there evidence that such a process is occurring in the kokako population?

Figure 6 shows the increase in the number of female-male pairs at Mapara when predators were being removed, reflecting the female population. The figure shows an increase from four territories to nearly 70 between 1991 and 2004 (an interlude when predators were let in during 1997–2000 is excluded). From these data we calculate the r in the absence of predators for this component of the population. Figure 7 shows that r per year for female-male pairs generally declines relative to population size, although with occasional years (e.g. 1995; Fig. 7) of high r one year after exceptional breeding seasons (1994–1995) caused by heavy fruiting. Thus, there is some evidence that supports predictions of density-dependent feedbacks at higher densities of the female kokako population.

An alternative explanation of these data is that declining r after 2001 is due to decreased recruitment of young after 3 years without pest management in 1997–2000. Kokako females recruit within 1–2 years of fledging (Basse *et al.*, 2003) and males within 2–4 years (I. Flux, Department of Conservation, Wellington, unpubl. data). Ongoing measurement of r in the absence
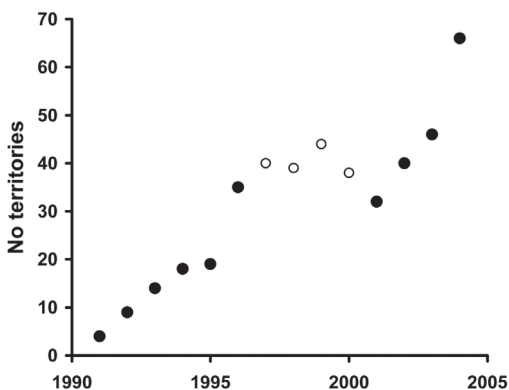

Figure 6. Kokako population at Mapara, as measured by number of male-female pair territories, increased during the periods when rat and possum nest predators were removed (closed circles) but declined when predators were let in (open circles).
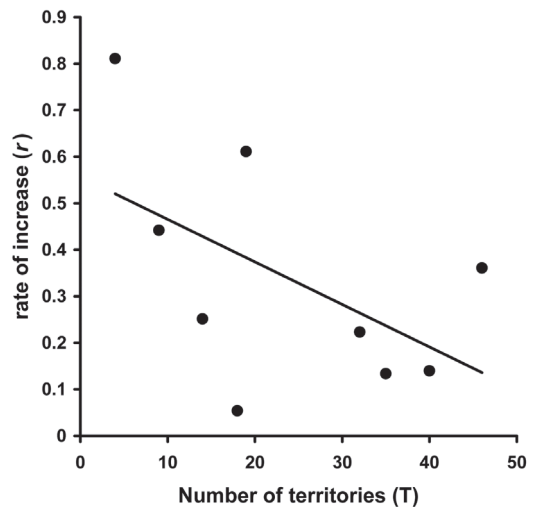

Figure 7. Instantaneous rate of increase of the Mapara population (r) is negatively related to population size (T), as indicated by number of male-female pairs in consecutive years of predator control (1992–1996; 2001–2104).

of any further pulsing of pest control would resolve whether *r* continues to generally decline as abundance increases.

However, a different picture emerges when all pairs, including male-male pairs are considered for the period 1991–1996 when these data are available. In this case there is an initial low rate of increase relative to the total number of territories. This is a reflection of the shortage of the number of females available to form reproductive pairs. This is one form of the Allee effect (Allee, 1931) in which rates of increase show a reverse trend, increasing *r* with population size before declining again. In essence, at very low population levels, widely

dispersed individuals have difficulty in finding mates and hence their reproduction should be lower than those living in higher numbers (Dennis, 1989; Courchamp *et al.*, 1999; Stephens and Sutherland, 1999).

