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POPULATION VIABILITY ANALYSIS OF BLUE DUCK
(HYMENOLAIMUS MALACORHYNCHOS)

(Short Answers in Conservation Science)

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Population Viability Analysis of Blue Duck *(Hymenolaimus malacorhynchos)*

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Summary

Data obtained from a fourteen-year study of blue ducks living in a section of the Manganuiateao River, central North Island, were used to develop and test a stochastic simulation model for investigating the viability of blue duck populations.

The Manganuiateao River population exhibited density dependence, operating through adult survival. That section of the river appears to have an equilibrium population size (carrying capacity) of 9 blue duck breeding pairs. The probability of an isolated population of this size surviving for 100 years was estimated at 87%.

Sensitivity analysis of the model indicated that variations in adult survival were the most powerful influences on predictions of the model. When adult survival rates were high or stable, populations persisted for longer than populations of a similar size with low or unstable adult survival rates. This result suggests we should attempt to discover causes of variation in adult survival rates in natural blue duck populations.

The model and its conclusions are limited by the generality of the data. First, blue ducks are long-lived birds with lifetimes approximating the length of the Manganuiateao River study. This means the relative importance of year-to-year variation in demographic parameters compared with environmental disturbance is still unknown. Second, we need estimates of demographic parameters from other blue duck populations in order to test and refine the model. Finally, we lack good measurements of dispersal within and between populations, parameters that may have large influences on population viability.

Introduction

What is PVA?

Population viability analysis (PVA) is a collection of procedures, usually including mathematical modelling, for exploring the dynamics of population extinctions.

Closed populations go extinct for one of two general reasons. Either the average death rate is consistently higher than the average birth rate, or the variability of birth and death rates is high relative to population size.

The research and management implications of these two different modes of extinction are quite different. In the first case, our priority is to find out why the growth rate is negative. Presumably some time in the past, growth rate was positive or zero. What has changed? Recruitment may have decreased or death rate increased. These population processes may be the result of environmental changes such as reduced food supply, increased predation, or reduction in available habitat. Once these factors have been identified, management procedures can be designed to reverse the trend (e.g. predator reduction).

In the second case, populations in which the average growth rate is not negative can still go extinct if populations are small and variability in population processes is large. Such stochasticity is conventionally partitioned into environmental and demographic components. The weather is clearly an environmental factor that can alter recruitment or death rates from year to year. Several bad seasons in succession might drive a population to extinction, even though over long time scales the climate is (on average) good enough for the population to survive. An example of demographic stochasticity is a biasede sex ratio of young. In a very small population with high turnover, skew in the sex ratio of the young might result in extinction due to loss of one sex by the binomial process of sex determination.

Other stochastic influences on populations are not so clearly environmental or demographic. The death rate may exhibit year to year variation. This might be due to weather, or perhaps simply be a product of a random death process. If a number of populations experience synchronous variations in death rates we would assign this to environmental effects. But there is no guarantee that environmental effects will be geographically consistent. A particularly cold year might be good for a population at a low altitude, but bad for one at high altitude. Such variation in parameters between, or within, populations may not be distinguishable from pure demographic stochasticity.

Both types of stochasticity, but particularly demographic stochasticity, are most important in small populations. In even moderate sized populations, the likelihood of all young being of one sex becomes vanishingly small, and other purely random processes become similarly swamped by population size. Large populations are likely to be dispersed over a greater geographic range, and thus there are more opportunities for small pockets to escape extreme climatic conditions or predator outbreaks. A population of 10,000 that loses 95% to an epidemic, is more viable than one of 20 that suffers the same percentage loss.

The aims of research in cases where stochastic processes may be important are thus to identify why the population is small (what limits its density or extent), and which population processes are variable, and why. The first step therefore is to establish the existence of density dependence, a notoriously difficult task (McCullough 1990).

The implications for management are manifold. First, managers might attempt to increase the population to a "safe" size, or to reduce the variability of population processes. Environmental stochastic effects might be reduced by spreading the risk in widely spaced populations. However, managers might also benefit from the understanding that extinction is a natural and inevitable process in small populations. If a small isolated population goes extinct, this may not be a reflection of the quality of the habitat, but simply its limited extent. Restocking of that population is thus not a waste of effort.

Population viability analysis has also been suggested as a means of putting the conventional categories of "endangered" or "threatened" on an objective and quantitative basis. This may then be used in the allocation of conservation resources and effort. Mace & Lande (1990) have suggested the following categories and definitions:

Vulnerable:	10% probability of extinction within 100 years
Endangered:	20% probability of extinction within 20 years
Critical:	50% probability of extinction within 5 years

Materials and Methods

The data

All data used to estimate parameters for the model were obtained from 14 years observation of a banded blue duck population on the Manganuiateao River, central North Island, New Zealand. Details of methods, and analysis of basic population parameters for the first 10 years, are provided in Williams (1991). The population is an arbitrary section of the river; blue duck exist above the range of the study area but not downstream. The population is open but movements are asymmetrical. Recruitment to the study area is predominantly from within that area but birds do move upstream where intrinsic productivity is very low (Williams 1991).

Territorial birds within the study area were found at intervals throughout the year and numbers of juveniles fledged by each pair were recorded each breeding season. The numbers of adult birds at the start of the breeding season (August) and the fledged young produced each year can be considered as a total census rather than an estimate. As most birds were identified with individual colour bands, losses between years could be determined.

Detailed data on nesting and fledging success are available from a sample of clutches. These data will be referred to as the 'monitored clutches' and comprises the number of eggs laid (25 clutches), the hatching rate (20 clutches), and the survival of hatched birds to fledging (24 clutches). The hatching rate will also be confounded by very early duckling mortality, before the clutch was first observed on the water.

Density dependence

Pollard & Lakhani (1987) proposed a randomization test for density dependence that overcomes the problems of serial correlation and non-independence in previously proposed tests (e.g. Bulmer 1975). Their test is based on the correlation between x_i and d_i from a series of annual censuses where x_i = logarithm of the population size at time i, and $d_i = x_{i+1} - x_i$.

The model

The model developed for this analysis is a discrete time, stochastic simulation model. The model is programmed in Microsoft Quickbasic and run on a 486-DX microcomputer under MS-DOS. The model simulates aspects of the life cycle of the blue duck for which data are available (see below). The steps in the model are:

1. Pairs attempting breeding
2. Nesting (clutches laid)
3. Hatching of eggs
4. Survival of hatched ducklings to fledging
5. Recruitment of fledged birds into the population of territorial birds
6. Survival of territorial adults

For most analyses, steps 2 to 4 were condensed into one step for reasons of data quality and computational simplicity explained later.

For each step in the model, parameters were obtained by the following procedure;

1. Examine data graphically for evidence of density dependence.
2. Test potential density dependence relationships with a randomization test on the correlation coefficient.
3. Fit models with error distribution from the binomial/Poisson/negative binomial family of distributions using maximum likelihood, to simultaneously estimate mean rates, slope (where density dependence was detected) and spread.
4. Use the likelihood support criterion to verify density dependence and to test non-linear density dependence models.
5. Determine the likelihood support surface for the estimated parameters and delimit the range of parameter values for sensitivity analysis.

Graphical exploration of the data was performed with SYSTAT (Wilkinson 1990) using distance weighted least squares smoothing (DWLS). The randomization tests were performed using a program based on that in Noreen (1989). All tests used 9999 random shuffles.

Maximum likelihood model fitting was carried out with a purpose written computer program employing an adaptive, systematic search procedure. This was preferred over more efficient maximum likelihood estimation methods because it can automatically generate the support surface as well as the maximum likelihood estimates, and is less likely to become trapped in local maxima. The search was terminated when parameters had been obtained to at least 3 significant figures.

The binomial family of distributions was chosen because they are discrete, constrained to non-negative values, and provide a range of 'shape'. For binomial distributions the variance is less than the mean, for negative binomials the variance is greater than the mean, and the Poisson is the limit case for mean equal to variance. Distributions of this family can be generalized to allow non-integer values of n. By varying n and p, a continuous range of distributions with different means and variances can be produced. Figure 1 shows three distributions from this family all with mean equal to 10. Binomial distributions will be the least variable, appropriate for tightly constrained population processes, e.g. clutch size. Negative binomial distributions will be appropriate for more variable or noisy processes. Negative binomial distributions can also be considered as compounded distributions, such as Poisson with parameter λ a random variable drawn from a Gamma distribution (Johnson & Kotz 1969). This could apply to death processes where deaths occur at random, but the probability of death varies among individuals or between years.

Since the binomial family of distributions described above are distinguished by the relationship of their means and variances, any distribution from within this class can be defined by a mean and the variance/mean ratio (abbreviated V/M hereafter). In the case of the binomial, this ratio is $1-p$, for the negative binomial it is $1/p$, and for the Poisson, equal to 1.

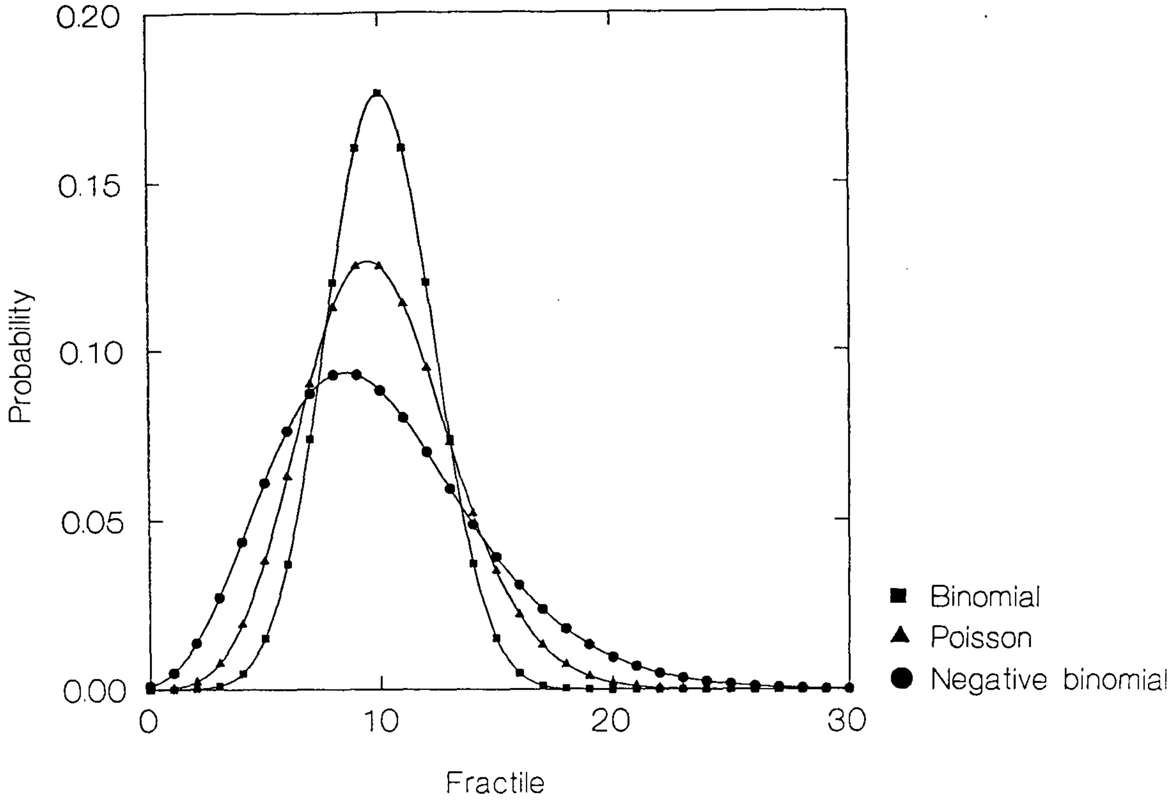

Figure 1. Comparison of a Binomial, a Poisson and a Negative Binomial distribution with mean equal to 10.

