CHAPTER 10

POPULATION VIABILITY ANALYSIS

INTRODUCTION

In managing any endangered species or population there is a need to assess how much risk it is in, and what is necessary to reduce the risk to an acceptable level. The latter often involves estimating the smallest population that would have an acceptable probability of survival over a given period of time. A second consideration is the loss of genetic variation that occurs over time in small isolated populations. This can affect both the fitness and reproductive ability of individuals and the population’s ability to adapt to environmental changes.

Such assessments are often complex and difficult, but they become much more so in very small populations. Small populations are very subject to stochastic effects, such as randomly fluctuating environmental conditions or rare “catastrophic” events. For these reasons a small population may be at high risk of extinction even when it has a positive growth rate. A second problem is the interaction of demographic and genetic effects, in which reduced population size leads to increased inbreeding, which causes lowered survival and reproduction, which in turn further reduces population size. Both of these problems make deterministic models ineffective for assessing risk in small populations.

Population Viability Analysis (PVA) is a set of techniques for designed to solve these problems using computer simulations. On the basis of a set of demographic, life history, and environmental parameters specified by the user, the computer program creates a simulated population and steps it through annual cycles of reproduction and death until either extinction occurs or a specified time limit is reached. The program repeats this process for many simulated populations, and combines the results to produce estimates of the likelihood of specific outcomes. More recent simulation programs include genetic factors, random environmental fluctuations, and catastrophic events, all of which are allowed to interact with one another. They can be used to predict effects of alternative scenarios on the population's genetic variability as well as its size. PVA is useful not only for predicting a population's fate or minimum viable size, but also for deciding how to use resources most efficiently in conservation efforts. By constructing "what-if" scenarios one can predict the impact of various potential management actions, and thus their cost effectiveness. This sort of "sensitivity analysis" can also show what kinds of missing information are most needed to accurately assess a population's status. For a review of PVA in wildlife management see Lindenmayer et al. (1993).

The VORTEX version 5.1 computer program (Lacy & Kreeger 1992) used in this study is currently the most widely used program for PVA, and has been used in the management of many species in Australia and other countries, including the Puerto Rican Parrot (Lacy et al. 1989) and the Orange-bellied Parrot (Clark et al. 1991). The program, which runs on IBM compatible microcomputers, is described in detail by Lacy (1993). Unless otherwise noted each simulation included 500 iterations.

STUDY 1: RISK OF EXTINCTION

In the first set of simulations, I attempted to model the population dynamics of the Kangaroo Island population of Glossy Black-Cockatoos using the available demographic and ecological information. Of particular interest were the population's intrinsic rate of growth and risk of extinction.

Methods

Because the demography of the Glossy Black-Cockatoo has not been studied in detail, estimates were unavailable for some parameters, and information from related species was used when necessary. For other parameters only educated guesses were possible. The numbers used in Study 1 and the sources they are based on are listed in Table 10.1. For the parameter "Percent of females fledging no young" an accurate estimate of 90% is available for the Stokes Bay area over several breeding seasons, but this may not be representative of the Island as a whole. Although it is probably less precise, I chose to use the estimate of 80% based on the number of females and juveniles recorded in three surveys by L. Joseph (1982, 1987, 1988) because it represents a much larger proportion of the total population. The "heterosis" model of inbreeding was used because it requires much less computation time than the "lethals" model and produced comparable results.

The most important demographic parameters for which reasonable estimates were not available are mortality rates. For the initial model mortality rates and standard deviations were calculated from Saunders' (1982) data on Carnaby's Cockatoo

(*Calyptorhynchus funereus latirostris*) in Western Australia, as this is the most closely related species for which mortality data are available.

Table 10.1: Parameters used for Study 1 (listed in the order requested by VORTEX program), and the sources of estimates. Values in parentheses are standard deviations of environmental variation.

