

A simulation of the future of kakapo

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Abstract The recent productivity and survival of the critically endangered kakapo (*Strigops habroptilus*) is summarised and its population trajectory in a variety of circumstances is modelled by simulation. Simulated kakapo population growth rates decline with decreasing intensity of management, and unmanaged kakapo on Codfish Island increase only slowly and have a significant risk of declining. Kakapo on islands where more than one fruiting species triggers their breeding have much higher growth rates than kakapo on islands where only rimu (*Dacrydium cupressinum*) triggers their breeding. The models predict that kakapo will reach a predetermined population milestone of 53 females in 2 - 6 years depending on the number of fruiting species that trigger breeding. At this milestone the intensity of conservation management will be reduced. Conservation management will be further reduced at a second predetermined milestone of 150 females in 19 - 37 years.

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INTRODUCTION

The kakapo (*Strigops habroptilus*), a large parrot endemic to New Zealand, is one of the world's rarest birds, with a total population (in 2005) of only 86. It possesses a suite of unusual features that have made it especially vulnerable to the ecological changes that have occurred in New Zealand since colonisation by humans less than 1000 years ago. Kakapo are large (1.5 - 4 kg), flightless, nocturnal, herbivorous, lek breeders, that breed only once every two - five years. Females are solely responsible for incubation and chick rearing, and leave their nests unattended for long periods at night when they feed. Eggs and nestlings are thus vulnerable to chilling and to predators, particularly when food supplies are low and females are forced to leave their nests for prolonged periods. Adults are also vulnerable to introduced mammalian predators because their cryptic coloration and nocturnal habit, while effective defences against diurnal, sight-hunting raptors, are ineffective against nocturnal predators which hunt by smell.

Kiore (*Rattus exulans*) and dogs (*Canis familiaris*) were introduced to New Zealand by the initial Polynesian settlers, and Norway and ship rats (*Rattus norvegicus*, *R. rattus*), cats (*Felis catus*), and three mustelids (stoats, *Mustela erminea*; ferrets, *M. furo*; and weasels, *M. nivalis*), were introduced by European settlers in the 19th century (King 1990). Although habitat loss through forest clearance and habitat modification by introduced browsing mammals has affected kakapo, the main cause of their decline has been predation (Lloyd & Powlesland 1984).

By the 1950s kakapo were known only from one remote area, Fiordland, and when intensive conservation management of this population began in the 1970s it was found to comprise only males. Fortunately, another population was discovered in southern Stewart Island in 1977 (Butler 1989). This population was the subject of intensive research and management for a decade until high rates of predation by cats led to the transfer of all surviving kakapo to three relatively predator-free islands (Lloyd & Powlesland 1994). Conservation managers hoped that these transfers would secure the kakapo's future, but although adult survival on these islands was high (98-99% per annum; Clout & Merton 1998), it was not until intensive management of the birds began in 1995 (Elliott *et al.* 2001) that kakapo numbers began to rise. Intensive management has comprised movements of birds between islands to maximise breeding opportunities, close monitoring and management of nests, and the provision of supplementary food (see Elliott *et al.* 2001).

In 2002 kakapo had a particularly productive breeding season on Codfish Island resulting in a 39% increase in the total population in just one breeding season (Elliott *et al.* 2006). This breeding season changed several pre-conceptions about kakapo behaviour and productivity and has necessitated a review of the direction and intensity of future kakapo management.

Most kakapo breeding in recent years has coincided with mast fruiting of rimu (*Dacrydium cupressinum*) trees, the only source of abundant fruit on Codfish Island where most kakapo are held. However, in 1981, kakapo on Stewart Island bred while feeding on the fruits of pink pine (*Halocarpus biformis*) and yellow-silver pine (*Lepidothamnus intermedius*) as well as rimu, and in the late 19th and early 20th century kakapo were recorded breeding in areas where southern beeches (*Nothofagus* spp.) provided the only source of abundant fruit (Hill & Hill 1987). All these species are mast fruiters and the

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Table 1 Survivorship of adult female kakapo carrying radio transmitters on predator-free islands since 1981.

