Using surrogate data in population viability analysis: the case of the critically endangered cranberry fritillary butterfly

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Population viability analyses (PVA) are central tools for the management of threatened populations. However, the parameterisation of effective PVA models is very demanding in high quality data, which are often impossible to collect on endangered populations. Here we propose the use of a generalisation strategy to bypass this limitation: management measures for an endangered metapopulation of the cranberry fritillary butterfly in the Netherlands are evaluated with RAMAS/GIS by using parameters estimated from a healthier metapopulation in Belgium. The Belgian metapopulation seems viable, with stable abundance and number of local populations, despite their erratic dynamics, whereas the Dutch metapopulation shows a continuous decline in the course of time, with many vacant habitat patches. Simulations of various scenarios indicated that (1) large scale restoration of habitat patches would be necessary to ensure long-term survival of the species in the Netherlands as not enough suitable habitats are currently remaining; and that (2) global warming is expected to put a major threat on both metapopulations by reducing the growth rate of this glacial relict species, and/or increasing environmental stochasticity (amplified climatic variations).

“Rarity precedes extinction” was already pointed out by Darwin nearly 150 years ago (Darwin 1859), and this assertion is more and more topical considering the current biodiversity crisis where a high proportion of all Earth’s species could disappear if nothing is done to protect them and their habitats (Pimm and Raven 2000). Management of threatened populations will be necessary to guarantee long-term survival of endangered species and ecosystems (Beissinger and Westphal 1998, Reed et al. 2002). Population viability analysis (PVA: Beissinger and McCullough 2002, Morris and Doak 2002) is becoming an ever more central tool in conservation biology. In a PVA, biological and landscape data are used to parameterise a population model which projects the dynamics, abundance and (meta)population structure of a focal threatened species into the future. From these projections, viability is estimated and compared under different scenarios of landscape or population management to design effective conservation guidelines.

We focus here on the cranberry fritillary Boloria aquilonaris (Stichel), a glacial relict specialist butterfly in western Europe, where it is restricted to active peat bogs with Vaccinium oxycoccos (L.), the only host-plant of caterpillars in this part of its distribution area. The distribution of these habitats is boreo-alpine: they are restricted to regions where altitude or the proximity of oceans provide the cold and wet climatic conditions necessary for peat formation, and are therefore naturally fragmented both at the regional and the landscape scale.
(Mousson et al. 1999, Vandewoestijne and Baguette 2002, Baguette and Schtickzelle 2003). This natural fragmentation has been enhanced at the landscape scale by human activities (mainly peat bog drainage and afforestation with conifers) and as a consequence B. aquilonaris has rapidly declined in western Europe since 1950 (Baguette et al. 1992, Mousson et al. 1999, Wallis de Vries 2003). In Belgium, it is present in a few (25) localities on four uplands; nevertheless the majority are located in the same landscape (The Plateau des Tailles upland), which is therefore the key area for its persistence in Belgium (Mousson et al. 1999). The situation in the Netherlands is even worse: B. aquilonaris is currently only found in a population network in the Drenthe region (Wallis de Vries 2003). This network has only been known since 1963 and earlier records from species with similar habitat suggest that colonisation occurred not much before that date from source populations >25 km away.

In a previous paper (Baguette and Schtickzelle 2003) on metapopulation dynamics of B. aquilonaris, we observed the local extinction of a large population and huge variations in growth rate between years. We hypothesised that such erratic local population dynamics may hamper the viability of the species in Belgium and explain its decline currently visible in the Netherlands. In continuity, we aim in this paper at investigating through PVA modelling its viability in these two countries. This is of direct application to design conservation and/or restoration measures for B. aquilonaris and the ecosystem it represents (peat bogs). Indeed, a species protection plan has been developed to promote a sustainable conservation of the species (Van Swaay and Wallis de Vries 2001). Furthermore, we use this PVA to illustrate how it is necessary and possible to generalise data available for related systems and/or species to elaborate conservation guidelines for species in systems where it is too late to collect the necessary data (Linacre et al. 2004).

