



The role of density regulation in extinction processes and population viability analysis

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Abstract. We review the role of density dependence in the stochastic extinction of populations and the role density dependence has played in population viability analysis (PVA) case studies. In total, 32 approaches have been used to model density regulation in theoretical or applied extinction models, 29 of them are mathematical functions of density dependence, and one approach uses empirical relationships between density and survival, reproduction, or growth rates. In addition, quasi-extinction levels are sometimes applied as a substitute for density dependence at low population size. Density dependence further has been modelled *via* explicit individual spacing behaviour and/or dispersal. We briefly summarise the features of density dependence available in standard PVA software, provide summary statistics about the use of density dependence in PVA case studies, and discuss the effects of density dependence on extinction probability. The introduction of an upper limit for population size has the effect that the probability of ultimate extinction becomes 1. Mean time to extinction increases with carrying capacity if populations start at high density, but carrying capacity often does not have any effect if populations start at low numbers. In contrast, the Allee effect is usually strong when populations start at low densities but has only a limited influence on persistence when populations start at high numbers. Contrary to previous opinions, other forms of density dependence may lead to increased or decreased persistence, depending on the type and strength of density dependence, the degree of environmental variability, and the growth rate. Furthermore, effects may be reversed for different quasi-extinction levels, making the use of arbitrary quasi-extinction levels problematic. Few systematic comparisons of the effects on persistence between different models of density dependence are available. These effects can be strikingly different among models. Our understanding of the effects of density dependence on extinction of metapopulations is rudimentary, but even opposite effects of density dependence can occur when metapopulations and single populations are contrasted. We argue that spatially explicit models hold particular promise for analysing the effects of density dependence on population viability provided a good knowledge of the biology of the species under consideration exists. Since the results of PVAs may critically depend on the way density dependence is modelled, combined efforts to advance statistical methods, field sampling, and modelling are urgently needed to elucidate the relationships between density, vital rates, and extinction probability.

Key words: Allee effect, Ceiling carrying capacity, Density dependence, Extinction, Population viability analysis, Software, Spatially explicit models, Stochastic population models

Introduction

Extinction of populations is of prime evolutionary and conservation interest and stochasticity is a decisive factor in the survival or extinction of populations (e.g., Goel and Richter-Dyn 1974; Goodman 1987a,b). Not surprisingly, theoretical research on stochastic extinction of populations and the application of stochastic models for population viability analysis (PVA) have become very popular within the last two decades (e.g., Leigh 1981; Soulé 1987; Lande and Orzack 1988; Hanski and Gilpin 1991; Mace and Lande 1991; Burgman et al. 1993; Wissel et al. 1994; Settele et al. 1996; Drechsler et al. 1998; Amler et al. 1999). The popularity of the PVA approach in conservation biology is reflected in the availability of several software packages and reviews (e.g., Goel and Richter-Dyn 1974; Akçakaya and Ferson 1990; Boyce 1992; Lacy 1993; Lindenmayer et al. 1995; Oostermeijer et al. 1996; Reich and Grimm 1996; Groom and Pascual 1997; Beissinger and Westphal 1998). Despite this attention, PVA as a practical tool for conservation management is not without its critics and has been the subject of a lively debate in the recent literature (e.g., Caughley 1994; Doak and Mills 1994; Hedrick et al. 1996; Beissinger and Westphal 1998; Asquith 2001).

Like stochasticity, density regulation can play a driving role in population dynamics as has been documented in a vast literature (e.g., May and Oster 1976; Dennis 1989a; Hanski 1990; Burgman et al. 1993; Dennis and Taper 1994). Opinions about the relevance of density regulation still diverge considerably, ranging from those believing that it is a ubiquitous and crucial element of population growth (e.g., Dennis and Patil 1984; Ferson et al. 1989; Dennis and Taper 1994; Grant and Benton 2000) to those that doubt its relevance (e.g., Andrewartha and Birch 1984; Foley 1994). There is similar disagreement about its relevance for PVAs [e.g., Ginzburg et al. (1982, 1990) and Foley (1994) contra Burgman et al. (1993) and Groom and Pascual (1997)]. Although some authors have compared the effects of different models of density regulation on population persistence (e.g., Gabriel and Bürger 1992; Wissel et al. 1994; Mills et al. 1996; Pascual et al. 1997), no comprehensive comparison or review exists as yet. Our aim is to provide such a review.

Scope and basis of the review

We summarise the types of density dependence included in extinction models and their availability in generic software. We review the effects of different

types of density regulation as used in extinction models and PVA case studies. We restrict our review to stochastic models, since population fluctuations inherently contain stochastic components often with significant influence on the persistence of populations (e.g., Goodman 1987a,b). We specifically include density regulation by spatial structuring of populations due to social behaviour and limited dispersal, since this can be a major mechanism for density effects (Allee et al. 1949). We do not consider spatial structure in the form of a metapopulation unless density regulation is explicitly addressed.

We base our review on an extensive reference collection of PVAs, stochastic extinction models, and density dependence. In addition we searched the 1996–2001 issues of the journals *Conservation Biology*, *Journal of Applied Animal Ecology*, *Journal of Wildlife Management*, and *Verhandlungen der Gesellschaft für Ökologie* for relevant publications and conducted a keyword search with ‘population viability analysis’, ‘extinction’, and ‘stochastic models’ in the BIOSIS database for the year 2000. We further tried to trace any citation that appeared to be relevant for our topic.

Density regulation in extinction models and PVAs

Four main approaches to including density dependence in extinction models can be identified: the use of empirical data, the use of a quasi-extinction level as a surrogate for an Allee effect, the description of density dependence by a mathematical function, and the modelling of the spacing behaviour of individuals. When using empirical data, a value for a demographic parameter is drawn at random from observed values for a particular density (population size) (e.g., Shaffer 1983; Armbruster and Lande 1993; Burgman et al. 1993). Obviously, this approach requires intensive data and can be applied only in simulation models. Often it has been assumed that the use of a quasi-extinction level $N > 1$ will account for an Allee effect (e.g., Ginzburg et al. 1982; Dennis et al. 1991; Akçakaya et al. 1995). Quasi-extinction level means that a population is considered extinct once it reaches or falls below that level. However, the use of a quasi-extinction level is dictated by the model structure (Ginzburg et al. 1982; Dennis et al. 1991) rather than by a consideration of biological processes, and levels are often set arbitrarily.

Decisions on how to model density dependence by a mathematical function are complicated. The researcher not only has to specify which function to use in the first place, but also has to choose whether the total population size or the size of one or several particular stages control the feedback mechanism to be modelled. Furthermore, one has to decide whether all or only particular stages are affected by density regulation and which demographic process (e.g., birth rate) will be density dependent.

Description of density dependence by a mathematical function is achieved by making the population growth rate (r) or any other demographic parameter a function of density dependence, usually by multiplying the demographic parameter with a density-dependent term, $f(N)$ (see Appendix A). Many functions that have been used to describe density regulation are mathematical generalisations or limiting cases of other functions for particular parameter values. We consider functions to be separate whenever they had been used as independent models of density regulation in the analysis of population extinction. Some authors have replaced the shape parameters of some models by driving or constraining variables, such as rainfall or food availability. Here, we do not regard them as separate models. Likewise, some models combine two different density-dependent terms (e.g., Jacobs 1984; Dennis 1989a). Again, these are not listed as separate models unless they form a fixed combination in widely available software.

A bewildering range of functions has been used in the literature to describe density regulation, 29 of them in stochastic extinction models (Table 1). Functions differ greatly in their flexibility and ability to describe density-dependent population processes (e.g., Bellows 1981; Schnute 1985; Dennis and Taper 1994). Most ideas have been driven more by mathematical tractability than by a thorough testing of the matching of the models with real data or derivation from biological processes (Dennis 1989b). Moreover, no statistically rigorous method exists to test between, and to select among, different models of density dependence (Dennis 1989a,b; Dennis and Taper 1994; but see Berryman and Turchin 2001).

In Appendix A, we briefly discuss biological assumptions and mathematical relationships of the density-dependent terms listed in Table 1. For ease of cross-referencing among the text and the tables and because several models lack names and others occasionally are labelled with the same name in the literature though they differ mathematically, we label different models of density dependence by numbers (#).

A recent alternative to the use of functions of density dependence is the explicit modelling of density effects of spatial structure on individuals for dispersal limited species (e.g., Lamberson et al. 1992; Lecomte et al. 1994; Ginsberg et al. 1995; Wiegand et al. 2001). Individual-based spatial models track the fate of each individual based on (empirically derived) biological rules on spacing behaviour and/or dispersal. Differences in survival, reproduction, and/or dispersal of different individuals due to local population structure (e.g., size, location, and occupancy of territories) lead to density regulation in these models. This approach drops the assumption of ideal mixing of individuals of a population, which is important for reproduction at low population sizes (Allee et al. 1949; McCarthy 1997; Stephens et al. 1999). In some metapopulation models the location of the subpopulations is spatially

Table 1. Summary of density-dependent terms $[f(N)]$ used in stochastic population extinction models (see Appendix A for details).^a

#	Type	$f(N)$	Description	Authors
1a	TC	For $N < K$: 1; for $N = K$: 0	Density-independent growth to a ceiling carrying capacity	MacArthur and Wilson (1967), Goel and Richter-Dyn (1974), Wissel et al. (1994)
1b	TD	For $N < K$: 1; for $N = K$: λ^{-1}	Density-independent growth to a ceiling carrying capacity	Goel and Richter-Dyn (1974), Dennis et al. (1991), Foley (1994), Wissel et al. (1994)
2	TD	For $N \leq K$: 1; for $N > K$: 1 (for K mature females); a ($0 < a < 1$) (for $N - K$ mature females)	Density independence below K and reduced probability of breeding for females in excess of female K	Beier (1993)
3	TD	For $N < K - d$: $1 + \frac{b}{\phi}$ (with $-\phi \leq b \leq 1 - \phi$); for $K - d \leq N \leq K + e$: 1; for $N > K + e$: $1 - \frac{c}{\phi}$ (with $0 < c \leq \phi$)	Model with a step function of survival; note that negative values of b result in an Allee effect	Harris et al. (1989)
4a	TC, TD	$1 - \left(\frac{N}{K}\right)$	Logistic growth model with a ceiling carrying capacity	Strebel (1985), Dennis (1989a,b)
4b	TC, TD	$1 - \left(\frac{N}{K}\right)^\theta$	θ -Logistic growth model	Strebel (1985), Dennis (1989a,b)

Table 1. (continued)

#	Type	$f(N)$	Description	Authors
4c	TC, TD	$1 - f\left(\frac{N}{K}\right)^\theta$ (with $0 < f \leq 1$)	Generalised θ -logistic model for survival or fecundity	Boyce et al. (1994)
5	TD	$\frac{1}{1 + xN}$ (with $x = \frac{\lambda - 1}{K}$)	Beverton–Holt model	Beverton and Holt (1957), Schnute (1985), Ferson et al. (1989)
6	TD	e^{-xN} (with $x = \frac{\lambda - 1}{K}$)	Ricker model	Ricker (1975), Ginzburg et al. (1990)
7	TD	$\frac{1}{(1 + xN)^\beta}$ (with $x = \frac{\lambda^{1/\beta} - 1}{K}$)	Classical contest ($\beta = 1$)/scramble ($\beta > 1$) competition model	Hassell et al. (1976), Gabriel and Bürger (1992)
8	TD	$\frac{1}{1 + (xN)^\beta}$ (with $x = \frac{(\lambda - 1)^{1/\beta}}{K}$)	Maynard-Smith and Slatkin contest/ scramble competition model	Maynard-Smith and Slatkin (1973), Poethke et al. (1996a,b)
9	TD	$e^{-a_0 - a_1 N}$	Ricker equation (logistic growth model without a ceiling carrying capacity)	Dennis et al. (1991), Dennis and Taper (1994), Berryman and Turchin (2001)
10	TD	$e^{-a_0 - a_1 e^{g/N}}$	Double exponential model relating population growth to the ratio of the environmental variable g and N	McCarthy (1996b)
11a	TD	For $N \leq N_{tr}$: 1; for $N \geq N_{tr}$: $\left(\frac{N_{tr}}{N}\right)^\alpha$ (with $\alpha > 0$)	Power model of contest/scramble competition above a threshold	Stelter (1997, 1998)

