Journal of Applied Ecology 2007
44, 725–736

Designing a network for butterfly habitat restoration: where individuals, populations and landscapes interact

ELIOT J. B. MCINTIRE*, CHERYL B. SCHULTZ† and ELIZABETH E. CRONE*

Wildlife Biology Program and Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA and †School of Biological Sciences, Washington State University, Vancouver, WA 98686, USA

Summary

1. Restoring biologically appropriate habitat networks is fundamental to the persistence and connectivity of at-risk species surviving in highly fragmented environments. For many at-risk species, this landscape planning problem requires combining detailed biological information about the species with the landscape, economic and social realities of the restoration effort.

2. Here, we assess the ability of potential restored landscapes to create persistent and connected populations of the federally endangered Fender's blue butterfly (*Icaricia icarioides fenderi*) in Oregon's Willamette Valley. Like many other at-risk species, a very small amount (0·5%) of historic habitat remains and much of this habitat is highly degraded.

3. To do this, we combine extensive demography and behaviour data from prior studies of Fender's blue with landscape maps of potential restoration sites by building and running a spatially explicit landscape model. We chose a simulation approach because previous attempts using more traditional population modelling did not provide sufficiently informative answers for this restoration problem.

4. From our simulations, we: (a) provide a solution to the general landscape restoration problem of determining whether patches that are available according to social, economic and ecological realities are sufficient to restore persistence and connectivity; (b) supported our predictions from our previous models about persistence of our large patches and expanded our inference to include connectivity and persistence of small patches; and (c) found several emergent properties of our system, including identifying stepping-stone patches, observing asymmetric connectivity and uncovering reciprocal effects of connectivity and population dynamics.

5. *Synthesis and applications.* Assuming no large disturbances, and relying on our 14 years of data collection and models, restoring all currently degraded and potentially available habitat patches to high quality native prairie would be sufficient for long-term persistence of Fender's blue butterfly in the West Eugene area, Oregon. This conclusion resolves many of the shortcomings of our previous population and metapopulation models that were not able to combine the necessary landscape complexity with species behaviour to address this restoration problem.

Key-words: Fender's blue butterfly, habitat connectivity, landscape model, reserve design, restoration, spatially explicit individual-based model, stepping stones.

Journal of Applied Ecology (2007) **44**, 725–736
doi: 10.1111/j.1365-2664.2007.01326.x

Correspondence: Cheryl B. Schultz, School of Biological Sciences, Washington State University Vancouver, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686, USA (fax: 360 546 9064; e-mail: schultzc@vancouver.wsu.edu).
*Current address: Département des sciences du bois et de la forêt, Université Laval, Québec, Québec, Canada, G1K 7P4.

Introduction

Restoration planning in highly fragmented landscapes requires careful consideration of both the biology of at-risk species and the status of the current and potentially restorable habitat network (Collinge 2001). This issue differs substantially from traditional reserve design approaches, which seek to identify minimum sets of remaining habitat patches that maximize biodiversity and minimize cost (e.g. Williams, Revella & Moloney 2004; Moilanen 2005; also see review in Kingsland 2002). In contrast, landscape planning for restoration of at-risk species requires a focus upon adding potential habitat that might achieve restoration goals, such as species persistence or connectivity, within the constraints of a unique landscape. Thus, on-the-ground restoration planning must be able to address species-specific biology, the economic realities of restoration costs and an explicit inclusion of the real, non-idealized habitat network in the landscapes of interest. As a result, evaluating options for restoration is fundamentally a spatial problem in which individual-, population- and landscape-level processes must be included (Huxel & Hastings 1999; Smallwood 2001).

Throughout its short history, planning for landscape restoration has been approached largely on a site-by-site basis, based on *ad hoc* judgement or rules (see review Holl, Crone & Schultz 2003), although planning has been directed by diffusion (e.g. Flather & Bevers 2002) and landscape models (e.g. Adriaensen *et al*. 2003; Carroll *et al*. 2003) in a few cases. Modelling has the benefit of being able to forecast the future impact of actions taken today, thereby potentially limiting the ecological and economic costs of restoration by trial and error. Different modelling approaches, however, will carry different assumptions and limitations and will have a particular scope of inference. For example, it is not straightforward for a population or a metapopulation model to address the landscape complexity often present in highly fragmented landscapes. Similarly, static geographical information systems (GIS)-based landscape models can be useful (Adriaensen *et al*. 2003) if there are no feedbacks within the system (e.g. social and population dynamics responding to the system, see this study). Spatially explicit, individual-based landscape models (SE-IBMs), on the other hand, provide a potentially important approach to examining the movement and demographic parameters of species in landscapes of realistic complexity, allowing for system properties to emerge from the model while incorporating species, population and individual data sources. These SE-IBMs have been used to address a variety of conservation issues, especially in large landscapes where multiple stakeholders must be considered. For example, some researchers have developed SE-IBMs that address general questions about spatial structure and conservation strategies (e.g. Fahrig 2001; Wiegand, Revilla & Moloney 2005). Other models have been developed to examine the spread of reintroduced populations in real landscapes (Gardner & Gustafson 2004; Kramer-Schadt *et al*. 2004; Wiegand *et al*. 2004). These approaches differ from spatially explicit metapopulation models (e.g. Ovaskainen 2002; Grimm *et al*. 2004; Heinz, Wissel & Frank 2006) because they explicitly include landscape complexities such as the actual shapes of landscape patches and animal behaviour that changes in different landscape locations. In particular, these individual-based simulation approaches are easily amenable to including species-specific biological information, such as mechanisms of habitat-specific movement and population dynamics (e.g. Grimm & Railsback 2005).

In general, restoration planning for at-risk species attempts to answer the two-part restoration question: is the remaining habitat enough for species persistence and connectivity and, if not, how much restoration and which patches would be needed to achieve persistence and connectivity? To date, there are few examples that we know where this restoration question has been answered using several alternative approaches, thereby demonstrating the uses and limitations of each (although see Stephens *et al*. 2002). In our system, over the past 14 years we have studied extensively field populations of the Fender's blue butterfly and used these studies to parameterize simpler diffusion (Schultz 1998; Schultz & Crone 2001), population (Schultz & Crone 1998; Crone & Schultz 2003; Schultz & Hammond 2003) and metapopulation (Schultz & Crone 2005; Winfree *et al*. 2005) models. The results of these studies have not been adequate to determine whether the extant patches or whether proposed restored networks of habitat patches are sufficient for subpopulation connectivity, nor have they been able to rule out this possibility.

Here, we attempt to resolve this general species-at-risk restoration problem of determining which patches should be chosen to restore population persistence and connectivity, given the limitations of on-the-ground patch availability and restoration potential. To do this, we build and use a spatially explicit, individual-based model of an endangered prairie butterfly, the Fender's blue (*Icaricia icarioides fenderi*). We then compare our conclusions from previous studies with predictions of this model. These previous studies did not yield unequivocal predictions for connectivity between butterfly subpopulations, a major inspiration for this current study. Finally, we highlight general ecological insights about the relationships between individual behaviour, population dynamics and landscape structure that emerge from our results that have not been recognized (or at least, not widely appreciated) in this or other systems.

