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## Population Viability Analyses with Demographically and Spatially Structured Models

H. Reşit Akçakaya

This paper presents a review of demographically structured (or, frequency-based) models, in which the individuals in a population are grouped into distinct classes. Structured models are used when vital rates (survival, reproduction, dispersal) of individuals depend on their age or physiological/morphological stage. Variation in these rates (environmental stochasticity) and the effect of abundance (density dependence) are important factors that determine population viability. Metapopulation models are built by adding information about spatial structure (number of populations, and the location, size, shape, and quality of habitat patches they inhabit). At the metapopulation level, the similarity of environmental fluctuations (correlation) and dispersal among patches become important variables determining viability. These modeling methods can be combined with habitat analyses that link landscape data with metapopulation models.

H. R. Akçakaya ([resit@ramas.com](mailto:resit@ramas.com)), *Applied Biomathematics*, 100 North Country Road, Setauket, New York 11733, USA

Population viability analyses often use models that simulate the future of the species based on parameters on the ecology and demography of its population(s). In demographically structured (also called frequency-based) models, the individuals in a population are grouped into distinct classes, based on their demographic characteristics, or their location, or both. This paper presents a review of structured models, including factors that such models can incorporate, the types of results they give and their advantages and disadvantages compared to the other types of models reviewed in this volume (Lacy 2000a, Sjögren-Gulve and Hanski, 2000).

Structured models that group individuals in a population according to their age (called age-structured models) incorporate age-specific vital rates such as probability of survival from one age class to the next, and fecundity in each age class. Age structure is inadequate to model some species with more complex life histories. These species may be better modeled with a stage-structured model, in which the individuals are classified according to characteristics such as size, weight, physiological, morphological or developmental state. Examples of stages used in such models include juvenile, subadult, adult; and seed, seedling, sapling, understory, canopy. Vital rates in a stage-structured model are rates of transition from one stage to another, which are used to model survival, growth and reproduction.

Spatial structure refers to the location of individuals, which are grouped into sub- or local populations. Different subpopulations may have different demographic characteristics, such as population size (abundance), carrying capacity, and vital rates.

I begin with a discussion of the type of results from structured models, and the type of questions such results may be used to address (see *Outputs from structured models*). In the section on *How to build structured models*, I discuss various factors that are incorporated into structured models, and the methods used for estimation of parameters related to these factors. In later sections, I discuss different uses of structured models, summarize their main assumptions and common data requirements, and review examples of models for different taxa and different type of life histories. In the *Discussion* section, I summarize the advantages and disadvantages of structured models, and discuss cases and questions for which structured models are most appropriate.

## Outputs from structured models

While discussing the details of building structured models in later sections, it is important to keep in mind the types of results such models produce, and how these results can be interpreted. The results of structured models can be expressed in several different ways. Some types of results are based on deterministic measures that attempt to make precise predictions about the fate of a population or species. Examples of deterministic measures include the predicted abundance, and the population growth rate (e.g., the finite rate of increase,  $\lambda$ , estimated as the dominant eigenvalue of the stage matrix; see Caswell [1989] and Burgman et al. [1993], pages 43-44, 127-132). Other types of results are based on stochastic measures, which incorporate variability and uncertainty by expressing the results in probabilistic terms. These measures include risk of extinction, risk of decline, and time to extinction.

Deterministic measures such as the finite rate of increase only reflect the state of the population at a given time, and may not anticipate the future behavior of the population. For example, a large but fluctuating population may have a higher risk of extinction than a smaller but less variable population. The deterministic growth rate ignores this variability as well as the distribution of individuals to age classes or stages. Because of these two factors, deterministic projections with finite rate of increase will be incorrect in the short-term (up to one generation or so). In the long term, factors such as density dependence and trends in habitat and vital rates may cause deterministic predictions to be biased. The only general statement that one can make about population growth rates is that for most species, the long-term average is around 1. When short-term growth rate is less than 1.0, it may mean that the population is declining because of a decrease in average values of vital rates (“systemic pressure” as defined by Shaffer 1981), or it is undergoing fluctuations (and in the period that it was observed, it happened to be declining), or it is returning to an equilibrium as a result of density dependent mechanisms. When short-term growth rate is above 1.0, this may be because of a temporary increase, and may not mean that the population is safe in any sense meaningful for conservation and management.

Natural variability in population dynamics is compounded by uncertainty in the population parameters due to lack of perfect information (i.e. ignorance). The consequent difficulty of making precise predictions has shaped the language of population viability analysis (e.g., see Shaffer 1990). The conservation-related problems and questions that PVA addresses are usually phrased in terms of probabilities; for example, we may want to assess the probability of extinction or the chance of recovery from a population bottleneck. Stochastic PVA measures are probabilistic expressions of population viability such as these. The concept of minimum viable population (MVP) is also phrased in terms of probabilities (Shaffer 1981), for example as the minimum size of a population that has a 90% chance of surviving for the next 100 years. Mace and Lande (1991) categorized levels of threat in probabilistic terms; they defined, for example, a “critical” population as one with a 50% chance of extinction in the next 10 years. Deterministic measures such as population growth rate or population size cannot address conservation questions in these probabilistic terms, but stochastic PVA models do.

### Extinction risk assessment

Risk is defined as the probability of an unwanted event (such as an extinction or population decline). Extinction risk assessment attempts to assess the likelihood of a population or species extinction (or decline) by some specified time in the future under various natural conditions and scenarios of management.

The results of risk assessment can be expressed in different terms. One of the commonly used variables is **extinction time**, i.e., predicted time until a population or species goes extinct. Reporting only the **mean extinction time** may be misleading, because distribution of extinction times is often skewed, with a heavy right tail (Fig. 1). Therefore, a proportion of populations go extinct at times much later than average, having a disproportional impact on the arithmetic mean. This also means there is a substantial probability that the population will go extinct much earlier than the mean extinction time.

This problem can be avoided to some extent by expressing the predicted extinction time in terms of the **median extinction time**. However, reporting only the median may lead to a wrong perception of the threat the population faces. The level of threat is communicated better by specifying the whole **distribution of extinction times**, e.g., by plotting is the *cumulative* probability distribution, which shows the probability of extinction *at or before a specific time step*. A cumulative distribution of extinction times increases

monotonically, and asymptotically reaches a probability of 1.0 for very long time periods (the probability often does not reach 1.0 in models with medium to long time horizons, especially if population is growing or immigration is assumed).

