CHAPTER 12

Predicting the dynamics of small and declining populations

> *There's an old adage, translated from the ancient Coptic, that contains all the wisdom of the ages – "Life is life and fun is fun, but it's all so quiet when the goldfish die".*
>
> **Beryl Markham (1983:218), *West with the Night***

INTRODUCTION

How well is a species doing? How likely is it that particular stressors will cause a wildlife population to decline or go extinct? What is the best way to reverse the trend? These are the big-picture questions commonly asked of applied population ecologists. Having built the foundation for understanding population biology and discussed factors causing large populations to decline, we can now consider ecological tools for predicting risks to small and declining populations.[1] Although interesting ecological questions can be generated from species that "naturally" persist at low abundance (e.g. Gaston 1994, Brown 1995), here the focus will be on applied situations where populations that were historically abundant are currently small and/or declining.

What is a small population (Mills et al. 2012)? Smallness is a meaningful concept only in relation to other species, to historical population sizes, or even to arbitrary management standards. For an exploited species such as the canvasback, conservation plans may call for corrective management to be implemented when population sizes decrease to the tens of thousands. In contrast, conservation efforts for threatened species may be delayed until the population falls below 100 or is putatively extinct (e.g. the Hawaiian honeycreeper with the two letter name: ʻōʻū).

In this chapter I will first review ecological characteristics that might predispose populations or species to extinction due to humans. The rest of the chapter will describe viability assessment for small populations, including quantitative approaches for population viability analysis (PVA).

ECOLOGICAL CHARACTERISTICS PREDICTING RISK

Are there broad ecological characteristics that can help classify population dynamics – and therefore risk – for particular populations or species? Obviously, smaller populations will be more vulnerable to extinction (all else being equal) than larger populations, an idea rooted in the classics of applied ecology (e.g. Leopold 1933, MacArthur & Wilson 1967). For example, Mace and Kershaw (1997) found that population size was the best predictor of extinction risk in a global survey of birds. In some (but not all) cases, having a restricted range or being endemic or highly specialized can serve as a proxy for small pop-

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[1] I will avoid the terms **rare** or **rarity**. These are often considered synonymous with low abundance, but can also sometimes refer to high habitat specificity, ecological specialization, and limited geographical distribution (Rabinowitz et al. 1986, Gaston 1994).When using rare or rarity the context should be defined precisely in terms of abundance, range size, and habitat use (Mace & Kershaw 1997).

Conservation of Wildlife Populations: Demography, Genetics, and Management, Second Edition. L. Scott Mills.

Box 12.1 The 50–500 rule

As an historical footnote in the use of abundance to predict extinction vulnerability, we must review the famous **50–500 rule**. This rule of thumb emerged from the application of conservation genetics to wild species (Franklin 1980, Soulé 1980, Frankel & Soulé 1981) and was swept up into management plans (e.g. the Puerto Rican parrot recovery plan) and a number of biological opinions (Mills et al. 2012). In essence, the rule provides a minimum genetic effective size for short- and long-term protection.

An effective size of 50 was proposed as a minimum to protect against short-term loss of fitness due to inbreeding, based on empirical observations of the decrease in fitness-related traits with incremental inbreeding domestic animal species.[2] Several caveats implicit in the original rule were lost as it became applied in management (Soulé 1987, Soulé & Mills 1992). For example, the 50 is the **genetic effective size** (N_e), typically about one-fifth to one-third that of the total population size (Chapter 9); thus an N_e of 50 translates to 150–250 or so actual animals. Second, the rule was proposed as a short-term guideline for captive breeding and similar holding operations, not for long-term survival of wild populations exposed to stochastic and deterministic stressors. Third, the rule was based purely on genetic factors, not incorporating the other factors that would again increase the minimum necessary size for persistence. Based on these considerations, it is untenable to argue that an actual population size of 50 is sufficient as a rule to support any wildlife population into the future.

A value of 500 was proposed as the minimum N_e necessary to ensure long-term maintenance of genetic variation, thereby preserving evolutionary options for future adaptation. In more formal terms, 500 was the estimated minimum genetic effective size where the loss of additive genetic variation of a quantitative character due to genetic drift would be balanced by new variation due to mutations. This number has received serious scrutiny by population geneticists, with arguments to increase it to as large as 5000 or more (Frankham et al. 2010). As Allendorf and Ryman (2002) note, this debate is likely to continue, but there is little doubt that the *actual* population size (as opposed to the genetic effective population size) necessary to maintain evolutionary potential for the long term should be thousands of individuals and not hundreds.

ulation size and therefore be a predictor of vulnerability to extinction for a species (Channell & Lomolino 2000, Purvis et al. 2000). There are no simple thresholds of population size that guarantee persistence (Box 12.1) and later in the chapter we will explore the best ways to assess risk for populations of different sizes.

Another predictor of extinction is the ratio of the variance in population growth rate to the mean growth rate (Chapter 5). Species with a low ratio of variability relative to growth rate are most resistant to extinction, while a high ratio is more predictive of local extinction (Fagan et al. 2001). A third predictor of extinction is body size, where larger-bodied animals tend to be more vulnerable to extinction both historically (as in the Pleistocene era) and currently (Brook & Bowman 2005, Cardillo et al. 2005). As body size increases for animal species, the population growth rate and density tend to decrease while the home-range size increases; furthermore, larger animals are more vulnerable to harvest and other human-caused threats. Finally, as we saw in the last chapter, a suite of characteristics predispose certain species to be able to adapt to human-caused stressors (Box 11.7: large abundance, short generation times, medium levels of gene flow, and a more generalist nature); species

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[2] To be exact, the 50 rule emerged from a literature review indicating that domestic animals experienced fitness problems when the inbreeding coefficient (F) exceeded about 1% per generation. Because F due to drift increases at a rate of $\frac{1}{2Ne}$ per generation (Chapter 9), $0.01 = \frac{1}{2Ne}$ is solved by $N_e = 50$.

without these traits would be less likely to adapt and persist.

Of course, all such rules of thumb for vulnerability are tempered by the reality that simple predictions may be overwhelmed by the specific situation. For example, vulnerability of primates and carnivores was underestimated by a model based on species characteristics in cases where the species had lost habitat, been commercially overexploited, or suffered from exotic species (Purvis et al. 2000). Similarly, extinction vulnerability for 145 Australian marsupial species depended more on geographical-range overlap with sheep than it did on species characteristics such as body size, reproductive rate, or habitat specialization (Fisher et al. 2003). Vulnerability may also derive in part from particular behavioral attributes such as Allee effects or naiveté toward predators (e.g. the passenger pigeon; Reed 1999).

THE EXTINCTION VORTEX

In managing small and declining populations, the overriding factors to consider are what caused the population to become small and how to reverse the decline. Whether the cause of decline was habitat loss or fragmentation, overharvest, exotic species, or some combination of these or other causes, reversing the human-caused deterministic stressors that led to the decline and that now limit recovery is of paramount importance (Chapter 11).

Unfortunately, a small population also becomes particularly vulnerable to a host of **stochastic** threats that interact with the deterministic stressors. Therefore, even if the deterministic stressors were reversed and a small population achieved a positive average population growth, the population could still stumble toward extinction. Three main types of stochasticity affect persistence: demographic, environmental, and genetic (Chapters 5 and 9). As a reminder, demographic stochasticity causes variation because mean vital rates are probabilistic, so as numbers of individuals become small the outcomes of births and deaths can substantially deviate from mean expectations. Environmental stochasticity refers to random changes in the mean vital rates across individuals from year to year, often driven by weather or other unexpected effects. Genetic stochasticity arises from genetic drift; harmful alleles randomly accumulate as homozygotes that may reduce demographic rates.

Both deterministic and stochastic factors interact in small populations to drive the **extinction vortex** (Fig. 12.1). The extinction vortex makes it very clear that when evaluating persistence we should not emphasize one factor (e.g. the cause of decline, genetic stochasticity, or environmental stochasticity) and disregard the others. Rather, management actions are best judged against the relative importance of the different factors and how they interact in any particular case (Lande 1988a, Mills & Smouse 1994).

The complex interactions among ecological factors and human-caused stressors make the extinction vortex hard to detect in the field. However, we saw some instances of the extinction vortex in the Chapter 9 case studies. Further, a review of 10 species with monitoring data documenting their demise showed key signatures that the extinction vortex kicked in at small numbers to exacerbate their collapse (Fagan & Holmes 2006). Finally, some manipulative laboratory studies have provided compelling evidence for the extinction vortex (Box 12.2).

