ORIGINAL PAPER

Habitat utilization by ovipositing females and larvae of the Marsh fritillary (*Euphydryas aurinia*) in a mosaic of meadows and croplands

Wenhua Liu · Yifei Wang · Rumei Xu

Received: 29 September 2005/Accepted: 12 April 2006/Published online: 17 October 2006 © Springer Science+Business Media B.V. 2006

Abstract The butterfly Euphydryas aurinia occurs as a classical metapopulation in Yanjiaping village, Heibei province, China. In the patch network under study there were 38 habitat patches. Most patches were uncultivated, consisting of meadows and fallows, while others had been cultivated, i.e., used as small croplands. In the cultivated patches, the habitat for the butterfly can be classified into two types: meadow type (MTH) and cropland type (CTH). In contrast, the uncultivated habitat patches consists only of MTH. We examined the habitat utilization of ovipositing females and larvae of E. aurinia to assess the effect of mixed land use on the butterfly's occurrence. More egg clusters and pre-hibernating larval groups were distributed throughout CTH than MTH. This dependence on CTH may be due to the preference of egg-laying females for large-sized host plants, which were mainly concentrated in CTH. Compared to the MTH, the mortality rate in CTH was lower. Therefore, for both eggs and pre-hibernating larvae, the quality of CTH was higher than that of MTH. The conditions in MTH, on the other hand, were important for the development of post-hibernation larvae. A combination of extensive farming and animal husbandry has created a mosaic of meadows and croplands in the habitats studied here, which is typical of rural areas in some developing

W. Liu · Y. Wang · R. Xu (⊠) Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Beijing Normal University, Beijing 100875, China e-mail: xurumei@bnu.edu.cn

Y. Wang

countries. This study implies that patchy land use typical of traditional agriculture facilitates the long-term persistence of *E. aurinia*.

Keywords Conservation · Cultivated patches · *Euphydryas aurinia* · Habitat types · Habitat utilization

Introduction

With the development of agriculture and urban life, more and more species inhabit fragmented landscapes, particularly in agricultural areas. Efforts to preserve biodiversity and to understand ecological processes in human-altered landscapes are becoming increasingly important. The theories guiding the studies of biodiversity in these systems have evolved from island biogeography to metapopulation theory and countryside biogeography (Daily 1997, 2001; Hanski and Gaggiotti 2004). Butterflies are among the best known and the most endangered taxa of temperate insects (van Swaay and Warren 1999). Considerable attention has been directed in recent years towards the investigation of optimal methods for protecting butterfly diversity in human-dominated agricultural landscapes (Dover 1991; Smallidge and Leopold 1997; Horner-Devine et al. 2003; Tews et al. 2004). Recent studies have shown that both habitat quality and landscape structure are important for the conservation of a given endangered butterfly (Thomas et al. 2001). In general, habitat quality for the most rare butterflies is determined by the specific conditions required by the juvenile stages. Consequently, the habitat requirements of ovipositing females and larvae should be considered to be an important aspect of butterfly conservation.

Research Institute of Forestry, Wetland Research Center, Chinese Academy of Forestry, Beijing 100091, China

The marsh fritillary *Euphydryas aurinia* (Rottemburg) was once widely distributed across the temperate Asian-European continent. In most European countries it suffered a severe decline and became endangered during the 20th century. Changes in traditional land use have been linked with the decline of *E. aurinia* (Thomas and Hanski 2004). At the present time this butterfly species depends on appropriate habitat management in unimproved habitats in Europe for its survival (Warren 1994; Anthes et al. 2003; Konvicka et al. 2003).

Habitat requirements of *E. aurinia* are of particular interest since there are marked geographical variations in the range of host plants and habitat use in several regions (Warren 1994; Lewis and Hurford 1997; Munguira et al. 1997; Wahlberg et al. 2001, 2002; Anthes et al. 2003; Konvicka et al. 2003). In addition, detailed studies have shown that this species is particularly sensitive to even minor changes in land use (Warren 1994) and that any change of habitat quality can greatly affect the persistence of the butterfly metapopulation (Wahlberg et al. 2002). This species has, therefore, a high potential as an indicator for monitoring environmental change.