Parameter	Value	Source of information
Populations	1	
Inbreeding	Yes	
Heterosis or Lethals	L	
Reproduction correlated with survival	Yes	
Number of catastrophes	0	
Breeding system	Monogamous	Forshaw 1989, pers. obs.
Females begin breeding	2	Connors & Connors 1988
Males begin breeding	6	Courtney 1986
Maximum age	50	Hill 1954
Sex ratio at birth	0.5	
Maximum clutch size:	1	Forshaw 1989, pers. obs.
Reproduction density dependent	No	Default
Percent females fledging no young	80%	Joseph 1982, 1987, 1988
SD in percent producing clutch	12.65%	Default
Mortality rates and (SD) by age & sex:	Saunders 1982 (Carnaby's Cockatoo)	
Juvenile	78.6% (10.8%)	Default
F subadult/adult	39.2% (9.9%)	Default
M subadult/adult	32.7% (15.5%)	Default
All adult males in breeding pool	No	Joseph 1982; Chapter 2
Percent males in breeding pool	70	Joseph 1982; Chapter 2
Start at stable age distribution	Yes	
Initial population size	150	Chapter 2
Carrying capacity (K)	200	
SD in K due to environmental variation	20	
Trend projected in K	None	
Will you harvest?	No	
Will you supplement?	No	

Results

Under the assumptions of Model 1 the population shrinks at an average rate of 51% per year, resulting in an average time to extinction of only 5.8 years and a 100% chance of extinction within 13 years (Fig. 10.1).

Discussion

These results suggest that the assumptions of this model were not accurate, because the population does not in fact appear to be declining rapidly (Chapter 9). The parameters likely to be most unrealistic are the mortality rates based on the Carnaby's Cockatoo. Saunders (1982) suggested that the rates he calculated were implausibly high for the population he studied, and that they may have been affected by the wing tags that were used. The very limited data available from Kangaroo Island Glossy Black-Cockatoos (Pepper, unpub. data) also suggest lower mortality rates there. This raises the question of how low mortality rates would have to be to produce a stable population if the other parameters are approximately correct. To address this question I conducted a series of simulations with the other values held constant and mortality rates systematically varied. The mortality rates shown in Table 10.2 resulted in a barely positive mean annual growth rate of 0.01 (before truncation to reflect carrying capacity), and a male biased sex ratio of 1.5:1, which is close to the observed ratio. These mortality rates are far lower than have been measured for other Australian cockatoos (e.g., Carnaby's Cockatoo: Saunders 1982, Galah: Rowley 1990, Major Mitchell Cockatoo: Rowley & Chapman 1991).

The only reliable conclusion from this exercise is that we do not currently have enough information to model the population accurately, and therefore cannot reliably predict its future.

Table 10.2. Mortality rates yielding a marginally positive annual growth rate of 1% and an age and sex distribution similar to those observed, using the assumptions of Table 10.1.

	Mean annual mortality	Standard deviation
Juveniles (first year)	10%	2.5%
Females (after year 1)	6%	1.5%
Males (after year 1)	3%	0.75%

STUDY 2: LOSS OF GENETIC VARIABILITY

The maintenance of genetic diversity is an important goal in conservation efforts, and several workers have proposed the goal of preserving 90% of genetic diversity (measured as heterozygosity) in managing small populations (e.g., Foose et al 1986, Soule et al. 1986). The current population of *Calyptorhynchus lathami halmaturinus* is probably too small to retain the genetic diversity present in the population over the long term. However, it is not clear how rapid the loss of diversity is under current conditions, and thus how urgent a need there is to increase its size for genetic reasons. To investigate this question I conducted a second set of simulations.

Methods

On the basis of the first simulation, the mortality rates were set to create a growth rate just sufficient to maintain the population (Table 10.2). The carrying capacity was set at 150 to keep the population size near that which exists presently. All other values were kept as shown in Table 10.1, and simulations were run over a period of 100 years.

Results

At the end of 100 years the average population size was 111. Over this period the expected heterozygosity declined by an average of 4.6% from the starting level, and the average inbreeding coefficient reached 0.019 (Fig. 10.2).

Discussion

These results should be interpreted with caution, because the model fails to account for several factors that would tend to increase the rate of loss of genetic variation. The long term pair bonds typical of the genus, and the unequal reproductive success of specific females (unpub. data) both reduce the effective population size (Crow & Kimura 1970). Reducing the effective population size would tend to accelerate the loss of genetic diversity, but the VORTEX program does not have provisions for modeling perennial versus serial monogamy, or highly skewed reproductive success among individuals.