PREDICTING RISKS IN SMALL POPULATIONS

To confront the extinction vortex requires a formal framework to assess viability. The intellectual roots for assessing viability in wildlife populations go back at least 80 years. Aldo Leopold (1933:47) noted the importance of recognizing "the minimum number of individuals which may successfully exist as a detached population." A few years later, our old friend W.C. Allee (Chapter 7) stated: "The general conclusion seems to be that different species have different minimum populations below which the species cannot go with safety, and that in some instances this is considerably above the theoretical minimum of one pair" (Allee 1938:82).

Viability assessments have more recently been placed into legal frameworks with names like **cumulative effects analysis** (Schultz 2010). Any framework to evaluate viability should place intuition, theory, and field data into an operational framework to allow insights into factors that caused decline and that may cause further decline in the future. At its best, viability assessments make both hard data and best guesses explicit, so that the input and output can be honestly debated. As a framework for incorporating

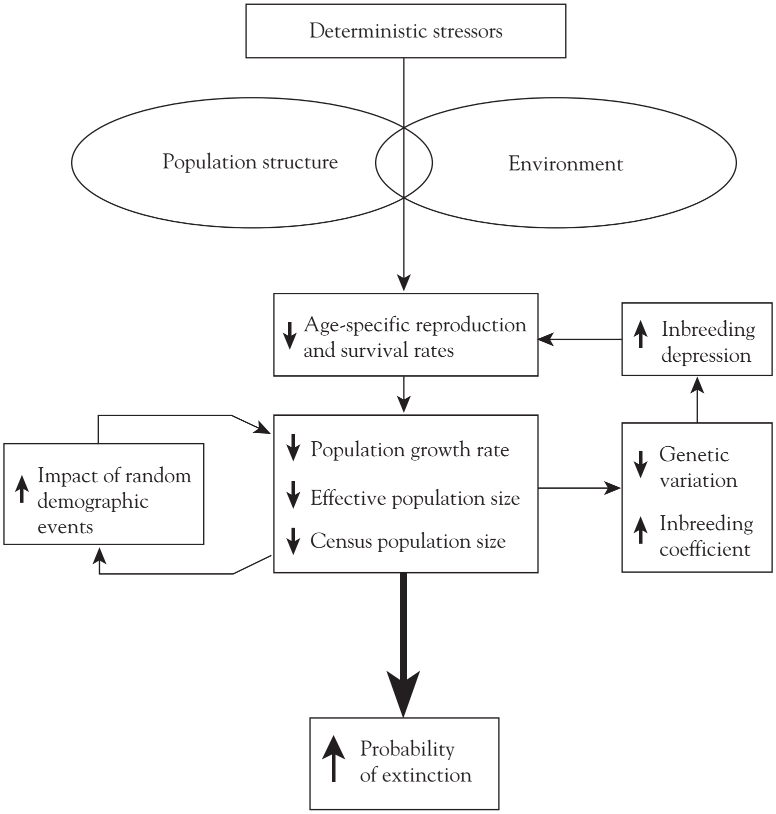

Fig. 12.1 A simplified representation of the extinction vortex. The effects of deterministic stressors are filtered by the population's environment (habitat as well as variable extrinsic factors such as weather, competition, predators, and food abundance) and by its structure (including age structure, sex ratio, behavioral interactions, density dependence, physiological status, and intrinsic birth and death rates). Each turn of the feedback cycle increases extinction probability (Gilpin & Soulé 1986). The extinction vortex model predicts that some small populations are more likely to become smaller and eventually go extinct with each generation due to the interaction of genetic and nongenetic factors. Modified from Soulé and Mills (1998). Copyright (1998) AAAS.

multiple, interacting processes, viability assessment can reveal nonintuitive and nonobvious outcomes that can assist management in surprising and important ways.

The quantitative branch of viability assessment is known as **population viability analysis** (**PVA**). We will consider PVA in some detail next. Because in many instances only a *qualitative* assessment of viability is possible – in contrast to the *quantitative* assessment of PVA – we will also consider qualitative alternatives to PVA.

POPULATION VIABILITY ANALYSIS (PVA): QUANTITATIVE METHODS OF ASSESSING VIABILITY

PVA defined

Broadly, PVA can be defined as *the application of data and models to estimate likelihoods of a population crossing thresholds of viability within various time spans, and to give insights into factors that constitute the biggest threats*. Key components in the definition include what is

Box 12.2 Insights into the extinction vortex from a model system

In a clever test of the extinction vortex, fruit flies were exposed to changing and stressful environments (Bijlsma et al. 2000). The replicated worlds were vials 22 mm in diameter holding up to about 120 flies. High temperature and different levels of ethanol produced stressful treatments. For each treatment of an environmental condition and inbreeding level 50 populations were followed over eight generations (imagine the difficulty of doing this experiment with your favorite wild mammal or bird species).

Control populations (Fig. 12.2, top panel) had relatively low extinction probabilities over time, although inbred populations (with inbreeding coefficients, *F*, greater than 0) had higher extinction rates. Under stressful conditions extinction rates increased (middle and lower panels), with inbreeding exacerbating the extinction risk. The researchers repeated the experiment 2 years later and found the same result: the extinction rate was elevated by environmental stress conditions and highly inbred populations were much more likely to go extinct when under environmental stress. Inbreeding and environmental stress act synergistically, making a convincing general case that the extinction vortex is real and that genetic effects should not be considered independently from environmental and demographic effects.

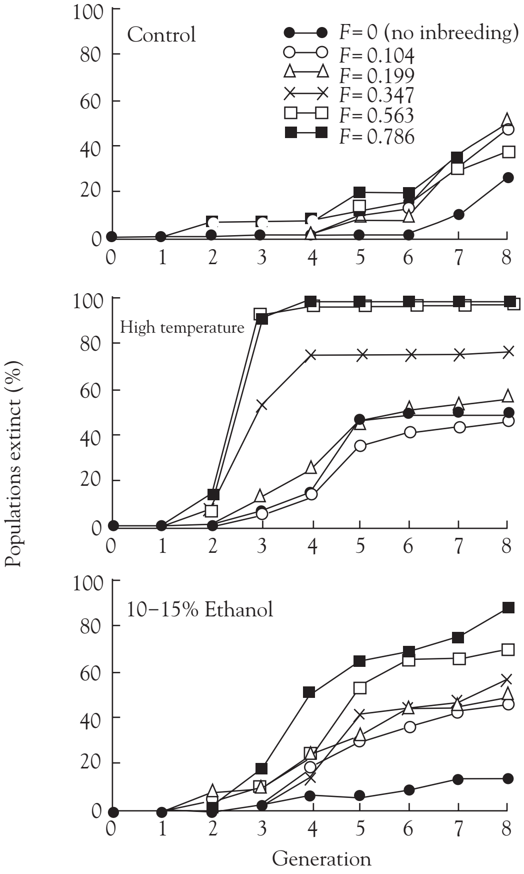

Fig. 12.2 Extinctions over time under various sets of conditions for outbred (F = 0) or inbred fruit flies. Modified from Bijlsma et al. (2000). Reproduced by permission of Blackwell Publishing Ltd.

meant by **viable**, **the time spans** of interest, and the **risk likelihoods** to be described. Each of these will be discussed in the next section. Clearly, a PVA incorporates virtually every concept of applied population biology discussed so far in this book.

Notice that this definition says nothing about a **minimum viable population** (**MVP**), a term that dominated much of conservation biology in the 1980s (see Gilpin & Soulé 1986, Soulé & Mills 1992). This is because PVA approaches capture the idea behind MVP, while making MVP itself obsolete. Although MVP has alluring simplicity as a single, simple number, the concept is problematic for both philosophical and scientific reasons. Philosophically, it seems questionable to presume to manage for the minimum number of individuals that could persist on this planet. Scientifically, the problem is that we simply cannot determine accurately a single minimum number of individuals that will be viable for the long term, because of the inherent uncertainties in nature and management arising from ecological processes, management scenarios, and measurement of population parameters in wild populations. Finally, the number of individuals required to carry out ecological functions – including nutrient cycling or limitation of prey numbers – may be much bigger than the minimum needed for that species to persist; without ecologically effective numbers, key ecological processes could be compromised (Soulé et al. 2003; see Chapter 13). Therefore, instead of a futile focus on a single number (MVP), a much more constructive and reliable philosophy evaluates a range of possibilities through PVA.

Three components of PVA

As defined above, three concepts central to the PVA definition include a criterion for viability, relevant time spans to evaluate, and the description of risk. The last part of the definition – insights into factors that constitute the biggest threats to the population – will be discussed for each of the types of PVA discussed below.

