Landscape Ecol (2008) 23:27–40
DOI 10.1007/s10980-007-9167-6

RESEARCH ARTICLE

Do corridors promote dispersal in grassland butterflies and other insects?

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Received: 13 March 2007 / Accepted: 27 September 2007 / Published online: 18 October 2007

Abstract Ecological corridors are frequently suggested to increase connectivity in fragmented landscapes even though the empirical evidence for this is still limited. Here, we studied whether corridors, in the form of linear grass strips promote the dispersal of three grassland butterflies, using mark-recapture technique in an agricultural landscape in southern Sweden. We found no effects of the presence of corridors or of corridor length on inter-patch dispersal probabilities. Instead, dispersal probabilities appeared to be related to the quality, areas and population densities of the source and recipient patches. For two of the species, the density of captured individuals along corridors was better predicted by the corridor length than by the straight-line distance from a pasture, suggesting that short-distance movements within habitat patches result in a diffusion of individuals along corridors. A literature review revealed that only 16 published studies had explicitly studied the effect of corridors on insect movement. The context in which studies were performed appeared to affect whether corridors facilitated dispersal or not. All seven studies where the corridors consisted of open areas surrounded by forest showed positive effects, while only two out of six studies where corridors consisted of grassland surrounded by other open habitats showed positive effects of corridors. Our results clearly demonstrate that corridors do not always have positive effects on insect dispersal and that the effect seems to depend on the quality of the surrounding matrix, on the spatial scale in which the study is performed and on whether true dispersal or routine movements are considered.

Keywords Connectivity · Habitat quality · Lepidoptera · Linear elements · Mark-release-recapture · Movement

Introduction

Metapopulation theory emphasizes the importance of dispersal and connectivity between local populations for long-term persistence of species at the landscape scale (Hanski 1999). Generally, metapopulation models assume that the probability of dispersal between two habitat patches depends solely on the straight-line distance between the patches

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Electronic supplementary material The online version of this article (doi:10.1007/s10980-007-9167-6) contains supplementary material, which is available to authorized users.

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(Hanski 1999). This may be true for some species and in some landscapes (Moilanen and Hanski 1998), but other studies have demonstrated that physical barriers and the structure and permeability of the surrounding "matrix" in the landscape may have significant effects on dispersal of some species (Ferreras 2001; Ricketts 2001).

Ecological corridors, consisting of tree rows, hedgerows or grassy field boundaries in agricultural land; roads, open tracks or power-line clearings in forests and strips of natural forest or grassland vegetation along streams have been suggested as a tool to increase connectivity between local populations in fragmented landscapes, and thereby contribute positively to (meta-) population persistence at the landscape scale (Diamond 1975; Bennett 1999; Jongman and Pungetti 2004; Damschen et al. 2006). Because of this, the concept of ecological corridors has received considerable attention among landscape planners and conservation practitioners (Bennett 1999; Crooks and Sanjayan 2006), even though the empirical evidence for positive effects of corridors on animal movements is still relatively limited (Beier and Noss 1998; Davies and Pullin 2007). There are very few studies exploring under which circumstances and for which species or groups of species corridors may be beneficial (Chetkiewicz et al. 2006; but see Baum et al. 2004).

Establishment and preservation of uncropped linear grass strips is a part of the agri-environmental schemes in several European countries (Kleijn and Sutherland 2003). Such strips have been shown to be beneficial for insect species richness and abundance (Feber et al. 1996; Pywell et al. 2004, 2005) but there are still very few studies investigating whether they also can act as dispersal corridors for species associated with grasslands.

In addition to landscape structure (e.g. barriers and corridors), characteristics of local patches or populations can affect the rates of dispersal between local populations (e.g. Wilson and Thomas 2002). A higher proportion of individuals may tend to leave patches of low quality and enter patches of high quality (Kuussaari et al. 1996; Matter and Roland 2002). Population density can have both positive and negative effects on emigration rates. Competition for scarce resources can induce emigration at high population densities, while at low densities individuals may emigrate to find mates (Matthysen 2005). A high population density may also attract dispersing individuals, thereby leading to a positive effect on immigration rates (Smith and Peacock 1990). Patch area has frequently been reported to affect migration rates (Kuussaari et al. 1996; Sutcliffe et al. 1997; Baguette et al. 2000; Wahlberg et al. 2002). This may partly be due to geometrical factors but the tendency to leave small patches, which usually also have small population sizes, may also be a way to avoid inbreeding (Clobert et al. 2004).

The aim of this study was (1) to investigate the effects of corridors in the form of open linear strips of grassy vegetation and of patch characteristics on the dispersal of three grassland butterflies in an agricultural landscape, and (2) to review the literature for evidence of effects of corridors on insect movement, specifically in relation to the landscape context in which the studies were performed.

