Influence of Colored Noise on the Extinction Risk in Structured Population Models

Heino, M. and Sabadell, M.

IIASA Interim Report
August 2002

Heino, M. and Sabadell, M. (2002) Influence of Colored Noise on the Extinction Risk in Structured Population Models. IIASA Interim Report. IIASA, Laxenburg, Austria, IR-02-056 Copyright © 2002 by the author(s). http://pure.iiasa.ac.at/6730/

International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

-

Interim Report IR-02-56

Influence of Coloured Noise on the Extinction Risk in Structured Population Models

Mikko Heino (mikko@imr.no)
Mireia Sabadell (mireiasabadell@hotmail.com)

Approved by

Ulf Dieckmann (dieckmann@iiasa.ac.at)
Project Leader, Adaptive Dynamics Network

August 2002

Contents

Abstract

We use simple models to compare extinction risk among basic life history types when environmental noise is either uncorrelated ("white") or positively autocorrelated ("red"). The metric of extinction is probability of extinction in 50 years; variability of noise is scaled such that its expected variance is independent of colour at this time scale. We compare annual, semelparous biennial, iteroparous biennial and perennial life histories. Given an identical equilibrium population size and basic reproductive number, annual life histories confer a much higher extinction risk than semelparous biennial life histories. Iteroparous biennial and perennial life histories have even lower extinction risks. Autocorrelated noise influences the life histories differently: the extinction risk of the annuals decreases with reddening noise, whereas the other life histories show an opposite response. We show that in a previously developed stage-structured population model for the Florida scrub jay *Aphelocoma coerulescens* ignoring the possibility of red environmental noise might result in a much too optimistic assessment of population viability. In conclusion, simplifications of population structure and ignoring red environmental noise in population viability analyses can result in serious biases.

About the Authors

Mikko Heino
Department of Ecology and Systematics
University of Helsinki
FIN-00014 Helsinki
Finland

and

Adaptive Dynamics Network
International Institute for Applied Systems Analysis
A-2361 Laxenburg
Austria

Mireia Sabadell
Department of Ecology
Faculty of Biology
University of Barcelona
Catalonia, Spain

Acknowledgments

We thank Tim Benton and Esa Ranta for very helpful comments on the manuscript. We acknowledge funding by the Academy of Finland (Project 45928).

Influence of Coloured Noise on the Extinction Risk in Structured Population Models

Mikko Heino
Mireia Sabadell

1. Introduction

What are the importance and the influence of environmental noise for population dynamics? These are salient questions both from the theoretical (Ranta et al., 2000) and from the applied perspective — environmental noise may have a major influence on extinction risk of populations (Wissel et al., 1993; Caughley, 1994; Foley, 1994; Lawton, 1997; Ripa and Lundberg, 2000). Consequently, numerical tools to assess extinction risk that explicitly account for environmental variability are an increasingly important part of population viability analysis (e.g., Shaffer, 1990; Boyce, 1992; Burgman et al., 1993; Caughley, 1994; Fieberg and Ellner, 2001).

One of the major questions in the recent theoretical research on the causes of extinctions has been the importance of the so-called “red noise” — noise characterized by positive autocorrelations. Many physical and ecological time series are red at decadal time scale (Steele, 1985; Pimm and Redfearn, 1988; Schroeder, 1991; Ariño and Pimm, 1995): consecutive years tend to be more similar than years far apart. Positive autocorrelations in physical systems reflect slow, quasi-cyclic fluctuations of global climate. Ecological systems are subject to climatic forcing and disturbances. Moreover, populations and communities have their own internal dynamics that may result in red time series. Even though the question how environmental variability is filtered to demographic parameters remains largely unresolved, the possibility that red environmental noise induces positively correlated fluctuations in demographic parameters should not be dismissed.

Despite the obvious relevance of autocorrelated noise for extinction risk, “white noise” where autocorrelations are absent is assumed in almost all earlier models on extinction risk. Consequently, much effort has recently been focused on trying to understand whether red-shifted noise tends to increase or decrease extinction risk. An intuitive argument is that because runs of bad years are likely when noise is reddened, red noise should be more dangerous for population persistence than white noise (e.g., Lawton, 1997). However, the published studies yield no consistent pattern with respect to the effect of red noise (Roughgarden, 1975; Mode and Jacobson, 1987a,b; Foley, 1994; Ripa and Lundberg, 1996; Johst and Wissel, 1997; Petchey et al., 1997; Heino, 1998; Cuddington and Yodzis, 1999; Halley and Kunin, 1999; Heino et al., 2000; Jonsson and Ebenman, 2001). The results have turned out to be sensitive both to model assumptions and to exact formulation of the question (Halley and Kunin, 1999; Heino et al., 2000; Lundberg et al., 2000).

Useful models for extinction times should be, to a sufficient degree, ecologically realistic. Therefore, it is striking that the theoretical studies on the influence of red noise on extinction risk have focused only on models assuming simple annual life history, whereas the majority of organisms show more complex life histories. Papers by Mode and Jacobson (1987a,b) and Jonsson and Ebenman (2001) seem to be the only exceptions, and only the latter paper focused on differences among life histories. However, it is even more striking how little population viability analyses have been influenced by the possibility of red environmental noise (e.g., Burgman et al., 1993; Fieberg and Ellner, 2001).

In this paper we want to study how structure of a population influences its extinction risk, particularly when red environmental noise is considered. This is a theoretically interesting question that is poorly understood. More importantly, there is a need for improving such understanding in conservation biology — most populations of conservation interest cannot adequately be described by an annual life history. We compare models representing four basic life history types: annual, semelparous biennial, iteroparous biennial and perennial. Despite the simplicity of these models, they are useful tools for providing insight on the qualitative effects of population structure on population viability. For a comprehensive treatment on construction and analysis of more complex and realistic population models, see Caswell (2001).

This paper is structured as follows. We will first introduce the different life history models. Then we start out analysis by exploring the behaviour of the different life histories when white environmental noise is assumed; these explorations are then extended to reveal the influence of autocorrelated noise for extinction risk in the different life history types. Finally, we show how red noise influences extinction risk in a complex life history model that is motivated by socially structured Florida scrub jay *Aphelocoma coerulescens* populations.

2. Life History Models

2.1 Deterministic Population Dynamics

We first introduce the deterministic skeletons of the life history models. We assume that the population census takes place immediately before reproduction. Fecundity is measured as the number of female offspring surviving to age one, thus including the effects of mortality during the first year of life. We keep track only on numbers of females and assume that shortage of males does not influence female reproductive success.

