A Spatially Explicit Population Viability Model using GIS

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Abstract: Population Viability Analysis (PVA) is a Monte Carlo simulation method for estimating the probability of extinction of threatened species. 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).

Keywords: PVA; Simulation; Stochasticity, Extinction; GIS

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 probability distributions 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 is threefold. Firstly, we require a seamless and robust interface between the GIS and the PVA simulation engine. This enables the user to more easily alter landscapes and initiate the PVA tool rather than importing new landscapes with every simulation. Secondly, this model is individual-based and models both sexes which is better suited for simulating small populations where the distance between potential breeding partners may be too great [Allee, 1949]. Finally, the model simulates some of the unique environmental characteristics of semi-arid environments including highly skewed rainfall distributions.

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 offspring $b_i(t)$ born in a particular time step is drawn from a binomial distribution where:

$$b_i(t) = \sim Binomial(f_i(x,t) * l, m_i(x,t))$$
 (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 offspring per female in each time step.

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

$$n_i(x+1,t+1) = \sim Binomial(n_i(x,t),s_i(x,t))$$
(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.

2.2 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 an "environmental variable" from a log-normal distribution in each time step for each cell.

The mean environmental variable and variance may be entered as two global parameters or alternatively selected as raster grids depicting changing environmental means and variances over a landscape. 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.

$$s_{i}(x,t) = S(x) \left(\frac{\exp(a_{s} + b_{s}u_{i}(t))}{1 + \exp(a_{s} + b_{s}u_{i}(t))} \right)$$
(3)

$$m_{i}(x,t) = M(x) \left(\frac{\exp(a_{f} + b_{f}u_{i}(t))}{1 + \exp(a_{f} + b_{f}u_{i}(t))} \right)$$
(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' can be used to experiment with different levels of inter-cell environmental correlation.

$$E_i = cE_g + sqrt(1-c^2)G_i$$
 (5)

Here E_i is the environmental variate at cell i, E_g is a global variate generated from the global mean and variance and G_i is a grid cell environmental variate separately generated from the global mean and variance. Equation 5 does not allow for spatial correlation between cells.

Density dependence is invoked by truncating the population (starting with younger individuals) at the end of each time step to the maximum carrying capacity defined as a multiple of a habitat quality variable in each grid cell.

2.3 Catastrophes

We define catastrophes as extreme environmental events such as fire or prolonged drought, which severely lower survival and fecundity. A more recent version of this model allows for catastrophes that affect either a proportion of the population (local catastrophes) or the entire population (global catastrophes). The advantage of separating 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 carrying capacity, survival and fecundity. The frequency of catastrophes is drawn from a binomial variate generator using a specified probability. 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 the environmental variable and the carrying capacities of each cell when a catastrophe occurs in that year.

2.4 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].

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

Here f(x) is the probability density of dispersal for distance x. Parameter 'a' is the inverse of the average dispersal distance specific to each sex. The dispersal algorithm simulates each dispersing individual moving from its natal (source) cell through the landscape. The disperser moves through the landscape by stopping at each cell and choosing the next cell in which to move according to a selection algorithm (Equation 7). An active disperser would choose to move to a surrounding cell with the highest habitat score. specifies n Bernoulli trials in Equation 7 as an indicator of search effort. This algorithm therefore incorporates an element of stochasticity in cell selection and is analogous to an individual searching the surrounding cells n number of times before making a decision. If n is zero the individual will move randomly to any of the surrounding cells. High values of n indicate a greater search effort. Separate binomial variates h_i are drawn for each surrounding cell j using the surrounding cell's habitat score as the probability for n Bernoulli trials. The cell with the highest integer value of h_i is selected for the next move.

$$h_j = \sim Binomial \left(n, p_j\right)$$
 (7)
Here p_j is the habitat quality of the j^{th} surrounding cell. 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. All moves by the individual to the final destination occur within one time step.

3. MODELLING DISPERSAL STRATEGIES

Spatially explicit Population Viability Analysis allows us to explore dispersal strategies in relation to landscape. By way example we use data collected in this study for the Yellow-footed Rockwallaby (*Petrogale xanthopus*). Field data collection is still in progress.

