MINIMUM VIABLE METAPOPULATION SIZE, EXTINCTION DEBT, AND THE CONSERVATION OF A DECLINING SPECIES

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Abstract. A key question facing conservation biologists is whether declines in species' distributions are keeping pace with landscape change, or whether current distributions overestimate probabilities of future persistence. We use metapopulations of the marsh fritillary butterfly *Euphydryas aurinia* in the United Kingdom as a model system to test for extinction debt in a declining species. We derive parameters for a metapopulation model (incidence function model, IFM) using information from a 625-km^2 landscape where habitat patch occupancy, colonization, and extinction rates for *E. aurinia* depend on patch connectivity, area, and quality. We then show that habitat networks in six extant metapopulations in 16-km^2 squares were larger, had longer modeled persistence times (using IFM), and higher metapopulation capacity (λ_M) than six extinct metapopulations. However, there was a >99% chance that one or more of the six extant metapopulations would go extinct in 100 years in the absence of further habitat loss. For 11 out of 12 networks, minimum areas of habitat needed for 95% persistence of metapopulation simulations after 100 years ranged from 80 to 142 ha (~5–9% of land area), depending on the spatial location of habitat. The area of habitat exceeded the estimated minimum viable metapopulation size (MVM) in only two of the six extant metapopulations, and even then by only 20%. The remaining four extant networks were expected to suffer extinction in 15–126 years. MVM was consistently estimated as ~5% of land area based on a sensitivity analysis of IFM parameters and was reduced only marginally (to ~4%) by modeling the potential impact of long-distance colonization over wider landscapes. The results suggest a widespread extinction debt among extant metapopulations of a declining species, necessitating conservation management or reserve designation even in apparent strongholds. For threatened species, metapopulation modeling is a potential means to identify landscapes near to extinction thresholds, to which conservation measures can be targeted for the best chance of success.

Key words: conservation; Euphydryas aurinia; *extinction threshold; habitat loss; incidence function model; metapopulation capacity; nonequilibrium metapopulations; transient dynamics.*

INTRODUCTION

Habitat networks of many species are declining because of the expansion and intensification of human land use (Groombridge 1992, Pimm et al. 1995, Brooks et al. 1997). If habitat is lost quickly, there may be a time lag before colonization and extinction dynamics reach equilibrium with current habitat distributions ("nonequilibrium dynamics" [Harrison 1991, Harrison and Taylor 1997]). As a result, species may persist for some time in habitat networks where they are expected to go extinct even without further landscape change ("extinction debt" [Tilman et al. 1994, Tilman and Lehman

1997]). The apparent survival of species in networks that are insufficient for their long-term persistence may cause underestimates of the area and quality of habitat needed to conserve threatened taxa (Hanski et al. 1996*a*, Harrison and Taylor 1997), and overestimates of the species richness that landscapes can support in the long term (Tilman et al. 1994, Helm et al. 2006). Therefore, the prevalence of nonequilibrium systems among rare species, and the implications for their conservation, need to be determined as a matter of urgency.

Metapopulation models represent one way to model species persistence in fragmented landscapes. Metapopulation theory considers local populations to be linked by migration, with the proportion of populated habitat patches dependent on local extinction and colonization rates (Hanski 1999). A common prediction of metapopulation theory is that beyond some threshold level of fragmentation remaining habitat patches will be too small and too isolated for long-term persistence, since

FIG. 1. The distribution of *Euphydryas aurinia* in England and Wales. (a) The 10-km grid squares distribution: white circles, 1970–1982 records only; black circles, 1995–1999 records, 97 cells also with records for 1970–1982, and 85 without 1970–1982 records (probably because of lower sampling intensity of earlier survey). (b) Population and habitat networks in this study: 1, Dorset, 625-km² focal system and 16-km² test networks; 2, Cumbria; 3, north Wales; 4, mid-Wales; 5, southwest A; 6, southwest B. Black squares show extant networks, and white squares show extinct networks.

extinction rates will exceed colonization rates (Nee 1994, Hanski et al. 1996*a*). Metapopulation models could be valuable tools for estimating minimum viable metapopulation sizes (MVM), and the likely prevalence of nonequilibrium metapopulations in fragmented landscapes, but in practice they have rarely been used in this manner (Hanski et al. 1996*a*, Biedermann 2000).

In this paper, we use a declining butterfly as an exemplar species to evaluate persistence and extinction debt in fragmented landscapes. We aim to determine (1) the minimum viable metapopulation size (MVM) needed to ensure long-term survival of the species in a habitat network; (2) whether remaining habitat exceeds MVM in landscapes subject to habitat loss and fragmentation; and (3) whether extant metapopulations of the species can be expected to survive in the absence of additional habitat management or restoration. We estimate MVM and network persistence times using a spatially realistic metapopulation model, the Incidence Function Model (IFM; Hanski 1994, 1999). We first estimate parameters for the IFM using information on occupancy, colonization and extinction of the butterfly over a large focal habitat network (625 km²) between 1981 and 2000. We then apply the parameterized model to 12 independent habitat networks in the United

Kingdom, six with extant populations of the species, and six where it has gone extinct since 1970. The IFM has previously been applied to a number of Lepidoptera (e.g., Wahlberg et al. 1996, Thomas et al. 2002) and other taxa (e.g., Moilanen et al. 1998, Biedermann 2000), but this is the first time, to our knowledge, that it has been used to estimate MVM for multiple independent networks of a rare and declining species.

METHODS

Study species

The marsh fritillary butterfly *Euphydryas aurinia* Rottemburg (Lepidoptera; Nymphalidae) is distributed from western Europe and north Africa to temperate Asia and Korea (Tolman and Lewington 1997). In the United Kingdom, *E. aurinia* larvae feed on large plants of *Succisa pratensis* Moench (Dipsaceae) growing in lightly grazed grassland that is untreated by chemical fertilizers and herbicides (Warren 1994). Lowland flower-rich grassland has declined in the United Kingdom by 97% since 1940 (Department of Environment 1995), and the butterfly has experienced a decline of 55% in the number of 10-km grid squares occupied since 1970 (Fig. 1) (Asher et al. 2001). Incomplete historical records mean that observed changes in

distribution size almost certainly underestimate the true level of decline. In Europe, *E. aurinia* has suffered a 20–50% decline over 25 years (van Swaay and Warren 1999) and is protected under the 1979 Bern Convention (Annexe II) and the EC Habitats and Species Directive (Annexe II).

E. aurinia has one annual flight period (May/June). Eggs are laid in batches, and larvae feed and hibernate gregariously in a web, before completing feeding the following spring, and pupating alone. The butterfly is relatively sedentary, with most adults flying no further than 50–100 m, but colonizations have been recorded 5–20 km from known populations (Porter 1981, Warren 1994, Wahlberg et al. 2002*a*). Patterns of occupancy, turnover, and population genetic structure provide evidence for metapopulation dynamics in most *E. aurinia* populations that have been studied (Lewis and Hurford 1997, Anthes et al. 2003, Joyce and Pullin 2003, Wang et al. 2004). In some cases, variation in population dynamics and rates of population turnover are so great that the small, fragmented networks where the species survives may not be viable in the long term (Hula et al. 2004, Schtickzelle et al. 2005).