Year	Survival	Variance	n
1983	1	0	3
1984	1	0	3
1985	1	0	2
1986	1	0	2
1987	1	0	2
1988	1	0	3
1989	1	0	3
1990	1	0	5
1991	0.8	0.032	5
1992	1	0	11
1993	1	0	14
1994	1	0	16
1995	1	0	17
1996	1	0	18
1997	1	0	18
1998	1	0	19
1999	1	0	19
2000	1	0	20
2001	1	0	20
2002	1	0	21
2003	1	0	21
2004	1	0	21
Mean survival	0.991	0.00182	22
Pooled survival	0.996	0.000014	263

fruiting frequency of rimu and southern beeches has been well documented (Wardle 1984; Norton & Kelly 1988). Kakapo have recently been transferred to two islands which have significant populations of all four of the fruiting species and it seems likely that, on these islands, kakapo will breed when any of these trees seed.

In this paper I review the productivity and survival of kakapo since intensive management began in 1995, and use stochastic simulation models to predict what is likely to happen to kakapo under a range of both managed and unmanaged scenarios in forests with only one fruiting species and in forests with more than one fruiting species. In particular, I attempt to assess the likely time it will take to reach some already determined population milestones.

Management milestones

These milestones occur between the four recognised stages in the management of the recovery of kakapo. In the first stage the causes of decline are identified and the management techniques necessary for recovery are developed. In the second stage kakapo are managed so that their population increases at the maximum possible rate. In the third stage the kakapo are managed to produce the most cost-effective population increase, not necessarily the fastest increase. In the fourth stage kakapo are managed at the minimum level necessary to produce a stable or slowly increasing population.

Why kakapo have declined is well known and documented (e.g., Butler 1989; Lloyd & Powlesland 1994) and techniques to make the population increase rapidly (the second milestone) have been developed (Elliott *et al.* 2001). Kakapo are currently managed to achieve the maximum possible rate of population increase. In this paper I estimate the likely time required until the transition to less intensive management at the ends of stages two and three.

Conservation milestones for species are inevitably determined by relative, rather than absolute extinction risks. A species moves to the next management stage not when its extinction risk drops below a predetermined threshold, but rather when it becomes less at risk of extinction than other endangered species with which it is “competing” for conservation funds (Jansen 2006). To determine with rigour when this transition should happen one would need to model the extinction risk of all endangered species and rank them against each other. New Zealand has a large number of endangered species (>600; Hitchmough 2002) and the extinction risk of only a few of them has been rigorously modelled. Thus conservation milestones for kakapo and other endangered New Zealand species have been qualitatively rather than quantitatively developed.

Managers of the Department of Conservation’s kakapo recovery programme consider that kakapo will have reached their second milestone when the population is sufficiently

Table 2 Kakapo breeding activity since 1996. In 1999 all kakapo on Codfish Island were transferred to Pearl Island to facilitate the eradication of rats from Codfish Island (Elliott *et al.* 2001).

No. females	Year	Island	No. females nested	No. nests	Eggs	Eggs hatched	Fledged naturally	Fledged hand-raised	Total fledged
10	1996	Codfish	0	0	0	0	0	0	0
10	1997	Codfish	6	6	12	5	2	1	3
13	1998	Codfish	0	0	0	0	0	0	0
13	1999	Pearl	5	7	14	5	0	3	3
12	2000	Codfish	0	0	0	0	0	0	0
11	2001	Codfish	0	0	0	0	0	0	0
21	2002	Codfish	20	24	67	26	20	4	24
13	2003	Codfish	0	0	0	0	0	0	0
13	2004	Codfish	0	0	0	0	0	0	0
20	2005	Codfish	10	10	26	6	0	4	4
8	2003	Chalky	0	0	0	0	0	0	0
8	2004	Chalky	0	0	0	0	0	0	0
1	2005	Chalky	0	0	0	0	0	0	0
2	1996	Maud	0	0	0	0	0	0	0
2	1997	Maud	0	0	0	0	0	0	0
3	1998	Maud	1	1	3	3	2	1	3
7	1999	Maud	0	0	0	0	0	0	0
8	2000	Maud	0	0	0	0	0	0	0
9	2001	Maud	0	0	0	0	0	0	0
6	1996	Hauturu	0	0	0	0	0	0	0
6	1997	Hauturu	0	0	0	0	0	0	0
4	1998	Hauturu	0	0	0	0	0	0	0
1	1999	Hauturu	1	1	3	3	0	3	3

