

RANKING METAPOPOPULATION EXTINCTION RISK: FROM PATTERNS IN DATA TO CONSERVATION MANAGEMENT DECISIONS

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Abstract. Viability analyses of large metapopulations are often hampered by difficulties in the parameter estimation. This leads to high uncertainty in parameter values and model outputs and complicates the formulation of clear recommendations for conservation management. We present a comprehensive procedure that is able to process spatiotemporal patterns of metapopulation occupancy to rank management scenarios. The first step of the procedure involves the formulation of the stochastic metapopulation model and the estimation of parameter values with a Bayesian approach, using a Markov chain Monte Carlo algorithm. In the second step, the model is used to predict the effects of different management actions, taking into account the uncertainty in the parameter estimates. Finally, in the third step, decision analysis is used to evaluate and aggregate the results of the previous step into a simple rank order of management scenarios. The procedure was applied to a metapopulation of the Glanville fritillary, *Melitaea cinxia*. Although the amount of available occupancy data was considerable, the uncertainty in the estimated model parameter values was so large that a precise estimate of the extinction risk of the metapopulation could not be made. However, the procedure was able to produce a rank order of management scenarios that was extraordinarily robust to the uncertainty. Application of the procedure to two other case studies revealed that, even though robust rankings cannot always be obtained, the results of the procedure are helpful in assessing the degree of uncertainty in the ranking and pointing to those factors most responsible for the lack of robustness. The results of this paper demonstrate very clearly, by way of example, both the limitations and the possibilities of model-based metapopulation viability analysis.

Key words: Bayesian analysis; extinction risk; Glanville fritillary; incidence function model; Markov chain Monte Carlo; *Melitaea cinxia*; metapopulation; multicriteria analysis; outranking; robustness; simulation model; uncertainty.

INTRODUCTION

Population modeling, as a part of population viability analysis (PVA), has become a well-established field in conservation biology. Most studies are concerned with either single populations or metapopulations with a moderate number of local populations. Viability analyses of larger metapopulations are hampered by two problems. First, it is difficult to rigorously estimate model parameters, and typically the uncertainty in the estimated parameter values is high. Second, exhaustive sensitivity analyses are necessary to understand the behavior of the model, but their results are difficult to interpret, especially if the parameters are poorly estimated.

In this paper, we introduce and demonstrate a comprehensive and general procedure for comparing different management actions. This procedure is able to cope with the problems of PVA and allows the ranking

of landscape scenarios with respect to the viability of metapopulations in the presence of uncertainty. Our procedure consists of three steps, starting with the analysis of field data and ending with the construction of a rank order of scenarios. The first step involves the formulation of the model and the estimation of parameter values, including their uncertainty. In the second step, the model and estimated parameter values are used to predict the effects of different landscape scenarios on persistence, taking into account the uncertainty in the parameters. Finally, in the third step, the results of the previous step are evaluated and aggregated into a simple rank order of scenarios that can be easily used by conservation managers and decision makers. As some of the details of the individual steps have already been described in previous papers (Hanski 1999, O'Hara et al. 2002), the primary focus of the present paper is on the procedure as a whole.

The data on which the analysis is based consist of patterns of occupancy of habitat patches of a metapopulation over several years. It is therefore appropriate to focus the modeling on extinction–colonization

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dynamics. Specifically, we will use the incidence function model (IFM; Hanski 1994, 1999), which is a stochastic patch occupancy model. The basic idea of the IFM is to relate the processes of local extinction and recolonization of empty habitat patches to the key landscape variables, typically the area and connectivity of the patches. The model parameters summarize the biology of a species, such as its extinction proneness in habitat patches of given size and its range of colonization. The model parameters are estimated from the observed occupancy patterns using a Bayesian approach (O'Hara et al. 2002). An important feature of the Bayesian analysis is that it provides probability distributions for the parameters, rather than just point estimates. This is important, because such distributions and the uncertainty that they summarize are indispensable when an honest judgement is made about whether or not the data are sufficient to support a particular decision.

The IFM has five parameters, which means that the Bayesian analysis will produce a five-dimensional probability distribution for where we believe the parameters to be. The estimation is carried out numerically, using a Markov chain Monte Carlo algorithm, which draws a large number of parameter combinations from the distribution. Each parameter combination is equally compatible with the observed pattern and thus has to be considered with equal weight in the model analysis (a region of the parameter space that is more compatible is represented by having more parameter combinations drawn from that region). For each parameter combination, the metapopulation dynamics are predicted using well-known Monte Carlo simulation techniques (e.g., Goel and Richter-Dyn 1974, Burgman et al. 1993) to assess the probability of the metapopulation surviving the period of time of interest.