Methods

Mark-recapture study

We performed mark-recapture studies on three butterfly species that are mainly associated with semi-natural grasslands, the ringlet *Aphantopus hyperantus*, meadow brown *Maniola jurtina* and small heath *Coenonympha pamphilus* (all in the subfamily Satyrinae). The mark-recapture study was performed in one study landscape, approximately 4 km^2 in size, situated 25 km SE of the city of Lund in southern Sweden (Fig. 1). In the study landscape, there was a total area of approximately 58 ha ($\approx$14%) of semi-natural grasslands, defined as areas dominated by grassy vegetation that have not been recently ploughed or fertilized. Most of this area (53.3 ha) consisted of eight relatively large (1.4–15.8 ha, mean = 6.6 ha, SE = ±1.0 ha) grazed patches, here referred to as pastures. There was also a total area of 4.8 ha of linear uncultivated elements with grassland vegetation comprising potential corridors for the three study butterfly species. The width of these potential corridors varied from about 1 m to more than 10 m, but the majority had a width between 2 and 3 m. Road verges along small roads are usually cut in late summer, while grassy boundaries between fields are not cut each year. Apart from the semi-natural grasslands and the uncultivated linear

Fig. 1 Map of the study area. Pastures are shown in light grey, forest patches in dark grey and possible corridors (grassy strips along roads and between fields) as black lines. White areas consist mainly of agricultural land. The pastures are labelled with capital letters. The situation of the study area in Sweden is indicated with a dot

elements, there were no other areas with grassland vegetation within the study region. For further details on the study species and the study area, see Öckinger and Smith (2007).

Between June 21st and August 1st 2004 (*M. jurtina* and *A. hyperantus*) and between June 2nd and July 1st 2005 (*C. pamphilus*) we searched for butterflies in all pastures and all linear habitat elements within the study area every day with suitable weather, i.e. ≥15°C and no rain. In total there were 28 capture-days for *M. jurtina*, 26 for *A. hyperantus* (which started flying a few days later than *M. jurtina*) and 19 capture-days for *C. pamphilus*. The search effort per unit area was kept constant in all, but due to uneven densities of butterflies, the time spent catching and handling butterflies differed both between habitat types and between separate pastures. All encountered butterflies of the study species were captured with a hand-held net, and all unmarked individuals were marked with a unique code on the ventral side of the hind-wings using a fine-tipped water-resistant marker pen and thereafter immediately released at the place of capture. For every captured butterfly we recorded species, sex, wing wear in two classes; new or old, where individuals with no significant signs of wing wear were classified as "new" and all other individuals as "old". The exact position of every butterfly was determined using a handheld GPS receiver (Garmin Geko 201), with 5-m accuracy.

Mark-recapture models

The local survival rates and dispersal probabilities between pastures were estimated by means of multi-strata models as implemented in Program MARK, version 4.2 (White and Burnham 1999). Multi-strata models allow independent estimation of local survival (S), capture probability (p) and probability of dispersal from one stratum to another (ψ) (Brownie et al.1993). Each pasture was considered a separate stratum, and all individuals captured somewhere in the study area outside any of the pastures (mainly in uncultivated field boundaries and similar "linear habitats", see Öckinger and Smith 2007) were pooled into one stratum. Due to low numbers of captured butterflies in a few pastures, these were excluded and pooled with the "linear habitats stratum". The "linear habitats" stratum was not included in any further analyses. In the analyses of *A. hyperantus* and *C. pamphiulus* 30 between-pasture intervals (six pastures with independent estimates for movements in both directions) were used and 12 between-pasture intervals (four pastures) were used for *M. jurtina*.

We used each day (with suitable weather, see above) as a capture period, except for days when less than 20 individuals of the study species were captured (marked and unmarked). Such days were pooled with the following capture day. Program MARK also makes it possible to indicate the interval between different capture periods. The fact that in some cases there was an interval of several days between capture days due to cold and rainy weather was accounted for in the models. We allowed local survival, capture probability and dispersal probability to vary with time (t = day) and groups (g = new males, new females, old males or old females), hence the fully parameterized model for each species was $S(g{\times}t)p(g{\times}t)\psi(g{\times}t)$. Constrained models are denoted by removing the letters indicating the excluded effect (g or t). We tested all models with all combinations of g, t, S, p and ψ, but always kept the variation between strata in all three parameters. Competing models were compared by means of the corrected Akaike's Information Criterion, $\mathrm{AIC_c}$. When the difference in $\mathrm{AIC_c}$ values is <2, then one cannot say with accuracy that one of the models is better supported than the other (Burnham and Anderson 2002). Because we used the outcome of the multi-strata models in the General Linear modelling, we performed separate analyses on the outcome of the competing models when a single best model could not be identified.

Local population sizes were estimated using Jolly–Seber models as implemented in the POPAN module (Arnason and Schwarz 1999) in Program MARK. Models of the Jolly–Seber type allow estimation of survival, capture probability, recruitment and population sizes. In two cases (both *A. hyperantus*), the number of recaptures were too low to estimate local population sizes with the Jolly–Seber method (the models did not converge) and we used Craig's method instead (Craig 1953; Southwood and Henderson 2000). Local population densities were calculated as the estimated local population size divided by pasture area.