Restoration context and past research

The West Eugene Wetlands Project (WEP; Anonymous 2004), an eight-agency partnership of public and private agencies, provides a specific, systematic vision for landscape restoration. The project has been lauded for its exemplary mix of habitat protection and land use planning (Duerkson & Snyder 2005). The area contains a matrix of historic wetland and upland prairie (Fig. 1). Fender's blue is an upland prairie specialist and it is not clear that the small and isolated upland habitat parcels that exist within the area comprising the Wetlands

Journal of Applied Ecology, **44**,
725–736

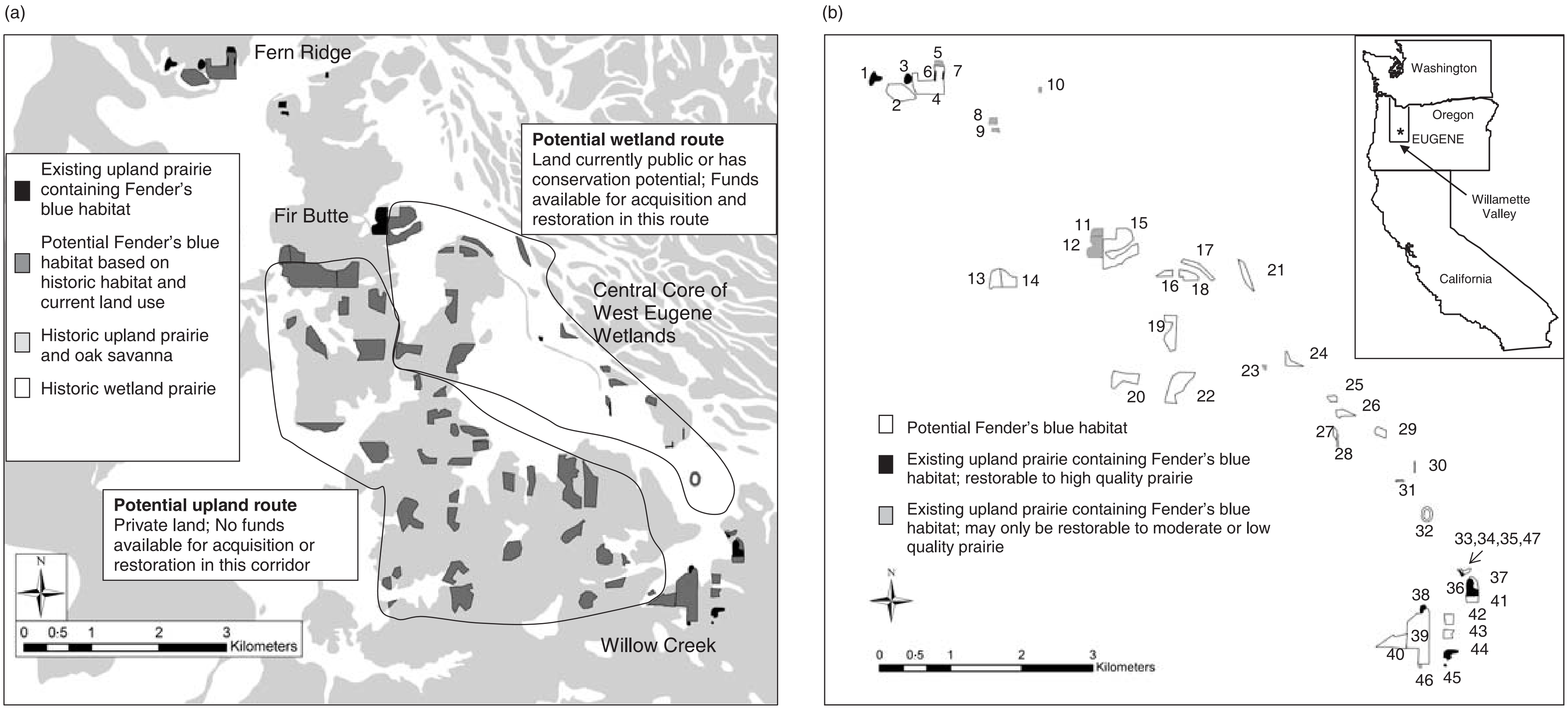

Fig. 1. Fender's blue butterfly habitat west of Eugene, Oregon. (a) Potential wetland and upland routes; (b) existing and potential Fender's blue butterfly patches modelled in FendNet. Numbers correspond to patches on *x*-axis in Figs 3 and 5. Butterfly occupancy over the past 10 years has included many extinctions and recolonizations; as a result, we have not identified 'occupied' patches on these maps. See Fig. 3 for geometric mean population sizes corresponding to patches in these maps.

Project are sufficient to connect existing Fender's blue populations. Land managers have suggested an upland route outside the Wetlands Project as an alternative for Fender's blue connectivity because the upland route contains substantially more historic upland prairie (Fig. 1). However, land within this potential upland route is private and thus expensive or impossible to restore in the public planning efforts. In contrast, substantial social and economic benefits would result if restoration within the West Eugene Wetlands could also contribute to Fender's blue recovery, because much of the land is already being acquired for wetland restoration, and the project has broad-based popular support (USFWS 2006; P. Johnston, personal communication). Thus, we evaluate whether achieving connectivity through the Wetlands is feasible by restoring these more easily restorable patches.

Our past research has not given a clear answer as to whether restoring patches within the WEP will connect subpopulations. For example, Schultz (1998) used an empirically parameterized diffusion model to compare two broad conservation options: a long narrow movement corridor vs. stepping stones, such as the potentially restorable upland patches within the WEP. She found that butterfly movement was not habitat-specific enough for a long, narrow corridor to be feasible, but that stepping stones might work, if they were within the average movement distance (1 km) of other patches. To refine this prediction, Schultz and Crone collected finer-scale observations of butterfly dispersal behaviour in response to habitat edges and calculated how long butterflies would remain in patches of different sizes, based on observed dispersal behaviour (Schultz & Crone 2001). These data were combined with estimates of survival and fecundity to calculate that high quality patches of less than ~5 ha would not persist in isolation, setting a minimum size for restoration projects outside existing habitat networks (Crone & Schultz 2003).

These first studies set two rules of thumb: to support Fender's blues, a habitat patch must be > 5 ha or within 1 km of large populations. Existing upland prairie remnants are generally both too small and too isolated to meet these criteria, confirming the need for habitat restoration to restore a habitat network. However, the large majority of potentially restorable habitat patches within the WEP also failed to meet one or both of these criteria (Schultz & Crone 2005), so it was not clear that restoration in this area would be sufficient. Thus, in this present study, we evaluate explicitly the population and connectivity consequences of restoration options in the WEP, using a spatially explicit individual-based simulation model of butterfly movement, reproduction and mortality.

Here, to address the restoration problem of determining which patches would be needed to create population persistence and connectivity, we develop restoration scenarios to address the following questions of increasing restoration effort. First, what is the persistence and connectivity of the current patch network? Second, what is the persistence and connectivity of the current network if all existing habitat patches were restored fully to high quality upland prairie? Third, if all patches that have high potential for restoration were restored, would this be sufficient to achieve persistence and connectivity? Fourth, if not, can we fill any large gap or gaps between the patches assessed above with a targeted suboptimal patch, and would this be sufficient to restore connectivity?