Viability versus extinction

The simplest criterion for a viable population is one that is **not extinct**, remaining above zero individuals (or one mating pair). Although extinction per se is obviously an important threshold, other viability thresholds may be more important for biological or management-based reasons. These **quasi-extinction thresholds** of viability might include biological thresholds below which Allee effects occur or where strongly interacting species become unable to carry out critical ecosystem functions. For example, the Marine Mammal Act (Section 2) explicitly incorporates a functional role into the viability threshold: "population stocks should not be permitted to diminish beyond the point at which they cease to be significant functioning elements of the ecosystem of which they are a part." The quasi-extinction threshold may also include **management thresholds** such as the triggering number to bring a wild population into captivity, or the abundance below which a threatened species would receive special management (Ginzburg et al. 1990). Therefore, when I refer to a viability threshold for avoiding extinction I mean it in the broad sense, including both true extinction as well as management or quasi-extinction thresholds.

Time

An assessment of population viability must also include a specified time element. As with many other predictions (e.g. weather or stock markets), the projections of PVA will be less reliable further into the future, reducing predictive accuracy. Therefore, PVA in endangered species recovery plans should incorporate short-term projections evaluated against a long-term goal (Scott et al. 1995, Goodman 2002). The long-term viability assessment includes management goals relatively free of political and legal considerations (i.e. biologically based). The short-term projections show tradeoffs for a range of options explicitly incorporating political, legal, social, and economic constraints; monitoring and the iterative use of short-term PVAs evaluate how well the goal of long-term persistence is being met. Thus public input (and political tradeoffs) can be incorporated in choosing short-term management strategies, but ultimate success is judged against the yardstick of the long-term, biologically based goal. An analogy is useful for thinking about the relative merits of short-term, more reliable projections compared with long-term projections: "We can see only as far as our headlights reach, but we need to be concerned about what lies beyond their reach" (Allendorf & Ryman 2002:77).

Likelihood of risk

As a forecasting tool, PVA relies on predicting likely outcomes. Therefore, the third critical issue to consider is confidence, or likelihood that the population will remain above the viability threshold for the specified time. Risks are often visually displayed with quasi-extinction curves (Groom & Pascual 1998, Akçakaya 2000) representing the probability (or cumulative probability) of reaching a quasi-extinction threshold over a range of time periods. For example, Figure 12.3(a) shows how the cumulative probability of declining to one California condor increases with time. The time that it takes to reach a 0.50 probability of quasi-extinction gives the median time to quasi-extinction.[3] In this case, we expect condors to have a

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[3] We tend to use median and not mean extinction time descriptions because extinction time distributions have a long tail, consisting of the small probability of lasting a very long time, which causes the mean to be much higher than the median and overestimates the probability of safety for the most likely population (see Akçakaya 2000).

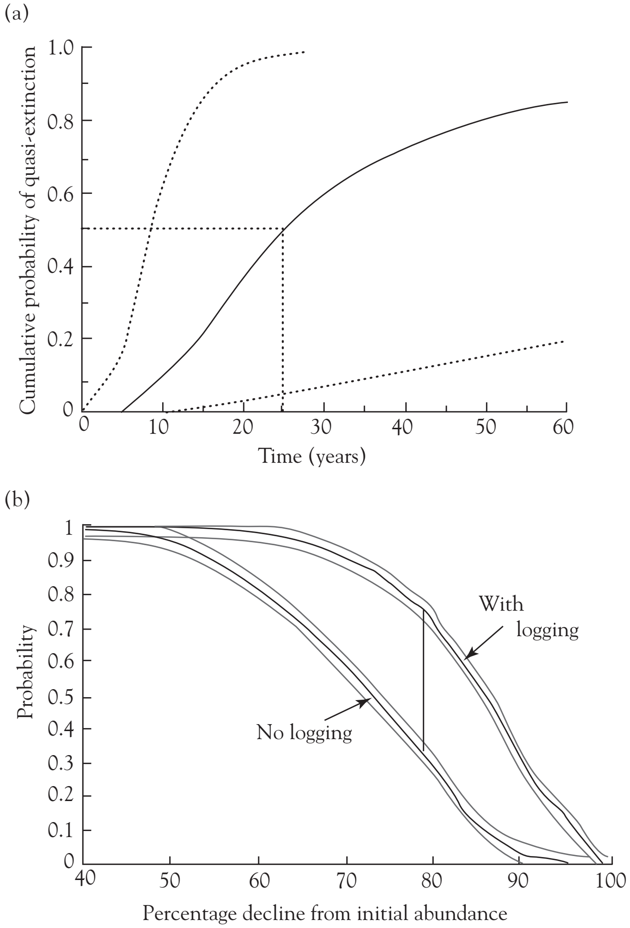

Fig. 12.3 Likelihoods of risk may be portrayed in different ways. (a) The cumulative probability of 12 California condors declining to one bird (the quasi-extinction threshold) as time passes (from Dennis et al. 1991; reproduced by permission of the ESA). The dotted lines represent the 95% confidence interval. The median time to extinction is 25 years, the time that it takes to reach a 50% quasi-extinction probability. (b) A different way of portraying risk: the probability of declining by some percentage of the original population size. The graph shows the risk of decline of a northern spotted owl metapopulation (modified from Akçakaya & Raphael 1998; reproduced by permission of Springer Science and Business Media). The top curve gives risk under a timber-harvest scenario and the bottom curve assumes no habitat loss. Each point on the curve indicates the probability that the overall abundance will decrease by some percentage from the initial abundance during a 100-year interval. In this example the maximum difference between the curves is at a 78% decline (marked by a vertical line); the probability of this level of decline from the initial abundance is approximately 77% with logging and 33% without logging.

50:50 chance of viability (as defined by our quasi-extinction threshold) in 25 years. Sometimes these cumulative probability curves are viewed in different ways, as shown later in Fig. 12.5, where we see the probability of the population reaching a range of abundances 5 years later.

Another way to portray risk is to display the probability of the population declining by some amount relative to the initial population size. For example, Fig. 12.3(b) shows that the risk of large percentage declines in spotted owls over the next 100 years is much higher with logging than without.

How to conduct a PVA

We have seen that various thresholds of viability or extinction may be considered over various times and probabilities. Clearly, the best PVAs will be those that consider multiple thresholds and alternatives with a range of inputs and outputs, instead of a single analysis with X data input for Y probability of persistence over Z years. Also, it should be clear that PVA has a strong biological basis but the selection of the thresholds arises from societal norms. Obviously, issues such as for how long we want to evaluate persistence and how secure that persistence should include social, cultural, economic, and political considerations (Shaffer 1987, Ludwig & Walters 2002).

Likewise, the spatial scale of any PVA should be linked to the population being analyzed and the management perturbations being considered (Ruggiero et al. 1994, Gärdenfors et al. 2001). These different scales may not match, for example if the PVA is for only one National Forest while the perturbations are occurring regionwide and the species persists across an even larger scale (say, continent-wide for a large carnivore species).

Once ranges of thresholds are set and the scale of analysis clearly articulated, we are ready to conduct a PVA. Two primary classes of formal, quantitative PVAs exist. One type uses time series, or abundance over time. The other uses vital rates linked to demographic processes such as density dependence and inbreeding depression. Both approaches can be extended to multiple populations.

Time-series PVA

A time series of abundance estimates can be used to estimate probabilities of a population reaching quasi-extinction. The mathematical approaches become complicated and beyond this book (see Dennis et al. 1991, Morris & Doak 2002, Staples et al. 2005), but the bedrock of the methods build off the estimation of average trend or growth rate ($\hat{\bar{\mathrm{r}}}$, often denoted in PVA as $\hat{\bar{u}}$) and its variance (σ^2), as described in Chapter 5. Assuming that the future will have similar growth and bounce (variation) as the past, one can calculate the future probability of a population bouncing its way down to some threshold quasi-extinction or management threshold.[4] The math captures the nonintuitive but important fact that stochasticity can cause populations with positive growth rates to decline to extinction (Chapter 5), implying that managing variability in population growth can be as important as managing the mean growth rate.

To see how time-series PVA works, consider estimates of abundance for gray whales off the central California coast from 1967 through 2001 (Fig. 12.4a). The population was depleted by commercial whaling in the late 1800s. Legal protection began in 1946 and by 1994 the population had recovered enough to be removed from the list of endangered and threatened wildlife (Gerber et al. 1999). The abundance estimates used in the time series were collected while whales were migrating south during the winter (Reilly 1992, Rugh et al. 2005). Trend analysis using the EGPN (exponential growth with process noise) method (Chapter 5) and translating $\hat{\bar{\mathrm{r}}}$ to λ provides an estimated λ of 1.008 with a 90% confidence interval of (0.97, 1.052). Thus the most likely trajectory of the gray whales has been an increase of just under 1% per year, with up to a 3% decrease or 5% increase being consistent with the data. The final step is to combine these estimates of growth and its variance with a quasi-extinction threshold. Suppose the quasi-extinction threshold were set at 10,000, a little smaller than the lowest number of whales observed during the the time series. The best estimate of the probability that the population will decline from its abundance of roughly 18,000 whales in 2001 to 10,000 is about 15% in 10 years and 28% in 20 years (Fig. 12.4b).