These caveats notwithstanding, the simulation indicates that although loss of genetic variation is expected while the population remains at its current size, it will be fairly slow due to the species' long generation times (averaging 14 years for females and 21 years for males) and long life span. The average inbreeding level reached in this simulation is also well below that at which deleterious effects on survival and reproduction usually appear. For this reason the risk of genetic loss appears to be a less critical concern in the short term than the threat of extinction.

In terms of setting targets for a long term population size, Lande & Barrowclough (1987) point out that simplistic models such as those employed here do not account for all types of genetic variation or all demographic variables, and argue that “every effort should be made to preserve evolutionarily important amounts of genetic variation by maintaining effective population sizes of at least several hundreds of individuals”. We do not yet have enough information to accurately calculate effective population size for *C. l. halmaturinus*, but estimates suggest that it is often as low as 10 to 30% of the total population (Lacy & Kreeger 1992).

STUDY 3: SENSITIVITY ANALYSES

One of the most practical uses of PVA is to ask “what-if” questions to investigate the effects of parameters that can feasibly be changed. For this purpose I conducted a set of simulations to model the effects of changing the nesting rate through a nest box program and changing the Island’s carrying capacity through tree planting.

Methods and Results

Mortality rates were set as shown in Table 10.2 and all other parameters were set as shown in Table 10.1. One parameter at a time was then varied to simulate the effect of a management action. To simulate the effect of a nest box program, the percent of females fledging young was systematically varied. To simulate the amount of foraging habitat available, carrying capacity was varied. For each different setting of the parameters, 100 iterations were performed.

Breeding rate

The effect of the percentage of females breeding in a given year was fairly linear over the range examined. Within the range of 10% to 25%, for each percentage point that the breeding rate increased, the annual population growth rate increased by about 2.5% (Fig. 10.3). The specific breeding rate producing a stable population (growth rate of zero) in this study is not meaningful, because the mortality rates used in the model had been selected to create a zero growth rate at close to the observed breeding rate of 20%. However, the results indicate how strongly the population growth rate would respond to a given change in breeding rate. The results also suggest that if food limitations do not prevent their use, providing artificial nest boxes could substantially increase in the population growth rate.

Another significant result is the slow drop in population size even with extreme changes in the breeding rate, as a result of the species' long life span and low reproductive potential. To investigate the effect of a sudden drop in breeding rate, I conducted a simulation beginning with the population's age distributed as it would be given a breeding rate of 20%, but with the current breeding rate set at zero. Under this scenario, a completely non-breeding population shrank by less than 5% per year for the first 20 years. This illustrates the danger that environmental changes could render a population no longer viable, yet have its effects go unnoticed for many years as the population ages without shrinking rapidly. This is of considerable concern, because this situation may have already been in effect on Kangaroo Island for some years (Chapter 9).

The fastest possible population growth is also quite constrained. To test the most extreme case I set the breeding rate for females to 100% and the carrying capacity to 10000 so that it would not be a limitation. Under these assumptions the annual population growth rate over 25 years averaged only 10.8%. This suggests that even heroic conservation efforts cannot be expected to produce very rapid population growth.

Carrying capacity

There is some uncertainty as to whether the carrying capacity of Kangaroo Island is sufficient to support the current population. A considerable amount of land has been cleared in the recent past, especially just before restrictions on land clearance were enacted in 1983 (T. Dennis, J. Anderson, pers. comm.). Furthermore, glossy black-cockatoos moved between the Island and the mainland up until the 1970's (Joseph 1989). This raises the possibility that refugees from the mainland increased the Island's numbers above what it could support as a breeding population.

In the simulation results actual population sizes were kept lower than the environmentally imposed limit by random fluctuations in environmental conditions and reproductive rates. Below a threshold carrying capacity of about 50 the population was virtually certain to become extinct within 100 years (Fig. 10.4). Above a carrying capacity of 100 there was no significant risk of extinction within 100 years and further increases only affected population size. However, if environmental fluctuations were greater than assumed, or if catastrophes such as major bush fires are likely, then carrying capacity would need to be much larger to minimize extinction risk.

