A Spatially Explicit Population Viability Model using GIS: Insights to Dispersal

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Abstract: Population Viability Analysis (PVA) is a Monte Carlo simulation method for estimating the probability of extinction of threatened species. There has been a shift in the use of PVA from absolute species risk measurement to relative risk assessment associated with a ranking of management strategies. Furthermore, PVA models have sought to include more spatially explicit information, like habitat structure and dynamics. Geographical Information Systems (GIS) have long been used as a spatial decision support tool. More recently there has been particular interest in the integration of GIS with simulation modelling. Integrating PVA with GIS will enable us to explore spatially explicit management strategies, eg. habitat restoration or predator control in particular places. We describe a new individual-based, spatially explicit PVA model that integrates with the Environmental Systems Research Institute's (ESRI) ArcView© and ArcInfo© GIS software. Environmental stochasticity is simulated in this model using normal or log-normal deviate random number generators. The model allows the user to choose from a variety of effects that environmental stochasticity and catastrophes have on fecundity and survival. The model simulates both sexes and allows for the Allee effect. This work is still in progress. We discuss the operation of this model and using preliminary data illustrate its application with a threatened species, the Yellow-footed Rock-wallaby (*Petrogale xanthopus*).

1. INTRODUCTION

Population Viability Analysis (PVA) is a Monte Carlo simulation modelling tool for assessing the probability that a species will become extinct in a particular region over a specific period (Possingham 1991). This involves randomly sampling demographic and environmental processes from defined probabilities and analysing their cumulative effects over time (Lacy 1993).

Given that species interact with their environment in space and time, PVA models should be explicitly spatial. Spatially explicit models combine population models with representations of the landscape (Wiegand et al. 1998). PVA models also incorporate stochasticity (Burgman et al. 1993). For example, small populations are particularly susceptible to chance events (Boyce 1992; Lacy 1993) and if the causes of decline are removed, a small population may still become extinct through demographic stochasticity (Shaffer 1981; Soulé 1987).

Many PVA software packages including ALEX, (Possingham and Davies 1995) RAMAS/GIS (Akçakaya 1994) and Vortex (Lacy 1993) have been used to assess the threat of species extinction in a range of applications including forest resource management (Lindenmayer 1996) and reintroduction/translocation strategies (Lindenmayer 1994; Southgate and Possingham 1995).

Our motivation for producing an alternative PVA model has been driven by the need to have a seamless interface between GIS habitat modelling tools and to better facilitate some of the unique characteristics of medium size mammals in semi-arid environments. Interfacing the model with a GIS allows us to more freely manipulate representations of real landscapes, demographic parameters and dispersal strategies and compare these configurations with species persistence without the need to migrate GIS landscape information across to a separate applications.

2. MODEL OVERVIEW

The PVA model we described here has been written in C++ and Avenue® as an extension to the Environmental Systems Research Institute (ESRI) ArcView® 3.2 Geographical Information System (GIS).

We divide the landscape into a regular grid of cells. Each cell holds a static habitat index, which represents the maximum carrying capacity in that cell. We separately model the demographic response of a species to changing environmental conditions by using a environmental variable drawn from a statistical distribution which relates resource availability at time *t* to survival and fecundity.

The model repeatedly steps through an annual cycle of chance environmental, dispersal and demographic events for a specified time period. The model then repeats the simulation and records the extinction and occupancy data at the end of each period.

2.1 Demographic Structure

The model is individual-based. This allows us to follow the fate of individuals throughout their lifetime. Both sexes are modelled using three age classes. Each age-class has a pre-defined survival probability and fecundity probability (females).

Modelling both sexes allows the user to specify the spatial proximity required between mating partners for breeding to occur. This is important for small populations where a lack of mating partners can contribute to a decline in the population (Allee et al. 1949). The mating system is polygamous.

Demographic stochasticity includes the chance fluctuations in survival, fecundity and sex determination. Chance birth and death events are simulated using a binomial pseudo-random variate generator. The number of births $b_i(t)$ born in a particular time step is drawn from a binomial distribution where:

$$b_i(t) = \sim Binomial\left(f_i(x,t) * l, m_i(x,t)\right) \qquad (1)$$

Here $f_i(x,t)$ is the number of potential breeding females of age class x in cell i at time t; $m_i(x,t)$ is the fecundity probability for that age class at time t and l is the maximum number of litters per female in each time step.