Elaborations of this basic density-independent PVA of time-series data can be extended to account for many real-world complexities, including correlations or changes in average trajectory over time, outliers, and density dependence (e.g. Bakker et al. 2009, Staples et al. 2005). In general, positive density dependence (e.g. Allee effects) will tend to increase extinctions in time-series PVA, while negative density dependence has more complicated effects: at low numbers it tends to reduce the extinction probability because population growth increases, but the regulatory effect of negative density dependence will also cap population growth, which could increase extinction probability.

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[4] How long a time series is needed to estimate the extinction risk for a single population? At the very least, 10–15 time steps (e.g. years) are needed to be able to characterize population growth and correlation structure, although considerably more may be necessary to properly capture variance in growth rates or determine density-dependence structure (Brook & Bradshaw 2006, Humbert et al. 2009).

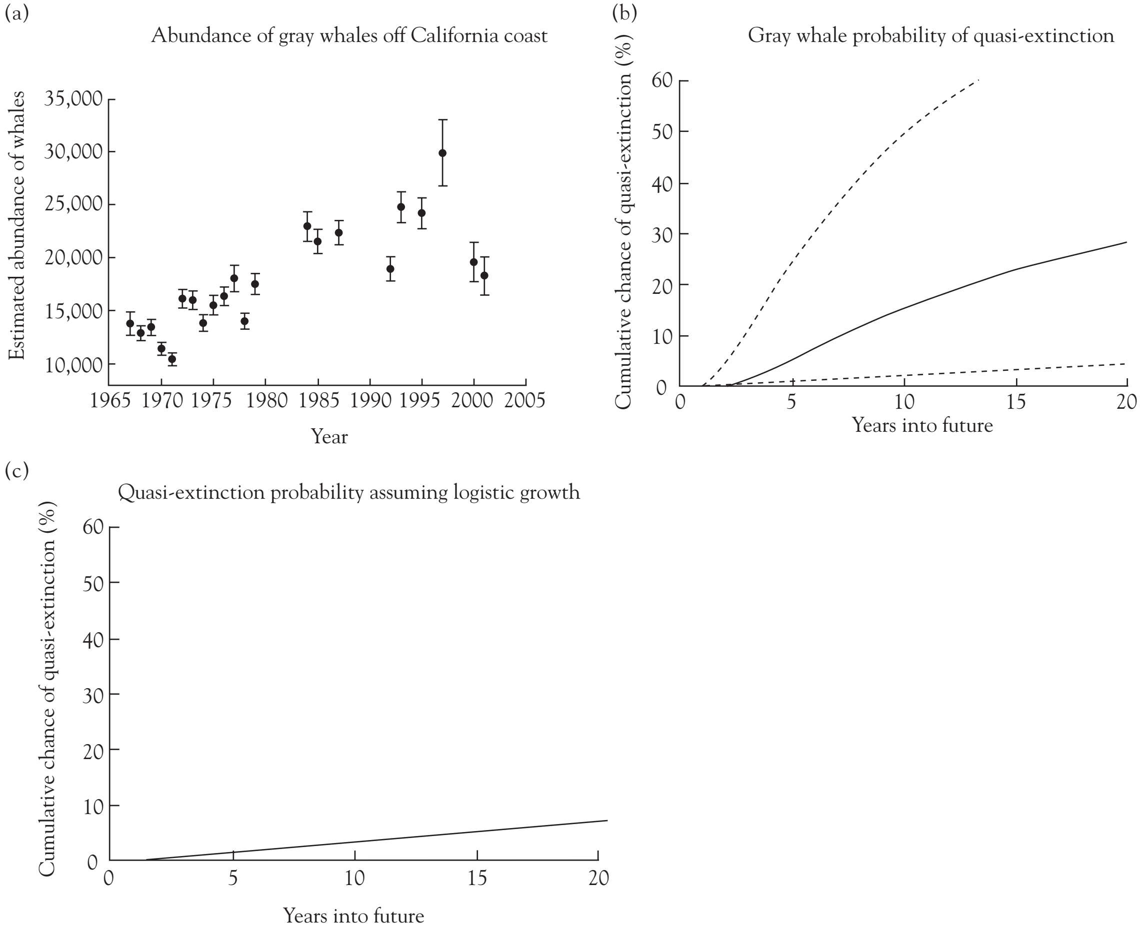

Fig. 12.4 Time-series PVA based on gray whales off the coast of California. (a) Abundance estimates over time, with SE bars representing sample variance (data from Rugh et al. 2005; see also Wade 2002). (b) The cumulative distribution function (and its 90% confidence interval) of the density-independent quasi-extinction probability of decline from the 2001 abundance of 18,178 to a quasi-extinction threshold of 10,000 or fewer whales. (c) Quasi-extinction probability, as in (b), except that a logistic growth model of negative density dependence is assumed.

One of three approaches are usually taken to deal with density dependence in PVA:

- Estimate the density-dependent structure and parameters from the field data using a model-fitting framework (e.g. Akaike's information criterion, AIC), which is undoubtedly the best approach but requires high quality and quantity of data.
- Use a density-independent model in the hope that it performs well enough to say something useful about real populations whether or not they are experiencing density dependence.
- Use an array of models with and without density dependence to bracket what might actually be occurring and see if management alternatives are robust to the model form used (Pascual et al. 1997).

When data quality and quantity do not allow the first approach (estimating the density dependence structure from the data), a combination of the second and third approaches can be reasonable. Simple density-independent models should perform well in a wide variety of conditions, such as the following (Sabo et al. 2004):

- Populations subject to density dependence are at abundance levels where density effects are not strong (e.g. at abundances well below *K* in cases of negative density dependence).
- The effects of density are similar in the past – when the parameters of population growth rate and its variance are estimated – and the future for which predictions are being made.
- The form of density dependence is a ceiling (Chapter 7), as might occur under competition for space such as nesting sites.
- The goal is to detect large declines as opposed to small ones.
- The population of interest is declining or only slowly recovering.

These conditions cover many instances where we would be interested in performing a PVA in the first place. In such cases, a density-independent time-series PVA model is likely to either correctly predict future dynamics or err toward the side of caution by overestimating the probability of reaching a quasi-extinction threshold (Sabo et al. 2004). If, however, you are interested in estimating chances of moderate declines, or if the population shows signs of recovery, or if biological intuition or sound data indicates the operation of more complex forms of density dependence with feedback across all population sizes (Chapter 7), then the best approach would use a density-independent model as well as different forms and shapes of density dependence. Figure 12.4(c) shows that logistic-type density dependence would decrease probabilities of quasi-extinction for the gray whales.

An extension of density-independent time-series PVA models is called **risk-based viable population monitoring** (Staples et al. 2005). This approach uses annually updated estimates of trend and variance to iteratively estimate probabilities of persistence or decline to a threshold of concern, thereby efficiently describing both population status and risk of potential future declines or extinction. In essence, trend and variance based on EGPN or EGSS estimators (Chapter 5) are used to estimate the probability that the population will fall below a specified quasi-extinction threshold within a specified time in the future; thus risk and recovery is not defined in a single long-term evaluation but rather as maintaining a low risk of decline over multiple updated risk assessments. Software is available to implement this methodology (Program PopGrow; http://www.cnr.uidaho.edu/population_ecology).

Time series PVA models have typically been limited to assessing risk without explicitly addressing the second part of the PVA definition of weighing how management actions might reduce the threats to a population. Because covariates can be incorporated into time series analyses (e.g. Dennis & Otten (2000) include rainfall and density in an analysis of kit fox trends), it should be possible to add management-relevant covariates and use model selection to ascertain which management actions most affect persistence. These approaches have been little used to date. The demographically explicit PVA method, described next, is more commonly used to evaluate the efficacy of various management techniques for recovering populations.

Demographically explicit PVA

This class of PVA model incorporates estimates of demographic vital rates, their variances and covariances, and other biological information such as stage structure, density dependence, and costs of inbreeding depression. A major benefit of demographically explicit PVA methods is that they move beyond merely predicting viability and allow constructive evaluation of actions that will most effectively reverse a declining population (Beissinger & Westphal 1998, Reed et al. 2002). Therefore, these approaches quantify effects of various management actions, thereby addressing the second part of the PVA definition (to give insights into factors that constitute the biggest threats).

As a striking example, consider the highly endangered northern right whales, which declined to about 300 worldwide due to female mortality from collisions with ships, entanglement with fishing gear, and fluctuations in food. The small size of the population means that every individual death has a large effect on survival. Ironically, therein also lies the hope: increasing current survival rates by preventing the deaths of just two or three individual female whales each year could actually reverse the decline of right whales and put them on the road to recovery (Fujiwara & Caswell 2001). When populations are very small, individuals matter (some more than others) and demographically explicit analysis can help show the most efficient path to recovery.