In some cases, models fitted to the data would occasionally generate survival rates (of a particular stage) greater than one. In these cases truncated distributions were fitted to eliminate such impossible cases while still maintaining a good fit to the data.

Density dependence was examined in a hierarchical sequence using the likelihood support criterion to select models. The simplest density dependent model is the logistic in which the demographic parameter changes linearly with population size. Theta-logistic (Gilpin et al. 1976) and piece-wise linear models ("plateau and ramp" of McCullough 1990) were also tested if graphical analysis suggested nonlinearity.

Model processes

The simulation begins with an initial number of paired adults (aged 2 years), set at the equilibrium population size (K) which is determined by the model parameters. Each year of the simulation begins with a check for 1 year old females, generation of the number of pairs breeding, and incrementing the ages of birds. Following this, numbers fledged are generated by sampling at random from the appropriate distribution, and assigned at random to male and female. Next, the number of fledged juveniles that will survive (recruited into the adult population next year) is generated. The number of adult deaths is generated and individual adult birds removed from the population.

Bereaved adults are then paired with another single territorial mate if available. Juveniles recruited into the adult population are preferentially assigned to territories held by a single bird, and then to vacant territories. Thus gaps in the adult population are filled while keeping within the limits of recruitment set by the fledging and juvenile survival stages. These procedures were implemented in order to mimic the tightly controlled sex ratio of territorial birds observed. Single adult birds are not seen in the study population apart from the occasional single male. In most years, all adult birds are paired, and a simple random assignment of recruited juveniles does not reproduce this.

The number of pairs surviving and single birds is counted. Loss of one sex of birds from the population is considered an extinction.

Random numbers were generated using the algorithm described in Noreen (1989). Algorithms for sampling from binomial, Poisson and negative binomial distributions were obtained from Ahrens & Dieter (1974).

Model outputs

The outputs from stochastic extinction models can be in a number of forms.

Time to extinction

This is generally not very useful because such times are highly variable, and computation times will be excessive for viable populations. It is important, however, to appreciate that the distributions of times to extinction are positively skewed so the mode or median is a more useful statistic than the mean (Boyce 1992). It must be remembered that in a simulated population where the median time to extinction is, say 100 years, many runs will result in extinction in less than 10 years while a few might survive for 10,000 years.

Probability of extinction

Instead of reporting the median of the time to extinction we could use any other percentile of the distribution that equates with a given area under the distribution curve. This is equivalent to finding the probability of extinction within a given time frame. Probabilities of extinction can be reported for any time frame and if these are relatively short (say 100 years) the computation time is not excessive.

Viable population sizes.

If a population exhibits density dependence, the population will be constrained by some approximate upper limit we can call the carrying capacity (K). At K, mean birth and death rates balance, so the population will fluctuate around, or just below, K. By varying density dependent parameters, populations of different K's can be simulated and a value of K that yields a particular median time to extinction, or probability of extinction, can be determined.

All three types of output are used in this report. Probabilities of extinction are estimated from runs of 1000. Viable population sizes were estimated by generating probabilities of extinction for a series of K values and a curve fitted with DWLS smoothing (Wilkinson 1990).

Intersection of the smoothed curve with an appropriate level of extinction probability gave the estimated population sizes for Critical (K_{cri}), Endangered (K_{end}) and Vulnerable (K_{vul}) following Mace & Lande (1990).

Sensitivity analysis

Accurate predictions from models require accurate estimates of parameters. We wish to understand how sensitive the model is to variation in these parameters. Such variation can take two forms. Firstly the real parameters may vary between populations, or over time and we need to know how this will affect our predictions. Secondly, our estimation of the parameters may not be very precise because the sample size of the data set is small and the process noisy. I have concentrated on this second aspect of sensitivity analysis; to determine which parameters are most important because of our lack of knowledge of them. Sensitivity analysis can also be used to determine which parameters in a complex model can be removed to reduce computation time while maintaining model performance.

I have used the likelihood approach to model fitting and testing (Edwards 1972) and employ 2-unit support limits as the range of parameter values acceptable in the light of the data. A selection of points from the 2-unit contour, including the most extreme points in each dimension, were evaluated.

Results

Density dependence

Using Pollard & Lakhani's (1987) procedure, I found r = -0.492, p = 0.0334. Similar figures are obtained if the $\mathbf{N_i}$ are pairs, rather than total birds.

Therefore we have strong evidence for density dependence in this population. The parameters of this relationship, and the life history stages where this dependence operates (e.g. mortality or natality), are determined in the following sections.

Parameter estimation

Pairs attempting breeding

Of 95 pair.seasons, 86 attempted breeding (see Williams, 1991 for definition of a breeding attempt). In 7 cases where pairs did not attempt to breed, the female was 1 year old. In the other two cases the age of the female was not known with certainty as they were new to the study area. All pairs in their second and subsequent years of observation attempted to breed. There were also 7 cases of 1 year old females attempting breeding.

In the model, all pairings in which the female is 2 years or older attempt breeding. Fifty percent of pairs in which the female is one year old will attempt breeding.

The data were very limited for this parameter (14 cases) so no attempt was made to search for density dependence or year to year variability. This component of the model has thus been implemented as a pure binomial process (n = number of pairs with 1 year old females, p = 0.5).

Clutch size

Williams (1991) recorded the average clutch size as 6.0. No new data on clutches has been added.

A plot of clutch size against number of adult birds suggests that clutch size increased with population size. The relationship is stronger with clutch size versus number of pairs attempting breeding (r = 0.502, p = 0.011). However, a linear increase in clutch size is not biologically realistic. No clutches greater than 7 have been observed but a linear model would predict average clutch sizes of 15 if the population was to rise to 30 pairs. Further evidence of the unsuitability of this model comes from attempts to fit the model with binomial errors. The fact that at the lowest bird densities (4 pairs breeding), both the lowest and highest clutch sizes were observed (Figure 2) precludes any significant slope (Table 1).

Nonlinear models yielded upward curvature, even less biologically acceptable, and were not supported by the likelihood criterion.

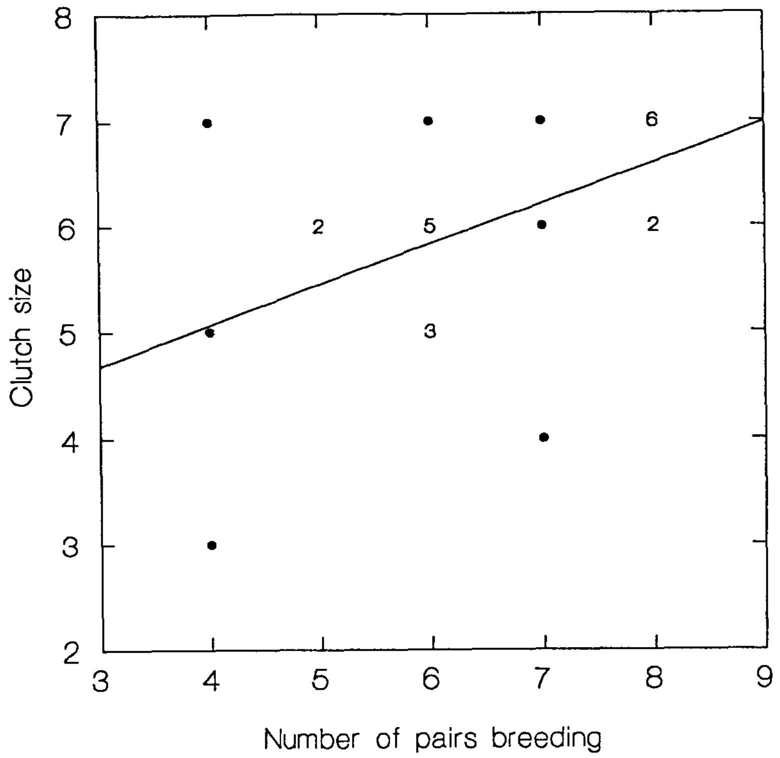

Figure 2. Clutch size and the number of breeding pairs of blue ducks in the Manganuiateao population.

Table 1. Likelihood estimation of models for clutch size

Model	Intercept	Slope	V/M	Log likelihood
Constant	6.00	-	0.143	-33.027
Linear	5.79	0.033	0.154	-32.996

Summary: Clutch production can be modelled as a binomial process with $n = 7, p = 0.86$ (mean = $np = 6$).

Hatch rate

No evidence of density dependence in hatching rate can be seen in graphical displays (Figure 3). However, hatching rate appears to be bimodal and can not be modelled adequately by any distribution from the binomial family. Of those nests observed, 35% did not produce any hatched ducklings. From all breeding attempts, 29% produced no ducklings on the water. In those clutches where there was some successful hatching, the hatch rate was 76%. This suggests two processes: complete loss of nests (perhaps predation or flooding) and a much lower rate of infertility or early loss of ducklings (see definition of 'hatching' above). Both processes can be modelled with binomial distributions (Table 2).