The analysis of many parameter combinations and landscape scenarios produces a large amount of output that has to be translated into management recommendations. Possingham et al. (2001a) and others have concluded that PVA would be most effective when used to support management decisions, for instance, to rank the consequences of different management actions with respect to a specific objective. To achieve this goal, it is preferable to link the model analysis with decision analysis (Maguire 1986, Ralls and Starfield 1995, Drechsler 2000, Possingham et al. 2001b). A major problem in conservation biology is that the impacts of human action are often small compared to the uncertainty in the data, and it is hence difficult in an environmental impact assessment to demonstrate the influence of certain human actions. As in most public decision making, the burden of proof usually lies with those stakeholders representing the interests of conservation. Thus, it is particularly important to exploit the scarce information available as efficiently as possible and to produce results that are as robust as possible. Here we will demonstrate that decision analysis

can considerably increase the robustness of conclusions derived from population viability analysis.

In the following sections, we describe the management problem, the model, the technique of parameter estimation, and the analysis and aggregation of model results by means of a decision analysis. We then apply this entire chain of steps to the particular data set used to demonstrate how the procedure works in practice. Following the analysis of this "pilot example," we briefly present and investigate two supplementary case studies to demonstrate the general applicability of the approach.

The management problem (pilot example)

As an example, we use a metapopulation of the Glandville fritillary butterfly, *Melitaea cinxia*, in the Åland Islands in southwestern Finland. This species has been the focus of a large-scale study since 1991 (summarized in Hanski 1999). The landscape is naturally highly fragmented, with the suitable habitat for the butterfly consisting of small dry meadows with the larval host plants *Plantago lanceolata* and *Veronica spicata*. There are altogether ~4000 such meadows in the Åland Islands, but here we focus on one particular patch network with 48 habitat patches that is relatively independent of the rest of the system dynamically. Fig. 1 shows the spatial configuration of the 48 patches in the focal network.

In our hypothetical management problem, we will focus on four components of the network: the three patches in the upper left corner of the network (Fig. 1, shape 1), the set of small patches in the middle of the network ("stepping stones," shape 2), and the cluster of patches in the lower right corner, which we have further divided into a left and a right component (shapes 3 and 4, respectively). We assume that some management actions may destroy some of the patches in the network. The key question is which of these hypothetical actions is most adverse to the survival of the metapopulation in the network. We compare four different scenarios: (1) removal of the three patches in shape 1; (2) removal of the eight stepping stone patches (shape 2); (3) removal of the three biggest patches in shape 3; and (4) removal of the three biggest patches in shape 4.

Readers who are familiar with metapopulation theory may have an intuition as to which management action would be most, and which one would be least, harmful to the long-term persistence of the species, but clearly such feelings would not be sufficient for management recommendations and, indeed, they might turn out to be wrong.

METAPOPOPULATION MODEL AND PARAMETER ESTIMATION

We use a discrete-time Markov chain model to describe the stochastic dynamics of the metapopulation in a network of N patches. The state of the metapopulation, $\underline{q} = (q_1, \dots, q_N)$, is determined by the states

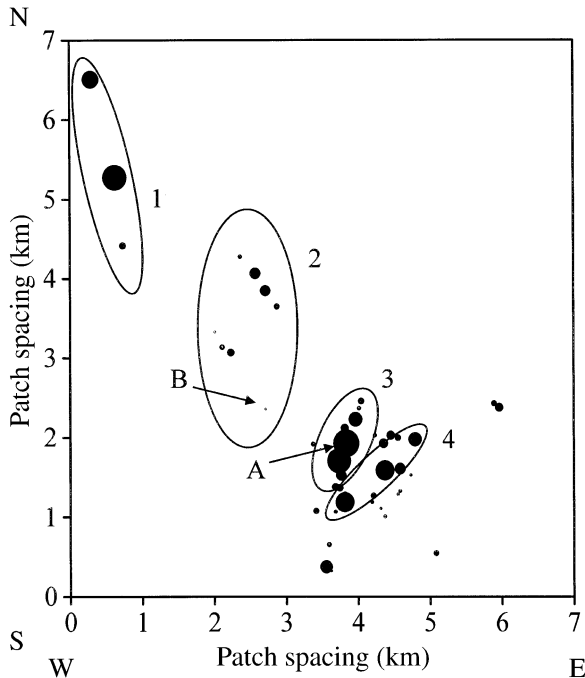


FIG. 1. The network of habitat patches of the pilot example for *Melitaea cinxia*, the Glanville fritillary. The coordinates on the axes give the east–west and north–south locations of the patches in the landscape; the scale is in kilometers. The sizes of the dots indicate the sizes of the patches, with the largest patch (arrow A) having an area of 0.91 ha and the smallest one (arrow B) having an area of 0.01 ha. The elliptical shapes and numbers are used to define landscape scenarios (see *Introduction: The management problem*).

q_i of the patches in the network. Each patch is assumed to be either occupied by a local population ($q_i = 1$) or empty ($q_i = 0$). The occupancy state of the patches may change at yearly intervals.