Methods

STUDY SPECIES AND SYSTEM

Fender's blue is a federally endangered butterfly that survives in upland prairie remnants in Willamette Valley, Oregon that maintain its primary larval host plant, Kincaid's lupine (federally threatened, *Lupinus sulphureus* spp. *kincaidii*). These prairies are highly endangered with less than 0·5% of prairies remaining, and many of these are highly degraded due to invasion by non-native species and absence of historic disturbance regimes (Noss, LaRoe & Scott 1995). Currently, 3000–5000 butterflies survive in about a dozen isolated prairie patches (Schultz, Hammon & Wilson 2003). The area west of Eugene includes one of the largest remaining populations of the Fender's blue, The Nature Conservancy's Willow Creek Natural Area and several smaller butterfly populations. In addition, there are several patches of Kincaid's lupine that are potential Fender's blue habitat which are not occupied currently by the butterfly. We have investigated site-level management required to convert a degraded patch to a restored patch (see Schultz & Crone 1998; Schultz & Dlugosch 1999; Schultz 2001), complementing our focus in this paper, where to restore these patches.

MODELLING APPROACH

To investigate the conservation effectiveness of potential habitat networks, we constructed an individual-based spatially explicit simulation using the Spatially Explicit Landscape Event Simulator (SELES; Fall & Fall 2001). SELES is a raster-based spatial modelling framework. Our model has four components: habitat maps, butterfly movement, reproduction (affected by patch quality) and mortality. We refer to our model of the Fender's blue network as FendNet. The base time scale for the simulation is the time required for one 'movement', as defined in our field data (Schultz 1998; Schultz & Crone 2001).

Habitat maps were assembled by identifying current and potential habitat in the West Eugene area (Fig. 1). Current habitat maps were created by combining field-based GPS site surveys with aerial photographs and are accurate to ~10–20 m resolution. To identify potential sites for restoration, we worked with local experts from The Nature Conservancy, City of Eugene and Bureau of Land Management (E. Alverson and E.

Wold, personal communication). Sites were included as potential Fender's blue habitat if sites were open fields (i.e. no human structures and no forests), soil maps indicated historic upland prairie and they were within the area considered for conservation by the West Eugene Wetlands Project. In addition, some sites of questionable history (i.e. previous human structures and highly degraded) were noted as possible restoration areas if simulations suggested that restoration of higher quality sites was insufficient for conservation goals. For each simulated scenario (see below), we added patches to the current patch map or filled in very spotty patches to reflect the restoration scenario. Each scenario had a single, unchanging base map for the entire simulation. We rasterized these base maps to a 1 m × 1 m pixel size (the scale of butterfly movement; Schultz 1998) for use in FendNet.

Butterfly behaviour and population dynamics in this model build on our previously published work in this system. Below, we refer readers to published models if we directly incorporated them into the landscape simulation, and provide more details on approaches not described elsewhere. We modelled individual butterfly movement using a biased, correlated random walk parameterized with field-collected observations of Fender's blue dispersal behaviour (Schultz & Crone 2001). We modelled butterfly population dynamics using annual adult-to-adult transitions. Following Crone & Schultz (2003), we assumed the number of eggs laid in each patch was proportional to the total number of moves made in that patch, with ~ 0·7 successful offspring produced per day in high-quality habitat, over a 15-day life span.

We incorporated environmental stochasticity into our predictions by modifying this deterministic relationship to reflect estimates of annual fluctuations in population growth rate, as measured by Schultz & Hammond (2003). Specifically, we multiplied fecundity by a log-normal random variable that differed among years and among patches, reflecting independent growth fluctuations between patches (Schultz & Hammond 2003). We solved numerically for the variance in fecundity that generated parameters equal to those measured by Schultz & Hammond (2003) by extracting population size in each year from FendNet, calculating the population growth rate and variance in population growth rate, and compared them to known population growth rates and variability. We repeated this, fitting in an iterative procedure by adjusting the variance parameter in the random number generator until the population variance from FendNet matched the observed variance from 1992 to 2001 across the range of Fender's blue butterfly populations.

We incorporated density dependence into predicted population dynamics by fitting simple population models to survey data from 1993 to 2003 in the West Eugene area (Fitzpatrick 2004; P. Severns, unpublished data). We fitted four models for population growth to annual abundance estimates: two without carrying capacity (exponential growth) and two with carrying capacity (logistic growth). Within each of these pairs (exponential vs. logistic), we tested a single model for all patches and a separate model for each patch (see Appendix S1 in Supplementary material for details). Comparison of the fit of these four models demonstrated that the simple logistic was clearly the best model (second best: logistic × patch, $\Delta_{\mathrm{AICc}} = 14{\cdot}5$), indicating that all the patches had a similar butterfly density and that there was a carrying capacity that could be estimated from the data (i.e. exponential growth models with no carrying capacity were not as good). The maximum likelihood estimate for the carrying capacity based on this best model was 613 butterflies per hectare (95% confidence interval: 313, 1310). We used this point estimate of carrying capacity as the maximum density that could be in a patch. When the patch was at carrying capacity, the patch population was calculated as the product of the carrying capacity (no./ha), the patch size and the same log-normal random number used in the calculation of the population size (see above). Thus, the same stochasticity approach was used to calculate population size irrespective of whether the patch was at carrying capacity. However, this does mean that the population size within a patch in year $t + 1$ will be independent of butterfly movement in that patch in year t, if it is calculated to be greater than the carrying capacity.

Existing prairie remnants differ in habitat quality (Schultz & Dlugosch 1999), and restoration may not fully restore high quality habitat. To incorporate this key variable, each patch was assigned qualitatively to one of three prairie qualities (low, medium, high) based on estimation of the abundance of Kincaid's lupine, nectar abundance and degree of degradation due to exotic species. In FendNet we assumed that lower patch quality reduced fecundity by 33% and 50% in medium and low-quality patches, respectively. This decision was subjective. However, it is validated empirically to the extent that FendNet was sufficient to reproduce historical patterns of Fenders blue population dynamics, with this model of habitat quality (see Results). We also echo Forrester (1961: 57), who commented that omitting unknown variables (e.g. patch quality) in simulations is equivalent to saying that there is a zero effect of differing patch quality on butterfly population dynamics – which is probably the only value that is certainly not true.

At initiation of the simulations, starting population sizes were chosen to reflect the population sizes in each patch estimated from spring 2003 abundance surveys. However, because population sizes fluctuate dramatically, selecting 2003 arbitrarily as the starting conditions may overemphasize the importance of the population sizes in that year. Also, the habitat quality is set to the simulated restored habitat quality at the start of each simulation (i.e. no time lag). To minimize the impacts of the starting conditions and to address the medium-term consequences of our management actions, we allowed all scenarios to run for 25 years, by which time we assumed that patches had reached their full restoration potential, and we interpret only the last 10 years of the simulations.