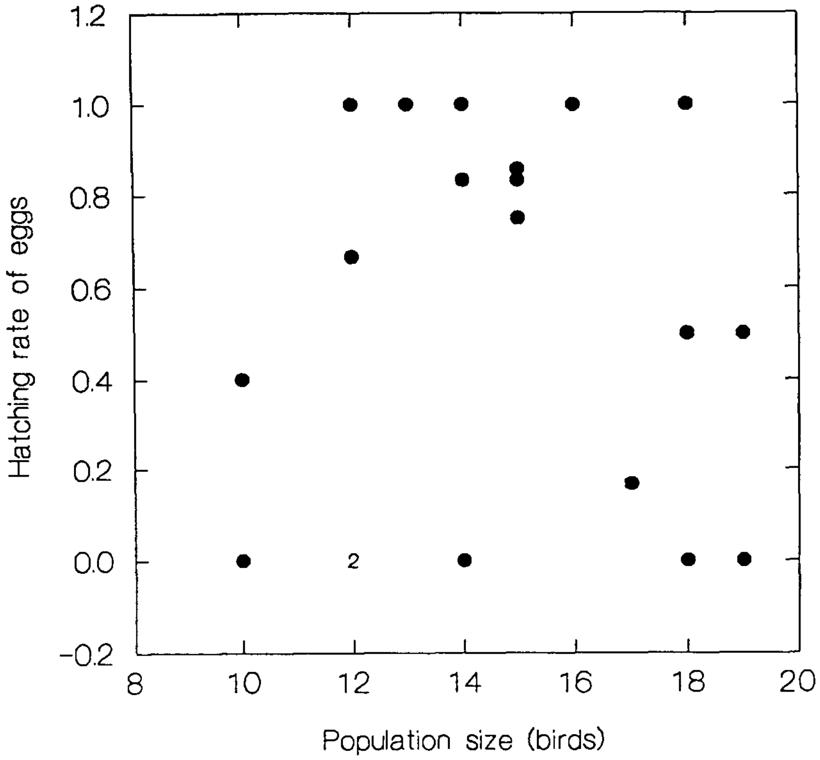

Figure 3. Hatching rate of eggs, and number of blue ducks in the Manganuiateao population.

Table 2. Likelihood estimation of models for monitored clutch data		
Model	Mean	V/M
Clutch loss	0.285	0.573
Hatch rate	0.756	0.371
Fledge rate	0.912	0.916 (truncated binomial)

Summary: Hatch rate of eggs in a clutch is modelled by compounding two processes; complete loss of clutches, and loss of eggs from remaining clutches. Both components modelled as binomial processes.

Fledging rate

Monitored clutches

No trends in fledging rate of hatched ducklings were apparent with either population size or clutch size (Figure 4).

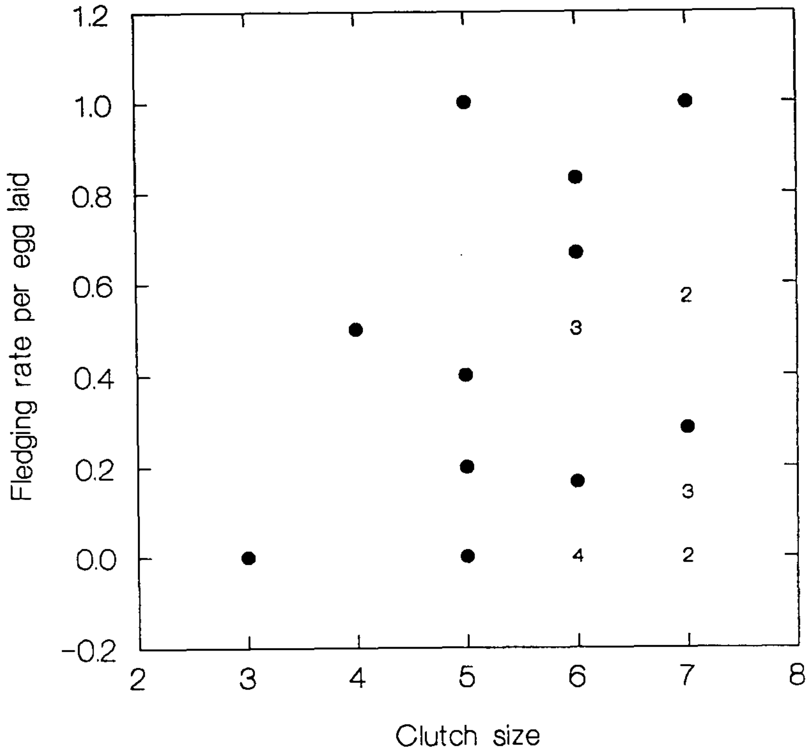

Figure 4. Fledging rate and clutch size of blue ducks in the Manganuiateao population.

The data for 1983 is clearly an outlier from the distribution of fledging rates. In that year population density was moderate, breeding occurred as usual and ducklings were seen on the water but no ducklings fledged. Williams (1991) attributed this to abnormally stable flows in the river that year associated with El Nino weather patterns. Thick growth of algae on stone surfaces in the river may have prevented ducklings from obtaining sufficient food. It was decided to treat this event as a special case of environmental stochasticity. Unfortunately, since another event of this kind has not occurred, we cannot estimate its probability with much precision. This component is implemented in the model as random event with probability 1/14 which results in zero recruitment.

Excluding the 1983 data, fledging can be modelled as a truncated binomial process (Table 2).

Full population

When the fledging rate from pairs breeding is obtained from the analysis in the previous sections, it is found to be significantly higher than the 1.414 observed for the whole population.

Clutch size * (1-clutch loss) * hatch rate * fledge rate = 2.118

(Note the true mean generated by the truncated binomial distribution for fledge rate, 1983 data included, is 0.653).

Most of the monitored clutches were those of two, long-lived and productive females and are clearly not an unbiased sample of the whole population. The results above have been presented as they may shed light on the process of fledging and duckling loss, but in simulation modelling the steps between nesting and fledging have been condensed into one step.

There is a suggestion of density dependence in the fledging rate from all breeding attempts when plotted against number of birds (r = -.373, p = 0.097) and the correlation between fledging rate and number of pairs is slightly stronger (r = -.456, p = 0.059, Figure 5). Maximum likelihood estimation of models with binomial or negative binomial errors provides similar results (Table 3)

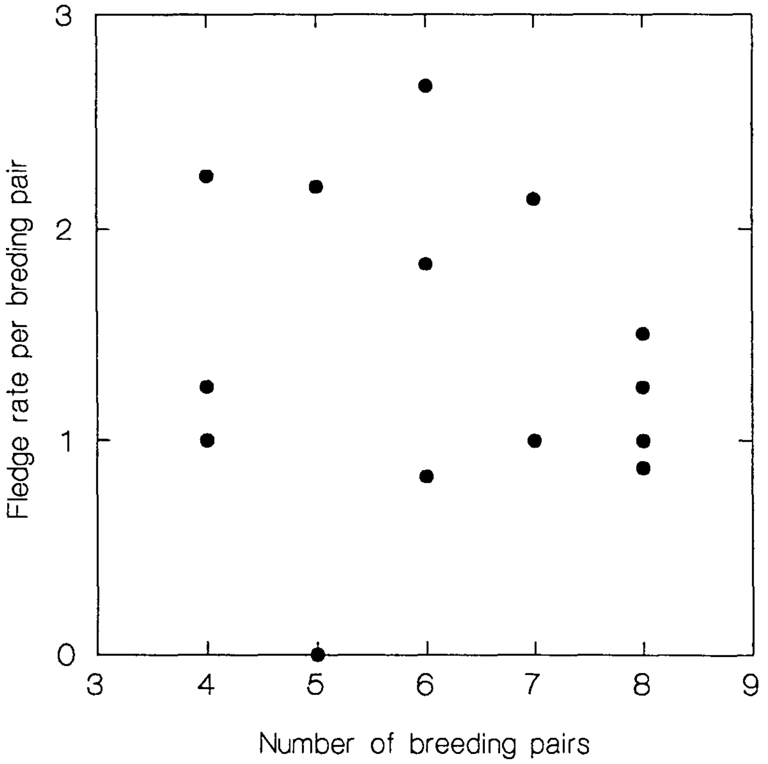

Figure 5. Fledging rate per breeding pair and number of pairs of blue duck in the Manganuiateao population.

Table 3. Likelihood estimation of models for fledge rate per breeding pair.

Model	Intercept	Slope	V/M	Log likelihood
Constant	1.481	-	1.384	-34.564
vs. birds	2.843	-.090	1.051	-32.723
vs. pairs	2.770	-.178	0.986	-32.383

Summary: Fledging is an approximately Poisson process (V/M ≈ 1) and may be a candidate for density dependence, fledging rate declining with increasing population size.

Juvenile Survival

Of those birds that fledged, less than half were recruited into the population of territorial adult birds within the study area. Evidence for density dependence in this component is very weak, the most promising aspect is a weak correlation between juvenile survival and the number of adults surviving to the next breeding season ($r = 0.393$, $p = 0.12$). Recruitment of juveniles into a territory may be dependent on gaps opened up by deaths of adults. This process is approximated by a truncated Poisson process (Table 4)

Table 4. Likelihood estimation of models for juvenile survival

Model	Intercept	Slope	V/M	Log likelihood
Constant	0.423	-	0.983	-23.925
vs. surv. adults	0.858	-.038	0.873	-22.978

Adult survival

Examination of a plot of adult survival rate against population size strongly suggests density dependence (Figure 6) and there is a significant correlation ($r = -0.588$, $p = 0.013$). However, this linear model would predict survival rates greater than one for low population sizes which is biologically impossible. We have no data on the adult survival rate for very small population densities in the study area which makes estimating non-linear models difficult. Non-linear models were greatly affected by one data point (lowest survival rate and highest number of birds). This resulted in very steep declines in survival at high population sizes, i.e. approximating an 'all-or-nothing' density dependence. However, neither non-linear approach provided significantly better fit than a linear model with truncated binomial errors. Note that the truncation of simulated adult survival rates above one, has the effect of lowering the actual survival rates in small populations and thus achieving a non-linear response (Figure 6).