large that, should all management cease, there is a 80% probability that at least 50 female kakapo would remain after 20 years. Kakapo will reach their third milestone, and management will further reduce, when there are 150 female kakapo - enough to confidently establish three self-sustaining populations.

Since kakapo are lek breeders (Merton *et al.* 1984) females are more likely to limit population growth than males and the population models are based only on females.

DEMOGRAPHIC PARAMETERS

Adult survival

Some female kakapo have been carrying transmitters on and off since 1981, and these birds provide the best estimates of survivorship (Table 1). Since kakapo are now confined to predator-free islands I have excluded survivorship data from before kakapo were transferred to them. To estimate annual survivorship I initially divided the number of female birds that have died while carrying a transmitter each year by the number of birds carrying transmitters that year and then averaged all of the estimates of annual survival. I used the method of White (2000) to attempt to apportion the

variance in the estimated grand mean survival amongst environmental (inter-annual) and parameter uncertainty variation, but the estimate of variance attributable to parameter uncertainty was greater than the variance about the grand mean, suggesting that environmental variation was insignificant. For this reason I pooled all the survival data and ignored inter-annual differences.

This estimate of survivorship is based on a group of unknown-age, but probably elderly, birds from a declining population. I would expect the survivorship of a sample of birds from a stable or increasing population to be even higher. On the other hand, the weights of kakapo are closely monitored and whenever a bird's weight drops significantly below average it is provided with supplementary food; kakapo are unlikely to die from starvation. This is likely to make my estimate of survivorship higher than would be expected from an unmanaged population.

Juvenile survival

Of the 40 young kakapo fledged since 1996, three have died, and six were rescued from almost certain death during their first two years.

Table 3 Kakapo productivity since 1997.

Year	Island	Females	Bred	Chicks produced per female				Chicks/ breeding female
				0	1	2	3	
1997	Codfish	10	6	4	1	1	0	0.5
1998	Maud	3	1	0	0	0	1	3
1999	Pearl	13	5	3	1	1	0	0.6
1999	Hauturu	1	1	0	0	0	1	3
2002	Codfish	21	20	7	5	5	3	1.2
2005	Codfish	20	10	7	2	1	0	0.4

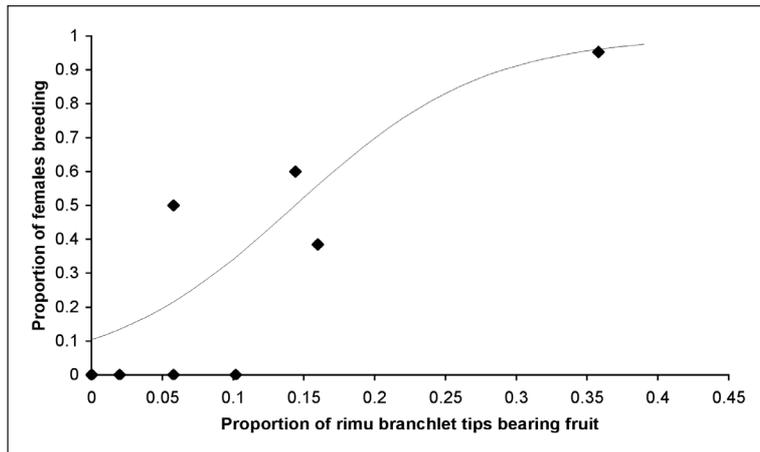


Figure 1 The relationship between the abundance of fruit on Codfish Island and the proportion of female kakapo that nested. The solid line is a fitted logistic curve.