Landslapes and choice of PVA model type

PVA models were designed for two separate landscapes (Fig. 1). (1) The Plateau des Tailles landscape (southeastern Belgium; designed below as B) consists of 14 patches totalling 26.2 ha of suitable habitat (peat bogs), all occupied by a local population and separated by an agricultural matrix interspersed with spruce plantations and small villages. (2) The Drenthe landscape (northeast of the Netherlands; designed below as NL) is a network of 45 habitat patches, of which 14 are currently occupied, 28 are suitable but vacant and three are unsuitable but may be restored; total area of suitable habitat currently covers only 3.0 ha. Habitat consists of heathland fens with peat bog formation, situated in former heathland areas, presently afforested. The population clusters of Dwingeloo, Grollo and Sleenerzand are separated by a predominantly intensively used agricultural matrix of arable land and pastures. Although the two landscapes are of comparable size, habitat fragmentation and destruction are more pronounced in NL, with smaller habitat patches and slightly longer between-patch distances.

Structured population models are particularly suitable for PVA when local dynamics are an important determinant of the overall metapopulation viability, especially when there are a few local populations with large variation in area or quality (PVA model types reviewed by Akçakaya and Sjögren-Gulve 2000). This is especially true in the present case (Baguette and Schtickzelle 2003). We chose RAMAS/GIS 4.0 (Akçakaya 2002) to design such spatially explicit PVA models for B. aquilonaris, as it presented no limitation concerning the PVA model structure and the use of available data; furthermore, its patch vs matrix way of habitat representation is adequate for a species which is tightly restricted to habitat patches (Lindenmayer et al. 2003), which is the case of B. aquilonaris: its unique host plant is living only in peat bogs. The metapopulation module of RAMAS/GIS is a user-friendly interface “used to build stage-structured, spatially-explicit metapopulation models, to run simulations with these models, and to predict the risk of extinction, time to extinction, expected metapopulation abundance, its variation and spatial distribution” (Akçakaya 2002 p. 1).

PVA model parameterisation

The present discrete-time PVA models were based on (1) a density dependence function giving population growth rate according to density, (2) the dispersal between habitat patches and (3) the correlation of local dynamics. Temporal stochasticity for these parameters was also included. The lack of data concerning larvae stages was circumvented by modelling the adult stage only, with no differentiation between males and females, through the use of the density dependence function. Both models were parameterised with available data on B. aquilonaris or a closely related surrogate species (Proclossiana eunomia) when necessary. These parameters were estimated in the B landscape; they were therefore generalised to the NL landscape given the absence of necessary information concerning population dynamics in NL.

Population growth according to density and weather conditions

The demography of B. aquilonaris was previously studied in the B landscape, based on capture–mark–
recapture (CMR) data during three generations (1995–1997; adults of this univoltine species fly during July in Belgium; Baguette and Schtickzelle 2003). Particularly, a density dependence function, giving the population growth rate ($R_t$) according to the population density the year before ($D_{t-1}$) was estimated:
\[ R_t = R_{\text{max}} \times e^{-\ln R_{\text{max}} \times D_{t-1}} \]  

This function is suitable to model scramble competition (Akcakaya 2002), as likely to occur in this non territorial species where factors responsible for density dependence are probably parasitoids or larval food resources (Baguette and Schtickzelle 2003). Parameter estimates are: maximum growth rate \( R_{\text{max}} = 1.24 \), carrying capacity \( K = 723 \) individuals ha\(^{-1}\) (Baguette and Schtickzelle 2003). We assumed that the \( K \) of each local population depends linearly on the area of the patch (i.e. homogeneous habitat quality); habitat patch area is therefore used as a surrogate for larval resource abundance.

