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Population Viability Analysis

Introduction

Population Viability Analysis (PVA) (sometimes referred to as extinction risk assessment, population vulnerability analysis, predictive simulation modelling, or stochastic population modelling) describes the process by which data and models are evaluated to determine the risk of population extinction over some given time-frame and under specified conditions. Understanding the risks of extinction faced by different populations can help to identify conservation priorities, whilst the formal consideration of how different interventions affect the probability of persistence can guide the choice of conservation actions. PVA has been a cornerstone of quantitative, species-focused conservation since the 1980s. Although it is sometimes characterized rather narrowly as simply the modelling of population trajectories, PVA is actually a much richer endeavour. For a given population, PVA requires the synthesis of quantitative information regarding the population's dynamics, as well as an explicit consideration of threats to its persistence and options for its management. More generally, the field of PVA provokes questions about realism, generality and sensitivity in modelling, about the key drivers of population dynamics and extinction, and about realistic time frames for population management. It exposes gaps in existing knowledge, about both general processes and specific populations, and thereby forces consideration of how best to deal with uncertainty. A strong theme in PVA research has been to characterise sources of variability in population dynamics, resulting in important contributions to the understanding of the roles of different types of stochasticity. A great diversity of methods exists for conducting PVA models and a significant challenge is to harmonise these, rendering their outcomes comparable. This has been the focus of recent research into the estimation of Minimum Viable Population size (MVP), one purpose to which PVAs have often been applied. Nonetheless, the estimation and utility of MVP estimates remains controversial. In spite of its long history, PVA remains widely used and integral to several ongoing developments in conservation biology. These include efforts to predict both the impacts of expected climatic change, and the consequences of management for interacting species. It is likely that PVA will remain an important analytical process for guiding conservation interventions for many years to come.

History

Amongst others, Beissinger & McCullough (2002) and Morris & Doak (2002) (both cited in *General overviews*) reviewed the origins of PVAs in some depth. In the 1970s, four factors focused attention on the problems of small populations. These included burgeoning interest in island biogeography and its implications for extinction – especially of populations confined to small areas, which was emphasised by Simberloff (1976); increasing recognition of the importance of variability in population dynamics, which was highlighted by May (1973); a developing science of the relationship between genetics and population size, stressed by Frankel (1974); and a growing awareness of the extinction crisis, which can be seen in Myers (1979) and in the retrospective overview by Simberloff (1988). Moving into the 1980s, these concerns dominated the developing field of conservation science, as seen in the treatments of Soulé & Wilcox (1980) and Soulé (1986). Questions associated with the vulnerability of small populations to extinction prompted consideration, by Shaffer (1981), of what constituted a small population and at what size a population ceased to be vulnerable. Ginzburg et al. (1982) emphasised the importance of stochastic modelling of quasi-extinction risk in environmental assessment. Shaffer (1983) used such a stochastic model to estimate the risks of population extinction and, thus, the *Minimum Viable Populations* for grizzly bears (*Ursus arctos*). From these beginnings, the concept of PVA emerged (see Soulé 1987, cited in *General overviews*). Early proponents, such as Burgman et al. (1988), saw population-focused models of extinction probabilities, informed by high quality autecological data, as an essential focus for larger questions about the design of reserves and the allocation of conservation resources. Subsequently, however, Caughley (1994) raised concerns about the dominant theoretical focus on small populations. Arguably, conservation biology still struggles to unite the disparate strands of research identified by Caughley (1994), and to ensure that work of academic appeal and theoretical interest contributes meaningfully to arresting rates of extinction. This remains a major challenge in the discipline.

Burgman, M.A., Akçakaya, H.R. & Loew, S.S. 1988. The use of extinction models for species conservation. *Biological Conservation*. 43:9-25

Summarises arguments against island biogeography as a predictively useful theory on which to base conservation decisions. The authors argue that population-focused conservation is likely to be more successful than conservation focused on communities or ecosystems. Conservation based on genetic and population dynamic models is promoted.

Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology*. 63: 215-244

This seminal paper identifies two parallel approaches to conservation biology: the small population paradigm, providing theoretical insights into the problems faced by small populations; and the declining population paradigm, focused on identifying and mitigating for the agents of a population's decline. Better integration of the two approaches is promoted.

Frankel, O. H. 1974. Genetic conservation: our evolutionary responsibility. *Genetics*. 78: 53-65

Embodies the growing awareness, in the 1970s, of the need to conserve genetic variability within species, not just the species themselves. Frankel argues that more information is needed on the genetic processes characterising natural populations, that we must safeguard the evolutionary potential of both wild and domesticated populations, and that genetical considerations can inform conservation practice.

Ginzburg, L.R., Slobodkin, L.B., Johnson, K. & Bindman, A.G. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis*. 2: 171-181

This paper promoted stochastic modelling as a key method in environmental risk assessment. The authors proposed measures for estimating the change in quasi-extinction probabilities as the consequence of an impact, and investigated the effects on time to quasi-extinction of aspects of stochasticity.

May, R.M. 1973. Stability in randomly fluctuating versus deterministic environments. *American Naturalist*. 107: 621-650

This paper was key to the increasing focus of conservation biologists on the importance of stochasticity in population dynamics, an important element in the developing science of conservation biology. May shows that stochastic population models can yield outcomes qualitatively different to those of their deterministic analogues.

Myers, N. 1979. *The Sinking Ark: A New Look At The Problem Of Disappearing Species*. Oxford: Pergamon Press

Influential treatment of the scale of the biodiversity crisis, focusing on explaining why so many species are doomed to extinction and what drives that fate. Focuses on tropical forests but the lessons are general, especially in regard to consumerism as the ultimate driver of extinction.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. *Bioscience*. 31: 131-134

The development of PVA was inextricably tied to the concept of the *Minimum Viable Population* (MVP). Posing the question, 'how much land is enough to achieve conservation objectives', Shaffer presents the first tentative definition for the concept of the MVP, and discusses methods available to derive MVPs.

Shaffer, M.L. 1983. Determining minimum viable population sizes for the grizzly bear. *Bears: Their Biology and Management*. 5: 133-139

Arguably the first PVA. Presents a stochastic simulation model, with demographic structure, in order to estimate the minimum population of Yellowstone grizzly bears that would have a 95% probability of persisting for 100 years. Uses those population size estimates to estimate the minimum area requirements of a viable population.

Simberloff, D. 1976. Experimental zoogeography of islands: effects of island size. *Ecology*. 57: 629-648

Presents empirical data from experimental manipulations of island size among mangrove islands in the Florida Keys. Data supported the principles of island biogeography, emphasising that extinction rates will be higher in smaller areas.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*. 19: 473-511

Discusses the background to the developing science of conservation biology, which also prompted developments in PVA. Simberloff identifies the importance of population ecology to that science – but also notes the complexities it introduces (for example, where it indicates that populations have very low probabilities of persistence).

Soulé, M.E. 1986. *Conservation Biology: the Science of Scarcity and Diversity*. Sunderland, Massachusetts: Sinauer Associates

This edited volume, including contributions from 45 authors, helped to define the modern discipline of conservation biology. It includes important contributions on elements of Caughley's (1994) small population paradigm and seeks to identify how those can contribute to conservation in the real world. Gilpin & Soulé's chapter introduced the term 'Population Viability Analysis'.

Soulé, M.E. & Wilcox, B.A. 1980. *Conservation Biology: An Ecological-Evolutionary Perspective*. Sunderland, Massachusetts: Sinauer Associates

Perhaps the first key text in developing the small population focus of conservation biology in the 1980s, this edited volume covers a range of topics and introduces some key definitions. It was this book which introduced Franklin's often-quoted 50/500 rule (see *Minimum Viable Populations*).

General overviews

Soulé (1987) was the first key treatment of scientific elements critical to this growing area of conservation-relevant research. Boyce (1992) provides a more critical consideration of the strengths and weaknesses of existing PVAs, and what they can realistically achieve for conservation. Beissinger & Westphal (1998) is also more cautious in its treatment of PVA, identifying a range of reasons for applying PVA as a qualitative, rather than a predictively quantitative, approach. In 2002, three further texts provided general overviews of PVA approaches: Beissinger & McCullough (2002) included contributions from a very large number of scientists active in the field of PVA, providing a comprehensive picture of the cutting edge of the subject; Morris & Doak (2002) proffered a more structured introduction to designing and conducting a PVA; and Reed et al. (2002) contributed further caution on how PVA should be used and interpreted. Sutherland

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(2006) provided a broader assessment of approaches for predicting the consequences of changes in environment or management, placing PVA in its wider context. [More recent overviews of PVA can be found in a range of textbooks on ecology and conservation, such as Gibson \(2015\).](#)

Beissinger, S.R. & McCullough, D.R. 2002. *Population Viability Analysis*. Chicago: University of Chicago Press

This edited volume contains contributions from a very large number of leading population and conservation biologists. It is the most recent – and, arguably, the most comprehensive – treatment of the science of PVA, across the whole range of issues that PVA raises.