Habitat quality

In order to examine possible differences in habitat quality between the semi-natural pastures in the mark-recapture study area we measured the proportion of area covered by shrubs, flower abundance, vegetation height, proportion of coarse-leaved grasses and the abundance of *Taraxacum* sect. *ruderalia*. *Taraxacum* abundance was included as a measure of nutrient status (c.f. Schneider and Fry 2001). The ratio of broad-leaved to thin-leaved grasses was included as a measure of habitat quality because larvae of all three butterfly species feed on several grass species but *C. pamphilus* and *M. jurtina* feed mainly on thin-leaved grass species while *A. hyperantus* feed mainly on broad-leaved species. The proportion of the pasture area covered by shrubs was measured from aerial photos using GIS, and the proportion was arcsine$\sqrt{}$-transformed before entered in any analysis. Flower abundance, proportion of coarse-leaved grasses and abundance of *Taraxacum* were measured in between 10 and 30 (depending on area) 50 × 50 cm plots per pasture, divided into 10 × 10 cm subplots and vegetation height was also measured adjacent to each plot. For further details on how the habitat quality variables were measured, see Öckinger and Smith (2007).

Because several variables related to habitat quality were highly correlated, and in this analysis we were mainly interested in the effects of the overall quality of each pasture, we used principal components analysis (PCA) to combine the habitat quality into principal components. The principal components were rotated with the Varimax option in SAS proc Factor. The first principal component (PC1) was most strongly correlated (positively) with the proportion of shrubs and the second principal component (PC2) was strongest correlated with the abundance of flowers (Table 1). Together, the first two principal components explained 84.5% of the total variation in the five habitat quality variables.

Landscape metrics

We used several landscape metrics as possible predictors of dispersal probability between pairs of pastures. First, we measured the Euclidean distance between (the closest borders of) two pastures using GIS. Second, we used a binary variable indicating whether or not the two pastures were directly connected (connected via corridors without any other pasture in-between and with no turning angels >90°) via linear elements ("corridors") with grassland vegetation. Third, we measured the shortest distance

Table 1 Eigenvectors and eigenvalues (percentage of total variation explained) for the two first principal components describing habitat quality

Variable	PC1	PC2
Vegetation height	0.110	–0.318
Taraxacum	–0.163	0.188
Broad leaved grasses	–0.365	0.461
Flower abundance	0.292	0.709
Proportion shrubs	0.666	0.367
Eigenvalues	0.621	0.224

between all pairs of pastures (even for those not considered directly connected) following potential corridors, but allowing gaps of up to 50 m. Fourth, we recorded whether or not a butterfly would have to pass through forest (“barrier”) in order to leave the source pasture in the direction of the recipient pasture. The forest was only considered a barrier if it was directly adjoining the source pasture. Finally, we measured the shortest distance a butterfly would have to travel between two pastures if it avoided passing through any forest patch but because this measure was strongly correlated with the corridor distance, it was not used in the analyses. For the pairs of pastures included in the analyses for the respective species, the Euclidean distance was significantly correlated with Corridor distance only for *A. hyperantus* (Pearson correlation: $r = 0.74$, $N = 16$, $P = 0.001$) but not for *C. pamphilus* ($r = 0.49$, $N = 15$, $P = 0.06$) or *M. jurtina* ($r = 0.23$, $N = 8$, $P = 0.58$). The binary variable Corridor was not significantly related to any of the distance measures for the pairs of pastures included in the analyses for any of the species (*t*-tests, see Table 2) and the binary variable Barrier was only significantly related to Corridor distance for *C. pamphilus* (Table 2). All distances were log-transformed, because a previous analysis (Öckinger and Smith 2007) showed that for all three species the proportion of individuals moving a certain distance followed an inverse power function.

Statistical analyses

To test whether the dispersal between pastures was affected by the distance and the presence of habitat elements that may act as barriers or conduits for dispersal we fitted alternative models to data. For example, if linear habitat elements acted as corridors, we expected the length of these corridors to better explain dispersal propensity between pastures than Euclidean distance, such that dispersal was high between pastures connected by short corridors. We used the log-transformed probabilities (separate for each species) as dependent variables in General Linear Mixed Models (SAS Proc Mixed) with pair of pastures as a random factor. First, we tested whether transformed or untransformed distance measures fitted the estimated dispersal probabilities best by means of AIC. Second, we used the forward selection procedure to enter the selected distance measures, the other landscape metrics described above, area, population density and the first two principal components describing habitat quality of both source and recipient pastures respectively as fixed variables in the models. To test if the habitat quality variables, landscape metrics or pasture area could explain the variation in local survival rates we used General Linear Models (SAS proc GLM). In all GLMs and GLMMs, the denominator degrees of freedom were estimated with the Satterthwaite method (Littell et al. 1996).