The probability that a currently empty patch becomes occupied (C, colonized) within one year is given by

$$P_{C,i} = 1 - \exp(-ys_i). \quad (1)$$

The parameter y is the inverse of the number of immigrants needed for a 63% chance of a successful recolonization. The quantity s_i represents the mean number of individuals immigrating into patch i in one year. We assume that it is given by

$$s_i = \sum_{j:q_j=1} A_j^b \exp(-\alpha d_{ji}) \quad (2)$$

(Hanski 1994) where the sum is taken over the patches j that are currently occupied by a local population and therefore are able to contribute to the recolonization of patch i . For each occupied patch, the number of emigrants from the patch is assumed to be related to patch area (A) through a power function with parameter b . The probability of an emigrant from patch j successfully reaching patch i is assumed to decline exponentially with the distance d_{ji} between the two patches, with the mean distance moved being α^{-1} . Note that the

probability that an empty patch is recolonized after one year is conditioned on the current occupancy state $\underline{q} = (q_1, \dots, q_N)$ of the whole metapopulation.

The probability of a currently occupied patch i becoming empty (E) within one year is given by

$$P_{E,i} = \min(1, e_i)(1 - P_{C,i}) \quad (3)$$

(Hanski 1994, 1999). The quantity e_i can be related to patch area A_i in a canonical way (Hanski 1994, Wissel et al. 1994, Foley 1997):

$$e_i = (A_0/A_i)^x. \quad (4)$$

This relation assumes that a larger patch can sustain a larger and, hence, more persistent, local population (Hanski 1994, 1999). The parameter A_0 is the critical patch area below which the annual extinction probability $P_{E,i}$ is one, while the power x is a measure of the strength of the environmental stochasticity (Hanski 1994, 1999). The weaker the fluctuations in the local population growth rate, the larger the value of x (Lande 1993, Hanski 1994, Wissel et al. 1994), and therefore the more the local population can benefit from an increase in the area of the patch. The second term on the right-hand side of Eq. 3 ($1 - P_{C,i}$) represents the rescue effect, i.e., it allows for immigration to reduce the probability of extinction (Hanski 1999).

In order to apply the model to our study system, the Glanville fritillary metapopulation shown in Fig. 1, the network-specific model parameters (α , b , x , y , and A_0) have to be estimated. Parameter estimation was done with the method described by O'Hara et al. (2002), which utilizes presence–absence data and yields a distribution of appropriate parameter combinations (α , b , x , y , and A_0). The heart of this method is a Bayesian analysis of the sequence of presence–absence snapshots of habitat patch occupancy. In addition to the model, one needs to specify prior distributions for the parameters, i.e., our guesses about the likely parameter values, based on previous knowledge. These values are combined with the data using Bayes' rule:

$$\Pr(\theta|r) = \Pr(\theta) \times \Pr(r|\theta) \quad (5)$$

where $\Pr(\theta|r)$ is the posterior distribution, i.e., where we think the parameters (θ) lie after we have obtained the data (r). This is a combination of where we think the parameters lie before we have the data, which is given as the prior distribution ($\Pr(\theta)$), and the contribution of the data (and the model) to our knowledge about the parameter, which is expressed through the likelihood ($\Pr(r|\theta)$).

It is not feasible to find an analytic expression for the posterior density of the parameters of the model. We therefore used a numerical method, Markov chain Monte Carlo (Gilks et al. 1996), to estimate the distribution of parameter values. The output from this analysis consists of a large number of parameter values drawn from the posterior distribution. All parameters were given exponentially distributed priors with mean

1. This is the simplest assumption for the priors. For real-life problems, one could choose more sophisticated prior distributions, reflecting genuine knowledge about the system (see O'Hagan [1998] for a discussion of approaches to choosing or "eliciting" prior distributions). For the estimation, five chains were run; after a "burn-in" of 5000 iterations, every 100th of the next 20 000 estimates was taken to give a total of 1000 draws from the posterior distribution. Further details about parameter estimation are given in O'Hara et al. (2002). The data used to estimate the values of the five model parameters (α , b , x , y , and A_0) consist of the observed occupancy patterns of the Glanville fritillary in the network shown in Fig. 1 from 1993 to 2000.

MODEL PREDICTIONS

We are interested in estimating the viability of the metapopulation for a given combination of model parameters (α , b , x , y , A_0) and a given spatial pattern of habitat patches in the network (Fig. 1). As a time frame in our analysis, we use 20 years and calculate the probability of the metapopulation surviving for this time. We calculate this probability with many stochastic simulations of the model, starting with all patches being occupied.