Density dependence is assumed to influence fecundity such that per capita offspring production is a decreasing function of the number of reproducing females. Density dependence at different stages may have different consequences (Hellriegel, 2000), but we chose fecundity because it is the only common parameter in all our models. We used a modified Ricker function to describe density dependence:

$$g(N) = \exp\left(-(N_c / k)^b\right), \tag{1}$$

where N_c is the abundance of the critical age-classes and k is a parameter scaling the population abundance. Parameter b determines the strength of density dependence: for $b = 1$ the equation takes the form of the Ricker equation; if $b<1$ the density dependence gets stronger at densities below N_c/k and weaker at densities above. The smaller is the parameter b, the less there is tendency for overcompensatory density dependence and non-equilibrium population dynamics.

We consider four different life history types (Fig. 1). Comparisons between the life histories are facilitated by standardizing them with respect to equilibrium population size and basic reproductive number (Appendix). The simplest life history is the annual type (Fig. 1) described by the equation

$$N(t+1) = f\exp\left(-\left(N(t)/k\right)^b\right)N(t)\,, \tag{2}$$

where $N(t)$ denotes the population size and f is maximum fecundity in absence of density dependence.

In the semelparous biennial life history, reproduction is delayed until age two (Fig. 1). This life history is described by the following two equations:

$$\begin{aligned} N_1(t+1) &= f\exp\left(-\left(N_2(t)/k\right)^b\right)N_2(t) \\ N_2(t+1) &= sN_1(t) \end{aligned} \quad . \tag{3}$$

Here N_1 and N_2 are the numbers of individuals of ages 1 and 2, and s is survival probability from age 1 to 2. In the iteroparous biennial life history the maximum life span is two years but reproduction starts already at age 1 (Fig. 1):

$$\begin{aligned} N_1(t+1) &= \exp\left(-\left((N_1(t)+N_2(t))/k\right)^b\right)\left(f_1N_1(t)+f_2N_2(t)\right) \\ N_2(t+1) &= sN_1(t) \end{aligned} \,, \tag{4}$$

where f_1 and f_2 denote the fecundities at ages 1 and 2 and s is the survival probability.

Our perennial life history (Fig. 1) is similar to the semelparous biennial life history except that the adults can survive to reproduce several times:

$$\begin{aligned} N_1(t+1) &= f\exp\left(-\left(N_2(t)/k\right)^b\right)N_2(t) \\ N_2(t+1) &= s_1N_1(t)+s_2N_2(t) \end{aligned} \quad . \tag{5}$$

In this model, N_2 denotes the number of individuals that are at least two years old. Annual survival probability from age 1 to age 2 is s_1 and from age 2 onwards s_2.

As an example of a more complex stage-structured life history model, we use a model developed by Root (1998) where the stage of an individual depends both on its social status (helper or breeder) and on age (juveniles do not breed or help). The life history graph illustrated in Fig. 2 gives raise to the following equations for the density-independent population dynamics:

$$\begin{aligned} N_J(+1) &= s_E f_E N_E(t) + s_W f_W N_W(t) + s_N f_N N_N(t) \\ N_H(t+1) &= s_J(1-P_{JN})N_J(t) \\ N_O(t+1) &= s_H(1-P_{HN})N_H(t) + s_O(1-P_{ON})N_O(t) \\ N_N(t+1) &= s_J P_{JN} N_J(t) + s_H P_{HN} N_H(t) + s_O P_{ON} N_O(t) \\ N_E(t+1) &= s_N P_{NE} N_N(t) + s_E N_W(t) \\ N_W(t+1) &= s_N(1-P_{NE})N_N(t) + s_W N_W(t) \end{aligned}$$

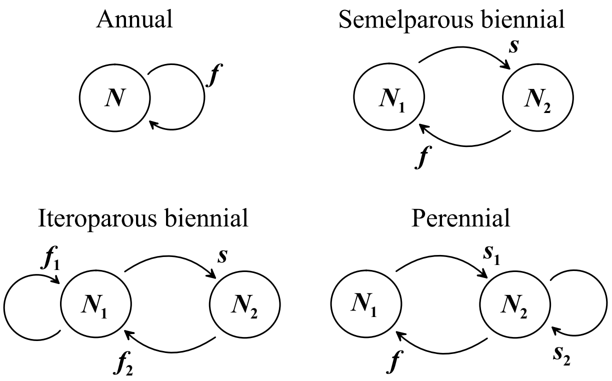


Figure 1. Life history graphs for simple life history models. Arrows indicate the two demographic processes taking place during one time step, reproduction (*f*) and survival (*s*). *N* denotes density.

where densities are denoted with *N*, fecundities with *f*, survival with *s* and transition probabilities with *P*. The subscripts refer to the individual states: *J* for juveniles, *H* for young helpers, *O* for old helpers, *N* for novice breeders and *E* and *W* for experienced breeders with and without helpers, respectively.

Density dependence works such that there is a fixed number of breeding territories that cannot be exceeded (Root, 1998). If the number of breeding females before reproduction would have exceeded the carrying capacity, breeding females were uniformly exposed to extra mortality such that the carrying capacity was respected. An undocumented feature of the original model is that the number of breeding females with helpers may exceed the number of helpers. In such cases, the excess breeders with helpers were transferred to the class of experienced breeders without helpers.

2.2 Demographic and Environmental Stochasticity

Discrete nature of individuals and probabilistic nature of birth and death events cause demographic stochasticity that cannot be ignored in small populations (e.g., Caughley, 1994). This requires two kinds of changes to deterministic models outlined in the previous section. First, the state variables must be integer numbers representing absolute abundance of individuals (as opposed to density in the deterministic formulation). Second, the rates related to births and deaths need to be taken from appropriate probability distributions.

The number of survivors follows a binomial distribution if all individuals within an age group have the same survival probability. Therefore, we modelled demographic stochasticity in survival by drawing the number of survivors from a binomial distribution with survival probability (*s*) and number of individuals (*N*) as the parameters, that is, $N(t+1)=\mathrm{Bin}(s, N(t))$. Probabilistic stage transitions in the Florida scrub jay model were treated similarly.