Beissinger, S.R. & Westphal, M.I. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*. 62: 821-841

Examines the application of PVA to endangered species management. The authors urge caution in interpreting the quantitative outcomes of PVAs, recommending – instead – an emphasis on predicting relative rather than absolute risk of extinction. The authors also make arguments for restricting predictions to short timescales.

Boyce, M.S. 1992. Population Viability Analysis. *Annual Review of Ecology and Systematics*. 23: 481-506

After the early enthusiasm following the establishment of PVA, this review strikes a note of caution. Although constructive and forward-looking, the review highlights the shortage of required data (and paucity of ecology informing many PVAs), the difficulty of predicting the future, and the danger to credibility of making unsupportable predictions.

Gibson, D.J. 2015. *Methods in Comparative Plant Population Ecology*. Oxford University Press, Oxford

This textbook gives, as the title suggests, a broad overview of plant population ecology. Nonetheless, the final chapter [covers relevant](#) advanced statistical techniques, including an introduction to, and critique of, PVA.

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Morris, W.F. & Doak, D.F. 2002. *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sunderland, Massachusetts: Sinauer Associates

This book is probably the best available general guide to developing and performing bespoke PVAs. The authors give an excellent overview of eight uses of PVA (pp2-8), then progress logically from simple, density-independent models, to models including density dependence, stochasticity and spatial structure. Importantly, the book includes abundant examples and related MATLAB code.

Reed, J.M., Mills, L.S., Dunning, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M-C. & Miller, P. 2002. Emerging issues in population viability analysis. *Conservation Biology*. 16: 7-19

Updates the arguments raised by Beissinger & Westphal (1998). The authors note the increasing ease with which PVA can be performed, and the resultant complexity of models used. They urge sensitivity analyses and appropriate measures of confidence, whilst echoing several recommendations of earlier more cautious treatments.

Soulé, M.E. 1987. *Viable Populations for Conservation*. New York: Cambridge University Press

Stemming from a workshop held in 1984, this is the first book devoted to the issue of PVA. It provides a good introduction to both the practical and theoretical backdrops from which PVA arose, as well as insight into the early questions provoked by PVA, many of which remain pertinent.

Sutherland, W.J. 2006. Predicting the ecological consequences of environmental change: a review of the methods. *Journal of Applied Ecology*. 43:599–616

Useful overview of the broader discipline within which PVA is situated: that of predictive ecology. The paper clarifies the need for predictive ecology and the methods available to make predictions, as well as their strengths and weaknesses. One conclusion is that quantitative modelling is often inadequate to guide management.

Journals

Articles on PVA can be found in a very wide range of conservation, ecology, biology and general science journals. The following are those that have, over the past decade, most frequently published articles on PVA, with relevant articles appearing in **Biological Conservation** and **Conservation Biology** substantially more frequently than in any other journal. Nevertheless, the journals listed account for little more than a third of articles on PVA from the last decade and most ecological journals will have published some. Two practitioner-focused journals that are intended to inform specific resource management issues, are **Ecological Applications** and **Journal of Applied Ecology**. As spatially-explicit and multi-species PVAs become more common (see *Emerging areas in PVA*), relevant articles are increasingly to be found in journals focusing on landscape- or global-scale issues for biodiversity such as **Landscape Ecology** and **Global Change Biology**.

Biodiversity and Conservation. 1992 –

Now published by Springer, this was the first intentionally multidisciplinary journal in biodiversity management and sustainable development. The journal was founded in recognition of the conflicting values of different stakeholders, and published PVAs will often (but not always) reflect some element of reconciling land management concerns. Available

online[<http://www.springer.com/life+sciences/evolutionary+%26+developmental+biology/journal/10531>]

Biological Conservation. 1968 –

This journal, one of the first scientific journals to make conservation biology its central focus, is published by Elsevier. The journal has published many examples of population-specific PVAs but has also been an outlet for some work generalising the outcomes of PVAs. Available *online[<http://www.journals.elsevier.com/biological-conservation/>]*

Bioscience. 1964 –

Published by Oxford Journals. Although this journal publishes relatively few papers on PVA, it has published some important and influential contributions. Those include Shaffer (1981) (cited under *History*), as well as a recent Forum and Commentary relating to the use of PVA in listing/delisting decisions in the USA (Vol. 65, issue 2). Available *online[<http://bioscience.oxfordjournals.org/>]*

Conservation Biology. 1987 –

Published by Wiley for the Society for Conservation Biology. Like Biological Conservation, this journal has published many population-specific PVAs. Despite a North American bias, it has a strong international influence. It was also the first journal to publish a paper focused on PVA. Available *online[<http://onlinelibrary.wiley.com/journal/10.1111/%28ISSN%291523-1739>]*

Ecological Applications. 1991 –

Published by the Ecological Society of America, this journal was founded to facilitate interactions between academic ecologists and practitioners of environmental management. As such, PVAs published in this journal are often intended to inform specific resource management issues. Available *online[<http://www.esajournals.org/loi/ecap>]*

Ecological Modelling. 1975 –

Published by Elsevier, this journal's focus is on the use of mathematical modelling to describe ecological processes and inform sustainable resource management. Articles tend to be quite mathematical but the journal has published a range of developments in PVA, including theoretical treatments of some PVA modelling considerations. Available *online[<http://www.journals.elsevier.com/ecological-modelling/>]*

Global Change Biology. 1995 –

Published by Wiley, this journal's focus is on understanding the interface between environmental changes that affect a substantial part of the globe and biological systems. As ecologists focus increasingly on the impacts of climate change on the future viability of

populations (see Emerging areas in PVA), more population viability analyses are likely to appear in this and similar journals. Available
online[[http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1365-2486](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1365-2486)]

Journal of Applied Ecology. 1964 –

Now published by Wiley for the British Ecological Society. The journal publishes quality ecological science with the potential to influence biodiversity management or policy. As with Ecological Applications, PVAs published in this journal are often intended to inform specific resource management issues. Available
online[<http://www.journalofappliedecology.org/>]

Journal of Wildlife Management. 1937 –

Now published by Wiley for The Wildlife Society. The journal's focus is on the management of vertebrates, together with their interacting species, but game management is emphasised. In spite of this, the journal has published some important general treatments of PVA (e.g., Beissinger & Westphal 1998, see General overviews). Available
online[<http://onlinelibrary.wiley.com/journal/10.1002/%28ISSN%291937-2817>]

Landscape Ecology. 1988 –

Published by Springer, this is an interdisciplinary journal exploring basic and applied research questions on landscapes as coupled human-environment systems. So far, it has published few articles concerned with PVA but concepts such as the impact of fragmentation on viability are clearly within the journal's remit. Available
online[<http://link.springer.com/journal/10980>]

Population Ecology. 1952 –

Originally 'Researches on population ecology', this journal is published by Springer for The Society of Population Ecology, Japan. The first three issues were in Japanese but the journal retains only a little of that original geographic bias. PVA articles include both straightforward population-focused assessments and some theoretical treatments. Available
online[<http://link.springer.com/journal/10144>]

Applications

PVAs can be broadly characterised as yielding predictions about the consequences of stasis in a population's environment, or of changes resulting from natural processes or interventional management. However, within that broad application, it is possible to identify a variety of purposes to which PVAs have been put (e.g., see the eight uses of PVA reviewed in Morris & Doak 2002, cited in *General Overviews*). A common and early application, arising from the importance of protected area size to early conservation biologists, was that of estimating the area requirements of

populations; examples include Armbruster & Lande (1993) and Burgman et al. (2001). Another primary focus of PVAs has been to determine the consequences of management interventions. For example, Beissinger (2014) investigated the consequences of captive breeding and reintroductions; Fordham et al. (2008) considered predator control and harvest; and Haydon et al. (2002) modelled the impacts of disease control. PVAs have also been used retrospectively, such as in the study by O'Regan et al. (2002) intended to unravel the reasons for past extinctions. Examples of using PVA to predict the feasibility of pest eradication, as in the studies of Andersen (2005) and Pertoldi et al. (2013), are considerably rarer. Demographic considerations are key to both PVA and to listing/delisting decisions (i.e., decisions about conferring protected status on, or removing it from, a population). As such, PVAs are important to efforts to classify the extent of threats, evident in Mace et al.'s (2008) overview of the IUCN's red list criteria. Listing/delisting targets provide fertile ground for debate: Frankham et al. (2014) (cited in *Minimum Viable Populations*) expressed concern that red list categories understate requirements for long-term viability; it also seems likely that listing/delisting decisions will need to be made with more explicit consideration of the distinction between a single-species focus on avoiding extinction, and a more community-focused approach to maintaining ecologically functional populations (Redford et al. 2011) (see, also, *Bioscience* under *Journals*).