The metapopulation dynamics are simulated for 20 years using standard Monte Carlo techniques (e.g., Goel and Richter-Dyn 1974, Burgman et al. 1993, Hanski 1999). At the end of each simulation, it is recorded whether the metapopulation has survived or gone extinct. For each parameter combination and landscape scenario, the simulation is repeated $L = 1000$ times; the fraction of these 1000 replicates in which the metapopulation survived is the probability of survival, P .

THE DECISION ANALYSIS

The Bayesian analysis does not provide a point estimate for each of the five model parameters, but instead a large number of parameter combinations compatible with the observed occupancy pattern. If we use these combinations to determine the survival probability, P , of the metapopulation, we obtain a range of values, one for each parameter combination. Similarly, for each parameter combination we can determine the metapopulation survival probability for each of the four landscape scenarios described in the section *The management problem*. For each parameter combination, we can compare the different landscape scenarios by ranking them with respect to the probability of metapopulation survival, P . Because the rank orders may differ and we do not know which parameter combination is the correct one, we are faced with a decision problem under uncertainty.

Formally, this particular decision problem can be regarded as a typical multicriteria decision problem (e.g., Bana e Costa 1990, Stewart 1992, Gal et al. 1999) in which a number of objects or alternatives must be ranked with respect to a number of criteria or objec-

TABLE 1. Multicriteria matrix with the metapopulation survival probabilities P_{ij} obtained for each of the four scenarios S_j ($j = 1 \dots 4$) for three selected parameter combinations ($i = 1 \dots 3$) from the metapopulation example for *Melitaea cinxia*.

Parameter combination, i	Survival probabilities, P_{ij}			
	S_1	S_2	S_3	S_4
1	0.423	0.497	0.124	0.287
2	0.212	0.250	0.046	0.155
3	0.088	0.076	0.008	0.046

tives. In the present case, each parameter combination can be regarded as a criterion. In multicriteria decision analysis (MCDA), the values of the alternatives in the various criteria are presented in a multicriteria matrix. Here these values are the survival probabilities of the metapopulation (Table 1).

In MCDA, there can be conflicts between different criteria, such that an alternative that is relatively good according to one criterion may be relatively bad by another criterion. In the same way, a scenario that is of relatively little harm, assuming one set of parameters, may be very bad for some other set of parameters. One task of MCDA is to identify an overall rank order of alternatives that agrees best with as many single-criterion rank orders as possible, i.e., to identify some kind of compromise solution. In the present study we are interested in a rank order of landscape scenarios that is compatible with as many parameter combinations as possible. In MCDA, decision makers often may feel that some criteria are more important than others and may give these higher weights in the search for a compromise rank order. In the present study, we have no reason to prefer one parameter combination (criterion) to another, so all parameter combinations receive equal weight.

Another task of MCDA is to identify how much conflict there is between the different criteria and the rank orders they produce. In particular, it is of interest to know how well the compromise rank order agrees with all single rank orders produced for the individual parameter combinations. In our case we want to know how robust the rank orders of landscape scenarios are with respect to the uncertainty of not knowing which parameter combination is the correct one.

The first task of MCDA can, by definition, be achieved by any method of MCDA, be it a utility-based method or a so-called outranking method (e.g., Bana e Costa 1990, Stewart et al. 1992, Gal et al. 1999). The second task can very conveniently be achieved with an outranking method. In this study we used the PROMETHEE method (Brans and Mareshal 1990), which is the simplest member of the family of outranking methods. The basic idea in PROMETHEE is to compare all actions separately and in a pairwise manner for each of the n criteria. The winner of such a pairwise comparison, i.e., the scenario with the most favorable re-

TABLE 2. Partial preference matrix with the pairwise preferences that refer to the survival probabilities for the first parameter combination in Table 1.

	S_1	S_2	S_3	S_4
S_1	0	0	1	1
S_2	1	0	1	1
S_3	0	0	0	0
S_4	0	0	1	0

Note: The numbers in the first row mean that scenario S_1 is not preferred to itself (by definition), not preferred to S_2 , but preferred to S_3 and S_4 (as it produces the higher survival probability).

sult, gains one point (is preferred) whereas the loser gets nothing (no preference). In a draw, no points are given at all (indifference). If we consider the first parameter combination in Table 1, with metapopulation survival probabilities $P_{12} > P_{11} > P_{14} > P_{13}$, then for this parameter combination (criterion) C_1 we obtain the pairwise preferences given in Table 2. This table is called the partial preference matrix for parameter combination (criterion) C_1 .

In the application of this concept to the results of the metapopulation model simulations, one must consider that the simulation results are subject to error. In a binary variable P , such as the survival probability, the simulation error is given by $[P(1 - P/L)]^{0.5}$ where L is the number of replicates (Sokal and Rohlf 1981). In the present study we have $L = 1000$ (see the section *Model predictions*); thus, the simulation error in each estimated survival probability P may be up to ~ 0.01 . In other words, we can distinguish scenarios only if the survival probabilities that they produce differ by more than 0.01. Within the decision-making framework, this means that one scenario is preferred to another only if the survival probability it produces exceeds that of the other scenario by at least 0.01. Otherwise both scenarios are considered as indifferent.

