Can the assumption of a non-random search improve our prediction of butterfly fluxes between resource patches?

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Abstract. 1. Understanding dispersal patterns that enable small, spatially isolated populations to survive in fragmented landscapes has become an important issue in conservation biology and landscape management. However, for most of the species of interest it is not known whether dispersing individuals navigate or follow systematic search strategies, as opposed to moving randomly.

2. Recently it was shown that individuals of the butterfly species *Maniola jurtina* do not seek resources by means of random flight. If true, this may be problematic for existing metapopulation models, including those based on the evolution of dispersal rates in metapopulations.

3. The study tested to what extent the non-random dispersal patterns described in the literature can explain *M. jurtina* fluxes in its natural habitat.

4. A model based on literature assumptions of *M. jurtina* movements is presented in the work reported here, and its predictions are compared with 2 years of capture–recapture data on its fluxes in two landscapes.

5. The model provides a good fit to the data and gives better predictions than the model based only on patch sizes and distances between patches.

6. Thus, if data are available about the actual landscape under consideration, the model should be preferred to simpler approaches; however, in general theoretical considerations the simple approach based on patch size and the degree of its isolation will retain its value.

Key words. Butterflies, capture–recapture, dispersal, grassland, *Maniola jurtina*, simulation model.

Introduction

Habitat loss and its fragmentation are seen as major threats to many species (Wilcove *et al.*, 1986; Jongman, 2000), especially in Western Europe, where expansion of farmland at the expense of uncultivated habitats such as permanent grasslands and hedgerows has led to drastic changes of agricultural landscapes. For species living in fragmented habitats, dispersal is a key process for survival (Wiens *et al.*, 1993;

McIntyre & Wiens, 1999). Understanding dispersal patterns that enable small, spatially isolated populations to survive has therefore become an important issue in conservation biology and landscape management (Fry, 1995; Cooper & Power, 1997). The metapopulation concept provides a general explanation for how species in fragmented landscapes can survive: movements of individuals between spatially isolated populations allow a metapopulation to survive due to colonisation or recolonisation of existing or vacant habitat patches (Gilpin & Hanski, 1991; Hanski & Gilpin, 1997). However, detailed information about how individual animals disperse is limited because of the difficulty in keeping track of dispersing individuals in the field (Zollner & Lima, 1999). Hence, for most of the species of interest to metapopulation

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biology it is not known whether dispersing individuals navigate or follow systematic search strategies, as opposed to moving randomly. Most metapopulation models therefore simply assume random movement (Hanski, 1998) and generate colonisation patterns for patches depending on variables such as patch size and isolation. This means that these models characterise landscape connectivity (the degree to which landscape facilitates or impedes movements – Taylor *et al.*, 1993) only by the degree of patch isolation (Verboom & van Apeldoorn, 1990; Moilanen & Hanski, 2001). However, several authors have shown that landscape connectivity depends not only on the distance between habitat patches, but also on the presence of corridors or stepping stones and on heterogeneity of the landscape (Pain *et al.*, 2000; Ricketts, 2001).

Many butterfly species live in fragmented habitats with networks of local populations. Therefore, they are especially threatened by loss and fragmentation of their habitats (Thomas, 1984, 1991; New *et al.*, 1995). Patch area, patch isolation, patch quality, and sex have been identified as factors influencing butterfly dispersal (Dover *et al.*, 1992; Hanski, 1994; Hill *et al.*, 1996; Kuussaari *et al.*, 1996; Baguette *et al.*, 1998, 2000; Petit *et al.*, 2001). In the special case of agricultural landscapes, patches can be seen as mosaic of crops and uncultivated land (Ricketts, 2001; Sutcliffe *et al.*, 2003). The meadow brown (*Maniola jurtina* L.) shows dispersal rates that are typical of butterfly metapopulations and has been the subject of several recent studies. Conradt *et al.* (2000) investigated their ability to return to a suitable habitat. They concluded that the meadow brown does not seek habitat by means of random flight. Their experimental butterflies used a non-random, systematic, search strategy in which they flew in loops around the release point and returned periodically to it. Conradt *et al.* (2000) point out that if dispersers actively orientate towards or search systematically for distant habitat, this may be problematic for existing metapopulation models, including models of the evolution of dispersal rates in metapopulations. Recently, Schneider *et al.* (2003) found that the distance decay curve (dependence of the frequency of flights on their distance) of *M. jurtina* fitted a negative exponential function and that the mean flight distance for both males and females was between 60 and 70 m.