Until recently, little was known about the ecology of this butterfly species in China. In YanJiaPing village, Hebei Province, *E. aurinia* had a classical metapopulation structure and dynamics in a mixed landscape (R.J. Wang et al. 2003; Y.F. Wang et al. 2003). Studies carried out between 1998 and 2002 revealed that *E. aurinia* exhibited a preference for the cultivated habitat patches. Consequently, the local population size in the cultivated patches was higher than that of uncultivated patches, and local extinction often occurred in uncultivated patches (Table 1).

Some of the *E. aurinia* meadow habitat patches in this patch network were fragmented by croplands. Most studies on conservation biology have shown that habitat fragmentation usually has a negative effect on population viability (Hanski and Gaggiotti 2004) and that, in general, a larger, continuous habitat area

provides a better chance for population survival. While conservation plans for invertebrates should clearly minimize habitat loss and fragmentation, it is equally important to give priority to habitat diversity, which may critically influence the capacity of habitat patches to maintain viable populations (Ehrich and Hanski 2004). Habitat diversity created by mixed land use may likely be one of the underlying causes for the preference of the butterflies for the cultivated patches.

The aim of this investigation was to study how ovipositing females and larvae utilize their habitat and, consequently, to clarify their habitat requirements. We also wished to test whether habitat diversity created by mixed land use within the habitat patches influenced the population dynamics of *E. aurinia*. Ultimately, we sought to investigate the effects of habitat quality on the metapopulation dynamics of *E. aurinia* and as such provide useful information for achieving the long-term conservation of the butterfly in this traditional agricultural landscape.

Materials and methods

Target species and study area

The study area is a basin roughly 10 km² in size and is located in Dahaituo National Natural Preserve, Hebei Province, China, at an elevation of approximately 1300–1600 m a.s.l. The target species, *Euphydryas aurinia*, is a univoltine species belonging to the family of Nymphalidae. Adults emerge from late May until late June. Females lay batches of eggs, and larvae hatch in late July. The larvae aggregate and spin a silken web from which they feed monophagously on a perennial host plant *Scabiosa tschiliensis* Grün (Dipsacaeae). The larvae hibernate in the fourth instar in a winter web by mid- or late September. In late March of the following year, the fourth instar larvae resume feeding gregariously after diapause. However, from the fifth to the

Table 1 Comparison of population size and turnover of *Euphydryas aurinia* between cultivated patches (n=12) and uncultivated patches (n=26) from 1998 to 2002 (Based on Y.F. Wang 2004)

Year	Number of local populations		Number of larval groups		Number of extinctions		Number of recolonizations	
	Cultivated patches	Uncultivated patches	Cultivated patches	Uncultivated patches	Cultivated patches	Uncultivated patches	Cultivated patches	Uncultivated patches
1998	8	7	53	17	0	6		
1999	8	2	31	2	0	2	0	1
2000	8	1	110	1	0	0	0	1
2001	9	3	78	3	0	3	1	2
2002	9	0	60	0	0	0	0	0

sixth instar they tend to feed singly. They then pupate in late April to early May.

Patches of meadows where the host plant grows were considered to be suitable habitat patches for *E. aurinia*. Altogether there were 38 such patches of meadows in the study area, which were isolated by valleys, shrubs, sparse woods, large croplands, roads, and a village. Patch sizes ranged from 0.025 to 3.2 ha (mean: 0.7 ha). The patch network was divided into southern, western, eastern and northern sub-regions according to their specific topographic features, and numbered accordingly (E01, E02, etc.) (Fig. 1) (Y.F. Wang et al. 2003).

Some habitat patches were cultivated; i.e., where local farmers grow corn or potatoes in small areas of croplands embedded within the habitat patches (Fig. 1). Other habitat patches were not cultivated. In the cultivated patches, the habitat for the butterfly can be classified into two types – meadow-type (MTH) and cropland-type habitats (CTH) (see Fig. 2). The MTH includes meadows proper and fallow land. In the embedded croplands, there are grass strips between the planted rows of crops as well as a marginal grass strip (defined as less than 3 m wide) outside the margin of the embedded cropland. These two components constitute the CTH. In contrast, the uncultivated patches consist only of MTH.





Fig. 2 Diagram of patch E03 as an example of the different types of habitats in a cultivated patch. The meadow type of habitat (MTH) includes meadows proper and fallow land. The grass strips between the planted rows of crops and the marginal grass strip constitute the cropland type of habitat (CTH)

Most patches were uncultivated (in 2003, for example, 22 patches, comprising about 80% of the overall area of the patch network, were uncultivated). The remaining patches (the other 16 patches, which comprised about 20% of the total area) were cultivated (Fig. 1).