11b	TD	For $N \leq N_{tr}$: 1; for $N \geq N_{tr}$: $1 + \frac{h}{DIEP} \left(\frac{N}{N_{tr}} \right)^\alpha$ (with $\alpha > 0$)	Power model of density-dependent emigration probability above a threshold	Stelter (1997, 1998)
12	TD	For $N \leq N_{tr}$: 1; for $N_{tr} < N < K$: $\left(1 - \frac{1}{\phi} \gamma \frac{(1 - N_{tr}/N)}{(1 - N_{tr}/K)} \right)$ for $N \geq K$: $\left(\frac{K}{N} - \frac{1}{\phi} \gamma \frac{(1 - N_{tr}/N)}{(1 - N_{tr}/K)} \right)$	Threshold model of scramble competition with additional contest competition above K	Drechsler et al. (1998)
13	TD	$\left(\frac{K}{N} \right)^\delta$ (constrained within $\phi_{min} \leq \phi \left(\frac{K}{N} \right)^\delta \leq \phi_{max}$)	Power model for survival with a 'baseline' survival at carrying capacity K	Beier (1993)
14	TD	$i + \frac{jk}{IN + k}$	Extension of Michaelis-Menten model	Mills et al. (1996), Pascual et al. (1997)
15a	TD	$[m(1 + e^{-a_0 - a_1 N})^{-1} + q]^x$ (with $ x = 1$);	Sigmoidal demographic rates multiplier	Swart and Lawes (1996)
15b	TD	$[1 + e^{-a_0 - a_1 N}]^{-1}$	Sigmoidal establishment multiplier	Chapman et al. (1989)
16	TD	$u + \frac{v}{1 + (N/K)^\varepsilon}$ (for $u, v > 0$ and ε integer)	Sigmoidal density dependence of the growth rate	Milton and Bélair (1990)
17a	TD	$a_4 N^4 + a_3 N^3 + a_2 N^2 + a_1 N + a_0$	Fourth-order polynomial growth model	Lacy (1993)
17b	TD	$a_2 N^2 + a_1 N + a_0$	Quadratic regression model	Nolet and Baveco (1996)
17c ₁	TD	$a_1 N + a_0$	Linear regression model	Shaffer (1983)

Table 1. (continued)

#	Type	$f(N)$	Description	Authors
17c ₂	TD	$a_1 N + a_0$ (for $N \leq K$); $a_1 K + a_0$ (for $N > K$)	Linear regression model with density independence once all territories are filled	Gaona et al. (1998)
17d	TD	a_0 (with $0 < a_0 < 1$ for $N_{t+1} > yK$; $a_0 = 1$ for $N_{t+1} \leq yK$; $y < 1$)	Reduction of population size by a constant factor if population size exceeds a threshold	Den Boer (1981)
18	TD	$1 + (\lambda - 1)(1 - N/K)$ (for $N \leq K\lambda/(\lambda - 1)$) 0 (otherwise)	Model of overshooting populations that crash to extinction	Gabriel and Bürger (1992)
19	TC	$1 - e^{-\eta N}$	Allee model: negative exponential	Dennis (1989a)
20	TC, TD	$\frac{N}{z + N}$	Allee model: rectangular hyperbola (z is the density at which half of the females mate)	Dennis (1989a), Burgman et al. (1994)
21	TD	$\frac{\langle A_{\min}(BN_m, N_f) \rangle}{N_f}$ (with $0 < A \leq 1$)	Male limited reproduction of females; $\langle x \rangle$ means integer value of x	Milner-Gulland (1997), Legendre (1999)
22	TD	$\frac{N_m}{K_m}(1 + \text{HRI})^{K_m - N_m}$ (with $N_m < K_m$)	Allee effect accounting for a compensatory expansion of male territories	Beier (1993)
23	TD	$1 - x^{-1} \frac{\text{SR}_O}{\text{SR}_N}$ (with $\text{SR}_O < \text{SR}_N$; $x = \mu, \phi$)	Model of disturbed mating systems in exploited harem species	Milner-Gulland (1997)

24	TD	$1 - (1 - s_a/s_t)^{n_s}$	Mate or territory encounter probability in a polygamous mating system	Lande (1987, 1988), Lamberson et al. (1992), Stephan and Wissel (1994), Wissel et al. (1994)
25	TD	$\left(\frac{N}{K}\right)^\varphi$	Probability of a vacant nest site becoming occupied	Andersen and Mahato (1995)
26	TD	$1 + \frac{CD}{r_0} \frac{N}{D + N}$	Allee effect: Jacobs' cooperation model	Jacobs (1984), Wissel et al. (1994)
27	TD	$\left\{1 - \left[\frac{(P_0 - P_K)}{P_0} \left(\frac{N}{K}\right)^\theta\right]\right\} \frac{N}{z + N}$	VORTEX model of breeding probability	Reed et al. (1998)
28	TD	$\frac{EN}{z + N}$ (with $E < 1$)	Density-dependent emigration model	Reddingius and den Boer (1970)
29	TD	$\frac{w_j/(n_j + 1)}{\sum_j w_j/(n_j + 1)}$	Density-dependent weighing function for the fraction of immigrants received by subpopulation j	Reddingius and den Boer (1970)

^a# is the model number used for cross-referencing throughout this publication. Type is time continuous (TC) or time discrete model (TD). DIEP: density-independent component of emigration probability; HRI: % home range increase of territorial males; K : carrying capacity, K_m : carrying capacity for adult males; n_j : number of individuals in subpopulation j ; n_s : number of sites searched; N : population size, $N_{f/m}$: number of (reproducing) females/(harem holding) males, N_{tr} : threshold population size, P_x : probability of breeding at a density close to x individuals with x either 0 or K , r_0 : intrinsic rate of increase at a population size close to zero, s_a : number of suitable unoccupied sites, s_t : total number of sites; SR_O : observed sex ratio; SR_N : 'normal' sex ratio in the absence of selective harvesting; w_j : weighing factor for subpopulation j ; C : effectivity of co-operation, D : saturation index, λ : finite rate of increase, μ : recruitment rate, ϕ : survival rate. The remaining parameters ($a, \dots, m, o, p, q, s, \dots, v, y, z, A, B, E, a_0, \dots, a_4; \alpha, \beta, \gamma, \delta, \varepsilon, \varphi, \eta, \theta$) are shape parameters. The Greek parameters specify strength of density regulation. See text for further explanations.

explicit but spatial structure is ignored in the subpopulations. We did not include them in the tally of models with explicit spatial structure accounting for density dependency, because the presence of interactions of spatial structure and density have been ignored in the metapopulation literature so far (see the Results section on metapopulations).

With the increasing popularity of PVAs, an increasing number of standard software packages have become available for routine PVA application. Software packages can diverge considerably in viability predictions for the same data set because of different ways in which stochastic variation in breeding structure (Brook et al. 1999) or density dependence (Mills et al. 1996) are incorporated in the underlying models. Therefore, in Table 2, we briefly summarise which forms of density dependence can be modelled with these software packages.

Summary statistics of density dependence used in PVA case studies

We analysed the characteristics of the PVA literature such as taxonomic groups investigated, or forms of density regulation used based on 219 published PVA case studies (see [http://www.ufz.de/\(en\)/spb/nat/](http://www.ufz.de/(en)/spb/nat/) for references and a comprehensive table). We included any paper that explicitly modelled population extinction for a particular species based on real data but limited our analyses to stochastic models. Frequently, authors have published several papers on PVAs of the same population/species. These were regarded as the same case study save for cases where model features changed (different software, different type of model, density dependence added in later publications). However, if several models were compared for one population in one publication, the publication was regarded as one case study but the models scored separately. The application of the same model to two or more species within the same publication was treated as two or more case studies.

The majority of case studies were made for mammals ($n = 91$) and birds ($n = 70$), followed by insects ($n = 25$) and plants ($n = 15$). PVAs for other taxonomic groups are rare (reptiles: $n = 8$, amphibians: $n = 4$, fish: $n = 4$, snails: $n = 2$). Density regulation has been included in 68% of the 247 models used in PVA case studies, 25% of them lacked any form of density dependence, and in 7% it is not stated whether density dependence had been included or not. The percentage of case studies that did not include density dependence was highest in 1991/1992 and lowest in 1993/1994. However, the temporal difference in the percentage of publications that incorporated some form of density dependence is not significant (Figure 1; $\chi_6^2 = 9.06$, $\alpha = 0.17$). Nevertheless there is a highly significant heterogeneity regarding the frequency of models with density dependence that included only a ceiling K or a more complex form of density dependence ($\chi_6^2 = 19.30$, $\alpha = 0.004$) with

Table 2. Types of density dependence incorporated in standard software.^a

Name	Model type	Density model (#)	Comments	Source
ALEX	Matrix; mp; p	1; ddd; probability of catastrophes can be density dependent	No breeding at K ; surplus individuals removed preferentially from younger age classes; density threshold for dispersal	Possingham et al. (1992), Lindenmayer et al. (1995), Possingham and Davies (1995)
GAPPS	Individual; p	User defined functions; models #1, 25, 28, 29 cannot be implemented		Mills et al. (1996), Brook et al. (1999)
META-X	Markov model; mp	Depending on external model used for sub-populations; models #1, 25, 28, 29, ddd cannot be implemented	Dynamics within sub-populations not modelled, but can use results from any external simulation model for subpopulation dynamics as input	Frank et al. (2003)
RAMAS	Matrix; mp; p	1, 4, 5, 6, 13, 19, ddd, od	K can vary stochastically; ddd only in RAMAS/GIS and RAMAS/space	Akçakaya and Ferson (1990), Akçakaya and Ginzburg (1991), Akçakaya (1992), Akçakaya et al. (1995)

Table 2. (continued)

Name	Model type	Density model (#)	Comments	Source
ULM	Matrix; p	User defined functions; models # 25, 28, 29 cannot be implemented	Software for matrix projections in which the matrix entries can be made functions of density	Legendre and Clobert (1995), Legendre (1999)
VORTEX	Individual; mp; p	User defined functions; models # 25, 28, 29 cannot be implemented; ddd	K can increase, decrease, and fluctuate stochastically; model # 27 implemented only in recent versions; dispersal above a density threshold but percentage dispersing density-independent	Lacy (1993, 2000), Lindenmayer et al. (1995, 2000), Reed et al. (1998)

^a Please note that additional options not described in the source cited may be available in more recent releases. Density model refers to the models listed in Table 1. ddd: threshold or unspecified density-dependent dispersal; K : carrying capacity; mp: metapopulation; od: observed distribution; p: single population.

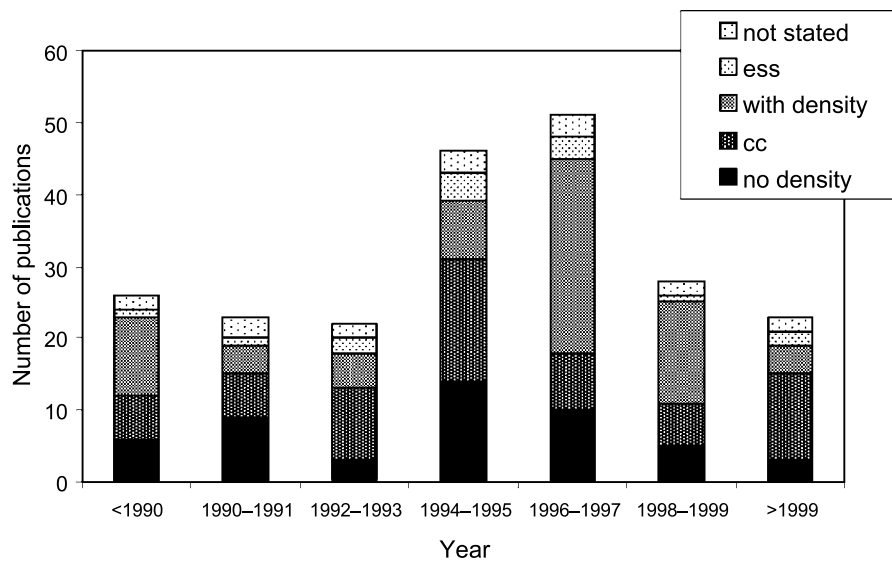


Figure 1. Temporal trend in the incorporation of density dependence in PVA publications. cc: density regulation in the form of a ceiling carrying capacity; ess: explicit spatial structure causing density dependence; no density: no form of density dependence included; with density: any other form of density regulation except for cc, ess, and density-dependent dispersal.

1996/1997 and 1998/1999 showing a strong preponderance of models with more complex forms of density dependence. These trends tend to indicate that the suggestion of Ginzburg et al. (1990) that models with density dependence result in conservative estimates of vulnerability, and later publications (e.g., Burgman et al. 1993; Mills et al. 1996; Groom and Pascual 1997) drawing attention to the importance of including density dependence in modelling population extinction may have had a mild influence on whether and how density dependence was included in published PVA models by later authors.