In the work reported here, it is being tested to what extent the non-random dispersal patterns described by Conradt *et al.* (2000) and Schneider *et al.* (2003) can explain *M. jurtina* fluxes between herbaceous areas in agricultural landscapes. A model is presented that assumes the non-random search described by Conradt *et al.* (2000) with both shape and parameters of the distance decay curve following Schneider *et al.* (2003), which assumes that the composition of the landscape between resource patches affects butterfly movements. The predictions of this model are then compared with 2 years of capture–recapture data on *M. jurtina* fluxes in two contrasting landscapes in terms of connectivity and with predictions of a simple regression model that includes sizes of departure and arrival patches and distances between these two as its variables.

Methods

The species

The meadow brown (*Maniola jurtina*) is one of the most abundant butterfly species in agricultural landscapes, found in a variety of habitats, although many populations have been lost due to agricultural intensification. It is a species of open grassland, heath land, hay meadows, roadside verges, hedgerows, and woodland clearings and rides. This butterfly is active even during dull weather when most other species are inactive. There is one generation per year with adults on the wing between mid June and September. The eggs are laid on a variety of grasses including fescues (*Festuca* spp.), bents (*Agrostis* spp.), and meadow grasses (*Poa* spp.). The young larvae feed during the day relying on their green colouring for camouflage. *Maniola jurtina* is classified as a sedentary species, with a minimal home range estimated as 0.5 ha (Brakefield, 1982), although in certain cases it can disperse over several kilometres (Schneider *et al.*, 2003). Landscape elements with tall vegetation such as woodland can act as a barrier of movement for grassland butterfly species, including *M. jurtina* (Sutcliffe & Thomas, 1995; Haddad, 1999), leading to changes in flight direction (Fry & Robson, 1994).

Study area

The study was conducted in two landscape units in western France (Northern Brittany), each 1 km² in size. These sites represent fine grain hedgerow network landscapes (bocage). Agriculture in both sites is oriented toward milk production; maize, wheat, and grasslands for pasture cover the majority of land. Sites 1 and 2 exhibit contrasted spatial structure. Site 1 is located in a dense hedgerow network and fine grain area with several woodlots, while site 2 is more open and contains a more reduced and fragmented hedgerow network. The sites also differ in the intensity of agricultural production. Site 2 is characterised by a high proportion of large cropped areas of maize and other cereals, compared to site 1 with more grassland. The studied landscapes are described using GIS (IDRISI; Eastman, 1997). Crops, woodland, temporary grasslands, permanent grasslands, hedgerows, and grassy field margins were distinguished.

Butterfly movement

At each study site, movement sampling was conducted in several herbaceous areas selected according to their nature (meadow, grassland, grassy field margin, hedgerow bank, road bank, and lane bank) and their spatial distribution. Sampled areas were distributed in square kilometre restricted areas in order to cover the average range of daily movements of *M. jurtina* (Brakefield, 1982). Eight and 10 patches were chosen at sites 1 and 2 in 1998, and 15 patches at each site in 1999.

Butterfly movement was recorded during 1998–1999 using mark–release–recapture experiments. Every day, one mark–release–recapture session was performed, which consisted of successive sampling of all the patches at each site in a fixed sequence and was performed within 1 day. Ten mark–release–recapture sessions and 21 mark–release–recapture sessions were conducted respectively in 1998 and 1999 at each site. During each session, butterflies that were captured for the first time were identified by individual numbers on their wing (using a no-odour pen), and released thereafter. At the same time, their capture location, i.e. patch number, was recorded. When recapturing butterflies, the individual's number and recapture location were recorded. The time spent in each patch was proportional to its surface area to maintain a constant sampling intensity. The flux from patch i to patch j was calculated as:

$$M'_{ij} = 100 \times \frac{M_{ij}}{\sum\limits_{k=1}^{n} M_{ik}}, i \neq j, \qquad (1)$$

where M_{ij} is the number of recaptures in patch j (at any time during the experiment) of individuals, which were captured in patch i; capture means the first capture of an individual – when it was marked – and recapture the subsequent recapture of this individual (no individual was recaptured more than once in the data).

Proportion of residents, M'_{ii}, was estimated for each patch as the proportion of individuals recaptured in the same patch:

$$M'_{ii} = 100 \times \frac{M_{ii}}{\sum\limits_{k=1}^{n} M_{ik}} \qquad (2)$$

Proportion of immigrants, I_i, was defined for each patch as the percentage of individuals entering patch i, out of the total number of recaptured individuals:

$$I_i = 100 \times \frac{\sum\limits_{j=1, j\neq i}^{n} M_{ji}}{\sum\limits_{k,l=1}^{n} M_{kl}} \qquad (3)$$