The inclusion of multiple interacting factors in a demographically explicit PVA almost always requires computer simulations, often following the framework of matrix models (Chapter 6). The computer builds

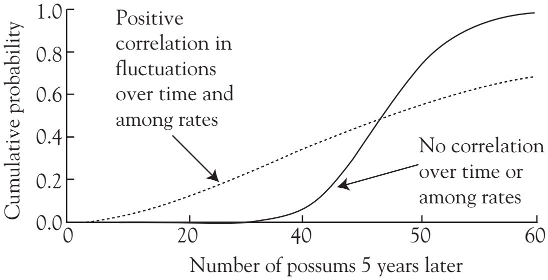

Fig. 12.5 Correlations among vital rates and over time can affect viability predictions. Based on data from the endangered Australian possum, the cumulative probability gives the risk that 30 possums will fall below some number of possums in 5 years. The solid line assumes independence (no correlation) both among rates and over time and indicates a high likelihood of persistence; for example, it appears that the chance of falling to less than 40 possums in 5 years is very small. The dotted line assumes perfect positive correlation in rates over time and among vital rates, and shows a much higher likelihood of declining to fewer than 40 possums, or even 30 possums, in 5 years. Modified from Ferson and Burgman (1995). Reproduced with permission from Elsevier.

thousands of "what if" scenarios, with each replicate being a possible projection of the population into the future. Replicates capture the many different paths a population could take, based on the real-world estimates of vital rates and other potential processes.

Factors that can be incorporated into demographically explicit PVAs include the many nuances of stochasticity, as well as inbreeding and density dependence. Demographic and environmental stochasticity can be incorporated into the replicate projections (Box 6.3), as can unusual fluctuations such as catastrophes with specified magnitudes and average timing for occurrence. Correlations among vital rates and over time (as discussed in Chapter 6) can also be incorporated (Fig. 12.5). Genetic stochasticity due to genetic drift and inbreeding depression can be incorporated by specifying how demographic rates decline with increased inbreeding (Box 12.3). The range of inbreeding expected for any species, as well as uncertainty in the shape of the curve relating inbreeding to fitness, means that incorporating genetic stochasticity is the same as with any other uncertain parameter in PVA (including, for example, dispersal rates, density dependence, breeding structure, correlations among rates and over time, and so on): you should include a range of plausible possibilities, including worst-case and best-case scenarios. Finally, as noted in the previous section, positive and negative density dependence can also affect PVA predictions and can be included based on field data and by bracketing with density-independent and density-dependent what-if scenarios (Mills et al. 1996).

How to conduct a demographically explicit PVA? In some cases, commercial or shareware PVA programs suffice. Two of the most popular are the matrix-based RAMAS (Akçakaya et al. 2004) and the individual-based VORTEX (Miller & Lacy 2003). In other cases, particular aspects of proposed management options or of the animal's life history or behavior require development of species-specific PVA programs (e.g. for cheetahs (Kelly & Durant 2000), red-cockaded woodpeckers (Daniels et al. 2000, Walters et al. 2002), and African wild dogs (Vucetich & Creel 1999); see Fig. 12.6).

Perhaps most importantly, demographically explicit PVAs allow the user to take the next step of evaluating efficacy of management actions across political, economic, and sociological contexts. Several case studies for practical sensitivity analyses to guide management based on PVA-like models are given in Chapter 6. Another example of management through viability analysis married PVA science with field data and management decision-making for the endangered island fox (*Urocyon littoralis*) on the Channel Islands (Bakker & Doak 2009, Bakker et al. 2009). First, acceptable risk and recovery criteria were established in a public forum, accounting for the inevitably complex sociopolitical and biological considerations. Next, readily monitored population attributes were selected (e.g. adult population size and adult mortality) and linked to quasi-extinction thresholds via PVA. This step clarified that uncertainty in the monitoring data will delay the delisting of a recovering population, giving incentives to all parties to reduce uncertainty. Finally, management actions that affect the population attributes were incorporated (e.g. how management of golden eagle predation would achieve delisting).

The biggest disadvantage of demographically explicit approaches is their need for extensive data. Clearly, there comes a point where ignorance of input values leads to futility in parameterizing a complex model with poor or nonexistent data; in such cases the time-series approach or one of the other approaches described below may be more appropriate. However, in the zone where the match between model needs and data availability is reasonable, one can embrace uncertainty by acknowledging it explicitly and considering

Box 12.3 Incorporating inbreeding costs into demographically explicit PVA models

Genetic drift in small populations can decrease heterozygosity and cause inbreeding depression (Chapter 9). The cost of inbreeding depression on fitness is incorporated in PVA models via **lethal equivalents** expressed either per gamete (per haploid genome) or per individual (per diploid genome; twice the number per gamete). Lethal equivalents include the effects of independently acting lethal alleles as well as the cumulative effects of partially deleterious alleles that would kill the individual if made homozygous. To bring this closer to home, humans have been found to carry enough deleterious alleles – lethal equivalents per individual – to kill each of us between two and five times over (Keller 1998). These deleterious alleles tend not to be expressed in individuals in large populations because natural selection holds them at low frequencies and they are usually recessive, so nondeleterious alleles mask their effects. However, inbreeding can increase expression of the deleterious recessive alleles, reducing survival or reproduction.

Lethal equivalents are estimated by determining (usually through regression) the relationship between the inbreeding coefficient and fitness. The difficulty of measuring both inbreeding level and fitness means that in many PVAs a range of values from other species are used to bracket possible effects. For example, for 40 different nondomestic mammal species in zoos the lethal equivalents per diploid individual for juvenile survival ranged up to 30.3, with a median of 3.1 (Ralls et al. 1988). Over the full range of lifetime reproductive success, field estimates of lethal equivalents may be closer to 12 (O'Grady et al. 2006).

When decrementing vital rates with loss of genetic variation in a PVA model, another consideration includes whether or not the cost of inbreeding is constant. The shape of the curve relating inbreeding to fitness is a complex topic that includes whether fitness interactions among genetic loci are synergistic and whether there is a threshold level of inbreeding above which the costs get worse (see Frankham 1995), as well as the extent to which inbreeding depression is purged over time (see Chapter 9). Different PVA programs account for synergistic effects and purging in different ways (e.g. Mills & Smouse 1994, Miller & Lacy 2003).

scenarios across a range of plausible values (Bakker et al. 2009).

PVA with multiple populations

The PVA approaches for single populations described above can be scaled up for multiple populations across the landscape (see Horne et al. 2011 for an example for endangered golden-cheeked warblers (*Dendroica chrysoparia*)). With sufficient data, multiple-population PVA models can be **spatially explicit**, incorporating exact locations of populations or individuals or other features (Reed et al. 2002). Levels of connectivity – and their positive and negative effects – as well as correlation in dynamics among the populations (Chapter 10) can be incorporated. The extent of positive correlation or coupling in environmental stochasticity is often facilitated by closer proximity. Correlations among population dynamics are also facilitated by movement of individuals; for example, Canada lynx populations across western North America are connected by gene flow (Chapter 10), which may facilitate the relatively synchronous dynamics of lynx populations at the continent-wide scale.

A different type of PVA builds off of presence/absence data across multiple populations over time. In the simplest form we might estimate the extinction probability to be the fraction of populations occupied in the past but no longer occupied in the present (e.g. of 100 sites historically occupied only 40 are still occupied, so the extinction probability is $1 - 40/100 = 0.6$). However, there is an important wrinkle in the real

