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Habitat use of the endangered butterfly *Euphydryas maturna* and forestry in Central Europe

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Abstract

The knowledge of ecological requirements of declining butterflies of European woodlands remains limited, which hinders conservation management of their localities. This also applies for continentally threatened scarce fritillary *Euphydryas maturna*. On the basis of the largest data set on its habitat use ever collected in Central Europe, we analyse habitat requirements of its populations in Austria (A), the Czech Republic (Cz) and Germany (D). All studied populations inhabit open-canopy sites within woodlands, but larval survival decreases under full sun and preferred sites are relatively humid and sheltered. Nests of pre-hibernation larvae occur at terminal branches of *Fraxinus excelsior*, 1.5–3 m above the ground. Pre-hibernation mortality reaches 70% (Cz, D). Another limiting factor is quality of woodland vegetation: post-hibernation larvae consume a wide range of herbs and shrubs, and adult distribution is linked to nectar availability. The butterfly thus depends on highly heterogeneous early successional stages of deciduous woods, historically maintained by coppicing (Cz, D) and forest pasture (A). Restoration of these traditional methods offers the only chance for survival of *E. maturna* in Central Europe, and the butterfly may become a flagship for other threatened organisms of open-canopy woodlands.

Introduction

Twelve per cent of European butterfly species are threatened on a continental scale (van Swaay & Warren, 1999). As many declining species have been associated with biotopes maintained for centuries via traditional land husbandry (Maes & Van Dyck, 2001; van Swaay, 2002), efficient conservation is unthinkable without understanding the historical land-use patterns. This is increasingly understood for grassland butterflies (e.g. Thomas, 1980; Dolek & Geyer, 1997, 2002; Balmer & Erhardt, 2000), but less so for species of other biotopes such as woodlands. This is of concern, because many woodland butterflies have declined dramatically, leading to the inclusion of five of them to annexes of the EU Habitats' Directive (van Helsdingen, Willemse & Speight, 1996). It has only recently been acknowledged that many woodland species depend on a continual supply of open-canopy structures, historically maintained by such practices as coppicing or forest pasture (Warren & Key, 1991; Sparks *et al*., 1994; Konvicka & Kuras, 1999; Bergman & Kindvall, 2004). The situation is complicated by economic considerations, because forestry practitioners view these forms of woodland management as wasteful.

All these complications affect the prospects of the scarce fritillary *Euphydryas maturna* (Linnaeus, 1758), one of the most critically threatened European butterflies (Kudrna, 2002). This inhabitant of sparse deciduous woodlands has become restricted to a handful of widely isolated populations in Central Europe. In contrast to ecologically distinct populations in Fennoscandia (Eliasson, 1991, 2001; Wahlberg, 1998, 2001*a*; Wahlberg *et al*., 2002), there is only vague information on their ecology, which hinders efficient conservation.

This study analyses habitat use by pre-adult stages, and, to a lesser extent, adult butterflies, in Austria (A), the Czech Republic (Cz) and Germany (D). Specifically, we describe the distribution of immature stages within woodlands with respect to woodland management, compare the size of egg batches and survival of immature stages, and analyse the distribution of larvae relative to that of adult butterflies. Data collecting was launched independently in the three countries and used slightly different methods, but the collated information represents the largest existing data set on habitat use of *E. maturna*, and the emerging patterns are directly transferable to management recommendations.

Methods

The butterfly

Euphydryas maturna (Lepidoptera: Nymphalidae, Melitaeinae) is distributed from France across Central and Eastern Europe to Siberia and Mongolia. It has always been described as local in Europe (Vogler, 1980; Essayan, 1999), but has declined dramatically during the past few decades. It is now extinct in three countries and critically endangered in five (van Swaay & Warren, 1999; Fig. 1). In Central Europe, adult flight lasts from late May until early July. The females lay eggs in batches on leaves of *Fraxinus excelsior*, or rarely *Ligustrum vulgare*. Elsewhere in Europe, other plant species may be used (Wahlberg, 1998). Young larvae feed communally in silk-woven nests, stop feeding in late summer and diapause in the leaf litter until early spring. A wide range of plants is reported as being used by solitary spring larvae, the range varies among locations, and some records may refer to captive rearing (cf. Weidlich & Schiller, 1987; Weidemann, 1988; Tolman & Lewington, 1998; Wahlberg, 2000).

Study sites

The study was carried out at seven sites in three countries between 1998 and 2004 (Tables 1 and 2). Plant nomenclature follows that of Rothmaler (1976).