Demographic stochasticity in birth events can be modelled in a similar manner by replacing the deterministic expectation with a random number from an appropriate distribution; Poisson distribution is a biologically feasible choice (Mode and Jacobson, 1987a; Burgman et al., 1993). This distribution has a single parameter, which is the

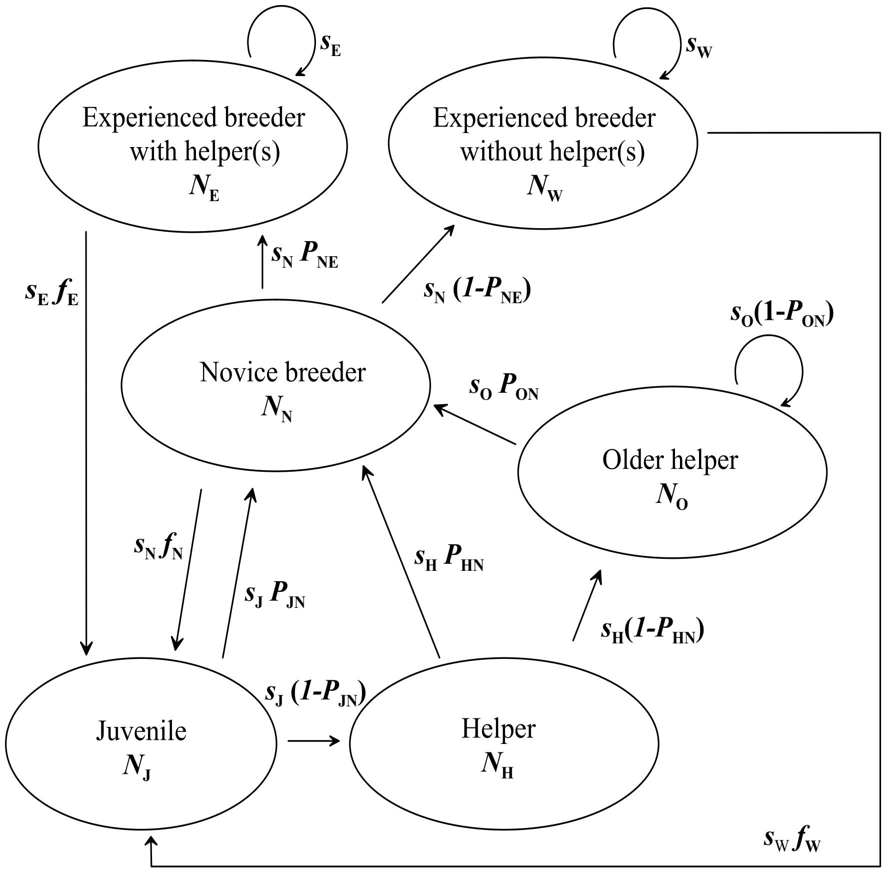


Figure 2. Schematic representation of the socially structured population model for Florida scrub jay (redrawn from Root, 1998). N_x denotes the number of individuals in stage x. Survival probability at stage x is denoted with s_x; P_{xy} is the transition probability from stage x to stage y and f_x is per capita fecundity of stage x.

expected number of offspring produced. Thus, if N females all produce on average f offspring, the total number of offspring produced follows $\mathrm{Poisson}(f\ N)$.

We generate the time series of environmental noise, $x(t)$, as a first-order autoregressive process. As compared to more complex and probably more realistic models noise, the so-called pink $1/f$ noise (Halley, 1996; Halley and Kunin, 1999), low-frequency fluctuations are under-represented in autoregressive noise. This difference becomes critical only at time scales that are longer than considered here, and we chose to use autoregressive model because it is an efficient way of generating noise with various degrees of autocorrelation. The first-order autoregressive process is given by the equation

$$\begin{array}{rl} x(t) = 0 & \text{if } t = 0 \\ x(t) = \kappa\, x(t-1) + \beta(\kappa)\,\varepsilon(t-1) & \text{if } t > 0 \end{array}, \qquad (6)$$

where κ ($0 \le \kappa < 1$) is the autocorrelation parameter that determines the colour of time series: for $\kappa = 0$, the time series is white noise, whereas for $\kappa > 0$ the time series becomes red-shifted. Random variables $\varepsilon(t)$ are normally distributed with zero mean and unity variance. Parameter β was chosen such that the expected variance of time series $x(t)$ was independent of its autocorrelation at the time scale of 50 years, which was also the time scale for scoring extinction risk (see Heino et al., 2000).

We assumed in the simple life history models that environmental stochasticity influences reproductive success, which in our models includes survival to age one. This choice enables comparisons between annual and the other life history types: annuals do not survive after age one. We considered two alternative ways of including the noise: either maximum fecundity *f* or parameter *k* determining carrying capacity was a stochastic parameter. Thus, we had either $f(t) = f + x(t)$ or $k(t) = k + x(t)$, with parameter β (equation 6) chosen to yield a desired coefficient of variation in the time series *f*(*t*) or *k*(*t*). The difference in the two formulations is in the distribution of fecundity after the effect of density dependence is included (recall equation 1): when noise is in *f*, environmental stochasticity is unfiltered, whereas when noise is in *k*, the function for density dependence filters the noise such that the distribution becomes skewed to the left (the longer tail is towards low values). In the Florida scrub jay model, we assumed either that noise affects fecundities or juvenile survival: $f_x(t) = f_x + x(t)$ or $s_J(t) = s_J + x(t)$.

2.3 Simulation Procedures

The measure of extinction risk chosen in our study is the probability that a population goes extinct during a period of 50 years, conditional that a population size at time zero followed a quasi-stationary distribution of the population dynamics accounting only for demographic noise. This probability was estimated with 1000 or 2000 replicate simulations for a given model and parameter combination, depending on the variability between the replicates.

To facilitate comparisons between different life history models (equations 2-5), we chose parameter *k* such that the total equilibrium population sizes in the deterministic versions of the life history models were identical. The population dynamics were then iterated for 20 generations without environmental stochasticity, such that stochastic demographic equilibrium was reached. If population went extinct, simulation was restarted. After having reached the quasi-equilibrium, environmental stochasticity was activated, and the trial period of 50 years was started. Similarly, the model with social structure was iterated to the quasi-equilibrium before the actual simulation.

When comparing behaviour of the four life history models, most parameter values and structural assumptions were varied following a simple factorial design, with two levels for each factor: the parameter influenced by environmental noise (fecundity or carrying capacity), reproductive ratio (low: $R_0 = 10$, or high: $R_0 = 50$), noise level (low: CV = 0.2, high: CV = 0.5) and strength of density dependence (weak: $b = 0.5$, or strong: $b = 1$). Finer grids were used for equilibrium population size (see Appendix) and colour of noise. When studying the socially structured model structure for Florida scrub jay, only carrying capacity and colour of noise were varied; other parameter values were obtained from Root (1998). The main effect of strength of density dependence is to influence the variability of population dynamics. When density dependence is weak, dynamics of the underlying deterministic models have stable point equilibria. Except for iteroparous biennial life history and low reproductive ratio, the point equilibria become unstable when density dependence is strong, and the dynamics display cyclic behaviour or chaos. Also in the stochastic models increasing the strength of density dependence tends to make dynamics fluctuate more strongly, but there are no qualitative changes in population dynamical attractors.

