THE ROYAL SOCIETY

doi 10.1098/rspb.2001.1693

The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes

J. A. Thomas[1*], **N. A. D. Bourn**[2], **R. T. Clarke**[1], **K. E. Stewart**[2], **D. J. Simcox**[1], **G. S. Pearman**[2], **R. Curtis**[1] **and B. Goodger**[2]

[1]*Natural Environment Research Council Centre for Ecology and Hydrology, CEH Dorset, Winfrith Technology Centre, Dorset DT2 8ZD, UK*
[2]*Butterfly Conservation, Manor Yard, East Lulworth, Dorset BH20 5QP, UK*

Habitat quality and metapopulation effects are the main hypotheses that currently explain the disproportionate decline of insects in cultivated Holarctic landscapes. The former assumes a degradation in habitat quality for insects within surviving ecosystems, the latter that too few, small or isolated islands of ecosystem remain in landscapes for populations to persist. These hypotheses are often treated as alternatives, and this can lead to serious conflict in the interpretations of conservationists. We present the first empirical demonstration that habitat quality and site isolation are both important determinants of where populations persist in modern landscapes. We described the precise habitat requirements of *Melitaea cinxia*, *Polyommatus bellargus* and *Thymelicus acteon*, and quantified the variation in carrying capacity within each butterfly's niche. We then made detailed surveys to compare the distribution and density of every population of each species with the size, distance apart and quality of their specific habitats in all their potential habitat patches in three UK landscapes. In each case, within-site variation in habitat quality explained which patches supported a species' population two to three times better than site isolation. Site area and occupancy were not correlated in any species. Instead of representing alternative paradigms, habitat quality and spatial effects operate at different hierarchical levels within the same process: habitat quality is the missing third parameter in metapopulation dynamics, contributing more to species persistence, on the basis of these results, than site area or isolation. A reorientation in conservation priorities is recommended.

Keywords: metapopulation; landscape; habitat quality; isolation; conservation; Glanville fritillary

1. INTRODUCTION

A priority in ecology and conservation is to explain why insect extinction rates in the Holarctic exceeded those of other recorded taxa during the 20th century in most ecosystems within cultivated landscapes (Thomas 1991; Thomas & Morris 1994; New *et al.* 1995). Two main hypotheses have been suggested, derived from butterfly population ecology (Thomas 1984; Hanski 1999):

(i) Changes in habitat quality within sites. In most insects, the immature stage occupies a narrow species-specific niche within its biotope. The same land-use changes that reduce and fragment ecosystems typically result in changed management, an altered vegetation structure and a deterioration in habitat quality for juveniles of the characteristic species within surviving ecosystem islands (Thomas 1984, 1991; Thomas & Morris 1994).
(ii) Changes in metapopulation structure. A species' populations are interdependent in any region. Long-term persistence depends on a balance across a landscape between local extinctions of individual populations and new colonizations of vacant habitat patches. Modern land use results in the survival or regeneration of too few, small or isolated ecosystem islands for persistence (Hanski 1998, 1999).

Although each approach to population ecology acknowledges the validity of the other (Thomas 1991; Hanski & Ovaskainen 2000), studies of habitat quality have often ignored metapopulation dynamics, and vice versa. Indeed, the development and testing of these hypotheses has been so separate that Hanski (1999, p. 201) described their emergence, in the 1970s and 1990s, respectively, as 'the [two] major reorientations in butterfly biology and conservation in 20 years'. Certainly, they have polarized the advice given to conservation organizations (Harrison & Bruna 1999). The former approach prioritizes the conservation of optimal habitat within patches, if necessary on fewer sites; the latter advocates the preservation of 10–20 biotope patches within every species' dispersal range, regardless of quality.

Recent theory suggests that, far from being alternative paradigms, these two processes are linked (Clarke *et al.* 1997; Thomas *et al.* 1998; Wiegan *et al.* 1999). We, for example, employed mechanistic spatial models of interacting ant and butterfly populations to predict that, in a typical landscape, the expected increased extinction rates associated with habitat loss and isolation could be reversed—provided that at least 25% of the ecosystems remained—if the quality of habitat within the surviving patches shifted from the normal (suitable, source) mixture to the optimum for both insects. On the other hand, metapopulation effects were enormously amplified if sites simultaneously became smaller, more isolated and deteriorated in quality (Thomas *et al.* 1998). Wiegan *et al.*

---

[*] Author for correspondence (jat@ceh.ac.uk).