Three birds died a few days after they were transferred to a new island, probably from a combination of recent exposure to the bacterium *Erysipelothrix rhusiopathiae* and the stress of transfer. Future deaths from this bacterium are unlikely in both managed and unmanaged populations because birds in managed populations will be vaccinated, and birds in unmanaged populations will not be subject to the stress of transfer.

The six birds rescued from almost certain death included one that was abandoned by its mother, two that became entangled in vegetation, two that received dangerous wounds, and one that suffered a serious cloacal infection. Our estimate of the survival rate of managed juvenile kakapo is therefore 1, but since this seems ridiculously optimistic I regard the survivorship of managed juvenile kakapo to be the same as that of adults. Our estimated survival rate of juvenile kakapo in their first two years without management is $30/36 = 0.91$ ($se = 0.06$).

Frequency of breeding

Table 2 summarises the nesting activity of kakapo since 1996. On Hauturu (Little Barrier Island) and Maud Island kakapo nesting has been associated with the provision of supplementary food (Elliott *et al.* 2001), but on Pearl and Codfish Islands it has been associated with the mast seeding and fruiting of rimu.

To measure seed production, fruit from the same four branches in 10 female rimu trees scattered over Codfish

Island have been sampled each year since 1997. Each November/December at least 250 branchlet tips on a healthy part of each branch were examined to determine whether or not they were bearing fruit, and fruit abundance determined as the ratio of fruit to tips. Figure 1 shows the relationship between fruit abundance and breeding intensity. Pearl Island is only 30 km from Codfish Island and has similar forest and climate, and I have assumed that the rimu abundance on Codfish Island is a good indicator of the fruit abundance on Pearl Island.

The relationship between rimu seed and kakapo breeding may be even closer than it appears. Not all of the seeds counted in the rimu trees were sound seeds containing endosperm that are likely to be worthwhile food for kakapo; some were unsound empty seeds. The proportion of sound rimu seed is correlated with the amount of seed produced (Norton & Kelly 1988), so that in years of heavy seedfall not only is there more seed, but a higher proportion is sound. Thus, when the number of seeds was low, it was likely that there was virtually no sound seed and no food for kakapo, hence the lack of breeding. When seeds were more abundant it is likely that there was some sound seed, breeding occurred, and the proportion of birds that bred was related to the amount of seed.

Norton & Kelly (1988) defined mast rimu seed events as years when more than 50% of the seed that fell was sound, and in Westland in a sample over 18 years they found that 50% were mast years.

Table 4 The age distribution of female kakapo alive in July 2005.

Age class	Number of birds
Chicks (0-1 year old)	3
1-2 years old	0
2-3 years old	0
3-4 years old	12
4-5 years old	0
5-6 years old	0
6-7 years old	4
7-8 years old	1
13-14 years old	1
24-25 years old	2
unknown	18

During the nine years that kakapo breeding and rimu seedfall have been closely monitored on Codfish Island, kakapo have bred in four years, but in only the year with the highest seedfall does enough sound rimu fruit appear to have ripened to enable kakapo to successfully raise chicks without a helping hand from conservation managers.

Clutch size and productivity

Table 3 summarises the clutch size and productivity recorded per female since 1997.

Nest management techniques changed substantially between 1997 and 2005. In 1999 it was discovered that kakapo would re-nest if their eggs were removed early in the breeding season, and in 2002 an attempt was made to get seven females to re-nest. Four of them laid second clutches producing an extra ten eggs and three fledged chicks. In 1997 conservation managers were cautious about interfering at nests, but by 2002 they had learned that kakapo have no adverse reactions to people at their nests and intervention happened much more quickly. In 1997 two of the females that laid were not taking supplementary food and three eggs/chicks died as a result. By 2002 all females had been trained to take supplementary food.

Age at first breeding

The age at first breeding is known for only three female kakapo; Heather at nine years old, Zephyr at 11, and Hoki at 10. Heather and Zephyr may have been physiologically capable of breeding earlier, but neither was in a situation where breeding was likely. Hoki was on Pearl Island in 1999 when five other female kakapo bred, but was then only seven years old and did not breed, and there was no breeding in the two subsequent years.