3. Results

Figure 3 shows how extinction risk depends on equilibrium population size in different life history models. Equilibrium refers here to the equilibrium of the deterministic skeleton; actual dynamics fluctuated because of both demographic and environmental noise. Environmental noise is assumed to be white. The general pattern is clear and not unexpected: the larger is the equilibrium population size, the lower is the risk of extinction. However, even when population sizes and basic reproductive numbers of the four life histories have been standardized, they often have strikingly different risk of extinction: typically, the annual life history shows the highest extinction risk, followed by the semelparous biennial life history. Iteroparous biennial and perennial life histories have much lower risks of extinction, but their respective ranks vary. However, when equilibrium population size is large, perennial life history always confers the lowest extinction risk. These results are qualitatively independent of the level of growth rate and strength of density dependence. Nevertheless, we note that extinction risk is increased by strong density dependence and high growth rate; these factors make dynamics more variable by increasing the tendency for strong intrinsic fluctuations and overshooting (see Ginzburg et al., 1990; Ripa and Lundberg, 2000). In contrast, if growth rate is very low (e.g., $R_0 = 1.5$), population fluctuations will largely be driven by external noise, and strength of density dependence becomes unimportant.

Mechanisms of extinctions differ between the life history types. On average, annuals go extinct from larger population sizes and after stronger environmental perturbations than the other types. Extinction process of the annuals is “fast”: typically extinctions are caused by a single unfavourable year. Population size prior the extinction is close to or above long-term average before extinction; high population size before extinction is observed when large fluctuations in population size occur, caused by the interaction between density dependence and environmental noise (cf. Ripa and Lundberg, 2000). In contrast, multi-stage life histories have a “slow” extinction process. Extinctions require at least two unfavourable years, and the population size the year before extinction is often well below long-term average.

Extinction risk depends on the way in which noise influences demography (Fig. 3). However, different life histories show different responses: perennial populations are more vulnerable to noise in fecundity, whereas other life history types tend to have higher extinction risk when noise influences carrying capacity. The extinction risk depends also on the strength of the environmental noise (not illustrated); when the amplitude of noise is decreased (from CV = 0.5 to CV = 0.2), extinction risk decreases strongly. In most of the cases, extinction risk becomes independent of equilibrium population size when equilibrium population size is higher than 30-60 individuals, indicating that demographic stochasticity contributes significantly to extinction risk only below that level.

Figure 4 illustrates the dependence of the extinction risk on temporal correlation in environmental noise. We note that irrespective of the colour of noise, annual life history