Received 11 December 2000 *Accepted* 6 April 2001

(1999) similarly predicted that the persistence of populations changed radically when a simple additional variable of within-site 'optimal' or 'suboptimal' habitat quality was included in metapopulation models of the brown bear.

Here, we present the first empirical confirmation that habitat quality and site isolation are both important predictors of where populations persist in modern landscapes. Using the colonial grassland butterfly species *Melitaea cinxia* (Glanville fritillary), *Polyommatus bellargus* (Adonis blue) and *Thymelicus acteon* (Lulworth skipper), we described the precise attributes of the habitat to which each species was limited, and measured the variation in carrying capacity within each species' niche. We then made detailed surveys to compare the distribution and density of every population of each species with the size, distance apart and quality of their specific habitats in all of their occupied and unoccupied habitat patches in topographically discrete landscapes in southern England. All were near these species' northern limits of range, where habitat quality and metapopulation effects are amplified (Thomas *et al.* 1999). We had previously established for each butterfly species that their population structure in these landscapes possessed all the attributes characteristic of metapopulations (Thomas & Simcox 1982; Thomas 1983*a*,*b*; Thomas *et al.* 1992; Hanski 1999; Bourn *et al.* 2000), and had available a similar number and area of habitat patches distributed across comparably sized landscapes to the benchmark description of a *M. cinxia* metapopulation on Baltic islands (Kuussaari 1998; Saccheri *et al.* 1998; Hanski 1999).

2. METHODS

(a) *Defining species' niches and habitat quality*

Previous studies had shown that each butterfly is restricted to a narrow ecological niche under British climates, defined by variation in the larval host-plant resource; nectar for adults was not a limiting factor on any site studied (Thomas 1991). *T. acteon* inhabits calcareous grassland in Britain, but only where its larval food-plant, *Brachypodium pinnatum*, grows in tall sheltered tussocks on southern aspects (Thomas 1983*a*); *P. bellargus* larvae eat *Hippocrepis comosa*, but only in well-grazed calcareous swards (Thomas 1983*b*); *M. cinxia* also prefer early-seral grassland, feeding on *Plantago lanceolata* on well-drained soils in the first years after landslips on mainly south-facing cliffs (Thomas & Simcox 1982; Thomas 1991).

We first quantified habitat quality (h) according to the preferences of ovipositing females or the distribution of larvae in the field. In each case, habitat preference (q) was classified as the probability of food-plants with different growth forms or microhabitats within sites containing eggs or larvae. We reanalysed published data describing the larval niche of *T. acteon* (Thomas 1983*a*), and made more precise new measurements for the other species. For *M. cinxia*, a total of 246 random $1\,\mathrm{m}^2$ quadrats, containing 3800 *P. lanceolata*, were examined on six occupied sites. Every plantain was classified as growing in one of five successional stages, and the mean leaf size was measured and assigned to one of five classes. The density of *M. cinxia* larval nests was recorded in the same samples, and the successional stage and plantain leaf size they used were measured. For *P. bellargus*, a total of 1560 randomly chosen $0.25\,\mathrm{m}^2$ quadrats were searched over four years on one site in Hampshire. In total, 2125 *P. bellargus* eggs were found on the 1853 *H. comosa* plants examined; the turf height and shelter category (as defined in Thomas 1983*b*) of every plant were recorded. In all species, the random sample of plants or quadrats used to derive the habitat-preference relationships from egg or larval distributions were from only small parts of a few sites and were made several years before the surveys; hence they were effectively independent of the census data on butterfly occupancy and density for each whole patch.

(b) *Defining habitat patches*

Mark–recapture estimates of adult butterfly vagility between patches (*M. cinxia* and *P. bellargus*, $n = 5$ sites; *T. acteon* $n = 3$ sites) were used to define as an individual patch and population any grassland of suitable aspect and soils containing the larval food-plant that was separated from another patch by more than 75 m of non-habitat for *M. cinxia*, and more than 100 m of non-habitat for *T. acteon* and *P. bellargus* (Thomas 1983*a*,*b*). These distances exceed the 30 m minimum used for *M. cinxia* on Baltic islands (Hanski 1999), but represent realistic barriers to trivial movements in these UK landscapes (i.e. less than 15% population exchange between patches; Bourn & Thomas 1992) and avoid the artefacts and biases inherent in smaller subdivisions of patches. In practice, very few patches were between 30 m and 75 m or between 30 m and 100 m apart; none was less than $500\,\mathrm{m}^2$ in area.