Extinction time can be made more general and useful by incorporating partial decline, or quasi-extinction (Ginzburg et al. 1982). Thus, the result becomes (the distribution of) the time (e.g., number of years) until the population declines below a predetermined threshold (see Fig. 2). This is useful because most models, and especially structured models, are unreliable at simulating the true dynamics of very small populations consisting of a handful of individuals. This is because there is often insufficient information to incorporate factors such as inbreeding depression and Allee effects (see *Adding density dependence* below) that affect small populations (see Lacy 2000a).

The threshold used in calculating quasi-extinction times depends on the question addressed and the biology of the species. A particular level may represent an anthropogenically significant threshold, as in the case of economically important species. It may also represent a biologically critical level of abundance. For instance, at low abundances, inbreeding depression can grow sharply in severity, or individuals may simply not be able to locate mates, or other Allee effects may come into play that were negligible at higher abundances. It is often very difficult to predict the behavior of a population once it reaches a very low level, because of these complicating demographic and genetic factors. It may be easier and more conservative to calculate quasi-extinction risk, i.e. the probability of a decline to a level where such effects are suspected of becoming dominant factors.

A different type of measure concentrates on the probability of extinction. The simplest measure of this type is simply the **extinction risk**, which is the probability that a population will go extinct within a specified time period. As with extinction time, it may be better to incorporate a partial decline. This is done by expressing the risk as **quasi-extinction risk**, which is the probability that the population will fall below a set of threshold population sizes *at least once during a fixed time period*. If the threshold is zero, then the quasi-extinction risk is the same as the extinction risk.

Alternatively, the risk can be expressed as a function of the amount of decline, i.e., as a function of the threshold abundance. The quasi-extinction risk can also be expressed as *the risk of declining by a given amount from the initial population*, i.e., as the probability of decline as a function of percentage decline from the initial population size (see Fig. 3).

These types of outputs can be used to assess the threat faced by a population or species, to compare different types of human impact, to evaluate different conservation or management options, and to plan fieldwork. These will be discussed in more detail below (see *How to use structured models*).

## How to build structured models

### Selecting demographic structure and estimating vital rates

In a demographically structured model, the population abundance is represented by a set of numbers (one for each age or stage class), instead of a single number for the whole population. See Box 1.

Using an age-structured model requires that the age of organisms is recorded when collecting the data necessary for estimating vital rates (survival rates and fecundities). Stage structure is more appropriate when

- (1) the available information is limited to cruder categories such as juvenile and adult,
- (2) the demographic characteristics of organisms (their probability of survival or fecundity) is determined by their size or other physiological characteristics, rather than their age,
- (3) growth is plastic, i.e., some individuals exhibit accelerated or retarded growth relative to others, or even regress (for example, decrease in size).

The first step in determining the stage matrix is to decide on what the stages are. This mostly depends on the life history of species studied. If the stages are defined on the basis of the size of organisms, then the number of stages, and the size limits for each stage must also be decided. This may be a complicated problem. On the one hand, it is necessary to define a sufficiently large number of stages so that the demographic characteristics

of individuals within a given stage are similar. On the other hand, it is necessary to have a sufficiently large number of individuals in each stage so that the transition probabilities can be calculated with reasonable accuracy (see Vandermeer [1978] and Moloney [1986]).

**Box 1.** Formulating an age-structured model of a species that lives for 4 years. The population abundance  $N$  is represented by a vector of 4 numbers:

$$\begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{bmatrix}$$

where  $N_i(t)$  represents the number of  $i$ -year-old individuals at year  $t$ . In models with age or stage structure, vital rates such as survivals and fecundities are often organized in a transition matrix. For an age-structured model, such a matrix is called a Leslie matrix. An example of Leslie matrix (for four age classes) is

$$\begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix}$$

where  $F_i$  and  $S_i$  are the fecundity and survival rate, respectively, of the  $i$ th age class. Each row (and column) corresponds to one age class. In a stage-structured model, each row (and column) of the transition matrix corresponds to one stage. The element at the  $i$ th row and  $j$ th column of the matrix represents the rate of transition from stage  $j$  to stage  $i$ , including survival, growth and reproduction.

Multiplying the transition matrix with the vector of abundances at year  $t$  gives the vector of abundances at year  $t+1$ :

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \end{bmatrix} = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix} \times \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{bmatrix}$$

Repeating this multiplication allows the model to predict the abundance in future years. For more information on matrix models, see Caswell (1989), Burgman et al. (1993) and Akçakaya et al. (1999).

The estimation of the matrix elements depends on the type of data available. If all individuals in a population can be followed through at least two time steps, and their age class or stage at each time step recorded, these data can be used to estimate each vital rate for each time step (except the last one). If, instead of following each individual, the abundance of individuals in different stages or age classes can be estimated for several time steps, these data can be used in a multiple regression analysis. For methods of data analysis using these approaches, see Caswell (1989) and Akçakaya et al. (1999).

Another commonly used method for estimating abundances and survival rates for an age or stage-structured model is a mark-recapture study (also called a capture-recapture study; see Pollock et al. 1990, Burnham and Anderson 1992, Lebreton et al. 1993). The analysis of mark-recapture data for estimating vital rates is facilitated by specialized software, such as the program MARK (<http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>), developed by Gary White.

When fecundity estimates are based on birth rates or nest surveys, these must be combined with the survival rates to calculate the fecundity element in the stage matrix (see Jenkins 1988, Caswell 1989, pages 8-15; Burgman et al. 1993, pages 127-129 and 140-142; and Akçakaya et al. 1999, pages 136-141). This is because, in a matrix model, fecundity is the average number, per individual alive at a given time step ( $t$ ), of offspring censused at the *next* time step ( $t+1$ ). Thus, fecundity depends on:

- (a) the proportion of the age class or stage that are breeders,
- (b) reproductive success (e.g., number of fledglings per nest in a bird species),
- (c) sex ratio (e.g., proportion of females at birth),
- (d) survival of breeders from census to next breeding, and
- (e) survival of newborns from birth to next census.

If, in a stage-structured model, the reproductive stage is “breeders” (instead of, say, “adults”), then (a) is obviously 1.0. If not all adults breed, then the transition rates between stages must reflect this. If only females are modeled (which is common; see *Adding sex structure* below), then (c) is the proportion of females at birth (i.e., 0.5 if 1:1 sex ratio is assumed). Most matrix models are parameterized either as post-breeding or pre-breeding census, and thus either (d) or (e) is assumed to be 1.0 (but never both). For parameterization of matrix models with post-breeding and pre-breeding assumptions, see Caswell (1989) and Akçakaya et al. (1999).

Fecundity may also be based on regression of the counts of first stage (the stage that individuals start their life in) on the counts of individuals in reproductive stages in the previous time step (see Akçakaya et al. 1999).