Andersen, M. (2005) Potential applications of population viability analysis to risk assessment for invasive species. *Human and Ecological Risk Assessment*. 11: 1083-1095

Andersen reviews models applied to invasive species and emphasises the strong link between these (often targeted at determining how the probability of extirpation can be maximised) and PVA (usually focused on minimising that probability). He concludes by calling for PVA to be applied more frequently to problems of invasive species control.

Armbruster, P. & Lande, R. (1993) A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? *Conservation Biology*. 7: 602-610

An early example of a PVA targeted at the specific problem of determining minimum areas required to conserve populations of a specific species. The model, parameterised from field data, includes density dependence and environmental stochasticity, and yields the recommendation that elephants need reserves of at least 1,000 square miles.

Beissinger, S.R. (2014) Digging the pupfish out of its hole: risk analyses to guide harvest of Devils Hole pupfish for captive breeding. *PeerJ*. 2: e549

An important analysis of management options for a critically endangered species. The complexity here is to conduct captive propagation, which involves removing individuals from the wild population without jeopardising it unduly. Shows why identifying which life stage to target (see further in *Influence of parameters*) can be relevant to captive breeding decisions.

Burgman, M.A., Possingham, H.P., Lynch, A.J.J., Keith, D.A., McCarthy, M.A., Hopper, S.D., Drury, W.L., Passioura, J.A. & Devries, R.J. (2001) A method for setting the size of plant conservation target areas. *Conservation Biology*. 15: 603-616

This paper offers rather more than just an example of using PVA to identify required reserve sizes. In the absence of all required information, the authors use expert judgement to identify parameters for their models. Unusually, they also include interspecific interactions of both predation and competition.

Fordham, D.A., Georges, A. & Brook, B.W. (2008) Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: managing a tropical freshwater turtle for sustainability and conservation. *Journal of Applied Ecology*. 45: 52-62

An example of how PVA can be used to inform real-world problems. The authors use PVA to explore the viability of an Australian turtle. They show that control of feral pigs can reduce mortality, enabling some traditional subsistence hunting of the species.

Haydon, D.T., Laurenson, M.K. & Sillero-Zubiri, C. (2002) Integrating epidemiology into population viability analysis: managing the risk posed by rabies and canine distemper to the Ethiopian wolf. *Conservation Biology*. 16: 1372-1385

An important example of a PVA for a critically endangered species that includes epidemiological dynamics. In the absence of disease, populations were stable, but rabies epidemics vastly inflated probabilities of extinction. The authors show that relatively low rates of vaccination could prevent the largest epidemics, potentially safeguarding the species.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J. & Stuart, S.N. (2008) Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species. *Conservation Biology*. 22: 1424-1442

A detailed exposition of the IUCN's threat categories and criteria used to assign species to those categories. One of the five IUCN criteria (Criterion E) is explicitly based on quantitative assessments of extinction risk. MVP theory explicitly informs Criteria C and D, which emphasise the dangers of small population size.

O'Regan, H. J., Turner, A. & Wilkinson, D. M. (2002) European Quaternary refugia: a factor in large carnivore extinction? *Journal of Quaternary Science*. 17: 789-795

Uses VORTEX (see *Modelling software*) to model the viability of an extinct large felid, using data from an extant analogue. The authors conclude that repeated confinement to glacial refugia could have led to a series of genetic bottlenecks and to inbreeding depression as an important driver of ultimate extinction.

Pertoldi, C., Rødjajn, S., Zalewski, A., Demontis, D., Loeschcke, V. & Kjærsgaard, A. (2013) Population viability analysis of American mink (*Neovison vison*) escaped from Danish mink farms. *Journal of Animal Science*. 91: 2530-2541

An unusual example of PVA used to assess the dynamics and control of an invading species, the American mink in Denmark. The authors show that feral mink populations cannot withstand harvest and, hence, that the population is sustained only by repeated escapes from fur farms.

Redford, K.H., Amato, G., Baillie, J., Beldomenico, P., Bennett, E.L., Clum, N., Cook, R., Fonseca, G., Hedges, S., Launay, F., Lieberman, S., Mace, G.M., Murayama, A., Putnam, A., Robinson, J.G., Rosenbaum, H., Sanderson, E.W., Stuart, S.N., Thomas, P. & Thorbjarnarson, J. (2011) What does it mean to successfully conserve a (vertebrate) species? *BioScience*. 61: 39–48

Distinguishes the attributes of successfully conserved populations to show that our understanding of conservation success lies on a continuum, depending on the extent to which we focus on merely averting crises. Argues for targets that go beyond the minimum, to a focus on conserving populations of ecologically and evolutionarily significant numbers of individuals.

Accuracy

There has been considerable research into the accuracy of PVA predictions, and whether PVA is usefully quantitatively predictive has proved to be – and arguably remains – a somewhat controversial subject. It is useful to consider both the assessments of accuracy and concerns that have been raised regarding their interpretation.

Assessments of accuracy

McCarthy et al. (2001) propose a variety of methods for assessing the accuracy of PVA predictions. Studies that have investigated the quantitative accuracy of PVA predictions have had rather variable outcomes. Among the earliest of these were those of Taylor (1995), Brook et al. (1997), Reed et al. (1998) and Ludwig (1999). All of these studies showed that both sparse data and uncertainty over population processes can lead to unacceptably wide confidence intervals around predictions of population persistence. In contrast to these, Brook et al. (2000a) conducted retrospective PVAs based on data from 21 well-studied populations and concluded that PVAs 'were surprisingly accurate' (Brook et al. 2000a, p.387) over mean time intervals of about 13 years. Although this has often been promoted as good evidence for the predictive accuracy of PVA, the paper provoked considerable criticism (see *Interpretation of PVA predictions*); moreover, the time-frames involved are short relative to the time-frames over which PVA is usually evaluated (often one or two orders of magnitude longer). Although various other studies have found some support for predictive accuracy, under some circumstances, the weight of evidence does not support quantitative accuracy of PVA over typical time-frames of decades to centuries. More recent focus

has shifted to explaining limitations on accuracy. Schiegg et al. (2005) focused on a single, well-studied species, the red-cockaded woodpecker (*Picoides borealis*). They found that a PVA provided very good predictions for the five years following a 13-year parameterisation period at the same site; however, differences in behaviour between populations prevented predictions for another site from achieving a similar level of accuracy (Schiegg et al. 2005). Consequently, it may be necessary to incorporate realistic behavioural decisions into PVA (see, also, Stephens et al. 2002, cited in *Complexity and realism*). Crone et al. (2013) found poor levels of accuracy among PVAs parameterised for large numbers of plant populations; they noted that predictive accuracy was most limited by changes in environmental conditions between data collection and forecast periods, recommending that PVAs should be linked to models capable of forecasting environmental changes also (see further in *Emerging areas in PVA*).

Brook, B.W., Lim, L., Harden, R. & Frankham, R. (1997) Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). *Biological Conservation*. 82: 119-128

Uses five different PVA packages to model the population trajectory of the Lord Howe Island woodhen, a flightless rail endemic to a single Pacific Island. The PVA predictions would have been inaccurate, given knowledge available at the time at which this population's recovery programme was conducted.

Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R. & Frankham, R. (2000a) Predictive accuracy of population viability analysis in conservation biology. *Nature*. 404: 385–387

Five PVA packages are used retrospectively to conduct PVA for 21 well-studied populations. Data sets were split in half, with the first period used for parameterisation. The numbers of populations predicted to decline in their second period was not significantly different from the number that did so.

Crone, E.E., Ellis, M.M., Morris, W.F., Stanley, A., Bell, T., Bierzychudek, P., Ehrlén, J., Kaye, T.N., Knight, T.M., Lesica, P., Oostermeijer, G., Quintana-Ascencio, P.F., Ticktin, T., Valverde, T., Williams, J.L., Doak, D.F., Ganesan, R., McEachern, K., Thorpe, A.S. & Menges, E.S. (2013) Ability of matrix models to explain the past and predict the future of plant populations. *Conservation Biology*. 27: 968–78

One of the largest assessments of PVA accuracy to date. Matrix models for 82 populations of 20 species of plants, spanning 3 continents, explained plant population dynamics well within the data collection period, but showed poor accuracy among forecasts of up to five years. Changes in environmental conditions between these periods underlay the limited accuracy of forecasts.