In summary, it is perhaps too early to properly assess the exact nature of negative feedback impinging on the kokako population. We view these early data as an illustration of possible processes, which we describe in Fig. 1, that should be investigated with future research programmes in this and other threatened species.
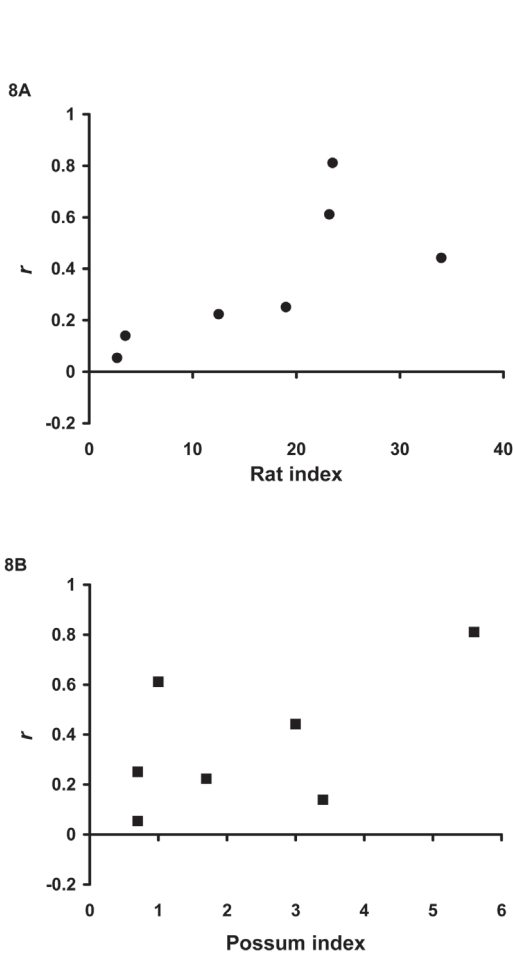

Figure 8. The instantaneous rate of increase (*r*) of the Mapara population does not decline as rat (8A) or possum (8B) indices increase, when these are at low values.
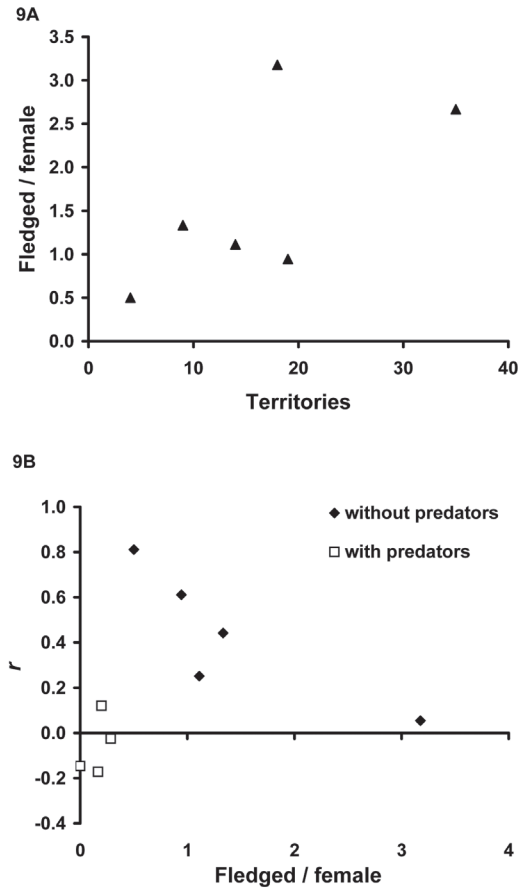
Figure 9. A. The production rate of the Mapara population is positively related to the population size (no. male-female territories, 1991–1996). B. The instantaneous rate of increase of the Mapara population declines as the production rate increases in the absence of nest predators, indicating that there is some other density-dependent mortality that overrides production. In the presence of nest predators both *r* and production are very low.

Mechanisms and causes of density dependence

The change in the rate of increase in female-male pairs is not obviously related to a lessening of rat and possum control, and so is not likely to be an artefact of the management programme (Fig. 8). The per capita production rate of kokako improved as the population increased (Fig. 9a). This meant that in the absence of predators the rate of increase actually declined as per capita production increased (Fig. 9b). Thus, the density-dependent decline in r was not due to changes in per capita production. Indeed, whatever the cause of density dependence it would have to be counteracting the inverse density-dependent effects of production.

Since the cause of density dependence in the absence of predators is not due to either changes in egg production or mortality in the nest (both are included in per capita production) the remaining possibilities are either adult or subadult loss, due to either non-predation mortality, the constraints on recruitment of territorial pairs, or emigration/dispersal.

At this point we have little evidence on causes of mortality at these two demographic stages, and mortality rates have not been measured in any high-density kokako population that can be compared with current data from low-density populations (Basse *et al.*, 2003). Both adult and subadult mortality could be reassessed at Mapara with its current high-density population with a substantial banding and resurvey effort over several years. Undernutrition is a possible candidate as a cause for the demographic responses. How this might work is not yet known. Kokako are highly territorial and so resource sequestering for space could be occurring through this behaviour, excluding non-territorial individuals from important food resources. The formation of territories and the process of pairing also need to be measured. Alternatively, possible concurrent increases in competing frugivores, such as kereru *Hemiphaga novaeseelandiae*, could be contributing to the per capita decline in food resources. These hypotheses need to be tested.