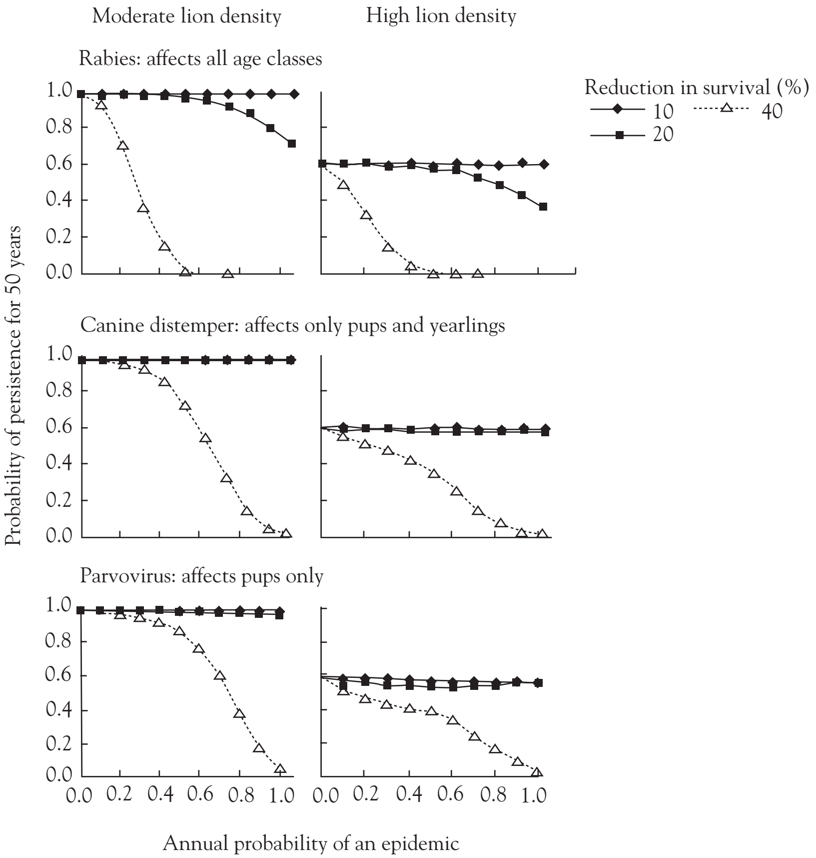

Fig. 12.6 An example output for a demographically explicit PVA, addressing how both predators (lions) and diseases of differing virulence would affect African wild dog populations. The panels (modified from Vucetich & Creel 1999, reproduced with permission by John Wiley and Sons, Ltd.) show the probability of persistence for 50 years for a population of 98 wild dogs, in cases where disease reduces wild dog survival by 10, 20, or 40%. The left-hand panels give results when wild dogs are in the presence of moderate lion density (100 adult lions/1000 km^2) and the right-hand panels represent high lion density (131 adult lions/1000 km^2). The top panels show results with rabies, which affects all age classes equally, the middle panels show the outcome of canine distemper, which primarily affects pups and yearlings (and adults only to a lesser extent), and the bottom panels are for canine parvovirus affecting only pups.

world: a presence is a presence; it was there. Does an "absence" truly indicate an extinction or was the species present but simply not detected? Just as we saw that raw count data must be adjusted by individual detection probability to estimate abundance (Chapter 4), with **occupancy modeling** we adjust raw counts of species detections across patches by the estimated probability of detecting a species (MacKenzie & Royle 2005). For occupancy, the probability of detecting a species that is actually present is derived from the pattern of detections and nondetections in a string of samples over time or space. After incorporating incomplete detection, the estimated occupancy at site *i* (site represents a patch or sampling cell), $\hat{\psi}_i$, becomes the probability that the site is occupied by the target species.

Now, suppose you have historic data that indicates where populations were known to be. Then you return to those previously occupied sites and estimate $\hat{\psi}_i$, the probability that it is still occupied in the present at that site. The extinction probability for that site is $\hat{E}_i = 1 - \hat{\psi}_i$. Finally, the average extinction probability for the species across all *n* sites that had previously been occupied is $\hat{\bar{E}} = \sum_{i=1}^{n} \hat{E}_i / n$ (Karanth et al. 2010). This gives the estimated proportion of sites at which local extinctions occurred.

A terrific example of this approach builds on >30,000 historic records (from museums, taxidermy, etc.) to identify areas where 25 mammal species in India were known to be present in the last 200 years. By returning to those sites in the present (2006) and applying occupancy modelling approaches, Karanth et al. (2010) could estimate the proportion of the historic sites still occupied, correcting for incomplete detection. From this they estimated local extinction probabilites for the 25 species ranging from 0.14 (jackal, *Canis aureus*) to 0.96 (lion, *Panthera leo*). They then modelled local species extinction rates relative to potentially important covariates and found that key variables led to decreased probabilities of local extinction for at least some of the species: the presence of protected areas (18 of 25 species), high forest cover (7 species), high elevation (8 species), and lower human population density (13 species). Extinction probabilities were higher for animals that were large-bodied, rare, and habitat specialists. Clearly, these approaches can be used to model population viability rigorously in cases where the only available data are presence and absence.

Big-picture thoughts about PVA

The primary benefit of using PVA to quantify viability is that it forces us to be explicit about the threats to a population. It puts assumptions on the table so that people can honestly debate and disagree. Sometimes the important factors for management focus turn out to be nonintuitive, emerging only when multiple factors are analyzed in the synthetic framework of a PVA. For the same reasons, PVAs also help identify surprising gaps in knowledge to target with research.

Practical advice for PVA may be found in Akçakaya and Sjögren-Gulve (2000), Burgman and Possingham (2000), and Reed et al. (2002). From these works and others, and from personal experience, I will distill three overlapping take-home messages.

(a) Remain acutely aware of the quality of the data available, and the match between the data and the model (Ludwig 1999, Fieberg & Ellner 2000, Sæther & Engen 2002). As we have seen in this book, variation in vital rates, abundances, and carrying capacities arises from both process variance and sampling variance (or observation error). Sampling error will make nature seem more variable than it really is, which will tend to overestimate the predicted probability of extinction. Also, if your attempt to parameterize a complex model hemorrhages with missing data, do not try to force a model that requires those data.

(b) Remember that PVA is more useful as a comparative tool for ranking management options than for making precise predictions of extinction. Although the scientific process underpinning PVA can provide a sound basis for predicting actual population trajectories, such precise predictions will typically be limited by the quality and quantity of data (Brook et al. 2000, 2002). In general, data quality will rarely be ideal, especially for the more realistic (detailed) models, and we will almost always be ignorant about the specific future changes (natural or human-caused) that should be included. Using PVA to evaluate the relative merits of different management options allows it to be incorporated into the decision-making that guides management action and policy (Maguire 1991, Noon & McKelvey 1996, Bakker & Doak 2009). Box 12.4 provides a case study of how a PVA was used to improve decision-making for Leadbeater's possum, an endangered marsupial at the center of a contentious forestry debate in Australia.

(c) Embrace uncertainty by considering a range of possibilities for every step with doubt about a process, a functional relationship, or a measured parameter. The worst PVAs are those that take one set of input data and provide one point estimate of extinction probabilities, while the best are those that consider a range of biological and management-based inputs, and a range of predictions (projection time span, probabilities of persistence, varying scenarios, etc.). Ideally, in addition to the range of input values and output metrics, a PVA should be performed with multiple methods. Sensitivity analysis in the broad sense, evaluating what inputs most affect the output, is perhaps one of the most useful contributions of PVA. Burgman and Possingham (2000:104) recall the epithet that "all models are wrong but some are useful" (from Box 1979:202) to emphasize their point that:

> . . . the only correct model is an entire reconstruction of the actual system – whereupon it ceases to be a model. The utility of a PVA is determined by several things, including the care taken to include

Box 12.4 An example of PVA as an input to decision analysis

The primary threat to Leadbeater's possums in Australia is loss of nest sites in trees over 150 years old. Early this century, fires burned more than 60% of the forest within the range of the species and clearcut logging subsequently occurred over 75% of its known distribution. The species now occupies an area 60 km by 50 km in the central highlands of the state of Victoria in southeastern Australia, where management avoids cutting in certain areas (including old growth patches) and allows it in others; areas that burn in the future may be salvage logged.

The viability of this species was assessed subject to current and potential future management options (Fig. 12.7) (Possingham et al. 2002). For each option, the number gives the percentage chance of extinction over the next 150 years (shown in parentheses in the figure) and over a period in the future when the forest has reached an equilibrium with the management actions (think of this as the period 500–650 years from now, assuming constant conditions).

Under current management, possums would be expected to persist for the next 150 years (only 38% chance of extinction), but not into the future (100% chance of extinction). If existing old-growth forest were not allowed to be salvage logged, the extinction risk decreases because damaged but

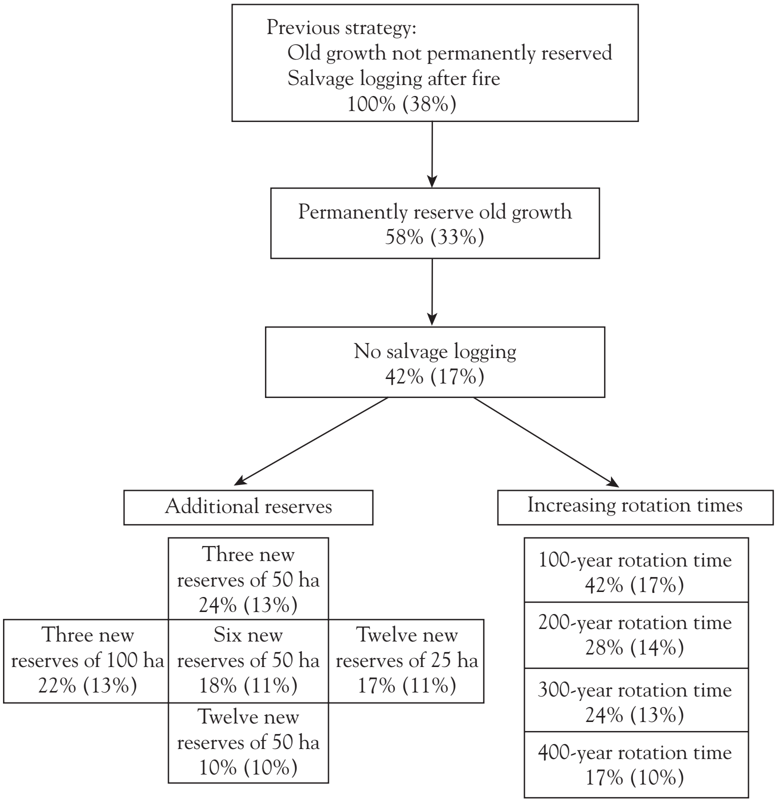

Fig. 12.7 Assessment of the viability of possums subjected to management options. From Possingham et al. (2002). Reproduced with permission of the University of Chicago Press.

alive trees remain. The next option also prevents salvage logging of other areas that can grow into old growth (see Fig 12.7, third box), further increasing possum viability.