Patch occupancy

The distribution of *S. pratensis* was mapped during 1998, using plant records and habitat maps (English Nature 1982) to identify potential habitat in a 625-km^2 (25 × 25 km) grid square in Dorset, United Kingdom (Fig. 1). Due to the large size of the study area, areas containing unsuitable habitats such as arable land were not intensively searched for *S. pratensis*. To test the validity of this approach, 20 1-km squares without "potential habitats" were randomly selected for intensive searches: no *S. pratensis* was found. Habitat patches were defined as areas containing 10 or more *S. pratensis* plants, which we estimated could support an *E. aurinia* population for at least one generation. Discrete patches were defined as areas separated by 50 m of open habitat without *S. pratensis*, or by 25 m if there was a scrub or woodland barrier, so that adults would on average not be expected to move between patches. The area of each patch was recorded, along with slope (degrees) and aspect (degrees). Depending on the size of the patch, between 30 and 40 stratified random 1-m^2 quadrats were used to record *S. pratensis* cover, leaf length and vegetation height (with a 30-cm drop disc [Stewart et al. 2001]). *S. pratensis* is the host plant in both chalk downland and wet grassland habitat types that support *E. aurinia* in the region, with late instar larvae very rarely observed using alternative host plants when there is a shortage of *S. pratensis* in chalk downland.

Surveys for adult, egg, and larval *E. aurinia* were carried out in 1998, 1999, and 2000 to establish whether habitat patches were occupied or vacant. Adult density at occupied sites was estimated using standard transect techniques adjusted for the flight period by weekly transects at two reference sites (Thomas 1983). Popula-

tions of *E. aurinia* in the region had been mapped using a similar approach in 1981, with suitable habitat identified based on host plant occurrence and vegetation height (M. S. Warren, *unpublished data*), providing population turnover information over 20 years.

Forward stepwise binary logistic regression (Norusis 1998) was used to determine the factors related to *E. aurinia* occupancy and turnover. Dependent variables for *E. aurinia* occupancy in 1998 were population presence (1) vs. absence (0). Dependent variables for population turnover from 1981–1998 were: for colonizations, colonized (1) vs. vacant (0) patches; for extinctions, extant (1) vs. extinct (0) populations. We used independent variables for the area, habitat characteristics, and connectivity of habitat patches. As one independent variable, we multiplied patch area by host plant cover to estimate resource area for each patch. To test for multicollinearity, we carried out Pearson correlations among the predictor variables selected by the models, and repeated logistic regressions using the variables alone and in combination: correlations were weak (ranging from −0.09 to 0.22), while regression coefficients did not change substantially and never changed sign.

Patch connectivity

Patch connectivity (S_i) was estimated as $S_i = \Sigma \exp^{-\alpha D_{ij}} A_j^B$ (Hanski 1994, Moilanen and Nieminen 2002), as a measure of potential immigration to each patch *i* from the sum total of source patches $j_{1...n}$ ($j \neq i$). Connectivity increases with the area of each patch *j* but decreases with its distance from patch *i*. The constant α estimates how migration from patch *j* declines with increasing distance, and is the slope of a negative exponential distribution of dispersal distances. D_{ij} is the distance between the centers of patches *i* and *j*; A_j is the area of patch *j*; *B* relates emigration rate to patch area (Hanski 1994, Moilanen and Nieminen 2002). We estimated connectivity using $\alpha = 2$, consistent with values used for the same species and close relatives in previous studies (e.g., Wahlberg et al. 1996, 2002*b*), rather than based on empirical dispersal data that tend to underestimate long-distance movement at a landscape scale (Wilson and Thomas 2002, Baguette 2003). Using values of $\alpha = 1$ or 3 did not alter results (see Table 3). *B* was set to 0.5, accounting for the tendency of per capita emigration to be greater from smaller habitat patches (Thomas and Hanski 1997, Moilanen and Nieminen 2002).

Two measures of connectivity that could influence *E. aurinia* occupancy were calculated for each habitat patch. First, connectivity was calculated to all *E. aurinia* populations in the intensively studied 625-km^2 study area, and in an additional 5-km buffer zone (using records from the Butterflies for the New Millennium database [Asher et al. 2001]). Second, we estimated connectivity to all patches in the 625-km^2 area, regardless of *E. aurinia* presence during the survey, as a measure of connectivity to habitat. The second
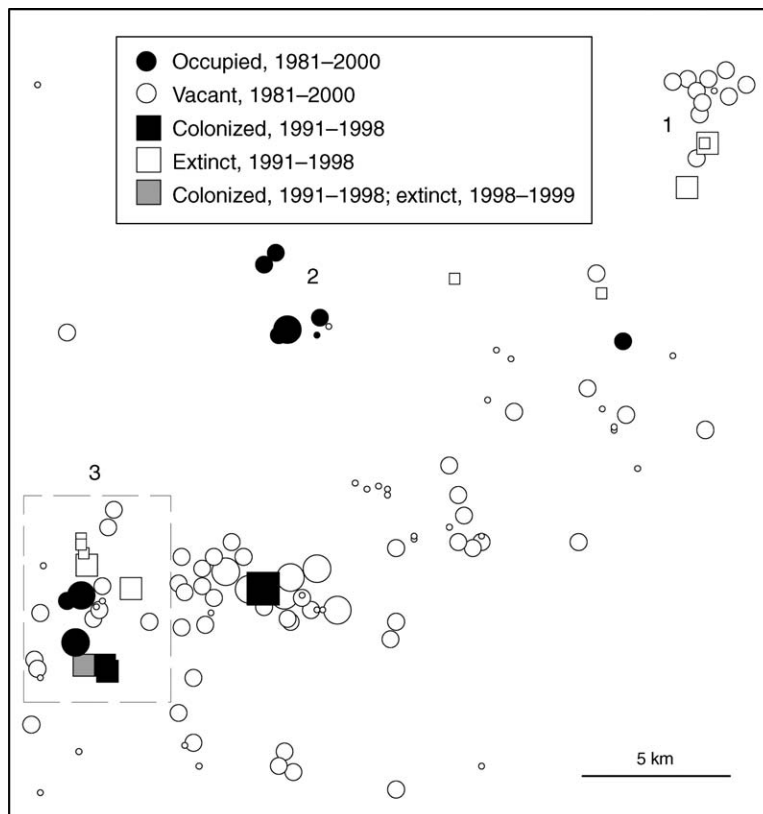
Fig. 2. Occupancy and turnover by *Euphydryas aurinia* in the focal 625-km² network. Black symbols are patches occupied by *E. aurinia* during 1998–2000; white symbols are vacant patches during 1998–2000; the patch represented by the gray symbol was occupied in 1998, vacant 1999–2000. Squares show turnover (extinction or colonization) from 1981 to 2000, circles show no change in status. Numbers indicate sub-networks described in *Methods: Incidence function model*. The dashed outline shows a sub-network used for IFM parameter estimation. Symbol sizes are scaled by patch area and exaggerate patch area.

measure of connectivity did not include information from the 5-km buffer zone, where habitat was not mapped comprehensively.