Pairwise preferences are calculated for all n parameter combinations and all scenarios, leading to a total of n partial preference matrices. These matrices are then added together to obtain a total preference matrix. For the example in Table 1 with the three parameter combinations $i = 1 \dots 3$ and the four landscape scenarios S_j ($j = 1 \dots 4$), we obtain the total preference matrix shown in Table 3.

The total preference matrix still needs to be evaluated in order to generate a rank order of landscape scenarios. First we take the row sums, F^+ . The sum of the first row is a count of how often (i.e., in how many parameter combinations) scenario S_1 is preferred to another scenario. If there are $m = 4$ scenarios and $n = 3$ criteria (parameter combinations), the maximum value that F^+ can assume is $n(m - 1) = 9$, which we would obtain if S_1 won the pairwise comparisons against all other scenarios in all criteria. In the same way, the other two rows are evaluated. Naturally, the larger the value of F^+ , the better the rank of the scenario

and we obtain: $S_2 > S_1 > S_4 > S_3$ where “ $>$ ” means “is better than.”

Alternatively, we can consider the column sums (F^-). The sum of the first column is a measure of how often another scenario is preferred to scenario S_1 . Again the possible maximum is $n(m - 1)$. The other two columns are assessed in the same manner. Naturally, a smaller value of F^- means that the scenario is better, and we obtain the same rank order of scenarios as previously shown.

Both rank orders are equally valid, in the sense that decisions based on either rank order are equally justifiable. In the application of PROMETHEE, it may happen that the two rank orders lead to contradictory results: in one rank order we obtain the result $S_u > S_v$ and in the other $S_v > S_u$. In this case, the two alternatives are called incomparable, i.e., it cannot be decided which one is better. A necessary mathematical condition for incomparability is that there are pairs of scenarios, S_u and S_v , such that the total preference of S_u over S_v plus the total preference of S_u over S_v is not constant. Otherwise, if $a_{ij} + a_{ji}$ is identical for all elements a_{ij} of the total preference matrix ($i, j = 1 \dots m; m = 4$), the sum $F^+ + F^-$ is identical for all scenarios and F^+ contains exactly the same information as F^- (Table 3 is an example of such a case). In the metapopulation example, if there were no simulation error (an infinite number of simulation replicates, L), then $a_{ij} + a_{ji}$ would equal the number of parameter combinations for all elements a_{ij} of the total preference matrix (cf. Table 3) and no incomparability would be possible. Only simulation error can reduce $a_{ij} + a_{ji}$. Thus, in the metapopulation example, incomparability can be avoided by reducing simulation error through an increased number of replicates, L .

RESULTS OF THE METAPOPOPULATION
VIABILITY ANALYSIS

Parameter estimation

The analysis produced a five-dimensional cloud of 1000 points, each being a plausible parameter combination. In some regions of the parameter space, the points occur more densely, indicating that parameter values in these regions have a higher posterior probability than those in the sparser regions. We can calculate several statistics from this five-dimensional like-

TABLE 3. Total preference matrix based on the three parameter combinations from Table 1.

	S_1	S_2	S_3	S_4	F^+
S_1	0	1	3	3	7
S_2	2	0	3	3	8
S_3	0	0	0	0	0
S_4	0	0	3	0	3
F^-	2	1	9	6	

Note: The last column and row give the row sums (F^+) and the column sums (F^-), respectively.

TABLE 4. Medians and bounds of the 95% confidence intervals of the model parameters.

Bounds and median	Parameters				
	α (km)	b	x	y	A_0 (ha)
Upper 95% confidence bound	0.812	4.140	0.606	0.219	0.031
Median	0.395	2.493	0.369	0.136	0.014
Lower 95% confidence bound	0.107	1.267	0.192	0.078	2.20×10^{-3}

Notes: Parameter α is the inverse dispersal distance; A_0 is the critical patch area. Parameters b and x are the exponents characterizing the relationships between patch area and emigration (Eq. 2) and between patch area and local extinction (Eq. 4), respectively. Parameter y is the inverse of the number of immigrants needed for a 63% chance of a successful recolonization (Eq. 1).

likelihood distribution. Basic results are given in Table 4. The variation in the parameter estimates (cf. Eqs. 1–4) is quite dramatic: mean dispersal distance (α), number of immigrants required for successful colonization ($1/y$), and critical patch size (A_0) below which annual extinction probability is one vary by an order of magnitude. The relationship between emigration rate and patch area ranges from a linear ($b \approx 1$) to a strong, quartic ($b \approx 4$) form and patch area can have a very weak ($x \approx 0.2$) or median ($x \approx 0.6$) influence on local extinction. It can be expected that these parameter uncertainties have a considerable effect on the results of the model simulation.