### Estimating initial abundances

Demographic models predict the abundance of individuals in each age (or stage) class through time, given the *initial* number of individuals in each age or stage. How much the total initial abundance affects extinction risks depends on other factors, particularly vital rates, density dependence and stochasticity. For some models, it may not have much of an effect. However, the distribution of the initial total abundance to classes (i.e., the initial proportion of individuals in each age or stage) may still have important effects on persistence of a population (Burgman et al., 1994).

There are various methods of estimating total abundance or its distribution to age/stage classes, including censuses, aerial surveys, mark-recapture studies and transect surveys. In variable-distance line-transect surveys, distances to the observed birds are used to fit a function of declining detection probability (Buckland et al. 1993). One program that does such fitting is DISTANCE (Laake et al. 1996; <http://www.ruwpa.st-and.ac.uk/distance/>). This program is used to analyze distance sampling data, including line transects, point transects (variable circular plots) and cue-counts, to estimate density and abundance of a population.

### Adding variability

Natural environments often change in an unpredictable fashion, causing changes in a population’s vital rates. Since these rates are partially a reflection of the suitability of the environment for growth, this type of variation is called *environmental stochasticity*. Extreme environmental events that adversely affect large proportions of a population are called *catastrophes*. Catastrophes may in some cases be considered to be a source of environmental variation that is independent of the normal year-to-year fluctuations in vital rates, carrying capacities, or other population parameters. When the number of individuals gets to be very small there is another source of variation that becomes important even if the population growth rate were to remain constant. This variation is called *demographic stochasticity*. For example, if there are 3 individuals in an age class, and if the survival rate for this particular time step is 0.4, the number of survivors can be calculated by assuming that each individual has an independent probability (0.4) of surviving. Thus, the number of survivors may be 3 (with probability  $0.4^3$ ) or 0 (with probability  $[1-0.4]^3$ ) or any other number in between (with the corresponding binomial probability).

Environmental stochasticity is usually modeled by sampling the vital rates (fecundity and survival rates) and other model parameters (such as carrying capacity or dispersal rate) in each time step of the simulation from random distributions with given means and variances. The variance of these distributions should be based on

temporal variance in the observed rates. This method is called “element selection” because each element of the matrix is selected randomly.

Another method of modeling environmental stochasticity is “matrix selection,” i.e., selecting randomly from a set of matrices (see e.g., Cohen 1979, Bierzychudek 1982). For example, if two different matrices are considered to represent good and bad years, one of the two can be randomly selected at each time step of the simulation and used in population projection. The advantage of this method is that it uses only observed vital rates, and does not make assumptions about the type of statistical distribution for these rates. The disadvantage is that, if the number of matrices is small, the range of the observed vital rates may underestimate their long-term ranges. Consequently, the matrix selection method can underestimate long-term variability, and hence the extinction risk. Matrix selection method is used in the simulation program POPPROJ2 (Menges 1992); in addition, the programs RAMAS GIS (Akçakaya 1998) and RAMAS Stage (Ferson 1990) can be used to model both element selection and matrix selection methods.

Demographic stochasticity can be modeled by sampling the number of survivors or dispersers from binomial distributions, and number of offspring (recruits) from Poisson distributions (Akçakaya 1991). Catastrophes are modeled by adding rare, random changes to model parameters or variables. For example, a 100-year-flood can be modeled by making these changes with a probability of 0.01 per year. If a flood kills half the population, its effect can be modeled by multiplying the number of individuals with 0.5 whenever a catastrophe occurs in the model.

There are several other important points to consider when adding variability to a model, see Box 2.

### **Adding density dependence**

As a population grows, the effect of limited resources on population growth results in density-dependent feedback that limits population growth. This type of density-dependence can be incorporated into a matrix model by allowing the matrix elements (vital rates) to decrease as population size increases. Density dependence may have significant effects on the risk of extinction of a population. For example, a density-independent model with growth rate of 1.0 and a density-dependent model may give similar average trajectories, but the variability (hence, the risk of decline) of the density-dependent model will often be less due to the stabilizing effects of density dependence. Thus, in the absence of information, a density-independent model may be used for conservative assessment (Ginzburg et al. 1990).

The simplest type of density dependence involves truncating total abundance at a ceiling. Modeling other types of density dependence requires selecting a function, and estimating its parameters. Some of the commonly used types of functions can be parameterized in terms of (1) a maximum rate of growth when density is low, and (2) a carrying capacity or an equilibrium abundance (Akçakaya 1998). However, detecting density dependence and estimating its parameters can be a complicated problem (Burgman et al. 1993, pages 87-91).

Population growth may also be affected negatively as population size reaches very low levels. The factors that cause such a decline (e.g., difficulty in finding a mate or disruption of social functions) are collectively called Allee effects (see Lacy 2000a). If a population declines to a critical level, if only by chance, then Allee effects can pull it down even further. Such phenomena can dramatically influence the risks of quasi-extinction, especially for small or fragmented populations. Modeling Allee effects involves more complicated density-dependence functions. A simple way is to use a quasi-extinction threshold instead of a threshold of zero, i.e., instead of extinction risk, to estimate the risk of decline to a level where Allee effects are suspected to become important.

### **Adding genetics**

Certain simplifying assumptions allow incorporating the effects of genetics to single-population structured models (Mills and Smouse 1994). For metapopulation models, this is complicated by exchange of individuals among populations by dispersal. Thus, realistic models that incorporate genetics are often individual-based (Lacy 2000a). However, for most species, a more fundamental problem is lack of information on the interaction between genetic and demographic factors, including the effects of inbreeding on demographic parameters. In the absence of this crucial information, one precautionary approach might be to model Allee

effects, or to use a relatively large threshold for extinction. Another option might be to consider the results as a lower bound estimate of the extinction risk. However, in a study designed to validate PVA models, Brook et al. (2000) found that even models that did not incorporate genetics did not underestimate risks.