Incidence function model

The incidence function model (IFM) is a spatially realistic stochastic patch occupancy model that can be used to simulate population turnover in habitat networks over time, based on the area and configuration of habitat patches and certain species-specific parameters (Hanski 1994, 1999). In the IFM, extinction rate (E_i) declines with increasing patch area according to the equation $E_i = (e/A_i^x)(1 - C_i)$, where A_i is patch area, e and x are parameters relating extinction rate to patch area (x refers to the strength of stochasticity and e is the extinction probability per generation in a patch of 1-ha area); at threshold patch area A_0, extinction rate $E_i = 1$; $1 - C_i$ simulates the rescue effect by the instantaneous recolonization of patches that would otherwise go extinct. Patch colonization rate (C_i) increases with patch connectivity (S_i) according to the equation $C_i = S_i^2/(S_i^2 + y^2)$, where y is a parameter relating colonization rate to patch connectivity (the greater the value of y, the higher the connectivity that is required for a given colonization

rate). Based on the assumptions that extinction is area dependent and colonization is connectivity dependent, IFM parameters e, y, and x can be estimated from snapshots of patch occupancy using maximum likelihood estimation (Moilanen 1999, 2000). Software for parameter estimation and metapopulation simulation was obtained from the Metapopulation Research Group at the University of Helsinki (*available online*).[6]

IFM parameters e, y, and x were estimated using patch occupancy and turnover data for 1981, 1998, and 1999, including all three distribution snapshots in parameter estimation. A 35-km² (7×5 km) sub-network (Fig. 2, network 3), that had been visited regularly since the 1980s and where population extinctions and colonizations were known to have occurred, was used for parameter estimation. This sub-network was considered more likely than other parts of the system to meet the IFM assumption of a stochastic steady state produced by colonization / extinction dynamics (e.g., all populations in network 1 had suffered extinction; Fig. 2). To meet IFM assumptions of approximate homoge-

neity in patch quality, patches with vegetation height ≤ 4 cm, shown to be unsuitable by field survey (*Results*), were removed from parameterization and simulations. Further parameters were estimated using information on the ecology of *E. aurinia* and previous applications of the IFM. Parameters α and B were set to 2 and 0.5, respectively (see *Patch connectivity*). Minimum patch area (A_0, where $E_i = 1$) was set to 0.1 ha (1000 m^2), because no patches ≤ 0.1 ha were occupied during the survey. To test model sensitivity to estimates of A_0 and α, parameters e, y, and x were also estimated using values of A_0 of 0.02, 0.05, and 0.3, and values of α of 1 and 3. IFM parameterization can include an estimate of "remote colonization probability," the chance per year of colonization from outside the parameterization system. We set this parameter to 0.001, bearing in mind that several populations were closer than 10 km to the 35-km^2 sub-network used for parameterization (e.g., network 2, Fig. 2).

Initial parameter estimates were obtained using nonlinear regression methods (NLR and BNLR [Moilanen 1999]), with 250 replicates in estimation, 300 function evaluations in initiation, and 1000 function evaluations in estimation. Final estimates were obtained using a Monte Carlo Markov Chain (MCMC) model with 1000 function evaluations in initiation and 4000 function evaluations in estimation, assuming quasi-stationarity (i.e., the estimations use turnover information but assume that single snapshots are representative of a stochastic steady state [Moilanen 1999, 2000]). The model estimated a value of 0.0005 for regional stochasticity, the extent to which environmental stochasticity is synchronized across all patches. Without detailed information on population synchrony in *E. aurinia*, and given that populations in the model system appeared to fluctuate independently of one another (C. R. Bulman, *unpublished data*), regional stochasticity was set to 0.0005 in all simulations. However, to test the effect of including a higher level of regional stochasticity, parameters e, y, and x were also estimated using a value of 0.3 for regional stochasticity.

Estimated IFM parameters were applied to the entire 625-km^2 Dorset focal system to test their predictions of occupancy patterns, for which 100 iterations of the model were run for 100 generations (years), with initial patch occupancy set at that observed in 1981.

Network occupancy

Five pairs of independent "test" networks were located in 16-km^2 (4×4 km) squares across the range of *E. aurinia* in England and Wales, with a sixth pair in the Dorset focal system (Fig. 1). One network of each pair was centered on an extant *E. aurinia* population, and the other on a recently extinct (post-1980) population, based on national data (Asher et al. 2001). The extant 16-km^2 networks were selected nonrandomly by consulting regional distribution records and conservation bodies, and were centered on nature reserves or

well-known *E. aurinia* populations that represented the best habitat in each region. Thus, any resulting bias in estimating the prevalence of extinction debt should be conservative, since the largest metapopulations in each region should have the highest chance of persistence. Comparison (extinct) 16-km^2 squares were the nearest available post-1980 extinct networks. Habitat was mapped in August–October 1999, using the same methods as in the 625-km^2 system. Field searches for larval webs were used to determine whether *E. aurinia* was present or absent in each habitat patch (Lewis and Hurford 1997, Schtickzelle et al. 2005).

Metapopulations of *E. aurinia* in the 16-km^2 networks were modeled using the IFM to test whether extant networks had longer modeled times to extinction than extinct networks, and whether extant networks were predicted to persist in the long term. Parameters estimated from the Dorset focal system were used to run 100 simulations of up to 500 generations (years) in extant and extinct networks. To allow comparison between extant and extinct networks, all patches were set as occupied at the start of simulations (therefore simulations may somewhat overestimate persistence times). Extant networks were also simulated starting with observed patch occupancy in 1999. To assess the sensitivity of results to parameter estimates, simulations were also run for all networks using parameter sets based on the same variations in the values of A_0, α, and regional stochasticity as used for the 625-km^2 network.

As a test for the existence of an extinction debt, we take the proportion of simulations surviving after 100 years for each network, and multiply these together as an estimate of the probability that all six extant networks would be extant after 100 years. This approach estimates the probability that all extant networks would be persistent in the absence of further habitat loss (i.e., that there is no extinction debt in any of the networks), assuming that the networks are independent and that the metapopulation model accurately describes the dynamics of the systems.

Metapopulation capacity

As an alternative estimation of relative ability to support metapopulations, each network's metapopulation capacity (λ_M) was calculated (Hanski and Ovaskainen 2000). Metapopulation capacity (λ_M) is a spatially explicit measure of potential metapopulation persistence based on an inverse relationship between population extinction rate and patch area, and a positive relationship between colonization rate and patch connectivity. Calculation of λ_M for a habitat network requires information on the size and spatial location of habitat patches, and an estimate of dispersal capacity (α) (for a full description see Hanski and Ovaskainen 2000). We calculated λ_M for each 16-km^2 network using $\alpha = 2$ (as for connectivity and IFM parameterization). Habitat networks with high λ_M have higher patch area and connectivity than networks with low λ_M.