Rank order of the four landscape scenarios

For each of the 1000 plausible parameter combinations produced from the Bayesian model fitting, the metapopulation survival probability was calculated for each of the four landscape scenarios. The most straightforward way of summarizing the outcome under the four scenarios is to determine the means and 95% confidence intervals for the metapopulation survival probability over all parameter combinations (Table 5).

The results in Table 5 indicate that only a very approximate estimate for the metapopulation survival probability can be obtained. For instance, the range of survival probabilities under scenarios S_1 or S_2 covers almost the entire interval $[0, 1]$, i.e., from certain extinction to certain survival. The data uncertainty is too high to accurately assess the viability of the metapopulation!

Looking at the mean survival probabilities, the highest value is found for scenario S_2 , followed by that under scenarios S_1 , S_4 , and S_3 . However, the differences between the survival probabilities are much smaller than the range of the confidence intervals. This means

TABLE 5. Metapopulation survival probability (mean and bounds of 95% confidence interval) for scenarios S_1 – S_4 .

Bounds and mean	Survival probability, P_{ij}			
	S_1	S_2	S_3	S_4
Upper 95% confidence bound	0.71	0.80	0.32	0.50
Mean	0.26	0.30	0.07	0.15
Lower 95% confidence bound	0.02	0.02	0.00	0.01

that these scenarios may not differ significantly in their effects. Again, the uncertainty in the data is too great to clearly distinguish the scenarios and even a relative assessment is not possible.

A clearer rank order can be obtained using the multicriteria approach outlined in the section *The decision analysis*. To do this, we regard each of the 1000 parameter combinations as an individual criterion. A scenario is better (less adverse) than another if in (almost) all criteria (parameter combinations) it produces a higher metapopulation survival probability than the other scenarios. The multicriteria analysis starts with a matrix with four columns and 1000 rows, where each element gives the metapopulation survival probability for the scenario in the corresponding column and the parameter combination in the corresponding row. Doing the appropriate calculations, we obtain the total preference matrix given in Table 6.

The results show that the least adverse landscape scenario with the highest F^+ value is scenario S_2 , followed by scenarios S_1 , S_4 , and S_3 . The same rank order is produced by the F^- values. The final rank order therefore is

$$S_2 > S_1 > S_4 > S_3.$$

This is the same rank order as in Table 5, but note that the result in Table 6 is much more conclusive. In Table 5 the scenarios S_1 and S_2 differ by only 4%, whereas in Table 6 scenario S_2 receives a score of 2835 out of 3000 (F^+) compared to S_1 with a score of 2022. On this basis, we may unambiguously conclude that scenario S_2 is better than scenario S_1 . An even stronger

TABLE 6. Total preference matrix for the four scenarios.

Scenario	Scenario				F^+	Rank
	S_1	S_2	S_3	S_4		
S_1	0	54	994	974	2022	<i>2</i>
S_2	856	0	994	985	2835	<i>1</i>
S_3	0	0	0	1	1	<i>4</i>
S_4	0	0	971	0	971	<i>3</i>
F^-	856	54	2959	1960		
Rank	<i>2</i>	<i>1</i>	<i>4</i>	<i>3</i>		

Notes: The boldface numbers indicate that, in 856 (54) parameter combinations, scenario S_2 (S_1) outperforms S_1 (S_2). Scenario rankings are italicized.

TABLE 7. Total preference matrix for the three scenarios of supplementary case study 1, another patch network for *Melitaea cinxia*.

Scenario	Scenario			F^+	Rank
	S_1	S_2	S_3		
S_1	0	60	84	144	<i>1</i>
S_2	39	0	98	137	<i>2</i>
S_3	16	0	0	16	<i>3</i>
F^-	55	60	182		
Rank	<i>1</i>	<i>2</i>	<i>3</i>		

Note: Scenario ranks are italicized.

argument for this conclusion comes from the direct comparison of the two scenarios (boldfaced numbers in Table 6): 856 out of 1000 parameter combinations support the ranking $S_2 > S_1$, whereas there are only 54 “votes” for the ranking $S_1 > S_2$. In the remaining 90 parameter combinations, simulation error is too high to rank S_1 and S_2 . Similarly, 974 against 0 parameter combinations support $S_1 > S_4$, and 971 against 1 parameter combinations support $S_4 > S_3$. In brief, the rank order derived from Table 6 can be regarded as very robust to the uncertainty in the model parameters. An identical rank order with the same robustness is found for longer time horizons of 40 and 100 years as well.

