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decision brief

A guide to good environmental decision making

Leadbeaters Possum (*Gymnobelideus leadbeateri*)
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Principles of population viability analysis (PVA)

A checklist of the basics

Population viability analysis (PVA) is a model-based protocol for characterising and predicting future fluctuations in a species' abundance. PVA is a potentially powerful tool for predicting a species' response to natural and human impacts and for evaluating management options in terms of their contribution to a species' long-term persistence. PVA can be based on models as simple as a single parameter population growth model through to quite complex simulation models that incorporate stochastic landscape and ecological processes, usually involving estimation of many parameters.

In its simplest form, a population growth model characterises the rate of change in the population using a single parameter called the finite rate of population growth R, so that the population size (N_t) at a time t is equal to R multiplied by the population size in the previous time step (t-1):

$$N_t = R * N_{t-1}$$

In most applications of PVA, we usually break down population growth into four components; births, deaths, immigrants, and emigrants. We then model those processes separately. In doing so, we are able to incorporate the range of natural and human influences on those four processes separately and attempt to analyse how each might impact on the long-term persistence of a species. This checklist outlines some of the key considerations and challenges involved in analysing a species' viability using population models.

Elements of good design

1. Vital rates
2. Initial population size
3. Carrying capacity and density dependence in vital rates
4. Life stage
5. Genetic variation
6. Variation over time
7. Immigration and emigration rates
8. Meta-population dispersal
9. Landscape change
10. Unpredictable events
11. Standard outputs
12. Sensitivity analysis

1. Vital Rates

Often we break down R into estimates of birth and death rates. At the population level, birth rate (fecundity: f) is defined as the average number of births in a given time period, and death (or mortality: m) rate is defined as the average number of deaths in a given period. Estimation of fecundity and mortality (often termed the vital rates), and predicting how these rates vary under a range of environmental conditions is at the heart of PVA. Poor estimates of vital rates lead to poor PVA.

For most listed threatened species, estimates of vital rates are published in the literature. Nonetheless, uncertainty about vital rates is often substantial due to natural/geographic/temporal variability, variation arising from environmental (including anthropogenic) forces and interspecific competition, and challenges associated with measuring these rates in the wild (especially for death rates of rare, long-lived species such as large forest owls).

Note that it is often desirable to explicitly model variation in vital rates within a population (among individuals) because differences in responses of individuals (or groups of individuals) to environmental changes or anthropogenic impacts can be very important in determining the fate of a population or species. For this reason, it is common to describe mortality as the probability that an individual will die during a given time period, and fecundity as the number of offspring expected to arise from any individual during a given time period. For convenience, survivorship (s); the probability that an individual will survive a given time period (equal to 1 – the mortality probability) is often used in PVAs instead of mortality.

2. Initial population size

Population models require an initial population size (N0) at a starting time (usually the present or some relevant reference time; t). A relevant starting time might be some 'pre-impact' state, if the aim of the analysis is to understand the role of an anthropogenic stressor on the long-term viability of the species.

For extremely well-studied species with known distributions and good population monitoring data, NØ may be relatively easy to obtain (eg, the orange-bellied parrot). However, for more widespread populations of species with low detectability, for which there exists little reliable population-level monitoring data (eg, southern brown bandicoot), NØ may be very difficult to estimate. For such species, a defensible strategy for estimating NØ is to utilise a species distribution model (SDM), in combination with an estimate (or observations) of the population densities at varying levels of habitat suitability, ranging from best habitat to marginal habitat in an average year.

3. Carrying capacity and density dependence in vital rates

The carrying capacity (K) of a population describes an upper limit on the number of individuals an area can support due to resource limitations such as food, space (in the case of territorial species), or shelter availability (eg, number of hollows for denning).

✓　Are estimates of vital rates based on published demographic data? Where published data are not available, have appropriate estimates been derived from unpublished data, expert opinion or new data?

✓　Is there a defensible estimate of the initial population size?

✓　Are estimates of K, the approach used to characterise variation in K as a function of habitat quality, and density dependence assumptions supported by published evidence?

K may be estimated on the basis of knowing how a limiting resource is distributed in space and time; however, it is more common to estimate K based on observed maximum densities in the wild and then model how K varies with habitat quality (usually defined using a species distribution model; SDM). Depending on the biology of a species and how individuals compete for resources, K may serve as a hard upper-bound population size, or it may be used to define how vital rates change as a population approaches K. When vital rates are based on the relationship between N (population size) and K, this is known as 'density dependence in vital rates'. There is guidance in the literature about how to define K and density dependence in vital rates given basic details about a species' biology.