TABLE 1. Forward conditional logistic regression for *Euphydryas aurinia* in the focal habitat.

								Model if term removed	
Model	−2LL	R^2	χ^2	df	P	Terms in model	B	−2LLR	P
A) Occupancy 1998	48.67	0.53	38.52	3	<0.001	constant	−6.26		
						vegetation height	+0.25	14.99	<0.001
						connectivity	+1.92	16.80	<0.001
						resource area[†]	+0.03	9.18	0.003
B) Survival 1981–1998	11.57	0.74	16.15	2	<0.001	constant	−5.76		
						vegetation height	+0.40	9.34	0.002
						resource area[†]	+0.11	10.96	0.009
C) Colonization 1981–1998	19.14	0.48	14.69	3	0.002	constant	−10.53		
						Succisa pratensis cover	+0.68	8.57	0.003
						connectivity	+1.53	7.65	0.006
						vegetation height	+0.29	4.29	0.038

Notes: (A) There were 14 patches occupied, 109 vacant; (B) 10 populations survived, 10 extinct; (C) four patches colonized, 99 remained unoccupied; −2LL is −2 log likelihood. For models using leaf length instead of vegetation height: (A) −2LLR = 45.48, R^2 = 0.57, χ^2 = 41.71, $P < 0.001$; (B) −2LLR = 13.03, R^2 = 0.69, χ^2 = 14.70, $P < 0.001$; (C) −2LLR = 18.14, R^2 = 0.51, χ^2 = 15.70, $P < 0.01$.

† Resource area = patch area of *Succisa pratensis* cover.

Binary logistic regression was used to determine whether area, habitat, modeled persistence times, and metapopulation capacity differed significantly between extant and extinct networks.

Minimum viable metapopulation size

Minimum viable metapopulation size (MVM) was defined as the area of habitat in a 16-km² network that resulted in ≥95% of simulations persisting for 100 years. MVM was first estimated based on IFM simulations for the twelve networks (six extant and six extinct), using linear regression of arcsine square-root survival after 100 years against habitat area (in hectares). Relatively few simulations survived for 100 years in any extinct and some extant networks, so the regression was relatively inaccurate at estimating area required for 95% persistence. Furthermore, different configurations of habitat require different total areas for persistence, because of effects of patch configuration on colonization rates. Therefore, MVM was estimated for each of the twelve habitat networks using IFM simulations with different simulated total areas of habitat, again using the linear regression of arcsine square-root survival after 100 years against habitat area (in hectares). The proportion of overall network area contributed by each patch was maintained by increasing or decreasing patch areas proportionately. Simulations were run for each network for total areas of 50, 60, 70, 80, 90, and 100 ha. Networks not achieving ≥95% persistence at 100 ha were also simulated with total areas of 110, 120, and 150 ha. Simulations were initiated with all patches occupied, and additionally with observed patch occupancy in 1999 for the surviving networks, to give more realistic estimates of MVM.

Recolonization of 16-km² networks

Species may persist in fragmented landscapes as groups of extinction-prone metapopulations ("megapopulations" [Hanski 1999]). If metapopulations of *E.* *aurinia* in the surviving 16-km² test networks were really part of larger networks, it would be unrealistic to estimate MVM for the 16-km² squares in isolation. A lower percentage of suitable habitat may be required to ensure persistence if a network is connected to a wider landscape containing *E. aurinia* habitat, than in a completely isolated 16-km² square. To test whether recolonization among 16-km² habitat networks may offset the extinction of individual networks, simulations were also run using model landscapes containing multiple copies of three surviving networks (southwest A, southwest B, mid-Wales). Model landscapes contained nine (144-km²) or 25 (400-km²) "tiles" of the individual network, arranged in squares, containing 10–100 ha of habitat per 16 km² unit. MVM was calculated for the central 16-km² unit, given that it was surrounded by comparably sized metapopulations that were able to recolonize it. One hundred IFM simulations were run for each model landscape, and the number of times that the central unit was occupied after 100 years was recorded.

RESULTS

Patch occupancy and turnover in the focal system

Succisa pratensis was found in 123 habitat patches in the focal system (area 408.5 ha; 0.65% of total land area). Fourteen patches were occupied by *E. aurinia* during 1998 (area 83.7 ha). In 1999 and 2000, 13 patches were occupied (one small population had gone extinct). Since 1981, when 20 patches were occupied, 10 populations had survived, 10 had gone extinct, and four patches had been colonized (Fig. 2).

Patch occupancy in 1998 was positively related to vegetation height, connectivity to *E. aurinia* populations, and resource area (patch area × host plant cover; Table 1A): populations occupied large, well-connected patches with tall and abundant *S. pratensis*. Total host plant quantity was important to patch occupancy: a small patch with high host plant density was as likely to

support a population as a large patch with low host plant density (a model including significant separate effects of patch area and host plant cover explained a comparable level of variation in patch occupancy).

The 10 populations that survived from 1981 to 1998 had taller vegetation heights and greater resource areas than the 10 that went extinct (Table 1B). The four patches colonized had greater host plant cover, higher connectivity to *E. aurinia* populations, and taller vegetation height than the 99 that remained vacant (Table 1C). Occupancy and colonization were positively related to population connectivity, but not to habitat connectivity. Models using *S. pratensis* leaf length, instead of vegetation height, included the same additional variables and explained similar levels of variation (Table 1, footnote). Results using vegetation height are presented in more detail because of its practical utility for conservation management.

Peak population density varied greatly from year to year in occupied patches, and mean peak density was not significantly related to any habitat variables ($n = 13$ occupied patches 1998–2000, Spearman's rank correlations, $P > 0.07$). No patches with vegetation height ≤ 4 cm were occupied in focal or test networks. Therefore, habitat patches with vegetation ≤ 4 cm were considered unsuitable and excluded from subsequent analyses.

Incidence function model: 625-km² system

The 35-km² sub-network used to estimate IFM parameters included 25 patches (88.24 ha; 2.5% of land area). Of these patches, three were occupied by *E. aurinia* and 14 were vacant in all surveys, and eight underwent turnover (three colonizations and six extinctions) (Fig. 2). IFM parameters estimated were: $x = 0.679$ (the strength of environmental and demographic stochasticity); $e = 0.209$ (extinction probability per unit time in a patch of 1 ha); $y = 4.483$ (the effect of connectivity on colonization rate).

IFM simulations across the entire 625-km² focal system produced occupancy levels comparable to those observed (10.6–16.3%), either starting with the 1981 distribution (median patch occupancy after 100 years = 6.1%, 95% CI [percentiles], 0–22.6%), or the 1999 distribution (median, 18.3%; 95% CI, 0–27.4%). Thirteen percent of iterations became extinct starting with the 1981 distribution, and 6% starting with the 1999 distribution. Differences between the two sets of simulations arose because several populations in 1981 were located in nonpersistent sub-networks (e.g., Fig. 2, sub-network 1) that declined to extinction in simulations.