APPLICATION OF THE RANKING METHOD TO OTHER EXAMPLES

The ranking of the scenarios in the previous case study is surprisingly robust to the uncertainty in the model parameters. This may not always be the case; it is of interest to know how the modeling and ranking approach that we have presented can be applied to cases in which the ranking is less robust. We will briefly analyze two more case studies in which high model parameter uncertainty obstructs the ranking of scenarios. The first case study is another patch network for *Melitaea cinxia* on the Åland islands. It consists of 67 patches that are arranged in a longish s-shaped manner and whose areas range from $2.5(10^{-3})$ to 1.1 ha (median ~ 0.5 ha). We considered three simple scenarios: remove the four largest patches (S_1); remove all but the four largest patches (S_2 ; “complement” to S_1); and halve the sizes of all 67 patches (S_3). It should be noted that the four remaining large patches in scenario S_2 are all relatively far apart from each other.

We determined 100 parameter combinations from the observed occupancy pattern and used them to rank the three scenarios S_1 – S_3 . Table 7 shows the total preference matrix. While scenario S_3 is clearly dominated by the other two scenarios, S_1 and S_2 perform very similarly, with S_1 having a slightly higher row sum F^+ and lower column sum F^- than S_2 . This suggests that parameter uncertainty is too high to obtain a robust ranking between these two scenarios; indeed, in 60 parameter combinations S_1 is better than S_2 and in 39 parameter combinations it is the other way round.

In such a situation, the decision analysis cannot provide a conclusive ranking, but it can quantify the degree of uncertainty in the ranking. It can also point to the main source of uncertainty. In a simple statistical analysis, we related the difference between the metapopulation survival probabilities for scenarios S_1 and S_2 (i.e., the performance of S_1 relative to that of S_2) to the magnitude of the model parameter values. We found quite a strong correlation with model parameters y and b (0.71 and 0.83, respectively), such that whenever y and b are large, scenario S_1 tends to be favored. In particular, if $y > 0.1$ and $b > 1$, scenario S_1 is most likely to outperform S_2 ; for $y < 0.1$ and $b < 1$, it is the other way around (Fig. 2). Therefore, the uncertainty in the ranking between S_1 and S_2 can be reduced most effectively by reducing the uncertainty in the parameters y and b .

The explanation for why the value of model parameter b sensitively affects the ranking of scenarios S_1 and S_2 is fairly simple. To maximize the probability of recolonization of an empty patch, the number of immigrants has to be maximized, which can be achieved by either having many small sources of dispersers in the neighborhood (scenario S_2) or few large disperser sources far away (S_1). Within the scope of the metapopulation model (Eqs. 1–4), naturally, the stronger the dependence of emigration on patch size is (i.e., the larger b), the more favorable are few large distant patches compared to many small near ones. The role

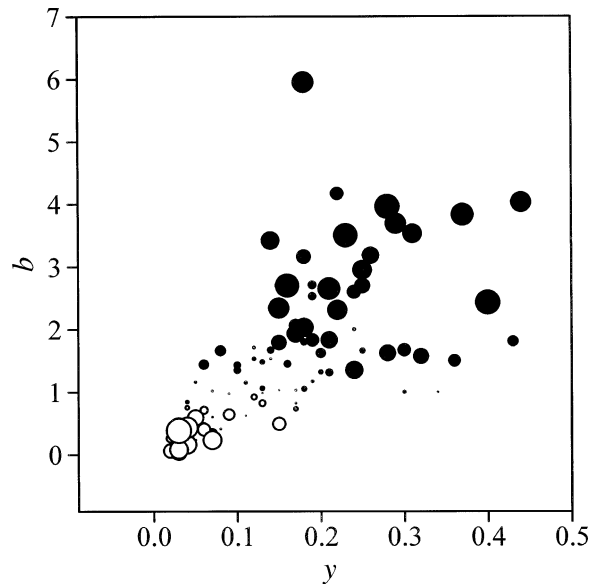


FIG. 2 Scatter plot of the values for the model parameters y and b for the first supplementary case study. Each circle represents one of the 100 parameter combinations produced by the Bayesian analysis. Closed circles mean that scenario S_1 outperforms S_2 , and open circles mean the opposite. The sizes of the circles indicate the absolute value of the difference between the metapopulation survival probabilities of scenarios S_1 and S_2 , i.e., how strongly the performances of S_1 and S_2 differ.

TABLE 8. Preference matrix for four actions (*A*, increase fecundity of breeding females; *B*, increase annual population survival; *C*, increase number of nest sites; *D*, increase size of wintering habitat), for the Orange-bellied Parrot *Neophema chrysogaster*.