4. Life stage

✓ Is the stage (or age) structure of the model and the vital rate estimates for each stage justified according to published accounts of the species' biology and vital rates?

For most organisms, fecundity and mortality vary depending on their age, or life-stage. For example, most large mammals have low (or zero) fecundity and high mortality rates in the early years of life, high fecundity and low mortality rates around the age of sexual maturity, and then declining fecundity and increasing mortality in the later years of life.

This variation in vital rates can be modelled by using a stage-based population model where each stage is modelled separately (using its own vital rates). Stages can be defined very flexibly. In some instances it is convenient to define vital rates for species as a function of age in years (or months or days), while for other species, stages are defined using uneven numbers of years (eg, the commonly used human stages of new-borns, toddlers, juveniles, and adults all imply age-categories of differing lengths).

5. Genetic variation

✓ The modelled relationships between population size and genetic influences on vital rates such as inbreeding or bottlenecks should be supported by published data.

Periodic reductions in population size and fragmentation of habitats have been shown to lead to impacts on genetic variation, which in turn may impact on the long-term viability of populations and/or a species. due to inbreeding or genetic bottlenecks that restrict adaptive potential. It is possible to characterise the impacts of restricted genetic variation using PVA, although formal analysis of genetic variation in PVA is not very common and tends to be important only when population sizes are very small. One of the challenges associated with incorporating genetic analyses into population viability is that it is expensive and time consuming to characterise population-level genetic variation, and then relate genetic variation to variation in vital rates. However, if appropriate genetic data are available, then it may provide valuable insights into the impacts of habitat and population fragmentation and reduction resulting from land-use decisions.

6. Variation over time

✓ In the absence of data to estimate temporal variation, has a range of values has been tested with sensitivity analysis?

K and the vital rates vary over time in response to changes in habitat availability and quality, weather, and other random processes such as disease, fire, and predation. This variation is known as 'environmental stochasticity' which can be explicitly modelled using sub-models such as those described in sections 9 and 10 below. 'Demographic stochasticity' is another source of variation in vital rates that results from random differences among individuals in survival and reproduction.

If explicit analysis of those random processes is not relevant to the planned use of the model, it is still necessary to incorporate this variation in K and vital rates because it does influence extinction risk. It is reasonable to implicitly incorporate observed temporal variation in K and vital rates using Monte-Carlo analysis. In the absence of data to support estimation of temporal variation in K and vital rates, it is reasonable to input a range of estimates and report on how sensitive the overall viability assessment is to uncertainty about natural variation in vital rates (see 12. Sensitivity analysis).

7. Immigration and emigration rates

✓ Has the approach to calculating meta-population dispersal probabilities been clearly documented (incl. analysis of geographic barriers to migration between populations)?

Populations that are completely isolated from other populations of the same organism are known as closed populations. If it is likely that a population is closed, then immigration and emigration rates must be estimated because they may have a strong influence on the long-term viability of populations, especially small ones. The process of migrating from one population to another is commonly referred to as dispersal.

8. Meta-population dispersal

✓ Has the approach to calculating meta-population dispersal probabilities been clearly documented (including analysis of geographic barriers to migration between populations)?

A meta-population is defined as a set of populations that are connected by dispersing individuals but which are separated by a geographic distance or barrier that precludes contact between individuals during normal home-range movements.

Habitat fragmentation resulting from habitat destruction or alteration can turn a single population into a meta-population if the process of fragmentation creates gaps between suitable habitat patches that cannot be crossed in the course of normal range movements of a species. Determining whether a species' viability should be analysed as a single-population, a meta-population, or a set of closed populations requires explicit analysis of the home-range movement and dispersal distances of a species.

A meta-population model includes home-range and dispersal distance estimates, which help define the probability that individuals will disperse between populations at each time step. How the probability that an individual will disperse between two patches varies as a function of the distance between the patches is usually represented using a graph called a 'dispersal kernel'. Advice on collecting and analysing range-movement and dispersal data, defining a meta-population structure, and calculating dispersal probabilities is widely available.