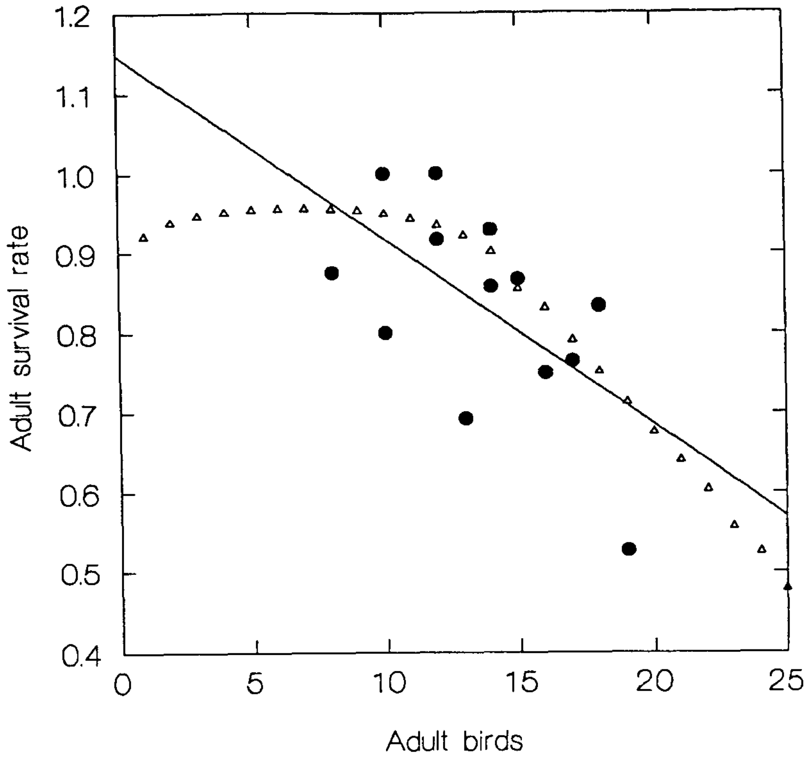

Figure 6. Density dependence of blue duck adult survival rate in the Manganuiateao population. Least squares linear regression line = solid line. Maximum likelihood model with truncated binomial errors = open triangles.

Table 5. Likelihood estimation models for adult survival				
Model	Intercept	slope	V/M	Log likelihood
Constant	0.814	-	0.214	-25.106
Linear	1.152	-.0234	0.129	-21.989
piece-wise	0.858	-.138 *	0.142	-21.167
θ-logistic	0.873	**	0.128	-19.568
Constant: males	0.850	-	0.151	-17.224
Linear: males	1.445	-.0384	0.152	-14.940
Constant: females	0.776	-	0.224	-17.817
Linear: females	1.239	-.0318	0.143	-14.380

* breakpoint at 17 birds
** x intercept = 19.8, θ = 21.3

Two lines of evidence suggest that male and female blue ducks might have different survival rates. In some years there has been an excess of males in the population but never an excess of females. The average age at death of males is greater than that of females (see model validation section). However, a model including separate parameters for male and female was only a marginal improvement (support gain = 1.857). Parameters for separate adult survival models for males and females are given in Table 5. Density dependence can be detected in the survival rates of both sexes.

Summary: Although the A-logistic model is best supported, this is dependent on the data from a single year. Decline in adult survival is definitely non-linear but more parsimoniously modelled by a linear relationship with truncated binomial error distribution.

Simulation modelling

The standard model referred to in this section contains the following components: Pairs breeding, fledging, juvenile survival, and adult survival. Adult survival is linear (logistic) density dependent. Although there was a suggestion of density dependence in fledging rate, this has not been implemented at present. A model with two interacting density dependent components presents problems for determining K and simultaneously varying parameters to simulate different K's.

Model Verification

Although we do not wish to test predictions of the model by observation of a series of real population extinctions, we can verify that the model is behaving in a way consistent with our knowledge of the population from which the data were obtained. Some predictions of the model, not directly related to the estimated model parameters, are examined in this section.

Population size

Table 6 compares basic statistics of the study area population with the results of a 500 year simulation. As expected, an extensive simulation yields greater extremes but the means and variances indicate that the model is reflecting the population adequately.

Carrying capacity

The parameters estimated from the study population indicate that the balance between recruitment and losses will be at a population size of 18.5 birds. Figure 7 shows that in the study area, population increased steadily until it reached 18 birds and has fluctuated around this level since.

Table 6. Comparison of population statistics from the Manganuiateao population and from simulations.

Statistic	Data	Model
Birds		
Mean	14.14	15.03
Variance	12.90	14.30
Max	20	32
Min	8	5
Pairs		
Mean	6.79	6.77
Variance	3.41	4.64
Max	10	14
Min	4	1

The carrying capacity does not equate with the mean population size (Figure 8). Some features of the model cannot be incorporated easily into a calculation of K. Truncation of the binomial or negative binomial sampling distributions will yield different mean values than those expected from the parameters alone. The recruitment rate will be affected by the proportion of pairs in which the female is in her first breeding year. This will be most evident in small populations with high turnover. If separate death functions for male and female are used, K will differ between sexes. Since females will most often be the limiting sex, the female K was used. Even if all these components of the model are disabled, mean population size is generally lower than the predicted K (Figure 9). This is because when the population exceeds K, adult deaths increase and the population rapidly declines, but when below K, it may take some time to grow back because recruitment is low and highly variable. The population thus spends most of its time below K. This should be borne in mind when considering the values of K for viable populations. K will be greater than the mean or median population size, closer to the upper quartile.

Age at death

Of the territorial birds that have lived in the study area over the period of observation, the age at death of only a few is known with certainty. Some birds were of unknown age when observations started, and many are still living today. One male is at least 12 years old and still alive. The age of death (or loss from the population) of 16 birds of each sex is known with reasonable certainty. The distributions are compared with those generated from runs of the model in Figure 10. When age categories are grouped, a chi-square test does not detect a difference (males $X^2_{3\ df} = 3.22$, p = .359, females $X^2_{3\ df} = 2.82$, p = .420).

The average age at death is also similar when the model predictions and actual data are compared (Table 7).

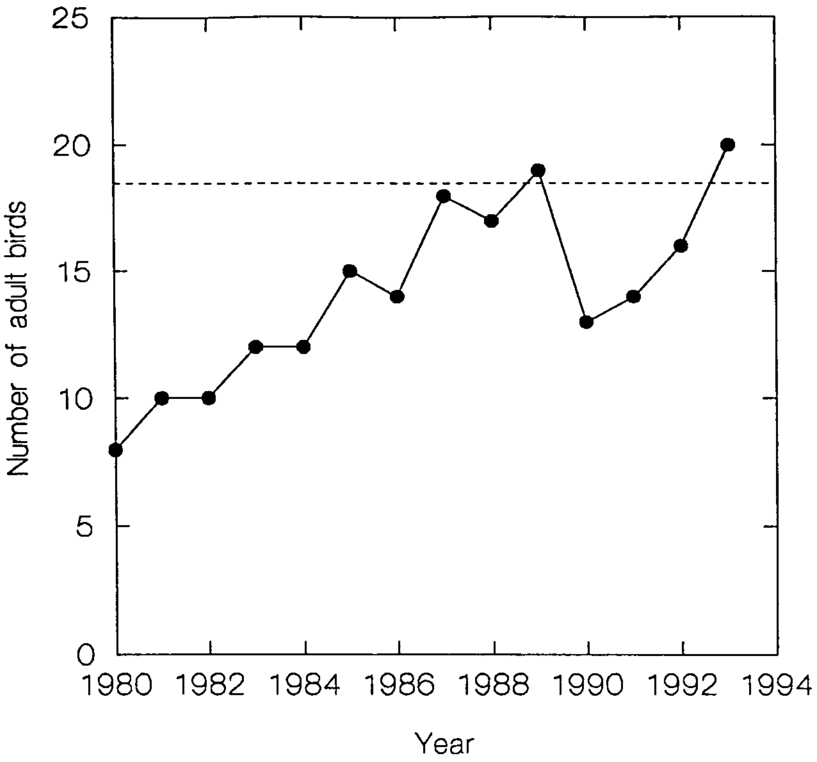

Figure 7. Number of adult blue duck in the Manganuiateao population from 1980 to 1993. Dashed line is the estimated equilibrium population size.

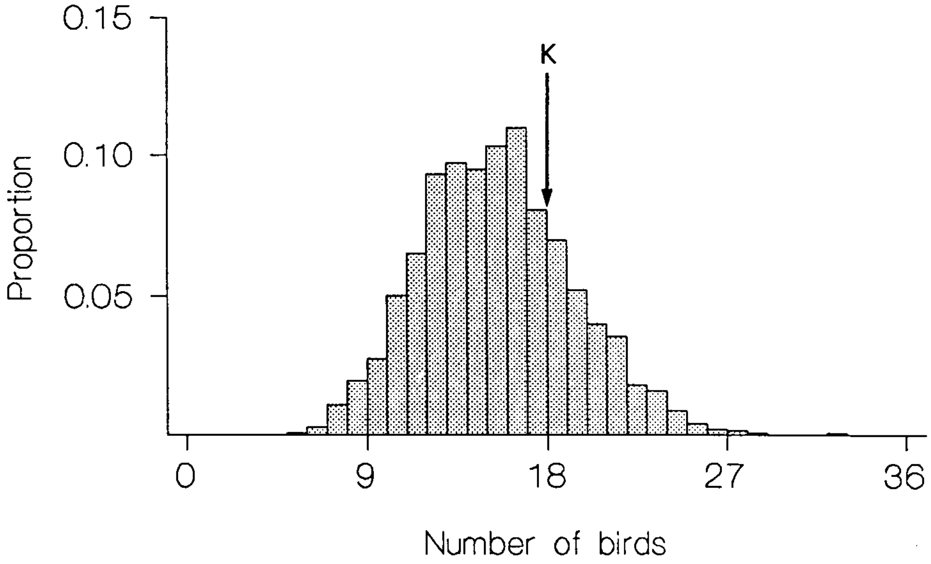

Figure 8. Distribution of population size from a simulation of 500 years of the Manganuiateao blue duck population. K is the equilibrium population size.