(c) *Survey methods*

Having described each species' preferences, we made a complete census of all its potential habitat patches in central southern England. *M. cinxia* was surveyed in 1996, *T. acteon* in 1997 and *P. bellargus* in 1999. Landscape boundaries were defined in order to encompass the entire UK ranges of *T. acteon* and *M. cinxia*; boundaries for *P. bellargus* encompassed its UK stronghold, the calcareous grassland of Dorset and south Wiltshire (Thomas 1983*b*). Within each study landscape, every potential habitat patch of the species in question was examined during the adult (*P. bellargus*, *T. acteon*) or late larval (*M. cinxia*) stages. Presence or absence and density of butterflies was recorded on every patch, using transects to record adult densities (Thomas 1983*c*) and absolute counts for *M. cinxia* larval nests (Thomas & Simcox 1982). Each patch was mapped using tested techniques and its area measured (Thomas 1983*c*); isolation (i) was represented by distance to the nearest patch, whether occupied or not. The quality of habitat in each patch was measured by recording food-plant density and growth form, microtopography and vegetation structure (including turf height) in 50 random $1\,\mathrm{m}^2$ quadrats ($n = 13\,350$ for the three species). Indexes for habitat quality for each patch were derived as weighted averages of the species' preference values for each vegetation and habitat type, weighted by the relative frequency of each type.

(d) *Statistics*

The relationships between the presence or absence of a species on a patch and the area, isolation and habitat quality of the patch were assessed using logistic-regression modelling techniques. The importance of each variable, both individually and when allowing for other variables, was measured by the statistical significance (p value) of its (partial) regression coefficient. The overall model fit was measured by the Goodman–Kruskal gamma (GKG) association using the MINITAB 13 statistical analysis package (Minitab Inc.), defined as $\mathrm{GKG} = (C - D)/(C + D)$, where C is the total number of pairs (j, k) of patches for