In total, 32 approaches have been used to model density regulation in theoretical or applied extinction models; 29 of them are mathematical functions of density dependence. Eight of the latter have been used only in theoretical extinction models. Model #1 (density-independent growth to a ceiling carrying capacity) was the most frequently used model in PVA case studies that incorporated density dependence. It accounted for 44% of the 205 density dependencies used, followed by the logistic growth model (model #4) with 8% and spatially explicit models with 7% (Table 3). The remaining approaches have been used only rarely. Only 13% of the 150 models that were based on mathematical functions of density dependence (density-dependent dispersal excluded) included an Allee effect. If only PVAs for re-introduction strategies or captive populations are considered ($n = 26$), 23% of the case studies accounted for an Allee effect and in 8% it is not clear.

Table 3. Summary of the use of different types of density dependence in PVA case studies.^a

Model number (#)	No. of case studies
1	91
2	1
3	1
4	17
5	11
6	5
7	1
9	9
10	1
11	3
12	1
14	1
15	3
17	7
20	1
21	9
22	1
23	1
24	3
25	1
27	4
Population extinct at K	2
Unspecified	4
ddd	9
ess	15
od	3
Unclear	17
None	62

^a Some case studies used different models for different demographic parameters. Model number refers to the models listed in Table 1. K : carrying capacity; ddd: threshold or unspecified density-dependent dispersal; ess: explicit spatial structure causing density regulation; od: observed distribution.

When does density dependence matter?

In the following sections we review the effects of density dependence on extinction probability of single populations and metapopulations and we

discuss the implications for PVAs. We present the review in the following order: effects of a ceiling carrying capacity, effects of a decrease of vital rates with density, Allee effects, effects of spatial structure, and stage-specific differences in density dependence.

Single populations

Density-independent growth to a ceiling carrying capacity

Introducing an upper limit for population size reduces persistence chances (Shaffer 1983) and the probability of ultimate extinction becomes 1 (Middleton et al. 1995). A constant ceiling carrying capacity leads to an upward or downward concave increase of mean time to extinction with carrying capacity (e.g., Belovsky 1987; Gabriel and Bürger 1992; Stephan and Wissel 1994; Wissel et al. 1994; Ginsberg et al. 1995). Shaffer (1987) suggested that the shape of the curve is indicative of the types of stochastic variability included in the model. According to Shaffer (1987) demographic stochasticity leads to an upward concave, demographic combined with environmental stochasticity to a linear, and the combination of demographic, environmental, and catastrophic stochasticity to a downward concave increase of mean time to extinction (T_m) with carrying capacity (K). Shaffer's (1987) results are still frequently cited (cf. Loeschcke 1990; Possingham et al. 2001). However, they were based on a limited number of studies in Soulé (1987), and Lande (1993) showed that they are not always correct.

Lande (1993) points out that previously reported differences can be understood based on the mean and the variance of the long-term population growth rate r . T_m exhibits an upward concave relationship to K if \bar{r} is larger than half its variance (σ^2) (Ludwig 1976; Goodman 1987a; Lande 1993; Wissel et al. 1994). Otherwise, T_m curves downwards with K unless the correlation time of the environment is high. In the latter case, there is an upward concave relationship even under very high environmental fluctuation (Wissel et al. 1994). However, with a negative average growth rate, T_m is always proportional to the logarithm of K independent of the degree of environmental stochasticity (Ludwig 1976; Lande 1993). T_m scales with the square of $\ln K$ for zero average growth rate (Lande 1993). Thus, different degrees of environmental stochasticity and growth rates explain why carrying capacity and mean time to extinction show different relationships in PVA case studies [e.g., compare Hildenbrandt et al. (1995) and Woolfenden and Fitzpatrick (1993) with Marmontel et al. (1997)].

Qualitatively similar results apply when K fluctuates stochastically (Foley 1994). Small stochastic fluctuations of K may not influence extinction risk but if the standard deviation of K is $>30\%$ of K , there is a rapid reduction in persistence probability (Reed et al. 1998). This result is not surprising,

since K is frequently close to zero under this condition. However, cycles of a deterministically fluctuating carrying capacity can increase population persistence slightly to considerably, as has been shown by Lindenmayer and Possingham (1994) for the survival of a metapopulation of Leadbeater's possum (*Gymnobelideus leadbeateri*) under various scenarios for the length of logging rotation times.

The effect of a ceiling carrying capacity also depends on the starting conditions. An influence is present for populations starting from values close to K but not for populations starting from low values (Middleton et al. 1995; Akçakaya and Baur 1996; Ludwig 1996; Marshall and Edwards-Jones 1998). Thus, the low starting size can explain why the introduction of a ceiling carrying capacity did not decrease median persistence time for the acorn woodpecker (*Melanerpes formicivorus*) (Stacey and Taper 1992), whereas such an effect was present in a simulation of the Lord Howe Island woodhen (*Tricholimnas sylvestris*) population that started from high values (Brook et al. 1997). Similarly, an increase in K did not increase the probability of survival of the Puerto Rican parrot (*Amazona vittata*) (Lacy et al. 1989) or the whooping crane (*Grus americana*) (Mirande et al. 1991) when populations were started well below K . When models of re-introduced populations of wild boar (*Sus scrofa*) were started at half K and K was small enough to make most populations go extinct within a short time period, an increase of K (without increasing the number of released animals) considerably reduced the probability of extinction (Howells and Edwards-Jones 1997).

The absence of an effect of K when starting from a small population size can be explained by a high initial extinction risk so that carrying capacity can exert an effect only on a limited number of population trajectories (cf. Wissel et al. 1994). For low environmental stochasticity, there is a critical population size below which the probability of extinction is very high and above which the probability of reaching K is high. This probability depends on the ratio of the death and birth rates (Wissel et al. 1994). Under high environmental stochasticity there is always a considerable risk of extinction before reaching K (Wissel et al. 1994).

Increasing reduction of vital rates with increasing density

Ferson et al. (1989) and Ginzburg et al. (1990) observed higher extinction risks in models of density-independent fish recruitment when compared to the Ricker (#6) and Beverton–Holt (#5) functions of density dependence. They hypothesised that density-independent models are always conservative. However, this hypothesis is not generally true. It was supported for the power model of survival (#18) when applied to cougars (*Felis concolor*) (Beier 1993), for the Maynard-Smith and Slatkin model (#8) applied to insect

populations (Poethke et al. 1996b), for the Beverton–Holt model (#5) applied to the California gnatcatcher (*Polioptila californica*) (Akçakaya and Atwood 1997), and for the Ricker model (#6) applied to the checkerspot butterfly (*Euphydryas editha*) (Harrison et al. 1991). However, it was contradicted by an individual-based model of the territorial gecko *Oedura reticulata* (Wiegand et al. 2002) and for the linear logistic when applied to the checkerspot butterfly (*E. editha*) (Harrison et al. 1991). Stacey and Taper (1992), in contrast, reported supportive results for the linear logistic and the θ -logistic model (#4a and b) when applied to the acorn woodpecker (*M. formicivorus*). However, they used a model code for their ‘density-independent’ model that introduced inversely density-dependent vital rates (Middleton and Nisbet 1997).

In other PVA case studies density dependence did not influence extinction probability (e.g., Nolet and Baveco 1996) or only marginally (e.g., Cross and Beissinger 2001). This is usually the case if a population starts well below carrying capacity (compare the previous section, but see *Allee effects and extinction probability*). Also, other processes may override any effects of density dependence and drive a population to extinction. This was the case in a PVA model for the marsh gentian (*Gentiana pneumonanthe*) (Oostermeijer 2000), which assumed a rapid decline in habitat quality due to succession.

The effect of density dependence on persistence probability depends on the strength of density dependence and its interaction with effects of the growth rate, carrying capacity, and stochasticity (Sæther et al. 1998) as well as on the function used. An increasing strength of density regulation increased the difference in extinction risk to the density-independent model in the θ -logistic, the Maynard-Smith and Slatkin, and the power function models (models #4b, 8, and 13: Stacey and Taper 1992; Middleton and Nisbet 1997; Beier 1993; Poethke et al. 1996b). The opposite was the case for the Beverton–Holt, Ricker, and the vacant territory occupation probability models (models #5, 6, and 25: Ferson et al. 1989; Ginzburg et al. 1990; Andersen and Mahato 1995).

If the reproductive rate is high, mean persistence times will be much shorter under strong compared to weak density dependence in the contest and scramble models #7 and #11a. The opposite is the case for low reproductive rates (Wissel et al. 1994; Stelter 1998). In contrast, there is only a small effect of the strength of density regulation on extinction probability in the θ -logistic model (#4b) under low growth rates and under growth rates that produce chaotic behaviour (Philippi et al. 1987).

Differences in persistence probability due to the introduction of density dependence further decrease with increasing variance in the growth rate in the linear logistic (#4a), θ -logistic (#4b), and the Maynard-Smith and Slatkin (#8) models (e.g., Goodman 1987a,b; Buckley and Downer 1992; Stacey and Taper 1992; Poethke 1996a,b). These observations most likely hold

generally true for any type of density dependence, because an increasing variance decreases persistence times and thus there is less opportunity for density dependence to exert a negative or positive influence on persistence.

A further factor complicating the effects of density dependence is the use of a quasi-extinction level. For example, in fish populations the extinction probability was higher for strong density regulation than for density independence under high quasi-extinction levels, whereas the opposite was true for low quasi-extinction levels (Ginzburg et al. 1990). The same relationship occurred for single populations of terns, but neither for metapopulations of terns nor for cormorants or albatrosses (Buckley and Downer 1992). These results caution against the use of arbitrary quasi-extinction levels for conservative risk estimation.

Moreover, different approaches to model density dependence can lead to vastly differing estimates of persistence times and may even result in qualitatively different conclusions. The few comparisons of the effects of different types of density dependence on extinction probabilities currently available show inconsistent results for some models of density dependence, as described below.

Models with density-independent growth to a ceiling carrying capacity (#1) predict marginally to several orders of magnitude higher persistence times than models that use the linear (#4a) or the θ -logistic (#4b) model (Richter-Dyn and Goel 1972; Leigh 1981). The difference increases with K and decreases with the strength of environmental stochasticity, σ (Wissel et al. 1994). These results are expected, since an increase in K and a decrease in σ increases the difference in opportunities for density dependence to act in the two models. Therefore, lower persistence times compared to density-independent growth to a ceiling K most likely hold generally for other models of density regulation that cause a reduction of the growth rate already well below K and thus keep the population consistently at lower sizes. However, the more optimistic prediction of model #1 does not hold for decreasing populations, that is, for populations with a negative growth rate (cf. Mills et al. 1996). We expect that the differences to model #1 are also small for models with weak density regulation that acts only once a population is close to carrying capacity.

Milton and Bélairs (1990) argued that populations in which density regulation produces a hump with a tail when N_{t+1} is plotted against N_t , such as model #16, have a lower risk of extinction than populations whose density regulation produces only one extremum, such as the linear logistic (#4a). This issue needs further exploration across a range of those model parameters that interact in determining extinction probability, such as growth rate, strength of environmental stochasticity, and strength of density dependence. For example, Gabriel and Bürger (1992) showed for models #4b, 7, and 18 that

the difference among model predictions depended on the growth rate and the strength of demographic stochasticity. Furthermore, the strength of density dependence changed the relationship between growth rate and mean time to extinction among and within models.

When comparing the Ricker equation (#9) and the double exponential model (#10) applied to red kangaroos (*Macropus rufus*) with and without harvest, McCarthy (1996b) obtained similar extinction risks for both models. Likewise, the Ricker (#6) and the linear logistic (#4a) model of density regulation gave similar quasi-extinction profiles for the Serengeti wildebeest (*Connochaetus taurinus*) (Pascual et al. 1997). These profiles were much higher than those resulting from the use of the Beverton–Holt (#5) and the Michaelis–Menten (#14) form of density regulation. However, Harrison et al. (1991) and Burgman et al. (1993) reported strikingly different results when contrasting the Ricker (#6) and the linear logistic (#4a) model for the checkerspot butterfly (*E. editha*) and the white-toothed shrew (*Crocidura russula*), respectively. In both cases, the former model predicted a low risk of extinction, whereas the latter predicted a high risk. Furthermore, though the Beverton–Holt (#5) and the Michaelis–Menten (#14) model gave similar predictions for the case of non-harvest of the Serengeti wildebeest, the former model resulted in a comparably much higher increase of quasi-extinction probabilities when 6% annual harvest was included. In contrast to these two models, the linear logistic and the Ricker model suggested only minor changes in extinction probability with harvest in *C. taurinus* (Pascual et al. 1997) and in *E. editha* (Harrison et al. 1991), respectively. This peculiar result arises because harvest reduces the likelihood of occurrence of extremely high populations and thereby mitigates overcompensatory population crashes that are characteristic of the logistic and Ricker model of density dependence. We expect similar results for other models that can show overcompensatory population crashes.

