

extinction of 0.05 (see Figure 13). This very clearly illustrates the importance of population fragmentation to species viability.

Now consider that we could move birds between the populations. The model has been adapted to move unpaired birds from the larger to the smaller population each year. The probability of both populations going extinct within 100 years is now 0.46, nowhere near as good as a single large population, but a significant improvement over 2 completely isolated populations.

Discussion

The process of modelling is at least as informative as the final results. While the most robust estimates of population viability are those generated by the simplified model, sensitivity analysis of a more complex model provides insight into the underlying demographic processes of viability and extinction.

The estimates of viable population sizes are somewhat smaller than those obtained from more general models (MacArthur & Wilson 1967, Richter-Dyn & Goel 1972, Soule 1987), i.e. an effective breeding population of 20 - 30 for protection against demographic stochasticity. Consideration of environmental stochasticity, genetic effects, and documented extinctions on islands suggest populations of 50 - 200 are required for long-term viability (Boyce 1992). The results presented here cannot be used to reject these 'rules of thumb', as shown by the sensitivity analysis. Rather, the most important achievements of the modelling exercise have been to demonstrate density dependence in a blue duck population, and identify variability in adult survival rate as the key to population viability in small blue duck populations.

A further, unexpected finding is that while the details of blue duck demography are highly variable (e.g. year to year variation in fledging rate), changes in the number of territorial adult birds in the Manganuiateao population were relatively slow and noise-free. This indicates strong compensation mechanisms exist within blue duck populations. For example, in 1983 when recruitment was zero in the Manganuiateao population, the population of adult birds remained static, and when large numbers of adults were lost from the population in 1989, they were replaced rapidly by higher fledging and juvenile survival rates. This finding gives further reason for optimism in assessing the viability of blue duck populations.

Limitations of the data

All the data used to determine the structure of the model and to estimate model parameters come from a single population of blue ducks. While fourteen years of monitoring of a banded population of between 8 and 20 birds is a major achievement, in statistical terms this is a small sample. The little information from other blue duck populations suggests that the Manganuiateao study area population performs consistently better in such parameters as fledging rate and adult survival (M.J. Williams pers. comm.). There is also evidence that in other North Island populations, site attachment and pair-bond fidelity is lower, and inter-catchment movements more likely than indicated by the Manganuiateao study (D. Towers pers. comm.). To make accurate predictions for blue duck populations in general we need a wider data set.

A particular limitation of the data is that we do not know whether the density dependent relationship for adult survival holds for very low and very high densities. It is possible that density dependence may be of the all-or-nothing type rather than a linear relationship.

Since the model is most sensitive to adult survival rate parameters, we especially need more precise estimates of these parameters. However, widening the scope to include other populations will likely uncover further variability in these parameters.

The Manganuiateao study area population is open to immigration and emigration upstream. It is important to find out what happens to unpaired adult females in a fully closed population.

Limitations of the model

Perhaps the main limitation of the model is that it assumes a closed population, when immigration and emigration is known to occur. A fixed value of K is another consequence of assuming a closed population. The simulated populations cannot grow by expanding their range, but must do so by increasing density. The results above will not apply to blue duck populations held at low densities by density independent factors (such as extreme environmental stochasticity).

The model does not adequately deal with correlations between demographic parameters. The combined sensitivity analysis is probably too pessimistic, but the simplified model approach too optimistic, in estimating the precision of viability predictions. The 'best' answer is somewhere between these extremes.

Only one source of density dependence was included in the model, that associated with adult survival. This was the parameter most clearly dependent on population size but there is also a suggestion that fledging rate declines with population size. Incorporating two density dependent components in the model would greatly complicate the analysis, particularly in setting values of K for simulated population which would be determined by the two slope parameters.

The use of negative binomial error distributions may not be appropriate. Although these distributions are the best fit to some components of the model, they have interesting consequences for modelling different sized populations. Unlike a binomial process which becomes more predictable with increasing population size, the variance of a negative binomial distribution continues to grow at a faster rate than the mean. This means that population processes become more unstable at higher densities. This may be appropriate when considering the same population at different densities, but not when a large population is the result of a large area of habitat. Under these conditions we would expect a large population to be buffered against stochastic processes. For this reason, the simplified model, which required only binomial error distributions, is expected to give more reliable predictions of viability for other blue duck populations.

A clear distinction between demographic and environmental stochasticity is not made in this model. This is a consequence of the difficulty in partitioning stochasticity in the limited data set. Although demographic parameters vary greatly from year to year, it is not apparent whether this is a result of, say, climatic variation between years, or simply reflects random

sampling from a very noisy process. Without confirmation of year-to-year variation from other populations, we are unable to make this distinction with any confidence. Both demographic and environmental stochasticity are accounted for by the variance/mean ratio of the parameter error distributions.

This model, and viability analysis, does not consider the deleterious genetic effects of small population size (Soule & Simberloff 1986). Triggs et al. (1992) have shown that blue duck populations are highly in-bred and within catchment genetic variability is virtually zero. However, since low genetic variability was found in the Manganuiateao population ('large' by blue duck standards), any deleterious effects are likely to occur equally throughout the range of population sizes considered in this report. It is hard to imagine how in-breeding depression in a population of 4 pairs could be more severe than in a population of 10 pairs in which nearly all birds are the offspring of two females, themselves closely related, which is the case in the Manganuiateao population.

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