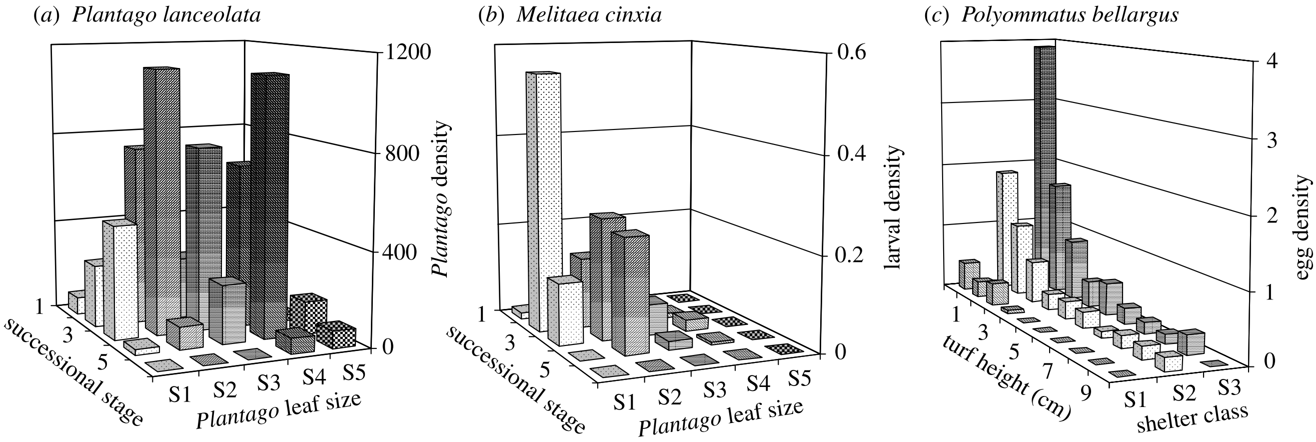

Figure 1. The niches selected by *Melitaea cinxia* and *Polyommatus bellargus* in UK grassland. (*a*) Distribution of *Plantago lanceolata*, the larval food-plant of *M. cinxia*, in five successional stages of grassland (1: $>90\%$ bare ground, turf height <5 cm; 2: 1–90% bare ground, turf height <15 cm; 3: 0% bare ground, turf height 15–20 cm; 4: 0% bare ground, turf height 20–25 cm; 5: 0% bare ground, turf height >25 cm) and in five classes of mean plant leaf size (S1: $<120\ \mathrm{mm}^2$; S2: 120–$500\ \mathrm{mm}^2$; S3: 501–$1800\ \mathrm{mm}^2$; S4: 1801–$3910\ \mathrm{mm}^2$; S5: $>3910\ \mathrm{mm}^2$). (*b*) Density of larval nests of *M. cinxia* in the same samples measured for *P. lanceolata* in (*a*); $n=368$ larval nests (mean ± s.d. $=89\pm56$ larvae per nest). (*c*) Density of *P. bellargus* eggs (q) on *Hippocrepis comosa* plants growing in turf of variable heights (cm) and shelter classes (S1: exposed, $q=0.71\mathrm{e}^{-0.48}$, $r^2=0.89$; S2: sheltered, $q=3.14\mathrm{e}^{-0.53}$, $r^2=0.98$; S3: very sheltered, $q=7.91\mathrm{e}^{-0.72}$, $r^2=0.99$; overall $r^2=0.986$).

which the butterfly is present on patch j but not on patch k, and the model predicted probability $P_j > P_k$; D is the number of pairs with $P_j < P_k$, using the same criteria as above.

3. RESULTS

(a) *Definitions of habitat quality*

Our reanalysis of published data (Thomas 1983*a*) showed that *T. acteon*'s preference for tall *B. pinnatum* is well described ($r^2>0.95$, $n=140$) by the relationship $q=0.00441\times(\text{turf height})^{1.46}$ over the observed height range from 0 cm to 40 cm, indicating at least ten times the larval density in turf over 25 cm tall compared with turf less than 5 cm tall.

As expected, *M. cinxia* larvae exploited only a small minority of the food-plants within sites, preferring small-leaved growths (S1) in short sparse turf and completely avoiding large plantains or any growing in later seral stages (turf heights of more than 25 cm) (figure 1*b*). This exploitation of a rare growth form of the food-plant (figure 1*a*) was so strong that we found no relationship between either the presence or the density of *M. cinxia* and the abundance of *P. lanceolata* in patches, but there were strong correlations ($p<0.001$) between seral stage and both butterfly parameters. We therefore calculated h for *M. cinxia*, on sites where *P. lanceolata* was present, using the relative abundance within the site of successional stages one to five, with estimated q values of 0.08, 0.54, 0.35, 0.03 and 0.00, respectively.

P. bellargus also showed strong habitat preference (q), in this case for examples of its food-plant growing not only in extremely short (1 cm tall) turf but also in the most sheltered micropockets available within sites (figure 1*c*). This variation is described for each of the three shelter categories (Thomas 1983*b*) by: S1 (exposed), $q=0.71\mathrm{e}^{-0.48}$, $r^2=0.89$; S2 (sheltered), $q=3.14\mathrm{e}^{-0.53}$, $r^2=0.98$; and S3 (very sheltered), $q=7.91\mathrm{e}^{-0.72}$, $r^2=0.99$; overall $r^2=0.986$.

(b) *The distribution of populations in landscapes*

The numbers of occupied and unoccupied topographically suitable patches containing the food-plant for each species in its landscape are listed in table 1. In each case, patches varied in area, isolation and habitat quality by similar orders of magnitude (table 1).

Butterfly density and habitat quality were correlated in each species ($p<0.05-p<0.0001$) even when the analysis was restricted just to the occupied sites (table 1), confirming that the egg-laying preferences reflect real variation in the carrying capacities of habitats. In no species was butterfly density correlated with patch size or isolation.

