
Importance of Buffer Mechanisms for Population Viability Analysis

VOLKER GRIMM,^{*,§} ELOY REVILLA,[†] JÜRGEN GROENEVELD,^{*} STEPHANIE KRAMER-SCHADT,^{*} MONIKA SCHWAGER,[‡] JÖRG TEWS,[‡] MATTHIAS C. WICHMANN,^{‡**} AND FLORIAN JELTSCH[‡]

^{*}UFZ Umweltforschungszentrum Leipzig-Halle, Department Ökologische Systemanalyse, PF 500 136, D-04301 Leipzig, Germany
[†]Department of Applied Biology, Estación Biológica de Doñana, Spanish Council for Scientific Research CSIC, Avenue Maria Luisa s/n, Pabellón del Perú, E-41013 Seville, Spain

[‡]Universität Potsdam, Institut für Biochemie und Biologie, Maulbeerallee 2, D-14469 Potsdam, Germany

Introduction

Population viability analysis (PVA) is widely used to assess the extinction risk of small populations for different management scenarios (Soulé 1986; Burgman et al. 1993; Beissinger & McCullough 2002). The stochastic population models used in PVA, however, are notoriously difficult to parameterize and test because data are usually poor. It has therefore been argued that simple models with fewer parameters should be preferred over more complex models that describe populations in more detail (e.g., Beissinger & Westphal 1998; Ralls et al. 2002; Reed et al. 2002).

Simple models inevitably ignore many features and processes of the real system, so their assessment of extinction risk cannot be taken literally. Nevertheless, it is argued that these assessments are still useful because PVA does not aim at absolute assessments of extinction risk (which are impossible) but at relative ones (Burgman & Possingham 2000; Reed et al. 2002; Grimm et al. 2004). If one compares two management scenarios and the error of the assessment of extinction risk is of the same order of magnitude for both scenarios, one might still identify the better management option to conserve the population (e.g., Ralls et al. 2002). But we have serious concerns about the ability of such relative assessments to rank the risks and benefits of management alternatives when the assessments are based on simple models that ignore existing buffer mechanisms. In the context of PVA, we define *buffer mechanisms* as those that reduce environmental noise (for a more general notion of buffer mechanisms, see Jeltsch et al. [2000]). *Environmental noise* refers

to the variation of a population's growth rate, which is caused by environmental variations (Burgman et al. 1993; Wissel et al. 1994); thus, environmental noise refers to the effect of the environment. Buffer mechanisms reduce this effect and, in turn, environmental noise.

To illustrate our concern, we considered a simple model that does not include a certain buffer mechanism and a more realistic model of the same population that does. In the simple model, environmental noise is thus higher than in the more realistic model. Higher environmental noise causes a higher risk of extinction (Lande 1993; Wichmann et al. 2003a; Wissel et al. 1994), so the extinction risk predicted by the simple model is higher than that of the more realistic model (Fig. 1).

Reduced environmental noise, however, changes not only the extinction risk in a given situation but also the functional relationship between extinction risk and habitat capacity (Lande 1993; Wissel et al. 1994). With high environmental noise, increases in habitat capacity reduce the extinction risk only slightly because environmental variation can still lead to population sizes so small that demographic noise causes extinction. With low or no environmental noise, however, even small increases in habitat capacity beyond a certain threshold can lead to a substantial decrease in extinction risk, to almost zero (Fig. 1).

For a certain larger habitat capacity, the more realistic model predicts a significant positive effect of increasing capacity, whereas the simple model predicts only a marginal positive effect (Fig. 1). The simple model may thus lead to the management decision of not increasing habitat capacity (and, for example, allocating resources to a captive breeding program) because the model predicts that it will not really pay. Thus, the claim that simpler models can be used to assess alternative management scenarios is not necessarily true.

Environmental noise is a key determinant of the extinction risk of any small population (Wissel et al. 1994). It is therefore critical for the management of threatened

§email volker.grimm@ufz.de

**Current address: CEH Dorset, Winfrith Tech. Centre, Winfrith Newburg, Dorchester; Dorset DT2 8ZD, United Kingdom.

Paper submitted March 3, 2004; revised manuscript accepted July 1, 2004.