RAMAS/GIS implements the environmental stochasticity by sampling \( R_t \) for each time step from a lognormal distribution with mean given by the density dependence function and a standard deviation (std\( R_t \)) indicating the magnitude of environmental stochasticity. To estimate std\( R_t \), we supposed that the mean growth rate is determined only by the density dependence function (Eq. 1) while its yearly variation is due only to climatic conditions, as done for \( P. \) eunomia where std\( R_t \) has been estimated at 0.74 in the same B landscape by extracting variation in \( R_t \) due to climatic effects only (Schtickzelle and Baguette 2004). This value was used in the present PVA models as surrogate for missing information on \( B. \) aquilonaris.

### Dispersal

The between-patch dispersal matrix input in RAMAS/GIS specifies the proportion of individuals in each patch \( i \) that successfully disperse to each patch \( j \) at each time step. Dispersal is the combination of two processes: emigration out of patch \( i \) and then successful dispersal to patch \( j \). It was estimated from CMR data with the virtual migration model (VM: Hanski et al. 2000), already applied successfully to estimate dispersal parameters in butterfly metapopulations (Petit et al. 2001, Wahlberg et al. 2002, Akcakaya 2002, Schtickzelle and Baguette 2003, Mennechez et al. 2004). VM estimates survival and dispersal parameters in a metapopulation based on capture histories from a multi-site CMR study. Connectivity of the patches is assumed to influence mortality during dispersal but not mortality within a habitat patch, allowing the separate estimation of these two mortalities. We present here a brief summary of the VM model and its equations to facilitate interpretation of results. The parameters of the VM model are:

- Survival in habitat patch: \( \varphi_p \)
- Emigration rate (\( \varepsilon_i \)) from patch \( i \) according to its area \( A_i \):

\[ \varepsilon_i = \eta \times A_i^{-\alpha} \]  

- Connectivity of patch \( i \) (\( S_i \)) as a power function of distance \( D_{ij} \) between \( i \) and each other patch \( j \) and area \( A_j \) of each other patch \( j \):

\[ S_i = \sum_{i \neq j} \frac{1}{(1 + D_{ij})^{3/2}} A_j^{3/2} \]  

- Survival during dispersal from patch \( i \) (\( \varphi_{mi} \)) as a sigmoidally increasing function of connectivity \( S_i \):

\[ \varphi_{mi} = S_i^2 / (\lambda + S_i^2) \]  

Six parameters (\( \varphi_p \), \( \eta \), \( \zeta_{sem} \), \( \alpha \), \( \zeta_{im} \)) are estimated, from which the overall probability \( p_{ij} \) of dispersing from patch \( i \) to patch \( j \) may be computed as the product of emigration probability from \( i \) (\( \varepsilon_i \)), survival probability from \( i \) (\( \varphi_{mi} \)) and probability of ending up in \( j \) \( (S_j/S_i \), i.e. contribution of patch \( j \) to connectivity of patch \( i \)):  

\[ p_{ij} = \varepsilon_i \times \varphi_{mi} \times \frac{S_j}{S_i} \]  

Three years of CMR data were available for a network of 24 habitat patches situated in the Grande Fange, one of the sites of B (Fig. 1b) (Baguette 2003); these three data sets totalled to 1063 marked individuals, 1425 (re)captures and 111 inter-patch movements. We pooled male and female data as well as the three years (to group data from different years, capture histories were put end to end, considering the first sample of year 2 as being after the last of year 1, as explained in Schtickzelle 2003) to allow the estimation of one set of mean parameters for these three generations. Parameter estimates (and their 95% confidence interval) are: \( \varphi_p = 0.7587 \) (0.7345–0.7809); \( \eta = 0.0415 \) (0.0085–0.1771); \( \zeta_{sem} = 0.1287 \) (0.0000–0.2737); \( \alpha = 4.6399 \) (3.4153–5.8763); \( \lambda = 0.0000 \) (0.0000–0.3967); \( \zeta_{im} = 0.2043 \) (0.0251–0.3784). These estimates were used to compute the dispersal matrix of both PVA models according to their landscape structure (patch area and location).