The key question was which variable best explained the pattern and proportion (range 0.46–0.75) of sites that were occupied by each species in its landscape? We found that the presence of a population in a patch was not correlated with patch area in any species (table 2). In contrast, strong correlations existed between presence and both isolation and habitat quality (figure 2 and table 2). Habitat quality was the best predictor for each species, with predictive association (GKG) values of between 62% and 85%, compared with between 23% and 51% for isolation. Moreover, isolation only improved the predictive association by between 3% and 6% beyond that explained by habitat quality (table 2). The same patterns were obtained when isolation was calculated as the distance from the nearest population (occupied patch) rather than from the nearest available patch.

4. DISCUSSION

This is the first time, to our knowledge, that within-site variation in habitat quality has been measured with precision in a metapopulation study. We believe that the results are also the first to show that this parameter predicts patterns of site occupancy across landscapes more strongly than the conventional metapopulation

Table 1. Summary of values of parameters recorded for the habitat patches of each species of butterfly in its landscape.

species	landscape area (km^2)	number of habitat patches	proportion of patches occupied	mean patch size, a (ha) (s.d.)	mean distance from the nearest patch, i (m) (s.d.)	mean index of habitat quality, h (s.d.)	rank correlation between h and population density
Melitaea cinxia	229	72	0.46	0.54 (1.1)	223 (467)	11.4 (8.4)	$r_{\text{occupied}} = 0.35$, $p < 0.05$ $r_{\text{all sites}} = 0.54$, $p < 0.0001$
Thymelicus acteon	507	96	0.75	6.51 (15.1)	747 (923)	0.34 (0.31)	$r_{\text{occupied}} = 0.39$, $p < 0.001$ $r_{\text{all sites}} = 0.62$, $p < 0.0001$
Polyommatus bellargus	1960	95	0.62	6.57 (9.3)	1716 (1913)	0.11 (0.10)	$r_{\text{occupied}} = 0.51$, $p < 0.01$ $r_{\text{all sites}} = 0.39$, $p < 0.001$

parameters of site isolation and area. It is important to note that it is the requirements of the (usually inconspicuous) immature stages that define habitat quality in most temperate insect species studied, and that adult resources are seldom limiting (Thomas 1991); thus Hanski (1999) found that flower abundance was a poor predictor of site occupancy by *M. cinxia* in the Baltic.

We obtained the same clear-cut result in each species studied (table 2 and figure 2), even though each had experienced very different trends in abundance, distribution and habitat availability across the study landscapes in recent decades. Between 1955 and 1980, *P. bellargus* experienced an 81% net reduction in patch occupancy, whereas *T. acteon* populations more than doubled in number; both changes were caused by reduced grazing of calcareous grassland, which led to an overall shift in sward structure from *P. bellargus*' preferred short turf towards the optimum tall habitat of *T. acteon* (Thomas 1983*a*,*b*). The opposite trends occurred from 1980 to 2000: grazing returned to many sites, *P. bellargus* spread to occupy twice as many patches as at its nadir and *T. acteon* experienced a net population loss (Bourn *et al.* 2000). *M. cinxia* was roughly stable in its landscape during these 45 years, but waxed and waned greatly on individual sites as landslips created new habitat patches, which subsequently became overgrown (Asher *et al.* 2001). As expected (Thomas *et al.* 1992), patch isolation is currently a better predictor of patch occupancy for the expanding species (*P. bellargus*) than for the contracting one (*T. acteon*). However, the fact that the metapopulation structures of both species and of *M. cinxia* are, by a factor of two- to three-fold, best described by variation in habitat quality (table 2) suggests that this parameter is more important than recent metapopulation models assume: most ignore it or treat it as a constant. It should now be possible to incorporate empirically derived values of habitat quality to future metapopulation models (Hanski & Ovaskainen (2000) provide a formula), but field validation will remain a problem: the present study, including the definition of the species' habitats, took 11 field seasons to complete.

It is surprising that site area was not a significant parameter in any analysis of the three species studied. In theory, large sites support more persistent populations than smaller sites not only for the obvious reason of their greater size but also because they are more likely to contain heterogeneous habitat, providing refuges to enhance population persistence through extreme perturbations or climatic events (Sutcliffe *et al.* 1997). Other empirical studies, including that of *M. cinxia* in the Baltic (Hanski 1999), have found that patch area partly explains site occupancy in certain landscapes, but in general the association is weaker than that with isolation. Patch area was not a significant factor in earlier landscape-scale analyses of *P. bellargus* or *T. acteon* (Thomas 1983*b*; Thomas *et al.* 1992). It is possible that the relative importance of these three parameters may be different in other climates, where species' habitat preferences may be less specialized, (Thomas *et al.* 1999) or in landscapes containing habitat patches more isolated than those studied. However, the fact that all the species studied showed the same strong pattern, despite their very different histories, suggests that this is a more general phenomenon. We suggest a mechanism to explain why this may be so.