Corridors may act as conduits for butterflies involved in short-distance movements (not resulting in between-pasture movements) rather than in the relatively long-distance dispersal between pastures. To see if this was the case, we tested whether the densities of captured individuals along the corridors were best explained by the Euclidean distance from a pasture or by the distance along corridors. The corridors were divided into 50-m intervals based on (1) the Euclidean distance to the edge of the nearest pasture, and (2) the distance along the corridors to the edge of the nearest pasture. All intervals at the same distance were pooled, and we calculated the density (individuals/100 m^2) of captured individuals of each species in each distance interval. To test whether the densities of individuals decreased with increasing distance from a pasture, three separate functions were fitted to the observed densities; a linear function, a negative exponential function and an inverse power function. The functions were fitted separately for each species and each of the two isolation measures, using SAS proc Reg. To test whether one isolation measure gave significantly better model fit we compared AIC-values for the same type of function

Table 2 The relationships between the binary variables Corridor and Barrier and the log-transformed Euclidean distance and Corridor distance for the pairs of pastures included in the analyses for the respective species

	Corridor		Barrier	
	$t_{\text{d.f.}}$	P	$t_{\text{d.f.}}$	P
A. hyperantus				
Distance	1.34_{14}	0.20	0.39_{14}	0.70
Corridor dist.	$1.42_{3.17}$	0.24	$1.57_{5.8}$	0.17
C. pamphilus				
Distance	0.10_{13}	0.93	0.69_{13}	0.50
Corridor dist.	1.59_{13}	0.14	2.31_{13}	0.038
M. jurtina				
Distance	0.01_{6}	0.99	0.72_{6}	0.50
Corridor dist.	1.21_{6}	0.27	1.06_{6}	0.63

See Methods section for details on how the variables were defined

(linear, negative exponential or inverse power) with different isolation measures, considering models with ΔAIC > 2 as significantly different.

Literature study

In order to investigate the empirical evidence for positive effects of corridors on insect movement we conducted a literature search for relevant papers (published up to and including 2005) in the databases BIOSIS and Web of Science using the combinations “corridor* AND movement*” and “corridor* AND dispers*”. We restricted the searches to empirical field studies dealing with terrestrial insects and studies that either quantified movement through corridors directly or studied the effects of movements, such as population densities in habitat patches connected by corridors and habitat patches not connected by corridors or pollen transfer through corridors. Studies that only recorded the presence of individuals in potential corridors were excluded, because the presence of a species in a potential corridor does not necessarily mean that they act as corridors. Studies performed in the laboratory, simulation studies and studies that focused on genetic effects of potential corridors on larger spatial scales were also excluded.

Results

Survival and dispersal probabilities

The numbers of captured and recaptured individuals of each species are shown in Table 3. In the multistrata analyses, the simplest models (i.e. $S(.)p(.)\psi(.)$), were the one that fitted the data best for both *C. pamphilus* (ΔAIC to second best model = 20.2) and *M. jurtina* (ΔAIC = 25.0), while for *A. hyperantus* the model with time-dependent capture probability ($S(.)p(t)\psi(.)$) had the best fit (ΔAIC = 271.0). This means that we found no evidence of differences in dispersal, survival or capture probabilities between males and females in any of the species. Because the difference in AIC between the best and second best models were large in all cases, we used only the results from the best models in the further analyses.

In all cases, transformed distance measures fitted the estimated between-pasture movement probabilities better than untransformed distance measures (all ΔAIC > 12), and all further analyses were performed with transformed measures. None of our landscape metrics (corridors, barriers or distance) were significantly related to the estimated dispersal probabilities (Table 4) and the hypothesis that corridors promote dispersal between habitat patches was not supported. Instead, there was a significant effect of habitat

Table 3 The number of captured and recaptured individuals (% of captured) of *Aphantopus hyperantus*, *Coeneonympha pamphilus* and *Maniola jurtina*, and the number of between-pasture movements and movements (% of recaptured) between multiple pastures (individuals with two or more between-pasture movements)

Species	Captured	Recaptured	Movements between pastures	Movements between multiple pastures
A. hyperantus	5333	971 (18.2%)	77 (7.9%)	4 (0.5%)
C. pamphilus	421	241 (52.7%)	19 (7.9%)	1 (0.4%)
M. jurtina	871	140 (16.1%)	14 (10.0%)	2 (1.4%)

Table 4 Results of General linear mixed models testing the effect of different variables on the estimated dispersal probabilities for *Aphantopus hyperantus*, *Coeneonympha pamphilus* and *Maniola jurtina* between pairs of grassland pastures