### Correlation of local dynamics

Estimation of the degree of correlation of local dynamics between local populations requires long-term temporal series of population growth rates. Such information was not available for \( B. \) aquilonaris. Nevertheless, it was for a closely related species, \( P. \) eunomia, for a habitat network located in the same landscape of B. Based on series of yearly change rates in demography in nine habitat patches, as estimated from CMR data, the correlation (\( p_{ij} \)) of local dynamics between patches \( i \) and \( j \) was...
estimated as a negative exponential function of between-patch distance ($D_{ij}$; in m; Schtickzelle and Baguette 2004):

$$\rho_{ij} = 0.906 \times e^{-D_{ij}/603.7}$$

(6)

This function was used to compute the correlation of local dynamics for all populations in the PVA models for *B. aquilonaris*, according to between-patch distances.

**Other parameters and model assumptions**

For each PVA model, the simulation was started with populations at their last known abundance level, estimated from available data. For *B*, all 14 habitat patches were occupied in 1997, with a density estimated at 206 individuals ha$^{-1}$ (5394 individuals for a total of 26.23 ha of habitat: Baguette and Schtickzelle 2003). For *NL*, the total abundance for each habitat patch was estimated as three times the maximum number of individuals observed during transect walk censuses done in 2000–2002. The uncertainty on the estimates of initial population size due to the use of this rule of thumb (Thomas 1983, Warren 1991) was not problematic as initial population size did not seem to affect model results (see below). The time horizon for prediction was fixed at 100 years (1 year corresponds to 1 generation and 1 simulation time step) and the number of replications used is 1000. Demographic stochasticity was included, i.e. numbers of individuals were sampled from binomial distributions (Akçakaya 2002). We did not consider the presence of an Allee effect as there is no data to assess it and it is known to be extremely difficult to detect in field data (Lande 2002).

**PVA model analysis**

Metapopulation viability was quantified using the following model results: (1) metapopulation size: total number of individuals in the metapopulation (sum of all local populations); (2) expected minimum metapopulation size: average over all replications of the minimum metapopulation size during all generations; (3) interval quasi-extinction risk: probability that the metapopulation size falls below a given abundance value during at least one generation; (4) interval percent decline risk: probability that the metapopulation size declines by a given percentage from the initial population. Thorough description and the way every variable is computed by RAMAS/GIS may be found in its user’s guide (Akçakaya 2002).

A model is never expected to tell the truth, just to be the best possible approximation of it (Burnham and Anderson 1998). Therefore, we remind the reader that the statements issued from the PVA models are conditional to these models. We focused on relative results such as sensitivity analysis or comparison of scenarios or landscapes as they are more robust than absolute results (Discussion). Nevertheless, the given results might be used in an absolute way; such interpretation may be biased and needs to be considered with caution, even if usually considerably more reliable that simple subjective judgement.

**Status quo scenario**

In a first step, the two PVA models were analysed in terms of metapopulation viability in case the current situation concerning landscape structure (number, area and location of habitat patches) and metapopulation dynamics (demography, dispersal, correlation and stochasticity) does not change in the future (Fig. 2). *B* metapopulation seems viable under these conditions, with quite stable metapopulation size and number of occupied habitat patches during all the 100 generations. Even if a substantial decline in metapopulation size is expected during some of the generations (50% chance of declining by 74%, from 5403 to 1405 individuals), the expected minimum metapopulation size is 1469 and the risk to decline below 500 is only 2%.