Hitherto, the habitat quality and metapopulation hypotheses have provided alternative paradigms to explain local extinctions in fragmented landscapes (Hanski 1999). Recently, Hanski & Ovaskainen (2000) suggested that habitat quality could act as a surrogate for patch area. We also conclude that both parameters are part of the same metapopulation process, but believe that habitat quality functions independently, at a lower hierarchical level than the conventional spatial parameters of area and isolation. It is axiomatic that a population inhabiting optimum habitat has a higher intrinsic rate of increase (r) and a higher equilibrium density (K) than those inhabiting sites with suboptimal habitat. In the case of UK butterfly species, measured K values of sites with optimum habitat are from 25 to > 200 times greater than those for occupied sites with suboptimal, yet suitable, habitat (Thomas 1984). These values were derived from species that were not living near to the edges of their ranges, and a similar range of intraspecific carrying capacities per unit area of habitat on managed sites have been reported among species of ant (Thomas

Table 2. Comparison of logistic regression models for the presence or absence of three butterfly species in relation to patch area (a), isolation (i) and habitat quality (h).

test	statistical (partial) significance p value based on the $z = b_j/se(b_j)$ statistic of each variable (a, i or h)									Goodman–Kruskal gamma measure of overall association			
model	1	2	3	4 ($a+i$)		5 ($a+h$)		6 ($i+h$)		1	2	3	6
variable	a	i	h	a	i	a	h	i	h	a	i	h	$i+h$
Melitaea cinxia	0.95	0.042	< 0.0001	0.41	0.064	0.31	0.003	0.031	< 0.0001	0.07	0.23	0.62	0.65
Polyommatus bellargus	0.35	0.001	< 0.0001	0.32	0.001	0.52	< 0.0001	0.01	< 0.0001	0.12	0.51	0.85	0.88
Thymelicus acteon	0.69	0.008	< 0.0001	0.13	0.004	0.54	< 0.0001	0.048	< 0.0001	0.08	0.39	0.74	0.80