In general, in most of the cultivated patches, the area occupied by the CTH was much smaller than that occupied by the MTH. Two representative cultivated patches, E03 and N11, were selected for a detailed investigation. Patch E03 faces south, with a gentle slope, and occupies a surface area of 1.48 ha. Patch N11 is on the east slope, and occupies a surface area of 0.53 ha. The ratio of the surface area of CTH to that of MTH was about 1:3 in patch E03 (Fig. 2) and 1:7 in patch N11. From April to October, cattle and sheep grazing was not allowed on CTH, and only mules were fastened to graze. However, groups of cattle and sheep were allowed to graze in MTH. Farmers mowed some CTH with scythes in the summer or autumn.

Census on egg clusters, pre-hibernating larval groups and post-hibernating larvae

Between 14 June and 24 June 2003, E. aurinia egg clusters were searched in the northern and eastern subregions, where the largest number of larval groups was usually found each year. When an egg cluster was found, the site was marked with a red stick, and the coordinate was recorded using a global positioning system. The distance to the boundary of the nearest cropland was then measured. The marked egg clusters were observed the every other day to check the status of the eggs until all members of the larval group had either disappeared or undergone diapause in the winter nest. Larvae from different egg clusters hatching on the same host plant often merged into a larger communal web in the early instars. It was impossible to distinguish individuals from different egg clusters. Therefore, the fate of the communal web was considered as the common fate of the original egg clusters.

In early September, winter nests were surveyed on the host plants throughout all the patches. In the following spring (early May) searches were made for larvae throughout patch N11 and E03.

Habitat quality of the two habitat types in cultivated patches

In late June, during the flight season of *E. aurinia*, all host plants surrounding egg clusters were surveyed. We

Table 2 Comparison of host
plant and vegetation
characteristics (mean \pm SE)
between the cropland-type
habitat (CTH) and the
meadow-type habitat (MTH).
Significance is based on *t*-test

also surveyed host plants in five and nine randomly selected transects in N11 and E03, respectively. Within each transect, $1 \times 1 \text{-m}^2$ quadrats (mean: 7.5, median: 9.0, SD = 3.2, range: 5–13) were checked. The total number of quadrats sampled was 109. The vegetation height and coverage, the number and height of host plants, and the number of shoots from the short rhizome of each plant were recorded.

The mean size of the host plants in CTH was larger than that in MTH, as assessed by the taller host plants and the increased number of shoots per plant (Table 2). However, CTH had a lower density of host plants. The vegetation in CTH was taller than that in MTH. No significant difference existed in the vegetation coverage between the two habitat types.

Data analysis

Associations between the occurrence of oviposition and habitat variables were investigated using logistic regression. We defined a dichotomous response variable as zero if no egg cluster was present in the quadrate, or as one if at least one egg cluster was present. *t*-tests were used to compare the means of variables between 'oviposited' and 'non-oviposited' quadrats. The variables that differed significantly were used to conduct step-wise logistic regression models to analyze their effects on the presence or absence of egg clusters (Hosmer and Lemeshow 1989).

t-tests were used to compare host plant and habitat variables between MTH and CTH.

We used SPSS ver. 10.0 for windows (SPSS, Chicago, Ill.) to conduct all statistical analysis.

Results

Factors affecting oviposition site selection

A comparison of habitat quality between quadrats in which oviposition occurred and those in which it did not occur – in both MTH and CTH – is shown in Table 3. Egg-laying females preferred to oviposit their eggs on large-sized host plants in both habitat types. In CTH, the number of shoots per host plant, the

	CTH (<i>n</i> =62)	MTH (<i>n</i> =47)	t	р
Height of vegetation (cm)	14.24±1.06	5.12 ±0.39	7.230	< 0.001
Vegetation coverage (%)	66.61±2.43	72.49±2.29	-1.877	0.071
Density of host $plant(/m^2)$	1.73 ± 0.32	7.96±1.35	-5.063	0.005
Height of host plant (cm)	12.53±0.71	5.37 ± 0.35	8.741	< 0.001
Shoots per host plant	3.93 ± 0.43	1.28 ± 0.01	5.730	< 0.001