To validate FendNet, we compare monitoring data from Fender's blue populations to results from the *status quo* scenario (with no added patches; see below) from the first 10 years of the simulations. For this assessment, we use data from 10 sites in West Eugene that were surveyed between 1993 and 2003. Because not all sites were monitored in all years, this data set includes 86 population estimates at 10 sites over the 11-year time interval. In addition, we note that at some sites a survey site corresponds to two nearby habitat patches identified in our mapping (e.g. sites 44 and 45 are one census site; see Fig. 1b). Thus these 10 sites correspond to the 19 patches in the *status quo* alternative that had Fender's blue butterflies in 2003. To compare FendNet to the observed census data, we report the number of censuses from 1993 to 2003 that fall within the 95% confidence intervals from the first 10 years of the simulations in the *status quo* scenario, as well as whether the geometric mean population size for any site over this interval fell within the 95% confidence interval produced by FendNet.

RESTORATION SCENARIOS

We used FendNet to simulate dynamics of Fender's blue populations under eight scenarios, ranging from no restoration to extensive habitat restoration (summarized in Table 1). In scenario 1, the landscape consists of existing upland prairie at current quality. In scenario 2, we assume all existing upland prairie patches are restored to high quality prairie (see Schultz 2001 for discussion of methods to restore degraded prairie). The next two scenarios add restoration of highly degraded uplands within these existing protected lands, increasing patch size of these sites, but not changing the number of habitat patches. In scenario 3, these are restored to the current quality of adjacent lands and in scenario 4 these and all existing lands are restored to high quality prairie. Scenarios 5 and 6 add restoration of potential upland sites within the West Eugene wetlands, as identified by Schultz & Crone (2005), to scenarios 3 and 4, respectively. Finally, scenarios 7 and 8 add a highly degraded patch with soil that may not be suitable for restoration (patch 32 in Fig. 1b, a former racetrack) to scenarios 5 and 6, respectively. These final two scenarios were added because this zone represents the largest area of scenarios 5 and 6 in which there is no habitat patch.

We assessed these restoration alternatives in terms of population dynamics and connectivity over the last 10 years of the 25 years' simulations. We reason that, given simulated full restoration at the beginning of the simulation, 15 years should be sufficient time for colonization dynamics if natural colonization drives dynamics and, given high extinction risks (Schultz & Hammond 2003), a conservation strategy should have a high likelihood of achieving success over this time-frame. If a restoration alternative is not likely to succeed within 2 decades, other restoration options should be pursued. To evaluate population dynamics, we report expected median population size with 95% confidence intervals for each patch and for the entire network over the last 10 years of the simulation. To evaluate connectivity, we divide the network into four subnetworks (see Fig. 2), even though FendNet treats each butterfly and each patch independently. We report connectivity as the number of butterflies moving between these subnetworks. We chose these subnetworks as a way to summarize and interpret the 48 × 48 matrix depicting movement among all sites. We know from

Table 1. Description of restoration alternatives. 'All high quality' habitat indicates that the model assumed that all patches of existing upland prairie can be restored to high quality Fender's blue habitat. 'Mixed quality' indicates that there are some patches of existing prairie for which local experts suggest that even with substantial restoration effort, restoring high quality Fender's blue habitat may not be feasible. In these scenarios, we assumed that these patches were restored to moderate or low rather than high quality prairie

Scenario	Landscape description	Patch quality	No. of patches	Total area (ha)
1	*Status quo* with an estimate of actual habitat quality. No additional management or restoration	Mixed quality	19	8·6
2	*Status quo* with assumed high quality in all current patches following restoration	All high quality	19	8·6
3	Restore all existing upland prairie to Fender's blue butterfly habitat	Mixed quality	19	21·0
4	Restore all existing upland prairie to Fender's blue butterfly habitat	All high quality	19	21·0
5	Restore all existing upland prairie and all high potential sites in West Eugene Wetlands area	Mixed quality	47	136·5
6	Restore all existing upland prairie and all high potential sites in West Eugene Wetlands area	All high quality	47	136·5
7	Restore all existing upland prairie and all high and the only moderate potential site in West Eugene Wetlands area	Mixed quality	48	138·1
8	Restore all existing upland prairie and all high and the only moderate potential site in West Eugene Wetlands area	All high quality	48	138·1

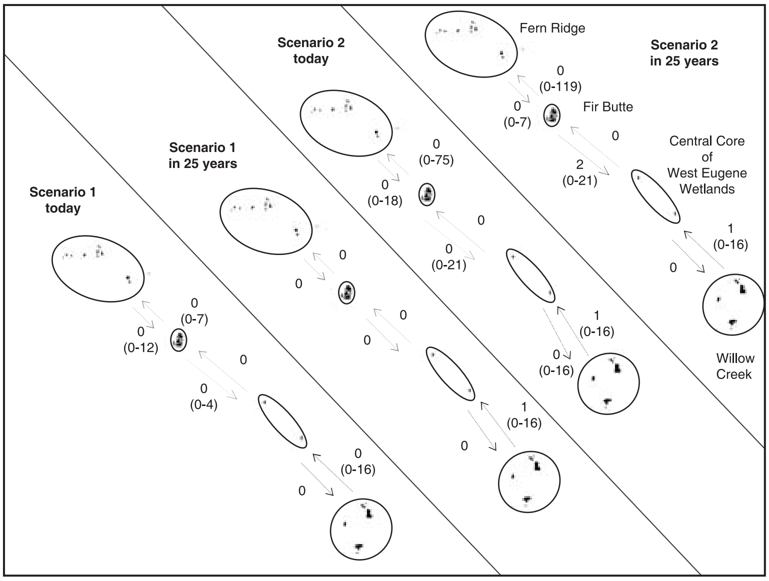

Fig. 2. Map comparing connectivity during the first and last 10 years of *status quo* simulations (scenarios 1 and 2). Numbers next to arrows indicate median number of butterflies moving between subnetworks each year. Numbers in parenthesis indicate 95% confidence intervals. Arrow shaft thickness increases with increasing numbers of butterflies moving along route described by the arrow. Sites enclosed by solid line polygons represent site groupings, with names written in top right panel of figure.

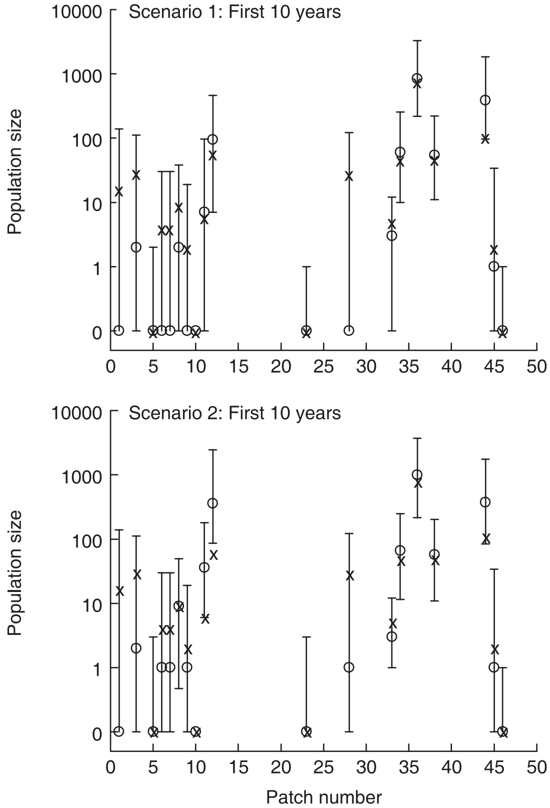

Fig. 3. Median with 95% confidence intervals for model output for the *status quo* simulations (scenarios 1 and 2) during the first 10 years of simulation. 'X' indicates geometric mean population size from Fender's blue butterfly surveys from 1993 to 2003. Patches are identified by number in Fig. 1.