**Box 2.** Important points to consider when adding variability to a structured demographic model.

1. The observed variance often includes effects of sampling variance (measurement error) and demographic stochasticity, which must be subtracted from total observed variance. Otherwise the model may overestimate variability, hence the extinction or decline risk.
2. The model should allow putting constraints on parameter values, such as limiting survivals to the [0,1] range, and constraining fecundities to be positive. In stage-structured models, the sum of all survival rates from a given stage (for example, probability of remaining in the same stage and growing to the next stage) must be constrained to be  $\leq 1$ .
3. Even if the sum of such transitions is less than 1.0, variation introduced by demographic stochasticity may make the number of individuals surviving from a given stage larger than the number in the stage in the previous time step. This must be corrected.
4. The truncation of sampled values may introduce a bias, so that the realized mean of, say a survival rate, is different from the average value used as the model parameter. This can be corrected by changing the shape of the distribution, by pooling the variance of all survival rates from a stage, or by introducing a different correlation structure. Changing correlation structure applies only in the case of stage-structured models in which transitions from one stage to two or more stages are possible. For example, suppose there are 2 survival rates from a particular stage (say, “small”) in a size-structured model: 60% of the individuals stay in the same stage, 35% grow to the next stage (say, “medium”). Because the total of these three transitions (0.95) is large, if each of them is sampled with large variances and with a correlation of 1.0 among them, truncations may occur. However, a large variance, combined with this mean can only mean that in years when a lot of individuals stay in the same stage, there are few that grow to the next stage, and vice versa. This suggests a negative correlation between the proportion that stay in the same stage and the proportion that grow to the next stage (Akçakaya 1998).
5. A high value for the correlation of vital rates among stages (or among populations of a metapopulation; see below) results in higher variability, and higher risk of decline. Thus, when correlations are not known, assuming full correlation rather than independence gives results that are more conservative or precautionary.
6. The number of replications determines the precision (but not the accuracy) of the risk estimates. Each simulation should be run with a minimum of 1000 replications (see Akçakaya & Sjögren-Gulve 2000). The accuracy of the risk estimates is determined by the measurement error in model parameters, including biases in estimation methods. Uncertainty should be incorporated in the form of ranges (lower and upper bounds) of each model parameter.
7. Simulations with catastrophes assume that such a catastrophe did not happen in the period when the demographic data was collected. If data included a catastrophe, then the estimates of demographic rates should exclude those catastrophe years (see Akçakaya and Atwood 1997). Otherwise, the combined effect of modeled catastrophes and environmental stochasticity would overestimate the actual variability in vital rates, and underestimate their means.

### Adding sex structure

Many structured models concentrate on a single sex; usually only the females are modeled. In species where one male can mate with several females, the number of males may not affect the total fecundity very much, and only females should be modeled. For other species, it is possible to develop models that include both sexes, but this requires additional information about reproduction. In particular, the contribution of males to fecundity (which is likely to be frequency-dependent) must be known. In models of monogamous species with only one breeding stage, fecundity can be expressed simply as number of offspring per breeding pair, multiplied by the minimum of the number of males and the number of females in the breeding stage. If more than one age class is reproductive, or if breeding is not monogamous, the frequency dependence will be more complicated.

### **Adding spatial structure**

In addition to the factors discussed above that affect the dynamics of populations, there are spatial factors that operate at the metapopulation level. These include, for example, the number and geographic configuration of populations within the metapopulation, distances and the rates of dispersal among populations, and the degree of similarity of environmental fluctuations experienced by different populations.

Dispersal refers to the movement of individuals among populations, which may lead to recolonization of vacant patches (i.e., extinct populations) by immigration from other (extant) populations. Such recolonization would have a positive effect on overall metapopulation persistence. In addition, dispersal may supplement local populations and stabilize local dynamics, thus preventing local extinctions (“rescue effect”; Brown and Kodric-Brown 1977).

Dispersal rates depend on many factors, for example species-specific characteristics such as the mode of seed dispersal, motility of individuals, ability and propensity of juveniles to disperse, etc. The dispersal rate between any two populations of the same species may also differ drastically, depending on a number of population-specific characteristics such as the distance between the populations, the surrounding habitat, topography, prevailing wind or water currents, the density of the source population, and habitat quality at the target patch.

When vital rates, carrying capacities or catastrophe-related parameters of two populations are different, increased dispersal between them may lead to decreased viability (even as it increases the occupancy rate). One reason this may happen is similar per-capita dispersal rates between a large and a small population in both directions. In this case, the number of dispersers from the large to the small population will overshoot the small population's carrying capacity (and thus not contribute much to its persistence). At the same time, the small number of dispersers from the small population to large population will not compensate for the number that leaves the large population. This effect would not occur if the dispersal rates in the two directions are unequal, which may be the case when there is a large difference in the areas of the two patches (see Hill et al. 1996, Akçakaya and Baur 1996, Kuussaari et al. 1996, Akçakaya and Raphael 1998, Kindvall 1999). Dispersal rates can be estimated by mark-recapture methods (see above).

The effectiveness of dispersal in reducing extinction risks depends largely on the degree of similarity of environmental fluctuations experienced by different populations (i.e., their correlation or interdependence). This is because when all populations decline simultaneously, there is less chance of recolonization of empty patches (Solbreck 1991). However if the fluctuations are at least partially independent (uncorrelated), then when some populations decline or become extinct others may remain extant or even increase, thus providing recolonization opportunities. A range of values for the correlation among populations can be estimated using the correlation of environmental factors causing the variability (e.g., LaHaye et al. 1994).

If the fluctuations are partially or substantially synchronous (correlated), then models based on an assumption of independent population dynamics among patches will underestimate extinction risk. As a result, correlation of environmental fluctuations among populations have important effects on metapopulation persistence and viability (Gilpin 1988, Akçakaya and Ginzburg 1991, Burgman et al. 1993).

### **Incorporating habitat characteristics**

There are various ways of adding spatial structure to a model to account for the spatial factors discussed above. At one extreme are simple occupancy models that are based on the number of occupied and unoccupied habitat patches, ignoring their location (see Sjögren-Gulve and Hanski 2000). At the other extreme are individual-based models that describe the spatial structure with the location of each individual in the population, or the location of territories or home ranges. Between these are spatially explicit metapopulation models that describe the dynamics of each population with structured demographic models, and incorporate spatial dynamics by modeling dispersal and temporal correlation among populations. Both dispersal and correlation between each pair of populations depend on the location of the populations, making these models spatially explicit. One type of spatially explicit metapopulation model is based on a regular grid, each cell of which is modeled as a subpopulation of a metapopulation (e.g., Price and Gilpin 1996). The major limitation of this approach is that the regular pattern of the grid is often arbitrary and does not correspond to the distribution of the species in the landscape.

Another approach expands spatially explicit metapopulation models by incorporating information about habitat relationships of the species and the characteristics of the landscape in which the metapopulation exists (e.g., Akçakaya and Atwood 1997). This method uses a habitat suitability map to determine the spatial structure of the metapopulation (number and location of habitat patches in which subpopulations of the metapopulation live) and population-specific parameters.

The habitat suitability map can be calculated in a number of different ways, including statistical analyses (such as logistic regression) that find the relationship between the occurrence or density of the species and independent variables that describe its habitat requirements. The relationship can be statistically validated by estimating the function from half of the available data, and predicting the habitat suitability of known locations in the other half (see Akçakaya and Atwood 1997).