Thus the butterfly fluxes, the proportions of residents, and the proportions of immigrants were calculated using the data from the whole study period (10 days in 1998 and 21 days in 1999).
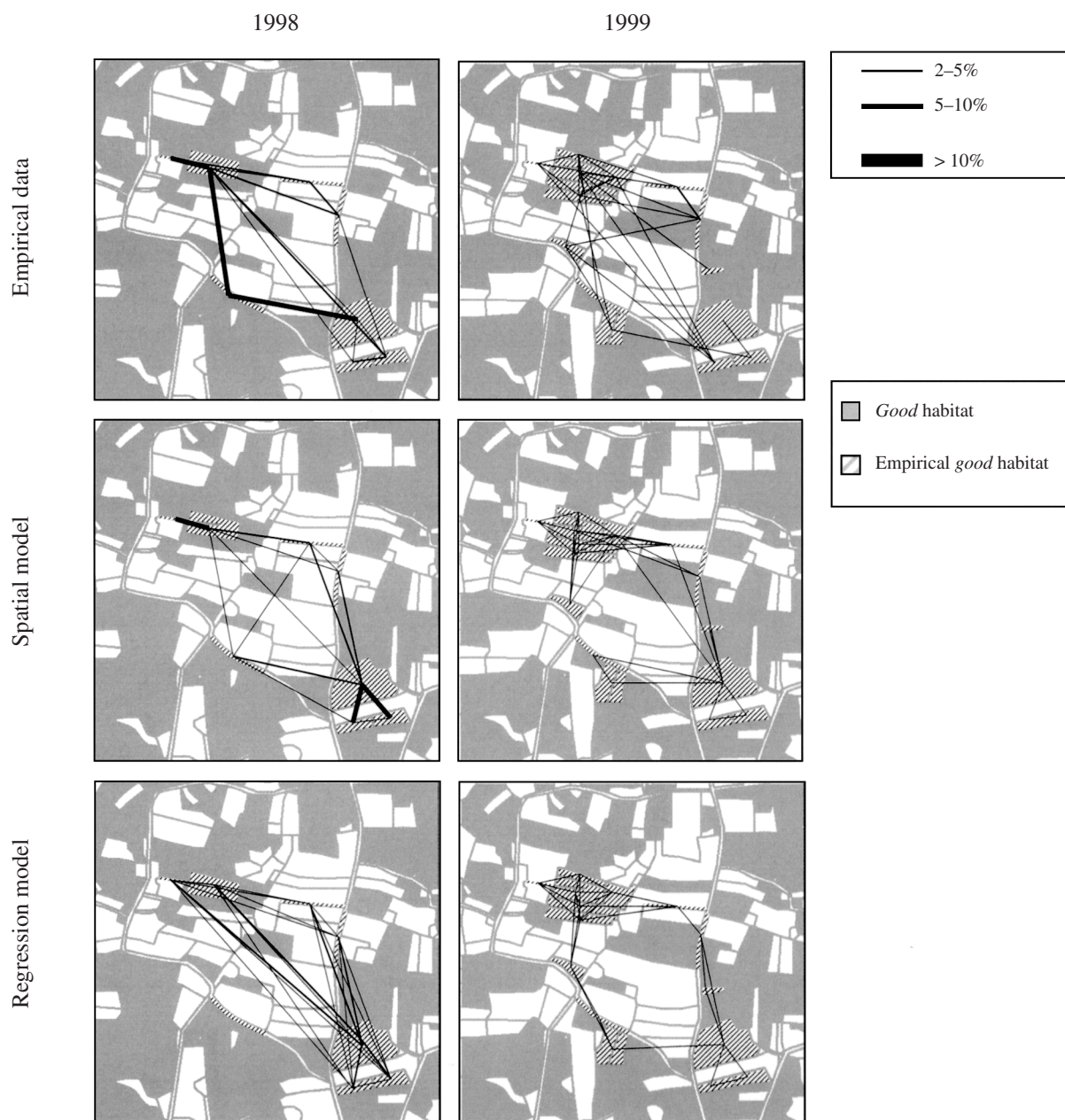
The spatial model

Each landscape studied was considered as a mosaic of 5×5 m pixels, so that each of the experimental patches consisted of many pixels. Each of the pixels was characterised by the type of its land cover: 1, water; 2, woodland and fallow land; 3, crops; 4, roads and buildings; 5, temporary grasslands; 6, permanent grasslands; 7, grassy field margin; 8, hedgerow. For the model purposes, however, only *good* habitats (grasslands, grassy field margins, and hedgerow margins) and *bad* habitats (water, woodland and fallow land, crops and roads, and buildings) were distinguished (see Figs 1 and 2). Landscape composition was different between the 2 years of observations in either of the sites due to crop succession, resulting in different spatial distribution of good and bad habitat for butterflies (see Figs 1 and 2). This made it possible to have different cases of landscape composition in the simulations. It was assumed that woodlands acted as a barrier for butterfly movements, according to the grassland status of the meadow brown. Consistent with Conradt *et al.* (2000), it was assumed that the butterflies are using a non-random, systematic search strategy in which they fly in loops around the starting point and return periodically to it, provided they do not find a good habitat. In the model, this was performed as follows:

1 In each step, the direction of flight, *Dir*, and its length, *Length*, were chosen at random.
2 Direction of flight was chosen from a uniform distribution, $Dir \in \,< 0; 360° > 0$.
3 Following Schneider *et al.* (2003), length of flight, *Length*, was chosen from a negative exponential distribution with a constant mean, *Mean*. $Mean = 70$ m was chosen for the main simulation, as it is the commonest mean distance of flight of *M. jurtina* (Schneider, 2003; Schneider *et al.*, 2003).
4 The individual was assumed to move linearly in the direction *Dir* for a distance *Length*. If at any time during the flight the individual hit a woodland or fallow land, it was assumed to land. If the individual hit area boundary during the flight, it was allowed to leave the system.
5 If the individual starting from pixel P_s did not hit any woodland or fallow land or area boundary during the flight in the direction *Dir* for a distance *Length*, and if after having completed the whole flight it arrived to a pixel P_a, it was assumed to land in P_a, if either P_a was good, or if P_s was bad (which might have happened, if it hit woodland during the previous flight). If P_s was good and P_a was bad, it was assumed to return to P_s and land there.
6 In the next step, the butterfly was assumed to take off from the point where it had landed in the previous step, as defined in points 4 and 5, and the whole procedure starting from point 1 was repeated.

In both experimental landscapes and in each of the experimental patches within the landscape, an initial position of the butterfly was chosen at random and the procedure described above (points 1–6) was performed 1000 times, so simulating 1000 flights of one butterfly, the first one starting in the pixel selected, the second one starting in the pixel where the butterfly landed after having performed the first flight (as defined in points 4 and 5), etc. This was repeated 1000 times for each landscape and each patch selected. Thus, in biological terms, 1000 experimental butterflies
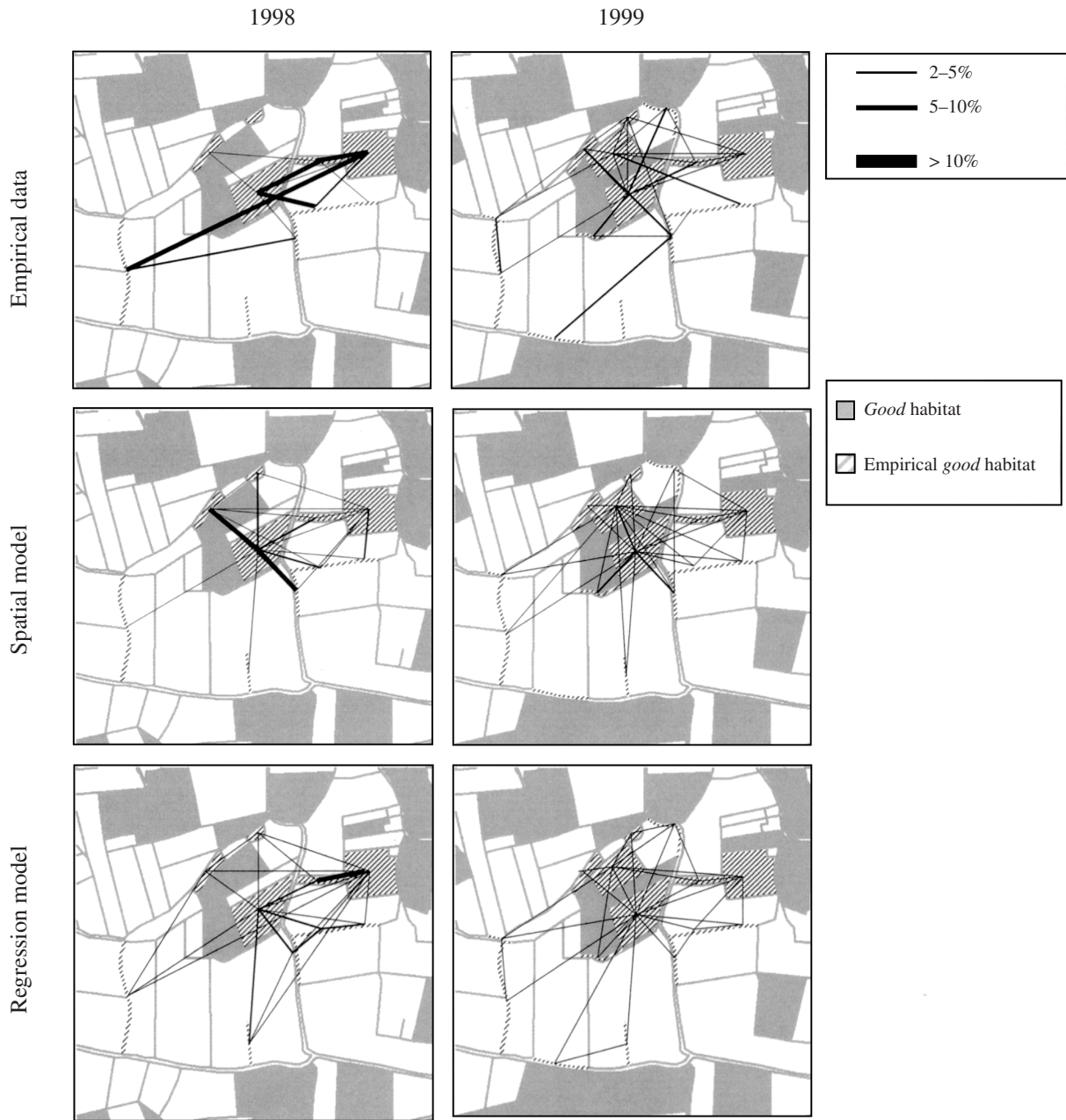
1998　　　　　　　　　　1999