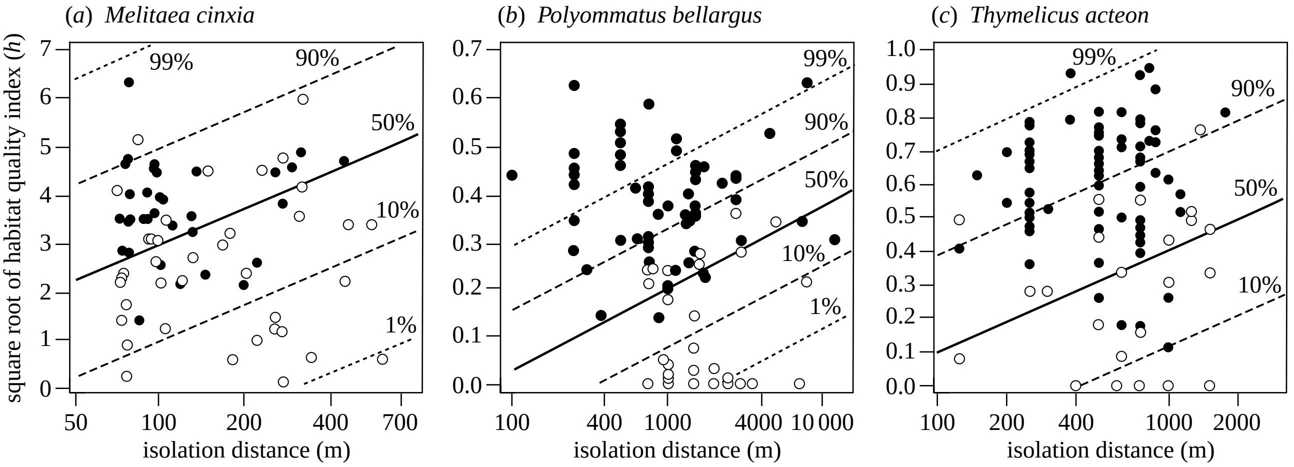

Figure 2. The distribution of occupied (solid circles) and unoccupied (open circles) habitat patches for three species of grassland butterfly in relation to the patch quality (h) and isolation (i). Lines indicate logistic-regression-model predicted probabilities (P) of a patch being occupied by a species. (a) *Melitaea cinxia*, $\log(P/(1-P)) = 2.16 + 1.11\sqrt{h} - 2.74i$. ($b$) *Polyommatus bellargus*, $\log(P/(1-P)) = 9.72 + 1.59\sqrt{h} - 3.52i$. ($c$) *Thymelicus acteon*, $\log(P/(1-P)) = 4.00 + 7.55\sqrt{h} - 2.36i$.

et al. 1998), aquatic invertebrate (Wright *et al.* 2000), fish (Hilton *et al.* 2001), bird (Goss-Custard 1996) and plant (Rose *et al.* 1998; and our current surveys). Measured or estimated maximum values of r for insects range from 3 to 29 (e.g. Brian 1965; Thomas *et al.* 1998), compared with $r = 1$ in the poorest source habitat, and from 30 to 100 in annual grasses (Crawley 1990). Clearly, in a landscape where patches have high r and K values, population persistence in individual patches is longer, between ten and 100 times more individuals are available for emigration from the strong sources and the offspring of females invading vacant patches are more likely to survive the initial period of establishment when the population is vulnerable to stochastic and inverse-density effects (Crawley 1986). In effect, variation in habitat quality is the missing third parameter in metapopulation dynamics—a parameter which, on the basis of these results, is more important than the conventional two parameters of isolation and area.

Although we suggest that these variables are part of the same process, the conservation messages are clear. The preservation of nearby groups of large sites is of course desirable, but small size and/or isolation are not *a priori* reasons for rejecting a site when the habitat quality within it is high. While metapopulation theory has usefully reorientated conservation priorities to the landscape scale (Harrison 1994; Hanski & Gilpin 1997; Margules & Presser 2000), it should not be employed as a substitute for within-site habitat management (Harrison & Bruna 1999). Our results suggest that it is at least as important to maintain high habitat quality through targeted management for valued types of community and species within individual sites as it is to maintain as many contiguous populations as possible in a landscape. Unfortunately, some conservationists have recently become so seduced by the elegance of metapopulation theory that they are neglecting 'the less interesting [problem] of the degradation of habitat within fragments' (Harrison & Bruna 1999).

We thank A. J. Gray and M. S. Warren for valuable comments. Surveys were part-funded by English Nature, The Countryside Council for Wales, Scottish Natural Heritage and The World Wide Fund for Nature.

REFERENCES

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. 2001 *The millennium atlas of butterflies in Britain and Ireland.* Oxford University Press.

Bourn N. A. D. & Thomas, J. A. 1992 The ecology and conservation of the Brown Argus butterfly in Britain. *Biol. Conserv.* **63**, 67–74.

Bourn, N. A. D., Pearman, G. S., Goodger, B., Thomas, J. A. & Warren, M. S. 2000 Changes in the status of two endangered butterflies over two decades and the influence of grazing management. In *Grazing management* (ed. A. J. Rook & P. D. Penning), pp. 141–146. Reading, UK: British Grassland Society.

Brian, M. V. 1965 *Social insect populations*. London: Academic Press.

Clarke, R. T., Thomas, J. A., Elmes, G. W. & Hochberg, M. E. 1997 The effects of spatial patterns in habitat quality on community dynamics within a site. *Proc. R. Soc. Lond.* B **264**, 347–354.

Crawley, M. J. 1986 The population biology of invaders. *Phil. Trans. R. Soc. Lond.* B **314**, 711–731.

Crawley, M. J. 1990 Population dynamics of plants. *Phil. Trans. R. Soc. Lond.* B **330**, 125–140.

Goss-Custard, J. D. 1996 *The oystercatcher: from individuals to populations*. Oxford University Press.

Hanski, I. 1998 Metapopulation dynamics. *Nature* **396**, 41–49.