To summarise, the strength of environmental variability, the growth rate, the strength of density dependence as well as the quasi-extinction level used and, for some models, the starting conditions all interact in determining extinction probability such that excluding density dependence from a PVA model may cause an increase, decrease, or no change in extinction probability compared with models that include density dependence. Furthermore, different types of density dependence may not only produce vast differences in quantitative predictions but may also lead to qualitatively different ones. Disturbingly, differences among two types of density regulation are inconsistent. Thus, PVA case studies lacking extremely good data must investigate a series of scenarios of density dependence appropriate to the species under investigation in order to understand the role of density dependence and to select an appropriate model in the case investigated (cf. Pascual et al. 1997).

Allee effects and extinction probability

Comparably few theoretical treatments have addressed an Allee effect in the study of population extinction (e.g., Lande 1987; Dennis 1989a; Stephan and Wissel 1994; Wissel et al. 1994). These studies observed the existence of an extinction threshold – called ‘critical density’ N_c by Dennis (1989a). Above N_c , populations grow fast towards K . Below N_c , r will become negative and populations decline rapidly to extinction. In the latter case increasing K might be a futile conservation strategy for an endangered species. Indeed, N_c even increased with K in a spatially explicit territorial model of the wall lizard (*Podarcis muralis*) (Hildenbrandt et al. 1995). The transition between densities that cause high extinction risks due to an Allee effect and densities that allow high probability of viability was narrower for high compared to low K (Bender 1999). Even very low immigration rates (0.5 individuals/year) can lower N_c and increase the probability of persistence (Hildenbrandt et al. 1995). Once a population is beyond N_c , the probability of establishment (growth to K) is high except under high environmental variability or low maximum growth rates (Stephan and Wissel 1994; Wissel et al. 1994).

The theoretical results discussed above also explain discrepancies in the relative importance of an Allee effect between PVA case studies on small, introduced populations and those on established populations. Burgman et al. (1994) and Legendre (1999) obtained a large increase in extinction risk in small populations of Leadbeater’s possum (*G. leadbeateri*) and re-introduced bird populations, respectively, when including an Allee effect (models #20 and #21, respectively). In contrast, the extinction probability of an established isolated black-footed ferret (*Mustela nigripes*) population was unaltered by the inclusion of an Allee effect (model #3) (Harris et al. 1989). Likewise, Wiegand et al. (2002) found that the Allee effect made only a small contribution to extinction probability in a spatially explicit model of large gecko populations. They explained this result by suggesting that the Allee effect comes into play only after a population has drifted to low densities, at which extinction risk is already high without density effects.

The influence of an Allee effect on persistence probability also depends on the growth rate. The probability of establishment once the population is above the critical size is smaller for low than for high growth rates (Wissel et al. 1994). For example, in a model of the helmeted honeyeater (*Lichenostomus melanops cassidix*), an Allee effect caused by limited availability of mates (model #20) considerably reduced persistence probability after adjusting demographic parameters downward such that the finite rate of growth $\lambda = 1$ (McCarthy et al. 1994).

In conclusion, Allee effects should always be considered if populations start from low numbers such as in re-introduction programs, but it may or may not matter for organisms with a low growth rate whose populations are

well below K but above N_c . In any case, the Allee effect has only a minor influence on mean persistence time for large established populations.

Stage-specific differences in density regulation

A considerable number of animal species develop through stages with strikingly different ecologies. It is very likely that such stages show different types of density regulation (Dempster 1983; Duellman and Trueb 1986). Though some spatially explicit individual-based age-structured population models incorporate differences in density dependence for adults and subadults (e.g., Beier 1993; Hildenbrandt et al. 1995; Letcher et al. 1998; Wiegand et al. 2001, 2002), we have found only one study in which the effects of differences in density regulation during different life stages on persistence probability are explicitly analysed (Stelter 1997, 1998). Stelter's (1997, 1998) model of butterfly populations included density regulation among caterpillars caused by food plants leading to an increase in mortality, a decreased body condition, and a reduced fecundity after having metamorphosed into female butterflies. The model also included density regulation in female butterflies in the form of a reduced fecundity and increased probability of emigration.

Stelter (1997, 1998) used an unusual form of density regulation (model #11) which includes a sudden jump of *per capita* effects on demographic parameters just above a threshold value where density starts to act. Biologically, this is not the most plausible form of density regulation but his analyses do provide an important lesson. Effects of density regulation in the caterpillar and butterfly stages on population persistence can exhibit complex interactions. For example, there was compensation between density effects on females and those on caterpillars such that mean time to extinction was maximal at an intermediate threshold level for density effects on females. This results in a paradox for the management of butterfly populations: an increase of female resources (improved habitat quality) will compromise the viability of a population due to stronger density driven fluctuations in caterpillar numbers. The compensatory effect leading to the paradox vanishes if density effects on caterpillars do not transcend to fecundity in the adult stage of females. Under weaker (contest-like) competition ($\alpha \leq 1.5$), persistence reached a maximum if resources were limiting both for females and for caterpillars. The stage for which there is strongest (scramble-like; α largest) competition most strongly reduced mean time to extinction and thus its resources should be largest to maximise persistence.

Stelter (1998) further analysed the effects of differences in density-dependent mortality of early and late stages of caterpillars. In this model competition among females was absent and female fecundity was affected by density only when older larval stages were concerned. He demonstrated that if both larval stages show the same strength of density dependence,

then only the rarer resource needs to be accounted for. However, weak (contest) competition among young caterpillars can buffer fluctuations caused by strong (scramble) competition among older caterpillars and thus considerably increase mean persistence time.

Metapopulations

Very little is known about the effects of density dependence on the persistence of metapopulations. Contrary to what one may expect, the effects of density regulation in single populations on persistence probability do not simply carry over to metapopulations. The introduction of density dependence often shows opposite effects for isolated populations compared to metapopulations. In density-independent models with only demographic stochasticity (Järvinen 1982) there is no difference between a single population and a metapopulation because the fate of individuals is independent of their compatriots and thus they might as well be isolated from each other. Under the linear logistic model of density dependence, however, survival will be better for a single population than for a metapopulation of the same total size (Burkey 1989). This is caused by a portion of subpopulations being near their local growth limits and experiencing little or no growth, while the total population is still well below its carrying capacity.

When environmental stochasticity is introduced, metapopulations slightly or considerably outperform single populations (Buckley and Downer 1992; Frank et al. 1994). However, in models of seabirds, the introduction of logistic density dependence in dispersal, survival, and reproduction (model #4) eliminated (albatrosses and cormorants) or decreased (terns) the advantage in persistence chance of metapopulations compared to single populations (Buckley and Downer 1992). This was caused by a marginally (albatrosses and cormorants) or dramatically (terns) increased probability of extinction of metapopulations under density dependence.

In contrast to the above situations in which the introduction of density dependence increased the probability of extinction of metapopulations, density dependence has the opposite effect in the logistic model (#4) when the growth rate is high enough to produce chaos. Although low densities lead to more frequent extinctions at the local level, the decorrelating effect of chaotic oscillations reduces the degree of synchrony among subpopulations, allows effective recolonisation and thus reduces the likelihood that all are simultaneously extinguished (Allen et al. 1993). The survival advantage is caused by the desynchronisation of the dynamics of subpopulations that allow recolonisation of frequently extinct subpopulations. The protection afforded by chaos fails under low level of environmental stochasticity in the reproductive rate or if the migration rate is high.

The spatial structure of metapopulations by itself can modify and cause density effects. The relative size and degree of connectedness determines the relative influence of a subpopulation on metapopulation persistence (e.g., Frank and Wissel 1998; Frank 2004 (this issue)). Therefore density regulation in 'important' subpopulations should be more consequential for metapopulation survival than in less important subpopulations. Furthermore, clusters of close subpopulations do form density attractors concentrating individuals within them while releasing individuals more rarely to more isolated peripheral subpopulations (Gruber, in preparation) unless density-dependent dispersal balances this spatial position effect. These interactions of spatial structure with density regulation have not yet received any attention in the metapopulation literature.

It is well known that dispersal is density-dependent in a wide range of animals (reviewed by, e.g., Dobson 1982; Lomnicki 1988; Hansson 1991). However, only very limited information is available about the effects of density-dependent dispersal on metapopulation persistence. Neither Reddingius and den Boer (1970) (model #28 for emigration, model #29 for immigration) nor Stelter (1997, 1998) (model #11b for emigration) observed any marked effects of density dependence in dispersal on metapopulation persistence of beetles or butterflies, respectively. In contrast, Amarasekare (1998) showed that an Allee-like effect of a reduced colonisation probability at low patch occupancy in a modified Levins' (1969) metapopulation model increased the threshold fraction of occupied patches below which the metapopulation goes extinct. However, it is not clear why colonisation probability of an empty patch should be reduced beyond the effect caused by the lower availability of dispersing individuals if fewer patches are occupied. In any case, it remains to be explored how Allee effects in subpopulations translate into an effect on extinction probability of the metapopulation.

Density regulation by spatial structuring

Exclusive territories, individual spacing behaviour together with limited dispersal power are major mechanisms for density regulation in many animal populations (e.g., Lomnicki 1988; Hansson 1991; Letcher et al. 1998). Models #24 and #25 are based on such effects and, with recent advances in simulation techniques, individual-based models are increasingly developed to explore the relationship between an explicit spatial structure, density-dependent dispersal, and extinction probability.

Lande (1987, 1988) developed such a model for the survival of the spotted owl (*Strix occidentalis caurina*) in fragmented landscapes that was increasingly refined by Doak (1989), Lamberson et al. (1992, 1994), Carroll and Lamberson (1993), and McKelvey et al. (1993). In these models, unmated

owls move from site to site until they find an empty territory or a territory occupied by a single of the opposite sex. There is a maximum number of sites that a dispersing owl can explore before it dies, thus making dispersal dependent on population structure and density. The model produces an extinction threshold, that is, a minimum percentage of landscape that must be suitable to allow population persistence (Lande 1987). This threshold decreased with search efficiency – an increasing search efficiency means that density starts to come into play only at increasingly high levels. In the limiting case in which individuals can search all sites, the threshold vanishes.

The inclusion of survival costs for each dispersal attempt within or among clusters of suitable habitat did not alter the qualitative results (Carroll and Lamberson 1993; McKelvy et al. 1993; Lamberson et al. 1994). Size of habitat clusters, the percentage of suitable sites per cluster, the total number of searches (3–20), and its interaction with cluster sites were significantly lower for extinct than for persisting model populations. Persisting populations also had significantly lower dispersal costs than populations that went extinct (Lamberson et al. 1994). Owls had a higher persistence chance in clustered habitats than in randomly distributed habitats (McKelvey et al. 1993). Furthermore, clusters with a low ratio of edge to area reduced extinction risk compared to continuous clusters of identical area but with varying degree of irregularity. McKelvey et al. (1993) explained the effects of habitat clustering with the difficulty of finding mates in a highly fragmented landscape. This difficulty will make positive growth rates at low density unlikely (an Allee effect). Qualitatively similar beneficial effects of habitat clustering were obtained for the red-cockaded woodpecker (*Picoides borealis*) by Letcher et al. (1998) with a spatially explicit model that allowed density-dependent changes in territory size.

The effect of habitat clustering, however, depends on net lifetime reproductive success (R_0), dispersal strategy, and dispersal power (With and King 1999). For species with limited reproductive output ($R_0 = 1.01$) extinction thresholds occurred sooner in clumped landscapes than in random landscapes – like for the spotted owl and the red-cockaded woodpecker – save for the most clumped landscapes, whereas they occurred increasingly later with the degree of contagion for species with high reproductive output ($R_0 > 1.1$) and low search efficiency. Increasing net lifetime reproductive success (R_0) reduced the extinction threshold and it vanished even in highly fragmented landscapes when combined with moderate search efficiency (numbers of dispersal attempts in the order of 10–20).

The effect of density dependence on persistence probability caused by spatial structure vanishes not only when search efficiency exceeds the scale of habitat fragmentation. The same holds for very low dispersal that happens on a scale much finer than that of habitat fragmentation, as in the hermaphroditic

snail *Trochoidea geyeri*. In this case, persistence time was also independent of habitat geometry and carrying capacity but grew rapidly with neighbourhood size (Pfenninger and Bahl 1997).

The models discussed so far assumed homogeneous habitat quality. Whereas an effect of spatial structure may or may not be present in these models depending on reproductive potential and dispersal, spatial structure seems to matter always in the presence of differences in habitat quality. McKelvey et al. (1993) suggested that marginal habitat surrounding suitable habitat will make (spotted owl) populations more extinction prone in spite of an increased mean population size, because juveniles settle in these marginal habitats instead of continuing to search for optimal habitat. A spatially explicit model of Bachman's sparrow (*Aimophila aestivalis*) supports this hypothesis. Persistence probability increased (marginally, but only 22 simulations were run) when only high quality habitat was selected for settlement (Pulliam et al. 1992). Nonetheless, even sink populations that cannot persist independently for much more than 10 years may show a considerable rescue effect for the source population (spatially explicit model for the grasshopper *Stenobothrus lineatus*; Samietz et al. 1996).