THE MODEL

I developed a stochastic model based on a Leslie Matrix incorporating 30 age classes, from chicks to adults up to 29 years old, and then a final class incorporating adults over 29 years and adults of unknown age. I simulated populations for 100 years, and repeated each simulation 1000 times incorporating both parameter uncertainty and

environmental variation (White 2000) where appropriate. I programmed the model in R 2.1.0 (R Development Core Team 2005). The starting point for simulations was the age structure of the existing kakapo population (Table 4).

Survivorship

I simulated parameter uncertainty by selecting a survivorship from a beta distribution with a mean and variance equal to the mean and variance of the survivorship estimate at the beginning of each simulation. I found no significant environmental variation (see above) so survivorship remained constant for all the years in a simulation. I have assumed that kakapo survivorship does not change with age after the first two years of life, for which I have a separate estimate (see above).

I simulated demographic variation in survivorship by determining whether each bird lived or died each year by choosing a random number between 0 and 1: if the random number was less than the survivorship the bird lived, if it was greater the bird died.

Breeding age and frequency

I assumed that birds could not breed before they were nine years old. After nine years whether or not they bred in any year was a function of the breeding frequency algorithm and simulated demographic variation.

I simulated variation in breeding frequency and intensity of kakapo in forests with only one fruiting species by assuming the breeding intensity was related to the level of seedfall of rimu.

At the beginning of each simulation I selected the proportion of rimu tips with fruit from a beta distribution with a mean equal to the mean of the rimu data and a variance equal to the parameter uncertainty portion of the variance of the rimu data which I apportioned using White's (2000) method. I estimated the standard deviation between years of rimu seedfall from the environmental variation portion of the variance of the rimu data (White 2000) and represented this uncertainty using a normal distribution centred on the between-year standard deviation and with a standard error equal to the between-year standard deviation divided by the square root of the sample size.

I modelled the relationship between the proportion of kakapo breeding each year and rimu seedfall by fitting a logistic regression mixed effects model with random annual variation in proportion of females breeding (Venables & Ripley 2002). The formula for the regression was: $\text{logit}(\text{proportion breeding}) = 16.596 * \text{Rimu} - 2.530 + \text{error}$ where error was normally distributed with mean = 0.0 and SD = 1.317. I simulated the proportion of kakapo breeding each year by inserting simulated rimu seedfall values into the above equation which includes some random normal error. As an additional refinement I assumed that some rimu seedfalls comprised mostly empty seeds that led to no kakapo breeding. At the beginning of each simulation I chose a value for this

Table 5 Estimated likely productivities of unmanaged nesting kakapo .

No. of chicks fledged	Frequency
0	11
1	6
2	3

proportion from a beta distribution with a mean and variance derived from Norton & Kelly’s (1989) estimate of the frequency of mast rimu fruiting, and if the rimu seeding in any year in my simulations was below this proportion I assumed there was no kakapo breeding. As a further refinement I assumed that unmanaged kakapo could only successfully raise chicks when the rimu seedfall was at least as heavy as was recorded in 2002, and I simulated this in the same way using data on the frequency of very heavy seedfalls.

Demographic variation was added in the same way as it was for survivorship.

There is no information on the relationship between kakapo breeding frequency and the seedfalls of pink pine, yellow-silver pine and southern beech, except that kakapo were reported to breed nearly every second year in beech forest-dominated parts of Fiordland in the late 1800s and early 1900s (Hill & Hill 1987), and kakapo ate pink and yellow-silver pine fruit during their breeding season on Stewart Island in 1981. Rather than explicitly model how kakapo might breed in the presence of these species I have simply contrasted how kakapo populations might perform in the presence of only rimu or rimu and one other fruiting species. I have assumed that kakapo breed at approximately the same frequency and intensity when their breeding is triggered by a second species, as when it is triggered by rimu, but to quantitatively acknowledge the lack of information on the relationship between kakapo breeding and other seeding species I doubled the standard error of both the parameter variation and environmental variation associated with the second fruiting species.