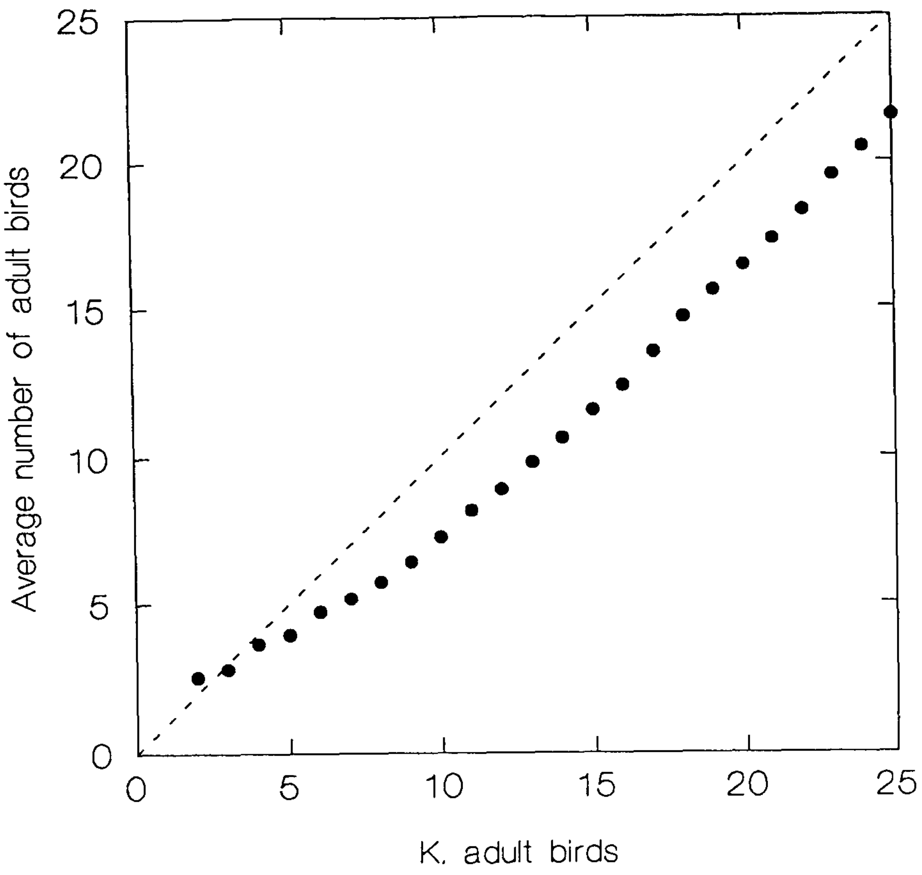

Figure 9. Average number of birds in simulated populations compared with equilibrium population size (K).

Table 7. Average age at death in simulated populations and in the Manganuiateao population

Sex	Data	Model
males	4.9	4.6
females	3.0	3.5

The model also predicts that, occasionally, a blue duck might live as long as 30 years. Only further long term monitoring can test this prediction. However, I expect this estimate of longevity to be too optimistic. Since the death rate is modelled as a density dependent process, at low densities death rates become lower and thus longevity increases, perhaps unrealistically. This is especially evident if the model is run with large K but without recruitment. As the population declines to extinction, age at death can be as high as 50 years (but with very low probability). Obtaining confirmation from observations of populations well below carrying capacity, will be difficult.

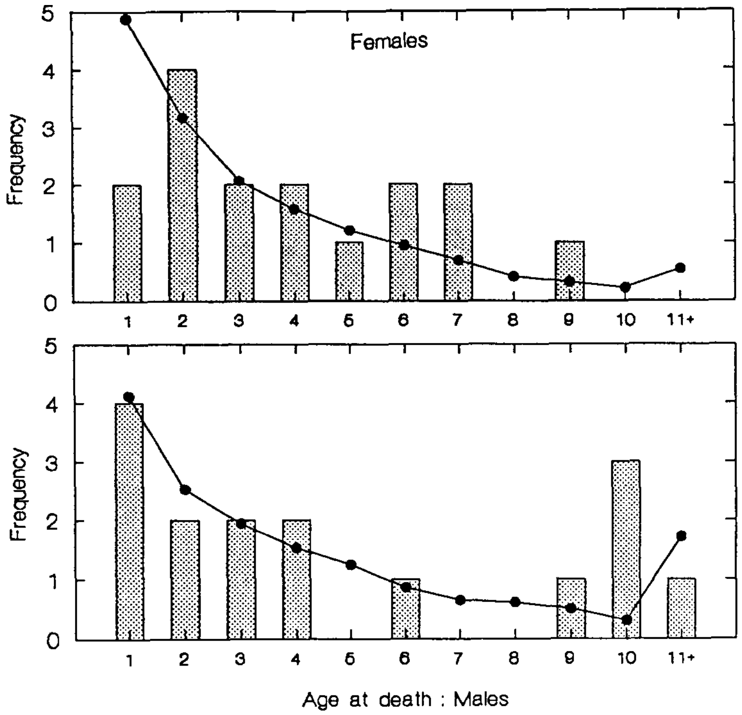

Figure 10. Longevity of blue ducks. Predictions from simulation modelling (filled circles) and data from the Manganuiateao population (bars).

Non-paired adult birds

As explained in the model description, the balance of male and female adult birds is tightly maintained in the study population and an effort was made to duplicate this in the model. Figure 11 shows the distribution of unpaired birds predicted from a simulation run of 500 years, compared with the data from the study population. The model is predicting the occurrences of occasional unpaired males accurately, but also predicts significant numbers of unpaired adult females, which have never been observed. The model also predicts that a population the size of the study population could (rarely) have as many as 6 unpaired males.

This discrepancy between the model and data (unpaired females) may be due to the fact that the study population is not closed. Excess birds, particularly females, probably find territories upstream.

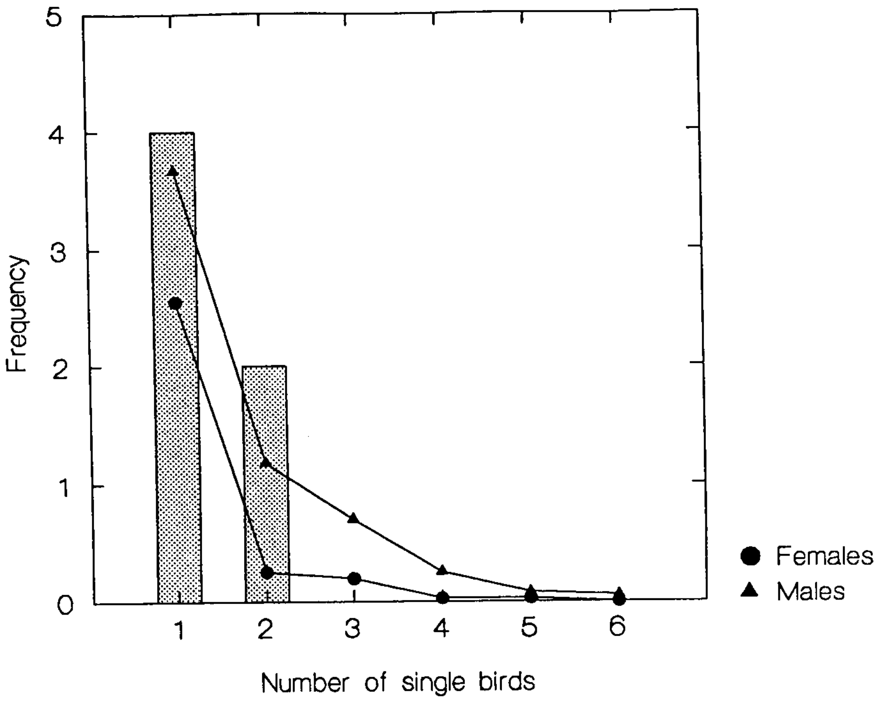

Figure 11. Unpaired adults in blue duck populations. Predicted frequencies of single males (filled triangles) and single females (filled circles) compared with numbers observed in the Manganuiateao population. No single females were observed.

Extinction modelling

Time to extinction

Using the maximum likelihood parameter values estimated from the Manganuiateao study population, 500 populations were simulated till extinction. The distribution of time to extinction is shown in Figure 12, summary statistics are given in Table 8.

Table 8. Statistics of time to extinction (years).

Minimum	4
Maximum	11286
Mean	1808
Variance	3012522
Standard deviation	1736
Skewness	1.65
Kurtosis	3.36
Median	1288

Figure 12. Distribution of time to extinction for 500 simulated blue duck populations.

The distribution is strongly positively skewed. While some populations lasted over 10,000 years, the modal lifetime is about 200 years and the mean time to extinction was exceeded only in 10% of simulated populations.

Probability of extinction

From simulation of 1000 populations, the probabilities of extinction within standard time frames are given in Table 9.

Table 9. Probability of extinction within some time periods

Time period	Probability of extinction
100 years	0.132
20 years	0.012
5 years	0.002

The population can thus be assessed as marginally vulnerable but not endangered by Mace & Lande's (1990) criteria.

Viable population sizes

Values of K that equate with levels of population risk were obtained by varying the slope parameter for adult survival rate. Probability of extinction curves are shown in Figure 13. Estimated critical population sizes are displayed in Table 10.

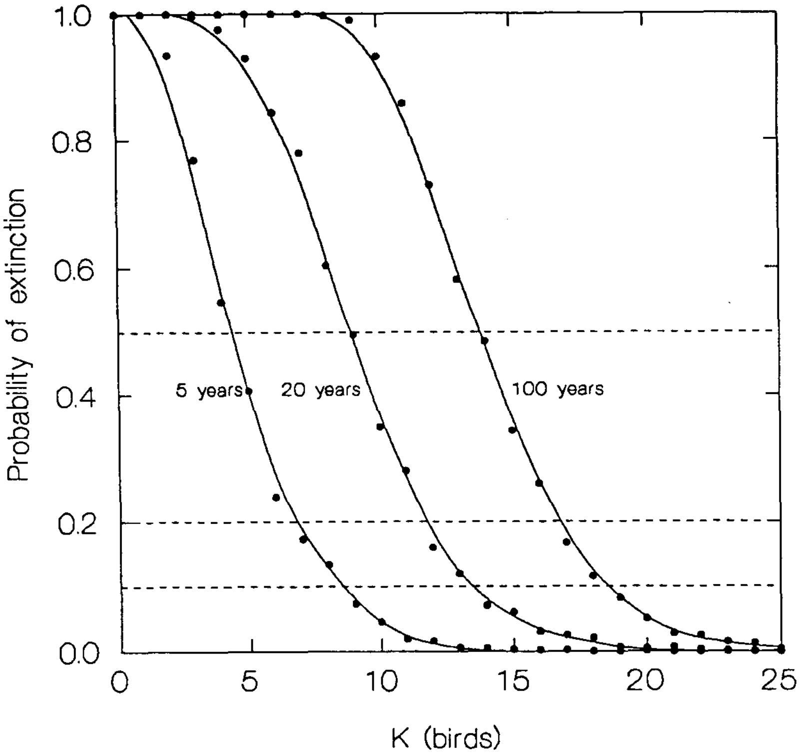

Figure 13. Probability of extinction curves for blue duck populations.

Table 10. Population size and risk of extinction. K is the number of adult birds at equilibrium.