Persistence and extinction debt in 16-km² systems

The six extant 16-km² systems generally had more, larger, and better-connected habitat patches than the six extinct systems (Fig. 3, Table 2). Total habitat area in the system was a better predictor of network occupancy than number of patches, average patch area, or habitat

connectivity, and was the only significant predictor in a forward conditional logistic regression (logit probability of network occupancy (P_O) = $-4.69 + 0.22$ total habitat area, -2 log likelihood = 5.85, $R^2 = 0.79$, $\chi^2 = 10.79$, $P = 0.001$). Only one extant network (Cumbria) had a smaller total habitat area than any extinct network. No measure of habitat quality differed significantly between extant and extinct networks.

Median time to metapopulation extinction in IFM simulations starting with 100% patch occupancy was greater for extant than extinct networks (Table 2, Fig. 4; logit probability of occupancy (P_O) = $-10.36 + 0.39$ median years to extinction, -2 log likelihood = 4.41, $R^2 = 0.85$, $\chi^2 = 12.23$, $P < 0.001$). In extinct networks, all simulations became extinct in less than 100 years, with the exception of southwest B. Four of the extant networks were also extinction prone, particularly Cumbria and southwest A, whose median times to extinction were ≤ 50 years. All simulations of the Cumbria and southwest A networks went extinct in ≤ 200 years, whereas only 1% of simulations for mid-Wales and Dorset survived for 500 years. The remaining two networks (southwest B and north Wales) had median times to extinction of >500 years.

Relative persistence times of the six surviving networks were unchanged when simulations were started with 1999 patch occupancy rather than full occupancy. However, median time to extinction in the four extinction-prone extant networks was reduced on average by 16.7% (Table 2). These four networks each had expected median times to extinction ("extinction debts") of 15–126 years based on current occupancy patterns.

Based on the IFM simulations, the probability that all six extant networks would be extant after 100 years in the absence of additional habitat loss was 0.005 (for simulations starting with full patch occupancy) or 0.004 (for simulations starting with occupancy in 1999). Thus, assuming that the model adequately described the underlying dynamics of *E. aurinia*, there was a >99% probability of an extinction debt in one or more of the extant population networks.

Metapopulation capacity (λ_M) was greater in extant than extinct networks (logit probability of occupancy (P_O) = $-5.27 + 2.57\lambda_M$; -2 log likelihood = 5.96, $R^2 = 0.79$, $\chi^2 = 10.68$, df = 1, $P = 0.001$). Thus, metapopulation capacity, total habitat area, and modeled time to extinction were closely correlated with each other and explained similar proportions of variation in network occupancy.

Minimum viable metapopulation size

Modeled survival after 100 years in the 12 test networks was related to habitat area by the equation: (arcsine square-root proportion persistence) = $-0.044 + 0.014 \times$ area ($R^2 = 0.92$, $F_{1,10} = 113.31$, $P < 0.001$; Fig. 5). Estimated minimum viable metapopulation size (MVM) based on observed habitat area in the 12
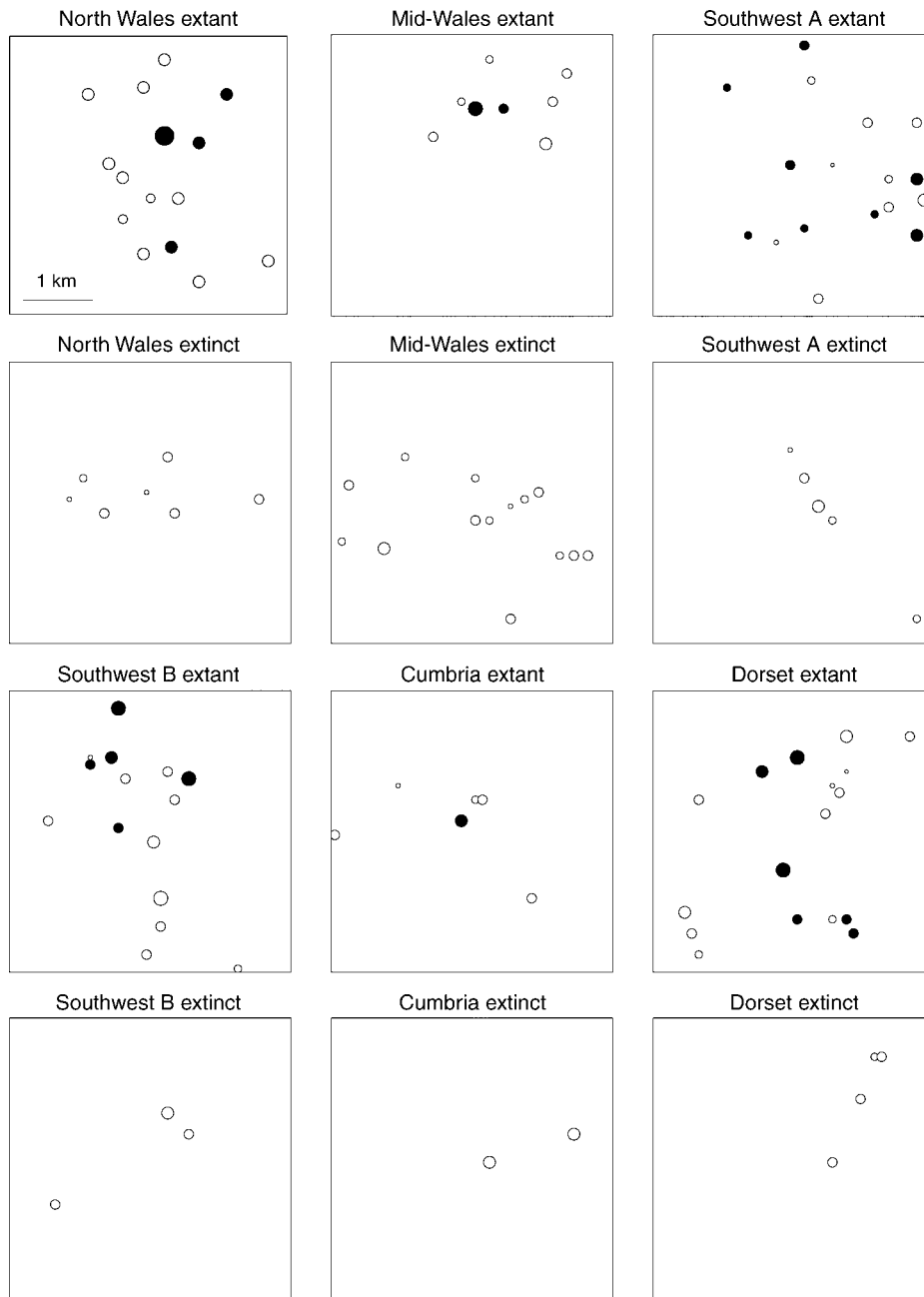
FIG. 3.   The distribution of habitat patches in 16-km² test networks. Black circles are patches occupied by *Euphydryas aurinia* in 1999; white circles are vacant. Symbol size is scaled by patch area and exaggerates patch area.

networks was 102.0 ha (6.4% of land area; 95% CI, 74.7–143.7 ha). Alternative IFM parameter estimates produced broadly similar estimates of MVM, ranging from 75 to 104 ha (Table 3).