previous empirical observations and analyses that there is movement within these subnetworks (C. Schultz, personal observation). These areas correspond to geographically contiguous areas that support current concentrations of butterflies and to management boundaries that are relevant to future conservation planning. These areas, from North-west to South-east, are: (1) Fern Ridge –Fender's blue habitat on land primarily owned by the US Army Corps of Engineers; (2) Fir Butte –Fender's blue habitat on land primarily owned by the US Bureau of Land Management; (3) Central Core of the West Eugene Wetlands – land that is part of the central part of the West Eugene Wetlands Project which has substantial potential to be restored as Fender's blue butterfly habitat; and (4) Willow Creek – Fender's blue habitat on land owned by The Nature Conservancy (see Fig. 1).

Results

VALIDATION

Model output suggests that FendNet reasonably captures Fender's blue population dynamics (Fig. 3), particularly when we included mixed quality habitat. For the *status quo* scenario assuming mixed habitat quality (scenario 1), geometric mean population size from annual surveys for each of the 10 sites fell within the 95% confidence interval from the simulation. In only one case for the *status quo* scenario assuming all high quality habitat (scenario 2) did the geometric mean population size over the interval fall outside the 95% confidence interval. Not surprisingly, this was a site which has moderate quality habitat and, in the scenario assuming the habitat was high quality, the 95% confidence interval produced by the simulation (91–2625 butterflies) was higher than the average of the observed populations (65 butterflies). In addition, 87% (75/86) of the observed censuses fell within the 95% confidence intervals for the first 10 years of predictions from scenario 1 and 84% (72/86) of the observed censuses fell within the 95% confidence intervals for the first 10 years of predictions from scenario 2. Seven of the observed censuses falling outside the confidence interval in scenario 2 were from the same site (i.e. the actual census estimates were lower than the predicted lower confidence limit).

POPULATION DYNAMICS

Simulations of alternative restoration networks indicate that all scenarios except scenarios 1 and 2 (no increase in existing habitat area) are likely to support Fender's blue butterfly populations. In scenarios 1 and 2, only 22% and 36% of the patches are occupied consistently (> 95% probability) in the last 10 years of the simulation. In contrast, for all other scenarios, more than 95% of the patches have a > 95% probability of occupancy in the last 10 years of the simulation. In addition, in scenarios 1 and 2, the median population

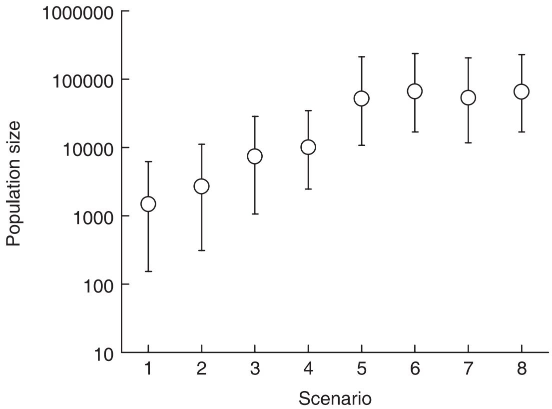

Fig. 4. Median population size of full network over last 10 years of simulation. Error bars are 95% confidence intervals. Scenarios are summarized in Table 1.

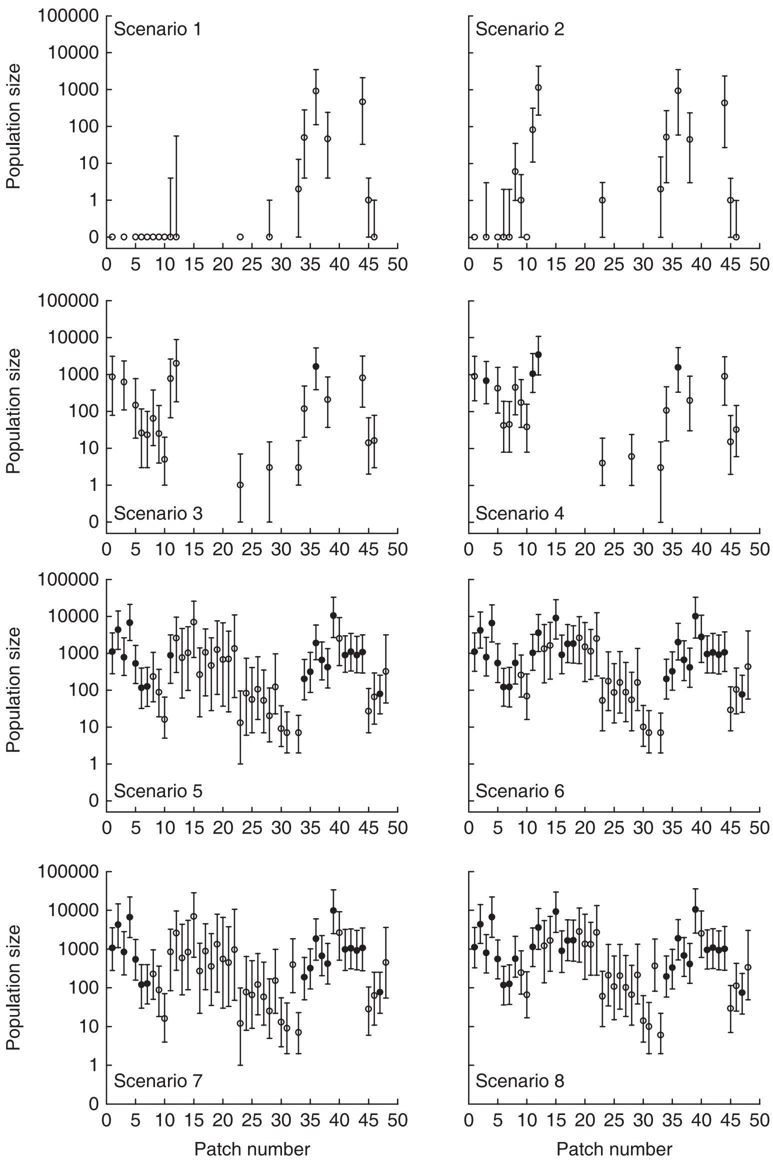

Fig. 5. Predicted population sizes during the last 10 years of each scenario (median with 95% confidence intervals). Odd-numbered scenarios assume that some habitat can only be restored to moderate quality; even-numbered scenarios assume that all existing upland prairie can be restored as high quality Fender's blue habitat. Solid circles indicate patches in which median population size was within 20% of carrying capacity.

sizes for the last 10 years is below 3000, with the lower 95% confidence limit suggesting the potential of only a few hundred butterflies (Fig. 4). In contrast, if a substantial network is restored (scenarios 5–8), the habitat supports 50 000–65 000 butterflies, with lower confidence limits suggesting at least 10 000 butterflies.