Table 3 Comparisonofvarious characteristics of the	СТН				
host plant and vegetation		Oviposited (n=64)	Non-oviposited (n=31)	t	p^{a}
between quadrats in which		6.00.0.52	14.02 1.20	6164	.0.001
oviposition occurred and	Height of vegetation (cm)	6.89±0.52	14.03 ± 1.30	6.164	< 0.001
those in which it did not.	Vegetation coverage (%)	64.22 ± 2.90	69.84±3.08	1.195	0.235
Values are the mean \pm SE	Density of host plant $(no./m^2)$	4.08±0.52	2.38±0.46	-2.079	0.040
for CTH and MTH	bt. Vegetation coverage (%) 64.22 ± 2.90 \pm SE Density of host plant (no./m ²) 4.08 ± 0.52 Height of host plant (cm) 13.10 ± 0.55 Shoots per host plant (no.) 8.63 ± 0.42 MTH Oviposited (n=3) Non-ovip	12.32±0.82	-0.794	0.429	
	Shoots per host plant (no.)	8.63±0.42	3.47 ± 0.50	-7.375	< 0.001
	MTH				
		Oviposited (n=3)	Non-oviposited (<i>n</i> =6)		
	Height of vegetation (cm)	5.23±0.95	4.84±0.40	-0.438	0.663
	Vegetation coverage (%)	47.69±5.73	73.39±2.36	4.937	< 0.001
	Density of host plant $(no./m^2)$	3.46±1.67	8.56±1.36	2.058	0.045
	Height of host plant cm)	10.00 ± 0.71	5.22 ±0.34	-6.709	< 0.001
^a Significance based on <i>t</i> -test	Shoots per host plant (no.)	6.46±0.76	1.23±0.01	-11.19	< 0.001

density of the host plants, and the height of vegetation were significantly different between the quadrats with oviposition and those with none, whereas the height of host plant and the vegetation coverage did not differ significantly (Table 3); in MTH, however, it was the vegetation coverage, the number of shoots per host plant, the height and the density of the host plants which were significantly different, while the height of vegetation did not differ significantly.

The results of stepwise logistic regression analysis indicated that in both habitats females preferred largesized host plants to lay their eggs (Table 4). The number of shoots per S. tschiliensis had significant positive associations with the presence of egg clusters in the quadrats in both habitat types. Also, the number of shoots per S. tschiliensis plant correlated positively with the number of egg clusters (Pearson correlation: R=0.27, p=0.002). Conversely, the height of the vegetation correlated negatively with the occurrence of egg clusters in the quadrats in CTH. However, the density of host plants did not significantly influence egg deposition decisions, even though the density of the vegetation differed significantly between the quadrats with oviposition and those with none in both habitat types.

Oviposition and larval habitat utilization

In 2003, 249 egg clusters were found on 140 *S. tschiliensis* plants in ten of the 23 habitat patches in the northern and eastern sub-regions. Egg clusters were found in nine of the 11 (81.8%) cultivated patches, and in only one of the 12 (7%) uncultivated patches. Accordingly, a higher percentage of cultivated patches than of uncultivated patches were occupied by *E. aurinia* larvae. In 2003, 11 of 16 (68.8%) cultivated patches were occupied by larvae, whereas five of 22 (22.7%) uncultivated patches were occupied (Fig. 1). The proportions of occupied cultivated patches and uncultivated patches differed significantly from each other (2×2 tables; Pearson's χ^2 =8.049, *df*=1, *p* < 0.01).

The distribution of the distance from each egg cluster to the edge of the nearest cropland is shown in Fig. 3. The average distance was 3.55 ± 0.33 m (n=249). A total of 179 egg clusters (71.9%) were found in CTH (less than 3 m from the croplands), whereas 70 egg clusters (28.1%) occurred in MTH.

A large number of pre-hibernating larval groups were also distributed throughout CTH. In 2003, 175 of 252 larval groups (69.4%) were found in CTH. The difference in the occurrence of larval groups between

Table 4 Forwardstepwiselogistic-regression^a of eggdeposition preferences of *E.aurinia* in the two habitattypes

^a β is the regression coefficient, SE is standard error of the coefficient, Model G² is the log-likelihood ratio of the model, *p* is the level of significance

Model	β	SE	р
СТН			
Constant	-0.562	0.953	0.556
Shoots per host plant	0.657	0.162	< 0.001
Height of vegetation (cm)	-0.242	0.071	0.001
Model: $G^2=52.305$; $df=2$, $p < 0.001$			
	β	SE	р
MTH			
Constant	-8.246	3.11	0.008
Shoots per host plant Model: G^2 =7.622; df=1, p < 0.001	2.867	1.29	0.003



CTH and MTH was highly significant (χ^2 =38.11, p < 0.001).