The number of animals in a particular age/sex class x that survive to the next age/sex class $x+1$ for grid cell i from time t to $t+1$, is given by:

$$n_i(x+1,t+1) = \sim Binomial\left(n_i(x,t), s_i(x,t)\right) \quad (2)$$

where, $n_i(x,t)$ is the number of animals in a particular sex/age class x for grid cell i at time t and $s_i(x,t)$ is the survival probability for that sex/age class.

The binomial generator uses the 'n' Bernoulli trial algorithm described by Kachitvichyanukul and Schmeiser (1988). This algorithm is also used to draw the sex of each offspring for a given sex ratio.

2.1 Environmental Stochasticity

The fecundity and survival probabilities, $m_i(x,t)$ and $s_i(x,t)$ in Equations 1 and 2 vary annually for a variety of reasons – changing rainfall, temperature or key resources. This is described as environmental stochasticity.

The temporal distribution of rainfall and resources in semi-arid environments tend to be highly skewed (McCallum 1994), hence environmental stochasticity in this model is simulated by sampling a pseudo-random number from a log-normal distribution in each time step.

The mean environmental variable and variance may be entered as two global parameters or alternatively selected as raster grids depicting variable environmental means and variances. The latter option enables us to model meta-populations, which are distributed over a range of environmental conditions.

The following logistic functions (from McCallum 1994) are used to link survival and fecundity probabilities to the generated environmental variates.

$$s_i(x,t) = S(x)\left(\frac{\exp\left(a_s + b_s u_i(t)\right)}{1+\exp\left(a_s + b_s u_i(t)\right)}\right) \qquad (3)$$

$$m_i(x,t) = M(x)\left(\frac{\exp\left(a_f + b_f u_i(t)\right)}{1+\exp\left(a_f + b_f u_i(t)\right)}\right) \qquad (4)$$

Here $u_i(t)$ is the environmental variable in cell i at time step t; $S(x)$ and $M(x)$ are the maximum attainable survival and fecundity probabilities for a sex/age class x; $s_i(x,t)$ and $m_i(x,t)$ are the derived survival and fecundity probabilities for a sex/age class x in cell i and time step t and a_s, b_s, a_f and b_f are fixed parameters.

When environmental variates are drawn from a global mean and variance, a correlation coefficient 'c' specifies the level of inter-cell environmental correlation.

$$E_i = cE_g + (1-c)G_i \qquad (5)$$

Here E_i is the derived environmental variate at cell i, E_g is a global variate and G_i is a grid cell environmental variate.

Density dependence is modelled by truncating the population (starting with younger individuals) at the end of each time step to the maximum carrying capacity defined by the habitat quality variable.

2.2 Catastrophes

We define catastrophes as extreme environmental events such as fire or prolonged drought, which severely lower survival and fecundity. We only allow for catastrophes that affect the entire population. In this context, the distinction between a catastrophe and an extreme environmental event or outlier is entirely academic. However, the advantage of separating global catastrophes from unusual environmental events is our ability to stipulate the probability (or frequency) of a global catastrophe, its maximum duration and net effect on survival and fecundity of all local populations. The frequency of catastrophes is drawn from a binomial variate generator using a specified probability. The duration of the catastrophe (in years) is drawn from a uniform random number generator up to a specified maximum duration. The user also specifies an

environmental modifier, which is a fraction multiplied by all environmental variables generated in the landscape when a global catastrophe occurs in that year.

2.6   Movement

Population models that incorporate landscape characteristics allow us to explore dispersal processes (Pulliam et al. 1992). Only movement related to natal dispersal has been incorporated in this model. The model accommodates active and passive dispersal strategies. An active dispersal strategy is when the individual seeks suitable habitat for survival and reproductive success (Pulliam 1996) whereas a passive dispersal strategy is random. The probability of dispersal also decays with distance. The following negative exponential distance probability function has been adapted from Okubo and Levin (1989).

$$f(x) = e^{-ax} \qquad (6)$$

Here $f(x)$ is the probability density of dispersal for distance x. Parameter a is a constant specific to each sex. For this distribution, the invert of parameter 'a' is the average dispersal distance. The dispersal algorithm simulates each dispersing individual moving from its source cell through the landscape. At each cell the active disperser chooses to move to a surrounding cell with the highest habitat score. The algorithm assumes the animal will search the surrounding cells n number of times before making a decision. This is achieved by drawing separate binomial variates h_j for each cell j using the cell habitat score as the probability in n Bernoulli trails. If n is zero the animal will move randomly to any of the surrounding cells. High values of n indicate a greater search effort. The cell with the highest integer value of h_j is selected for the next move.

$$h_j = \sim Binomial \; (n, p_j) \qquad (7)$$

Here p_j is the habitat quality of the jth surrounding cell and n is used as a measure of the animal's search effort. The individual cannot move back into the cell from where it last moved.

