Population Viability Analysis: Theoretical Advances and Research Needs

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Abstract

Population viability analysis (PVA) is a set of tools for forecasting population growth and estimating extinction risk. Recent methdological advances include assessing model reliability by estimating model parameters from time series with observation errors, synthesis of PVA with decision theory, extension of models to sex-structured populations and to density dependence in age-structured populations, and experimental validation of qualitative model predictions. Future research should focus on developing biologically based models of population growth, model selection, and model averaging; extension of models to species with complicated life histories including quiescent stages and seasonal life histories; and developing tools for validly incorporating additional information about species' demography from knowledge of their ecologies and natural histories. PVA is a rapidly developing methodology and users should recognize that a large variety of models and techniques are available for population forecasting.

Resumen

El análisis de la viabilidad de poblaciones (PVA-en ingles) es un juego de herramientas para pronosticar el crecimiento de las poblaciones y para estimar su riesgo de extinción. Avances metodológicos recientes incluyen la evaluación de la validez de los paramentos de modelos de « time series » con errores de observación, síntesis del análisis de viabilidad poblacional con la teoría de decisiones, la extensión de modelos a poblaciones estructuradas por sexo con poblaciones estructuradas por edad, y la validación experimental de modelos cualitativos de predicción. Modelos futuros de investigación deberían enfocarse en el desarrollo de modelos biológicos de crecimiento poblacional, la selección de modelos, el promedio de modelos, la extensión de modelos a especies con historias de vida complejas incluyendo historias de vida temporales y etapas de quiescente, y el desarrollo de herramientas de validación incorporando información adicional sobre la demografía de especies usando conocimiento de su ecología y su historia natural. El PVA es un método en rápido desarrollo y los usuarios deben darse cuenta que disponen de una larga lista de modelos y tecnologías para la predicción de poblaciones.

Population Viability Analysis (PVA) arose in the 1980's as a set of tools for conservation biologists to determine the risks faced by threatened and endangered species (Soulé 1987, Shaffer 1981). Development of PVA was prompted by the emerging extinction crisis and especially by concern for three endangered North American species—Grizzly bear (*Ursus Arctos*), Northern spotted owl (*Strix occidentalis*), and Loggerhead sea turtle (*Caretta caretta*), all of which were featured in early applications of PVA. During this period, important theoretical developments from the 1970's and early 1980's were widely publicized and the first case studies were conducted.

In the early 1990's two important developments occurred. First, Dennis *et al*. (1991) demonstrated how the parameters of the stochastic exponential population growth process could be estimated with regression analysis and how error in these estimates could be propagated through model equations to estimate uncertainty in the chance of extinction. The results from propagating sampling errors are now sometimes called population projection intervals (Lande *et al.* 2003) and are crucial if management actions are to be adequately informed. Second, software for simulating population trajectories on desktop computers became widely available (Lacy 1993). Notwithstanding more recent developments, especially for the analysis of metapopulations and for nonlinear models of population growth, the combination of the stochastic exponential population growth models and publicly available simulation software probably still represent the majority of PVA's being conducted now, a decade later.

The apparent simplicity of PVA, especially when it relies heavily on these two techniques, has repeatedly raised concern that it will be used incorrectly when deciding conservation actions. Recently, Reed *et al.* (2002) reviewed four well-known and common shortcomings of PVA models: (1) Models generally do not consider the spatial distribution of individuals in the population. (2) The practical consequences of uncertain parameter estimates are generally not sufficiently explored through sensitivity analysis. (3) Genetics is rarely considered, even though the deleterious effect of inbreeding on individual fitness is well established. And, (4) the appropriate models for plants are poorly understood compared to models for vertebrates. Importantly, methods to accommodate each of these obstacles exist and are outlined and advocated by Reed *et al.* (2002) as well as in other introductions to PVA (*e.g.* Morris and Doak 2002). There is no reason therefore for future PVAs to overlook these issues, and one hopes that our confidence in model predictions will increase commensurately.

Additional areas of active research are the reliability of model forecasts (Ludwig 1999, Fieberg and Ellner 2000), the synthesis of PVA and tools for structured decision analysis (Possingham *et al.* 2002, Ludwig and Walters 2002), density-dependence in age-structured stochastic populations (Lande *et al.* 2002), experimental validation of model predictions (Drake and Lodge 2004, Belovsky *et al.* 1999), and sex-structured models (Lande *et al.* 2003). No doubt, I have overlooked some topics and still others will be forthcoming. In this active stage of research therefore it is imperative that the practice and theory of PVA develop simultaneously. So, in conclusion, I identify three areas in which research is most desperately needed.

First, PVA's would be greatly improved by the development of more realistic, nonlinear models of population growth, where model forms are derived from the underlying biology of the population growth process, rather than because of phenomenological fit. It is well known that nonlinearity can have important consequences for the predictability of population dynamics, even over very short periods of time. The assumption that population growth is exponential at small sizes is therefore unwarranted, especially among sexually reproducing species or species whose survival depends on cooperation among individuals (Lande *et al.* 2003). Of course, once a set of models has been developed and is reasonably well understood, it still remains to decide which models to use for forecasting (Burnham and Anderson 1998). Finally, it will often be the case that a single model is not obviously best when compared with observed data. Under such considerations, methods for averaging model forecasts will be required if predic-

tions are to be reliable (Burnham and Anderson 1998). This is presently an active area of research in statistics (*e.g.*Hoeting *et al.* 1999) though these techniques have rarely been brought over to conservation biology.

Second, PVA methods should be extended for species with complicated life histories. The standard models allow for age-structure, which is important, but generally assume that population growth is not density-dependent and therefore asymptotically exponential. This is the basis of the Leslie/Lefkovitch matrix formulation of structured population growth. See Caswell (2001), chapters fourteen and fifteen, for an introduction to this topic. Lande *et al.* (2002) have extended the concept of density-dependence to age-structured populations, however other issues remain. Many species, especially non-vertebrates, exhibit quiescent life stages of indeterminate duration. Other species exhibit periodical life histories, while still others exhibit life histories that are determined by environmental conditions. A particularly challenging problem for these species is how to obtain precise and unbiased estimates of parameter values for stages that are not easily observed. This problem is exacerbated when population dynamics are confounded by large sampling error, sometimes the result of extremely large population sizes, *e.g.* seed production wherein every seed constitutes an individual organism, or heterogeneous environments.

Finally, we need better ways of incorporating natural history data when estimating model parameters. Sometimes, the biology of species for which PVA are conducted is very well understood because the species is of great conservation interest. But, because the more familiar techniques for estimating growth rates and variances depend on time series, parameter estimates are wildly uncertain because time series are short. Unfortunately, the timeframe for accurate forecasts attenuates rapidly with parameter uncertainty (Ludwig 1999, Fieberg and Ellner 2000). Therefore, especially when background information is available pertaining to such important factors as the frequency of disturbance events, rates of development, inter-specific interactions, mating system, and behavior patterns, such information should be carefully considered. What we require therefore are statistically meaningful ways of incorporating existing data into the modeling and decision-making process to improve the reliability of long-term forecasts.

PVA's proponents sometimes give the impression that it is a panacea; while it's detractors imply that it is futile. It is neither. It is a tool that through practice and refinement can become increasingly useful. It is just important that practice and theory continue to develop together.

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