Mean net kokako natal dispersal distance is small (1.62 km based on 174 kokako at Kapiti Island, Mapara, Te Urewera and Rotoehu; max. 5.4 km; J. Innes et al. unpubl. data) but total movements before settlement are likely to be far larger. One radio-tagged juvenile at Mapara moved at least 20.2 km between September 1992 and March 1993 (I. Flux, P. Bradfield, unpubl. data), and a radio-tagged adult translocated to Trounson Forest in 1996 subsequently travelled *c.* 70 km to end up *c.* 15 km away in Marlborough Forest (A. Gardiner, Department of Conservation, Northland, pers. comm.). If they are capable of such movements in search of more suitable habitat, then density-dependent emigration in response to crowding is a possible mechanism for density dependence.

Predator control

Once prey populations have reached high density, they experience reductions through non-predation mortality or emigration, as we outline above. If some predators are allowed back into the system, the mortality they impose (on the nests in the case of kokako) will then be compensated for in the short term by a reduction in either subsequent non-predation mortality or emigration. In contrast, at very low densities of prey, virtually all predators must be removed.

Therefore, if a population of the threatened species is allowed to reach high density, the management effort involved in predator reduction to maintain the population can be reduced, such as by intermittent pulsed removals of predators in the case of kokako (Basse *et al.*, 2003). Effort and cost of control is unlikely to be linear with predator density, but rather closer to exponential—the per-predator cost of removing the last few predators will be considerably greater than that for the first few. The cost of management is likely to be an optimisation function of per capita cost of predator removal, the density of the endangered species, the risk of extinction, and the stochasticity of the environment (specifically the distribution of events such as mast years, bad weather, and predator outbreaks). Estimating these costs, as Davis *et al.* (2004) have done for the costs of predicting rodent outbreaks in Australia, is something that should be addressed in future.

Conclusions

At least some populations of threatened species should be maintained at high density as a safeguard against sudden, unpredictable perturbations. At high density there are compensatory demographic mechanisms that can buffer or counteract disturbances, whether these are abiotic weather events or pulses of exotic predators. Such compensation is not available at low density.

Research is needed to understand the mechanisms and causes of such density-dependent negative feedbacks on all threatened species in New Zealand. At present there is very little evidence because such populations have not been seen at their normal density for the past century or more.

The kokako at Mapara may provide an indication of negative feedback, perhaps through the mortality or emigration of post-fledgling subadults or adults. More research is required to understand these causes and to generalise across species.

In addition to the increased resilience of a threatened species when at high density, the degree of predator removal can be relaxed. Consequently, the cost of management will also decline.

Acknowledgements

References

Allee, W.C. 1931. *Animal aggregations.* University of Chicago Press, Chicago, U.S.A.

Atkinson, I.A.E. 2001. Introduced mammals and models for restoration. *Biological Conservation 99:* 81-96.

Basse, B.; Flux, I.; Innes, J. 2003. Recovery and maintenance of North Island kokako (*Callaeas cinerea wilsoni*) populations through pulsed pest control. *Biological Conservation 109:* 259-270.

Burbidge, A.A.; McKenzie, N.L. 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation 50:* 143-198.

Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology 63:* 215–244.

Chamberlain, D.E.; Fuller, R.J.; Bunce, R.G.H.; Duckworth, J.C.; Shrubb, M. 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology 37:* 771–788.

Clout, M.N.; Craig, J.L. 1994. The conservation of critically endangered flightless birds in New Zealand. *Ibis 137:* S181-S190

Clout, M.N.; Saunders, A.J. 1995. Conservation and ecological restoration in New Zealand. *Pacific Conservation Biology 2:* 91-98.

Courchamp, F.; Clutton-Brock, T.; Grenfell, B. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution 14:* 405-410.

Davis, S.A; Leirs, H.; Pech, R.; Zhang, Z.; Stenseth, N.C. 2004. On the economic benefit of predicting rodent outbreaks in agricultural systems. *Crop Protection 23:* 305-314.