For each move, a random distance is drawn from the distribution in Equation 6. If the cartesian distance the individual has travelled from the origin cell reaches a variate distance drawn from this distribution, the individual ceases to move further. Destination cells are also tested to see if existing occupants have reached carrying capacity.

3.   Modelling the Yellow-footed Rock-wallaby (*Petrogale xanthopus*) in South Australia.

The Yellow-footed Rock-wallaby (*Petrogale xanthopus*) lives in isolated populations in semi-arid rangelands of south-eastern Australia. Predation and habitat degradation from native and introduced herbivores have caused a decline in *P. xanthopus* numbers in the last 100 years.

3.1   Demographic Parameters

Demographic data have been collected from mark and re-capture sampling resulting in 156 captures over seven six-monthly trap seasons at the three sites. Trapping was carried out between March 1998 and February 2001. This work is still in progress. Sites 1 & 2 are 4km apart in the Flinders Ranges National Park S.A. Site 3 is located in pastoral country approximately 24km from Site 2. All sites fall along a linear geological formation. Preliminary data analysis of mark and re-capture data indicates that the average adult survival and trapability is not significantly different between sites {P= 0.063, c^2=8.92(4)} or sexes {P= 0.083, c^2=4.978(2)}. The pooled average adult survival was calculated to be 0.88. Adult survival was also found to best link to the previous 12 months of rainfall (using Equation 3, a = -2.83, b = 0.033, R^2=0.82, 4 trap periods, 23 adults) although few data are available for this to be reliable. Juvenile survival was difficult to measure because few individuals were trapped after being marked as pouch young and the fate of these individuals is unknown. Using crude estimates, juvenile survival at sites 1 & 2 (with fox control) could be as high as 65% and at site 3 (with no fox control), 20%. Fecundity data did not link as well to rainfall (using Equation 4, a = 0.064, b = 0.009, R^2 = 0.37, 4 trap periods, 31 females).

3.2   Dispersal Parameters

There is still little information available on the long term and long distance movement of *P. xanthopus.* Microsatellite and mitochondrial DNA data collected at sites 1, 2, and 3 are currently be analysed by Macquarie University (NSW). Preliminary findings suggest that only a very small proportion of males have moved between sites 1 and 2 (4km) and little or no movement is evident between sites 2 and 3 (24km) (Eldridge, pers comm, 2001.)

3.3   Habitat

Habitat data and areal survey data of *P. xanthopus* collected by the Department for Environmental & Heritage (S.A.) have been collected over a 40x30 kilometre area. Using this information, a habitat index for 1kilometre grid cells has been derived using a technique known as Geographically Weighted Regression (Fotheringham et al. 1998).

4.0   RESULTS

Despite the scarcity of data, the application of PVA modelling can still provide us with early insights to parameter interactions, model performance and priorities

for further field data collection. Sensitivity analysis involves varying parameter estimates and analysing the resulting extinction probabilities (Possingham et al. 2001). Parameter uncertainty includes variations in process and errors in observation and sensitivity analysis can improve our understanding of how these uncertainties might affect model performance. In spatially explicit PVA, sensitivity analysis must also account for uncertainties in the habitat model particularly habitat connectivity, which is important for species movement (Taylor et al. 1993). An exhaustive sensitivity analysis of all model parameters has not yet been carried out and we present the results of only a few parameters.

4.2   Dispersal and Landscape Interaction

Using historical abundance information to guide habitat models is difficult in marginal habitat areas. In these areas there are few animals and the detection of species presence and absence using aerial data is often negatively biased. Grid A in figure 1 was derived using Geographically Weighted Regression and 5 years of estimated abundance data from aerial surveys. However, if species were undetected by aerial surveys in these marginal areas, the habitat scores of these cells could be higher. To test the effect of this, Grid B was modified to include connecting cells capable of supporting only one or two individuals. These two habitat models were then compared with a range of dispersal parameters (Equation 6). Figures 2 and 3 describe the median time to extinction for males and female with equal dispersal parameters 'a'.