The opposite is true for the *NL* metapopulation: the model predicts a continuous decline in the course of time, both in terms of metapopulation size and number of occupied habitat patches; on average never more than half the available habitat patches are occupied at the same time. A very large decline is expected to occur at some time in the next 100 years (50% chance of declining by 96%, from 549 to only 20 individuals), which would lead the metapopulation to extremely low abundance (17% risk of complete extinction, 79% risk of falling below 50 individuals); the expected minimum metapopulation size is as low as 30 individuals in this network of 42 habitat patches. This is further illustrated by the number of generations during which each habitat patch is occupied (Fig. 3). It is relatively low: only six of the 42 habitat patches are occupied during more than half the generations and some habitat patches are nearly never occupied. And it is correlated with the area of suitable habitat in the patch (Pearson’s $r = 0.39$, $P = 0.012$, $n = 42$) but not to the connectivity $S_j$ (Eq. 3) ($r = 0.40$, $P = 0.009$, $n = 42$; but this correlation is an artefact: it vanishes when two outliers are discarded: $r = 0.13$, $P = 0.409$, $n = 40$): the bigger the habitat patch, the higher the proportion of generations during which a local population was present.

**Sensitivity analysis of model parameters**

In a second step, the two PVA models were analysed using a sensitivity analysis: what is the effect on
metapopulation viability when changing the value of some model parameter? We chose to analyse the effect on the interval quasi-extinction risk of a change in six of the main parameters (Fig. 4): (1) the maximum growth rate ($R_{\text{max}}$), (2) the standard deviation of the growth rate ($\text{std}_R$), which reflects the strength of the environmental

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Fig. 2. Metapopulation viability in the two landscapes for the status quo scenario (no change in landscape structure and metapopulation dynamics in the future), as expressed by four viability variables (see text for definition). Line: mean value of the 1000 replications; bars: ±standard deviation (for a and b), ±95% confidence interval (for c and d); dots: minimum and maximum.
stochasticity, (3) the carrying capacity (\(K\)), (4) the dispersal rates, (5) the cv of dispersal rate, which reflects the strength of the stochasticity on the dispersal rate, and (6) the slope of the correlation-distance function (\(b\) of Eq. 6). For each parameter, we imposed first an increase and a decrease of 25 and 50\% to the parameter value and we compared the interval quasi-extinction risk. When no difference occurred in this first sensitivity analysis, we imposed an increase and a decrease of 95\%. We also tested the effect of total absence of dispersal between sites to assess the consequences of metapopulation structure (as opposed to isolated populations).

Essentially the same effects are observed in the two landscapes. The major conclusion is that metapopulation viability depends primarily on local dynamics (\(R_{\text{max}}\), std\(R_{\text{at}}\) and to a lesser extent \(K\)) and far less on dispersal, it may be argued that it is an artefact of the dynamics had a really small effect, while no effect occurred from changes in (6) the stochasticity on dispersal or (7) the initial population size (results not shown). Concerning the relatively small impact of dispersal, it may be argued that it is an artefact of the way sensitivity analysis was done: when modifying parameters according to x\% of their value, a “0” always remains “0”: unconnected pairs of patches will remain unconnected. Nevertheless the increase in viability was limited even when adding to each pair of patches a value corresponding to the average dispersal probability (0.34\% for B and 0.05\% for NL), a truly enormous increase at the metapopulation scale.

Evaluation of scenarios

Finally, viability of the metapopulation was assessed for each landscape under specific scenarios, representing possible future situations, either natural or following management. The first three scenarios were applied to both landscapes while the others were concerned only with the NL landscape where some habitat patches were vacant and/or to be restored. (1) The “status quo” scenario, corresponding to the current situation as explained before, was used as a comparison basis for the other scenarios. (2) The “full occupancy” scenario differed from the “status quo” scenario by the initial abundance fixed at the carrying capacity \(K\) for each population, as if every habitat patch was occupied by a local population at equilibrium. (3) The “global warming” scenario simulated the consequences of a 2°C increase in mean temperature in case it would have the same negative effect on demography (−15\% decrease of \(R_{\text{max}}\); from 1.240 to 1.063 and −22\% decrease of \(K\) from 723 ha\(^{-1}\) to 566 ha\(^{-1}\)) as observed on \(P.\ eunomia\) in the same B landscape (Schtickzelle and Baguette 2004); this assumption might not be verified in the absence of adequate data on \(B.\ aquilonaris\) but seemed plausible considering that both species are evolutionarily closely related and glacial relicts inhabiting peat bogs.