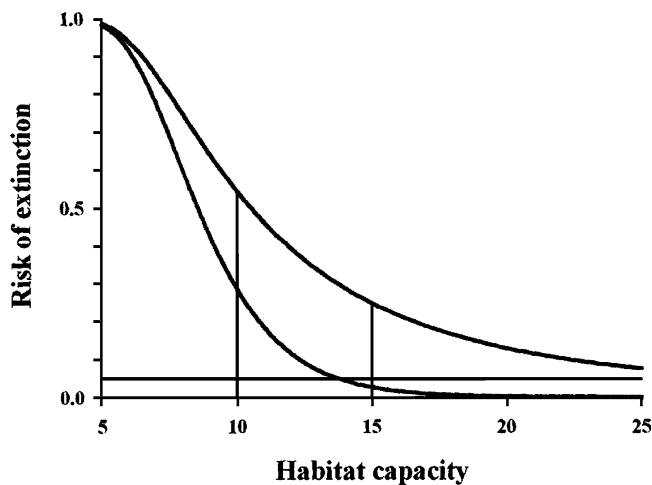


Figure 1. Risk of extinction over a certain time horizon (e.g., 50 years) versus carrying capacity of the habitat for two hypothetical models of the same real population. The lower curve is produced by a model that includes buffer mechanisms; thus, environmental noise is reduced. The model of the upper curve does not include the buffer effect. The lower curve predicts that an increase in capacity from 10 to 15 (arbitrary units) would reduce extinction risk under a certain threshold (here 5%), whereas the upper curve predicts that the extinction risk cannot be reduced to the threshold. The relative difference between the predictions of the simple and the more realistic model is about 50% for the capacity of 10 and about 90% for the capacity of 15.

populations to model environmental noise and demographic stochasticity (Kendall & Fox 2002, 2003) in a sufficiently realistic way. Currently, the practice is to assign environmentally caused variation to one or more demographic parameters. We conclude from the considerations mentioned previously, however, that considering buffer mechanisms is critical. The question is: What mechanisms may limit the environmentally induced variation of demographic parameters? Four examples follow:

- (1) Safe sites (or territories or home ranges) in the habitat can buffer environmental noise because individuals on these sites are less affected by environmental variation (McLaughlin et al. 2002; Greene 2003).
- (2) Group living can buffer environmental noise in social species (e.g., in the alpine marmot [*Marmota marmota*]; Grimm et al. 2003) because subdominant individuals (helpers) that do not reproduce usually contribute to the survival of the alpha individuals and their offspring.
- (3) Nonbreeding individuals (floaters) can buffer environmental noise in territorial species because they rapidly occupy territories that have become vacant because of the death of a breeder. This effect is de-

scribed for Red-cockaded Woodpeckers (*Picoides borealis*; Walters et al. 2002) for which the previous use of simple genetic models led to incorrect management decisions (Lande 1988).

- (4) An overshooting of the long-term average population size of the habitat in good years can buffer environmental noise because in the following years, extinction risk resulting from demographic noise will be reduced. Thus, “storing” the effect of good years is a buffer mechanism, which has been demonstrated in a model of the Tawny Eagle (*Aquila rapax*) in the southern Kalahari (Wichmann et al. 2003b).

The first two examples are typical of buffer mechanisms that reduce the correlation between individuals. The detrimental effect of strong environmental noise is that it causes strong correlation in the demographic rates of all individuals (e.g., high mortality or low birth rates). Buffer mechanisms reduce this correlation (i.e., some individuals are less affected by environmental variations). The importance of correlation and decorrelation on the extinction risk of populations has been addressed in metapopulation theory (Hanski 1999) and in theoretical population models (e.g., Ferson & Burgman 1995; Heino 1998; Johst & Drechsler 2003).

We call for the explicit consideration of buffer mechanisms because they may be crucial when evaluating alternative management options based on PVA results. The aim is not to include all conceivable buffer mechanisms and aim at absolute predictions of extinction risk. These are impossible in principle and in particular in PVA, which often has to be based on messy and scarce data. The point is to keep in mind that buffer mechanisms might exist and that they should be included if they can be identified, parameterized, and to some degree tested.

Often, one automatically tries to identify buffer mechanisms as soon as one tries to understand the outcome of a PVA model. For example, if a certain model predicts that a high risk of extinction cannot be reduced by a certain increase in habitat capacity, one should ask why. If the answer is because environmental noise is very strong, one can ask whether it is realistic to assume such strong environmental noise (i.e., does the population’s growth rate really undergo sharp fluctuations?). If the answer is no, one can ask which mechanism ignored in the model so far might be responsible for buffering environmental noise. Sometimes, when one analyzes models that already include a minimum amount of structure and mechanism, one might even have captured real buffer mechanisms in the model without knowing it. Only thorough model analysis and a strong incentive to understand what the model does will reveal these buffer mechanisms.