Fig. 1. Spatial distribution of butterfly fluxes (% of moving individuals) as predicted by the spatial model (middle) and the regression model (bottom) compared with spatial distribution of observed fluxes (top). Results are presented for two years, 1998–1999 and site 1. Fluxes lower than 2% are not depicted.

were simulated for each patch and each site, each of which completed 1000 flights. Point 2 above means that the experimental butterflies were not assumed to be able to learn from unsuccessful flights, as follows from Conradt *et al.* (2000). Note that different types of behaviour described in points 4 and 5 above reflect two different situations: hitting a woodland during the flight is only a signal to changing flight direction and continuing the search, while arrival to a bad

pixel at the end of the flight is a signal to return to the take-off pixel.

N_{ij} was then calculated as the number of times any of the experimental butterflies, the initial position of which was in patch i, landed in patch j during the simulation. In order to make this value comparable with the empirical fluxes, M'_{ij}, and with the empirically obtained proportions of residents, M'_{ii}, the transformation was used

Fig. 2. Spatial distribution of butterfly fluxes (% of moving individuals) as predicted by the spatial model (middle) and the regression model (bottom) compared with spatial distribution of observed fluxes (top). Results are presented for 2 years, 1998–1999 and site 2. Fluxes lower than 2% are not depicted.

$$N'_{ij} = 100 \times \frac{N_{ij}}{\sum\limits_{k=1}^{n} N_{ik}}, \qquad (4)$$

and N'_{ij} was then compared with M'_{ij}.

The number of flights used in the simulations might have affected the model predictions of the proportion of butterflies that decide to disperse, and of the proportion of individuals not recaptured; however, no data was available about the actual number of flights of the real butterflies. Therefore, the proportions of resident individuals, N_{ii}, were taken out of all further analyses with the only exception of calculating correlations between the proportions of residents observed and those predicted by the spatial model, and the proportions of residents observed and patch area. This is reasonable, as the ratios $N'_{11}:N'_{22}:\ldots:N'_{nn}$ and $M'_{11}:M'_{22}:\ldots:M'_{nn}$ are not likely to be affected by either the

sampling effort or the number of flights in the simulation (while their actual values might be). Therefore the correlation coefficients between these, or between these and patch area, are not affected either.

As Schneider (2003) reports a broad variation in the mean distance of flight of *M. jurtina*, model sensitivity to the parameter *Mean* was explored and additional simulation runs were performed in which this parameter was varied by 5 m from 5 m to 100 m.

The regression model

The empirical data was then fitted by a regression model

$$\overline{M}'_{ij} = \frac{aA_i^b A_j^c}{D_{ij} + d} \tag{5}$$

that includes sizes of departure (A_i) and arrival (A_j) patches and distances between these two (D_{ij}) as its variables, a, b, c, and d model parameters, and $\overline{M}'_{ij}$ as the flux predicted by the regression model by minimising the residual sum of squares,

$$\sum_{i,j} (M'_{ij} - \overline{M}'_{ij})^2$$

Similar to usual assumptions of metapopulation models, it is assumed here that fluxes are positively associated with sizes of the departure and arrival patches, and negatively associated with the distance between these two. Thus the model parameters a, b, c, and d were not obtained from an independent data set, as was the case of the spatial model, but by means of fitting the data. In addition, the regression model includes four parameters (a, b, c, and d), while the spatial model only one (*Mean*); the latter was not fitted and its value was obtained from an independent data set: $Mean = 70$ m (Schneider *et al.*, 2003). For all these reasons, one would therefore expect a better fit in the regression model, represented, for example, by lower residual sum of squares.