Ludwig, D. (1999) Is it meaningful to estimate a probability of extinction? *Ecology*. 80: 298–310

Uses empirical data on a range of populations to show the wide uncertainty that characterises predictions made on the basis of demographic models parameterised with those data. The author concludes that this level of uncertainty threatens to render predictions of PVA 'meaningless'.

McCarthy, M.A., Possingham, H.P., Day, J.R. & Tyre, A.J. (2001) Testing the Accuracy of Population Viability Analysis. *Conservation Biology*. 15: 1030–1038

A review of methods to test the predictive accuracy of PVA. The authors propose that testing should be a part of the PVA process, in order to define model weaknesses, leading to model improvement.

Reed, J.M., Murphy, D.D. & Brussard, P.F. (1998) Efficacy of population viability analysis. *Wildlife Society Bulletin*. 26: 244–251

The example of the California gnatcatcher *Poliioptila californica* is used to illustrate typical problems with parameterising PVA models. The authors argue that the numerical approach of PVA is prone to the 'fallacy of illusory precision' and that, for populations prone to high levels of environmental stochasticity, PVA outcomes are likely to be so uncertain as to be meaningless.

Schiegg, K., Walters, J.R. & Priddy, J. A. (2005) Testing a spatially explicit, individual-based model of red-cockaded woodpecker population dynamics. *Ecological Applications*. 15: 1495–1503

Data collected at one colony during a 13-year period was used to parameterise spatially explicit, stochastic individual based models. The model performed well for a 5-year period at the site used for parameterisation, but poorly for another site. A major difference between sites was in the frequency of behaviours underlying territory formation.

Taylor, B.L. (1995) The reliability of using population viability analysis for risk classification of species. *Conservation Biology*. 9: 551-558

Using data on the Steller sea lion *Eumetopias jubatus*, Taylor provides an early example of how realistic data availability yields uncertain, inaccurate and biased models of population viability. The results caution against the use of quantitative PVA outcomes to inform listing decisions for conservation.

Interpretation of PVA predictions

Boyce (1992) and Beissinger & Westphal (1998) (both cited in *General overviews*) emphasised the difficulties of making accurate quantitative predictions, and the latter authors, in particular, recommended that predictions were used qualitatively, rather than quantitatively. As seen in the previous section, many models of specific populations endorse that view, whilst theoretical simulations by Fieberg & Ellner (2000) led to similar conclusions, and the recommendation that quantitative predictions should be made only for very short time frames. The high profile work of

Brook et al. (2000a) (cited in *Assessments of accuracy*) provided a more optimistic view of the potential accuracy of PVA. However, various authors questioned whether their findings legitimised the use of PVA to make quantitative predictions. Coulson et al. (2001) noted the high demand for data (which had motivated the choice of data sets used by Brook et al. 2000a) and pointed to the importance of rare events in the dynamics of many populations. Ellner et al. (2002) showed that the analyses used by Brook et al. (2000a) might have been adequate to show that PVA could predict the total loss rates across an ensemble of species, but were not appropriate to justify the use of PVA for specific populations. Consensus now endorses the views of early critics: qualitative predictions are useful and relative predictions informative (McCarthy et al. 2003); PVA remains an important tool for conservation management, less subject to bias than is subjective judgement (Brook et al. 2002; McCarthy et al. 2004). Importantly, PVAs require careful checking before their implications can be used to guide legislation and management (Patterson & Murray 2008).

Brook, B.W., Burgman, M.A., Akçakaya, H.R., O'Grady, J.J. & Frankham, R. (2002) Critiques of PVA ask the wrong questions: Throwing the heuristic baby out with the numerical bath water. *Conservation Biology*, 16, 262–263.

Summarises correspondence about PVA over the previous few years suggesting that, whilst critics of PVA are right to point to its shortcomings, they seldom point to suitable alternatives. Indeed, Brook et al. assert that the main alternatives identified (historical and predicted future habitat loss, recent population trends, and genetic considerations) are all types of information that can be used in PVAs.

Coulson, T., Mace, G.M., Hudson, E., & Possingham, H. (2001) The use and abuse of population viability analysis. *Trends in Ecology & Evolution*. 16: 219–221

This response to Brook et al. (2000a) discusses why that study does not justify the use of PVA to make quantitative predictions of the fates of specific populations. The authors emphasise that the detailed data available for Brook et al.'s study are not typically available for studied populations.

Ellner, S.P., Fieberg, J., Ludwig, D. & Wilcox, C. (2002) Precision of Population Viability Analysis. *Conservation Biology*, 16: 258–261

This study, also provoked by that of Brook et al. (2000a), shows that analyses of the predictive accuracy of PVA that are conducted at the level of an assemblage of species, do not justify the use of PVA to make quantitative predictions for individual populations.

Fieberg, J. & Ellner, S. (2000) When is it meaningful to estimate an extinction probability? *Ecology*. 81: 2040–2047

Theoretical and simulation approaches are used to assess the data requirements of PVA. Even with detailed data, short time-frames are urged. For example, even ignoring census

error and process uncertainty, 40 years of grizzly bear *Ursus arctos* census data would enable estimates of extinction risk to be made over only 4-8 year horizons.

McCarthy, M.A., Andelman, S.J. & Possingham, H.P. (2003). Reliability of Relative Predictions in Population Viability Analysis. *Conservation Biology*. 17: 982–989

PVAs are parameterised using simulated data and predictions are made regarding the risk of population decline within 100 years. Relative risks predicted using data from 10 years of simulation correlate well with simulated fates; the strength of that correlation increases with data availability. Abilities of PVA to identify appropriate management strategies are also explored.

McCarthy, M.A., Keith, D., Tietjen, J., Burgman, M.A., Maunder, M., Master, L., Brook, B.W., Mace, G., Possingham, H.P., Medellin, R., Andelman, S., Regan, H., Regan, T. & Ruckelshaus, M. (2004) Comparing predictions of extinction risk using models and subjective judgement. *Acta Oecologica*. 26: 67–74

Uses simulations to provide data on hypothetical species. Modelled forecasts of population trajectories are compared with expert opinions (based on the same information). Predictions based on models are slightly more accurate than those based on subjective judgement and the latter are shown to be more biased.

Patterson, B.R. & Murray, D.L. (2008) Flawed population viability analysis can result in misleading population assessment: a case study for wolves in Algonquin park, Canada. *Biological Conservation*. 141: 669–680

Illustrates the sensitivity of PVA to the data and analyses used to parameterise it. The authors provide a general overview of PVA critiques and suggest that the case study of a PVA for wolves (*Canis lupus*) should provide a framework for considering the application of population risk assessments.

Modelling considerations

Boyce (1992, p492; cited in *General overviews*) noted that “the simplest possible model of population growth is an exponential population growth model. It has no ecology.” This is the start point for a fundamental concern in PVA: simple models lack key processes required to capture a population’s behaviour but more complex models are difficult to parameterise, increasing uncertainty. There is widespread agreement that models should capture uncertainty from a range of sources, including demographic and environmental stochasticity. However, other aspects of a population’s ecology can have substantial impacts on persistence and are less routinely included in PVAs. Models often consider only one sex and may not account fully for age structure. Intrinsic factors like density dependence and genetic processes may be ignored or treated only simplistically. More commonly, extrinsic threats from predators, competitors, declining prey or

disease are overlooked (but, for example, see Burgman et al. 2001 and Fordham et al. 2008, both cited in *Applications*). These considerations pose two questions: what factors should be included in a PVA model and, given that, how can those aspects be robustly parameterised?

Complexity and realism

Models cannot capture every aspect of a population's ecology; attempts to do so would result in high uncertainty and complexity that would defy sensitivity analyses. Nevertheless, in addition to demographic and environmental stochasticity, a range of processes has been identified as important. Boyce (1992; cited in *General overviews*) suggested that an assumption of logistic growth should be the default in population models, with dynamics assumed to be density independent (up to some ceiling carrying capacity) only if the null expectation of logistic growth could be rejected. Gilpin & Ayala (1973) suggested that the theta-logistic provides a more versatile function, capable of capturing different forms of negative density dependence. Density dependence is further complicated by the importance of positive density dependence to the dynamics of small populations (Boyce 1992; cited in *General overviews*). This form of density dependence arises from mechanisms broadly described as 'Allee effects'. To find evidence for Allee effects is difficult because it requires identifying a deterministic signal in transient dynamics characterised by high stochasticity. Nonetheless, Kramer et al. (2009) showed that Allee effects appear to be widespread and, as reviewed by Courchamp et al. (2008), they have major implications for processes of extinction. The role of genetic processes in population viability was initially controversial and treatment of those processes in PVA was often simplistic (Allendorf & Ryman 2002). However, the important role of both inbreeding depression and drift is now widely recognised and, as Frankham et al. (2010) discuss, these processes can readily be incorporated into PVA models. Many PVAs are based on matrix models, which have the benefit of being well characterised mathematically, computationally rapid and readily analysed (Caswell 2006). Further complexity can be added by splitting the population into ever-finer stages (based on age, developmental status, physiological state, behavioural experience, location, social setting, or some combination of these attributes). The end point of this process is to create individual-based models (IBMs), which have often been applied to conservation problems, such as PVA, as reviewed in DeAngelis & Mooij (2005). IBMs have the advantage of flexibility in the face of increasing evidence that not all individuals of a given age or stage will make the same choice in a particular situation. However, if individual fates are modelled as contingent on different behavioural decisions in a given situation, great demands are placed on data availability to parameterise these processes. Furthermore, there is evidence that empirically-derived rules for individual behaviours may be inadequate to capture realistic patterns of behaviour, thereby giving rise to misleading population dynamics (Stephens et al. 2002). A final, and major, source of both complexity and realism arises from including multiple species-interactions in PVAs. This is a relatively new enterprise (see further in *Emerging areas in PVA*).