Results again change if the suitability of habitat patches does not remain constant. If two habitats have the same average quality but are marginal, respectively, optimal in different years, habitat heterogeneity can improve the survival chances of populations (Krug et al. 1996). Again, the effect of spatial structure of habitat quality on population persistence depends on the occupancy strategy used. A beneficial effect of habitat heterogeneity can be seen if individuals establish territories in the second habitat only once the first (preferred) habitat is completely filled or if settlement is equally likely in both habitats. No such effect was obtained when the chance to occupy a territory in the second habitat linearly increases with occupation density in the preferred habitat.

The models discussed above removed a spatial effect by changing movement into a scale that no longer matched the scale of habitat structure. However, this procedure concomitantly reduces mortality so that the effects of density and those of changes in vital rates are confounded to some degree. In contrast, Wiegand et al. (2002) maintained matching of scale when testing the effects of spatial structure on extinction probability for the territorial gecko *O. reticulata*. Instead, they removed the mortality costs of movement and adjusted total mortality such that it was equivalent in the spatial and the non-spatial model. In the spatially explicit model, the search for empty territories led to an increase in mortality, pushing down population size. Stochasticity caused the population trajectories to reach even lower levels, resulting in considerably lower persistence time than in the non-spatial model without density dependence.

In summary, the effects on extinction probability of density dependence caused by spatial structure depend on reproductive potential, search efficiency, occupation strategy for empty territories, landscape pattern, fragmentation scale, and habitat quality. Furthermore, there are interactions among these factors. These effects vanish if dispersal happens on a scale much finer or much coarser than that of habitat structure.

Discussion

How to deal with density dependence in PVAs?

Should density dependence be included in PVA models and, if so, how? Since all models are wrong, scientists should be concerned with what is importantly wrong (Box 1976). Of critical importance is the robustness of models to departures from assumptions (Vucetich and Creel 1999). Contrary to previous suggestions (e.g., Ginzburg et al. 1990), the assumption of density independence does not always result in pessimistic predictions about population persistence. Whether models without density dependence are conservative depends on the biological details of the species under consideration, particularly the growth rate, the type and strength of density dependence assumed, the strength of environmental variation, the quasi-extinction level used, and, in some models, the initial conditions. In addition, these factors may interact in determining extinction risks. Spatially explicit models further show that reproductive output, search efficiency and occupation strategy, habitat structure and quality, and the relative scales of habitat structure and dispersal can all have important influences on spatially mediated density effects on population persistence. Moreover, density effects in single populations do not simply carry over to metapopulations. Indeed, they may act in opposite directions. Finally, there can be complex interactions of density regulation in different life-stages of a species.

Because of the potential for widely divergent quantitative and qualitative predictions, how density regulation is to be modelled in PVAs is a crucial issue. Models with density-independent growth to a ceiling carrying capacity tend to produce optimistic predictions compared to most other possibilities of density regulation, but this is not invariably the case. Similarly, high environmental variability tends to decrease the influence of density dependence on extinction probability, but does not remove it completely. When populations start at low numbers, modelling the Allee effect is crucial. The lower the population growth rate the more important is its inclusion. In contrast, if populations start at high numbers, the type of density regulation assumed at high density mainly determines the probability of extinction, and the Allee

effect has only a mild influence (e.g., Wiegand et al. 2002). Judged by the few analyses available, density effects seem to operate in opposing directions in single populations compared to metapopulations. However, this hypothesis needs testing with systematic comparisons.

We also noticed an interesting opposing trend between models that use a mathematical function for density dependence and spatially explicit models. Whereas density independence tends to result in pessimistic predictions in the former, the opposite tends to be the case in the latter. Similarly, the former seem to predict no important effects of density-dependent dispersal on metapopulation survival, the latter show that dispersal crucially interacts with density dependence on determining persistence. Unfortunately, there are no standardised comparisons available for the same species. Therefore, it is not possible to evaluate whether this tendency results from the different approaches to modelling density dependence or from the different types of organisms involved. It could be highly instructive for the understanding of density processes and for the application of PVAs to set up a series of spatially explicit population models, analyse the distribution of population persistence, fit various functions of density dependence to randomly selected population trajectories, and then compare the ability of these different density models to predict persistence adequately.

So how to proceed in a PVA without such knowledge? First, biological knowledge should be carefully screened to identify likely, and to discard unlikely types of density regulation. For example, empirical data provided by Fowler (1981) and Stubbs (1977) indicate that most density-dependent change occurs close to carrying capacity for species with low reproductive rates, long life expectancy, and with populations that are mainly limited by resources. In contrast, species with high reproductive potential, short life-span, and with populations frequently below the limits of environmental resources exhibit most density-dependent change at low population levels. Thus, for the former type of species, functions of density dependence with a strong *per capita* change at high population size may be adequate whereas functions with a strong *per capita* change at low density may be more suitable for the latter group of organisms.

Second, statistical methods should be used to identify biologically possible types of density regulation that do not fit the data well. Unfortunately, as yet no test exists to discriminate between different forms of density regulation. Indeed, it has been difficult to demonstrate the presence of any type of density regulation (Gaston and Lawton 1987; Pollard et al. 1987; Burgman et al. 1993; but see Dennis and Taper 1994). So far, alternatives are usually chosen because of familiarity with a particular equation or availability of software (Burgman et al. 1993). One *ad hoc* approach is the selection of the model that explains most of the variance of the data when fitted with non-

linear regression (e.g., Bellows 1981; Eberhardt 1987). However, this is not a satisfactory approach and may easily lead to the selection of inadequate models (Burgman et al. 1993). Modern model selection approaches based on information theory do not seem to be helpful either, since all functions of density regulation contain similar numbers of parameters (cf. Pascual et al. 1997). At least a robust method is now available to identify the dimension of density dependence in time series analyses (Berryman and Turchin 2001), but this will help only to differentiate between a small number of possible models.

Groom and Pascual (1997) suggested comparisons among multiple models to obtain best possible portraits of future outcomes of a management strategy or a particular disturbance. However, given the wide range of possible effects of density regulation on persistence, an objective method for limiting the number of plausible alternatives is important. For example, a comparison of as wide a range of model output as possible with existing data that were not part of the model input may allow a further rejection of some models and increase confidence in the model chosen for inferences (Wiegand et al. 1998, 2004 (this issue)). The consequences of pessimistic versus optimistic predictions may further help in model selection.

In the absence of hard field data it is difficult to achieve a realistic representation of density dependence in spatially unstructured models. An alternative may be to account for density dependence by modelling individual behaviour in spatially structured models. In many cases the most natural way to model density dependence of territorial species will be by imitating the effects of the inherent causes of density dependence, that is, the spatial structure of populations (cf. McKelvey et al. 1993; Hildenbrandt et al. 1995; Letcher et al. 1998; Wiegand et al. 2002). Particularly in the case of sparse data the explicit consideration of spatial population structure has the following advantages. If data are scarce, it is important to make use of structural knowledge that cannot be easily incorporated into more abstract models (Wiegand et al. 2004 (this issue)). This requires the matching of the model scale to the scale of population structure. With similar model and observational scale, one can use secondary model predictions to test whether the model rules are plausible. For example, one might look at patterns such as the number of occupied territories as a function of population size (density) (Wiegand et al. 2002).

Where to from here?

Further systematic comparisons of the effects of different types of density regulation on persistence probability are of considerable importance to establish better guidelines for when and which form of density dependence should be included in a PVA. Systematic comparisons are particularly needed across

a range of density functions and life history strategies using complete extinction as a currency. Furthermore, the effect of density dependence on metapopulation persistence and the complex interactions of density regulation in different stages have hardly been touched. Likewise, very few comparisons of spatially explicit to non-spatial models exist. It is non-trivial to design the models in such a way that they are really comparable (Wiegand et al. 2002), and this has not yet been resolved for any functional representation of density dependence. Also, testing the robustness of predictions from spatially explicit models to deviations from assumptions about individual behaviour (and landscape structure) is still in its infancy (Reed 1999, but see Wiegand et al. 2004 (this issue)).

Although they require considerable effort, carefully planned field experiments to elucidate the relationships of vital rates with density are of paramount importance. Advances in field methods and in statistical methods are also required. Given that most PVAs include a ceiling carrying capacity in their model assumptions, it is of considerable relevance to have reliable methods for estimating carrying capacity. Most frequently, the highest observed population size is used as an estimate of carrying capacity (e.g., Ferrière et al. 1996). Reed et al. (1998) estimated the carrying capacity of a metapopulation as the sum of the maximum sizes of the discrete subpopulations observed at any time. This almost certainly is an overestimate, since in equilibrium metapopulations some suitable patches are always unoccupied (Hanski 1991). An alternative to the use of observed population sizes is to estimate carrying capacity in units of 'lots' (smallest patch sizes that are able to support an individual) and modelling the occupancy of empty 'lots' by floaters and territorial neighbours from observational data of contests (Hildenbrandt et al. 1995; McCarthy 1996a). The resulting distribution of the number of 'lots' occupied by an individual can be transformed into a carrying capacity in terms of territorial individuals. None of these approaches accounts for (stochastic) fluctuations in carrying capacity and little is known about the reliability of any of the methods used so far to estimate carrying capacity. Brook et al. (1997) showed for the Lord Howe Island woodhen (*T. sylvestris*) that estimates of carrying capacity based on habitat size alone were incorrect since habitat requirements were inadequately known. They assumed that for many endangered species the same applies and concluded that care must be taken to estimate carrying capacity from habitat size alone (see also Vos et al. 2001). Further research on this topic is urgently required.

Statistical analyses should address the question of how different sources of data are best combined to increase our ability to not only detect density dependence but to select among alternative models. It may be fruitful to explore the joint development of models and statistical methods that can be used to test model forecasts with smaller sets of time series (cf. Dennis et al.

1995). Such analyses may ultimately allow the development of guidelines for field biologists to optimise their sampling strategies. Combined efforts to advance statistical methods, field sampling, and modelling will improve considerably the decision making basis for selecting PVA approaches that will ensure robust management strategies for the world's highly endangered species.

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Appendix A. Biological assumptions of and relationships among mathematical functions of density dependence used in extinction models

Description of density dependence by a mathematical function is achieved by making the population growth rate (r or λ) or any other demographic parameter a function of density. The most common way to achieve this is by using a term that is a function of density, $f(N)$, as a multiplier for the population growth rate. In this case, time continuous (TC) models are of the form $\partial N = f(N)rN\partial t + \sigma N\partial W$, with the second term describing stochastic noise, and time discrete models (TD) take the form $N_{t+1} = f(N)\lambda_t N_t$. In TD models, stochasticity often is introduced by replacing the shape parameters of the density terms by an environmental variable such as rainfall.

The growth rate can be decomposed into its components: birth rate (b), death rate (d), immigration rate (i) and emigration rate (e), that is, $r = b + i - d - e$ in the TC case and $\lambda_t = (1 + b_t + i_t - d_t - e_t)$ in the TD case. The term $f(N)$ can be used as a multiplier to each or only some of these demographic parameters. Furthermore, different terms may be used for different demographic rates and only some classes within a population may be affected by or control the feedback mechanism.

Instead of using multiplicative terms, TD models may use terms that are added to a baseline value of a demographic parameter, usually its value for

a population size close to zero or carrying capacity K . For the purpose of this review, we converted published additive terms into multipliers to allow a consistent representation of the term $f(N)$ in Table 1. Please note that different constraints of the shape parameters of the density terms may be necessary depending on the demographic parameter to which they are multiplied and transformations may be necessary if applied to different demographic parameters, for example, to death rates instead of survival rates. The density-dependent terms also can be used in individual-based models by interpreting them as probabilities, for example, as the probability of survival of an individual.

The simplest model of density regulation is a ceiling K (model #1 in Table 1) that functions as an upper boundary for population size. Under this model, populations grow without density regulation until they reach K , where growth stops (Leigh 1981; Caughley and Sinclair 1994). The model assumes that there are no reproductive or survival costs associated with finding or competing for the limiting resource until K is reached. Biologically, this is an unlikely assumption, although it may be approximated in some populations that are limited only by a non-consumable resource such as nest sites.

A ceiling carrying capacity may affect only the number of reproducing females in a population through the limited availability of sites for reproduction (e.g., nesting sites). In this case, surplus individuals may join a pool of floaters (e.g., Lamberson et al. 1992; Beier 1993; Hildenbrandt et al. 1995) instead of dying or emigrating. Model #2 extends model #1 to allow some female floaters to reproduce.