3.1 Demographic Parameters

P. xanthopus lives in isolated populations in semiarid 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. 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 and is still work in progress. Sites 1 & 2 are 4km apart in the Flinders Ranges National Park S.A and 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, χ^2 =8.92(4)} or sexes {P= 0.083,

 $\chi^2 = 4.978(2)$. Of course and non-significant result does not mean there is no difference... Could the differences be large? 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, R²=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 being analysed by Macquarie University (NSW). Preliminary findings using an assignment test suggest that approximately 4 males (n= 19 females, n=22 males) have moved between sites 1 and 2 (4km) with no movement detected between sites 2 and 3 (24km) in ecological time [Eldridge, pers comm, 2001].

3.3 Habitat

Habitat data have been collected from field surveys and compared with aerial survey data of *P. xanthopus* collected by the Department for Environmental and Heritage (S.A.). Using this information, a habitat index for 1 kilometre grid cells (Figure 1) has been derived using a technique known as Geographically Weighted Regression [Fotheringham et al., 1998].

4. RESULTS

Despite the scarcity of data, the application of PVA modelling can still clarify our understanding of the ecological processes that effect species persistence and extinction. 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. An exhaustive sensitivity analysis of all model parameters has not yet been carried out.

4.1 Understanding Dispersal Strategies

To illustrate the potential of spatially explicit PVA modelling, we describe a few dispersal simulation experiments. Johnson [1990] hypothesised that dispersal is male biased in macropods and although the genetic data sampled in this study does not negate this hypothesis there are too few data to substantiate any claims. Figure 2 shows the results of 500 simulations for a range of dispersal parameters. An active dispersal strategy has been selected in this example (n= 10 in Equation 7), and although little or no data is known about the way this species selects habitat, other experiments using a more passive strategy will be trialed at a later stage for comparison. In Figure 2, high average male and female dispersal distances at line (a) markedly increase the probability of extinction. Conversely, low female dispersal distances for a varying range of average male dispersal distances (line (c) in Figure 2) appear to exhibit a reduction in extinction probabilities. The turning points at approximately 2000m for lines (a) & (c) are interesting and worth further investigation but may be an artefact of the cell size (1000m).

The effect of both males and females dispersing larger distances may therefore decrease the chance of males and females breeding hence increase the probability of extinction.

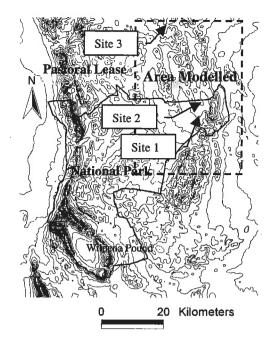


Figure 1. Study Site.

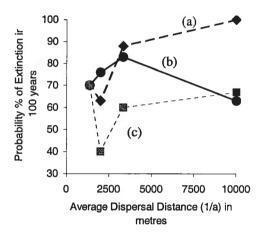


Figure 2. Average dispersal distance verses probability of extinction in 100 years; 500 simulations; adult survival = 0.88, Juvenile Survival = 0.4. Line (a) both male & female dispersal parameters vary; line (b) average male dispersal fixed at 1500 metres and female dispersal varying; line (c) average female dispersal fixed at 1500 metres and male dispersal varying. Similar experiments were conducted for cells with an 80% correlation between environmental variables and a range of other juvenile survival rates. An 'Allee' effect parameter was set so that female breeds only if a male is present in the same cell or a surrounding cell (including diagonals).

4.2 Model Limitations

The approach we have described does not include a genetic sub-model and the effect of limited dispersal would lead to genetic isolation and inbreeding, that may ultimately lead to decline. The inclusion of a genetic sub-model may also provide some insights about the importance of different dispersal strategies for gene flow in different landscape structures.

The survival parameters we used in equation 3 apply to all age classes because only a small amount of data was available to measure the response of juvenile survival to environmental stochasticity however, this could severely affect our predictions and further field work is required. 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.

5. CONCLUSIONS

While PVA are primarily used to model the risk of extinction, it is also useful as a tool to explore hypotheses and help clarify ecological processes when data may be scarce. Spatially explicit PVA enables us to explore the movement and dispersal strategies in relation to the landscape and sensitivity analysis that focuses on dispersal also provides us with a better understanding of the importance of different dispersal strategies and accordingly directs future data collection efforts.

These results are only preliminary but lend support to the hypothesis that dispersal may be male biased. While this is a commonly accepted paradigm for most macropods, few data have been available to support this hypothesis for *P. xanthopus*. Illustrating this through model simulation is not an attempt to prove this hypothesis but through model simulation we may be able to gain further insights to the process that drive these strategies.

This work is still in progress and further work will test a range of dispersal strategies different habitat types and catastrophes frequencies. This may shed some light on the role of dispersal in local population rescue.

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