The distribution of egg clusters, pre-hibernating larval groups, and post-hibernating larvae in patches E03 and N11 is shown in Table 5. Thenumbers of both the egg clusters and pre-hibernating larval groups were significantly higher in CTH than in MTH (egg clusters: χ^2 =26.797, p < 0.001; larval groups: χ^2 =23.405, p < 0.001). However, most of the post-hibernating larvae occurred in the CTH (χ^2 =46.44, p < 0.001).

Mortality of egg clusters and pre-hibernating larval groups

The mortality of egg clusters was 10.1% (*n*=177) in CTH and 15.9% (*n*=69) in MTH; this difference was not significant (χ^2 =2.862, *p*>0.05). However, the mortality of pre-hibernating larval groups in CTH (23/164 = 14.0%) was significantly lower (χ^2 =16.49, *p*<0.01) than that in MTH (21/59 = 33.3%).

The mortality factors differed between the two habitat types, and between life stages (Fig. 4). Mortality due to grazing was higher in MTH (90.9% for egg clusters; 38.1% for pre-hibernating larvae) than in CTH (22.2% for egg clusters; 4.3% for pre-hibernating larvae).

For egg clusters, mortality due to predation by stinkbug and lacewing was low in both habitats (11.1% for CTH and 9.1% for the MTH). In CTH, mowing destroyed a substantial number of egg clusters (33.3%). Heavy rainfall, which washed egg clusters off the host plants (33.3%), may have been the reason for the death of another proportion of egg clusters.

The high mortality rate of pre-hibernating larvae during the first and second instars (73.9% in CTH and 57.1% in MTH) was due to larvae falling off the host plants onto the ground: death occurred very quickly after exposure to the hot soil (Moore 1989). The difference for this mortality rate between CTH and MTH is not significant (χ^2 =2.23, *df*=1, *p*>0.05).

Table 5 The distribution ofegg clusters, pre-hibernatinglarval groups and post-hibernating larvae in patchesE04 and N11

Patch	Life stage	CTH	MTH	χ^2	р
E04	Egg cluster	50	5	36.818	< 0.001
	Pre-hibernating larval group	53	2	47.291	< 0.001
	Post-hibernating larvae	26	73	22.313	< 0.001
N11	Egg cluster	16	8	2.667	0.102
	Pre-hibernating larval group	11	4	3.267	0.071
	Post-hibernating larvae	12	52	χ ² 36.818 47.291 22.313 2.667 3.267 25.000 26.797 23.405 46.44	< 0.001
Total	Egg cluster	66	13	26.797	< 0.001
	Pre-hibernating larval group	63	52 25.000 13 26.797 5 23.405	< 0.001	
	Post-hibernating larvae	38	125	χ ² 36.818 47.291 22.313 2.667 3.267 25.000 26.797 23.405 46.44	< 0.001

Fig. 3 Distribution of the

distance from each E. aurinia

egg cluster to the edge of the nearest cropland (n=249)



Fig. 4 Relative frequency of mortality factors acting on egg clusters (a) and pre-hibernating larval groups (b) in CTH and MTH. Egg clusters: CTH, n=18; MTH, n=11. Pre-hibernating larval groups: CTH, n=23; MTH, n=21

During the pre-diapause period, the webs of a few groups of larvae were destroyed, which resulted in the larval groups being frozen to death (4.8% in the CTH and 13.1% in the MTH). In CTH, only one larval group died of starvation. Parasitizing rate of larval groups was 4.2%, caused by the braconid wasp *Cotesia melitaearum* (Wilkinson).

Movement of pre-hibernating larval groups

From July to September, 62.1% of the pre-hibernating larval groups stayed on the same host plant (n=116). In cases of dispersal, the distance between the oviposited host plant and the over-wintering host plant was usually less than 1 m, and only about 3.4% of the dispersed distance was more than 1 m. The maximal dispersal distance was 1.3 m. Pre-hibernating larvae dispersed over significantly (t=-2.640, p=0.009) shorter distances in CTH (0.17±0.03 m, n=95) than in MTH (0.37±0.09 m, n=21).