Another straightforward extension of model #1 assumes that survival, reproduction, or growth rate will decrease in a stepwise fashion at specific values of density (model #3). In the general case of this extension, population size can grow to infinity. However, an upper boundary is retrieved by setting the survival rate zero for surplus individuals when a specified density value beyond $K + e$ is reached. Model #3 can account also for an Allee effect if survival, birth, or growth rates are reduced instead of increased at low density. Strictly speaking, the biological assumption of a stepwise change in reproduction, survival, or growth rate is unrealistic, but the model may be a reasonable approximation to a steep sigmoidal change of density effects over a limited range of population sizes (cf. Harris et al. 1989).

A more realistic assumption than a stepwise change is a continuous change of survival, reproduction, population growth, and/or emigration with density. Most of the remaining models (#4–28) assume such continuous changes at least across certain ranges of density. These models use the carrying capacity K as a descriptor of equilibrium population size and not as a ceiling boundary.

Several of these models (#4–8) are generalisations of the logistic growth model first introduced by Verhulst (1838). In the basic logistic growth model

(model #4a), the *per capita* growth rate is a linearly declining function of population size. Therefore, it is often referred to as the linear logistic or linear density regulation model. Density regulation is symmetric, that is, the relative importances of density regulation at high and low densities are equal. In a generalised form (model #4b), the θ -logistic, the parameter θ specifies the relative importance of density regulation at high versus low densities and the strength of density regulation. Density regulation decreases in strength with increasing θ and its importance shifts more towards regulation at high densities. Model #4c is a further generalisation that allows a scaling of density effects.

The θ -logistic is generally used in cases where the linear logistic model does not fit the data well (e.g., Eberhardt 1987; Stacey and Taper 1992). This is particularly often the case for insect populations (Dempster 1983). The linear logistic model is strictly applicable only in the special case when a population's limiting resources are produced at a rate independent of the number of individuals using it (Dennis 1978; Caughley and Sinclair 1994). It is sometimes assumed that the linear logistic may provide a suitable approximation to many unspecified growth models (Dennis and Patil 1984). However, the striking differences that different types of density regulation may exert on population viability warn against using such an assumption in the modelling of extinction processes. In any case, the model is not suitable for species whose densities are regulated by successful dispersal to empty territories (Noon and McKelvey 1996). Model #24 may be suitable in this case; notwithstanding, the θ -logistic may still be applicable to those species whose territories are of variable quality, are compressible, or if there is a cost to territory defence (Stacey and Taper 1992).

Models #5–8 are descendants of a generalised time discrete logistic growth model. Models #5 (the Beverton–Holt model) and #6 (the Ricker model) are widely used biologically. They relate total reproductive effort to reproductive success such that after a peak of success additional effort is actually counter-productive and causes a decrease in reproductive success. The Beverton–Holt model always results in contest competition, whereas the Ricker model represents scramble competition. In contest competition, resources are partitioned so that an individual obtains a parcel necessary for survival, or not. Contest competition models may be useful for species in which the survival of young is limited by the number of territories or the number of nesting sites so that a more or less fixed number of young will be recruited irrespective of the number of young produced. If, in contrast, resources are shared more or less equally among all members of the population, scramble competition results. Under scramble competition, not all resources available contribute to population growth since some are won by individuals that do not survive. Scramble competition can result in overcompensatory population crashes; that is, if

some initial density is exceeded, fewer and fewer individuals in a population survive because the share becomes smaller and smaller.

Models #7 and #8 are different generalisations of the Beverton–Holt model. Both models assume that the strongest *per capita* effect of density occurs at low density. With increasing strength of density dependence (β), the models shift along the continuum from contest towards scramble competition. Model #8 has a very flexible shape and Bellows (1981) showed that this model is better able to describe a wide range of data than a set of alternative models tested, including model #5. It should be kept in mind that, as shown by Burgman et al. (1993), a density regulation model with a better fit does not necessarily mean that such a model is more suitable for predicting changes in population size. This can happen because the census data are too short to extract the underlying density regulation correctly.

Model #9 is known as the Ricker equation because of its similarity with the Ricker model of recruitment (model #6). Instead of a reflecting boundary at carrying capacity, this model uses an exponentially decreasing population growth at high densities. The behaviour of this model is very similar to the TD Verhulst model: the first-order Taylor series expansion of the exponential function in this model yields the Verhulst model for $a_1 = r/K$.

Model #10, a modification of model #9, is derived from the theory of ratio-dependent consumer–resource interaction (Arditi and Ginzburg 1989) relating population growth to the ratio of the environmental variable g and population size. Density effects usually are slightly weaker than in model #9.

Another contest–scramble competition model is #11 (Stelter 1998). It is based on a power function and assumes that density effects come into play only above a threshold value of population size (N_{tr}). At this threshold value the *per capita* effects of density are highest and then decrease with density as in the classical contest–scramble model. Whereas it may be biologically reasonable that density effects appear only above a threshold value, it is very unlikely that the *per capita* effects are suddenly very strong and then decrease again.

Drechsler et al. (1998) suggested another threshold contest–scramble model (#12). In this model contest competition comes into play at K and reduces mortality such that K is a ceiling limit. Additionally, scramble competition sets in above a threshold value of population size but less abruptly than in model #11.

Beier (1993) introduced another power function (model #13) to model density effects on survival, with survival being constrained between fixed maximum and minimum values. The function was chosen for its computational simplicity. The biological implication of the function is a rapidly declining survival with increasing density at low densities and a slow

approach to the minimum survival rate, which is reached at a population size beyond carrying capacity.

The next four functions have been used in PVAs also mainly because of their flexibility. Model #14 relates the density-dependent demographic parameter to the ratio of the environmental parameter k (e.g., rainfall) and population size (cf. Pascual et al. 1997), as is the case in model #10. Model #14 can display a wide range of behaviours. If the shape parameter $i = 0$, the function passes through the origin, becoming the Michaelis–Menten equation. By constraining the remaining shape parameters as well, the model can be converted into the Beverton–Holt model. The model further includes density independence (for $j = 0$).

Models #15 and #16 allow a flexible modelling of a sigmoidal change in demographic parameters with density. Models #15a and #15b have been suggested independently, but model #15b is a special case of model #15a. In model #15a, the density effects are scaled by m and the curve is shifted upwards by q compared to model #15b. In model #15a, the exponent x is $+1$ and -1 depending on whether the demographic rate increases (e.g., mortality) or decreases (e.g., reproduction), respectively, with density. The parameters in these two models may be re-scaled such that N is replaced by N/K . Model #16 shows similar properties as model #15a and has been used instead of model #15a because it is better suited for analytical studies.

The fourth-order polynomial (model #17a) allows a close fit to most plausible density dependence curves. Both positive and negative (Allee effect) responses, or more complex relationships can be modelled (Lacy 1993) but there is no underlying biological process assumed that produces a fourth-order polynomial relationship of demographic parameters with density. Quadratic functions (model #17b: e.g., Nolet and Baveco 1996), linear regression models (#17c: e.g., Shaffer 1983), or the use of a constant multiplier (model #17d) are special cases of model #17a. These special cases are also used mainly because of mathematical convenience. Sometimes different functions are applied to particular ranges of density.

The next model (#18) has been introduced mainly for theoretical reasons with assumptions that are unlikely for the majority of (endangered) species. In this type of density regulation overshooting of the carrying capacity can occur and is followed by a crash to extinction.

The models of density dependence discussed so far assume that increasing density will result in decreased survival or reproduction. However, it is well known that at low density the effects may be reversed and survival or reproduction will decline with decreasing density. This Allee effect has been observed in many taxa (reviewed, e.g., by Allee et al. 1949; Dennis 1989a). Many functions have been used to describe an Allee effect (Jacobs 1984; Dennis 1989a; McCarthy 1997) and eight (#19–27) of them in the context of modelling population extinction. As an alternative, Swart and Lawes (1996)

treated the occurrence of the Allee effect probabilistically by specifying a probability value that very small troops will go extinct. Furthermore, the inclusion of inbreeding effects in extinction models could be considered as a kind of Allee effect (cf. Burgman and Lamont 1992; Lacy 1993; McCarthy 1996a); however, genetic effects are not considered in this review.

The Allee effect has been modelled mainly for reproduction, most frequently using various assumptions on the mating system and encounter probabilities of individuals. If the mating system is promiscuous and the reproductive rate increases with the encounter rate, models #19 or #20 result. Whereas model #19 assumes that all females have the same effective search area (= area searched \times proportion of males in the population), model #20 results if the effective search area varies among females.

In contrast to the two previous models, model #21 assumes that search area is not limited and that the number of reproducing females depends only on the number of available males. In a monogamous mating system $B = 1$, whereas in polygamous species B is the average harem size. The competition coefficient A in the model accounts for females remaining unpaired for any reason in the presence of unpaired males. Note that the expected percentage of females breeding increases with density in this model. Model #22 assumes that monogamy is the result of matching male and female territories (instead of pair bonding) and that males expand their territories when some male territories are unoccupied. In this model, a larger percentage of females breed than under model #21. Model #23 is a male limited model developed for exploited harem species in which hunters harvest males preferentially, leading to a disturbance of the natural mating system. It assumes that juvenile survivorship or female fecundity decline as a linear function of the degree of disturbance of the natural sex ratio.

Model #24 has been used for modelling the mating probability of a particular female in a polygamous mating system and for the probability of successful dispersal to a suitable empty territory. It assumes that individuals search a number of sites for unoccupied territories or territories with a suitable partner. Individuals that fail to find a suitable territory perish. Likewise, individuals that do not encounter a mate have no mating success. Implicitly, the model also assumes that there are no other costs involved with searching for territories or mates. Consequently, survival during dispersal or mating success increase with the percentage of sites that are suitable or occupied by a single of the opposite sex. Likewise, dispersal survival and mating success increase with search efficiency (the number of sites searched). If applied to non-territorial species, the number of sites searched is replaced by the number of adult males and the ratio of suitable available to total sites is replaced by the probability that a particular female finds a particular male.

Whereas the previous model takes the perspective of a searching individual, model #25 addresses the probability that a vacant nesting site will

become occupied. Please note that here the dynamics of site occupation is modelled instead of the demography of the population. The model allows a rapid increase of colonisation with density at either low or high density depending on the exponent (φ). No other biological or mathematical justification for the model was presented.

The co-operation model of Jacobs (1984) (model #26) assumes that there is a minimal growth rate at very small population sizes, r_0 , that may be positive or negative. Co-operation in the widest sense, that is, any increase in natality or survival by virtue of the interaction of two or more individuals, increases this minimal growth rate. The magnitude of this increase depends on the efficiency of co-operation, C , and an index of sociality, D . Asymptotically, the product CD is the maximum *per capita* growth rate. The model does not make any assumption about encounter probabilities, though mathematically it is similar to, but not a generalisation of, model #20.

Model #27, the VORTEX model of breeding probability, combines the rectangular hyperbolic model of an Allee effect (model #20) with the generalised θ -logistic model (model #4c with $f = (P_0 - P_K)/P_0$) applied to breeding probability. In this model, the breeding probability of females varies between a maximum of $P_0 \leq 1$ when population size is close to 0 and a minimum of $P_k \geq 0$ when the breeding size is at carrying capacity.

The final two models have been suggested for density-dependent emigration, respectively, immigration. (In addition, model #11b and a threshold density for dispersal with no dispersal below and density-independent dispersal beyond the threshold have been suggested.) Though model #28 is a mathematical extension of the rectangular hyperbola function used for Allee effects, it is not a generalisation of this model and lacks a mechanistic basis. Indeed, it assumes that emigration probability increases with density, which is opposite to an Allee effect. The only biological justification was that the model results in an increase of dispersal mortality with density if a fraction of the dispersing individuals do not find a new subpopulation. However, any other function of an increase in emigration probability with density would achieve the same effect. Model #29 distributes the pool of surviving migrating individuals across subpopulations such that each receives a fraction inversely proportional to its density.

References

- Akçakaya H.R. 1992. Population viability analysis and risk assessment. In: McCullough D.R. and Barrett R.H. (eds), *Wildlife 2001: Populations*. Elsevier Applied Science, London, pp. 148–157.
- Akçakaya H.R. and Atwood J.L. 1997. A habitat-based metapopulation model of the California gnatcatcher. *Conservation Biology* 11: 422–434.