For the NL landscape, where some patches are vacant and/or to be restored, five extra scenarios were studied. (4) The “reintroduction” scenario consisted in introducing at year one five individuals in each vacant but suitable habitat patch (caught outside of the system, in a region where the withdrawal would not harm persistence of \(B.\ aquilonaris\)); five individuals may be considered as enough for the settlement of a population as successful colonisations were observed after such introductions in \(P.\ eunomia\) (Barascud et al. 1999). Three scenarios explored the effect of restoration of various amounts of suitable habitat in existing patches: (5) the “restoration” scenario implied that the total area of suitable habitat is almost doubled (3.0 to 5.5 ha) by enlarging all patches to 0.1 ha, if smaller, for all 45 sites (including the three sites currently completely unsuitable but which may be restored); (6) the “maximum restoration” scenario simulated the effect of restoring suitable habitat covering 80\% of the area of the peat bogs where the 45 patches are situated (or to 0.1 ha if still smaller),

![Fig. 3. Local occupancy for the Drenthe (NL) metapopulation: number of generations during which each habitat patch is occupied by a local population. Squares: mean value of the 1000 replications; bars:± standard deviation; dots: minimum and maximum.](Image 60x538 to 251x682)
which increased the total area of suitable habitat by a factor 7 (3.0 to 20.7 ha); (7) the “delayed maximum restoration” scenario implied that the restoration of suitable habitat covering 80% of the area of the peat bogs (with 0.1 ha minimum) would be achieved progressively on a 10 yr period, i.e. the carrying capacity progressively increased from the current value at year one to the value after restoration (723 individuals/ha) on year 11; (8) the “maximum restoration + global warming” scenario simulates the combination of maximum habitat restora-
tion and global warming. In all these scenarios, restoration and the associated increase in area of suitable habitat affected both the demography through the carrying capacity but also the dispersal probabilities through emigration and immigration (Eq. 2 and 3).

Viability of the metapopulation sometimes varied greatly between specific scenarios (Table 1, Fig. 5). Concerning the B metapopulation, the viability would not be increased compared with current situation ("status quo” scenario) if all the local populations were currently saturated ("full occupancy” scenario). In contrast, it would largely decrease in case global warming had negative effects on demography ("global warming” scenario), putting the metapopulation into immediate danger of extinction. In NL, a negative impact of global warming on demography would have an even more disastrous effect in this metapopulation which is already threatened by extinction. Starting with more individuals in all local populations ("full occupancy” scenario) would increase viability but this difference seemed limited, as would be the effect of reintroduction of individuals in vacant habitat patches ("reintroduction” scenario). As expected, habitat restoration increased overall viability ("restoration” scenario); the restoration of suitable habitat covering 80% of the area of the peat bogs where patches are situated ("maximum restoration” scenario) improved metapopulation viability quite more importantly. If it took 10 years for the land to be restored into suitable habitat ("delayed maximum restoration” scenario), viability would be decreased compared to immediate restoration; the decrease was most marked during the transition period to complete restoration. The positive effects of habitat restoration would nearly completely vanishes in case global warming negatively affects population demography ("maximum restoration+global warming” scenario).

Finally, given that some habitat patches of the NL landscape were nearly all the time vacant (Fig. 3), we a posteriori tested whether these patches might be discarded without affecting metapopulation viability. We removed habitat patches with mean occupancy time lower than 20, 40 and 50 years, with and without restoration of remaining habitat patches. It appeared that this would have a limited effect on overall viability, whether habitat restoration took place or not and whatever its intensity was (results shown only for “maximum restoration without patches with <20 yr occupancy”; Fig. 5). It means that these habitat patches are nearly useless for metapopulation persistence in the NL landscape. Furthermore, the more often a patch is vacant, the less important it is for overall metapopulation viability: the decrease in viability was more and more pronounced as patches with longer occupancy time were removed.