Network-specific MVM estimates, retaining patch spatial locations and relative sizes but varying habitat area systematically, ranged from 66 ha (4.1% of land area) to 136 ha (8.5%) (mean 98.8 ha, 6.2%) in 11 of the 12 networks (Table 2). The extinct Cumbria network's estimate was 202.6 ha (95% CI, 142.6–302.8 ha) and may

be less reliable because only two patches remain in the system, so that MVM depends largely on estimated local extinction rate. Simulations for the six extant networks starting with 1999 patch occupancy gave slightly higher MVM estimates (80–142 ha [5–9%]). All extinct and four extant networks contained habitat areas that were lower than their network-specific MVM estimates. For the extant networks, habitat areas in Cumbria (14.1 ha) and Dorset (79.8 ha) were less than their lower 95% CIs for MVM (80.1 ha and 86.9 ha, respectively). Habitat areas

TABLE 2. Comparison of extant and extinct metapopulations of *Euphydryas aurinia*.

Network	Year of last record	No. patches	Total area (ha)	Median time to extinction (years)†	Metapopulation capacity	Estimated MVM (ha)†
Extant						
North Wales	‡	15	114.88	>500	5.30	88.4 (96.3)
Mid-Wales	‡	8	40.98	116 (97)	3.83	66.3 (81.0)
Southwest A	‡	17	32.53	50 (45)	2.84	71.1 (79.7)
Southwest B	‡	15	116.12	>500	4.68	92.5 (93.8)
Cumbria	‡	6	14.12	24 (15)	1.48	115.8 (141.8)
Dorset	‡	18	79.79	130 (126)	4.02	113.7 (123.7)
Extinct						
North Wales	1986	7	10.30	15	0.64	135.5
Mid-Wales	1987	14	19.54	21	1.03	87.5
Southwest A	1989	5	9.46	17	2.00	92.1
Southwest B	1994	3	7.50	22	1.17	133.2
Cumbria	1992	2	16.65	26	1.68	202.6
Dorset	1981	4	5.90	11	0.35	90.7

† Main values for simulations starting with full patch occupancy; value in parentheses refers to simulations starting with 1999 occupancy.

‡ Still extant in 1999.

exceeded the lower 95% CIs in mid-Wales (41.0 ha > 35.9 ha) and southwest A (32.5 ha > 17.4 ha) because habitat patches were clustered in the landscape, increasing colonization rate, but were still well below estimated network-specific MVM. Only two extant networks (southwest B and north Wales) contained larger areas of habitat than their MVMs, but habitat losses of only 20% would cause both networks to fall below these estimated thresholds for persistence.

Recolonization of 16-km² networks

We modeled the impact of long-distance colonization on estimated MVM by centering each 16-km² network in model landscapes of nine (3 × 3) or 25 (5 × 5) repeated 16-km² "tiles," representing 144-km² or 400-km², systems respectively. In 144-km² systems, MVM for the central 16-km² unit was 57.7 ha for network southwest A (3.6% of land area), 69.7 ha for southwest B (4.4%), and 62.2 ha for mid-Wales (3.9%). Thus, estimated MVM was reduced slightly in comparison with estimates based on 16-km² networks in isolation (Table 2) but remained around 3.5–4.5% of land area. Estimates of MVM for the central unit in 400-km² systems differed by less than 1 ha from those of the 144-km² systems, showing that further increasing network extent did not increase recolonization of the central 16-km² cell. Three of the extant networks contain less habitat than this 57–70 ha range, indicating that they would fail to meet MVM criteria even if they were surrounded by other identical networks with the same survival probabilities (in fact, they are surrounded by landscapes with much lower levels of survival probability).

DISCUSSION

We estimated minimum viable metapopulation size (MVM) for a declining species breeding in fragmented landscapes. Threshold MVM was greater than total habitat area in four out of six extant metapopulations of the butterfly *Euphydryas aurinia*. Metapopulation sim-

ulations of these four networks suggest that they are declining to extinction, with "extinction debts" expected to last median times of 15–126 years.

Turnover and persistence in a fragmented landscape

Euphydryas aurinia showed a low level of habitat occupancy, substantial population turnover, and evi-
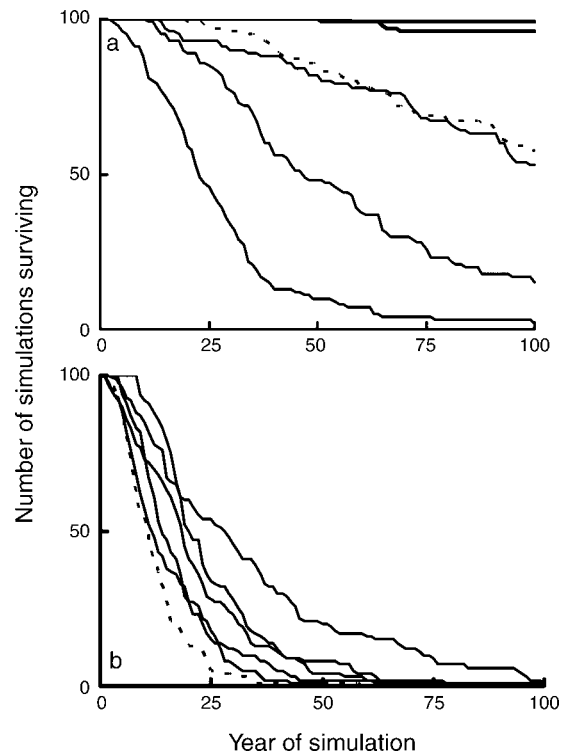