- Akçakaya H.R. and Baur B. 1996. Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. *Oecologia* 105: 475–483.
- Akçakaya H.R. and Ferson S. 1990. RAMAS/Space User Manual: Spatially Structured Population Models for Conservation Biology, Exeter Software. Applied Biomathematics, New York.
- Akçakaya H.R. and Ginzburg L.R. 1991. Ecological risk analysis for single and multiple populations. In: Seitz A. and Loeschcke V. (eds), *Species Conservation: A Population Biological Approach*. Birkhäuser, Basel, Switzerland, pp. 73–87.
- Akçakaya H.R., McCarthy M.A. and Pearce J.L. 1995. Linking landscape data with population viability analysis: management options for the helmeted honeyeater *Lichenostomus melanops cassidix*. *Biological Conservation* 73: 169–176.
- Allee W.C., Emerson A.E., Park O., Park T. and Schmidt K.P. 1949. *Principles of Animal Ecology*. Saunders, Philadelphia, Pennsylvania.
- Allen J.C., Schaffer W.M. and Rosko D. 1993. Chaos reduces species extinction by amplifying local population noise. *Nature* 364: 229–232.
- Amarasekare P. 1998. Allee effects in metapopulation dynamics. *The American Naturalist* 152: 298–302.
- Amler K., Bahl A., Henle K., Kaule G., Poschlod P. and Settele J. 1999. *Populationsbiologie in der Naturschutzpraxis. Isolation, Flächenbedarf und Biotopansprüche von Pflanzen und Tieren*. Ulmer, Stuttgart, Germany.
- Andersen M.C. and Mahato D. 1995. Demographic models and reserve designs for the California spotted owl. *Ecological Applications* 5: 539–647.
- Andrewartha H.G. and Birch L.C. 1984. *The Ecological Web*. University of Chicago Press, Chicago, Illinois.
- Arditi R. and Ginzburg L.R. 1989. Coupling in predator–prey dynamics: ratio dependence. *Journal of Theoretical Biology* 139: 311–326.
- Armbruster P. and Lande R. 1993. A population viability analysis for African elephant (*Loxodonta africana*): How big should reserves be? *Conservation Biology* 7: 602–610.
- Asquith N.M. 2001. Misdirections in conservation biology. *Conservation Biology* 15: 345–352.
- Beier P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7: 94–108.
- Beissinger S.R. and Westphal M.I. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62: 821–841.
- Bellows T.S. 1981. The descriptive properties of some models for density dependence. *Journal of Animal Ecology* 50: 139–156.
- Belovsky G.E. 1987. Extinction models and mammalian persistence. In: Soulé M.E. (ed), *Viable Populations for Conservation*. Cambridge University Press, New York, pp. 35–57.
- Bender C. 1999. *Populationsgefährdungsanalyse der Mauereidechse (Podarcis muralis): demographische und genetische Grundlagen*. Ph.D. Thesis (on microfiche), Universität Frankfurt, Germany.
- Berryman A. and Turchin P. 2001. Identifying the density-dependent structure underlying ecological time series. *Oikos* 92: 265–270.
- Beverton R.J.H. and Holt S. 1957. On the dynamics of exploited fish populations. *Fisheries and Food, Fishery Investigations (Series 2)* 19: 5–533.
- Box G.E.P. 1976. Science and statistics. *Journal of the American Statistical Association* 71: 791–799.

- Boyce M.S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23: 481–506.
- Boyce M.S., Meyer J.S. and Irwin L. 1994. Habitat-based PVA for the northern spotted owl. In: Fletcher D.J. and Manly B.F.J. (eds), *Statistics in Ecology and Environmental Monitoring*. University of Otago Press, Dunedin, New Zealand, pp. 63–85.
- Brook B.W., Lim L., Harden R. and Frankham R. 1997. Does population viability analysis software predict behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). *Biological Conservation* 82: 119–128.
- Brook B.W., Cannon J.R., Lacy R.C., Mirande C. and Frankham R. 1999. Comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the whooping crane (*Grus americana*). *Animal Conservation* 2: 23–31.
- Buckley P.A. and Downer R. 1992. Modelling metapopulation dynamics for single species of seabirds. In: McCullough D.R. and Barrett R.H. (eds), *Wildlife 2001: Populations*. Elsevier Applied Science, London, pp. 563–585.
- Burgman M.A., Ferson S. and Akçakaya H.R. 1993. *Risk Assessment in Conservation Biology*. Chapman & Hall, London.
- Burgman M.A., Ferson S. and Lindenmayer D. 1994. The effect of initial age-class distribution on extinction risks: implications for the reintroduction of Leadbeater's possum. In: Serena M. (ed), *Reintroduction Biology of Australian and New Zealand Fauna*. Surrey Beatty, Sydney, Australia, pp. 15–19.
- Burkey T.V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. *Oikos* 55: 75–81.
- Carroll J.E. and Lamberson R.H. 1993. The owl's odyssey. A continuous model for the dispersal of territorial species. *SIAM Journal of Applied Mathematics* 53: 205–218.
- Caughley G. 1994. Direction in conservation biology. *Journal of Animal Ecology* 63: 215–244.
- Caughley G. and Sinclair A.R.E. 1994. *Wildlife Ecology and Management*. Blackwell Science, Cambridge, UK.
- Chapman S.B., Rose R.J. and Clarke R.T. 1989. The behaviour of populations of the marsh gentian (*Gentiana pneumonanthe*): a modelling approach. *Journal of Applied Ecology* 26: 1059–1072.
- Cross P.C. and 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.
- Dempster J.P. 1983. The natural control of populations of butterflies and moths. *Biological Revue* 58: 461–481.
- Den Boer P.J. 1981. On the survival of populations in a heterogeneous and variable environment. *Oecologia* 50: 39–53.
- Dennis B. 1978. Analytical solution to an open-system model of population-growth. *Mathematical Biosciences* 40: 167–169.
- Dennis B. 1989a. Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource Modeling* 3: 481–538.
- Dennis B. 1989b. Stochastic differential equations as insect population models. In: McDonald L., Manly B., Lockwood J. and Logan J. (eds), *Estimation and Analysis of Insect Populations*. *Lecture Notes in Statistics* 55: 219–238.
- Dennis B. and Patil G.P. 1984. The gamma distribution and weighted multimodel gamma distributions as models of population abundance. *Mathematical Biosciences* 68: 187–212.

- Dennis B. and Taper M.L. 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* 64: 205–224.
- Dennis B., Munholland P.L. and Scott J.M. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 61: 115–143.
- Dennis B., Desharnais R.A., Cushing J.M. and Costantino R.F. 1995. Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. *Ecological Monographs* 65: 261–281.
- Doak D. 1989. Spotted owls and old growth logging in the Pacific Northwest. *Conservation Biology* 3: 389–396.
- Doak D.F. and Mills L.S. 1994. A useful role for theory in conservation. *Ecology* 75: 615–626.
- Dobson F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behavior* 30: 1183–1192.
- Drechsler M., Burgman M.A. and Menkhorst P.W. 1998. Uncertainty in population dynamics and its consequences for the management of the orange-bellied parrot *Neophema chrysogaster*. *Biological Conservation* 84: 269–281.
- Duellman W.E. and Trueb L. 1986. *Biology of Amphibia*. McGraw-Hill, New York.
- Eberhardt L.L. 1987. Population projections from simple models. *Journal of Applied Ecology* 24: 103–118.
- Ferrière R., Sarrazin F., Legendre S. and Baron J.-P. 1996. Matrix population models applied to viability analysis and conservation: theory and practice using the ULM software. *Acta Ecologica* 17: 629–656.
- Ferson S., Ginzburg L. and Silvers A.A. 1989. Extreme event risk analysis for age-structured populations. *Ecological Modelling* 47: 175–187.
- Foley P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8: 124–137.
- Fowler C.W. 1981. Density dependence as related to life history strategy. *Ecology* 62: 602–610.
- Frank K. 2004. Ecologically differentiated rules of thumb for habitat network design – lessons from a formula. *Biodiversity and Conservation* 13: 189–206 (this issue).
- Frank K. and Wissel C. 1998. Spatial aspects of metapopulation survival – from model results to rules of thumb for landscape management. *Landscape Ecology* 13: 363–379.
- Frank K., Drechsler M. and Wissel C. 1994. Überleben in fragmentierten Lebensräumen – Stochastische Modelle zu Metapopulationen. *Zeitschrift für Ökologie und Naturschutz* 3: 167–178.
- Frank K., Lorek H., Köster M., Sonnenschein M., Wissel C. and Grimm V. 2003. *Meta-X: Software for Metapopulation Viability Analysis*. Springer, Berlin, Germany.
- Gabriel W. and Bürger R. 1992. Survival of small populations under demographic stochasticity. *Theoretical Population Biology* 41: 44–71.
- Gaona P., Ferreras P. and Delibes M. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecological Monographs* 68: 349–370.
- Gaston K.J. and Lawton J.H. 1987. A test of statistical techniques for detecting density dependence in sequential censuses of animal populations. *Oecologia* 74: 404–410.
- Ginsberg J.R., Mace G.M. and Albon S. 1995. Local extinction in a small and declining population: wild dogs in the Serengeti. *Proceedings of the Royal Society of London, Series B* 262: 221–228.
- Ginzburg L.R., Slobodkin L.B. and Bindman A.G. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis* 2: 171–181.
- Ginzburg L.R., Ferson S. and Akçakaya H.R. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4: 63–70.

- Goel N.S. and Richter-Dyn N. 1974. Population growth and extinction. In: Goel N.S. and Richter-Dyn N. (eds), *Stochastic Models in Biology*. Academic Press, New York, pp. 73–91.
- Goodman D. 1987a. The demography of chance extinction. In: Soulé M.E. (ed), *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK, pp. 11–34.
- Goodman D. 1987b. Consideration of stochastic demography in the design and management of biological reserves. *Natural Resource Modeling* 1: 205–234.
- Grant A. and Benton T.G. 2000. Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* 81: 680–693.
- Groom M.J. and Pascual M.A. 1997. The analysis of population persistence: an outlook on the practice of viability analysis. In: Fiedler P.L. and Kareiva P.M. (eds), *Conservation Biology for the Coming Decade*. Chapman & Hall, New York, pp. 4–27.
- Hanski I.A. 1990. Density dependence, regulation and variability in animal populations. *Philosophical Transactions of the Royal Society of London* 330: 141–150.
- Hanski I.A. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society* 42: 17–38.
- Hanski I.A. and Gilpin M. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42: 3–16.
- Hansson L. 1991. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnean Society* 42: 89–103.
- Harris R.B., Clark T.W. and Shaffer M.L. 1989. Extinction probabilities for isolated black-footed ferret populations. In: Seal U.S. and Thome E.T. (eds), *Conservation Biology and the Black Footed Ferret*. Yale University Press, New Haven, Connecticut, pp. 69–82.
- Harrison S., Quinn J.F., Baughman J.F., Murphy D.D. and Ehrlich P.R. 1991. Estimating the effects of scientific study on two butterfly populations. *The American Naturalist* 137: 227–243.
- Hassell M.P., Lawton J.H. and May R.M. 1976. Patterns of dynamical behaviour in single-species populations. *Journal of Animal Ecology* 45: 471–486.
- Hedrick P.W., Lacy R.C., Allendorf F.W. and Soulé M.E. 1996. Directions in conservation biology: comments on Caughley. *Conservation Biology* 10: 1312–1320.
- Hildenbrandt H., Bender C., Grimm V. and Henle K. 1995. Ein individuenbasiertes Modell zur Beurteilung der Überlebenschancen kleiner Populationen der Mauereidechse (*Podarcis muralis*). *Verhandlungen der Gesellschaft für Ökologie* 24: 207–214.
- Howells O. and Edwards-Jones G. 1997. A feasibility study of reintroducing wild boar *Sus scrofa* to Scotland: Are existing woodlands large enough to support minimum viable populations. *Biological Conservation* 81: 77–89.
- Jacobs J. 1984. Cooperation, optimal density and low density thresholds: yet another modification of the logistic model. *Oecologia* 64: 389–395.
- Järvinen O. 1982. Conservation of endangered plant populations: single large or several small reserves. *Oikos* 38: 301–307.
- Krug R.M., Johst K., Wissel C. and Märtens B. 1996. Wirkung der räumlichen Heterogenität innerhalb eines Habitats auf die mittlere Überlebensdauer einer Zauneidechsen-Population. *Verhandlungen der Gesellschaft für Ökologie* 26: 447–453.
- Lacy R.C. 1993. VORTEX: a computer simulation model for population viability analysis. *Wildlife Research* 20: 45–65.
- Lacy R.C. 2000. Structure of the VORTEX simulation model for population viability analysis. *Ecological Bulletins* 48: 191–203.