Two popular suggestions for further aiding this species, to increase rotation times and to make more reserves, were considered next. Although increasing rotation time does reduce extinction probabilities, it requires an almost complete halt of logging for the next 150 years, hardly a politically realistic possibility. By contrast, setting aside reserves improves viability even more but reduces logging very little; for example, setting aside just six 50-ha reserves (5% of the forest block) reduces the extinction probability to 18% over the long term but reduces logging by only 5% at most. With the identification of additional permanent reserves as a viable approach, a number of scenarios were considered, trading off size and number of reserves. The authors assessed the sensitivity of conclusions by modeling a range of possibilities for processes about which they were uncertain. The recommendations emerging from this work have been implemented on the ground.

all ecological intuition faithfully, the care taken to represent all views (hypotheses) as structural alternatives, the detail and transparency of statements about assumptions, and the role of the model within the decision-making framework. One of the most important steps in establishing the credibility of a PVA is to communicate the uncertainties embedded in the model and its assumptions.

OTHER APPROACHES TO ASSESSING VIABILITY

The worst-case scenario for a biologist is to conduct an assessment of viability when time is short and data are scarce to nonexistent. However, it is not unusual for biologists to be asked to conduct a PVA with neither the time nor the data to conduct quantitative PVA using the time-series, demographically explicit, or multiple population models and analyses described above. For example, in 1993, President Clinton appointed a Forest Ecosystem Management Assessment Team (FEMAT) to evaluate the effects of large-scale timber-harvest options on wildlife species in western Washington, Oregon, and northern California (Meslow et al. 1994, Thomas 1994). More than 1000 plant and animal species were to be included in the assessment, even though little was known about many of the species. The team had 3 months to complete the job.

In the case of the 1000 species assessed as part of FEMAT, the best that could be done was a subjective expert-panel-type approach to assess viability. This method had evolved from earlier use in analyses in the Pacific northwest of the US (e.g. Thomas et al. 1993) and continued to evolve after FEMAT (Marcot et al. 1997). **Expert opinion** or other subjective approaches to assess viability are problematic because humans are inherently bad at guessing risks, even when they are informed guesses. We are led astray by how visible or controllable the risk appears and by the consequences of the risks (Burgman et al. 1993). Thus, we overestimate many low-level risks (e.g. death by tornado or anthrax) and underestimate high-level risks (e.g. death by heart disease or automobile accident). Also, subjective decision-making is idiosyncratic to the experiences of the expert making the decision: the term severe risk will mean different things to different people. This means subjective judgment decisions are neither transparent nor amenable to testing their logic, mechanisms, predictor variables, or sources of uncertainty (McCarthy et al. 2004). In short, expert-opinion assessments of viability remain an uncomfortable and insufficient last resort.

Therefore, to close the discussion of viability assessment, we will consider two less data-intensive methods that are not part of PVA per se, but that can be used to assess viability when detailed population data are not available.

Rules of thumb

Rule-of-thumb approaches assign qualitative rankings of risk based on specified, operational criteria. Two widely used programs based on rule-of-thumb viability assessments include those developed by the Nature Conservancy (Master et al. 2000, Samson 2002) and the World Conservation Union (the International

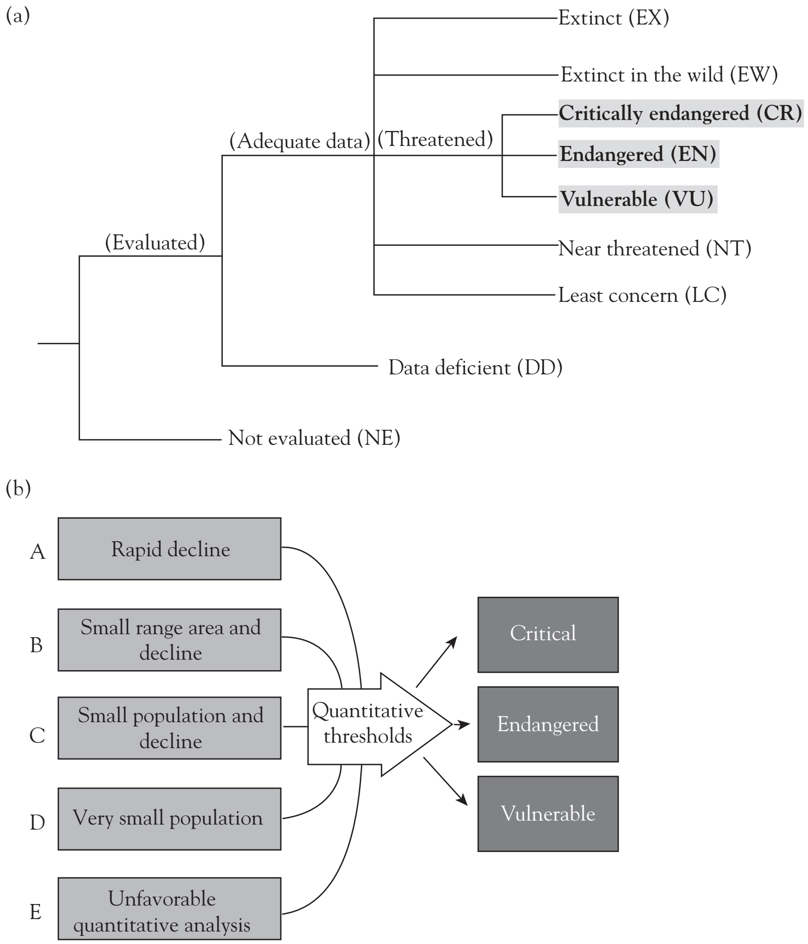

Fig. 12.8 The IUCN Red List population-assessment procedures. (a) Evaluated species are classified into one of nine categories. The three categories at risk of extinction are shown in bold. Modified from IUCN (2011). (b) The five rule-of-thumb criteria are used to place a species in one of the three categories of risk, see the **highlighted** categories in panel (a). Categories are from Mace et al. (2008) and IUCN (2011).

Union for the Conservation of Nature and Natural Resources, IUCN) Red List Categorization system (Mace et al. 2008, IUCN 2011; www.iucnredlist.org).

I will focus on the IUCN system, which forms the basis for Red Lists assessing the conservation status of more than 25,000 vertebrate species worldwide (Hoffmann et al. 2010). The IUCN approach assigns species to one of nine categories (Fig. 12.8a). To be placed in one of the three categories at risk of extinction (critically endangered, endangered, or vulnerable) at least one operational criterion must apply: (i) deep declines in abundance, (ii) reduction or fluctuation in geographic range or number of populations, (iii) small population size coupled with decline or fluctuations, (iv) very small or restricted population, or (v) quantitative analysis (Fig. 12.8b). Each of these criteria are based on specified, operational, rule-of-thumb thresholds. For example, the first criteria assesses declines in the past 10 years or three generations (whichever is longer); if the causes of reduction have stopped and are reversible then triggers into risk categories are: 90% decline = critically endangered, 70% decline =

endangered, and 50% decline = vulnerable; if the causes of decline have not stopped or may not be reversible the triggers are: 80% decline = critically endangered, 50% decline = endangered, and 30% decline = vulnerable (IUCN 2011). The fifth criterion for assigning species – quantitative analysis – may include a PVA if sufficient data exist, but may also use other analyses that directly quantify obvious threats; for example, if an endemic forest-dependent species occupies an area slated to be clearcut within 20 years (Mace et al. 2008).

A recent assessment of 25,780 vertebrate species worldwide – including all described bird, mammal, and amphibian species on earth – indicates that almost one-fifth fall into one of the at-risk categories (critically endangered, endangered, or vulnerable), with amphibians the group with the highest risk (Fig. 12.9). Furthermore, threatened vertebrates are disproportionately concentrated in tropical regions, where large numbers of species with restricted distributions coincide with high anthropogenic pressures (Hoffmann et al. 2010).