The habitat suitability map is then used to calculate the spatial structure of the metapopulation. This is done by identifying cluster of cells in a raster map that are suitable (e.g., above a threshold value of habitat suitability), and that are close to other suitable locations. This patch recognition is based on species-specific characteristics such as the home range size, dispersal distance and minimum habitat suitability for reproduction. The demographic parameters (such as carrying capacity and average vital rates) of the population inhabiting each habitat patch can be determined as functions of patch-specific characteristics, such as the total habitat suitability in the patch (Akçakaya 1998). This provides a link between the spatial and demographic components of the model, and makes it easier to parameterize models with large number of populations, based on limited data.

Often, habitat loss or degradation results in deterministic changes (such as temporal trends) in population characteristics that are different from random environmental fluctuations. Such changes can be incorporated by trends in model parameters such as carrying capacities or vital rates (e.g., see Akçakaya and Raphael 1998).

## How to Use Structured Models

Structured models can be used to assess the threat of extinction or decline faced by a population or metapopulation. Such assessments can be used to prioritize species, for example in the context of the IUCN (1994) threatened species categories. Other uses of structured models involve sensitivity analyses or comparison of “What if...” scenarios for evaluating management options and assessing human impact. These uses are discussed below.

### Sensitivity analysis and planning field research

Because of lack of sufficient data and measurement errors, parameters of a model are often known as ranges instead of single estimates. In such cases, collecting more data makes these ranges narrower, and consequently the results become more certain. Given that there is a cost associated with additional fieldwork, the question is: Which parameter should be estimated better first? In other words: Which of the several uncertain parameters should be given priority for more precise estimation with additional fieldwork?

Such questions can be addressed by sensitivity analyses. There are two common methods of sensitivity analysis:

- Deterministic *eigen-analysis* is based on the effect of each vital rate on the eigenvalue of the stage matrix (i.e.  $\lambda$ , the finite rate of increase). For example, elasticity analysis quantifies the proportional change in  $\lambda$  caused by a proportional change in each vital rate (de Kroon et al. 1986, Caswell 1989, Burgman et al. 1993).
- *Risk-based sensitivity analysis* is based on the effect of changes in vital rates (or other parameters) on population extinction risk or recovery chance.

As discussed above, deterministic methods ignore variability, density dependence and the initial distribution of individuals to stages. In addition, they focus on the deterministic growth rate, rather than the more relevant results such as the risk of extinction.

An important consideration in deciding which parameters are more important to estimate more precisely is the

uncertainty in each parameter. Other things being equal, it makes sense to spend more time and money for additional data on a more uncertain parameter. With the risk-based method described above, this consideration is accounted for by changing each parameter to the lower and upper values of its estimated range, instead of changing them plus and minus a fixed percentage. This way, a parameter with a wider range will contribute more to uncertainty about the risk of extinction (other things being equal). With the deterministic methods (such as elasticities), it is not always possible to take this consideration into account, because those methods are based on linear approximations, which means they assume that growth rate changes linearly with changes in vital rates. This is often a good approximation for small changes, but may not be valid for large ones (e.g., when a survival rate is known as a wide range).

Another disadvantage of the deterministic methods is that they are often applied only to single matrix elements. However, some matrix elements may have to be estimated as products of two vital rates. For example, fecundity may be estimated as the product of maternity (e.g., number of fledglings per adult) and survival of the juveniles until the next census. If we want to decide whether the fieldwork should focus on maternity or juvenile survival (which may require different types of study design), then the sensitivity of the population growth rate to their product (fecundity) is not very useful.

Finally, the risk-based sensitivity approach can be extended to parameters other than those in the stage matrix (average vital rates). Often, the variances of vital rates are known even more poorly than their averages. We may be uncertain about the type of density dependence, or the number of stages to use in the model. In each of these instances, the strategy is the same: change parameter values or model structure to their alternatives and measure the importance of the change by the effect it has on the risks of decline.

### **Assessing impacts and evaluating management options**

Another application of sensitivity analysis involves decisions about which vital rates to focus on in management and conservation efforts. The evaluation of management options requires considerations similar to those for planning field research. The first is the contribution of each vital rate to the expected growth rate, and the chances of decline or recovery of the population. Thus, a formal sensitivity analysis of a model can provide some insight into how best to manage a population.

The second consideration is how much each vital rate (or other model parameter) can be changed with management. Other things being equal, it makes sense to base management actions on those aspects of the life history that are practical to manipulate. Further complicating this issue is the fact that each management or conservation action may affect more than one vital rate. For example, protecting nest locations of a bird species may improve fecundity, and to a lesser extent survival rates, whereas restoring dispersal habitat may improve dispersal rates, juvenile survival, and to a lesser extent adult survival. In these cases, a parameter-by-parameter analysis of sensitivity does not make sense, because the parameters cannot be changed independently (or in isolation from others). It is much better to do a *whole-model sensitivity analysis*, and compare management options instead of single parameters. This can be done by developing models for each management or conservation alternative. Each model incorporates changes to all the parameters affected by that particular alternative. The results of these models than can be compared to each other, as well as to a “no-action” scenario (e.g., Berglind 2000).

The same approach can be used when assessing the impact of a disturbance or human activity, by comparing a “no impact” scenario with the results of a model that incorporates effects of the simulated impact on model parameters (see Fig. 4). As with management options, an impact is likely to affect more than one parameter, each to a different degree. Thus, a whole-model sensitivity analysis is more appropriate than one based on single parameters.

Both in planning future fieldwork and in evaluating management actions, a non-biological consideration is the relative cost of each research objective or management action. Population viability analyses do not explicitly incorporate economic factors but, because of quantitative nature of PVA results, it is possible to jointly consider ecological and economical objectives (see Akçakaya and Sjögren-Gulve 2000).

When structured models are used in this comparative mode, the results can be expressed in relative terms, e.g., as the relative increase in the risk of extinction due to an impact. Such relative measures are less sensitive to uncertainties in the data compared to absolute measures such as the risk of extinction (Lindenmayer and Possingham 1996, Hanski 1997, Akçakaya and Raphael 1998).

## Assumptions of structured models

The type of structured models reviewed in this paper assume discrete time steps, i.e., are based on difference equations. Most of these models address a single species; thus, they cannot explicitly represent competition, predation, mutualism or other interspecific interactions. These interactions can be modeled as constant, fluctuating, or cyclic influences on the demographic parameters.

Structured models group individuals into distinct categories such as age classes, stages, subpopulations, or a combination of these (e.g., stages within subpopulations). Within a group, the individuals are assumed to be identical. For example, the basic assumption of stage-structured models is that the demographic characteristics of individuals are related to their developmental stage. They assume that there is little variation among individuals in the same stage with respect to their demographic characteristics such as chance of surviving, chance of reproducing, and the number of offspring they produce.