Risk category	Population size (K)
Vulnerable	18.5
Endangered	11.6
Critical	4.4

Sensitivity analysis

Pairs breeding

The likelihood support function for the parameter of a simple binomial distribution can be easily obtained analytically (Edwards 1972). The 2-unit support limits for $n = 14$ and $x/n = .5$ are $p = 0.25 - 0.75$. Simulation results obtained from varying this parameter within 2 support units, and some more extreme values, are given in Table 11.

Table 11. Sensitivity analysis for pairs breeding. p100, p20 and p5 = probabilities of extinction within 100, 20, and 5 years respectively, of the Manganuiateao population. Status: V = vulnerable, E = endangered, C = critical, safe = not vulnerable. K_{end} = critical population size for endangered status.

Parameter (p)	p100	p20	p5	Status	K_{end}
0.0	.174	.028	.000	V	
0.25	.121	.011	.001	V	11.5
0.5 (ML)	.132	.012	.002	V	11.6
0.75	.099	.016	.001	safe	11.9
1.0	.065	.007	.001	safe	

Summary: The proportion of pairs not breeding due to age of the female has little effect on the model predictions.

Fledging rate

The likelihood support surface for the two parameters of fledging rate are shown in Figure 14. Simulation results obtained from selected points on the 2 support unit contour are shown in Table 12.

Estimates of fledging rate parameters have quite broad support limits. The average fledging rate may be anywhere between 1.17 and 1.87 birds fledged per pair, and the error distribution type ranging over binomial and negative binomial. However, this has limited effect on simulation outputs, mainly through altering the predicted carrying capacity. There is a strong relationship between K and the probability of extinction, but predicted K's for endangered status are very uniform.

Table 12. Sensitivity analysis for fledging rate. Label refers to the point identified in Figure 14, K is the equilibrium population size for the Manganuiateao population, other abbreviations as in Table 11.

Label	Parameters mean	 V/M	K	p100	p20	p5	Status	K_{end}
ML	1.481	1.384	18.5	.132	.012	.002	V	11.6
a	1.17	1.70	16.7	.359	.050	.000	V	12.3
b	1.35	3.00	17.7	.294	.032	.002	V	12.7
c	1.59	3.40	19.1	.155	.023	.001	V	12.6
d	1.80	3.00	20.3	.070	.013	.001	safe	12.2
e	1.87	2.15	20.7	.041	.005	.000	safe	12.3
f	1.73	1.00	19.9	.045	.005	.000	safe	11.7
g	1.50	0.65	18.6	.067	.013	.000	safe	11.6
h	1.26	1.00	17.2	.227	.031	.000	V	12.5

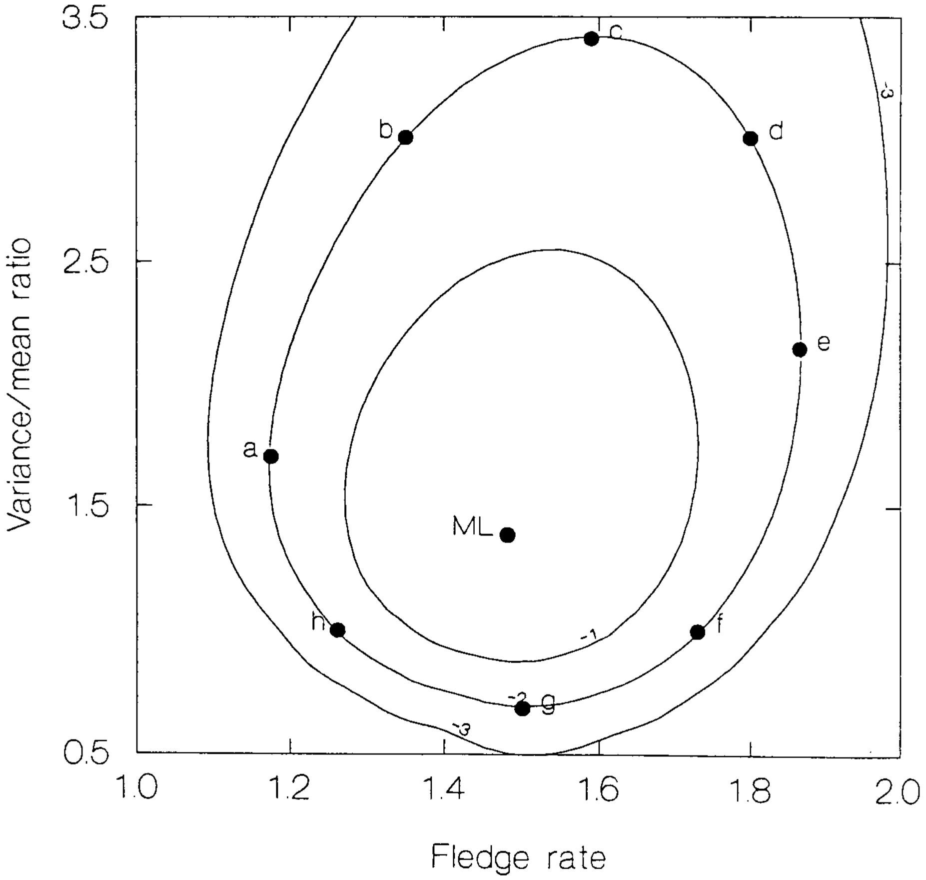

Figure 14. Likelihood support surface for the parameters of fledging rate. Points labelled on the 2-unit contour were selected for sensitivity analysis.

Components of fledging rate

Separate sensitivity analyses of the four components of the fledging were not attempted. Considering the low sensitivity to overall fledging rate, this would add little. However, examination of the V/M parameters (Tables 1 and 2) for these components can indicate their relative contributions to overall variability in fledging rate. Clutch size is apparently very tightly constrained and cannot have a significant role in stochastic extinction. The hatch rate of eggs is more variable, but it is the fledge rate of hatched birds that is the major source of variability in overall fledging rate.

Summary: The model is relatively insensitive to fledging rate parameters.

Juvenile survival

The likelihood support surface for the two parameters of juvenile survival are shown in Figure 15. The support surface is bounded by regions where the likelihood is undefined for the given data, however, extrapolation of the 2-support unit contour into this zone is feasible. Simulation results obtained from selected points on the 2 support unit contour are shown in Table 13.

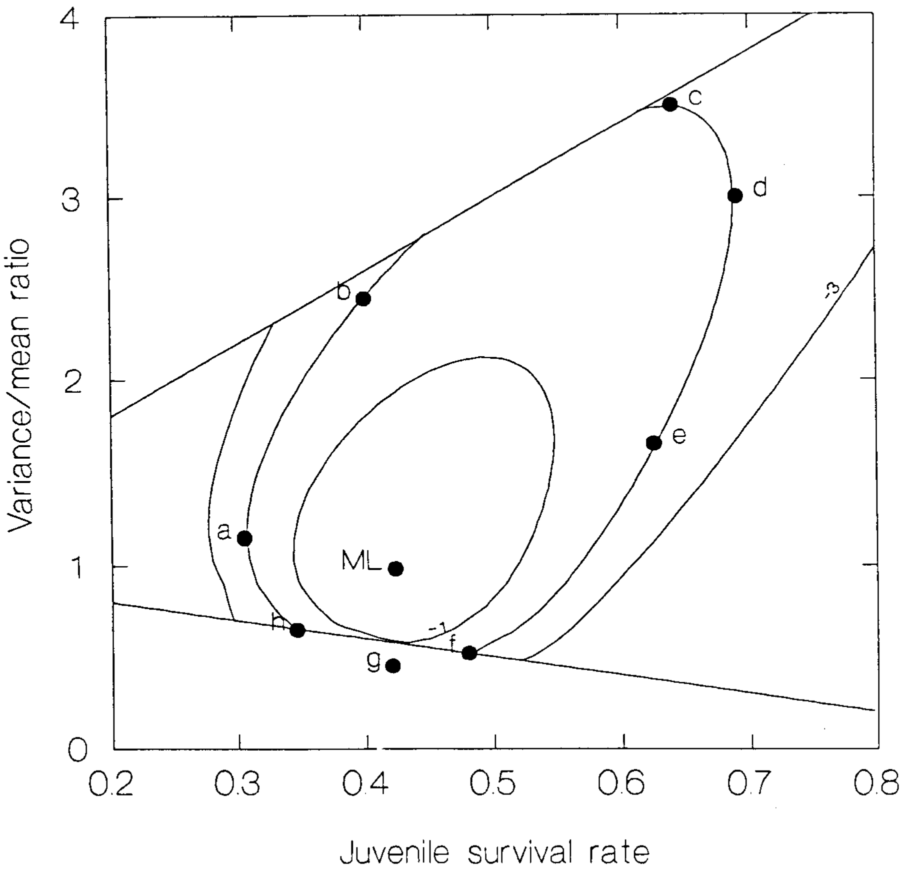

Figure 15. Likelihood support surface for the parameters of juvenile survival rate. Points labelled on the 2-unit contour were selected for sensitivity analysis.

Table 13. Sensitivity analysis for juvenile survival, abbreviations as in Table 11.

Label	Parameters mean	 V/M	K	p100	p20	p5	Status	K_{end}
ML	.423	0.983	18.5	.132	.012	.002	V	11.6
a	.31	1.15	16.3	.398	.043	.000	V	12.0
b	.40	2.45	18.0	.376	.047	.001	V	11.8
c	.64	3.50	22.7	.187	.026	.000	V	14.8
d	.69	3.00	23.7	.171	.020	.002	V	16.5
e	.63	1.65	22.5	.108	.018	.003	V	13.9
f	.48	0.50	19.6	.018	.005	.000	safe	10.5
g	.43	0.45	18.6	.038	.006	.001	safe	10.7
h	.34	0.65	16.9	.134	.018	.000	V	10.7

The estimated mean survival rate of juveniles ranges between 0.31 and 0.69 and the error distribution may be binomial or negative binomial. Varying the parameters within these limits has a similarly small effect on probabilities of extinction as the fledge rate sensitivity analysis, but varying the error distribution does have a noticeable effect on predictions of K for endangered status (between 10 and 16 birds).

Summary: Juvenile survival parameters are more important for predicting extinctions than fledging rates. Juvenile survival is a more variable process and thus has a greater impact on stochastic population dynamics, and at the same time is a more difficult parameter to estimate with precision.