FIG. 4. Number of 100 IFM iterations surviving against time for (a) extant and (b) extinct 16-km² networks. All patches were occupied at initiation. Dashed lines show the focal system (Dorset) networks.
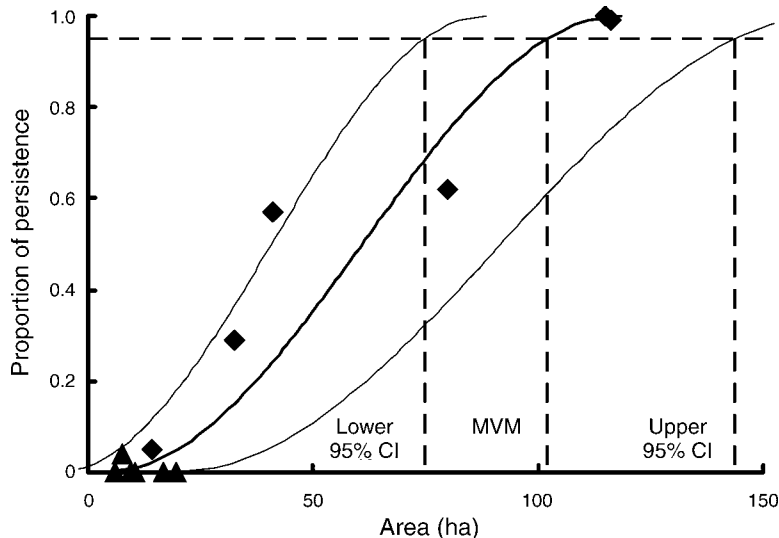
FIG. 5. Proportion of IFM iterations persisting for 100 years against habitat area in 16-km^2 networks. Triangles show extinct networks, diamonds show extant networks. The thick line is the linear regression of arcsine square-root proportion survival against area, used to estimate minimum viable metapopulation size (MVM) at which ≥95% of simulations persist for 100 years (thin lines show 95% CI). Dashed lines show 95% CI of estimated MVM.

dence of metapopulation dynamics in a 625-km^2 landscape. Of 123 habitat patches, only 10 contained populations in all of four distribution surveys, with 11 extinctions and four colonizations. Populations had a greater risk of extinction in patches with smaller areas of poorer quality habitat; while patches with good quality habitat and high connectivity to *E. aurinia* populations had a higher probability of colonization. Occupied patches had larger areas of high quality habitat and higher connectivity than vacant patches, as in many empirical studies of species in fragmented landscapes (Hanski 1999 and references therein).

The spatial pattern of turnover events and metapopulation simulations in the 625-km^2 system suggest that there are several semi-independent population networks in the landscape (Fig. 2, networks 1, 2, 3). Between 1981 and 2000, one isolated network (1) went extinct, and is unlikely to be recolonized; another network (2) retained

a high level of occupancy, with no extinctions observed; a further network (3) included several extinctions and colonizations. Most turnover occurred in the longest interval between sampling (1981–1998), and, given that extinctions and colonizations are relatively rare events, the observed turnover in this period is probably an underestimate (see Thomas et al. 2002). Only one patch showed turnover between 1998 and 2000 (the extinction of a patch colonized after 1981) but, since then, several colonizations have been observed in network 3, with four patches that suffered extinction during 1981–1998 occupied by *E. aurinia* in 2006 (C. R. Bulman, *unpublished data*).

Applications and limitations of the metapopulation approach

Low occupancy and relatively high turnover in the 625-km^2 network suggested that it was appropriate to

TABLE 3. Estimated incidence function model parameters and associated estimates of *Euphydryas aurinia* minimum viable metapopulation size.

Parameters entered into model			Parameters estimated by model			Minimum viable metapopulation size (ha)		
A_0	α	Regional stochasticity	x	y	e	Estimate	Lower 95%	Upper 95%
0.1	2	0.0005	0.679	4.483	0.209	102.0	74.7	143.7
0.1	1	0.0005	0.236	3.083	0.581	91.6	66.4	130.0
0.1	3	0.0005	1.002	3.221	0.100	77.6	35.9	189.1
0.02	2	0.0005	0.753	8.674	0.052	75.7	40.0	153.8
0.05	2	0.0005	0.811	7.007	0.088	84.1	51.8	144.0
0.3	2	0.0005	0.823	3.400	0.371	103.6	80.2	136.6
0.1	2	0.3	0.760	4.674	0.174	80.1	37.6	194.3

Note: Parameters are: A_0, threshold patch area; α, a constant estimating how migration from a patch declines with increasing distance, and the slope of a negative exponential distribution of dispersal distances; x, the strength of stochasticity; y, a parameter relating colonization rate to patch connectivity (the greater value of y, the higher the connectivity that is required for a given colonization rate); e, the extinction probability per generation in a patch of 1-ha area.

use a metapopulation approach to model *E. aurinia*'s spatial dynamics. Studies using demographic modeling (Schtickzelle et al. 2005) and genetic approaches (Joyce and Pullin 2003) support this approach, since they indicate large fluctuations and high turnover for *E. aurinia* populations in fragmented landscapes. In addition, even though the incidence function model (IFM) parameters were estimated from occupancy and turnover data for the 35-km^2 sub-network (Fig. 2, network 3), the model recreated occupancy patterns well in the entire 625-km^2 system. However, despite providing a useful means of modeling *E. aurinia*'s dynamics in independent habitat networks, uncertainty in model parameters and possible differences in habitat among landscapes mean that model results should be interpreted with caution.

In the 625-km^2 network, *E. aurinia* was more likely to occupy habitat with abundant, tall, *S. pratensis* plants, but other features of habitat were not clearly related to its abundance. Instead, population densities varied greatly and asynchronously between patches, possibly depending on levels of larval parasitism (influenced by parasitoid metapopulation dynamics and the weather [Porter 1983, Bulman 2001]). When the population dynamics of species vary widely for reasons other than habitat variation, patch area may be a reasonable estimate of average expected population size, and unpredictable local population dynamics may be approximated by simulated environmental and demographic stochasticity in a metapopulation model (Moilanen and Hanski 1998). Nevertheless, the integration of temporal and spatial variation in habitat quality in metapopulation models is an important area for research (Thomas et al. 2001). Possible approaches include the combination of resource density and habitat area to provide a measure of resource area for each habitat patch (as we used for the 625-km^2 system), and synchronous variation in modeled patch size such as is used in the IFM to simulate regional stochasticity (Moilanen 1999).

In this study, we excluded habitat with short (<4 cm) vegetation from our analyses, to ensure that habitat areas in all networks corresponded to suitable *E. aurinia* habitat. Differences in vegetation height and *S. pratensis* cover among patches and networks produce uncertainty in absolute estimated survival times and minimum viable metapopulation size. For example, the total habitat area required for metapopulation persistence can be reduced by increasing habitat quality. However, for metapopulations to survive in consistently smaller areas of habitat in the 16-km^2 networks than in the network used for parameter estimation, habitat quality would have to be systematically better in the 16-km^2 networks. There were no significant differences in average *S. pratensis* cover between the Dorset network (mean = 4.4%) and the independent extant 16-km^2 networks (mean = 4.1%) (Mann-Whitney tests between networks, *P* > 0.2), suggesting that our identification of an extinction debt

in the 16-km^2 networks should be robust to variation in habitat quality.

Minimum viable metapopulation size

Patch networks in five out of six extant 16-km^2 systems had greater habitat areas, longer modeled times to extinction, and higher metapopulation capacities than six extinct systems. Habitat area may be a good indication of likely metapopulation persistence for conservation, as long as habitat quality is maintained at an adequate level. Nevertheless, for ranking persistence among networks with comparable habitat areas but different patch locations, IFM and metapopulation capacity are useful because they consider the effects of patch connectivity on colonization rates. Of these two methods, metapopulation capacity has the advantage over the IFM in that it requires the estimation of fewer parameters, and hence includes fewer potential sources of error. However, IFM is useful for generating expected persistence times, with the practical value of estimating minimum viable metapopulation size (MVM).