Matrix models assume that what an organism will do (its demographic rates) depends only on the stage it is in now, and not on what stage it was in the previous time steps, or how long it had remained in each stage.

## Data requirements

The main disadvantage of structured models is that they require more data, such as survival rates and fecundities and their variabilities, compared to unstructured demographic models and occupancy models. However, in many cases (especially for vertebrate populations), the types of data needed are more readily available (from the literature or from data bases maintained by various agencies), than data required for occupancy models (e.g., observations of local extinction and recolonization). If not available, the demographic data required by structured models are more easily collected, and can be obtained by a variety of methods, including censuses, mark-recapture studies, surveys and observations of reproduction and dispersal events. Note that these methods are also used for monitoring, which is an important component of any conservation plan.

Structured models allow various levels of detail. For example, if age-specific data are available, models can be age-structured. If not, or if the demography of the species makes it more appropriate, the model can be stage-structured (including, for instance, only juveniles and adults, instead of each age class). If there are sufficient data, each population can be assigned to a specific set of vital rates (i.e., a different age or stage matrix for each population). If not, the available data can be pooled to estimate a common matrix for all populations. Another option is to calculate vital rates as functions of habitat characteristics. This requires estimation of the vital rates from a few representative populations, and extrapolating the relationship between vital rates and habitat attributes to other populations (see Akçakaya and Raphael 1998 for an example). Similarly, dispersal rates can be specified for each pair of populations, or they can be assigned as a function of the distance between populations, based on studies designed to monitor dispersal among a few populations.

## Examples

Structured models have been applied to populations and metapopulations of a variety of organisms, including plants, marine and terrestrial mammals, birds, reptiles, amphibians, fishes and invertebrates. Applications within the last 8 years included the species listed in Box 3. This list is representative but not comprehensive. For previous applications, see Boyce (1992).

The basic principles of building structured models discussed above apply to most of the cases in Box 3. However, some types of life histories present special problems. For example, in modeling some marine species, delineating populations (stocks) is a difficult task, compounded by the high connectivity of populations in some species through larval dispersal and currents. In marine environments, seasonality (regular cycles with a year) is often less important than long-term regular oscillations of environmental variables.

Some plants and other species have life history stages that are invisible or otherwise difficult to detect. In plants, the seed bank is often modeled as one or more separate stages. Estimating parameters related to these stages often presents difficulties. In addition, time-dependent contingencies and rules of transition (e.g., from

seed to seedling following fire) make the application of a simple matrix structure difficult (e.g., Drechsler et al. 1999; also see Menges 2000).

Many of the applications of structured models in Box 3 have aimed at providing management recommendations for rare, endangered or harvested populations. Drechsler et al. (1999) used a stage-structured, stochastic metapopulation model to determine factors affecting the viability of a rare shrub, and to make management recommendations. Maschinsky et al (1997) used a stage-structured single-population model to compare the dynamics of a endangered plant before and after protection from trampling. Kokko et al. (1997) evaluated harvesting strategies for seal populations in the Baltic with age-structured models. They showed that deterministic models can give a false impression of safety while the same strategies are often judged to be risky when a more realistic, stochastic model is used. Armbruster and Lande (1993) analyzed the effect of culling on the viability of the African Elephant with an age-structured, stochastic model. Litvaitis and Villafuerte (1996) used an age-structured, stochastic metapopulation model to evaluate the impact of habitat fragmentation and loss, environmental correlations and management options on the likelihood of persistence of New England cottontails (*Sylvilagus transitionalis*). They recommended a management program to maintain a network of suitable habitat patches, and defined the ages and sizes of patches that would be sufficient to achieve acceptably small risks of decline. Akçakaya et al. (1995) used a stage-structured, stochastic metapopulation model to explore the feasibility of translocating Helmeted Honeyeaters (*Lichenostomus melanops cassidix*) from their current locations to a new habitat patch. Reed et al. (1998) used the qualitative results of their metapopulation model of the Hawaiian Stilt (*Himantopus mexicanus knudseni*) to argue that the current conservation status of the species should be maintained. Crowder et al. (1994) used a stage-structured model to analyze the effect of turtle excluder devices on the growth rate of loggerhead sea turtle populations. Additional examples are provided by Berglind (2000), Ebenhard (2000) and Lennartsson (2000) in this volume.

**Box 3.** Applications of structured models in population viability analysis. The list is representative but not comprehensive. Some examples are commented further in the text.

**Plants:** *Andropogon* spp. (annual grass; Silva et al. 1991, Canales et al. 1994), *Ascophyllum* (seaweed; Aberg 1992), American ginseng and wild leek (Nantel et al. 1996), sentry milk-vetch (Maschinsky et al. 1997), golden heather (Gross et al. 1998), *Banksia goodii* (Drechsler et al. 1999), *Gentianella campestris* (Lennartsson 2000). See Menges (2000) for other examples.

**Marine mammals:** Mediterranean monk seal (Durant and Harwood 1992), killer whale (Brault and Caswell 1993), northern sea lion (York 1994), Steller sea lion (Pascual and Adkinson 1994), grey and ringed seals (Kokko et al. 1997).

**Terrestrial mammals:** roan antelope (Beudels et al. 1992), the African elephant (Armbruster and Lande 1993), rabbit (Palomares et al. 1995), red deer (Benton et al. 1995), asiatic wild ass (Saltz and Rubenstein 1995), cottontail rabbit (Litvaitis and Villafuerte 1996).

**Birds:** peregrine falcon (Wootton and Bell 1992, Ebenhard 2000), California spotted owl (LaHaye et al. 1994), helmeted honeyeater (Akçakaya et al. 1995), red-cockaded woodpeckers (Maguire et al. 1995), golden-cheeked warbler and black-capped vireo (U.S. Fish and Wildlife Service 1996a, 1996b), California gnatcatcher (Akçakaya and Atwood 1997), Florida scrub-jay (Root 1998), Hawaiian stilt (Reed et al. 1998), northern spotted owl (Akçakaya and Raphael 1998).

**Reptiles and amphibians:** pool frog (Sjögren 1991), salamanders (Gibbs 1993), loggerhead sea turtle (Crowder et al. 1994), desert tortoise (Doak et al. 1994), yellow mud turtle and Kemp's ridley sea turtle (Heppell et al. 1996), spadefoot toad (Hels 1999), sand lizard (Berglind 2000).