Adult survival

The likelihood support function for the three parameters of adult survival is a four-dimensional surface. Figure 16 shows a sample of points on the 2-unit support boundary. These points define a hollow, 3-dimensional ellipse which is bounded by regions where the likelihood is undefined for the given data. Extrapolation of the 2-support unit boundary into these zones was not attempted. The support surface is narrow and elongated due to the high correlation between slope and intercept parameters. Simulation results obtained from selected points on the 2 support unit boundary are shown in Table 14.

Adult survival is clearly the most important component in this model. Variation of adult survival parameters within their support limits gives widely differing assessments (from fully viable through to endangered) of the status of the Manganuiateao study population, and estimates of a viable population size vary widely.

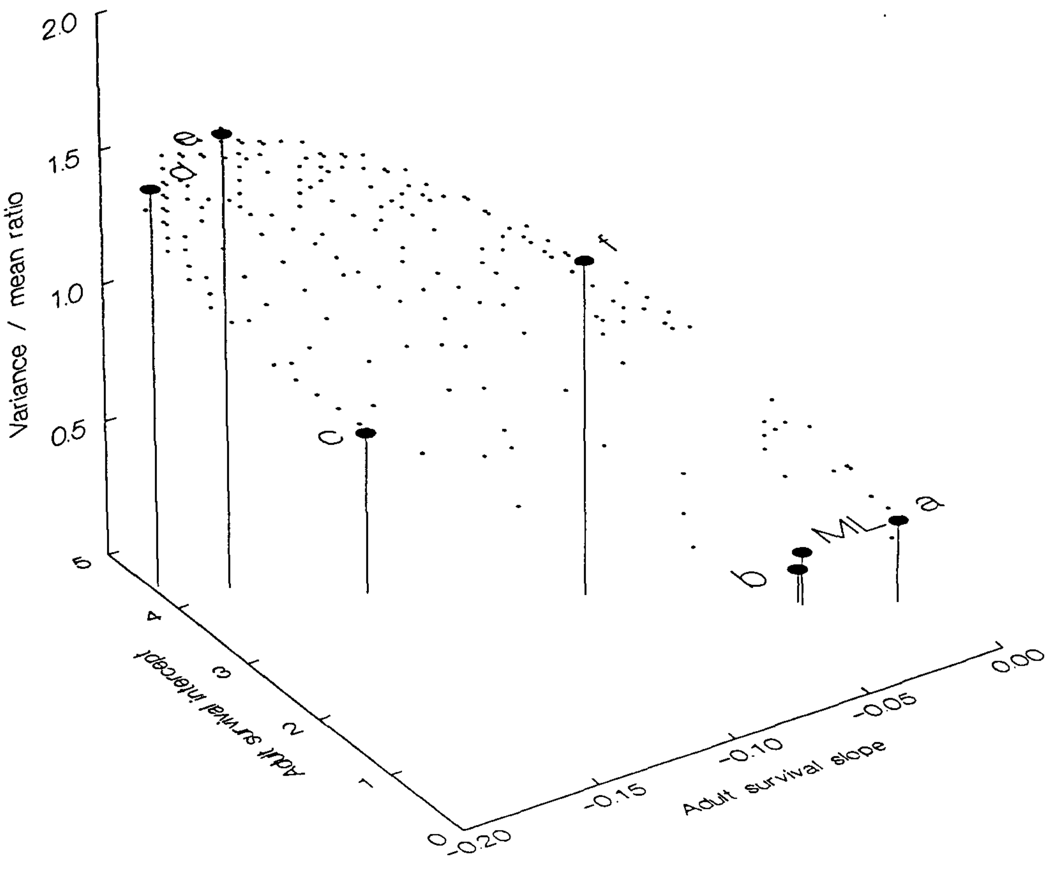

Figure 16. Likelihood support 2-unit contour surface for the parameters of adult survival rate. Labelled points were selected for sensitivity analysis.

Table 14. Sensitivity analysis for adult survival, abbreviations as in Table 11.

Label	Parameters			K	p100	p20	p5	Status	K_{end}
	int.	slope	V/M						
ML	1.387	-.0379	0.194	18.5	.132	.012	.002	V	11.6
a	1.02	-.014	0.32	23.8	.825	.142	.002	V	20.9
b	1.44	-.038	0.12	19.8	.008	.002	.000	safe	10.3
c	3.38	-.147	0.70	18.3	.757	.205	.042	E	19.0
d	4.34	-.198	1.47	18.5	.954	.469	.092	E	25.0
e	4.04	-.180	1.66	18.6	.985	.536	.093	E	26.5
f	2.43	-.091	1.23	19.2	.997	.570	.058	E	25.2

There may be two reasons underlying the great sensitivity of the model to adult survival parameters. Firstly, blue duck are relatively long lived birds, with high potential, but low actual, recruitment rate. A population can sustain several successive years without recruitment, as long as adults continue to survive. High recruitment may be of no value to the population if it is near carrying capacity and available territories are filled, so we can expect adult survival to be an important component in the model. However, adult survival is the one density dependent component in this model, and thus has an extra parameter, an extra degree of freedom with which to vary. Because of this, our estimates of adult survival rates from a small data set are very imprecise. As an indication of this, the initial detection of density dependence was only just significant at the 5% level, so the slope parameter could be close to zero. This has a big effect on the estimation of K (see Table 14), but the biggest effect on extinction probabilities is due to estimates of the error distribution (V/M). As expected, low variability (low V/M) predicts low extinction rates and the higher variability of negative binomial models predicts very high extinction rates. Note that the V/M parameter for adult survival does not range as high as those for fledge rate or juvenile survival (see Tables 12 and 13) so this cannot be the complete explanation for the high sensitivity to adult survival.

Combined sensitivity

The analyses carried out in the previous sections deal with one component of the model at a time. If all components are allowed to vary within their support limits simultaneously, the range of extinction estimates will be even greater. Table 15 shows the best and worst combinations of parameters within these limits and Table 16, the results from simulation. The best and worst combinations differ depending on whether the output is probability of extinction of the study area population, or estimation of K_{end}.

Table 15. Best and worst case parameter combinations for sensitivity analysis

Case	yr. 1 breed	fledge		Juv. survival		Adult survival		
		mean	V/M	mean	V/M	Int.	slope	V/M
best p.ext	.742	1.87	2.15	.48	0.50	1.44	-.038	0.12
worst p.ext	.246	1.17	1.70	.31	1.15	2.43	-.091	1.23
best K	.742	1.50	0.65	.48	0.50	1.44		0.12
worst K	.246	1.35	3.00	.69	3.00	4.04		1.66

Table 16. Sensitivity analysis of best and worst case parameter combinations.

Case	p100	p20	p5	Status	K_{vul}	K_{end}	K_{cri}
best	0.009	.002	.001	safe	13	8	3
worst	1.000	.899	.116	E	?	> 70	12

The results of the combined sensitivity analysis are not very encouraging. Estimates of extinction probabilities and viable population sizes have very wide ranges, beyond reasonable limits. For example, the worst case suggests that we would see many local extinctions of blue duck populations, even on a 5 year time frame, and that the study area population has little chance of surviving for 20 years. Excessive computation times prevented accurate estimation of viable population sizes for the worst case.

A simplified model for sensitivity analysis

Clearly the assumption of independence of model components, implicit in the above analysis, is invalid. For example, we could conceive that juvenile survival and adult survival would be negatively correlated. Loss of territorial birds would provide opportunities for juveniles to establish, thus extreme combinations of adult and juvenile survival are unlikely. Estimating all the correlations between parameters and incorporating this into the model, would make the model unwieldy, and we have a limited data base with which to estimate these correlations. An alternative strategy is to simplify the model by collapsing components of the model, so that correlations between parameters are incorporated into the combined parameter and its error distribution. The simplest such model would have only one component, survival of pairs from one year to the next, and three parameters (intercept, slope and V/M) estimated simultaneously from the series of annual censuses. This 'black box' model will not be as useful for investigating the underlying processes involved in population viability, but it will provide more robust estimates of model sensitivity. A drawback of this approach is that, since all the data (including implicitly the correlations between demographic processes) are estimated from a population that has not gone extinct (it has grown), this simplified model is likely to be too conservative in predicting extinction probabilities.

The same methods for parameter estimation and simulation model construction described in the Methods section were used to construct a one component stochastic population model. It has already been established that, at this level, density dependence can be detected. Figure 17 shows the likelihood support surface for the three parameters and Table 17, the results of sensitivity analysis using the procedures established above.

Table 17. Sensitivity analysis of a simplified model. All parameters and results relate to pairs of birds.

Label		Parameters		K	p100	p20	p5	Status	K_{vul}	K_{end}	K_{cri}
	int.	slope	V/M								
ML	1.711	-.091	.224	7.8	.001	.000	.000	safe	4.9	3.0	1.4
a	1.68	-.09	.56	7.6	.107	.021	.005	V	8.0	4.9	1.9
b	1.40	-.04	.43	10.0	.048	.009	.000	safe	8.9	5.6	1.4
c	1.18	-.02	.30	9.0	.181	.022	.003	V	10.3	4.3	1.5
d	1.59	-.06	.19	9.8	.000	.000	.000	safe	4.7	2.8	1.3
e	1.81	-.09	.18	9.0	.000	.000	.000	safe	4.5	2.7	1.3
f	2.05	-.13	.20	8.4	.000	.000	.000	safe	4.3	3.0	1.3
g	2.31	-.17	.29	7.7	.002	.000	.000	safe	5.0	3.3	1.7
h	2.10	-.15	.47	7.3	.051	.008	.001	safe	6.5	4.5	2.0
i	1.90	-.13	.43	6.9	.033	.004	.001	safe	6.3	4.1	1.7

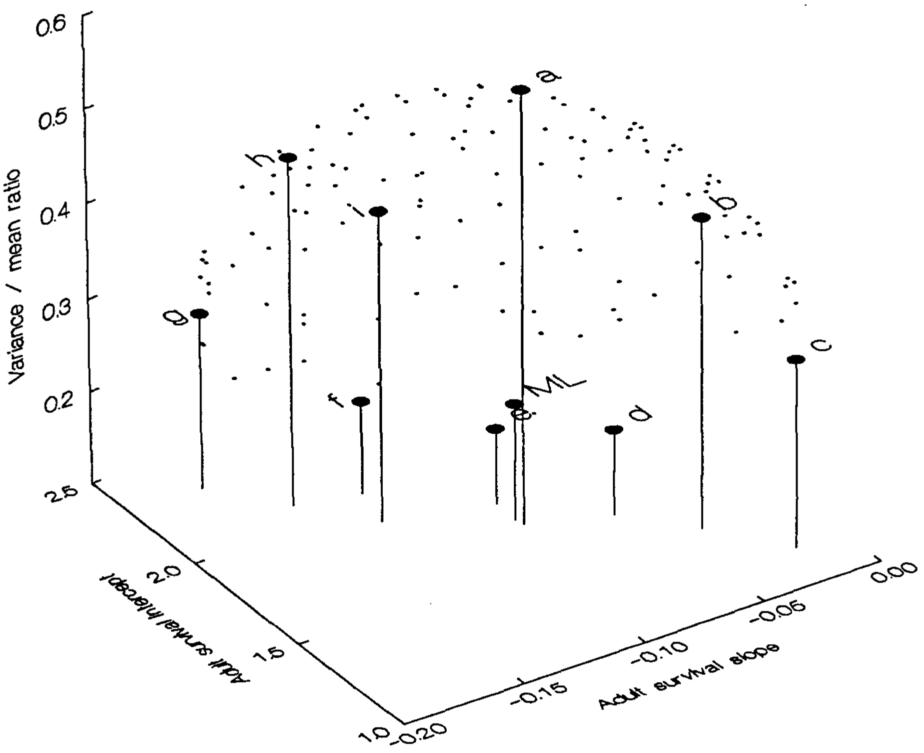

Figure 17. Likelihood support 2-unit contour surface for the parameters of a simplified model. Labelled points were selected for sensitivity analysis.