Allendorf, F.W. & Ryman, N. (2002) The role of genetics in population viability. pp. 50–85 in *Population Viability Analysis* (Beissinger, S.R. & McCullough, D.R., eds). Chicago: University of Chicago Press

A useful summary of early controversy over the relative importance of genetic processes in extinction and possible reasons for that controversy. Also a helpful introduction to the basics of conservation genetics, the ways in which key processes can be included in PVA, and the difficulties of parameterising those processes.

Caswell, H. (2006) *Matrix Population Models: Construction, Analysis and Interpretation*, 2nd Ed. Sunderland, Massachusetts: Sinauer Associates

A comprehensive overview of the use of matrix models, which are at the heart of most PVAs. In addition, this book should be required reading for anyone studying population dynamics more generally.

Courchamp, F., Berec, L. & Gascoigne, J. (2008) *Allee Effects in Ecology and Conservation*. Oxford: Oxford University Press

Comprehensive, entertaining and readable summary of the causes and consequences of Allee effects, as well as ways of modelling them. The latter will be useful reading for those who wish to incorporate Allee effects into PVA models.

DeAngelis, D.L., & Mooij, W.M. (2005) Individual-Based Modeling of Ecological and Evolutionary Processes. *Annual Review of Ecology, Evolution and Systematics*. 36: 147–168

A thorough overview of the uses of IBMs in ecology and evolution. Several sections detail applications of IBMs in conservation settings, with comprehensive overviews of examples. A good start point for anyone considering an individual based PVA.

Frankham, R., Ballou, J.D., & Briscoe, D.A. (2010) *Introduction to Conservation Genetics*, 2nd Ed. Cambridge: Cambridge University Press

Detailed overview of the entire discipline of conservation genetics. Chapter 22 focuses on PVA and includes a complete listing of input parameters for an example PVA in VORTEX (see *Modelling software*) of the Golden Lion Tamarin. This will be particularly helpful to those embarking on using VORTEX and keen to get going with a real data set.

Gilpin, M., & Ayala, F. (1973) Global Models of Growth and competition. *Proceedings of the National Academy of Sciences*. 70: 3590–3593

The origin of the theta-logistic function, often used as a more flexible version of the logistic function to describe negative density dependence. The model is actually developed in the context of modelling competition between species but was required to capture the within-species dynamics. Not easy reading for the mathematically-averse.

Kramer, A.M., Dennis, B., Liebhold, A.M., & Drake, J.M. (2009) The evidence for Allee effects. *Population Ecology*. 51: 341–354

The most recent and most comprehensive attempt to catalogue and describe the outcomes of studies that have sought evidence for Allee effects. Obviously hampered by publication bias away from studies reporting 'no effect' but, nonetheless, presents evidence for widespread Allee effects arising from many different mechanisms.

Stephens, P., & Frey-Roos, F., Arnold, W. & Sutherland, W.J. (2002) Model complexity and population predictions: the alpine marmot as a case study. *Journal of Animal Ecology*. 71: 343–361

Four models, with complexity ranging from a standard matrix model to an individual based model with behavioural optimisation, are parameterised from the same data set. The radically different predictions of transient dynamics show the dangers of IBMs in which behaviours do not adapt to circumstances unlike those experienced during collection of the data.

Parameterisation

The difficulties of parameterising PVA models have long been recognised. These difficulties arise from the lack of detailed, long-term field studies of the demography and genetics of most taxa (Shaffer et al. 2002). Even where those studies exist, it is often difficult to characterise adequately all of the key processes affecting a population's viability. Many PVAs use matrix models in which matrix elements are presented as point estimates, concealing underlying uncertainty, as noted by both Taylor (1995, cited in *Accuracy*) and Devenish-Nelson et al. (2010). Gould & Nichols (1998) showed that variation in transition probabilities should be partitioned between true variation and sampling uncertainty, or the magnitude of environmental stochasticity may be substantially exaggerated. As discussed (in *Complexity and realism*), positive density-dependence is extremely difficult to identify. However, even negative density dependence can be difficult to parameterise with confidence: Shenk et al. (1998) showed that the apparent role of negative density dependence in time series data may be an artefact of census error, whilst Clark et al. (2010) illustrated that the versatile theta-logistic function describing density dependence cannot easily be fitted to ecological data. Methods for robust fitting of density dependent functions now emphasise estimating it jointly with process and observation errors, using state-space models (Dennis et al. 2006) often analysed with Bayesian approaches (Kery & Schaub 2012; Wade 2002). Even with these approaches, long time series are necessary to estimate the true magnitude of environmental stochasticity, especially for rare catastrophic events that often play an important role in extinctions. Estimates of genetic parameters affecting extinction are available for relatively few populations. As a result, default parameters are often used (e.g., see Frankham et al. 2010, cited in *Complexity and realism*; O'Grady et al. 2006). Some consolation in the face of concerns about parameterisation might be found in a shift of emphasis in conservation. Specifically, Gaston & Fuller (2008) highlighted that, for ecosystem function, being able to predict changes in the abundance of relatively common species may be substantially more important than focusing on rare

species. Common species have the advantage of yielding large data sets more rapidly than rare species.

Clark, F., Brook, B.W., Delean, S., Akçakaya, H.R. & Bradshaw, C.J.A. (2010) The theta-logistic is unreliable for modelling most census data. *Methods in Ecology and Evolution*. 1: 253–262

An important contribution to debate over the form of density dependence. Earlier, high profile publications had used the theta-logistic to suggest that negative density dependence was typically concave in natural populations. This study demonstrates why those results are unreliable.

Dennis, B., Ponciano, J. & Lele, S. (2006). Estimating density dependence, process noise, and observation error. *Ecological Monographs*. 76: 323–341

An important paper, identifying methods by which different forms of noise can be differentiated in time series data. Not easy reading but worth persevering with because it leads to the important result that the majority of noise in time series is often attributable to observation error (see also Gould & Nichols 1998).

Devenish-Nelson, E.S., Harris, S., Soulsbury, C.D., Richards, S.A. & Stephens, P.A. (2010) Uncertainty in population growth rates: determining confidence intervals from point estimates of parameters. *PLoS One*. 5: e13628

Illustrates that population models are often based on point estimates of vital rate parameters, without accompanying acknowledgement of uncertainty. Presents simple techniques for identifying the extent of overall uncertainty – although this would more usefully be partitioned between process and sampling uncertainty.

Gaston, K.J. & Fuller, R.A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*. 23: 14–19

Thought-provoking review regarding the focus of conservation biology. Promotes much greater emphasis on the fates of common species in response to the commonly invoked drivers of extinction. Presents evidence for the impacts of those drivers on common and widespread species, and the consequences for ecosystem structure, function and services.

Gould, W.R. & Nichols, J.D. (1998). Estimation of temporal variability of survival in animal populations. *Ecology*. 79: 2531–2538

Focuses on estimating variance in survival rates for three bird species with rather different life histories. Shows that apparent temporal variation in survival is overwhelmingly due to sampling variation in each case. Presents methods for separating out the sources of variation. Should be widely read by anyone dealing with vital rates and their variation.

Kery & Schaub 2012 Bayesian Population Analysis using WinBUGS: A Hierarchical Perspective.

Academic Press

Much-praised introduction to Bayesian methods for parameterising and running population models. Clearly written with code (in R) provided. Arguably, worth it to develop a better understanding of population modelling, whether or not the reader intends to use Bayesian approaches.

O'Grady, J.J., Brook, B.W., Reed, D.H., Ballou, J.D., Tonkyn, D.W. & Frankham, R. (2006) Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation*. 133: 42–51

A meta-analysis of the impacts of inbreeding on vital rates (specifically, fecundity, first year survival and survival to sexual maturity) and viability. Useful resource for anyone seeking justification for default values for genetic effects in PVA models.