- Lacy R.C., Flesness N.R. and Seal U.S. 1989. Puerto Rican Parrot *Amazona vittata* Population Viability Analysis and Recommendations. Captive Breeding Specialist Group, Species Survival Commission, IUCN, Apple Valley, Minnesota.
- Lamberson R.H., McKelvey R., Noon B.R. and Voss C. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology* 6: 505–512.
- Lamberson R.H., Noon B.R., Voss C. and McKelvey K.S. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. *Conservation Biology* 8: 185–195.
- Lande R. 1987. Extinction thresholds in demographic models of territorial populations. *The American Naturalist* 130: 624–635.
- Lande R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75: 601–607.
- Lande R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* 142: 911–927.
- Lande R. and Orzack S.H. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proceedings of the National Academy of Science USA* 85: 7418–7421.
- Lecomte J., Clobert J., Massot M. and Barbault R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard. *Écoscience* 1: 300–310.
- Legendre S. 1999. Demographic stochasticity: a case study using the ULM software. *Bird Study Supplement* 46: S140–S147.
- Legendre S. and Clobert J. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics* 22: 817–834.
- Leigh E.G. 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90: 213–239.
- Letcher B.H., Priddy J.A., Walters J.R. and Crowder L.B. 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. *Biological Conservation* 86: 1–14.
- Levins R. 1969. The effect of random variations of different types on population growth. *Proceedings of the National Academy of Science USA* 62: 1061–1065.
- Lindenmayer D.B. and Possingham H.P. 1994. *The Risk of Extinction – Ranking Management Options for Leadbeater’s Possum using Population Viability Analysis*. Australian National University, Canberra, Australia.
- Lindenmayer D.B., Burgman M.A., Akçakaya H.R., Lacy R.C. and Possingham H.P. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife metapopulations. *Ecological Modelling* 82: 161–174.
- Lindenmayer D.B., Lacy R.C. and Pope M.L. 2000. Testing a simulation model for population viability analysis. *Ecological Applications* 10: 580–597.
- Loeschcke V. 1990. Evolution und Artenschutz. In: Streit B. (ed), *Evolutionsprozesse im Tierreich*. Birkhäuser, Basel, Switzerland, pp. 239–254.
- Lomnicki A. 1988. *Population Ecology of Individuals*. Princeton University Press, Princeton, New Jersey.
- Ludwig D. 1976. A singular perturbation problem in the theory of population extinction. *SIAM-AMS Proceedings* 10: 87–104.
- Ludwig D. 1996. The distribution of population survival times. *The American Naturalist* 147: 506–526.
- MacArthur R.H. and Wilson E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Mace G.M. and Lande R. 1991. Assessing extinction threats: towards a reevaluation of IUCN threatened species categories. *Conservation Biology* 5: 148–157.

- Marmontel M., Humphrey S.R. and O'Shea T.J. 1997. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976–1991. *Conservation Biology* 11: 467–481.
- Marshall K. and Edwards-Jones G. 1998. Reintroducing capercaillie (*Tetrao urogallus*) into southern Scotland: identification of minimum viable populations at potential release sites. *Biodiversity and Conservation* 7: 275–296.
- May R.M. and Oster G.F. 1976. Bifurcations and dynamic complexity in simple ecological models. *The American Naturalist* 110: 573–599.
- Maynard-Smith J. and Slatkin M. 1973. The stability of predator–prey systems. *Ecology* 54: 384–391.
- McCarthy M.A. 1996a. Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and spatial structure. *Ecological Modelling* 85: 151–163.
- McCarthy M.A. 1996b. Red kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology* 33: 45–53.
- McCarthy M.A. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modelling* 103: 99–102.
- McCarthy M.A., Franklin D.C. and Burgman M.A. 1994. The importance of demographic uncertainty: an example from the helmeted honeyeater *Lichenostomus melanops cassidix*. *Biological Conservation* 67: 135–142.
- McKelvey K., Noon B.R. and Lamberson R.H. 1993. Conservation planning for species occupying fragmented landscapes – the case of the northern spotted owl. In: Kareiva P.M., Ingsolver J.G. and Huey R.B. (eds), *Biotic Interactions and Global Change*. Sinauer, Sunderland, Massachusetts, pp. 424–450.
- Middleton D.A.J. and Nisbet R.M. 1997. Population persistence time; estimates, models, and mechanisms. *Ecological Applications* 7: 107–117.
- Middleton D.A.J., Veitch A.R. and Nisbet R.M. 1995. The effect of an upper limit to population size on persistence time. *Theoretical Population Biology* 48: 277–305.
- Mills L.S., Hayes S.G., Baldwin C., Wisdom M.J., Citta J., Mattson D.J. and Murphy K. (1996) Factors leading to different viability predictions for grizzly bear data set. *Conservation Biology* 10: 863–873.
- Milner-Gulland E.J. 1997. A stochastic dynamic programming model for the management of the saiga antelope. *Ecological Applications* 7: 130–142.
- Milton J.G. and Bélair J. 1990. Chaos, noise, and extinction in models of population growth. *Theoretical Population Biology* 37: 273–290.
- Mirande C., Lacy R.C. and Seal U.S. 1991. *Grus americana* Whooping Crane Conservation Viability Assessment Workshop Report. Captive Breeding Specialist Group, Species Survival Commission, IUCN, Glen Rose, Texas.
- Nolet B.A. and Baveco J.M. 1996. Development and viability of a translocated beaver *Castor fiber* population in the Netherlands. *Biological Conservation* 75: 125–137.
- Noon B.R. and McKelvey K.S. 1996. A common framework for conservation planning: linking individual and metapopulation models. In: McCullough D.R. (ed), *Metapopulations and Wildlife Conservation*. Island Press, Washington, DC, pp. 139–165.
- Oostermeijer J.G.B. 2000. Population viability analysis of the rare *Gentiana pneumonanthe*: the importance of genetics, demography and reproductive biology. In: Young A.G. and Clarke G.M. (eds), *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, UK, pp. 313–334.
- Oostermeijer J.G.B., Berholz A. and Poschlod P. 1996. Genetical aspects of fragmented plant populations. In: Settele J., Margules C.R., Poschlod P. and Henle K. (eds), *Species Survival in Fragmented Landscapes*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 93–101.

- Pascual M.A., Kareiva P. and Hilborn R. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* 11: 966–976.
- Pfenninger M. and Bahl A. 1997. Influence of habitat size on the viability of spatially structured populations of the landsnail *Trochoidea geyeri*. *Verhandlungen der Gesellschaft für Ökologie* 27: 469–473.
- Philippi T.E., Carpenter M.P., Case T.J. and Gilpin M.E. 1987. *Drosophila* population dynamics: chaos and extinction. *Ecology* 68: 154–159.
- Poethke H.J., Gottschalk E. and Seitz A. 1996a. Gefährdungsgradanalyse einer räumlich strukturierten Population der Westlichen Beißschrecke (*Platycleis albopunctata*): Ein Beispiel für den Einsatz des Metapopulationskonzeptes im Artenschutz. *Zeitschrift für Ökologie und Naturschutz* 5: 229–242.
- Poethke H.J., Seitz A. and Wissel C. 1996b. Species survival and metapopulations: conservation implications from ecological theory. In: Settele J., Margules C.R., Poschlod P. and Henle K. (eds), *Species Survival in Fragmented Landscapes*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 81–92.
- Pollard E., Lakhani K.H. and Rothery P. 1987. The detection of density-dependence from a series of annual censuses. *Ecology* 68: 2046–2055.
- Possingham H.P. and Davies I. 1995. ALEX: a model for the viability analysis of spatially structured populations. *Biological Conservation* 73: 143–150.
- Possingham H.P., Davies I., Noble I.R. and Norton T.W. 1992. A metapopulation simulation model for assessing the likelihood of plant and animal extinctions. *Mathematics and Computers in Simulation* 33: 367–372.
- Possingham H.P., Lindenmayer D.B. and McCarthy M.A. 2001. Population viability analysis. In: Levin S.A. (ed), *Encyclopedia of Biodiversity*. Academic Press, London, pp. 831–843.
- Pulliam H.R., Dunning J.B. and Liu J. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2: 165–177.
- Reddingius J. and den Boer P.J. 1970. Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia* 5: 240–284.
- Reed J.M. 1999. The role of behaviour in recent avian extinctions and endangerments. *Conservation Biology* 13: 232–241.
- Reed J.M., Elphick C.S. and Oring L.W. 1998. Life-history and viability analysis of the endangered Hawaiian stilt. *Biological Conservation* 84: 35–45.
- Reich M. and Grimm V. 1996. Das Metapopulationskonzept in Ökologie und Naturschutz: Eine kritische Bestandsaufnahme. *Zeitschrift für Ökologie und Naturschutz* 5: 123–139.
- Richter-Dyn N. and Goel N.S. 1972. On the extinction of a colonizing species. *Theoretical Population Biology* 3: 406–433.
- Ricker W.E. 1975. *Computation and Interpretation of Biological Statistics of Fish Populations*. Fisheries Research Board of Canada Bulletin 191.
- Sæther B.E., Engen S., Islam A., McCleery R. and Perrins C. 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *The American Naturalist* 151: 441–450.
- Samietz J., Berger U. and Köhler G. 1996. A population vulnerability analysis of the stripe-winged grasshopper, *Stenobothrus lineatus* (Caelifera: Acrididae). In: Settele J., Margules C.R., Poschlod P. and Henle K. (eds), *Species Survival in Fragmented Landscapes*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 299–311.
- Schnute J. 1985. A general theory for analysis of catch and effort data. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 414–429.
- Settele J., Margules C., Poschlod P. and Henle K. 1996. *Species Survival in Fragmented Landscapes*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

- Shaffer M.L. 1983. Determining minimum viable population sizes for the grizzly bear. *International Conference on Bear Research and Management* 5: 133–139.
- Shaffer M.L. 1987. Minimum viable populations: coping with uncertainty. In: Soulé M.E. (ed), *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK, pp. 69–86.
- Soulé M.E. 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK.
- Stacey P.B. and Taper M. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2: 18–29.
- Stelter C. 1997. Persistenz von kleinen Schmetterlingspopulationen in dynamischer Landschaft – ein Populationsdynamik-Modell. Cullivier, Göttingen, Germany.
- Stelter C. 1998. Genügt die Modellierung der Habitatqualität durch eine einzige Kapazität, um die Populationsdynamik von Schmetterlingen zu verstehen? *Verhandlungen der Gesellschaft für Ökologie* 28: 161–168.
- Stephan T. and Wissel C. 1994. Auslöschung von Populationen: Ein Modell mit Berücksichtigung einer Ressource. *Verhandlungen der Gesellschaft für Ökologie* 23: 391–397.
- Stephens P.A., Sutherland W.J. and Freckleton R.P. 1999. What is the Allee effect? *Oikos* 87: 185–190.
- Strelbel D.E. 1985. Environmental fluctuations and extinction – single species. *Theoretical Population Biology* 27: 1–26.
- Stubbs M. 1977. Density dependence in life-cycles of animals and its importance in *k*-strategies and *r*-strategies. *Journal of Animal Ecology* 46: 677–688.
- Swart J. and Lawes M.J. 1996. The effect of habitat patch connectivity on samango monkey (*Cercopithecus mitis*) metapopulation persistence. *Ecological Modelling* 93: 57–74.
- Verhulst J.H. 1838. Notice sur la loi que population suit dans son accroissement. *Correspondences mathématiques et physiques* 10: 113–121.
- Vos C.C., Verboom J., Opdam P.F.M. and Ter Braak C.J.F. 2001. Toward ecologically scaled landscape indices. *The American Naturalist* 157: 24–41.
- Vucetich J.A. and Creel S. 1999. Ecological interactions, social organization, and extinction risk in African wild dogs. *Conservation Biology* 13: 1172–1182.
- Wiegand T., Naves J., Stephan T. and Fernandez A. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. *Ecological Monographs* 68: 539–570.
- Wiegand K., Sarre S., Henle K., Stephan T., Wissel C. and Brandl R. 2001. Demographic stochasticity does not predict persistence of gecko populations. *Ecological Applications* 11: 1738–1749.
- Wiegand K., Henle K. and Sarre S. 2002. Extinction and spatial structure in simulation models. *Conservation Biology* 16: 117–128.
- Wiegand T., Revilla E. and Knauer F. 2004. Dealing with uncertainty in spatially explicit population models. *Biodiversity and Conservation* 13: 53–78 (this issue).
- Wissel C., Stephan T. and Zschke S. 1994. Modelling extinction and survival of small populations. In: Remmert H. (ed), *Minimum Viable Populations*. Springer, Heidelberg, Germany, pp. 67–103.
- With K.A. and King A.W. 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13: 314–326.
- Wolfenden G.E. and Fitzpatrick J.W. 1993. Florida scrub jay ecology and conservation. In: Perrins C.M., Lebreton J.-D. and Hirons G.J.M. (eds), *Bird Population Studies*. Oxford University Press, Oxford, UK, pp. 542–565.