Hanski, I. 1999 *Metapopulation ecology*. Oxford University Press.

Hanski, I. & Gilpin, M. E. 1997 *Metapopulation biology*. London: Academic Press.

Hanski, I. & Ovaskainen, O. 2000 The metapopulation capacity of a fragmented landscape. *Nature* **404**, 755–758.

Harrison, S. 1994 Metapopulations and conservation. In *Large-scale ecology and conservation biology* (ed. P. J. Edwards, R. M. May & N. R. Webb), pp. 111–128. Oxford, UK: Blackwell.

Harrison, S. & Bruna, E. 1999 Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* **22**, 225–232.

Hilton, J., Welton, J. S., Clarke, R. T. & Ladle, M. 2001 An assessment of the potential for the application of two simple models to salmon stock management in chalk rivers. *Fish. Manag. Ecol.* **8**, 189–205.

Kuussaari, M. 1998 *Biology of the Glanville fritillary butterfly* (*Melitaea cinxia*). Helsinki: University of Helsinki.

Margules, C. R. & Presser, R. L. 2000 Systematic conservation planning. *Nature* **405**, 243–253.

New, T. R., Pyle, M., Thomas, J. A., Thomas, C. D. & Hammond, P. C. 1995 Butterfly conservation management. *A. Rev. Entomol.* **40**, 57–83.

Rose, R. J., Clarke, R. T. & Chapman, S. B. 1998 Individual variation and the effects of weather, age and flowering history on survival and flowering of the long-lived perennial *Gentiana pneumonanthe*. *Ecography* **21**, 317–326.

Saccheri, I. J., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. 1998 Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491–494.

Sutcliffe, O. L., Thomas, C. D., Yates, T. J. & Greatorex-Davis, J. N. 1997 Correlated extinctions, colonisations and population fluctuations in a highly connected ringlet butterfly metapopulation. *Oecologia* **109**, 235–241.

Thomas, J. A. 1983*a* The ecology and status of *Thymelicus acteon* (Lepidoptera: Hesperidae) in Britain. *Ecol. Entomol.* **8**, 427–435.

Thomas, J. A. 1983*b* The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. *J. Appl. Ecol.* **20**, 59–83.

Thomas, J. A. 1983*c* A quick method for estimating butterfly numbers during surveys. *Biol. Conserv.* **27**, 195–211.

Thomas, J. A. 1984 The conservation of butterflies in temperate countries: past efforts and lessons for the future. In *Biology of butterflies* (ed. R. I. Vane-Wright & P. Ackery), pp. 333–353. London: Academic Press.

Thomas, J. A. 1991 Rare species conservation: case studies of European butterflies. In *The scientific management of temperate communities for conservation* (ed. I. Spellerberg, B. Goldsmith & M. G. Morris), pp. 149–197. Oxford, UK: Blackwell.

Thomas, J. A. & Morris, M. G. 1994 Patterns, mechanisms and rates of decline among UK invertebrates. *Phil. Trans. R. Soc. Lond.* B **344**, 47–54.

Thomas, J. A. & Simcox, D. J. 1982 A quick method for estimating larval populations of *Melitaea cinxia* L. during surveys. *Biol. Conserv.* **22**, 315–322.

Thomas, C. D., Thomas, J. A. & Warren, M. S. 1992 Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92**, 563–567.

Thomas, J. A., Clarke, R. T., Elmes, G. W. & Hochberg, M. E. 1998 Population dynamics in the genus *Maculinea*. In *Insect population dynamics: in theory and practice* (ed. J. P. Dempster & I. F. G. McLean), pp. 261–290. London: Chapman & Hall.

Thomas, J. A., Rose, R. J., Clarke, R. T., Thomas, C. D. & Webb, N. R. 1999 Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. *Funct. Ecol.* **13**, 55–64.

Wiegan, T., Moloney, K. A., Naves, J. & Knauer, F. 1999 Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *Am. Nat.* **154**, 605–627.

Wright, J. F., Gunn, R. J. M., Winder, J. M., Blackburn, J. H. & Wiggers, R. 2000 The response of chalk stream macroinvertebrates to a prolonged drought: the value of a long-term dataset. *Verhandlungen Internationale Vereinigung Limnologie* **27**, 912–915.