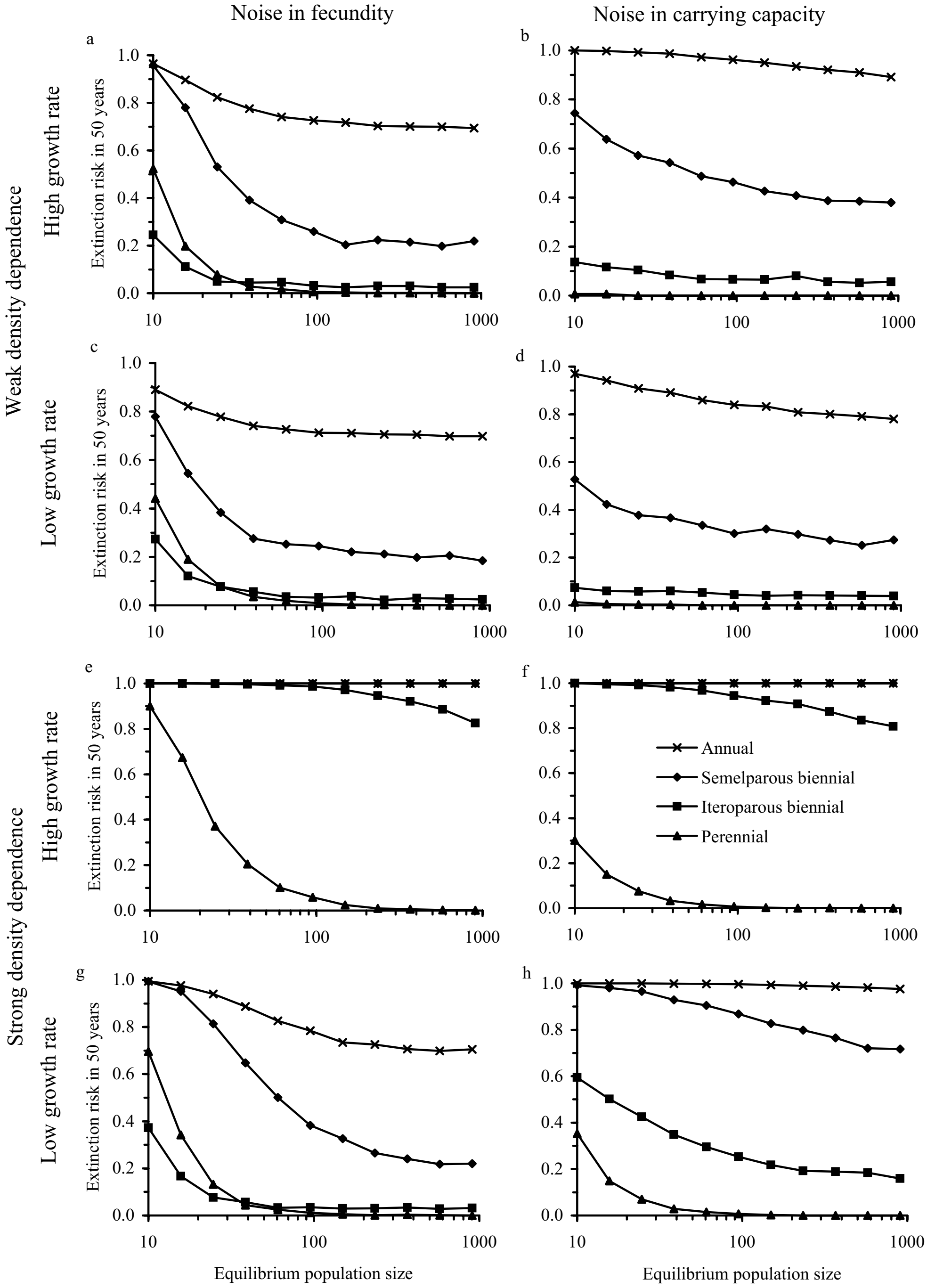


Figure 3 Extinction risk in 50 years for the four simple life history types subject to white environmental noise. Equilibrium population size refers to the equilibria in deterministic skeletons of the stochastic models used in the simulations. The parameter values are varied following a factorial scheme with three factors, each with two levels: strength of density dependence (weak: b = 0.5, or strong: b = 1); reproductive ratio (low: R_0 = 10, or high: R_0 = 50) and the demographic parameter influenced by noise (fecundity or carrying capacity). Noise level was high, such that the coefficient of variation of the stochastic parameter was 0.5; the results for lower noise level are not shown but were qualitatively similar. The number of replicates was 1000. Survival probabilities: semelparous and iteroparous biennial life history, s = 1; perennial, s_1 = 1 and s_2 = 0.1. Fecundities: annual and semelparous biennial life history, f = 10 or f = 50 (low and high R_0, respectively); iteroparous biennial life history f_1 = f_2 = 5 or f_1 = f_2 = 25; perennial f = 9 or f = 45.