**Fishes:** striped bass (Cohen et al. 1983, Bulak et al. 1995), cod (Ginzburg et al. 1990), brook trout (McFadden et al. 1967, Marschall and Crowder 1996), *Fundulus* sp. (Munns et al. 1997).

**Invertebrates:** marine bryozoan *Membranipora* (Harvell et al. 1990), gorgonian coral *Leptogorgia* (Gotelli 1991), bush cricket (Kindvall 1995, 2000), land snail *Arianta* (Akçakaya and Baur 1996), estuarine polychaetes (Levin et al. 1996), marine snail *Umbonium* (Noda and Nakao 1996), pea aphid (Walthall and Start 1997), marine bivalve *Yoldia* (Nakaoka 1997), burrowing mayfly (Madenjian et al. 1998).

## Discussion

### Advantages and disadvantages of structured models

The main advantage of structured metapopulation compared to occupancy models is their realism. Structured models are not constrained in terms of the number of populations or turnover rate in metapopulations, making them more flexible. Unrealistic assumptions about the species or (meta)population being modeled can be avoided with structured models, which use all the available demographic data to estimate species viability. As a result, structured models have been applied to a variety of organisms (see Examples, above).

Another advantage, especially as compared to individual-based models, is that, despite their flexibility, structured models are based on a number of common techniques or frameworks that allow their implementation as generic programs. These include the matrix-based approach to model local age or stage-structured dynamics, generating random variates for vital rates to simulate environmental variation and catastrophes, and using replicate trajectories to calculate risk-based viability results. This common framework becomes an advantage when models and viability analyses are needed for a large number of species, and time and resources limitations preclude detailed modeling and programming for each species, as it allows generic programs (e.g., RAMAS; <http://www.ramas.com>). In contrast, using the full flexibility of individual-based modeling approaches often requires writing a different program for each species modeled. However, some individual-based models (such as VORTEX; see Lacy 1993, 2000a, 2000b) solve this problem by having a fixed, age-based structure.

The main disadvantage of structured models compared to occupancy models is that they require more data, such as survival rate and fecundity of each age class or stage and estimates of the temporal and spatial variation in these rates (see *Data requirements*, above).

### When are structured models most appropriate?

The appropriate level of detail for a PVA model depends on the ecology of the species, the availability of data, and the questions addressed (see Akçakaya and Sjögren-Gulve 2000).

Structured models are more appropriate than occupancy models if “internal” (within-population) dynamics are important, there are few subpopulations, or local extinctions and recolonizations are relatively rare (see Akçakaya and Sjögren-Gulve 2000). However, it is important to note that these are only general guidelines, and there may be exceptions. For example, structured models can also be appropriate when there are frequent local extinctions, or over 100 populations, depending on the data, the question, and the species.

Structured models are more appropriate than individual-based models if data at the individual-level (e.g., on dispersal behavior) are not available, or if the population size is not too small. In general, the smaller the population size, the more appropriate are individual-based approaches. What is “too small” depends on: (1) what is known about the population, and about each individual, (2) how complex is the social structure, and (3) question to be addressed.

For example, even a scalar (unstructured) model may be suitable for a population as small as 2 individuals, if the population dynamics and social organization are simple enough (think of a model for a *Paramecium* population). But, for species with complex social structure, and plenty of reliable data, populations that are much larger than this may be better modeled by individual-based models.

The more information there is about each individual (such as age, size, sex, location, reproductive status, social status, genetics, relationship to other individuals, etc.), and about the behavior of the species (social structure, dispersal patterns, reproductive behavior) the more appropriate are individual-based models. If such information is not available, it may be unnecessary, even counter-productive, to attempt to build complex individual-based models.

Individual-based models are especially sensitive to the dispersal behavior of individuals. Small errors in dispersal mortality, mobility and habitat suitability may result in large errors in predicting dispersal success (Ruckelhaus et al. 1997). In structured models, dispersal is modeled at a coarser scale, as the proportion of individuals moving from population to another between two successive time steps, which can be estimated

with mark-recapture studies. Dispersal mortality is incorporated into the vital rates (e.g., specified in a stage matrix; see Akçakaya 1998, 2000).

Finally, the questions addressed should also affect the decision about the complexity of the model. If the PVA aims to address questions about future distribution of occupied territories, or the optimal pairing of individuals for captive breeding, then an individual-based approach may be more appropriate. If the goal of the PVA is population or species-level assessment of extinction risk, a structured model may be more appropriate. However, in many cases, both structured and individual-based models can be used. For example, in a study designed to validate the PVA approach, Brook et al. (2000) modeled 21 populations, using both structured programs such as RAMAS and INMAT, and individual-based programs such as GAPPS and VORTEX for each population. They found that the PVA predictions were accurate, and the predictions of different PVA programs were consistent with each other.

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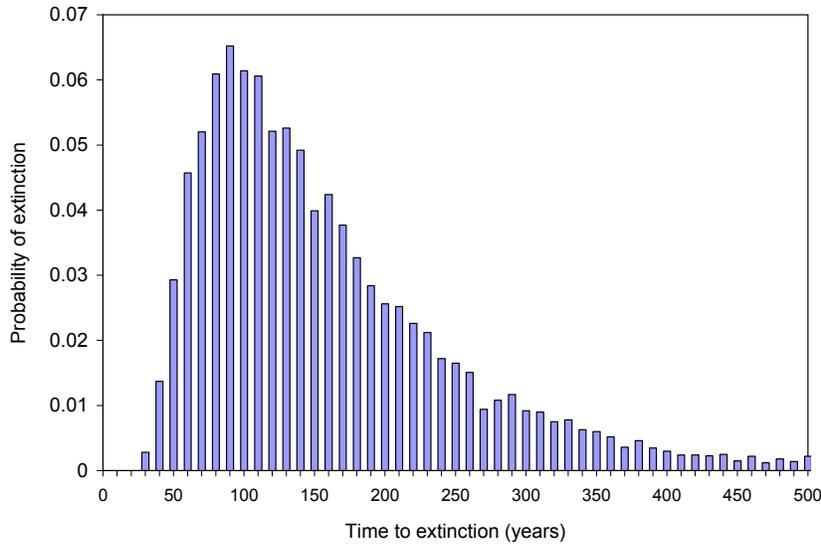


Fig. 1. Example of a distribution of extinction times. The height of each vertical bar gives the probability that the population will go extinction in the 10-year period ending with the year shown on the x-axis. For example, there is about 1.4% chance that the population will go extinction between years 30 and 40, and about 2.9% chance that it will go extinct between years 40 and 50. The median of this distribution is about 131 years.