Variable	*A. hyperantus*			*C. pamphilus*			*M. jurtina*		
	Regression coefficient	$F_{\text{d.f.}}$	*P*	Regression coefficient	$F_{\text{d.f.}}$	*P*	Regression coefficient	$F_{\text{d.f.}}$	*P*
Distance	–1.89	$0.51_{1,12}$	0.49	–2.69	$1.13_{1,11.4}$	0.31	–0.41	$0.01_{1,3.7}$	0.95
Corridor	–2.73	$0.25_{1,12.9}$	0.63	6.01	$1.44_{1,13.2}$	0.25	6.02	$0.17_{1,8.0}$	0.69
Barrier	2.73	$0.04_{1,23.9}$	0.53	1.42	$0.13_{1,25.7}$	0.73	–7.14	$0.80_{1,5.5}$	0.41
Corridor dist.	0.17	$0.00_{1,13.7}$	0.96	–2.41	$0.51_{1,11.5}$	0.49	–7.65	$0.28_{1,4.1}$	0.63
Source PC1	–3.69	$2.59_{1,21.1}$	0.12	–1.90	$0.24_{1,25.4}$	0.63	–18.1	$0.94_{1,7.7}$	0.36
Source PC2	4.62	$1.97_{1,22.7}$	0.17	0.61	$0.03_{1,21.3}$	0.86	10.9	$2.99_{1,5.1}$	0.14
Source density	23.6	$0.27_{1,22.9}$	0.61	2404.6	$1.68_{1,21.0}$	0.21	250.5	$2.57_{1,3.9}$	0.19
Source area	0.020	$0.22_{1,22.2}$	0.64	–0.21	$0.17_{1,20.3}$	0.69	–0.90	$1.79_{1,6.3}$	0.23
Recipient PC1	**–8.73**	**$5.49_{1,22.0}$**	**0.029**	3.36	$0.49_{1,21.3}$	0.49	**–59.0**	**$9.50_{1,6.8}$**	**0.018**
Recipient PC2	**–16.4**	**$11.0_{1,23.0}$**	**0.003**	5.56	$2.79_{1,22.0}$	0.11	12.2	$3.29_{1,4.5}$	0.14
Recipient density	–1.00	$0.00_{1,21.4}$	0.96	**7964.7**	**$18.5_{1,21.8}$**	**<0.001**	297.0	$3.94_{1,4.4}$	0.11
Recipient area	–0.03	$0.19_{1,22.7}$	0.67	**1.30**	**$14.4_{1,21.8}$**	**0.001**	–0.51	$0.52_{1,6.9}$	0.49

The regression coefficient is the slope the regression line for continuous variables and the difference between levels of binary factors. The numerator (first) and the denominator (second) degrees of freedom are given as subscripts after the F-values. Statistically significant results are indicated with bold text

quality in the recipient pastures in *A. hyperantus* and *M. jurtina* and of population density and area of the recipient pastures in *C. pamphilus* (Table 4).

There was a high variation in estimated dispersal probabilities between pastures, and for all three species the dispersal probabilities were asymmetric (i.e. $\psi_{\text{AB}} \neq \psi_{\text{BA}}$, where A and B are two separate pastures) in several cases (see Supplementary material). The overall dispersal probability differed between species ($F_{2,48.7} = 6.62$, $P = 0.003$) with higher dispersal probabilities in *A. hyperantus* than in *C. pamphilus* (linear contrast: $F_{1,53.2} = 10.7$, $P = 0.002$), but with no significant differences between *A. hyperantus* and *M. jurtina* ($F_{1,33.9} = 1.54$, $P = 0.22$) or between *M. jurtina* and *C. pamphilus* ($F_{1,7.1} = 0.78$, $P = 0.39$). Moreover, the dispersal probabilities between pairs of pastures were not correlated for any of the species (Pearson Correlation *A. hyperantus–M. jurtina*: $\rho = 0.27$, $N = 11$, $P = 0.42$; *A. hyperantus–C. pamphilus*: $\rho = 0.24$, $N = 11$, $P = 0.47$; *M. jurtina–C. pamphilus*: $\rho = 0.17$, $N = 11$, $P = 0.62$), indicating that the dispersal of the three species is affected by different factors.

The pasture-specific survival rates differed among species (see Supplementary material), but we could not relate the local survival rates to any measured pasture characteristics for any of the species (all $P > 0.1$). Local survival rates per pasture were correlated in *A. hyperantus* and *C. pamphilus* (Pearson Correlation, $\rho = 0.96$, $N = 6$, $P = 0.002$) but not between *A. hyperantus* and *M. jurtina* ($\rho = 0.46$, $N = 5$, $P = 0.80$) or between *M. jurtina* and *C. pamphilus* ($\rho = 0.21$, $N = 5$, $P = 0.74$).