If degraded lands within the existing network were restored (scenarios 3 and 4), one to a few patches would probably reach and maintain population sizes close to carrying capacity (Fig. 5, scenarios 3 and 4). If all potential upland habitat within the West Eugene wetlands were acquired and restored, several of the patches have the potential to reach and maintain population sizes near carrying capacity (Fig. 5, scenarios 5–8). In these scenarios, more existing patches reach carrying capacity because nearby patches are restored, so immigration is more likely to balance emigration. Thus, from a population dynamics perspective, restoration of upland habitat in the West Eugene wetlands is sufficient to support Fender's blue populations.

CONNECTIVITY

Given the *status quo* habitat network, movement of butterflies between subnetworks is low today and is likely to drop over time as population sizes decline (Fig. 2; scenarios 1 and 2). If existing protected uplands were restored to functioning habitat (scenarios 3 and 4), there would be connectivity between the Fern Ridge and Fir Butte subnetworks, but not full connectivity through the Central Core of the West Eugene Wetlands (Fig. 6). If most potential habitats were restored (scenarios 5 and 6), there would be enhanced connectivity between the subnetworks (Fig. 6). However, there would be asymmetric movement between two subnetworks; butterflies would travel from Willow Creek to the Central Core of the West Eugene Wetlands, but not in the reverse direction. Restoring connectivity depends on restoring the low-potential habitat patch added in scenarios 7 and 8 (Fig. 6). Only scenarios with this patch predict full connectivity between subnetworks (Fig. 6).

Discussion

Based on our previous approaches (Schultz & Crone 2001; Crone & Schultz 2003), we expected persistence of our larger subpopulations in the simulations. This study confirmed this prediction. Our previous studies, however, were equivocal with respect to connectivity between these persistent patches. Here, we found that connectivity would be achievable within the constraints of availability of patches for restoration, complex movement behaviours, realistic habitat quality estimates, social momentum and economic costs. This key result did not emerge from our previous approaches, perhaps because the landscape and biological complexity of our system warranted this added model complexity. Thus, in this and other restoration planning situations,

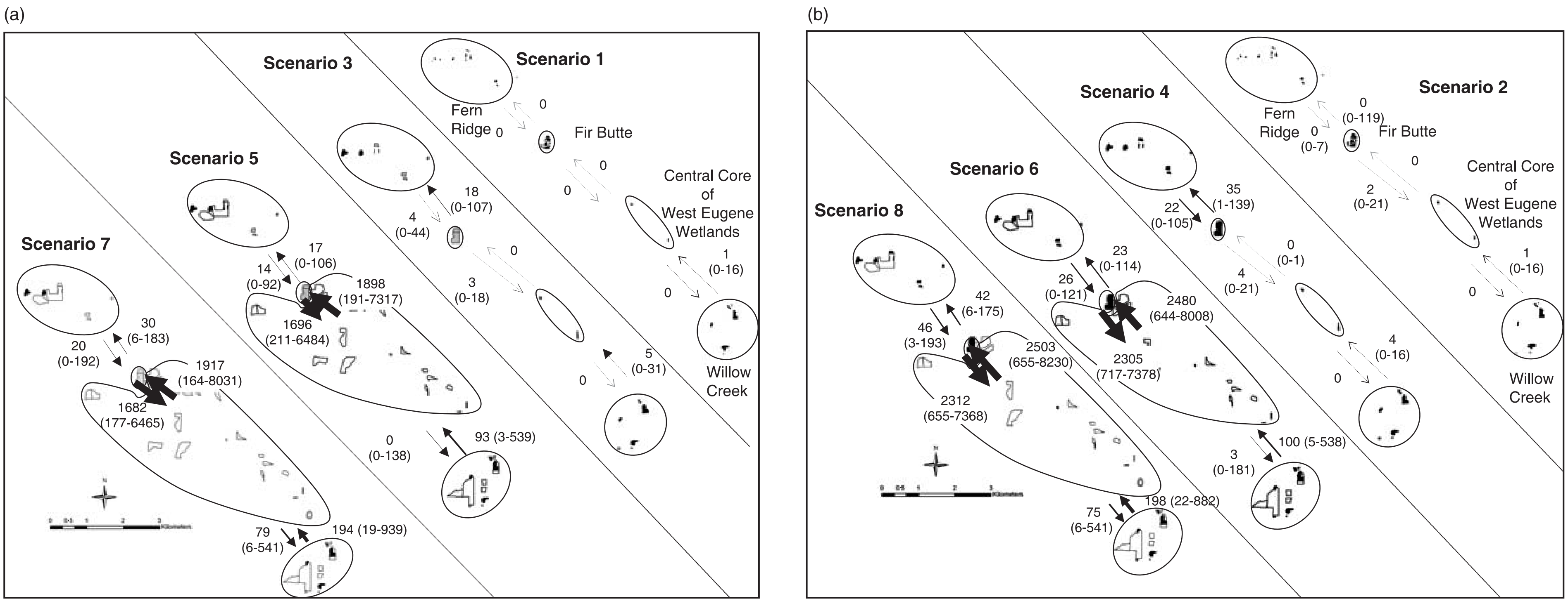

Fig. 6. Map of connectivity during the last 10 years of each simulated scenario. (a) Odd-numbered scenarios (assuming that some existing upland prairie can only be restored to moderate quality); (b) Even-numbered scenarios (assuming all existing upland prairie can be restored as high quality). Other symbols follow fig. 2.

the complexity of the system and the social needs will define the complexity of model needed to assist in planning.

Our results build on and increase dramatically our ability to infer about the functioning of a fragmented system. Previously, our simpler diffusion and landscape models demonstrated that successful restoration of a connected and persistent system in the West Eugene Wetlands would depend upon successful movement among habitat patches (Schultz 1998; Crone & Schultz 2003). Similarly, our past research showed that restoring small, connected habitat patches was more important than restoring large, isolated habitat patches (Schultz & Crone 2005). These results are generally true and were corroborated here, but did not inform us sufficiently about the functioning of this system. In other words, we could not tell how much dispersal limitation, population dynamics, habitat limitation or connectivity would drive the dynamics of our system and to what extent these effects would interact. Here, for example, several small patches in the core wetland area were found to be essential because of their role as stepping stones. These patches did not, nor could not, maintain populations in isolation, nor were they close enough to large patches to receive immigrants directly from them. We were able to tell in which patches population dynamics drives connectivity, in which patches connectivity and dispersal drive population dynamics and where lack of habitat prevents system-wide connectivity.