Figure 1 Distribution of *Euphydryas maturna* in Central Europe. Based on Vogler (1980), Ebert & Rennwald (1991), Huemer & Tarmann (1993), Essayan (1999), Höttinger & Pennerstorfer (1999), van Swaay & Warren (1999), Lafranchis (2000), Bayer LfU (2001), Schmidt (2001), Gallo & Gianti (2003), Reinhardt (2003) and data by the authors.

In A two sites in the calcareous Alps of Salzburg (altitude 460–700 m) were used. Both sites are wet woodlands with *Alnus glutinosa* and *F. excelsior*, situated within a forested region dominated by beech and spruce forests. The wet woodlands were formerly used for forest pasture and litter collecting, and contain numerous litter meadows with spontaneous growth of *F. excelsior*. Multiple scattered clearings (0.25–1.5 ha) provide re-growth areas where *F. excelsior* usually occurs abundantly. Forest patches are cut at irregular intervals of *c.* 100 years.

In Cz two closely adjoining (2.5 km apart) insular humid deciduous woods in an intensively farmed lowland (altitude 230 m) were used. The tree layer consists of *Quercus* spp., *F. excelsior* and *Carpinus betulus*. Both woods were coppiced until 80 years ago; they are now managed as high forests with a rotation of 100–120 years. The harvested plots do not exceed 1 ha; they are afforested either by oak or by conifers. Natural regeneration of diverse assemblages of trees and shrubs, including *F. excelsior*, occurs.

In D three sites (altitude 390 m), all in the region ‘Vorderer Steigerwald’, Bavaria, were used. The region consists of a mosaic of arable land and deciduous woodlands, where the historical forest management of coppicing with standards is still practised locally. Under the management, most trees are cut in a rotation of 35 years to produce firewood, whereas a few standards are allowed to reach maturity and are harvested for timber. The management creates a sparse canopy layer and a dense and species-rich understory. *Fraxinus excelsior* grows abundantly in moister parts of these managed woods.

Larval requirements

We searched intensively for communal nests, locating all nests using a global positioning system (GPS) and/or detailed forest maps. For each nest, we recorded (1) position within the wood, that is ‘light forest stand’, ‘clearing’, ‘dark forest stand’, ‘along pathway/road’, ‘inner edge’ (= between a clearing and a high forest) and ‘outer edge’, (2) position above the ground, (3) height of the nest-bearing tree and (4) topographic aspect (Table 2: 1–4). To quantify aggregation of the nests, we used the standardized Morisita index of dispersion (SMID) separately for sites and years (Krebs, 1989; Table 2: 5). To do so, we overlaid a grid of 100 × 100 m onto forest maps and considered every grid cell within a line connecting the outermost nests [n(D1) = 139, n(D2) = 19, n(D3) = 24, n(A1) = 266, n(A2) = 156, n(Cz1) = 90]. In Cz and D, data on canopy cover and age of stands were extracted from forest management plans (Table 2: 6). At Cz1, we used the composition of vegetation to compare abiotic conditions of occupied versus unoccupied clearings (Table 2: 7), using Ellenberg’s plant indicator values (Ellenberg *et al.*, 1991). The values describe, on ordinal scales, habitat requirements of most of the higher plants of the Central European flora (e.g. Schönhaar, 1952; Oostermeijer & van Swaay, 1998). A botanist spent 40 min at each clearing, recording all the higher plants present. We then calculated the unweighted indicator values for light,

Table 1 Study sites of *Euphydryas maturna* in Austria, the Czech Republic and Germany, with study years, number of larval nests and extent of inhabited area

Country	Site	Studied in	Number of nests	Mean per year	Min./max.	Inhabited area (ha)
Austria	A1	1998–1999	123	61.5	59/64	200
	A2	1999	88	–	–	110
Czech Republic	Cz1	2002–2003	152	76	31/121	114
	Cz2	2003	18	–	–	2
Germany	D1	2000–2003	284	71	13/197	100
	D2	2001–2003	36	12	3/30	19
	D3	2002–2003	23	11.5	2/21	5

Table 2 Overview of data available for analysing habitat requirements of *Euphydryas maturna* in Austria (A), the Czech Republic (Cz) and Germany (D)