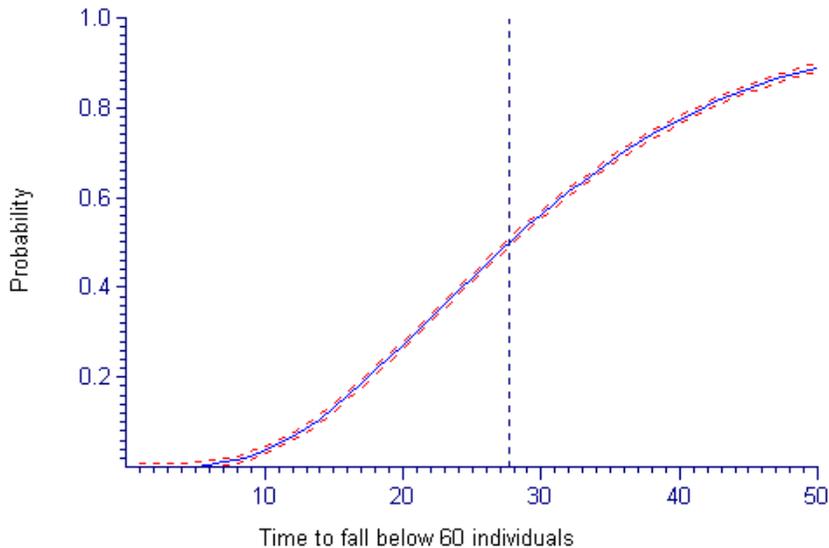


Fig. 2. Example of a cumulative time to quasi-extinction curve: each point in the curve gives the probability that the population will decline to 60 individuals by the end of the time step (given in the x-axis). The vertical line indicates the median time to quasi-extinction (the time step when the probability reaches 0.5), which is 27.6 years in this example. This means that there is about a 50% risk that the total abundance will fall to or below 60 individuals sometime in the next 28 years.

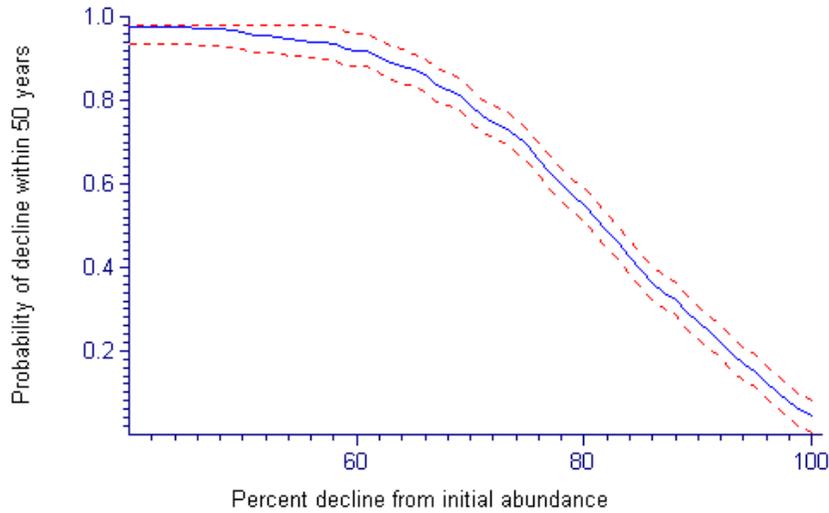


Fig. 3. Example of a risk of decline curve: each point on the curve shows the probability that the population will fall by the given percentage from the initial abundance anytime during the next 50 years. For example, the curve indicates that the probability of an 80% decline (from initial abundance) in the next 50 years is about 0.56. If the total abundance in year 2000 was, for example, 1000 individuals, this means that there is about a 56% risk that the abundance will fall to or below 200 individuals sometime before the year 2050. Dotted curves give 95% confidence intervals based on Kolmogorov-Smirnov statistic,  $D$ .

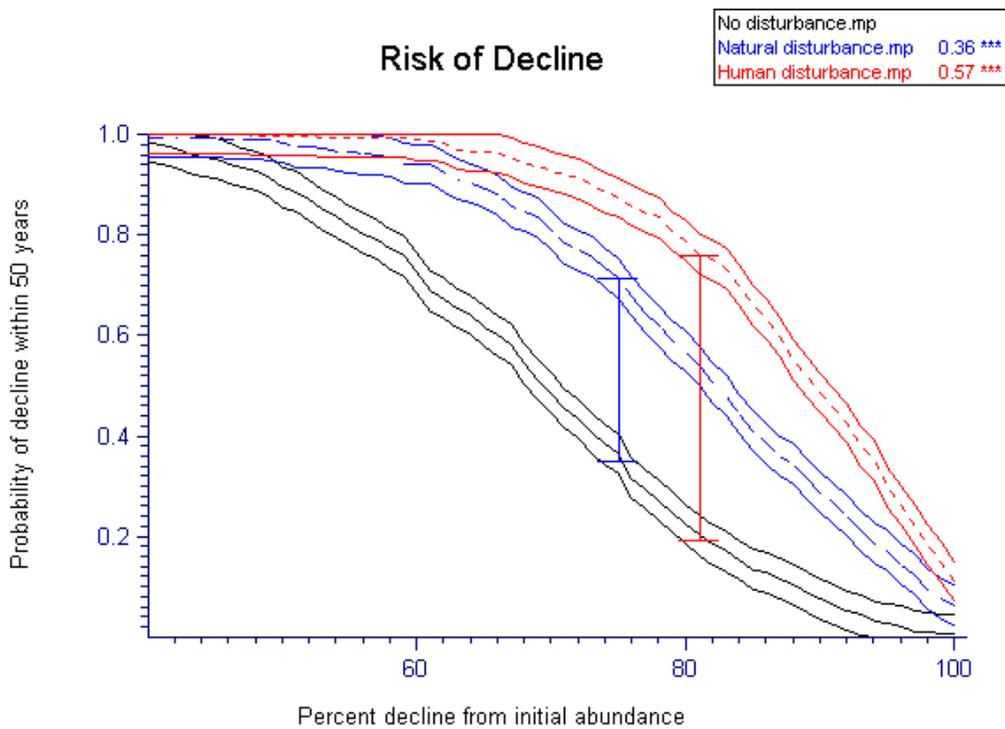


Fig. 4. Example of risk-based impact assessment: each curve gives the risk of decline (as in Fig. 3) under a different scenario. Each vertical bar shows the maximum difference between two curves. In this example, human disturbance increases risk of an 80% decline (from initial abundance) in the next 50 years by 0.57 (from about 0.20 to 0.77). If the current total abundance is, for example, 1000 individuals, this means that there is about a 57% *additional* risk, attributable to human disturbance, that the abundance will fall to or below 200 individuals sometime in the next 50 years.