Densities of individuals along corridors

In all three species, the densities of captured individuals along the corridors decreased with increasing isolation (Table 5), even though not statistically significant in the case of the effect of Euclidean distance for *C. pamphilus* and the corridor distance for *M. jurtina*. In *C. pamphilus* a linear function fitted the observed densities best and in *M. jurtina* the negative exponential function fitted the observed densities best, for both isolation measures (Table 5). In *A. hyperantus* the negative exponential function fitted the observed densities best for the Euclidean distance while the linear function fitted the data best for the corridor distance. In *A. hyperantus* ($\Delta\text{AIC} = 8.8$) and *C. pamphilus* ($\Delta\text{AIC} = 19.4$) the distance along corridors was a better predictor of butterfly density than the Euclidean distance, while

Table 5 R^2 and P-values for the regression models describing the effect of isolation from the nearest pasture on the number of captured individuals of *Aphantopus hyperantus*, *Coeneonympha pamphilus* and *Maniola jurtina*, using two different isolation measures, the Euclidean (straight-line) distance and the distance along a corridor

Isolation measure	Model	*A. hyperantus*		*C. pamphilus*		*M. jurtina*	
		R^2	P	R^2	P	R^2	P
Euclidean distance	Linear	0.264	0.050	0.208	0.077	0.003	0.330
	Negative exponential	0.463	0.009	0.099	0.17	0.339	0.047
	Inverse power	0.280	0.044	0.070	0.21	0.203	0.080
Corridor distance	Linear	0.520	0.008	0.585	0.004	0.042	0.530
	Negative exponential	0.491	0.011	0.472	0.013	0.319	0.056
	Inverse power	0.316	0.057	0.377	0.034	0.254	0.095

there was no significant difference between the two isolation measures in *M. jurtina* (ΔAIC = 0.2).

Literature study

In total, we found 17 studies in 16 papers fulfilling our search criteria (Table 6). Eleven of these showed positive effects of corridors on insect inter-patch movement, while four studies did not find any such positive effects. In one study there was a positive tendency, but the sample size was too low to allow any statistical tests. Seven of the studies dealt explicitly with butterflies and all of these also showed positive effects of corridors, but in all these seven papers the study design consisted of open patches and open corridors surrounded by forest. Only two studies (Berggren et al. 2002; Baum et al. 2004) out of six showed positive effects of corridors consisting of grassy vegetation surrounded by an open matrix.

Discussion

In contrast to our expectations and to the finding of several other studies (reviewed by Bennett 1999), we found no positive effect of corridors on the dispersal between pastures for any of the three studied butterfly species. Instead habitat quality seemed to be a more important factor. Despite this, the distance from a pasture measured along a corridor explained the number of individuals captured in corridors better than the straight-line distance in two of the species, *A. hyperantus* and *C. pamphilus*. This indicates that the linear elements are still used as corridors to some extent.

One reason for this discrepancy may be that the exchange of individuals between pastures and the movement of individuals from pastures to the linear elements are influenced by two different types of movement (c.f. Van Dyck and Baguette 2005). The decreasing density of individuals with increasing distance along the corridors may mainly be caused by short-distance movements ("routine movements" sensu Van Dyck and Baguette 2005) within a more or less continuous area of habitat (pastures and linear elements directly connected to them), resulting in a diffusion of individuals along the corridors. In contrast, the exchange of individuals between separate pastures may primarily depend on "special movements" (directed movements aimed at leaving the current habitat patch for another one; Van Dyck and Baguette 2005). The low numbers of movements between multiple pastures (Table 3) and the low proportion of individuals moving long distances (Öckinger and Smith 2007) indicate that between-pasture movements mainly represent real dispersal events, and based on our results this type of movement seems to take place regardless of the presence of corridors. Unfortunately, our data does not allow us to test whether our contrasting results are explained by different types of movements. This would require more detailed, behavioural studies.

The scale of study relative to the dispersal potential of the studied species could also influence whether corridors influence movements or not. In small-scale studies, movement distances may be too short to detect any effects of corridors. For example, the small-scale experiments by Collinge (2000) failed to find positive effects of corridors. Interestingly, most of the published corridor studies including butterflies were performed on smaller spatial scales

Table 6 Empirical studies addressing the question whether corridors increase the inter-patch movement of terrestrial insects

Group	Context	Scale	Method	Response variable	Effect	Comments	Reference
Coleoptera	Road verge	250 m	Mark-recapture	Movement distances and direction in the road verge	0	No control.	Vermeulen (1994)
Lepidoptera	Open patches and corridors in forest	97–532 m	Mark-recapture	Exchange rates as an effect of euclidean distances or distances via corridors	+		Sutcliffe and Thomas (1996)
Coleoptera	Hedgerows and forest patch in farmland	35 m	Radar tracking	Movement distances within forest and hedgerows	0	Shorter distances moved in hedgerows	Charrier et al. (1997)
Coleoptera	Hedgerows and forest patch in agricultural land	Approx. 1500 m	Pitfall traps	Density as an effect of euclidean distances or distances via hedgerows	0		Petit and Burel (1998)
Lepidoptera	Open patches and corridors in forest	64–384 m	Mark-recapture	Exchange rates between patches connected or not connected by corridors	+		Haddad (1999a)
Lepidoptera	Open patches and corridors in forest	64–384 m	Surveys	Densities of the study species in patches connected or not connected by corridors	+	Positive effects on three of four species	Haddad and Baum (1999)
Coleoptera	Hedgerows in farmland	Approx. 200 m	Mark-recapture	Movement at hedgerow nodes and in linear hedgerow fragments	+		Joyce et al. (1999)
Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera	Un-mowed grassland patches and corridors in mowed matrix	10 m	Sweep-netting	Extinctions after isolation (mowing) in connected and unconnected patches Re-colonization in connected and unconnected patches	0		Collinge (2000)
Coleoptera, Orthoptera	Un-mowed grassland patches and corridors in mowed matrix	10 m	Direct observations of marked individuals	Movement rates and distances	0		Collinge (2000)
Lepidoptera	Open patches and corridors in forest	16–192 m	Release of marked individuals in corridors and forest	Colonization of the focal patch by individuals released at different distances	(+)	At long (128–192 m), but not at shorter distances corridors had a positive effect on colonization	Haddad (2000)