The simplified model yields more optimistic and less variable predictions than sensitivity analysis performed on the full model. The status of the study area population as either viable or vulnerable is confirmed. Limits on predicted population sizes for viable populations are relatively wide (4 to 10 pairs) but these predictions closely follow the estimates for K in the study population. Support limits for the V/M parameter are very narrow (all well within the range for binomial processes) so the overall population growth process is quite tightly constrained (low 'noise'). The main limitation to accurate predictions of population viability seems to be the difficulty in estimating K (i.e. density dependence).

Differential survival of males and females

The above sensitivity analyses were performed using the same adult survival parameters for males and females. Table 18 compares the output of the full simulation model, using the maximum likelihood estimates for all parameters, with and without differential survival rates for males and females

Table 18. Sensitivity to differential survival rates of males and females

Model	K	p100	p20	p5	Status	K_{vul}	K_{end}	K_{cri}
same	18.5	.132	.012	.002	V	18.5	11.6	4.4
different	17.4	.079	.013	.000	safe	16.9	10.2	3.3

Perhaps surprisingly, incorporation of different survival rates produces more optimistic estimates of population viability. This is because females are usually the limiting sex in pair formation and although the death rate of females is higher, it has a less variable error distribution than for males (see Table 5). The higher variability in the adult male death process has little impact on the population if there is an excess of males. However, when this higher variability is incorporated in a single parameter for both sexes, it does lower the viability slightly.

Recruitment failure

In one of fourteen years of monitoring the study population, no recruitment occurred. This has been attributed to the effects of an El Nino weather pattern in that year, but we have no idea how often such an extreme demographic event will occur. All simulations with the full model have incorporated this type of event as a binomial process with p = 1/14. Figure 18 shows the results obtained when this parameter is varied over its full range.

Events of this type do not result in immediate extinction since adult survival remains high. However, if they become too frequent (every fourth year on average) population viability will be compromised. In the study area, this type of demographic event was due to abnormally stable river flows. In other populations floods or predator irruptions may be the cause of similar events. Catastrophic events that also affect adults, e.g. volcanic lahar or disease epidemic, will have greater impacts.

Extensions of the model

While this model has been designed to answer questions of viability and extinction of isolated populations it can be easily modified to investigate other problems. Three such extensions are briefly considered.

Population establishment.

So far all simulations have begun with a population size equal to the carrying capacity. If the initial population size is much smaller, we can simulate the establishment of a population, and ask questions of the appropriate propagule size for translocation.

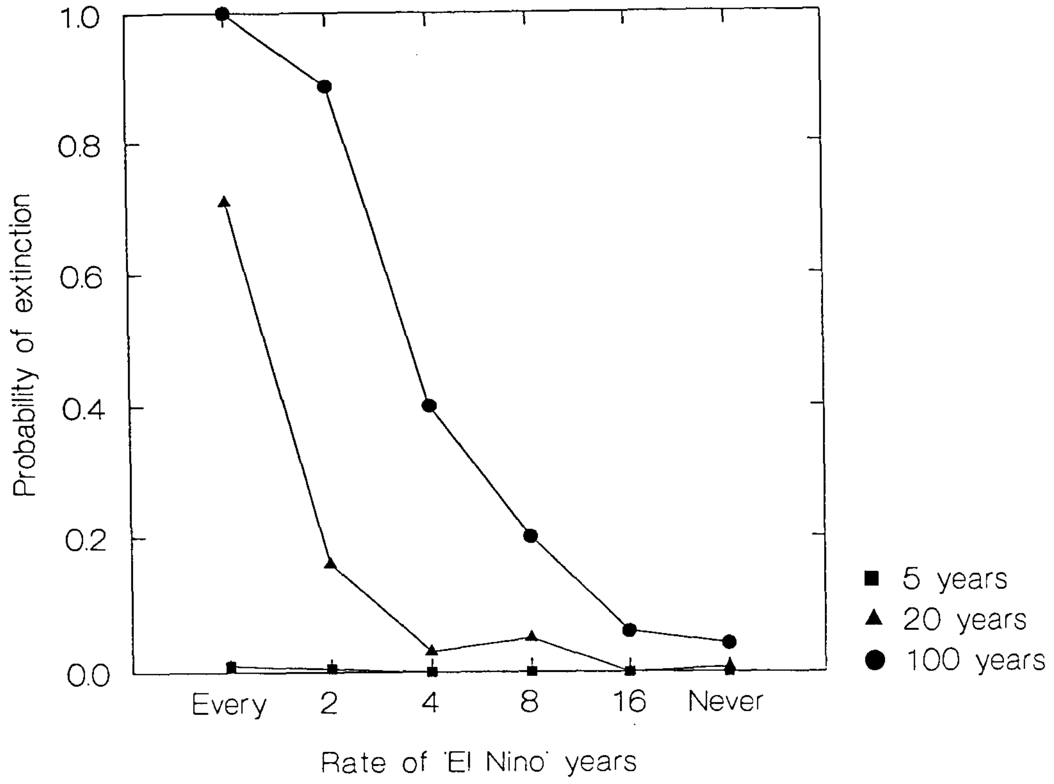

Figure 18. Sensitivity analysis for rate of catastrophic recruitment failure.

Figure 19 shows the results of varying the initial number of pairs while holding all other parameters of the model (including K = 18.5 birds) to their standard values. Three or more pairs in the initial propagule can be considered an acceptable size as their probability of extinction within 100 years is approaching that of a population starting at K. A population started by single pair has a 40% chance of reaching K. These predictions will vary depending on the carrying capacity of the new environment, and also assume that survival and recruitment rates are not affected adversely by the translocation.

Removal of birds for translocation.

If birds are removed from one population to establish a new population (or for some other reason), we will be interested in the impact on the source population. For example the effects of regular removal of unpaired adults, or of pairs could be evaluated. The analysis of recruitment failure provided above can also be used to estimate the impact of removal of juveniles from a population. Removal of all juveniles produced in one year would have the same effect on the population as a year with total recruitment failure (perhaps less if removal is early and the ducks re-nest). If this were to happen less frequently than every fourth year, the model predicts that long term viability of the population would not be significantly compromised. This prediction only applies to a source population with the characteristics of the Manganuiateao study population. Effects of removal of juveniles from smaller populations, or those with lower adult survival, may be more serious but could be estimated with further modelling.

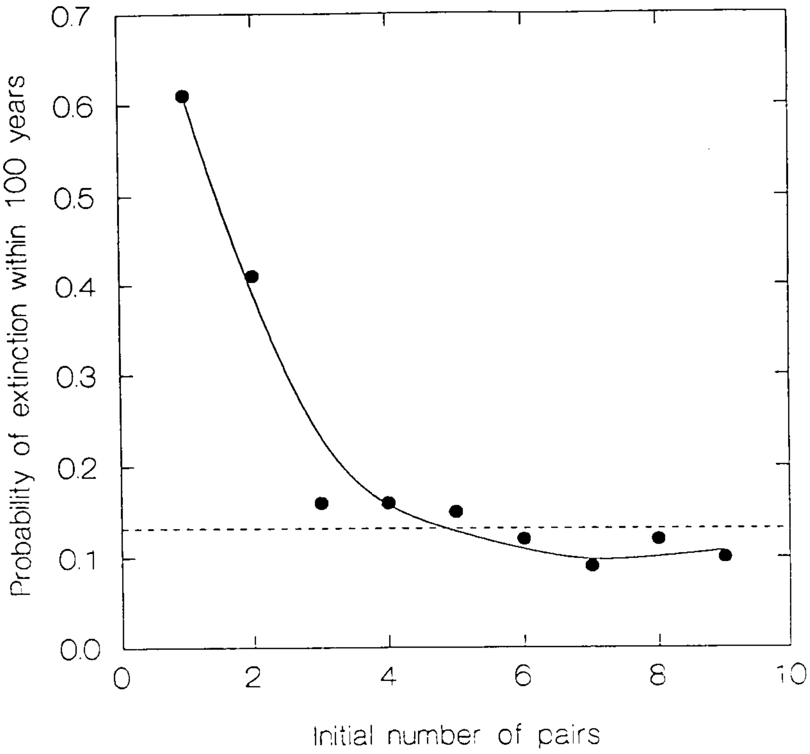

Figure 19. Probability of extinction of small populations established in a habitat with carrying capacity of 9 pairs. Dotted line is the probability of extinction of populations initiated at carrying capacity.

Meta-population analysis.

Blue ducks do not exist in completely closed populations. There is a low rate of movement between river catchments. The viability of the species is a function of the viability of its constituent populations. The results of the modeling suggest that while individual populations of blue duck may be vulnerable or endangered, the species as a whole is viable unless catastrophic events affect all populations simultaneously. However, if all populations are isolated, the extinction of the species is possible through attrition. Meta-population simulations can help assess the importance of inter-population movements (including management-induced movements) to overall species viability. The following exercise illustrates the possibilities.

Consider two isolated populations each with K = 10. From the results of previous modelling, the probability of one population going extinct within 100 years is 0.93 (see Figure 13). The probability of both populations going extinct independently is 0.93 * 0.93 = 0.86. If the populations could be combined, the single population with K = 20 would have a probability of

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