Discussion

Habitat utilization by ovipositing females and pre-hibernating larval groups

Butterfly abundance in a given area is often related to the abundance of host plants under specific conditions rather than to the total abundance of host plants (Bourn and Thomas 1993). We found more egg clusters and pre-hibernating larval groups in CTH (Fig. 3, Table 5), and even though the density of host plants was relatively higher in MTH than CTH, only a few ovipositions and a small number of larvae were found in the former (Table 5). The preference for larger host plants rather than the abundance of host plants can help explain the preference of E. aurinia for ovipositing in CTH (Table 3). Local farmers avoid placing grazing animals on croplands but not on open meadows. Thus, with only light grazing in CTH, the host plants are able to grow larger and become more mature (Table 2). Females tend to select the larger host plants because they provide sufficient food for pre-hibernating larval groups to survive until hibernation. This strategy may also reduce mortality due to predation or bad weather when the larvae need to vacate the silk web to search for a neighboring host plant. Conversely, in MTH, heavy grazing prevented the host plant from growing large (Table 2). Consequently, we conclude that grazing intensity caused the discrepancy between the CTH and MTH with respect to the quality and abundance of S. tschiliensis plants.

A second reason for the higher concentration of larval groups of *E. aurinia* in CTH may be that larval survival is higher in this habitat than in MTH. The main mortality factor for the larval groups in MTH is grazing; for example, heavy grazing by sheep destroyed not only the host plants but also egg clusters or larval groups. In contrast, only mule grazing was occasionally allowed in CTH; consequently, fewer egg clusters and larval groups were destroyed. Partial mowing in the CTH may cut down some host plants and could cause the death of some egg clusters and larval groups. However, short turf still remains and keeps the vegetation open, which is helpful to egg-laying females (Table 4). This result is similar to that of previous studies on E. aurinia (Anthes et al. 2003; Konvicka et al. 2003).

These results suggest that the concentration of *E. aurinia* in CTH may be ascribed to two factors: (1) the higher abundance of large-sized host plants; (2) the lower larval mortality. Previous studies have also shown that *E. aurinia* prefers to oviposit at the edge of some habitats. In England, the butterfly prefers to

breed around scrub edges (Warren 1994). In Germany, optimal oviposition conditions were found to be present in recently abandoned calcareous fen meadows and at the edges of such meadows currently in use (Anthes et al. 2003). The edge of these habitats can be regarded as a refuge for the larger host plants and thus for egg clusters and pre-hibernating larvae.

Habitat diversity, habitat quality, and population persistence

Our results show that prior to diapause, habitat suitability is better in CTH than in MTH. However, MTH is primarily utilized by post-hibernating larvae and as such may be an important habitat component even though heavy sheep grazing destroys most of the larger host plants, rendering it unsuitable for the pre-hibernation stages. Short turf provides the warm microhabitat necessary for larval development in the spring (Porter 1982); however, the density of host plants is higher in MTH than CTH, and most of the posthibernating larvae are found in the former (Table 5). Furthermore, grazing promotes short turf and maintains the level of soil disturbance suitable for germination of the host plants in early spring (see Konvicka et al. 2003). We conclude that both CTH and MTH are necessary complementary components of a suitable habitat patch.

Habitat diversity is crucial to the persistence of many butterflies (Thomas and Hanski 1997). However, the factors leading to habitat heterogeneity have been shown to vary. Slope (Murphy and Weiss 1988; Murphy et al. 1990), shade (Sparks et al. 1994; Grundel et al. 1998; Lane and Andow 2003), and type of vegetation (Thomas 1994) have all been shown to contribute significantly to habitat heterogeneity. In our study, the habitat heterogeneity created by patchy land use due to traditional agricultural practices appears to improve habitat quality within the cultivated patches.

This heterogeneity in time and space has significant effects on the metapopulation dynamics of the butterfly (Table 1). Most of the cultivated patches were occupied. In contrast, few uncultivated patches were occupied, and extinction occurred more frequently there. This difference was especially prominent in 2002 when larval groups were only found in the cultivated patches. In uncultivated patches with heavy grazing, the shortage of large host plants may result in fewer locations for females to oviposit and insufficient food for pre-hibernating larvae.