Sophisticated methods for making uncertainty explicit in the risk-assessment procedure have been proposed for IUCN categorization (Akçakaya et al. 2000, Taylor et al. 2002). The IUCN uses the precautionary principle as one way to deal with uncertainties: the credible estimate that gives the highest risk of extinction is used, so that uncertainties favor more cautious management approaches.

Another key philosophy behind the IUCN approach underscores an important general point about management of small populations: a distinction is made between assessing the severity of threat and setting conservation priorities (Mace 1994, 1995, Gärdenfors et al. 2001). Categories of threat established by the rules of thumb are just one piece of information used to set conservation priorities. Other important criteria might include the likelihood of success in restoring the species, the number of other threatened species occupying the same habitat, taxonomic uniqueness, availability of funds, and the legal and political framework for conserving a particular species.

Despite obvious limitations to any rule-of-thumb approach, they may be the best available method at times. Mace and Hudson (1999:244) report that

> . . . although the IUCN system may be efficient at picking up different species facing diverse threats, it is not designed to be an accurate tool for measuring extinction risk, for projecting population status, or

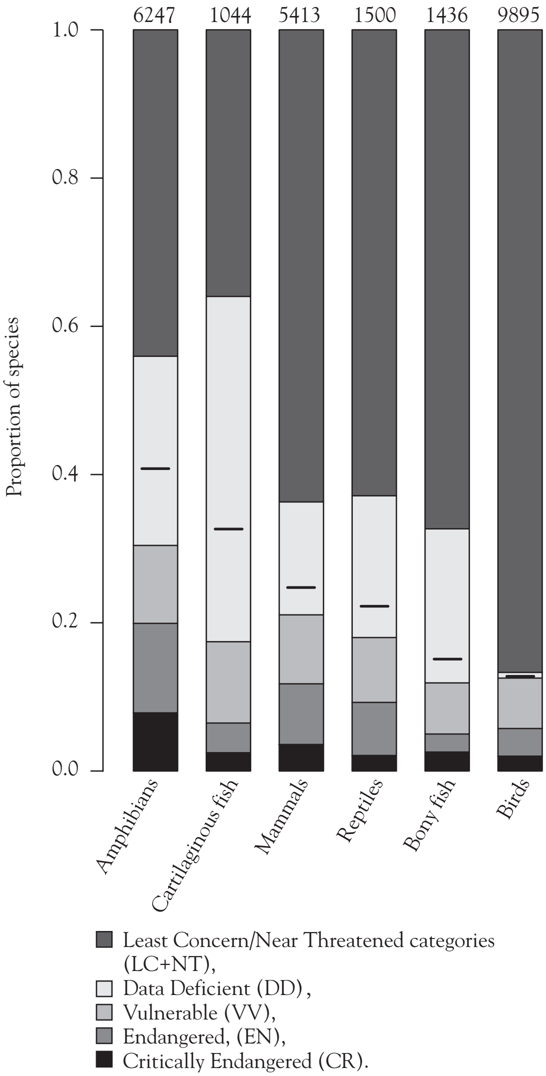

Fig. 12.9 Proportion of 25,780 vertebrate species assigned to various IUCN Red List categories. Included are all extant mammals, birds, and amphibians, and representative samples of reptiles and fish (the number of species assessed in each group is at the top of each bar). The bars, from the bottom up, represent Critically Endangered (CR), Endangered (EN), vulnerable (VV), Data Deficient (DD), and Least Concern/Near Threatened categories (LC + NT). The horizontal line in each bar represents the estimated percentage of species that would be considered at risk of extinction (i.e. placed in critically endangered, endangered, or vulnerable categories) if the data-deficient species were assigned to categories in the same percentage as data-sufficient species. Modified from Hoffmann et al. (2010). (See Color Plate 11)

> for designing population management plans. Its role is to highlight species exhibiting one of several symptoms of pending extinction and to classify species according to the relative severity of the apparent threat. The Red List is a useful conservation tool only when listing leads to measures to assess the causes of threat and to develop, where necessary, appropriate management responses and species recovery plans. In short, the IUCN Red List criteria are designed to be robust and precautionary across a wide range of circumstances, to operate when data are scarce, and to pinpoint species in need of attention.

Approaches based on habitat and other information

The presence of habitat alone cannot constitute an assessment of population viability. As Kent Redford (1992) noted for wildlife in tropical forests: "The presence of soaring, buttressed tropical trees, however, does not guarantee the presence of resident fauna . . . although satellites passing overhead may reassuringly register them as forest, they are empty of much of the faunal richness valued by humans. An empty forest is a doomed forest." Habitat is necessary, but not sufficient, to guarantee population persistence or to predict what will happen to the population in the future. In the US this principle was captured in legislation when the first federal Endangered Species Act of 1966, which focused entirely on habitat and ignored taking and commercial activities on wildlife populations, was modified to include population-level impacts (Goble 2006).

Nevertheless, for certain species at certain times more information exists for habitat relations than for demographic vital rates, and the habitat information alone can contribute useful information to assessments of viability (Boyce 1992). Habitat associations can be combined with other information for region-wide or species-wide assessments in a **Bayesian belief network** (Marcot et al. 2001, Suring et al. 2011). The inputs include associations with habitat and other variables, as well as expert opinion and ancillary models (including true PVA models), incorporated in a transparent way. Using a Bayesian statistical framework (Chapter 2), input variable values are combined to estimate our belief, represented as a probability, of a response relevant to population status. Risks associated with alternative courses of actions can be explored. For example, viability of 28 species was assessed as part of land planning for the 58 million ha Interior Columbia River basin (see Wisdom et al. (2002) for an assessment of greater sage-grouse and Rowland et al. (2003) for wolverine).

Marcot et al. (2001:29–30) describe both the utility and limitations of these approaches, noting that when scant scientific data are available but decision-making is nevertheless moving forward:

> . . . the experts must provide their best professional evaluation or step aside and let activities proceed without their input . . . Our [Bayesian belief network] models of wildlife population response, however, do not substitute for empirically based, quantitative, stochastic analyses of population demography, genetics, and persistence such as those used in population viability analysis . . . [the Bayesian belief network approach is] most useful when empirical data on population trends, demography, and genetics are unavailable.

SUMMARY

Often the most vulnerable wildlife populations have high susceptibility to human-caused stressors, have gone from being large to being small, and have high variability relative to growth rate. In such cases, the most important actions are to reverse the decline and increase numbers. However, a population that has become small may also be sucked into the extinction vortex, whereby demographic, environmental, and genetic randomness exacerbate the potential for extinction even if the causes of decline are reversed. Viability assessment procedures provide a framework to capture the intuition, theory, and field data comprising the extinction vortex. The quantitative branch of viability assessment, known as population viability analyis (PVA), incorporates multiple interacting factors, providing transparent and often nonintuitive outcomes of management.

Quantitative PVAs are often conducted with time series or with demographically explicit models. Time-series analysis estimates quasi-extinction probability (decline to numerical thresholds of importance) based on counts of abundance over time. By contrast, quasi-extinction probabilities for demographically explicit PVAs are based on a range of vital rates and their correlations, density dependence, inbreeding costs, and other information relevant to population dynamics. Demographically explicit scenarios are also preadapted to provide what-if scenarios or sensitivity analysis to identify specific management actions of greatest benefit to species persistence, and perhaps highest economic or political efficiency. Quantitative PVAs can be extended across multiple populations, where persistence can also be modeled with presence/absence data in an occupancy modeling framework.

In more data-sparse situations, less quantitative approaches are often used to assess viability. For example, the IUCN Red List method assigns qualitative ranks of risk using specified, rule-of-thumb thresholds based on trend, abundance, fluctuations, and degree of connectivity. Bayesian belief networks provide a different framework to consolidate and make transparent field data, expert opinion, and models for management decision-making. Although these methods do not fall under the formal rubric of quantitative PVA, they accommodate uncertainty, make input explicit, and assess risks associated with alternative courses of action.

Small-population management includes peeking into the crystal ball to fathom how particular scenarios will affect the likelihood of extinction. In so doing, we should (i) remain acutely aware of data quality, (ii) use models as comparative tools, and (iii) embrace uncertainty, using all of the data and population-biology concepts and theory at our disposal to make good predictions while acknowledging and making transparent the assumptions underlying the assessments. Through viability assessment, population biology can and should be a vital part of decision-making for small and declining populations.

FURTHER READING

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Staples, D.F., Taper, M.L.,and B. B. Shepard, B.B. (2005) Risk-based viable population monitoring. *Conservation Biology* **19**, 1908–16. A nice overview of time-series PVA approaches and a provocative proposal for a new way to conduct them.