We estimated that the threshold area to achieve 95% probability of *E. aurinia* persistence for 100 years ranged from 66.3 to 202.6 ha (4.1–12.6%), depending on the number of patches in a network and their spatial locations, and whether networks were assumed to be fully occupied at the start of simulations. Testing the sensitivity to parameters of species dispersal and minimum area requirements led to fairly consistent estimates of MVM, between 75.7 and 103.6 ha (4.7–6.5%) in a 16-km^2 cell (Table 3). The inclusion of only negligible regional synchrony in population dynamics may underestimate extinction risk (Moilanen 1999), but simulations using greater estimated regional synchrony increased the confidence intervals around the estimate rather than increasing estimated MVM (80.1 ha; Table 3). In larger regions, a smaller percentage of land may need to be protected, because of colonizations across wider networks of habitat (Wilson et al. 2002, Thomas and Hanski 2004). However, simulations across wider landscapes suggested that some 4% of land area still had to be habitat to ensure metapopulation persistence, even in 144-km^2 or 400-km^2 networks. Thus, reduction in habitat density from 6% to 4% required a 10-fold increase in the size of region required for the same level of persistence. With less than 4% habitat cover, increased landscape size may still not permit species persistence.

Caution must be taken when interpreting absolute area for MVMs, while the relative values of different landscapes are likely to be more robust (Dreschler et al. 2003). Nonetheless, IFM simulations and sensitivity analyses suggest that *E. aurinia* will almost always experience a serious extinction risk in 16-km^2 landscapes with <50 ha of habitat, whereas persistence is likely for most reasonable parameter combinations when >150–200 ha are present. In between, the chance of persistence will depend on factors such as the spatial locations of

habitat, the density and size of host plants within habitat, and effects of the intervening landscape on dispersal by *E. aurinia* and its natural enemies. Unfortunately, three of the extant metapopulations contain <50 ha of habitat (14–41 ha) and have a high predicted risk of extinction, and all three of the others fall within the zone of uncertainty (80–116 ha). None of them can be considered to be "safe" from extinction. In general, very few *E. aurinia* metapopulations in Britain (Asher et al. 2001) and northwestern Europe (van Swaay and Warren 1999, Schtickzelle et al. 2005) are so large that persistence can be guaranteed. This study showed that further habitat degradation of only 10–20% even in apparent strongholds will cause networks to fall below their estimated MVM. For this and other declining species, it makes sense to target conservation measures on the most persistent, "core" metapopulations: first, because it may be impossible to carry out enough management and restoration in the smaller networks to ensure long-term persistence; and second, because core metapopulations may themselves be at some risk of extinction.

Nonequilibrium metapopulations and extinction debt

After processes of habitat loss and fragmentation, populations may not go extinct instantaneously from all remaining habitat, instead remaining for some time as "nonequilibrium metapopulations" in networks that are below the threshold required for long-term persistence (Harrison 1991, Harrison and Taylor 1997). Occupancy patterns lag behind those expected at equilibrium (i.e., extinction), in what is known as an "extinction debt." Until now empirical evidence for extinction debts has been deduced from four sources: biogeographic patterns such as species–area curves (e.g., Brooks and Balmford 1996, Cowlishaw 1999, Helm et al. 2006); rates of species extinction following habitat fragmentation (e.g., Soulé et al. 1988, 1992); species distributions that are more closely related to former than current habitats (Petit and Burel 1998); and metapopulations modeled in conjunction with known changes in habitat distributions (Hanski et al. 1996b, Thomas and Hanski 2004). Theory predicts that the length of the transient period of non-equilibrium dynamics, after habitat degradation but before metapopulation extinction, is greatest for systems where the network size is close to the extinction threshold (Ovaskainen and Hanski 2002, 2004). We provide evidence for an extinction debt in *E. aurinia* by modeling metapopulation dynamics in six extant meta-populations that have suffered rapid habitat loss and fragmentation, and which are now close to (or below) the extinction threshold for the species.

Suitable habitat for *E. aurinia* has declined markedly in the United Kingdom since the start of the 20th century due to changing agricultural practices. These changes have taken two forms: fertile lowland habitats have been lost to agricultural improvement (drainage, plowing, reseeding, and fertilization), while land that is marginal to modern agriculture has become too overgrown for the host plant *S. pratensis*, because of abandonment and declines in livestock grazing. Culm grassland, a habitat used by *E. aurinia* in southwest England, has declined by 92% since 1900, with a 48% decline between 1984 and 1991 (Department of Environment 1995). The Culm grassland networks that we surveyed (southwest B) included an extant network of 116 ha (still extant in 2006, but with some population loss since 1999 because of habitat abandonment), and a 7.5-ha network that went extinct in 1994. Habitat declines in most landscapes will have been similar, exposing metapopulations of *E. aurinia* to marked habitat fragmentation over short periods of time.

Assuming that the metapopulation simulations adequately describe the underlying dynamics of *E. aurinia*, there is a >99% chance that the species has an extinction debt in one or more of the extant networks studied in the United Kingdom. In particular, the simulations suggest that *E. aurinia* is carrying an extinction debt in four of the six extant networks. Habitat area in these networks was below the estimated MVM (in two cases below the estimated lower 95% CI), and metapopulation simulations had median times to extinction of 15–126 years based on habitat and occupancy in 1999. It is unlikely that the extant metapopulations that we studied are maintained by colonization across wider landscapes, since we selected the largest known metapopulations in each region, and because modeled persistence was barely increased by modeling the effects of immigration from nearby metapopulations. Thus, there is strong support for the hypothesis that some extant networks of *E. aurinia* will decline to extinction in the absence of further habitat loss. Indeed, the extant metapopulation with the shortest modeled time to extinction (Cumbria) effectively went extinct in 2004, when the two remaining larval groups were taken into captivity for captive breeding until habitat has been restored.

Conclusion

In many currently surviving networks of rare or declining species, even maintaining the status quo may not prevent regional extinction. But the transient time before a species reaches extinction represents a challenge and an opportunity to conservationists. Approaches such as metapopulation or population viability modeling can allow estimation of the amount, type, or spatial location of habitat maintenance or restoration that will most favor persistence in the long term (e.g., Dreschler et al. 2003, Schtickzelle et al. 2005). Improving habitat quality by changed management, or improving habitat area and connectivity by habitat restoration, can then be practically employed to reduce extinction rates and increase colonization rates. Such approaches are already being employed for *E. aurinia* in several population networks in England and Wales (Fowles and Smith 2006, Fox et al. 2006). In order to implement such approaches for other species of conservation concern,

the prevalence of species suffering from transient, non-equilibrium, population dynamics is a matter for urgent research.

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