Action	Action				<i>F</i> ⁺	Rank
	<i>A</i>	<i>B</i>	<i>C</i>	<i>D</i>		
<i>A</i>	0	0	1	0.55	1.55	<i>2</i>
<i>B</i>	1	0	1	1	3.00	<i>1</i>
<i>C</i>	0	0	0	0.47	0.47	<i>4</i>
<i>D</i>	0.45	0	0.53	0	0.98	<i>3</i>
<i>F</i> ⁻	1.45	0.00	2.53	2.02		
Rank	<i>2</i>	<i>1</i>	<i>4</i>	<i>3</i>		

Note: Action rankings are italicized.

of the number of immigrants required for successful recolonization ($1/y$) is less obvious. In general, it may be difficult to identify the ecological reason for the impact of a certain model parameter on a particular ranking. Nevertheless, even if a ranking is not robust, the ranking procedure can be a valuable decision aid to conservation managers by pointing to those issues that are most relevant to the management decision.

In the second supplementary case study, Drechsler (2004) ranked four different management actions to increase the viability of the endangered Orange-bellied Parrot *Neophema chrysogaster* in southeastern Australia: increase of the fecundity of breeding females (*A*); increase of mean annual population survival (*B*); increase of the number of nest sites (*C*); and increase of the size of winter habitat (*D*) (for details about the population model analysis, see Drechsler et al. [1998]). In a rather heuristic manner, a small number of “key parameter combinations” and their corresponding likelihoods (i.e., probabilities of correctly describing the real population) were determined. For each key parameter combination, the impacts of the four actions were determined and a partial preference matrix was established as described. The preference matrices were added, but in contrast to the previous two case studies, the partial preference matrices were weighted; i.e., before the summation, each partial preference matrix was multiplied by the likelihood of the corresponding parameter combination. The resulting total preference matrix, Table 8, shows that action *B* clearly outperforms all of the other actions, whereas the ranking “*A* > *D*” and the ranking “*D* > *C*” is not robust at all. Similar to the previous case study, the analysis identified which management actions can be ranked conclusively and which cannot. If it turned out, for some reason, to be necessary to decide between actions *A* and *D*, more information on the species would have to be collected before a safe decision could be made.

DISCUSSION

We have presented a procedure that integrates all three essential components of a model-based conservation effort: the development and parameterization of

an appropriate model; the fitting of the model to data; and the aggregation of model results into a ranking of the alternative conservation or management actions. The analysis was applied to habitat patch occupancy data for the Glanville fritillary butterfly living in a fragmented landscape, and it produced a robust ranking of the alternatives.

In our example, the estimated values of the model parameters turned out to be subject to considerable uncertainty, with the posterior distribution of the parameters having a large variance. In the predictions from the metapopulation model, the uncertainty in the parameter estimates translated into large uncertainty in the predicted probability of metapopulation survival. These probabilities ranged practically over the entire unit interval, from certain metapopulation extinction to certain survival.

Uncertainty has rightly been regarded as one of the major problems in PVA, and the great uncertainty that typically characterizes results has caused several authors to be pessimistic about the applicability of PVA in the assessment of population extinction risk (e.g., Taylor 1995, Beissinger and Westphal 1998). However, estimating population lifetimes or extinction risks is only one, and arguably not the most useful, purpose of PVA. The more practical and helpful goal is the comparison of management actions to obtain the one that maximizes the viability of a (meta)population. It has been suggested that such rank orders are more robust to uncertainties than are absolute estimates of population lifetimes or extinction risks (e.g., Hanski 1999, Possingham et al. 2001a), but this suggestion has never before been tested properly.

We used multicriteria decision analysis (MCDA) to calculate the rank order of four hypothetical landscape scenarios with respect to their effect on the survival probability of the Glanville fritillary metapopulation. The rank order produced by MCDA indeed turned out to be much more robust than that derived from an independent analysis of the individual landscape scenarios (compare Tables 5 and 6). The reason is that not all of the uncertainty occurring in the data is really affecting the ranking of the landscape scenarios, although it does affect the probability of survival. MCDA served to extract from the vast amount of uncertain data the tiny bit of relevant information: the relative effects of the landscape scenarios on the species.

Even though the procedure was able to extract the relevant component of the uncertainty, it does not necessarily produce robust rank orders in all instances. We outlined two examples in which uncertainty was too high to rank all scenarios. Here the presented modeling and ranking procedure cannot give a definite answer to the decision problem. However, even in these two cases, the method proved useful by identifying those pairs of scenarios whose rankings are not robust, and by providing a quantitative measure of the degree of uncertainty in these rankings. This helps the decision

maker to determine whether the current ranking is sufficiently robust or whether more information is required before a decision can be made. In the latter case, the results of the MCDA can be the basis of a statistical analysis that points to those factors that are most responsible for the ambiguity in the ranking and indicates where additional research should be concentrated.

Although the procedure presented here can deal with the problem of statistical uncertainty, it cannot solve problems concerning systematic errors. Such errors may arise from an incorrect model structure or biases in the field data. They can best be eliminated by further research to identify the most appropriate model structure and to improve the quality of the data. These considerations highlight the importance of qualitative knowledge about the ecology of the species in the assessment of human impacts and conservation measures.

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