Discussion

This sensitivity analysis examined only two parameters accessible to human interventions. Many others could have been included, but the most important is probably the effects of bush fires. A single fire can remove a large proportion of the population's foraging habitat for many years, and often has in the past (Chapter 2). This analysis is also limited in ignoring potentially important interactions between parameters. For example, incorporating the likelihood of catastrophic fire damage would greatly increase the carrying capacity required to ensure survival; if life span is shorter than assumed then breeding rates must be higher to achieve population growth, and so on.

CONCLUSIONS

The specific numbers generated by these simulations are not very reliable both because of the inherent limitations of simulations that fail to include many real-life factors, and because of the uncertainty of some of the input parameters. Rather they are useful in producing rough estimates and revealing general trends. PVA is a dynamic tool, and models can be refined as better information becomes available on the species and its environment and as conservation goals evolve. Several conclusions can be drawn from these studies however, as follows.

1) Modeling the population accurately will require better demographic data, particularly on mortality rates.
2) Evidence that the population is not declining steeply does not necessarily mean it is viable.
3) Population growth is expected to be relatively slow even under optimal conditions, probably well under 10% per year.
4) To reach the goal of an effective genetic population size of several hundred would probably require an actual population of at least several times that number.
5) The population is not currently stable unless mortality rates are exceptionally low, suggesting that it may be declining or at risk of decline.
6) The risk of inbreeding and loss of genetic variability is a concern if the population remains small, but is less pressing in the short term than the risk of extinction.

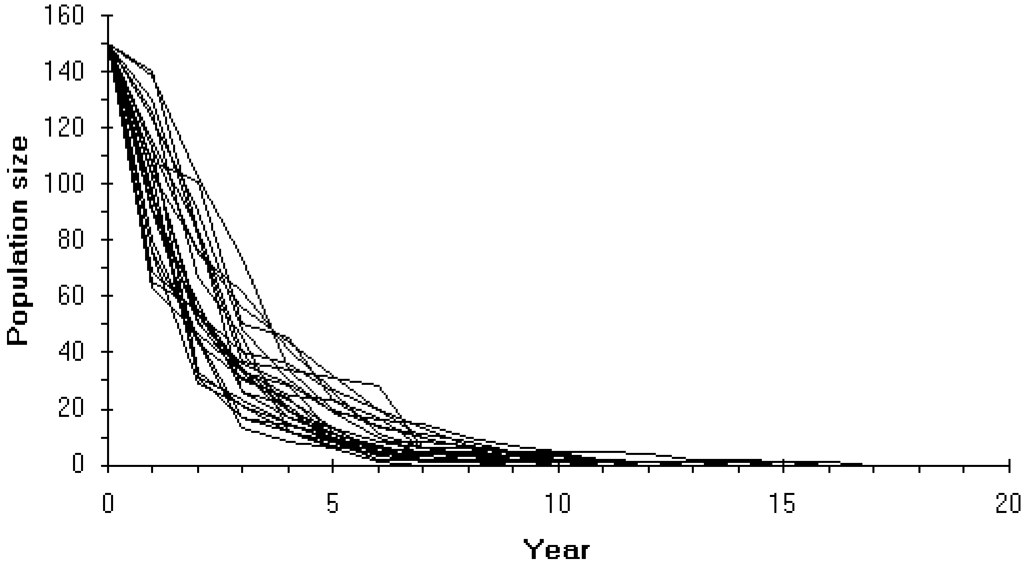

Figure 10.1. Results of 25 iterations of VORTEX simulation using the parameters listed in Table 10.1. On the basis of 500 iterations, the average growth rate was -0.51, and the mean time to extinction was 5.8 years.