Shaffer, M., Hood-Watchman, L., Snape III, W.J. & Latchis, I.K. 2002. Population viability analysis and conservation policy. pp. 123–146 in *Population Viability Analysis* (Beissinger S.R. & McCullough D.R., eds). Chicago: University of Chicago Press

Surveys the use of PVA in policy and management. Highlights the lack of availability of required data, the possibility that Minimum Viable Population size is routinely underestimated in policy, and the lack of consistency in the time horizons and probabilities of persistence used to assess viability.

Shenk, T., White, G. & Burnham, K. (1998) Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological Monographs*. 68: 445–463

A depressing read! Highlights the problem that measurement error affects, with opposite sign, estimates of population size and population growth; thus, apparent negative density dependence may result from nothing more than noise in survey data. Provoked a significant reappraisal of how time series population data are analysed.

Wade, P.R. 2002. Bayesian Population Viability Analysis. pp. 213–238 in *Population Viability Analysis* (Beissinger S.R. & McCullough D.R., eds). Chicago: University of Chicago Press

A relatively short, highly readable introduction to Bayesian PVA. Wade comes across as a patient tutor and demonstrates some significant advantages of Bayesian approaches over more standard frequentist methods.

Influence of parameters

Viability analyses based on standard matrix models are often analysed to determine the vital rates that have the greatest influence on population growth rates. In particular, two common measures of influence are sensitivity (the impact on population growth of a small absolute change in a given vital rate) and elasticity (the impact of a small relative change in a given vital rate) (see Caswell 2006, cited in *Complexity & Realism*). Of these measures, elasticities are deemed more appropriate for

inferring the relative importance of vital rates for population growth (de Kroon et al. 1986). Despite widespread use of elasticity analyses to guide appropriate targets for conservation interventions, several concerns are often expressed regarding that approach. These usually focus on the facts that elasticities change as vital rates (and population growth rates) change, and that proportional changes in vital rates are not equally achievable by management (de Kroon et al. 2000). In addition, Fieberg & Ellner (2001) show that vital rates may covary in more or less predictable ways, making it hard to isolate the impacts of manipulating a single rate. Bayesian techniques overcome some of these problems (see, for example, Wade 2002 cited in *Parameterisation*). In addition, Wisdom et al. (2000) proposed Life-stage Simulation Analysis (LSA) to ameliorate problems associated with estimating parameter influence; to some extent, LSA represents the coming together of PVA and perturbation analysis. LSA yields a number of measures of the impacts of varying vital rates simultaneously, through plausible ranges. The distribution of population growth rates associated with variation in any individual vital rate can be explored, with interventions favoured when they have the largest positive effect on the overall distribution of outcomes. An overview of methods for assessing the influence of parameters is given by Cross & Beissinger (2001), who also present an example of using logistic regression to examine sensitivity.

Cross, P.C. & Beissinger, S.R. (2001) Using logistic regression to analyze the sensitivity of PVA models: a comparison of methods based on African wild dog models. *Conservation Biology*. 15: 1335–1346

A useful case study and review of methods (Table 1 gives an overview of the range of approaches in use at the time). The authors also showcase the approach whereby model outcomes are reduced to a binary variable (extinction or persistence) and binary logistic regression is used to analyse the effects of parameter values on this outcome. Overcomes many of the limitations for which other methods have been criticised.

de Kroon, H., Plaisier, A., van Groenendael, J. & Caswell, H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*. 67: 1427–1431

A short and highly readable explanation of problems with sensitivity as a measure of the influence of matrix elements on the population growth rate. Introduces elasticity with a compact explanation and illustrates its use with an empirical example.

de Kroon, H., van Groenendael, J. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology*. 81: 607–618

Comprehensive discussion of elasticities in the analysis of matrix models. This article includes critical consideration of the limitations of conventional elasticity analysis, exposing the need for alternative approaches (such as that proposed by Wisdom et al. 2000).

Fieberg, J. & Ellner, S.P. (2001) Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters*. 4: 244–266

An unexpectedly long and comprehensive review. This article exposes the problems that can arise when vital rates are treated as independent, and their covariation ignored. The authors also suggest that environmental covariates might help to explain variation in vital rates, thereby improving the precision of viability estimates in PVAs.

Wisdom, M., Mills, L. & Doak, D. (2000) Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology*. 81: 628–641

Describes an approach by which meaningful measures of parameter influence on population growth rate can be obtained, by resampling vital rates from plausible distributions that reflect their variation and covariation. Uses an empirical case study to show how this can inform management interventions. Straightforward and a useful advance over elasticity analyses.

Modelling software

Many users of PVA might prefer to construct their own models. Reed et al. (2002, cited in *General overviews*) cautioned that the ease with which PVA could be conducted by non-modellers using software packages increased the potential for misuse. However, Brook et al. (1997, cited in *Accuracy*) noted that bespoke models are unlikely to have been tested with the rigour of generic software packages. For those who prefer to use existing frameworks to make predictions of viability, a number of possibilities exist. These have been reviewed in detail by Keedwell (2004), amongst others, and the predictions of some packages have been compared on a number of occasions with varied findings. Mills et al. (1996) and Brook et al. (1997, cited in *Accuracy*) found that packages differed substantially in their predictions of extinction risk, even when the same underlying data were used; this was attributed to subtle differences in input formats and to substantial differences in the way that different packages handled density dependence. By contrast, Brook et al. (2000a, cited in *Accuracy*) found that different packages gave “highly concordant” predictions (Brook et al. 2000a, p385). This difference is likely to have arisen because both Mills et al. (1996) and Brook et al. (1997, cited in *Accuracy*) focused on comparisons of predictions made for single populations, whereas Brook et al. (2000a, cited in *Accuracy*) were interested in comparisons of predictions across an assemblage of species (hence, consistency was judged by different criteria). Brook et al. (2000b) noted that PVA packages gave more similar results when only females were modelled. This arose because individual-based PVA packages incorporate stochasticity in sex ratio, unlike matrix-based PVAs; obviously, single sex PVAs are not prone to those differences (Brook et al. 2000b). Despite the wide range of PVA software that has been tested (see Keedwell 2004 for an overview) and promoted more recently, few packages have seen widespread use in peer-reviewed literature. Of these, the most commonly used are VORTEX and RAMAS (and its variants). Finally, PVAs can be run using two packages available for the modelling language R. The “popbio” package (Stubben & Milligan 2007) facilitates most of the analyses of matrix models that are discussed in Caswell (2006, cited in *Complexity and Realism*)

and Morris & Doak (2002, cited in *General overviews*). The “PVAClone” package enables PVAs based on time series of census data to be run (based on the methods of Nadeem & Lele 2012).

Brook, B.W., Burgman, M.A. & Frankham, R. (2000b) Differences and congruencies between PVA packages: the importance of sex ratio for predictions of extinction risk. *Conservation Ecology* 4: 6

Compares the predictions of five PVA packages for the viability of five extant vertebrate species and one hypothetical vertebrate life history. Individual based PVAs consistently estimated higher extinction risks than matrix based PVAs. The resultant recommendation is that only females should be modelled in matrix based PVAs.

Keedwell, R.J. (2004) Use of population viability analysis in conservation management in New Zealand. Wellington, NZ: Department of Conservation

A useful and readable, general overview of PVA that compares eight PVA software packages in some detail. Packages are most variable in their ability to incorporate stage (rather than age) structure, in the way that they deal with inbreeding depression, and in their ability to incorporate management such as harvesting or supplementation.

Mills, L., Hayes, S., Baldwin, C., Wisdom, M., Citta, J., Mattson, D. & Murphy, K. (1996) Factors leading to different viability predictions for a grizzly bear data set. *Conservation Biology*. 10: 863–873

Compares the predictions of four PVA packages regarding the viability of grizzly bear populations in a variety of scenarios of overall growth rate. An early attempt to understand consistency and variation among PVA packages.

Nadeem, K. & Lele S.R. (2012) Likelihood based population viability analysis in the presence of observation error. *Oikos*. 121: 1656–1664

Builds on the methods of Dennis et al. (2006, cited in *Parameterisation*) to illustrate the importance of observation error to the predictions of PVA. Presents methods for estimating the form of density dependence and the extent of observation error from time series of counts, and applying these to estimate extinction risks. Essential reading for users of the R package “PVAClone”.

RAMAS(<http://www.ramas.com/software.htm>)

RAMAS includes a wide range of software, including stage (as opposed to age) based versions that can be adapted to many different life histories, versions that can include metapopulation dynamics and versions that can be integrated with landscape data from a Geographic Information System. The software is typically user friendly with accessible online help and tutorials – but users will need to pay for its use.