For situations with rimu and another fruiting species the model simulates the two species seeding independently of each other and the proportion of females breeding was simulated using the logistic equation above but inserting the sum of the seedfalls of the two species.

In my model females that bred successfully in one year were not available to breed in the following year, as kakapo take a long time to raise chicks and have never been recorded attempting to breed when they raised chicks in the previous year.

Productivity

Each breeding female whose nest was deemed to be intensively managed in the model was assigned a productivity by bootstrap sampling from the productivities recorded in 2002 and 2005 (Table 3). Females whose nests were deemed to have been unmanaged were assigned a

productivity by bootstrap sampling from Table 5. These data were derived from the 2002 data but with the following changes that reflect our guess at what productivity is likely to be at unmanaged nests: No females laid a second clutch, and one chick died in nests that initially contained more than one chick.

For both managed and unmanaged nests the sex ratio of kakapo chicks was assumed to be 50:50. There is evidence that sex ratio is influenced by the provision of supplementary food, with the sex ratio of chicks produced by birds not receiving supplementary food being female-biased, and that of supplementary-fed birds being male-biased (Clout *et al.* 2002). Recent changes in the provision of supplementary food have resulted in a sex ratio of approximately 50:50 (Robertson *et al.* in press) so for managed birds the assumption of a 50:50 sex ratio is at least approximately correct. An estimate of the sex ratio of chicks produced by unmanaged birds can only be based on eight clutches and is female-biased, so the 50:50 ratio used in the models is precautionary. Demographic variation in sex ratio was simulated in the same way that it was for survivorship.

Identifying population milestones

I simulated unmanaged populations with increasing starting population sizes until 80% of the simulations had 50 or more female kakapo after 20 years.

Scenarios

I modelled eight scenarios:

1. *Rimu fruit with full management.* Kakapo bred in response to rimu fruiting and got the same intensive management as they received in 2002. The productivities of nests were bootstrap sampled from Table 3. Juvenile survivorship was assumed to be the same as adult survivorship because young birds are rescued from any life-threatening circumstances.
2. *Rimu fruit with 20 managed nests.* The same as scenario 1, but no more than 20 nests were managed intensively. The productivities of managed nests were bootstrap sampled from Table 3, and productivities of unmanaged nests from Table 5. Twenty nests was about the maximum number of nests that could be managed with existing funding.
3. *Rimu fruit with some management.* Kakapo bred in response to rimu fruit with no intensive management of nests, but female kakapo were supplied with supplementary food so that they could successfully raise chicks even when rimu crops failed. Kakapo bred as often as for the intensively managed scenario and female productivity was bootstrap sampled from Table 5. Juvenile survivorship was assumed to be lower than adult survivorship, in particular about one of every six chicks was assumed to die in its first two years.

Table 6 Median number of years to reach kakapo population milestones 2 and 3 under 8 different scenarios (95% confidence intervals in brackets), and the percentage of simulations declining over 100 years..

Scenario	Years to milestone 2	Years between milestones 2 & 3	% of simulations declining
5 Two species, full management	2 (1-8)	11 (8-16)	0.0
6 Two species, 20 managed nests	2 (1-9)	13 (9-19)	0.0
7 Two species, some management	4 (1-12)	17 (12-29)	0.0
1 Rimu, full management	6 (2-20)	22 (16-39)	0.0
2 Rimu, 20 managed nests	6 (2-21)	27 (18-56)	0.0
8 Two species, no management	9 (2-100+)	37 (19-100+)	3.4
3 Rimu, some management	10 (2-38)	31 (27-62+)	0.2
4 Rimu, no management	32 (2-100+)	78+ (27-100+)	20.5