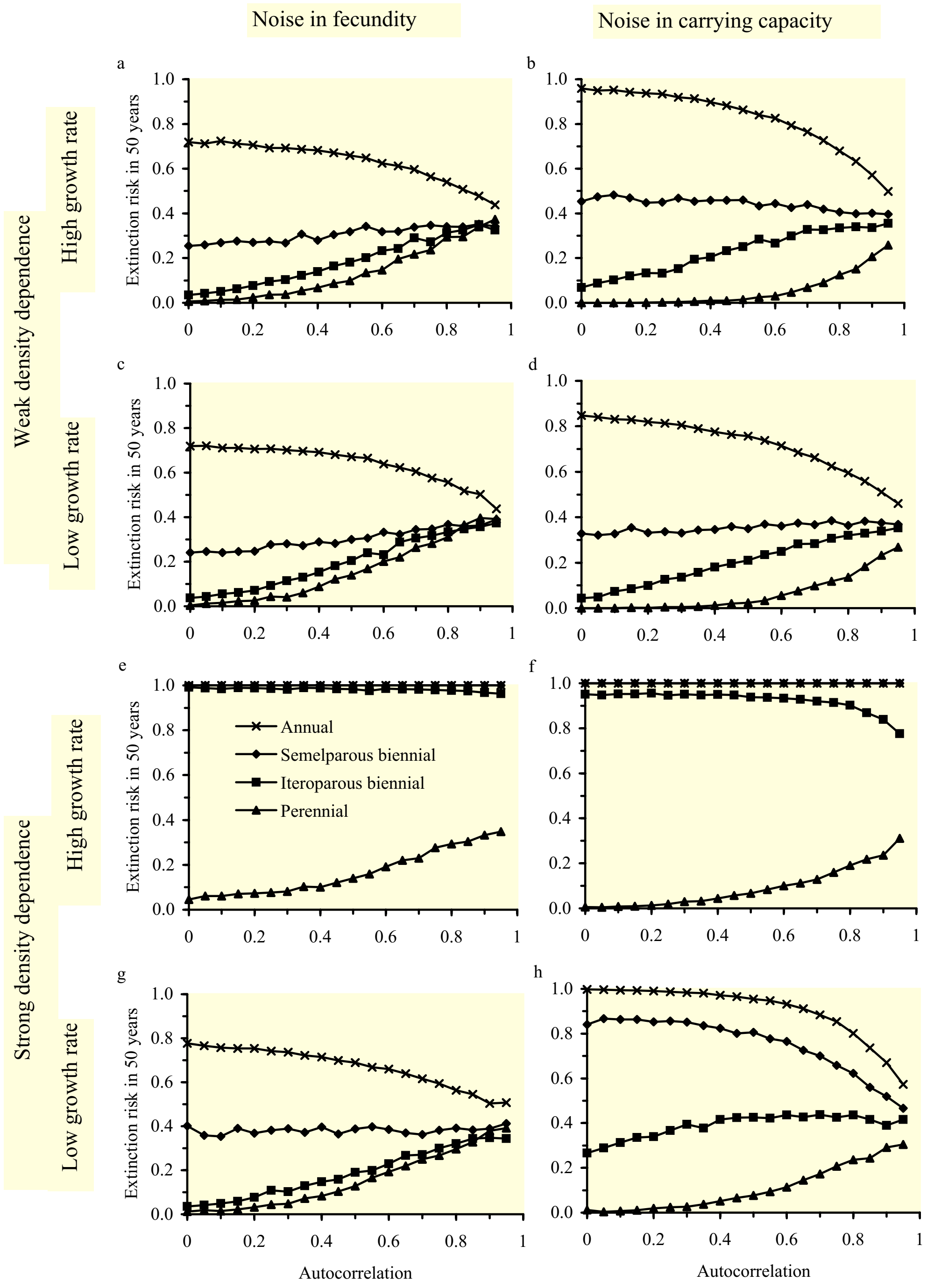


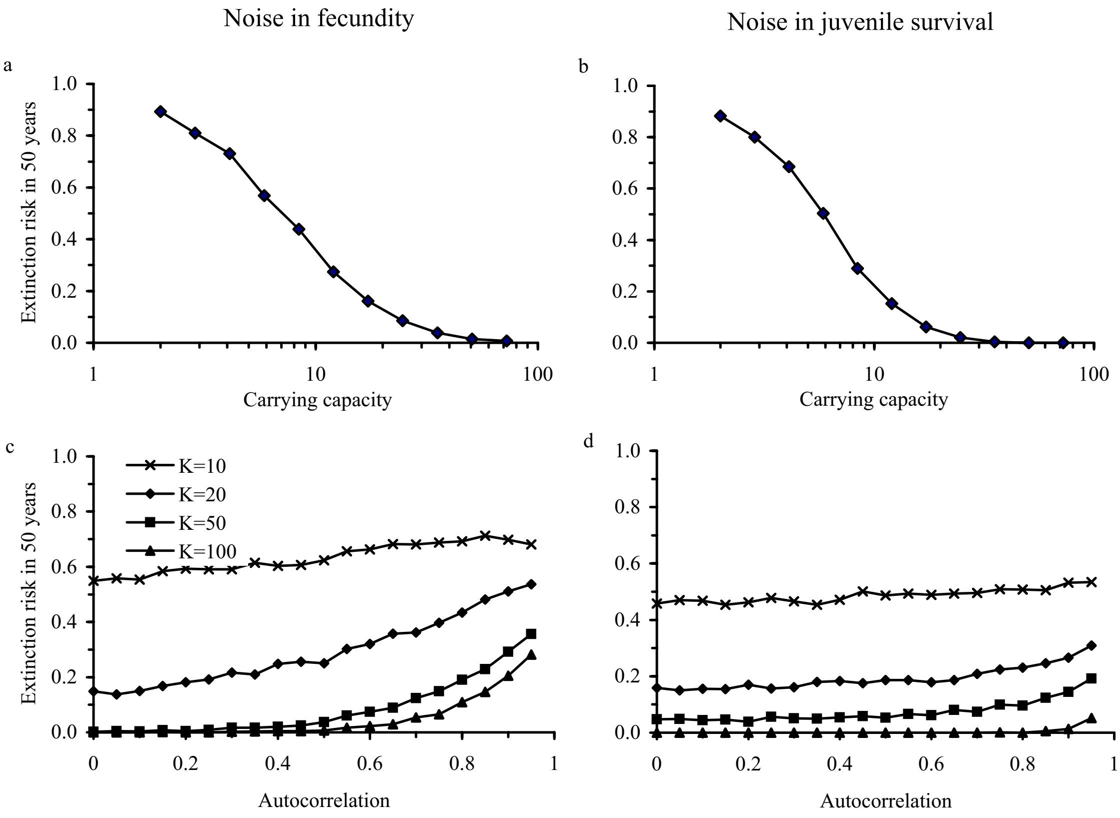
Figure 4. Extinction risk in 50 years for the four simple life history types when the colour of environmental noise ranges from white (no autocorrelation) to strongly red ($\kappa = 0.95$). Deterministic equilibrium population size was scaled to 100 in all simulations. Other parameter values are the same as in the Fig. 3.

type has higher extinction risk than semelparous biennial, iteroparous biennial and perennial types; the latter have the lowest probability to go extinct. However, the most notable finding in Figure 4 is that the four life histories show qualitative differences in the way in which extinction risk depends on the colour of environmental noise. In a population with annual life history the extinction risk decreases with increasing temporal correlation. In contrast, this probability steadily increases with autocorrelation in the other life history types. However, the higher is the autocorrelation, the lower are the differences between the models. This effect occurs because when autocorrelation of type has higher extinction risk than semelparous biennial, iteroparous biennial and perennial types; the latter have the lowest probability to go extinct. However, the most notable finding in Figure 4 is that the four life histories show qualitative differences in the way in which extinction risk depends on the colour of environmental noise. In a population with annual life history the extinction risk decreases with increasing temporal correlation. In contrast, this probability steadily increases with autocorrelation in the other life history types. However, the higher is the autocorrelation, the lower are the differences between the models. This effect occurs because when autocorrelation of environmental noise increases, extinctions are more and more frequently caused by prolonged adverse environmental conditions (f or k staying below the average values). These periods pose a high risk to multi-stage life histories with the slow extinction process. However, the story is different for annual life history. Annuals are prone to extinctions that are caused single, large perturbations that are unlikely if noise is sufficiently red: when autocorrelation of noise increases, short-term variability of noise decreases (Halley and Kunin, 1999; Heino et al., 2000).

We now turn to a slightly more concrete example. Figure 5 shows how the extinction risk varies when the carrying capacity or the autocorrelation is changed in the socially structured model motivated by Florida scrub jay. We consider two cases: environmental noise affecting fecundity (f_x) or juvenile survival probability (s_J). Our results demonstrate that the extinction probability depends on the carrying capacity, the type of noise (whether noise affects f_x or s_J) and the colour of noise. In the models assuming white noise, extinction risk decreases rapidly when carrying capacity increases, and it becomes negligible if the habitat supports more than few tens of breeding territories. The decrease of the extinction risk with increasing carrying capacity is faster when environmental noise affects juvenile survival than when it affects fecundities. When temporal correlation is introduced, the results show that the extinction risk increases with the autocorrelation, although the increase is significant only when noise is affecting fecundities. It is noteworthy that red noise can make extinction risk high even when white noise model would predict negligible risk.

4. Discussion

We have demonstrated that extinction risk strongly depends on the life history type. Moreover, we have also shown that the colour of environmental noise varies the extinction risk, but that the effect is qualitatively different between annual life history and the others: extinction risk of biennials and perennials increase with reddening noise, but the opposite is true for annuals. Positive relationship between extinction risk and red noise is also observed in a “socially” structured model, i.e., a stage-structured model where individual stage is partly determined by its social status. Thus, increasing awareness on the possibility that assuming white environmental noise may yield biased results is required. On the other hand, the good news is that the bias caused by assuming white noise is usually small, as long as autocorrelation in noise is only moderate (κ<0.3).


Noise in fecundity

Noise in juvenile survival

Figure 5. Extinction risk in 50 years in the Florida scrub jay model with ‘social’ structure. Panels a and b show the dependence of extinction risk on carrying capacity (number of breeding territories) when white environmental noise is assumed. In c and d, the influence of coloured noise on extinction risk is shown for four different carrying capacities. Environmental noise influences fecundity in the left column (CV = 1.2) and juvenile survival in the left column (CV = 0.26). We used the parameter values given by Root (1998) for the optimal habitat. The annual survival probabilities are: $s_J = 0.34$; $s_H = 0.64$; $s_O = 0.74$; $s_N = 0.74$; $s_W = 0.77$; $s_E = 0.85$. The transition probabilities are: $P_{JN} = 0.52$, $P_{HN} = 0.31$, $P_{ON} = 0.23$ and $P_{NE} = 0.52$. The stage-specific fecundities are $f_N = 0.88$, $f_W = 0.90$ and $f_E = 1.29$. The number of replicates is 2000.