The maintenance of habitat diversity within the patch scale has been shown to be important for the long-term persistence of local populations in the Czech Republic (Konvicka et al. 2003). On a regional scale, one successful conservation strategy has been to include management programs that varied according to the type of habitat (Anthes et al. 2003).

Management and conservation

In this study, *E. aurinia* exists in a patch network where both farming and animal husbandry occurs regularly in some patches. This mixed land use provided a setting that is different from those described in previous metapopulation studies on *E. aurinia* in Europe (Warren 1994; Lewis and Hurford 1997; Wahlberg et al. 2002) where the habitat patches can be considered to be pure improved grasslands or clear-cuts. The landscape in this study can be regarded as a countryside habitat for the butterfly and as such includes agricultural plots, forest, and different habitat types devoted primarily to human activities (Daily 1997).

Although the farmers have conserved the habitat unintentionally rather than deliberately, the maintenance of habitat diversity through a small-scale mosaic of diverse traditional management programs may offer insights into successful habitat management. CTH is regarded as a refuge for the large host plants, egg clusters, and pre-hibernating larvae. At this stage in our management program, it is very important to maintain suitable areas containing high-quality S. tschiliensis in order to preserve E. aurinia. The occupied grass strips in the MTH should be lightly mowed once a year at the beginning of adult flight because this will expose rather than destroy the rosettes of the host plant. Ploughing the crop edge in late autumn and early spring should be maintained as it disturbs the soil at such sites, thereby facilitating the germination of host plants. Heavy sheep grazing is harmful to the butterfly's conservation. A reduction in sheep grazing or a shift from sheep grazing to cattle grazing is necessary to restore this butterfly's breeding habitat in MTH. The post-hibernating larvae primarily utilize MTH. Thus, moderate grazing intensity should be maintained to produce a suitable habitat for posthibernation larval development.

The spatial arrangement of CTH and MTH within the patch, which may influence the viability of the local population, requires further study. For example, the positioning of CTH closely adjoining MTH is of particular importance and should be maximized.

Patchy land use typical of traditional agriculture was once a very widely accepted practice, but it has been lost in many parts of Europe (Robinson and Sutherland 2002). The resulting reduction in habitat diversity as a result of intensified agriculture is one of the main threats to biodiversity, including that of butterflies, in developed countries (Robinson and Sutherland 2002; Benton et al. 2003; Thomas and Hanski 2004). Consequently, the creation of habitat diversity by various human activities in the human-dominated landscape is very important to the concept of biodiversity conservation (Daily 2001; Horner-Devine et al. 2003). Meadows in mountain areas in developing countries are often of a mixed character, with cropping and animal husbandry coexisting in close proximity. Traditional mosaic land use, which is still practiced in these areas, has functioned to enhance habitat diversity. How to maintain this habitat diversity for biodiversity conservation is an important issue given the increasing intensity of modern agriculture practices.

Acknowledgments We are grateful for helpful corrections and comments on the manuscript from I. Hanski and M. R. Shaw. We also thank Guofa Zhou, Weiping Zeng and P. Gongal for helpful comments and language corrections. This research is supported by the National Natural Science Foundation of China (Grant No. 30270241).

References

- Anthes N, Fartmann T, Hermann G, Kaule G (2003) Combining larval habitat quality and metapopulation structure – the key for successful management of pre-alpine *Euphydryas aurinia* colonies. J Insect Conserv 7:175–185
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182–188
- Bourn NAD, Thomas JA (1993) The ecology and conservation of the brown argus butterfly *Aricia agestis* in Britain. Biol Conserv 63:67–74
- Daily GC (1997) Countryside biogeography and the pro-vision of ecosystem services. In: Raven P (eds) Nature and human society: the quest for a sustainable world. National Research Council National Academy Press, Washington, D.C., pp. 104–113
- Daily GC (2001) Ecological forecasts. Nature 411:245
- Dover JW (1991) The conservation of insects on arable farmland. In: Collins NM, Thomas JA (eds) The conservation of insects and their habitat 980. Academic Press, London, pp 293–318
- Ehrilch PR, Hanski I (2004) On the wings of checkerspots, a model system for population biology. Oxford University Press, New York
- Grundel R, Pavlovic NB, Sulzman CL (1998) The effect of canopy cover and seasonal change on host plant quality for the endangered Karner Blue butterfly (*Lycaeides Melissa* samuelis). Oecologia 114:243–250
- Hanski I, Gaggiotti OE (2004) Ecology, genetics, and evolution of metapopulations. Elsevier, San Diego
- Horner-Devine CM, Daily GC, Ehrlich PR, Boggs CL (2003) Countryside biogeography of tropical butterflies. Conserv Biol 17:168–177
- Hosmer DW, Lemeshow S (1989) Applied logistic regression. John Wiley and Sons, New York