Table 6 continued

Group	Context	Scale	Method	Response variable	Effect	Comments	Reference
Orthoptera	Tall-grass patch and corridor in a short-grass matrix	5 m	Release-resighting	Corridor use, turning angles	+		Berggren et al. (2002)
Several famiilies	Vineyards with and without intersecting corridor	300 m	Malaise traps, sticky traps	Population gradients in vineyard blocks with and without intersecting corridor	+	Only one replicate of each vineyard type	Nicholls et al. (2001)
Lepidoptera and multiple	Open patches and corridors in forest	150 m	Mark-recapture and recording of fruit set	Movement rates and fruit set in patches connected or not connected by corridors	+		Tewksbury et al. (2002)
Hymenoptera	Open patches and corridors in forest	64–384 m	Mark-recapture	Exchange rates between patches connected or not connected by corridors	?	Small sample size	Haddad et al. (2003)
Hemiptera	Patches and corridor of native grass in matrix of bare ground or exotic grass	2 m	Release-recapture	Colonization of target patches with corridors in different matrix types or without corridors	+	Corridors in low-resistance matrix (exotic grass) was more beneficial than corridors in high-resistance matrix (bare ground)	Baum et al. (2004)
Lepidoptera, Hymenoptera	Open patches and corridors in forest	150 m	Marked pollen	Transfer of marked pollen between patches connected or not connected by corridors	+		Townsend and Levey (2005)
Diptera	Open patches and corridors in forest	150 m	Release-recapture	Recapture rates in patches connected or not connected by corridors from the release patch	+		Fried et al. (2005)

+ indicates positive effects of corridors on the response variable(s), 0 indicates that there were no positive effects of corridors. The scale of study refers to (maximum) corridor lengths. Where an approximate number is given, the corridor length has been measured from figures in the respective paper than ours. In the studies that found positive effects of corridors on butterfly movements, the length of the movements ranged from 16 m (Haddad 2000) to 532 m (Sutcliffe and Thomas 1996). In our study area, the Euclidean distances between pastures that were connected by corridors varied between 70 and 1090 m, with corridor lengths between 215 and 2200 m. This means that too short distances are unlikely to be the reason why we found no positive effects of the corridors. It is possible that corridors have the most influence on dispersal at intermediate distances, relative to the dispersal capacity of the species under study. Unfortunately, we do not know the movement capabilities of most of the species in the reviewed studies, so we can not test that hypothesis.

Another factor that appears to influence whether corridors increase dispersal is the spatial context in which the studies were performed. The majority of studies in which the corridors and the source and target patches consisted of open land surrounded by a matrix of forest showed positive effects of the corridors on insect movement. In contrast, only two of the six studies where corridors were surrounded by an open-land matrix showed positive results and one of these was performed on a species, *Metrioptera roeseli* (Orthoptera), that does not fly (Berggren et al. 2002). Only one study (Baum et al. 2004) showed positive effects of corridors in an open matrix on a flying insect species. A number of studies have shown that forests or tree-lines may act as physical barriers to dispersal of flying insects living in open habitats (Keyghobadi et al. 1999; Roland et al. 2000; Ricketts 2001; Ries and Debinski 2001; Schmitt et al. 2005). For these species, open corridors are likely to enhance dispersal between patches (Haddad 1999b). Similar arguments can be used for ground-living insects that tend to avoid edges between vegetation types (Berggren et al. 2002). At least some butterfly species tend to avoid crossing boundaries between two open habitats, such as the ones between grasslands and arable fields (Ries and Debinski 2001; Schultz and Crone 2001; Schtickzelle and Baguette 2003). Based on this behaviour and because arable fields surrounded most the pastures in our study area, it could be assumed that linear strips of grassy vegetation could function as corridors, but obviously this was not the case.

The patches in our study area were relatively large. This could also partly explain why we found no positive effect of corridors. Those studies that found positive effects of corridors on butterfly movements had patch areas ranging from 0.04 (Sutcliffe and Thomas 1996) to 1.64 ha (Haddad and Baum 1999; Haddad 1999a; 2000). In our study area, the patch areas varied between 1.4 and 15.8 ha with a mean of 6.6 ha. Because larger patches constitute a larger target area for dispersing individuals, it is possible that corridors are more important in directing dispersing individuals to a habitat patch in landscapes where most patches are small. Unfortunately, our data set is too small to test this hypothesis.