Of the studied life history types, the annual life history conferred the highest probability of extinction. This is understandable because in the annual life history there is only one cohort present at time, whereas in the other types the number of concurrent cohorts is at least two. Semelparous biennial type had a much lower extinction risk that the annual type. The special feature of the biennial semelparous life history is that two concurrent cohorts, “even” and “odd” year cohorts, never mix. Thus, the overall extinction risk is lowered by the presence of two cohorts, but the surviving cohort cannot rescue the cohort that goes extinct. In contrast, in iteroparous biennial and perennial life histories cohorts are mixing (i.e., an individual can contribute to more than one future cohort), safeguarding populations from isolated failures in reproduction or survival. However, iteroparous biennial type goes extinct after two consecutive failures. Therefore it usually has a higher extinction risk than the perennial type, which can overcome more than two years of recruitment failure, because reproducing adults may survive for many years. Because we only considered environmental stochasticity in reproductive success, perennials are immune to white environmental noise when adult population is large enough. However, even perennials populations are vulnerable to red noise, because in that case adverse conditions can persist for a long time. Undeniably, some of these results are contingent on our specific assumptions on density dependence and on how noise influences demographic parameters, but they nevertheless show that details of population structure may matter a lot. This is in line with the experience in life history theory where it is well established that evolutionary performance of various life history types depends on strength of environmental fluctuations (e.g. Caswell, 2001).

We also studied the influence of autocorrelated noise on extinction risk. We observed once more that the annual life history type has the highest extinction risk among the considered life histories, irrespective of the colour of noise. A more striking observation is that even though extinction risk in the annuals is decreasing with reddening noise (e.g., Roughgarden, 1975; Ripa and Lundberg, 1996), in the other life history types extinction risk is almost invariably increasing. Thus, the intuitive argument that red noise is bad for population persistence (e.g., Lawton, 1997) holds for structured populations. However, the intuitive argument fails for the annuals. This discrepancy is caused by differences in the mechanisms of extinctions among the life history types. Annuals, with their fast extinction process, are sensitive to even single unfavourable years, whereas in multi-stage life histories extinction process is slow, and extinctions require at least two unfavourable years.

To evaluate the significance of red noise in a setting that is motivated by a concrete example, we modified the population model developed for the Florida scrub jay by Root (1998). It is doubtful whether these models are “good” in the sense that the quantitative predictions are reliable; yet, they can provide valuable insight to importance of various factors on viability of the Florida scrub jay populations. In particular, our results show that the model-predicted extinction risk can significantly increase with increasing autocorrelation of the environmental noise. Even if a model assuming white noise predicts negligible extinction risk (i.e., when carrying capacity is large), the extinction risk can be very high if environmental noise is strongly autocorrelated.

Our analysis of the Florida scrub jay model was based on the simple assumption that environmental variability can be represented as a stochastic demographic variable — without considering what is the actual mechanism linking environmental variability (e.g., habitat change or variations in temperature or rainfall) and demography. However, in some other studies a mechanistic link has been established and used when modelling extinction risk. For example, Wiegand et al. (1998) studied the influence of rainfall on mortality and probability of breeding in the European brown bear. Griebeler and Gottschalk (2000) considered fluctuations in temperature that influenced development rate and daily fecundity in the grey bush cricket. Griebeler and Gottschalk (2000) also found that different ways of modifying autocorrelation structure of real and artificial temperature data had a large influence on extinction risk.

Our results highlight the fact that extinction risk may be strongly influenced by the life history type. In this respect, our results are in line with a recent paper by Jonsson and Ebenman (2001) who also emphasized the differences in the extinction risk between life histories with different demographies. They also noted that it is important which one of the demographic parameters is subject to stochasticity. For example, semelparous species are more prone to extinction than iteroparous when noise affects developmental rate or juvenile survival, whereas iteroparous species are more prone to extinction than semelparous ones when noise varies adult survival. Jonsson and Ebenman (2001) also observed the effects of life history type on the dependence between extinction risk and noise colour. However, their study differs from ours in a number of important assumptions: Jonsson and Ebenman (2001) assumed density-independent dynamics and zero average growth rate, and stochasticity in other demographic variables than in our models. Further, their model dealt only with quasi-extinctions and ignored demographic stochasticity.

The effect of life history on extinction risk has also been observed in some earlier studies on age-structured population models (e.g., Orzack, 1993; Pascual et al., 1997), and population viability analysis software supporting structured population models have been available for many years. However, most theoretical studies on extinction risk in stochastic environments assume either annual life history or homogeneous population with overlapping generations, especially when the focus has been on coloured noise (e.g., Roughgarden, 1975; Wissel et al., 1993; Foley, 1994; Ripa and Lundberg, 1996; Johst and Wissel, 1997; Petchey et al., 1997; Halley and Iwasa, 1998; Cuddington and Yodzis, 1999; Halley and Kunin, 1999; Heino et al., 2000; Ripa and Lundberg, 2000). Nevertheless, theoretical papers usually aim at finding generalities rather than solving specific real-life problems. Starting from simple models is completely legitimate with such strategic goals. However, sticking to simple models may also hide patterns that would be important when trying to apply the results to more concrete problems. Specifically, here we have observed that simplifying assumptions on population structure may qualitatively influence conclusions about the influence of coloured noise on extinction risk.

We have considered environmental noise that influences only reproductive success. In multi-stage life history models this assumption enables a “storage effect”: there are individuals unaffected by noise that can rescue population from extinction. Although sensitivity of age-classes to environmental variability may differ because of differences in habitat, behaviour or body size (Hellriegel, 2000; Benton et al., 2001; Coulson et al., 2001), this mechanism may not apply commonly. In future elaborations it would be valuable to study environmental noise that simultaneously influences several demographic parameters at different ages, with different correlations between the parameters — in order to have models that reflect better what likely happens in natural populations. However, transforming variability of observed environmental variables properly to variability in demographic rates is a complex problem (Laakso et al., 2001). Further, our approach relying only on simulations could be complemented with more analytical methods, e.g., utilizing elasticity analysis to study the sensitivity of dynamics to variations in demographic parameters (Grant and Benton, 2000; Caswell, 2001).

Analyses of extinction risk under coloured noise are complicated by the fact that variance of a time series of red noise increases with time. This is not true for white noise, which has a constant variance. Thus, choices of scaling the variance of noise and time scale used to score extinctions will influences the results. We have chosen to scale noise such that its variance is independent of its colour at the time scale used to score extinction risk. We acknowledge that this assumption may have influenced our conclusions. However, analysis of the effects of the time scales is beyond the scope of this paper. These issues are discussed by Halley and Kunin (1999) and Heino et al. (2000) in the context of unstructured population models.

Our results emphasize the need to take the population structure adequately into account when assessing importance of various factors modulating extinction risk, such as colour of environmental noise. Our results also warn against relying on too simple models ignoring population structure in population viability analysis, even when poor knowledge about population structure or stage-specific demographic parameters would seemingly warrant gross simplifications. Depending on the life history type and the strength of temporal correlation in the environment, extinction risk may vary drastically.