- Konvicka M, Hula V, Fric Z (2003) Habitat of pre-hibernating larvae of the endangered butterfly *Euphydryas aurinia* (Lepidoptera: Nymphalidae): what can be learned from vegetation composition and architecture? Eur J Entomol 100:313–322
- Lane CP, Andow DA (2003) Oak Savanna subhabitat variation and population biology of *Lycaedes melissa sammuelis* (Lepidoptera: Lycaenidae). Ann Entomol Soc Am 96:799– 809
- Lewis OT, Hurford C (1997) Assessing the status of marsh fritillary (*Eurodryas aurinia*): an example from Glamorgan, UK. J Insect Conserv 1:159–166
- Moore SD (1989) Patterns of juvenile mortality within an oligophagous insect population. Ecology 70:1726–1737
- Munguira ML, Martin J, Barros EG, Jose LV (1997) Use of space and resources in a Mediterranean population of the butterfly *Euphydryas aurinia*. Acta Oecol 18:597–612
- Murphy DD, Weiss SB (1988) Ecological studies and the conservation of the bay checkerspot butterfly, *Euphydras editha bayenis*. Biol Conserv 46:183–200
- Murphy DD, Freas KE, Weiss SB (1990) An environment metapopulation approach to population viability analysis for a threatened invertebrate. Conserv Biol 4:41–51
- Porter K (1982) Basking behavior in larvae of the butterfly *Euphydryas aurinia*. Oikos 38:308–312
- Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. J Appl Ecol 39:157–176
- Smallidge PJ, Leopold DJ (1997) Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated landscapes. Landscape Urban Plan 38:259–280
- Sparks TH, Porter K, Greatorex-Davies JN, Hall ML, Marrs RH (1994) The choice of oviposition sites in woodland by the Duke of Burgundy butterfly *Hamaeris lucina* in England. Biol Conserv 70:257–264
- Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92
- Thomas CD (1994) The ecology and conservation of butterfly metapopulations in the fragmented British landscape. In: Pullin AS (eds) Ecology and conservation of butterflies. Chapman and Hall, London, pp 46–63
- Thomas CD, Hanski I (1997) Butterfly metapopulations. In: Hanski I, Gilpin ME (eds) Metapopulation biology: ecology genetics, and evolution. Academic Press, San Diego, pp 359–386
- Thomas CD, Hanski I (2004) Metapopulation dynamics in changing environments: butterfly responses to habitat and climate change. In: Hanski I, Gaggiotti O (eds) Ecology, genetics, and evolution of metapopulations. Academic Press, London, pp 489–514
- Thomas JA, Bourn NAD, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc Roy Soc Lond Ser B Biol Sci 268:1792–1796
- van Swaay C, Warren M (1999) Red Data Book of European Butterflies (Rhopalocera). Nature and Environment, No. 99, Council of Europe, Strasbourg, France
- Wahlberg N, Kullberg J, Hanski I (2001) Nature history of some Siberian melitaeine butterfly species (Nymphalidae: Melitaeini) and their parasitoids. Entomol Finn 12:72–77

- Wahlberg N, Klemetti T, Hanski I (2002) Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography 25:224–232
- Wang RJ, Wang YF, Lei GC, Xu RM, Painter J (2003) Genetic differentiation within metapopulations of *Euphydryas auri*nia and Melitaea phoebe in China. Biochem Genet 41:107–118
- Wang YF (2004) Difference in metapopulation structure and dynamics of two species of coexistent melitaeine butterflies. PhD thesis, Beijing Normal University, China
- Wang YF, Chen JJ, Wang RJ, Lei GC, Xu RM (2003) Difference in metapopulation structure and dynamics of two species of coexistent melitaeine butterflies. Chin Sci Bull 48:1239–1246
- Warren MS (1994) The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary *Euroydryas aurinia*. Biol Conserv 67:239–249