In addition to this increased understanding of our system, we also were able to answer the landscape restoration question – which patches are necessary for creating persistent and connected populations within the constraints of an ongoing restoration programme? To answer this question, however, we found that we needed the relatively complex modelling approach used here, a result also found elsewhere. Stephens *et al.* (2002) compared four models ranging from simple matrix approaches to detailed spatially explicit models with and without behaviour. They found that only the more complex model with behaviour adequately predicted observed populations of the alpine marmot (*Marmota marmota*) from a 13-year study. In addition, they note that including behaviour in the model was a critical step for predicting transient rather than equilibrium dynamics. This observation is particularly relevant for studies investigating the potential of restoration strategies because many at-risk populations are not near equilibrium (cf. Fox & Gurevitch 2000). Lindenmayer *et al.* (2002), in their review of landscape-scale population models, found that there was a reasonable fit between model predictions and field data only when sufficient complexity was added to the model. This complexity included matrix effects on dispersal and the influence of habitat quality on population dynamics.

Several population- and landscape-scale insights emerged from our study, in spite of the fact that mechanisms driving the model were at the individual scale. One key result was that population dynamics were influenced substantially by connectivity and vice versa. The importance of connectivity for population dynamics has been well documented in population ecology and was confirmed here. At several of the smaller patches in our data set, population sizes are well below carrying capacity. However, these patches maintain populations at or close to carrying capacity when nearby areas are restored in the model (Fig. 5). Much less attention has been paid to the importance of population dynamics for connectivity. Our results demonstrate that connectivity depends on population size within each patch, not merely patch location, patch size and movement behaviour. Although only a small fraction of individuals move across gaps between disparate patches, large populations make this unlikely individual event likely at the population level. Thus, the large population in the south-east corner of our system provides a source of dispersers into the large area with only small patches. This source of dispersers effectively connects the butterflies in this section to all other areas within the fully restored landscapes.

Asymmetric dispersal between patches is commonly discussed in the conservation literature in the context of source–sink dynamics and dispersal between patches driven by patch selection based on habitat quality (e.g. Boughton 1999; Kauffman, Pollock & Walton 2004), but is discussed less commonly between patches maintaining different population sizes. A corollary of the result that population size affects connectivity is that we found asymmetric dispersal in the south-east corner of our system driven by differences in population size and patch size not active habitat selection based on patch quality. Similar patterns have been observed in genetic assessments of population structure. For example, Fraser, Lippe & Bernatchez (2004) observed asymmetric movement of brook charr (*Salvelinus fontinalis*) from a population with a large effective population size (N_e) towards two smaller populations. At larger scales, directional asymmetry in dispersal is a common consideration in biogeography and the colonization of distant islands (e.g. Cook & Crisp 2005). Our findings emphasize the importance of considering asymmetric dispersal between patches in developing landscape-scale conservation plans.

The utility of models for conservation planning depends on knowledge of life history and ecology, as well as model complexity. A common conclusion from many studies investigating potential conservation strategies is the need to begin with a solid understanding of species-specific biology. We found that population dynamics and connectivity interacted in species-specific ways indicating that both must be assessed where there are restoration strategies for at-risk species. Elsewhere, Baguette, Petit & Queva (2000) found that species-specific differences in dispersal of three butterfly species within the same network in Belgium had implications for population viability and recommended that design of regional conservation strategies focus on the most fragile species. Similarly, Wang *et al.* (2004)

Journal of Applied Ecology, **44**, 725–736

contrasted the movement behaviour of two checkerspot species in network of meadows in China. In years of high overall butterfly numbers the more mobile species, *Euphydryas aurinia*, had higher numbers of patch colonization events while populations of the less mobile species, *Melitaea phoebe*, tended to increase in local abundance, but not regional abundance. These results are consistent with findings from a broad range of taxa. For example, in their studies of fragmentation effects on three closely related species pairs of birds and mammals in Australia, Lindenmayer *et al*. (2003) found that model predictions for one species were not informative for the other member of the species pair.

Constructing simulation models for use with real landscape maps raises potential future complexities that may need to be dealt with for restoration planning. Our work to date has been based on Fender's blue behaviour in primary prairie habitat, in abandoned fields with few host plant or nectar resources, and at the boundaries between these habitats. These habitat types represent a substantial amount of the habitat in the West Eugene area. However, we have not estimated butterfly response to other matrix habitat types and barriers such as woodlands, light industrial development and roads. The influence of the matrix has attracted substantial attention in recent literature (e.g. Ricketts 2001; Adriaensen *et al*. 2003; Baum *et al*. 2004; Antongiovanni & Metzger 2005; Berry *et al*. 2005). We are currently undertaking field studies to estimate the effect of the woodlands and topography on butterfly movement because understanding the effect of the matrix is a priority.

In conclusion, we were able to resolve the general landscape restoration problem of determining which patches are required for species persistence and connectivity, given social, economic and ecological constraints, under the aforementioned assumptions. Furthermore, we assessed and corroborated our predictions from previous simpler approaches in this system, and found restoration solutions where our previous attempts had not. In particular, connectivity in all directions should be obtainable, creating links between subpopulations and probably providing longer-term stability of Fender's blue butterfly. To obtain these results and have predictions for landscape management, our study required combining individual behaviour within frameworks of population and landscape ecology. We also illustrated the general importance of the reciprocal effects of movement on population dynamics, and of population dynamics on connectivity. Although the former has been recognized widely, the latter needs more attention, particularly in landscape studies for which very little population ecology is known.

Acknowledgements

We thank Eric Wold and Ed Alverson for helping put together the map of potential Fender's blue habitat and for comments on early drafts of the manuscript. We thank Paul Severns and Greg Fitzpatrick for contributing census data for this effort. Funds for the project were provided by Washington State University Vancouver and an NSERC Postdoctoral Fellowship to E. J. B. McIntire. We thank N. Chacoff for commenting on an earlier draft of this manuscript. We also thank Paul Giller and Andreas Erhardt and three anonymous reviewers for their valuable comments that improved this manuscript.

References

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H. & Matthysen, E. (2003) The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, **64**, 233–247.

Anonymous (2004) *West Eugene Wetlands Plan, Eugene, Oregon*. City of Eugene, Eugene, OR.

Antongiovanni, M. & Metzger, J. (2005) Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. *Biological Conservation*, **122**, 441–451.

Baguette, M., Petit, S. & Queva, F. (2000) Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology*, **37**, 100–108.

Baum, K., Haynes, K., Dillemuth, F. & Cronin, J. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**, 2671–2676.

Berry, O., Tocher, M., Gleeson, D. & Sarre, S. (2005) Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology*, **19**, 855–864.

Boughton, D. (1999) Empirical evidence for complex source–sink dynamics with alternative states in a butterfly metapopulation. *Ecology*, **80**, 2727–2739.

Carroll, C., Phillips, M.K., Schumaker, N.H. & Smith, D.W. (2003) Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. *Conservation Biology*, **17**, 536–548.

Collinge, S. (2001) Spatial ecology and biological conservation – introduction. *Biological Conservation*, **100**, 1–2.

Cook, L. & Crisp, M. (2005) Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography*, **32**, 741–754.

Crone, E. & Schultz, C. (2003) Movement behavior and minimum patch size for butterfly population persistence. *Butterflies as Model Systems: Ecology and Evolution Taking Flight* (eds C. Boggs, P. Ehrlich & W. Watt), pp. 561–576. University of Chicago Press, Chicago.