The dispersal probabilities of both *A. hyperantus* and *M. jurtina* were affected by habitat quality in the recipient pastures (Table 4). Previous studies of butterfly dispersal have found that aspects of patch quality, such as host plant abundance and abundance of nectar-providing flowers, may affect both immigration and emigration rates (Kuussaari et al. 1996; Matter and Roland 2002; Schneider et al. 2003). The dispersal probability of *C. pamphilus* was positively related to the population density in the recipient pasture. This could be a result of con-specific attraction, as has been demonstrated for several animal species (Smith and Peacock 1990), including butterflies (Välimäki and Itämies 2003). On the other hand, if population densities reflected habitat quality and we failed to measure habitat quality appropriately, the observed effect could also have been caused by attraction to patches of high quality.

The positive relationship between recipient pasture quality and dispersal probability in combination with the lack of isolation effects indicate that butterflies were able to distinguish between and select among habitat patches of different quality within the study area. Previous studies that have found effects of patch quality on butterfly migration rates (Kuussaari et al. 1996; Matter and Roland 2002; Schneider et al. 2003) appear to have been conducted in study areas with shorter distances between pastures than in our study area. Our results suggest that individuals involved in "true" dispersal movements may fly long distances in order to find a high quality habitat patch. Similar results were found by Harrison (1989), studying the otherwise relatively sedentary (comparable to our study species) butterfly *Euphydryas editha bayensis*. She found that individuals released outside its habitat were able to locate and reach nearest habitat patch, situated up to 5.6 km from the release point. In an experiment where butterflies were released outside a habitat patch, Conradt et al. (2000) found that individuals of *M. jurtina* returned to the habitat patch at higher rates than expected from random flight at release distances up to 150 m, suggesting that dispersing butterflies are able to locate habitat patches at relatively large distances. Van Dyck and Baguette (2005) argued that since the study of Conradt et al. (2000) was performed on a relatively small spatial scale, the released butterflies may mainly have been involved in "routine" movements. If so, it is unclear whether their results are valid for individuals involved in directed dispersal.

It is important to notice that the lack of isolation effects in this study does not imply that isolation is not an important factor for the dispersal of the studied species. Our study was performed in a relatively small area with a relatively high proportion of habitat suitable for the studied species. Previously (Öckinger and Smith 2007) we showed that individuals of all three species are able to move distances at least as long as the maximum possible distance in our study area, even though the number of dispersers decreased significantly with increasing distance. This means that in a larger study area we would expect to find isolation effects. Also, in a landscape with a lower proportion of habitat, more long-distance dispersers than in our study area would fail to reach a suitable habitat patch, leading to more pronounced isolation effects. It should also be noted that because our study landscape contained relatively few (but large) pastures, we cannot exclude the possibility that the lack of isolation and corridor effects depends on low statistical power.

Conclusions and implications

Ecological corridors are often suggested as a means to mitigate negative effects of habitat fragmentation, and the concept is widely used in conservation planning (Bennett 1999; Crooks and Sanjayan 2006). Here, we have shown that corridors do not always have the assumed positive effects on dispersal. We do not claim that corridors never facilitate butterfly movement. Instead, we agree with Davies and Pullin (2007) that more controlled studies on the effect of corridors are needed. Especially, future studies should address under which circumstances and at what spatial scales corridors might facilitate dispersal. Our data indicated that the effect of the corridors may depend on which type of movements that is dominating, because we found that corridors influenced short-distance movements but not the longer movements between pastures. This means that whether corridors facilitate insect movement may also depend on the spatial scale on which the study is performed. Furthermore, our review of the literature shows that whether corridors have a positive effect or not may depend on the geographical context of the study. Corridors appear to be more efficient if they connect patches surrounded by a matrix that act as a physical barrier to dispersal, as dense forests do for many species associated with open habitats.

The influence of corridors may also differ among populations and landscapes depending on the conditions to which species are adapted. In a highly fragmented landscape, there may be a selection against long-distance dispersal because a very small proportion of dispersing individuals are likely to find a suitable habitat patch (Van Dyck and Matthysen 1999; Travis and Dytham 1999; Merckx et al. 2003). If this is the case, it is possible that corridors of suitable habitat could increase the exchange of individuals between patches.

Acknowledgements L. Bomark, E. Cronvall, M. Edlund, S. Gödderz, K. Mellbrand, H. Millsjö, C. Ronnås and N. Syde assisted with the field work. S.G. Nilsson, M. Franzén, D. Levey, D. Anderson and two anonymous reviewers gave valuable comments on the manuscript. This study was financed by the Swedish Environmental Protection Agency through the research program "The Conservation Chain" and by Lunds Djurskyddsfond. H.G.S. was supported by a grant from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS).

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