Discussion

The efficiency of PVA in conservation planning is regularly questioned, the question being still open (Beissinger and Westphal 1998, Brook et al. 2000, Coulson et al. 2001, Reed et al. 2002). A consensus is nevertheless emerging to state that relative results of PVA (e.g. sensitivity analysis or ranking management options) are better than absolute results (e.g. value of extinction risk; Dunning et al. 1995, Ralls and Taylor 1997). Recently, a simulation modelling study has confirmed that relative PVA results may reliably contribute to conservation planning (McCarthy et al. 2003), as we do in the present study.

Data are lacking to formally validate the present PVA models, as is generally the case for threatened species and systems, where PVA is by definition useful. Never-

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<th>Scenario</th>
<th>Metapopulation viability</th>
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<td>Average final metapopulation size after 100 years</td>
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| a) Plateau des Tailles (B)  
1) status quo | 5021 | 1469 | 0.00 | 0.00 |
| 2) full occupancy | 5012 | 1536 | 0.00 | 0.00 |
| 3) global warming | 270 | 33 | 0.43 | 0.80 |
| b) Drenthe (NL)  
1) status quo | 107 | 30 | 0.17 | 0.79 |
| 2) full occupancy | 172 | 68 | 0.04 | 0.44 |
| 3) global warming | 1 | 0 | 0.99 | 1.00 |
| 4) reintroduction | 133 | 47 | 0.10 | 0.62 |
| 5) restoration | 304 | 114 | 0.02 | 0.24 |
| 6) maximum restoration | 2420 | 399 | 0.00 | 0.00 |
| 7) delayed maximum restoration | 2271 | 313 | 0.00 | 0.01 |
| 8) maximum restoration+global warming | 10 | 2 | 0.88 | 1.00 |
| 9) maximum restoration without patches with <20 yr occupancy | 2443 | 388 | 0.00 | 0.00 |
theless, a model of the same type parameterised from similar data using similar methods has been successfully validated on a closely related species living in the same landscape (B), *Proclossiana eunomia* considered by some taxonomists (Kudrna 1986) as congeneric to *Boloria aquilonaris* (Schtickzelle and Baguette 2004). Furthermore, again due to lack of data, we were forced to generalise some parameters: (1) across species, taking a few parameters (correlation by distance function and strength of environmental stochasticity) estimated on *P. eunomia* in B; and (2) across landscapes generalising parameters from B to NL. Such generalisations are frequently necessary as studies are quite rare where all the required information is available to perform a complete PVA analysis on a species. It is therefore advocated to use other sources of data, provided it is reasonable to assume that they may apply to the species of concern (Bart 1995, White 2000, Frankham 2002, Hanski 2002). Even if such generalisations may influence the absolute results (e.g. extinction risk), we believe that relative results are still trustworthy in the present case. (1) Across species generalisation: *B. aquilonaris* and *P. eunomia* are closely related species sharing many ecological traits; parameters for *P. eunomia* were estimated in the same landscape (Plateau des Tailles) as occupied by *B. aquilonaris* in B; the parameters generalised either do not much affect viability (correlation of local dynamics) or are likely to be similar for both species (environmental stochasticity, mainly driven by regional climatic conditions). (2) Across landscape generalisation: information is generalised on the basis of landscape configuration (area of suitable habitat and location of patches), whose meaning is the same in the two landscapes; the effect of sensitivity analysis is very similar between the two landscapes studied, which means ranking of parameter importance to metapopulation viability is independent of the landscape.