Appendix

We give here densities at the point equilibrium of deterministic population dynamics and the expressions for basic reproductive number (R_0, expected lifetime reproduction of offspring in absence of density dependence) that were used to standardize the population size and effective reproductive capacity of the life histories being compared. The point equilibrium was mostly unstable if density dependence was strong (b = 1); in such cases the equilibrium densities still gave reasonable estimates of the average population sizes.

	Equilibrium density	Basic reproductive number
Annual	$N^* = k\ln(f)^{1/b}$	$R_0 = f$
Semelparous biennial	$N_1^* = ks^{-1}\ln(fs)^{1/b}$ $N_2^* = k\ln(fs)^{1/b}$	$R_0 = fs$
Iteroparous biennial	$N_1^* = k(1+s)^{-1}\ln(f_1 + f_2 s)^{1/b}$ $N_2^* = ks(1+s)^{-1}\ln(f_1 + f_2 s)^{1/b}$	$R_0 = f_1 + f_2 s$
Perennial	$N_1^* = \frac{1-s_2}{s_1} k \ln\left(\frac{fs_1}{1-s_2}\right)^{1/b}$ $N_2^* = k\ln\left(\frac{fs_1}{1-s_2}\right)^{1/b}$	$R_0 = fs_1/(1-s_2)$

References

Ariño, A., Pimm, S.L., 1995. On the nature of population extremes. Evolutionary Ecology 9, 429--443.

Benton, T.G., Lapsley, C.T., Beckerman, A.P., 2001. Population synchrony and environmental variation: an experimental demonstration. Ecology Letters 4, 236--243.

Boyce, M., 1992. Population viability analysis. Annual Review of Ecology and Systematics 23, 481--506.

Burgman, M.A., Ferson, S. Akçakaya, H.R., 1993. Risk Assessment in Conservation Biology. Chapman & Hall, London.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation, 2nd edn. Sinauer Associates, Sunderland MA.

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

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J., Grenfell, B.T., 2001. Age, sex, density, winter weather, and population crashes in Soya sheep. Science 292, 1528--1531.

Cuddington, K.M., Yodzis, P., 1999. Black noise and population persistence. Proceedings of the Royal Society of London Series B 266, 969--973.

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

Foley, P., 1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8, 124--137.

Ginzburg, L.R., Ferson, S., Akçakaya, H.R., 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. Conservation Biology 4, 63--70.

Grant, A., Benton, T.G., 2000. Elasticity analysis for density-dependent populations in stochastic environments. Ecology 81, 680--693.

Griebeler, E.M., Gottschalk, E., 2000. The influence of temperature model assumptions on the prognosis accuracy of extinction risk. Ecological Modelling 134, 343--356.

Halley, J.M., Iwasa, Y., 1998. Extinction rate of a population under both demographic and environmental stochasticity. Theoretical Population Biology 53, 1--15.

Halley, J.M., Kunin, W.E., 1999. Extinction risk and the $1/f$ family of noise models. Theoretical Population Biology 56, 215--230.

Heino, M., 1998. Noise colour, synchrony and extinctions in spatially structured populations. Oikos 83, 368--375.

Heino, M., Ripa, J., Kaitala, V., 2000. Extinction risk under coloured environmental noise. Ecography 23, 177--184.

Hellriegel, B., 2000. Single- or multistage regulation in complex life cycles: does it make a difference? Oikos 88, 239--249.

Johst, K., Wissel, C., 1997. Extinction risk in a temporally correlated fluctuating environment. Theoretical Population Biology 52, 91--100.

Jonsson, A., Ebenman, B., 2001. Are certain life histories particularly prone to local extinction? Journal of Theoretical Biology 209, 455--463.

Laakso, J., Kaitala, V., Ranta, E., 2001. How does environmental variation translate into biological processes? Oikos 92, 119--122.

Lawton, J.H., 1997. The science and non-science of conservation biology. Oikos 79, 3--5.

Lundberg, P., E. Ranta, J. Ripa, and V. Kaitala. 2000. Population variability in space and time. Trends in Ecology and Evolution **15**:460-464.

Mode, C.J., Jacobson, M.E., 1987a. A study of the impact of environmental stochasticity on extinction probabilities by Monte Carlo integration. Mathematical Biosciences 83, 105--125.

Mode, C.J., Jacobson, M.E., 1987b. On estimated critical population size for an endangered species in the presence of environmenatal stochasticcity. Mathematical Biosciences 85, 185--209.

Orzack, S.H., 1993. Life history evolution and population dynamics in variable environments: some insights from stochastic demography. In Adaptation in Stochastic Environments, eds. J. Yoshimura, C. Clark, pp. 63--104. Springer, Berlin.

Pascual, M.A., Kareiva, P., Hilborn, R., 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology 11, 966--976.

Petchey, O.L., Gonzalez, A., Wilson, H.B., 1997. Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. Proceedings of the Royal Society of London Series B 264, 1841--1847.

Pimm, S. L., Redfearn, A., 1988. The variability of animal populations. Nature 334, 613--614.

Ranta, E., Lundberg, P., Kaitala, V., Laakso, J., 2000. Visibility of the environmental noise modulating population dynamics. Proceedings of the Royal Society of London Series B 267, 1851--1856.

Ripa, J., Lundberg, P., 1996. Noise colour and the risk of populations extinctions. Proceedings of the Royal Society of London Series B 263, 1751--1753.

Ripa, J., Lundberg, P., 2000. The route to extinction in variable environments. Oikos 90, 89--96.

Root, K.V., 1998. Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. Ecological Applications 8, 854--865.

Roughgarden, J., 1975. A simple model for population dynamics in stochastic environments. The American Naturalist 109, 713--736.

Schroeder, M., 1991. Fractals, Chaos, Power Laws: Minutes from an Infinite Paradise. W. H. Freeman, New York.

Shaffer, M.L., 1990. Population viability analysis. Conservation Biology 4, 39--40.

Steele, J.H., 1985. A comparison of terrestrial and marine ecological systems. Nature 313, 355—358.

Wiegand, T., Naves, J., Stephan, T., Fernandez, A., 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. Ecological Monographs 68, 539--570.

Wissel, C, Stephan, T., Zaschke, S.-H., 1993. Modelling extinction and survival of small populations. In Minimum Viable Populations, ed. H. Remmert, pp. 67—103. Springer, Berlin.