9. Landscape change

✓ Planned management activities or unplanned environmental changes that alter K and vital rates should be incorporated in the PVA model in a way that is supported by published precedents.

The distribution of suitable habitat for a species (and hence, the spatial variation in K) varies over time in response to predictable landscape changes such as forest growth, succession and disturbance. Disturbances include the predictable (manageable) disturbances such as timber harvesting and prescribed burning, and less predictable, random processes such as wildfire.

The influence of predictable changes in the landscape on K, vital rates and dispersal (meta-population structure) can be represented using GIS maps of planned activities. These maps can be used to modify estimates of K, s, f and dispersal at specific locations and future times, enabling explicit inclusion

within the population model. It is often analysis of the impact of these planned management activities such as timber harvesting or prescribed burning on species viability that is being assessed with the PVA.

There are numerous published examples of how to go about incorporating planned alterations to habitats in PVA in a spatially explicit way. A particular type of unplanned, but predictable environmental change that may impact on species viability via changes to K and vital rates is long-term changes in weather brought about by climate change. Examples of how to model the impacts of climate change on species viability are now readily available in the peer-reviewed scientific literature.

10. Unpredictable events

✓ Have the range of possible stochastic impacts on a species' viability been considered and included using methods justified by published precedents?

Many of the disturbances that impact on species viability through changes to K and vital rates are highly unpredictable events such as wildfire, disease, and drought. These sort of impacts on K and vital rates can be handled implicitly (see 5. Variation over time) or explicitly using stochastic simulation models. It is possible to incorporate such processes in a PVA because, while it is not possible to know exactly where and when the next unpredictable catastrophe will occur, it is possible to analyse the statistical properties of catastrophes, such as the mean and variance in the time interval between fires, and the mean and variance of wildfire sizes for a particular region. These statistical properties can be used to simulate multiple future landscape scenarios, providing a picture of the likely fate of a species that is subject to random disturbance events. The value of PVA based on landscape scenario models that integrate both predictable disturbance (eg, timber harvesting) and unpredictable disturbance (eg, wildfires) is that the synergistic or additive impacts of multiple disturbance types on viability can be assessed.

11. Standard outputs

✓ Has the choice of model outputs been justified with respect to the aim of the study?

PVA models produce a range of standard outputs including the probability of population or meta-population extinction within a particular time period, the minimum population size that the population is expected to reach within a particular period, or the predicted population size at the end of the simulation which is usually considered in relation to the initial population size (N0).

Graphical outputs include plots of how the population size is predicted to change over the simulation period, predicted changes in K over the simulation period. The result that is most highly emphasized depends on the purpose of the model and the extinction risk status of the species in question. It has been demonstrated that the expected minimum population size (EMP, also known as expected minimum abundance: EMA) is a relatively robust statistic for use in comparing the outcomes of management options. Low extinction probability over a specified period does not equate to low impact; a population might be reduced by 75% in 20 years but still have a low probability of extinction within that period. Predictions of extinction risk or time-to-extinction are seldom reliable because small population sizes are highly susceptible to random disturbances, which are by their nature quite difficult to predict. This is another reason to focus reporting on EMA.

✓   Have sensitivity analyses been undertaken across all uncertain parameters, and the sensitivity of the findings to uncertainty in parameters been described in the report?

12. Sensitivity analysis

Sensitivity analysis provides a picture of how robust PVA model predictions are to uncertainty about model parameters. For example, if there was concern about the reliability of the survivorship estimates used in a PVA for the powerful owl, then it would be reasonable to see how much owl EMA varied under the highest and lowest plausible estimates of survivorship. If the difference in EMA obtained using the high and low estimates of survivorship were trivial, then a reviewer could be confident that the findings of the PVA were not sensitive to uncertainty in the estimate of survivorship.

A similar logic can be applied when considering how sensitive ranking of management options is to uncertainty about estimates of key parameters. If the ranking of management options (based on EMA) do not change across plausible values of a particular parameter, then it is fair to assert that the ranking is not sensitive to that parameter estimate. When uncertainty about parameters is found to be critical in determining the ranking of management options, then the result is said to be sensitive to uncertainty about that parameter. In this case, it may be necessary to (i) invest in obtaining a better estimate of that parameter, or (ii) utilise a decision strategy that accounts for the uncertainty in the parameter estimates (beyond the scope of this checklist!).

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Resources

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