Analysis

Similarity between the matrices of predicted vs. observed fluxes, i.e. between the matrices $N = (N_{ij}')$, $M = (M_{ij}')$, and $\overline{M} = (\overline{M'_{ij}})$ was then tested by means of Mantel's test (Mantel, 1967). As a formal hypothesis test, Mantel's test can be used to compare an observed data matrix to one posed by a conceptual or numerical model; the test is to summarise the strength of the correspondence between the two matrices (see, e.g. Shirley *et al.*, 2003). Significance levels were determined by performing 1000 permutations for each test. As the diagonals of the matrices (proportions of residents) were clearly strongly dominant and because of the possible bias mentioned in The spatial model section, they were deleted from the permutation tests, which lowered

the test significance levels. In other words, if the test including only non-diagonal elements has shown that the two matrices were significantly different at significance level α, then the same test with diagonals included would show that these matrices are even more significantly different – at an even lower significance level $\alpha' < \alpha$.

In addition, to compare the goodness of fits of the spatial and regression models, residual sums of squares of non-diagonal terms for the pairs of matrices N and M (measure of fit of the spatial model) and M and $\overline{M}$ (measure of fit of the regression model) were calculated.

Pearson's correlation coefficients in the SYSTAT (Systat Software Inc., Chicago, Illinois) package were used to calculate the correlations between the proportions of residents and immigrants predicted by the spatial model and those observed, between the patch surface area and observed proportions of residents and immigrants, between the proportions of immigrants and those predicted by the regression model, between the inter-patch fluxes and those predicted by each of the two models, and between the inter-patch distance and observed fluxes.

Results

Figures 1 and 2 enable comparison of the predictions of the spatial model for *Mean* = 70 m, and of the predictions of the regression model, with the empirical capture–recapture data for sites 1 and 2 respectively, and for 2 years, 1998 and 1999.

Table 1 shows values of Pearson's correlation coefficients between the proportions of residents and immigrants predicted by the spatial model and those observed, between the patch surface area and observed proportions of residents and immigrants, between the proportions of immigrants and those predicted by the regression model, between the inter-patch fluxes and those predicted by each of the two models, and between the inter-patch distance and observed fluxes. The results of the spatial model for the mean flight distance equal to 70 m were consistently used here.

Comparison of predictions of the spatial model with observed data

Results of Mantel's tests of the significance of differences between the matrices of observed fluxes vs. those predicted by the spatial model for both sites, 2 years, and each of the 20 simulation runs (differing in the mean distance of the butterfly flight, *Mean*, which was varied by 5 m from 5 m to 100 m) are shown in Table 2. Butterfly fluxes as predicted by the spatial model were similar to the observed data ($P < 0.01$), the exception being site 2 in 1998, where the fluxes predicted differed from observed data for each mean flight distance considered in the simulations. A very weak dependence of the significance level on the mean flight distance, *Mean*, is evident.

Figures 1 and 2 also demonstrate that the spatial distribution of butterfly fluxes, in terms of presence or absence of

Table 1. Pearson's correlation coefficients between observed proportion of residents (proportion of individuals that were recaptured in the same patch) and those predicted by the spatial model (S, column 3), between the observed proportion of residents and patch area (A, column 4), between the empirical proportions of immigrants and those predicted by the spatial model (S, column 5) and the regression model (R, column 6), the empirical proportion of immigrants and patch area (A, column 7), the empirical fluxes and those predicted by the spatial model (S, column 8) and regression model (R, column 9), and the empirical fluxes and inter-patch distance (D, column 10) for both sites and both years.

| | | Correlation coefficient | | | | | | | |
| | | Residents | | Immigrants | | | Fluxes | | |
Site	Year	S	A	S	R	A	S	R	D
1	1998	0.48	0.54	0.65	0.165	0.73	0.563*	0.165	−0.328*
1	1999	0.74*	0.58	0.61*	0.426*	0.31	0.379*	0.426*	−0.311*
2	1998	−0.22	−0.02	0.53	0.242	0.88*	0.155	0.242	0.094
2	1999	0.24	0.26	0.92*	0.534*	0.72*	0.499*	0.534*	−0.275*

*$P < 0.05$

movements, was relatively well predicted by the spatial model, especially at site 1 in 1998 and at site 2 in 1999. There were some differences between the spatial distributions of predicted and observed fluxes in terms of movement intensity.