Dennis, B. 1989. Allee effects: population growth, critical density and the chance of extinction. *Natural Resource Modeling 3:* 481-537.

Dowding, J.E.; Murphy, E.C. 2001. The impact of predation by introduced mammals on endemic shorebirds in New Zealand: a conservation perspective. *Biological Conservation 99:* 47-64.

Elliott, G.P.; Merton, D.V.; Jansen, P.W. 2001. Intensive management of a critically endangered species: the kakapo. *Biological Conservation 99:* 121-133.

Fowler, C.W. 1981. Density dependence as related to life history strategy. *Ecology 62:* 602-610.

Fowler, C.W. 1987. A review of density dependence in populations of large mammals. *In:* Genoways, H. (Editor), *Current mammalogy.* pp. 401-441. Plenum Press, New York, U.S.A.

Griffith, B.; Scott, J.M.; Carpenter, J.W.; Reed C. 1989. Translocation as a species conservation tool: status and strategy. *Science 245:* 477-480.

Hoosen, S.; Jamieson, I.G. 2003. The distribution and current status of New Zealand saddleback *Philesturnus carunculatus. Bird Conservation International 13:* 79-95.

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.

Johnson, K.A.; Burbidge, A.A.; McKenzie, N.L. 1989. Australian macropodoidea: status, causes of decline, and future research and management. *In:* Grigg, G.; Jarman, P.; Hume, I. (Editors), *Kangaroos wallabies and rat-kangaroos.* pp. 641-657. Surrey Beatty and Sons, Chipping Norton, N.S.W., Australia.

Kerr, J. T.; Deguise, I. 2004. Habitat loss and the limits to endangered species recovery. *Ecology Letters 7:* 1163-1169.

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.

Mduma, S.A.R.; Sinclair, A.R.E.; Hilborn, R. 1999. Food regulates the Serengeti wildebeest: a 40-year record. *Journal of Animal Ecology 68:* 1101-1122.

Moorhouse, R.; Greene, T.; Dilks, P.; Powlesland, R.; Moran, L.; Taylor, G.; Jones, A.; Knegtmans, J.; Wills, D.; Pryde, M.; Fraser, I.; August, A.; August, C. 2003. Control of introduced mammalian predators improves kaka *Nestor meridionalis* breeding success: reversing the decline of a threatened New Zealand parrot. *Biological*

Conservation 110: 33-44.

Pierce, R.J.; Westbrooke, I.M. 2003. Call count responses of North Island brown kiwi to different levels of predator control in Northland, New Zealand. *Biological Conservation 109:* 175-180.

Serena, M. (Editor). 1994. *Reintroduction biology of Australian and New Zealand fauna.* Surrey Beatty and Sons, Chipping Norton, N.S.W., Australia.

Short, J.; Bradshaw, S.D.; Giles, J.; Prince, R.I.T.; Wilson, G.R. 1992. Reintroduction of macropods (Marsupialia: Macropodoidea) in Australia - a review. *Biological Conservation 62:* 189-204.

Sibly, R.M.; Barker, D.; Denham, M.C.; Hone, J.; Pagel, M. 2005. On the regulation of populations of mammals, birds, fish and insects. *Science 309:* 607-610.

Sinclair, A.R.E. 1989. Population regulation in animals. *In:* Cherrett, J.M. (Editor), *Ecological concepts. Symposia of the British Ecological Society 29:* 197241.

Sinclair, A.R.E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. *In:* Floyd, R.B.; Sheppard, A.W. (Editors), *Frontiers and applications of population ecology.* pp. 127-154.

CSIRO, Melbourne, Australia.

Sinclair, A.R.E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. *Philosophical Transactions of the Royal Society, London 358:* 1729-1740.

Sinclair, A.R.E.; Pech, R.P. 1996. Density dependence, stochasticity, compensation and predator regulation. *Oikos 75:* 164-173.

Sinclair, A.R.E.; Pech, R.P.; Dickman, C.R.; Hik, D.; Mahon, P.; Newsome, A.E. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology 12:* 564-575.

Stephens, P.A.; Sutherland, W.J. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution 14:* 401-405.

Sutherland, W.J. 1998. Managing habitats and species. *In:* Sutherland, W.J. (Editor), *Conservation science and action.* pp. 202-219. Blackwell Science, Oxford, U.K.

Towns, D.R.; Broome, K.G. 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. *New Zealand Journal of Zoology 30:* 377-398.