Stubben, C. & Milligan, B. (2007) Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*. 22: 1-23

Original description of the "popbio" package for R. The paper describes the package and its capabilities, including the potential to run many analyses of matrix population models useful for PVA, including stochastic projections and quasi-extinction analyses.

VORTEX(<http://vortex10.org/Vortex10.aspx>)

PVA software based on individual based simulations. VORTEX is free to download and is probably the most widely used generic PVA software. Comes with an extensive handbook but, nevertheless, can take a while to achieve familiarity. Can now be linked via MetaModel Manager (<http://www.vortex10.org/MeMoMa.aspx>) to facilitate models of interacting species (see further in *Emerging areas in PVA*).

Minimum Viable Populations

Arguably, the whole enterprise of PVA emerged from US legislation that required that national forests maintain viable populations of vertebrates (Reed et al. 1998 cited in *Accuracy*). The question naturally arose, what constitutes a viable population and how low can that population become without compromising its viability? This question had concerned agricultural economists since the 1960s (Ciriacy-Wantrup 1968) but did not appear in mainstream conservation literature until the 1980s. Franklin (1980) first developed the 50/500 rule based on the genetic viability of populations. Shaffer (1981, cited in *History*) then introduced the concept of the Minimum Viable Population (MVP), defining it as "the smallest isolated population having a 99% chance of remaining extant for 1000 years, despite the effects of demographic, environmental, and genetic stochasticity, and natural catastrophes" (Shaffer (1981, p132). A dominant early application of PVA, therefore, was to estimate MVPs. As concerns grew about the predictive accuracy of PVA, emphasising that PVA was best used as a qualitative rather than a quantitative tool (see *Accuracy*), many biologists focused on how PVA could guide management, rather than on estimates of 'safe' small population sizes. Recently, however, there has been a resurgence of interest in MVP. In particular, a series of papers has promoted the idea that the lack of clear taxonomic or life history differences in MVP estimates, together with existing genetic evidence, supports the utility of a rule of thumb MVP size (numbering approximately 5,000 individuals), equally applicable across all populations (see Traill et al. 2010). This assertion has been criticised on the grounds that neither demographic theory and existing MVP estimates (Flather et al. 2011), nor current understanding of genetic processes (Jamieson & Allendorf 2012 but see Frankham et al. 2014) support widespread applicability of a generic MVP value. There is, thus, considerable opposition to the notion that conservation funding should be allocated according to a population's numerical distance from the suggested rule of thumb MVP (see Clements et al. 2011 and subsequent correspondence in *Frontiers in Ecology and the Environment*). Overall, most biologists agree that viable populations will tend to number in the thousands of individuals; however, this is

context specific, contingent on current threats and management, and likely to be affected by the details of the population's biology.

Ciriacy-Wantrup, S.V. (1968) *Resource Conservation: Economics and Policies*, 3rd ed. Berkeley & Los Angeles: University of California

Regarded as a classic of conservation economics. Introduces arguments for conserving the unique phenomena of nature and develops the idea of the 'safe minimum standard' (SMS) of conservation, a precursor of the MVP concept.

Clements, G.R., Bradshaw, C.J., Brook, B.W. & Laurance, W.F. (2011) The SAFE index: using a threshold population target to measure relative species threat. *Frontiers in Ecology and the Environment*. 9: 521–525

Builds on Traill et al. (2007) to suggest that standardised MVP estimates "show marked consistency among taxa" (p523). Promotes the idea that 5,000 adult individuals is an appropriate guideline MVP across taxa and that a sensible measure of the extent of threat to a population is the difference between its logged population size and $\log(5000)$. Provoked considerable critical correspondence.

Flather, C.H., Hayward, G.D., Beissinger, S.R. & Stephens, P.A. (2011) Minimum viable populations: is there a "magic number" for conservation practitioners? *Trends in Ecology & Evolution*. 26: 307-316

Reassesses the evidence for, and approaches used by Brook and colleagues to, support a generally-applicable MVP of 5,000 adult individuals. Finds that the guideline MVP is not supported by demographic theory or data. Questions the utility of quantitative MVP estimates for conservation. See, also, subsequent correspondence.

Frankham, R., Bradshaw, C.J.A. & Brook, B.W. (2014) Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation*. 170: 56–63

Suggests that Franklin's (1980) 50/500 rule should be updated in light of data gathered over recent decades. Highlights that inbreeding can be a problem for effective population sizes (N_e) well in excess of 50 and suggests that alternative approaches to estimating the N_e required to avoid loss of genetic variation yield numbers in excess of 1,000. See, also, correspondence subsequent to this article.

Franklin, I.R. (1980) Evolutionary change in small populations. pp. 135–150 in *Conservation Biology: an Evolutionary–Ecological Perspective* (Soulé, M.E. & Wilcox, B.A., eds). Sunderland, Massachusetts: Sinauer Associates

A cornerstone of conservation genetics (but see Frankham et al. 2014). Proposes rules for effective population sizes (N_e) that are robust against short term decline owing to

inbreeding depression ($N_e = 50$) and long term net loss of genetic variation owing to genetic drift ($N_e = 500$).

Jamieson, I.G. & Allendorf, F.W. (2012) How does the 50/500 rule apply to MVPs? *Trends in Ecology & Evolution*. 27: 578–84

Reassesses evidence for the 50/500 rule (Franklin 1980) and finds no evidence that the rule is in need of upward revision. Raises intriguing questions about the use of a general rule for relating census population size to effective population size across taxa, and concerning the relationship between variability at neutral genetic loci and the genetic diversity required to safeguard a population from future threat.

Trall, L.W., Brook, B.W., Frankham, R.R. & Bradshaw, C.J.A. (2010) Pragmatic population viability targets in a rapidly changing world. *Biological Conservation*. 143: 28–34

Reviews recent literature on the MVP concept, concluding that it is “a useful benchmark” (p32) for conservation. Builds on various earlier papers by the same group to promote the use of a generalised MVP of 5,000 individuals in conservation triage and the allocation of funding.

Emerging areas in PVA

Conservation biology, the broader discipline within which PVA is situated, is a dynamic and burgeoning field. It is impossible to do justice to the many ways in which population models are being developed for management and conservation purposes. Two broad types of issue are likely to play a dominant role in coming years. These include developments in modelling approaches, and developments in the treatment of risk and uncertainty, especially in light of data deficiencies.

Emerging issues for PVA modelling

A range of developments sets the stage for increases in the complexity of PVAs, or integration of PVA with other modelling techniques. First, techniques that enable modellers to incorporate more nuanced aspects of a population's life history and evolution are increasingly available. Easterling et al. (2000) proposed integral projection models as alternatives to less flexible age- or stage-structured models. Coulson et al. (2011) provided an example of how these can be used to project population responses to environmental change, together with correlated life history changes. These eco-evolutionary changes can be modelled in greater detail by accounting explicitly for genetic changes. The field of genomics offers potential to provide the level of detail required, enabling a shift from PVAs that incorporate genetics in an often-rudimentary manner, to models that can encapsulate the complexities of the eco-evolutionary process (Pierson et al. 2015). Second, as discussed in *Modelling considerations*, there is growing recognition that PVAs based on modelling populations in isolation are unlikely to capture key processes governing the population's fate or that of the wider community of which that population is part. This has prompted the development of

'metamodels' that seek to integrate models of interacting species (e.g., Shoemaker et al. 2014), as well as the emerging field of community viability analysis (e.g., Ebenman & Jonsson 2005). Third, developments in climate change biology suggest that PVA approaches could substantially improve current predictions of the impacts of climate change on populations. Hitherto, those predictions have emphasised the consequences of climate change for phenology and geographical range but have largely neglected more demographic approaches to the viability of populations (Brook et al. 2009). Keith et al. (2008) argued that models that integrate bioclimate and demography should unite the previously disparate fields of population dynamics and bioclimate modelling. Projections of viability in the face of climate change are necessarily linked to changes in the quality and availability of habitat. This suggests that PVAs that explicitly account for spatial processes are likely to become more common (McCarthy 2009). Finally, conservation is increasingly framed within an economic context. This has been less overt within the field of PVA, but Bode & Brennan (2011) provided an example of how to incorporate costs, and return on investment, into PVA.

Bode, M. & Brennan, K.E.C. (2011) Using population viability analysis to guide research and conservation actions for Australia's threatened malleefowl *Leipoa ocellata*. *Oryx*. 45: 513–521

Intriguing example of an ongoing conservation programme within which the principal threats remain complex and unclear. The PVA is used to begin to tease apart these threats. More importantly, costs associated with different management interventions are estimated explicitly, so that the efficacy of different but financially equivalent strategies can be compared. More PVAs incorporating explicit economics can be expected in the future.