Table 1 shows that the spatial model predictions of the proportions of residents were significantly positively correlated with the observed data at site 1 in 1999. Spatial model predictions of the proportions of immigrants were always positively correlated with the observed data, but significantly so only in 1999 at both sites. Spatial model

Table 2. Results of Mantel's test – probabilities that the matrices of fluxes predicted by the spatial model and observed fluxes are independent of each other. The diagonals of the matrices were not considered.

| Mean flight distance (m) | Site 1 | | Site 2 | |
	1998	1999	1998	1999
5	0.001	0.001	0.099	0.001
10	0.002	0.001	0.100	0.001
15	0.001	0.001	0.082	0.001
20	0.003	0.001	0.100	0.001
25	0.002	0.001	0.100	0.001
30	0.002	0.001	0.106	0.001
35	0.002	0.001	0.102	0.001
40	0.003	0.001	0.121	0.001
45	0.001	0.001	0.093	0.001
50	0.001	0.001	0.101	0.001
55	0.002	0.001	0.081	0.001
60	0.003	0.001	0.091	0.001
65	0.003	0.001	0.088	0.001
70	0.002	0.001	0.078	0.001
75	0.003	0.001	0.080	0.001
80	0.001	0.001	0.071	0.001
85	0.005	0.001	0.076	0.001
90	0.002	0.001	0.064	0.001
95	0.003	0.001	0.083	0.001
100	0.005	0.001	0.066	0.001

predictions of the inter-patch fluxes were always significantly positively correlated with the observed data, with the exception of site 2 in 1998, when the positive correlation was not significant.

Comparison of predictions of the regression model with observed data

Mantel's tests have shown that the differences between the matrices of observed fluxes vs. those predicted by the regression model for both sites in the 2 years were not statistically significant ($P < 0.01$), which means that even the predictions of the regression model were similar to the observed data.

Table 1 shows that the proportions of immigrants and inter-patch fluxes predicted by the regression model were significantly positively correlated with the observed data at both sites in 1999, that the patch area was significantly positively correlated with the proportion of immigrants at site 2 in both years, and that the observed inter-patch fluxes were significantly negatively correlated with inter-patch distance except at site 2 in 1998. Table 3 shows that the proportions of residents and those of immigrants were larger in large patches.

Comparison of the predictions of the spatial and regression models

Results of Mantel's tests suggest that both models are able to satisfactorily predict the fluxes between the empirical patches at a very high significance level ($P < 0.01$); however, Mantel's test is rather conservative for the purpose of comparison of goodness of fit, as the difference between the pair of matrices tested has to be relatively large for the test to be significant. Thus comparison of residual sums of squares between the observed values and those predicted by the two models seems to be more adequate.

Table 3. Observed proportions of residents and immigrants in empirical patches for both sites and both years.

	Site 1			Site 2		
	Patch no.	Residents	Immigrants	Patch no.	Residents	Immigrants
1998	1	40	2	1	63	13
	2	85	60	2	86	75
	3	79	3	3	100	6
	4	85	18	4	75	4
	5	89	42	5	91	4
	6	75	19	6	0	
	7	80	13	7	50	9
	8	50	1	8	85	30
				9	100	10
				10	100	0
1999	1	0	0	1	24	39
	2	62	126	2	47	38
	3	13	47	3	50	0
	4	11	34	4	100	19
	5	89	35	5	29	78
	6	53	16	6	0	0
	7	75	35	7	82	55
	8	25	2	8	60	229
	9	37	96	9	57	54
	10	45	79	10	50	34
	11	47	86	11	0	24
	12	58	72	12	0	0
	13	86	3	13	20	1
	14	77	61	14	6	6
	15	70	61	15	62	135

Table 4 shows the residual sums of squares of the non-diagonal terms for the pairs of matrices N and M (measure of fit of the spatial model) and M and $\overline{M}$ (measure of fit of the regression model). The regression model consistently gives a worse fit and in three out of the four cases the residual sum of squares for the regression model is 1.3–2.5 times larger than that for the spatial model. In addition: the regression model fits four parameters to the empirical data, while the spatial model makes its completely independent prediction, without fitting any parameters (the parameter *Mean* was not fitted – the value used was suggested by the literature instead, rather than fitting it to the data, and subsequently it is being shown that the spatial model results are not sensitive to changes of its value). Rules of statistics suggest that a model that either yields a smaller residual sum of squares or has fewer parameters, or both, should be

Table 4. Residual sums of squares of non-diagonal terms for the pairs of matrices N and M (measure of fit of the spatial model) and M and $\overline{M}$ (measure of fit of the regression model) for the two empirical sites and years 1998 and 1999.

	Site 1		Site 2	
	1998	1999	1998	1999
Spatial model	4627	11 843	18 795	18 186
Regression model	11 546	17 331	24 585	19 169

preferred. Thus in this case, both criteria are in favour of the spatial model.

This is further supported by the correlation coefficients presented in Table 1. Predictions of the inter-patch fluxes are better correlated with the empirical data for the spatial model (three statistically significant correlation coefficients for the spatial model, compared with only two for the regression model), while the correlations between the predictions of the proportions of immigrants and empirical data are comparable for both models.