Provided the current situation (in terms of landscape structure and metapopulation dynamics) remains unchanged in the future, the threat of a rapid extinction of the species appears obviously in the Netherlands, but less clearly in Belgium. Large-scale restoration of habitat patches is required to ensure long-term survival of the species in the NL region. In terms of importance of the parameters for metapopulation viability, both landscapes share similar features, mainly the prime role of demography and the threat due to global warming. Would the average population growth rate be higher, the
viability would be largely increased; would it be lower, the extinction would be deterministic. Metapopulation viability is also drastically and negatively affected by the strength of the environmental stochasticity: temporal variation in population growth rate may lead several local populations and even the whole metapopulation to extinction. This was already suggested from the erratic dynamics (high temporal and spatial variation) observed in population growth rates in the B metapopulation (Baguette and Schtickzelle 2003). Increased extinction risk due to environmental stochasticity has also been observed in theoretical models (Foley 1994). The low population growth rate and its large yearly variations may be due to global warming which is expected to negatively affect a glacial relict species such as B. aquilonaris. Indeed, such a negative effect of an increase in temperature on local demography has previously been shown in the same landscape for a closely related species, P. eunomia (Schtickzelle and Baguette 2004); if a comparable effect affects B. aquilonaris, extinction of the species in Belgium and the Netherlands is highly probable, even if large habitat restoration is achieved. This is not unexpected as the combined effect of climate change and habitat loss has been shown to have disastrous effects on specialist species: the negative effect of climate change is more pronounced when habitat loss is important, which means that species may not anymore be able to overcome the current rapid climate change as they may have done in the past (Warren et al. 2001, McLoughlin et al. 2002, Travis 2003). Furthermore, climate change has been shown to lead populations of Euphydryas editha bayensis to extinction due to amplified population fluctuations caused by amplified climatic variations (McLaughlin et al. 2002). The low and erratic demography of B. aquilonaris currently observed may then be a first sign of a degradation of peat bog ecosystems in western Europe due to global warming (e.g. excessive desiccation during summer), which may eventually lead to the regional disappearance of this ecosystem and its community of living organisms. This may be of considerable significance for the overall biodiversity as small wetlands have been shown to be particularly important to maintain present levels of biodiversity (Semlitsch and Bodie 1998).

Population viability analysis models are of direct application to managers, in order to determine guidelines for efficient conservation. In the present case, it appears that a considerable effort is urgently required to save the last metapopulation of B. aquilonaris in the Netherlands as not enough habitat is remaining. Restoration of a large area of land into high-quality suitable habitat would be necessary to obtain a reasonable long term persistence probability. Recent projects show that restoration of active peat bog from heathland is well possible (B. Takman, pers. comm.) but relatively costly (ca €20.000 ha⁻¹: Dumont and Champluvier 1990); restoration of all habitat patches in NL would require a funding of around €400.000, less if only some patches are restored. This nevertheless is a feasible restoration proposal, because government policy in the Netherlands attaches a great importance of preserving threatened species such as B. aquilonaris and its peat bog habitat. Survival of the species in Belgium may be achieved with a lesser effort by constant site protection, provided global warming does not reduce too much habitat quality or demography of B. aquilonaris. We hope our models will be used in collaboration with managers to determine the best actions to take in the field for conservation of the species in Belgium and the Netherlands.

In conclusion, we would like to stress that it is possible to elaborate conservation guidelines for species in systems where it is too late to collect the necessary data, provided data are available for related systems and/or species. It has of course to be done cautiously but represents the best solution in the crisis situation faced by highly threatened species.

Acknowledgements – We thank Luc Mousson and Bénédicte Gérard for previous work as well as the people involved in data collection; Mark Burgman helped to improve the manuscript. This work was funded by the National Fund for Scientific Research through a ‘Scientific Research Worker’ grant (mandat de Collaborateur scientifique FNRS) to N. Schtickzelle, by a grant from the Ministère de la Région Wallonne and by a grant from the Office of Scientific and Cultural Affairs (Belgian Federal Government) (contract OSTC-SPSDII EV10/16A 2000–2004) to M. Baguette. Special capture licenses for B. aquilonaris and site access in Plateau des Tailles were provided by the Ministère de la Région Wallonne. We are grateful to the National Forest Service of the Netherlands (Staatsbosbeheer) for cooperation and access to the study areas in Drenthe. This is contribution BRC057 of the Biodiversity Research Centre.

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