Brook, B.W., Akçakaya, H.R., Keith, D.A., Mace, G.M., Pearson, R.G. & Araújo, M.B. (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters*. 5: 723–5

Report detailing the outcomes of a meeting between demographers and climate envelope modellers. Identifies the underlying concern that, at present, approaches to listing the threat status of species (e.g., the IUCN Red List) do not adequately incorporate the extent to which populations are threatened by climate change. Proposes modelling as a solution to that problem.

Coulson, T., MacNulty, D.R., Stahler, D.R., VonHoldt, B., Wayne, R.K. & Smith, D.W. (2011) Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. *Science*. 334: 1275–8

Clear example of how integral projection models can be applied, even to species generally viewed as typically stage-structured, in order to make projections of coupled eco-evolutionary changes.

Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: applying a new structured population model. *Ecology*. 81: 694–708

First exposition of the potential of integral projection models. Describes problems associated with stage-based matrices, arising as a result of having either too many or too few, often arbitrary, stage classes. Suggests that parameterising continuous relationships with an underlying state variable might sometimes be less demanding than estimating separate parameters for each stage class.

Ebenman, B. & Jonsson, T. (2005) Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology & Evolution*. 20: 568-575

Community viability analysis involves characterising communities with respect to the strength of interactions between their constituent species and the extent to which those interactions are compartmentalised between subsections of the community. Static or dynamic models are analysed to yield insights into the likelihood of secondary extinctions and chains of extinctions.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B. & Rebelo, T.G. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*. 4: 560–563

Uses species distribution modelling to predict future availability and suitability of habitat under climate change. Habitat suitability and availability determine carrying capacities, which are then used in stochastic population models to assess viability under climate change. Mainly a methodological paper but provides clear avenues for future research.

McCarthy, M.A. (2009) Spatial population viability analysis. pp. 122–134 in *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools* (Moilanen, A., Wilson, K.A. & Possingham, H., eds). Oxford & New York: Oxford University Press

An overview of spatial PVA (or SPVA). Reviews examples of SPVAs and of the insights that can be gained by incorporating spatial processes in PVA. Identifies some important challenges for users of SPVA including, of course, constraints on data availability, but also highlights the difficulty of identifying the best strategy for all contingencies.

Pierson, J.C., Beissinger, S.R., Bragg, J.G., Coates, D.J., Oostermeijer, G.B., Sunnucks, P., Schumaker, N.H., Trotter, M.V. & Young, A.G. (2015) Incorporating evolutionary processes into population viability models: Eco-Evo PVAs. *Conservation Biology*. 29: 755-764

Discusses the potential of genomics to enable evolutionary processes to be parameterised and, hence, fully integrated into PVAs. Presents the possibility to discriminate between processes affecting functional versus neutral regions of the genome, using individual based models to translate gene frequencies to phenomena such as genetic rescue and local adaptation.

Shoemaker, K.T., Lacy, R.C., Verant, M.L., Brook, B.W., Livieri, T.M., Miller, P.S., Fordham, D.A. & Resit Akçakaya, H. (2014) Effects of prey metapopulation structure on the viability of black-footed ferrets in plague-impacted landscapes: a metamodeling approach. *Journal of Applied Ecology*. 51: 735–745

Uses linked models of plague dynamics, prairie dog metapopulation dynamics and black-footed ferret population dynamics to assess ferret viability under different scenarios. Shows that habitat assumed to be good (because of high densities of prairie dog colonies) facilitates plague transmission, reducing ferret dynamics. This finding would not have emerged from conventional, single species PVA.

Data deficiencies, risk and uncertainty

Many of the developments highlighted under *Emerging issues for PVA modelling* will place greater demands on available data, further highlighting the need for detailed, long-term field studies of demography and genetics (see *Parameterisation*). This is underlined by Devenish-Nelson et al. (2013), which showed that data substitution (where missing parameters for population models are derived from similar populations) is likely to prove highly misleading. One consolation in the face of data shortages comes from work on decision-making in the face of uncertainty; for example, Nicholson & Possingham (2007) showed that qualitative uses of PVA are often robust to uncertainty. Although they are not novel fields, decision-making in the face of uncertainty, and meeting the demands of models when data are in short supply, remain major challenges for the future of PVA. Burgman (2005) introduced the theoretical backdrop and many of the tools required for decision-making under uncertainty. Although this work has been available for some time, its use remains restricted to a very small subset of conservation biologists. Martin et al. (2005) provided an example of how expert opinion can be used to augment Bayesian projections of population persistence. Martin et al. (2012) reviewed how to elicit expert opinion to aid environmental risk assessment, whilst Yokomizo et al. (2014) reviewed the use of formal decision theory, more broadly. Both of these should make the methods more accessible to conservation biologists. In addition, McBride et al. (2012) illustrated how expert opinion and consensus techniques could be used to inform the IUCN's Red Listing process. As McBride et al. (2012) noted, expert judgements often underlie assessments for data-poor taxa but levels of investment in conservation demand that these use a formal, transparent and robust process. In light of this, it seems likely that expert opinion and decision-making under uncertainty will become more widely used in assessing populations' futures.

Burgman, M.A. (2005) *Risks and Decisions for Conservation and Environmental Management*. Cambridge: Cambridge University Press

Wide-ranging overview of how to take transparent decisions in the face of uncertainty. Covers the psychology of risk and the use of expert judgement. Highlights difficulties in being objective in risky situations. Provides an authoritative introduction to technical tools available to facilitate decision-making under uncertainty.

Devenish-Nelson, E.S., Harris, S., Soulsbury, C.D., Richards, S.A. & Stephens, P.A. (2013) Demography of a carnivore, the red fox, *Vulpes vulpes*: what have we learnt from 70 years of published studies? *Oikos*. 122: 705-716

Assesses the insights gained into the demography of the red fox, a species of considerable management interest. Identifies limitations to parameterising population models for foxes (despite the long history of research into the species) and illustrates problems that arise from the gambit of 'data substitution', when demographic parameters are 'borrowed' from similar populations.

Leung, B. & Steele, R.J. (2013) The value of a datum - how little data do we need for a quantitative risk analysis? *Diversity and Distributions*. 19: 617-628

An intriguing investigation into the question of when data should be considered to be so scant that they are not worth incorporating into decision-making. The authors use simulations based on known situations to assess how small amounts of data can be used to improve the inferences of various risk assessments, including PVA.

Martin, T.G., Kuhnert, P.M., Mengersen, K. & Possingham, H.P. (2005) The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. *Ecological Applications*. 15: 266-280

An early illustration of how expert opinion can be used to provide informative priors in Bayesian models of population persistence under different management strategies. When expert opinions were highly congruent, credible intervals around predictions were greatly reduced in magnitude. Divergent expert opinions produced results similar to those obtained in the absence of expert opinion.

Martin, T.G., Burgman, M. a., Fidler, F., Kuhnert, P.M., Low-Choy, S., McBride, M. & Mengersen, K. (2012) Eliciting expert knowledge in conservation science. *Conservation Biology*. 26: 29-38

Review of the process of eliciting expert knowledge. Contains useful pointers to a variety of examples of this practice within the field of conservation. Emphasises the importance of planning structured elicitation processes, and reducing bias by eliciting interval bounds and associated confidence rather than point estimates.

McBride, M.F., Garnett, S.T., Szabo, J.K., Burbidge, A.H., Butchart, S.H.M., Christidis, L., Dutson, G., Ford, H.A., Loyn, R.H., Watson, D.M. & Burgman, M.A. (2012) Structured elicitation of expert judgments for threatened species assessment: a case study on a continental scale using email. *Methods in Ecology and Evolution*. 3: 906-920

Illuminating example of the use of expert judgement to assign IUCN Red Listing categories (see Mace et al. 2008, cited in *Applications*) to Australian birds in nine different taxa.

Combines the use of expert opinion with a modified (email-based) Delphi process to attain consensus. Identifies how time consuming and labour-intensive this process can be.

Nicholson, E. & Possingham, H. (2007) Making conservation decisions under uncertainty for the persistence of multiple species. *Ecological Applications*. 17: 251–265

Considers the problem of land acquisition for protected areas given budgetary constraints, the need to satisfy targets for different species simultaneously, and limitations on available data (with consequent uncertainty). Identifying the nature of uncertainty permits robust decisions to be made and provides management recommendations that contrast with those obtained if uncertainty is ignored.

Yokomizo, H., Coutts, S.R. & Possingham, H.P. (2014) Decision science for effective management of populations subject to stochasticity and imperfect knowledge. *Population Ecology*. 56: 41–53

Reviews the use of decision science as an essential framework for making objective decisions in the face of missing or uncertain data. Identifies that, in PVA, the best decision may often be relatively robust to parameter uncertainty, highlighting that further investment in reducing uncertainty might be less worthwhile than investing in management actions.