4. *Rimu fruit with no management.* No management occurred, and kakapo successfully raised chicks only when rimu fruited heavily and ripened. Their productivities were bootstrap sampled from Table 5. Juvenile survivorship was the same as in 3 above.
5. *Two fruiting species with full management.* Kakapo bred in response to seeding by rimu and another species and received the same intensive management as they received in 2002. Productivities and survivorships were as in 1 above.
6. *Two fruiting species with 20 managed nests.* The same as scenario 5, but only 20 nests are managed intensively. The productivities of managed nests were bootstrap sampled from Table 3, and productivities of unmanaged nests were sampled from Table 5. Juvenile survivorship as in 1 and 5 above.
7. *Two fruiting species with some management.* Kakapo bred in response to rimu and another species with no intensive management of nests, but female kakapo were supplied with supplementary food so that they could successfully raise chicks even when the seed crop failed. Kakapo bred as often as in the intensively managed scenario and female productivity was bootstrap sampled from Table 5 as in scenario 2. Juvenile survivorship as in 3 and 4 above.
8. *Two fruiting species with no management.* No management occurs, kakapo successfully raised chicks only when rimu and or another species seeded and ripened, and their productivities were drawn from Table 5. Juvenile survivorship as in 3, 4 and 7 above.

For each scenario I present the median number of years taken to reach the second population milestone ($\pm 95\%$ confidence intervals), the median number of years between the second and third population milestones ($\pm 95\%$ confidence intervals) and the risk of population decline over 100 years.

Parameter uncertainty

To assess how much of the variation in the results of the simulations was attributable to process variation (i.e., inter-annual variation and demographic stochasticity) and how much was attributable to parameter uncertainty associated with the small sample sizes from which many of the parameters were estimated, I repeated the simulations of scenario 1 for 40 years with and without parameter uncertainty included in the model.

RESULTS

Population milestone

Eighty percent of simulated unmanaged populations had not declined below 50 females when their starting population comprised at least 53 female kakapo. I therefore define the second population milestone as 53 female kakapo.

Scenarios

The results of simulations of the eight scenarios are shown in table 6.

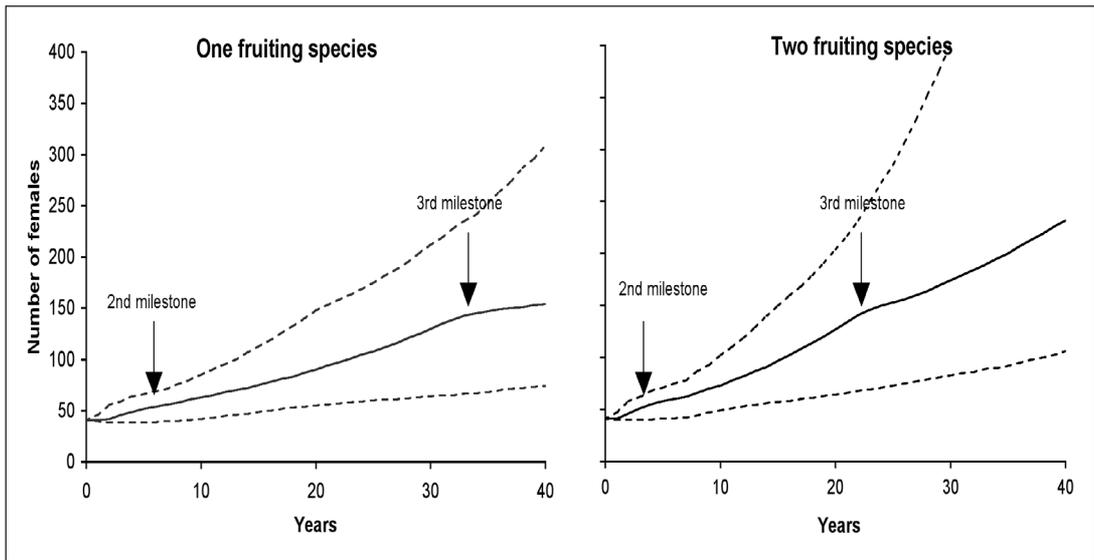
As expected, increasing intensity of management increased modelled kakapo population growth rates, but modelled scenarios with two fruiting species and minimal management produced more optimistic population trajectories than did any of the scenarios with only one fruiting species. All scenarios predicted population increase, and only one, "rimu with no management", had a significant risk of decline.