Discussion

No previous knowledge derived from this data was incorporated into the spatial model. For spatial model building, literature predictions exclusively on *M. jurtina* flight behaviour were used, so that the spatial model predictions are verified by using a completely independent data set. The results of Mantel's test show that the spatial model fits the empirical data well and is not too sensitive to the value of mean flight distance, *Mean*. This is further supported by the correlation coefficients presented in Table 1 and by the residual sums of squares in Table 4. Visual inspection of Figs 1 and 2 suggests a reasonable similarity between model's predictions and empirical data.

The spatial model was based on two assumptions. The first hypothesis was that *M. jurtina* adopts a non-random, systematic search strategy in which it flies in loops around the release point and returns periodically to it (Conradt *et al.*, 2000). Second, it was assumed that the landscape composition between habitat patches affects butterfly movements, i.e. that woodlands act as a barrier (Sutcliffe & Thomas, 1995; Haddad, 1999) and resource patches act as stepping stones or corridors for butterflies. In the spatial model, hitting the barrier was simulated by changing the flight direction (point 4 in the model) and assumption of landing in a good patch and performing further flight afterwards (point 5 in the model and assumption of the total of 1000 flights for each butterfly) simulated good patches acting as stepping stones. Despite some obvious differences between the spatial model predictions and empirical data, the results show that the spatial model gives better predictions of butterfly movements than did the regression model based only on patch area and isolation. This indicates that the assumptions made in the spatial model might be important for describing how butterfly movements are affected by landscape composition.

The differences between the spatial model predictions and the observed spatial distribution and intensity of *M. jurtina* fluxes between habitat patches can be attributed to simplifications in the assumptions of the spatial model. All hedgerow margins were considered as suitable habitats for the meadow brown and thus as potential corridors used by butterflies for reaching other habitat patches (Dover, 1994). However, the banks of some hedgerows consist of high, dense woody and shrubby vegetation, which makes them impermeable for butterflies (Fry & Robson, 1994),

depending on the orientation of the hedgerow relative to the direction of butterfly movement. In addition, differences in resource quality between different habitat patches were not taken into account. In agricultural landscapes, local abundance and diversity of flowering plants is related to the farming practices conducted here: different management regimes lead to different plant species assemblages (Le Coeur *et al.*, 2002). Thus, the good habitats such as temporary and permanent grasslands may in reality differ in quality – as perceived by butterflies – because of differences in the diversity and abundance of flowering plants here. The management regimes of herbaceous areas might influence *M. jurtina*'s behaviour and distribution in resource patches, as demonstrated in previous studies for other butterfly species (Sparks & Parish, 1995; Dover, 1997). Finally, it was assumed that all non-herbaceous areas other than woodland influenced butterfly movement in a similar way, which is a simplification of reality. As the type of the inter-patch matrix influences butterfly movements (Ricketts, 2001), a potential improvement of the model might be assigning different viscosities to the different land covers composing the landscape matrix. For this, however, lots of extensive data sets about actual viscosity would be needed. Thus although there is potential for improvements of the spatial model, the results show that both detailed information about flight behaviour of individuals and landscape connectivity between habitat patches are important factors, worth being integrated into models of butterfly movements.

The differences between spatial model predictions and observed fluxes can also be explained by certain limitations inherent to butterfly sampling. Studying movement at the landscape scale is problematic because of the difficulty to realise exhaustive and large-scale sampling in the field. The surface area of the studied landscapes was thus limited to 1 km^2 for practical reasons. The scale of the study area has a major impact on the results of mark–release investigations, and large-scale studies are recommended to get a more accurate view of butterfly dispersal ability (Schneider, 2003). Mark–release–recapture methods can underestimate long-distance dispersers, especially for species that live in patchy habitats in fragmented landscapes (Wilson & Thomas, 2002). Thus, because of the relatively small scale of the sampling caused by limitations in manpower and the bias inherent to mark–release–recapture methods, the study might thus underestimate long-distance movements of butterflies in the landscape.

The question remains of whether the spatial model gives a significant improvement, compared with much simpler approaches, which generate colonisation patterns for patches depending on variables such as patch size and isolation (the regression models). Figures 1 and 2, Table 1, and especially Table 4, provide a partial answer. In most cases, the spatial model based on the assumptions of Conradt *et al.* (2000) and Schneider *et al.* (2003) gives either a considerably better, or at least comparable, prediction of actual butterfly fluxes than a simple prediction of the regression model based on patch size and distance between patches. Thus, if data are available about the actual landscape under

consideration, the spatial model should be preferred to the regression model; however, in general theoretical considerations the regression model based on patch size and the degree of its isolation will retain its value.

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