Although models including buffer mechanisms do indeed require more data and empirical knowledge than simpler models, powerful modeling strategies and techniques exist to deal with this challenge (pattern-oriented

modeling; Grimm et al. 1996; Grimm & Berger 2003; Mooij & DeAngelis 2003; Wiegand et al. 2003). The question of which kind of model is more appropriate for PVA is not so much a question of simple versus complex but rather of the ability of the model to capture, in a testable way, essentials of the mechanisms that determine population persistence so that the most effective management recommendations can be made.

Acknowledgments

We thank M. Burgman and two anonymous reviewers for helpful comments. E.R. was supported by a Ramón y Cajal contract from the Spanish Ministry of Education and Science.

Literature Cited

- Beissinger, S. R., and D. R. McCullough. 2002. Population viability analysis. The University of Chicago Press, Chicago.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62**:821–841.
- Burgman, M. A., and H. Possingham. 2000. Population viability analysis for conservation: the good, the bad and the undescribed. Pages 97–112 in A. G. Young and G. M. Clarke, editors. *Genetics, demography and viability of fragmented populations*. Cambridge University Press, Cambridge, United Kingdom.
- Burgman, M. A., S. Ferson, and H. R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman & Hall, London.
- Ferson, S., and M. A. Burgman. 1995. Correlations, dependency bounds and extinction risks. *Biological Conservation* **73**:101–105.
- Greene, C. M. 2003. Habitat selection reduces extinction of populations subject to Allee effects. *Theoretical Population Biology* **64**:1–10.
- Grimm, V., and U. Berger. 2003. Seeing the forest for the trees, and vice versa: pattern-oriented ecological modelling. Pages 411–428 in L. Seuront and P. G. Strutton, editors. *Handbook of scaling methods in aquatic ecology: measurement, analysis, simulation*. CRC Press, Boca Raton, Florida.
- Grimm, V., N. Dorndorf, F. Frey-Roos, C. Wissel, T. Wyszomirski, and W. Arnold. 2003. Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*. *Oikos* **102**:124–136.
- Grimm, V., K. Frank, F. Jeltsch, R. Brandl, J. Uchmanski, and C. Wissel. 1996. Pattern-oriented modelling in population ecology. *Science of the Total Environment* **183**:151–166.
- Grimm, V., et al. 2004. META-X: a generic software for metapopulation viability analysis. *Biodiversity and Conservation* **13**:165–188.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, United Kingdom.
- Heino, M. 1998. Noise colour, synchrony and extinctions in spatially structured populations. *Oikos* **83**:368–375.
- Jeltsch, F., G. E. Weber, and V. Grimm. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology* **150**:161–171.
- Johst, K., and M. Drechsler. 2003. Are spatially correlated or uncorrelated disturbance regimes better for the survival of species? *Oikos* **103**:449–456.
- Kendall, B. E., and G. A. Fox. 2002. Variation among individuals reduces demographic stochasticity. *Conservation Biology* **16**:109–116.
- Kendall, B. E., and G. A. Fox. 2003. Unstructured individual variation and demographic stochasticity. *Conservation Biology* **17**:1170–1172.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* **241**:1455–1460.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* **142**:911–927.
- McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. The route to extinction: population dynamics of a threatened butterfly. *Oecologia* **132**:538–548.
- Mooij, W. M., and D. L. DeAngelis. 2003. Uncertainty in spatially explicit animal dispersal models. *Ecological Applications* **13**:794–805.
- Ralls, K., S. R. Beissinger, and J. F. Cochrane. 2002. Guidelines for using population viability analysis in endangered-species management. Pages 521–550 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. The University of Chicago Press, Chicago.
- Reed, J. M., L. S. Mills, J. B. Dunning, E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M.-C. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. *Conservation Biology* **16**:7–19.
- Soulé, M. E. 1986. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Walters, J. R., L. B. Crowder, and J. A. Priddy. 2002. Population viability analysis for red-cockaded woodpeckers using an individual-based model. *Ecological Applications* **12**:249–260.
- Wichmann, M. C., F. Jeltsch, W. R. J. Dean, K. A. Moloney, and C. Wissel. 2003a. Implication of climate change for the persistence of raptors in arid savanna. *Oikos* **102**:186–202.
- Wichmann, M. C., K. Johst, K. A. Moloney, C. Wissel, and F. Jeltsch. 2003b. Extinction risk in periodically fluctuating environments. *Ecological Modelling* **167**:221–231.
- Wiegand, T., F. Jeltsch, I. Hanski, and V. Grimm. 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and conservation practice. *Oikos* **100**:209–222.
- Wissel, C., T. Stephan, and S.-H. Zschke. 1994. Modelling extinction and survival of small populations. Pages 67–103 in H. Remmert, editor. *Minimum animal populations*. Ecological studies 106. Springer-Verlag, Berlin.