Figures 2 and 3 both show that at higher levels of juvenile survival, the median time to extinction increases at higher average dispersal distances (low values of 'a'). In figure 3, the median time to extinction appears to be marginally higher in the less fragmented landscape, Grid B.
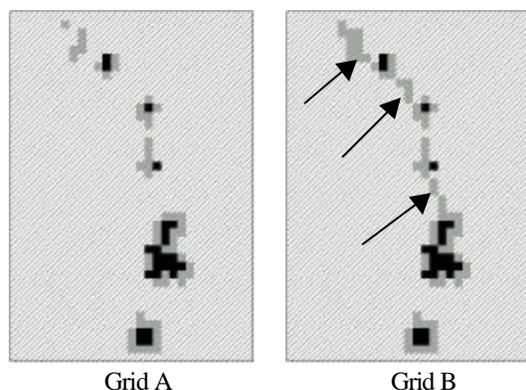

Grid A   Grid B

Figure 1: Habitat grids of 1 km cell size. Darker cells indicate higher carrying capacities. (arrows indicate additional connectivity).
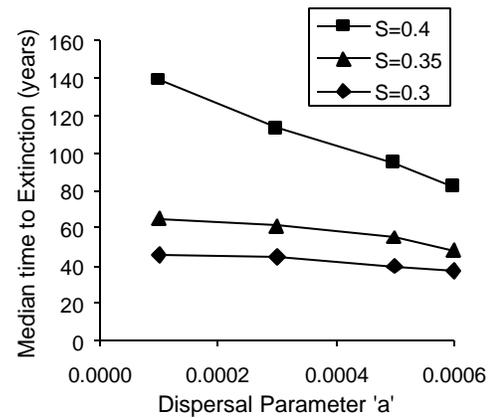

Figure 2: Dispersal parameter 'a' verses median time to extinction for Grid A. S is juvenile survival. Adult survivals kept constant at 0.88.

Johnson (1990) hypothesised that dispersal is male biased in macropods and the genetic data sampled in this study does not negate this hypothesis although there are too few data. Interestingly, further simulations have shown that the median time to extinction was much higher for a range of male dispersal parameters when females had lower dispersal distances.

Not surprisingly, lower male dispersal distances (a = 0.00065) and high female dispersal distances yield lower median times to extinction.

5.0   CONCLUSIONS

These simulations provide some insights about the relationship between dispersal strategies and landscape structure.

For example, at low juvenile survival rates, habitat connectivity and dispersal strategies have little effect on persistence .
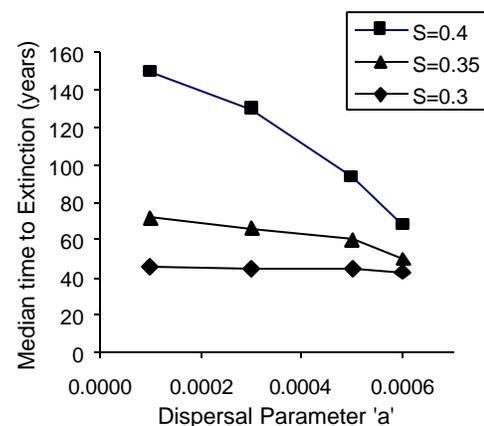

Figure 3: Dispersal parameter 'a' verses median time to extinction for Grid B. S is juvenile survival only. Adult survival kept constant at 0.88.

Further work will focus on the hypothesis of limited female dispersal, modelled for a range of habitat types and juvenile survival probabilities.

The importance of habitat corridors has been reinforced in this study and further field work will focus on gathering abundance and habitat data in the more marginal habitats types where habitat model uncertainties may have arisen from negative biases in aerial abundance estimates.

The approach we have described does not include a genetic sub-model and the effect of limited dispersal would lead to genetic isolation and in-breeding, that may ultimately lead to decline.

The survival parameters we used in equation 3 applied to all age classes because little data was available to measure the response of juvenile survival to environmental stochasticity – this could severely affect our predictions and further field-work is required in this area.

Finally, the dispersal decay function does not penalise the individual's chances of survival with distance and a future version of this model will consider survival associated with dispersal. Future modelling will also need to include all parameters in the sensitivity analysis. Aerial survey data collected by the Department for Environment and Heritage (S.A.), will also be used to investigate other model inadequacies.

6.0   ACKNOWLEDGMENTS

7.0   REFERENCES

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