Parameter uncertainty

The variance of simulated populations of scenario 1 for 40 years was 18949, whereas the variance of the populations simulated with no parameter uncertainty was 7777, suggesting that parameter uncertainty accounted for about 59% of the variation in simulated population size, and process variation accounted for 41%.

DISCUSSION

Of necessity these models make many assumptions about kakapo demography, fruiting tree phenology, and the relationships between them. In particular the independence or otherwise of the fruiting of the four tree species is unknown, and the relationship between kakapo breeding and the fruiting of three of the four tree species



► **Figure 2** Modelled population trajectories of kakapo that breed in response to the fruiting of one and two fruiting species. Dashed lines are the upper and lower 95% confidence intervals of the modelled populations. The arrows indicate changes in management practices associated with population milestones.

is unknown. For these reasons these models cannot be expected to produce reliable predictions of future population trajectory. However, the models can appropriately be used to explore the implications of moving kakapo to islands with more fruiting species, and to other changes in their management.

Even with the assumptions, there is considerable uncertainty about the predictions of these models, but counter-intuitively there was less uncertainty in the simulations of two fruiting species than there was in those with rimu alone. This is because the addition of a second masting species, regardless of the uncertainty in its effect, reduces the frequency of years where no kakapo breeding occurs and thus reduces the variability of the proportion of kakapo breeding.

Because of the small samples sizes on which most of the parameter estimates were made, more than half of the uncertainty in the predictions of the models results from parameter uncertainty. The reliability of the predictions of these models will increase as sample sizes increase with time, but even with very large sample sizes the inherent variability in kakapo productivity means that modelled kakapo population trajectories will always have large confidence intervals.

The only scenario with a significant risk of decline is the unmanaged population with only rimu, but this scenario is of considerable significance because the main stronghold of kakapo (Codfish Island) has only rimu.

The models predict that the population growth rate of kakapo on islands with more than one fruiting species will be substantially higher than on islands with rimu alone and that transferring kakapo to islands with multiple

fruiting species will lead to greater productivity gains than will intensive management. However, lack of knowledge about the response of kakapo to seeding of southern beeches, pink pine, and yellow-silver pine means there can be no great confidence in this prediction. Fortunately, testing this prediction involves little risk. The islands suitable for kakapo that have more than one fruiting species have significant amounts of rimu, thus the productivity of kakapo on these islands is very unlikely to be less than on Codfish Island where there is only rimu. It is a sensible conservation strategy to transfer as many birds as possible to islands with more than one fruiting species.

In 2002, the nests of 20 female kakapo on Codfish Island were intensively managed and this was about the maximum number of nests that could be managed within the funding then provided for kakapo conservation. Fortunately, it seems that increasing the number of managed nests will have very little impact on the rate at which the kakapo population milestones are achieved. This is simply because when population levels are less than the milestones there are normally fewer than 20 female kakapo attempting to breed in any one year.

Intensively managing about 20 nests per island costs about 50% more than the “some management” option, yet it increases the rate of population growth by only 24 - 40%. Intensive management is not, therefore, the most cost effective way of increasing kakapo numbers, but it is the most prudent strategy when the species is critically endangered. Once kakapo numbers have risen to a level where their extinction risk is acceptable, more cost-effective management techniques are possible.

If the kakapo population follows the population trajectory predicted by these models, and if kakapo management changes at the milestones of 53 and 150 female birds, then likely trajectories of kakapo are as in Figure 2. If rimu is the only fruiting tree that triggers kakapo breeding, then kakapo will be managed intensively for six years and then less intensively for a further 31 years, after which there will be almost no management. The change in population trajectory at the second milestone will be almost undetectable, but

there will a considerable drop in kakapo population growth when all management ceases with the population growing only slowly thereafter. If more than one species triggers kakapo breeding then kakapo will be managed intensively for only two years, and less intensively for a further 17 years after which there will be no management. There will be conspicuous reductions in kakapo population growth rate at each of the milestones, but even with no management the population should continue to increase quite rapidly.

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