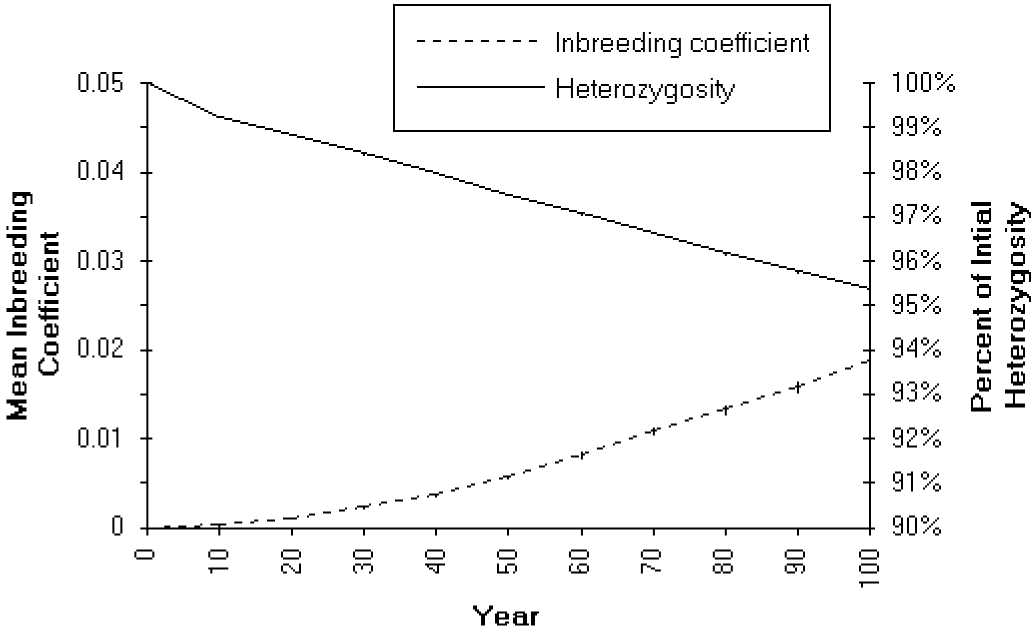

Figure 10.2. Predicted inbreeding and loss of genetic diversity over 100 years. Carrying capacity was set at 150, and all other parameters were as shown in Table 10.1.

Figure 10.3. Predicted response of the population growth rate to varying rates of breeding by females. Negative growth rates indicate a shrinking population. Based on mortality rates shown in Table 10.2, with all other parameters as shown in Table 10.1.

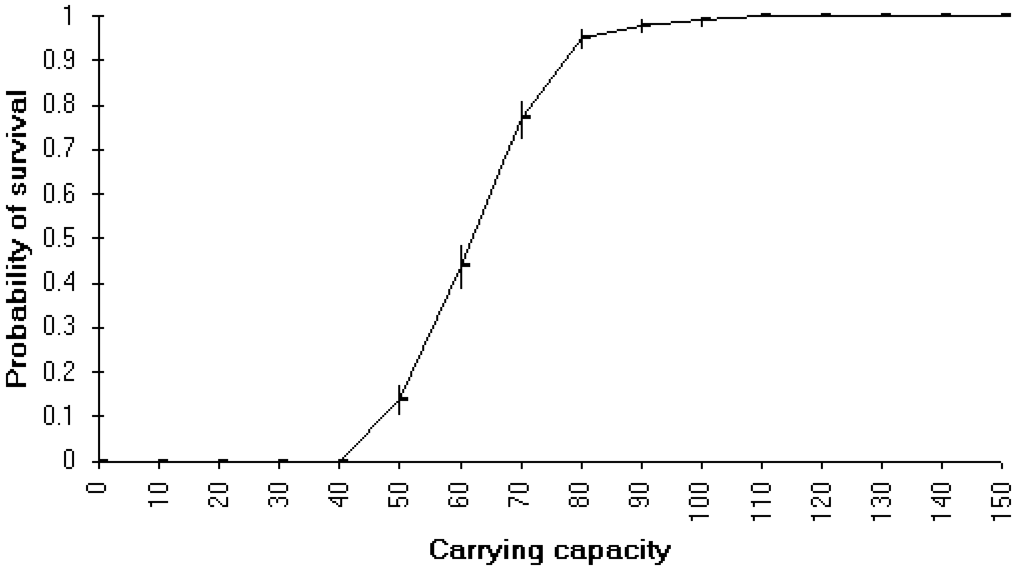

Figure 10.4. Probability of the population persisting for 100 years as a function of carrying capacity. Error bars show one standard error. Simulations were based on the mortality rates shown in Table 10.2, with all other parameters as shown in Table 10.1.

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