Duerkson, C. & Snyder, C. (2005) Eugene, Oregon: shining star of wetlands preservation. *Nature-Friendly Communities: Habitat Protection and Land Use Planning* (eds C. Duerkson & C. Snyder), pp. 197–220. Island Press, Washington, DC.

Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65–74.

Fall, A. & Fall, J. (2001) A domain-specific language for models of landscape dynamics. *Ecological Modelling*, **141**, 1–18.

Fitzpatrick, G.S. (2004) *2003 Status of the Fender's Blue Butterfly (Icaricia Icarioides Fenderi) in Lane County, Oregon: Population Estimates and Site Evaluations (Part 1) and Effects of Mowing on the Fender's Blue Butterfly: Implications for Conservation and Management* (Part 2). Report to the Oregon Natural Heritage Program and the US Fish and Wildlife Service, Eugene, OR.

Flather, C.H. & Bevers, M. (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *American Naturalist*, **159**, 40–56.
Forrester, J. (1961) *Industrial Dynamics*. MIT Press and John Wiley & Sons, Inc., Cambridge, MA.
Fox, G. & Gurevitch, J. (2000) Population numbers count: tools for near-term demographic analysis. *American Naturalist*, **156**, 242–256.
Fraser, D., Lippe, C. & Bernatchez, L. (2004) Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology*, **13**, 67–80.
Gardner, R. & Gustafson, E. (2004) Simulating dispersal of reintroduced species within heterogeneous landscapes. *Ecological Modelling*, **171**, 339–358.
Grimm, V., Lorek, H., Finke, J., Koester, F., Malachinski, M., Sonnenschein, M., Moilanen, A., Storch, I., Singer, A., Wissel, C. & Frank, K. (2004) META-X: Generic software for metapopulation viability analysis. *Biodiversity and Conservation*, **13**, 165–188.
Grimm, V. & Railsback, S. (2005) *Individual-Base Modeling and Ecology*. Princeton University Press, Princeton.
Heinz, S.K., Wissel, C. & Frank, K. (2006) The viability of metapopulations: individual dispersal behaviour matters. *Landscape Ecology*, **21**, 77–89.
Holl, K., Crone, E. & Schultz, C. (2003) Landscape restoration: moving from generalities to methodologies. *Bioscience*, **53**, 491–502.
Huxel, G.R. & Hastings, A. (1999) Habitat loss, fragmentation, and restoration. *Restoration Ecology*, **7**, 309–315.
Kauffman, M., Pollock, J. & Walton, B. (2004) Spatial structure, dispersal, and management of a recovering raptor population. *American Naturalist*, **164**, 582–597.
Kingsland, S. (2002) Designing nature reserves: adapting ecology to real-world problems. *Endeavour*, **26**, 9–14.
Kramer-Schadt, S., Revilla, E., Wiegand, T. & Breitenmoser, U. (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, **41**, 711–723.
Lindenmayer, D., Manning, A., Smith, P., Possingham, H., Fischer, J., Oliver, I. & McCarthy, M. (2002) The focal-species approach and landscape restoration: a critique. *Conservation Biology*, **16**, 338–345.
Lindenmayer, D., Possingham, H., Lacy, R., McCarthy, M. & Pope, M. (2003) How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecology Letters*, **6**, 41–47.
Moilanen, A. (2005) Methods for reserve selection: interior point search. *Biological Conservation*, **124**, 485–492.
Noss, R., LaRoe, E. III & Scott, J. (1995) *Endangered Ecosystems of the United States: a Preliminary Assessment of Loss and Degradation*. US Department of Interior Biological Report 28. National Biological Service, Washington, D.C.
Ovaskainen, O. (2002) The effective size of a metapopulation living in a heterogeneous patch network. *American Naturalist*, **160**, 612–628.
Ricketts, T. (2001) The matrix matters: effective isolation in fragmented landscapes. *American Naturalist*, **158**, 99.
Schultz, C.B. (1998) Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology*, **12**, 284–292.
Schultz, C.B. (2001) Restoring resources for an endangered butterfly. *Journal of Applied Ecology*, **38**, 1007–1019.
Schultz, C.B. & Crone, E. (1998) Burning prairie to restore butterfly habitat? A modeling approach to management trade-offs for the Fender's blue. *Restoration Ecology*, **6**, 244–252.
Schultz, C.B. & Crone, E. (2001) Edge-mediated dispersal behavior in a prairie butterfly. *Ecology*, **82**, 1879–1892.
Schultz, C.B. & Crone, E. (2005) Patch size and connectivity thresholds for butterfly habitat restoration. *Conservation Biology*, **19**, 887–896.
Schultz, C.B. & Dlugosch, K.M. (1999) Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. *Oecologia*, **129**, 231–238.
Schultz, C.B. & Hammond, P. (2003) Using population viability analysis to develop recovery criteria for endangered insects: case study of the Fender's blue butterfly. *Conservation Biology*, **17**, 1372–1385.
Schultz, C.B., Hammond, P. & Wilson, M. (2003) Biology of the Fender's blue butterfly (*Icaricia icarioides fenderi* Macy), an endangered species of western Oregon native prairies. *Natural Areas Journal*, **23**, 61–71.
Smallwood, K. (2001) Linking habitat restoration to meaningful units of animal demography. *Restoration Ecology*, **9**, 253–261.
Stephens, P., Frey-Roos, F., Arnold, W. & Sutherland, W. (2002) Model complexity and population predictions. The alpine marmot as a case study. *Journal of Animal Ecology*, **71**, 343–361.
US Fish & Wildlife Service (USFWS) (2006) Endangered and threatened wildlife and plants; designation of critical habitat for Fender's blue butterfly (*Icaricia icarioides fenderi*), *Lupinus sulphureus* spp. *kincaidii* (Kincaid's lupine), and *Erigeron decumbens* var. *decumbens* (Willamette daisy); final rule. *Federal Register*, **71**, 63862–63977.
Wang, R., Wang, Y., Chen, J., Lei, G. & Xu, R. (2004) Contrasting movement patterns in two species of chequerspot butterflies, *Euphydryas aurinia* and *Melitaea phoebe*, in the same patch network. *Ecological Entomology*, **29**, 367–374.
Wiegand, T., Knauer, F., Kaczensky, P. & Naves, J. (2004) Expansion of brown bears (*Ursus arctos*) into the eastern Alps: a spatially explicit population model. *Biodiversity and Conservation*, **13**, 79–114.
Wiegand, T., Revilla, E. & Moloney, K. (2005) Effects of habitat loss and fragmentation on population dynamics. *Conservation Biology*, **19**, 108–121.
Williams, J., ReVelle, C. & Levin, S. (2004) Using mathematical optimization models to design nature reserves. *Frontiers in Ecology and the Environment*, **2**, 98–104.
Winfree, R., Dushoff, J., Crone, E.E., Schultz, C.B., Budny, R.V., Williams, N.M. & Kremen, C. (2005) Testing simple indices of habitat proximity. *American Naturalist*, **165**, 707–717.

Received 4 November 2005; final copy received 9 March 2007
Editor: Andreas Erhardt

Supplementary material

The following supplementary material is available for this article.

Appendix S1. Model fitting for calculating carrying capacity.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01326.x

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.