			1	2	3	4	5	6	7	8	9	10	11	12	13
Country	Site	Year	Habitat type	Height of nest	Height of used ash tree	Exposition of nest	Dispersion of nests	Tree cover percentage	Vegetation characteristics of forest openings	Food-plants of spring larvae	Eggs per batch	Egg-batch position on leaf	Mortality of young larvae	Insolation of nests	Mark–recapture survey
A	1	1998	X	X	X	X	X								
A	1	1999	X	X	X	X	X			X	X				
A	2	1999	X	X	X	X	X			X	X				
Cz	1	2002	X	X	X	X	X	X	X						X
Cz	1	2003	X	X	X	X	X		X		X	X	X		X
Cz	1	2004								X					
Cz	2	2002	X	X	X	X		X							
Cz	2	2003	X	X	X	X									
Cz	2	2004								X					
D	1	2000	X	X	X	X	X				X	X	X		
D	1	2001	X	X	X	X		X			X	X	X		
D	1	2002	X	X	X	X	X				X	X		X	
D	1	2003	X	X	X	X	X				X	X	X		
D	1	2004								X					
D	2	2001	X	X	X	X									
D	2	2002	X	X	X	X		X				X		X	
D	2	2003	X	X	X	X	X				X	X			
D	3	2002	X	X	X	X		X				X		X	
D	3	2003	X	X	X	X	X				X	X			

Year, year of investigation; recorded parameters 1–13, see Methods for explanations.

temperature, moisture, pH and nitrogen for all recorded plants and compared each using Mann–Whitney *U*-tests.

The use of host plants by solitary spring larvae was assessed by searching for actively feeding larvae during April and May (Table 2: 8).

Reproduction and mortality

For detected egg batches, we recorded the number of eggs per batch and the position of egg cluster on ash leaves (Table 2: 9, 10). Randomly selected batches were visited at intervals of 2–4 days to assess the mortality of autumn larvae by counting the larvae surviving until the second instar (Table 2: 11); later on, it becomes impossible to distinguish mortality from emigration.

Microclimatic parameters affecting mortality were investigated for 20 nests at D1 (Table 2: 12). The potential duration of sunshine and half-shadow was measured by a horizontoscope. This instrument reflects the horizon (with trees, hills, etc.) and allows estimates of the time of day and year when the sun reaches the locality of measurement. For every 15-min interval, we distinguished whether a nest was sunlit or shaded completely or partly. Additionally, inlays of the horizontoscope give details of insolation energy that a normal area receives at any time of a day. The insolation energy at a nest site was calculated using time and duration of sunshine: nothing was added during a time of shading and half of the given value was added during a time with half-shadow. To estimate the development success of the thus studied nests, we recorded nest sizes after the larvae left for hibernation in autumn, assuming that the less the caterpillars that die, the more the leaves consumed and the larger the nest becomes. We distinguished tiny (leaflets of one leaf), small (one to five leaves), medium (five to 10 leaves) and large ($>$10 leaves) nests.

Larval versus adult distribution

To compare habitat conditions suitable for larvae and adults, we used data from an intensive mark–recapture survey at Cz1 (Konvicka *et al.*, 2005; Table 2: 13). During the survey, we repeatedly visited all forest openings (69 in total), trying to mark all observed butterflies and counting all butterflies that escaped capture. Each opening was characterized by area; biotope (road/glade, clearing, edge); nectar (ordinal scale from 0, none, to 5, rich); cover of *F. excelsior* in 3 m height bands; covers of canopy, shrub and herb layer; exposition to wind on a scale from 1, wind protected, to 3, windy; percentage of high forest; percentage of clearings; and percentage of open vegetation per perimeter. We then regressed (1) total numbers of adults seen at each opening during the mark–recapture study weighted by the number of visits to the respective opening, (2) number of larval webs found in 2002 and (3) in 2003, against the above variables. We used generalized linear models with Poisson's distribution of dependent variables (S-Plus 2000, 1999) and, following single-term regressions, constructed multiple regression models via a (manual) forward stepwise procedure.

Results

Larval nests and forest structure

A majority of the nests was situated at open-canopy sites (Fig. 2), but the pattern differed among the countries [frequency table: $\chi^2_{12} = 603.95$, $n(\mathrm{A}) = 211$, $n(\mathrm{Cz}) = 172$, $n(\mathrm{D}) = 344$, $P<0.001$]. In D, a vast majority of nests was situated within light forest stands maintained by coppicing, 93% ($n = 344$) being situated in stands with canopy cover $<$30%. Stand age since the last cut ranged from 7 to 27. Additionally, all nests occurred in stands with relatively sparse coppice re-growth ($<$75%). In A and Cz, the prevailing biotopes were clearings created by timber harvest. However, the clearings were not preferred, as nests situated near pathways and at inner forest edges were nearly as frequent as those situated at clearings. The differences are attributable to differences in forest management and therefore vegetation structure. In D, the proportion of light forest stands was about seven times higher ($26 \pm 13.9\%$) than in Cz ($4 \pm 0.3\%$) and the proportion of clearings in Cz was quite small ($10 \pm 1.6\%$). Despite the differences, the nests exhibited aggregated distribution for all sites/years with $>$20 nests (SMID: 0.51–0.59, $P<0.001$ for all χ^2 tests).

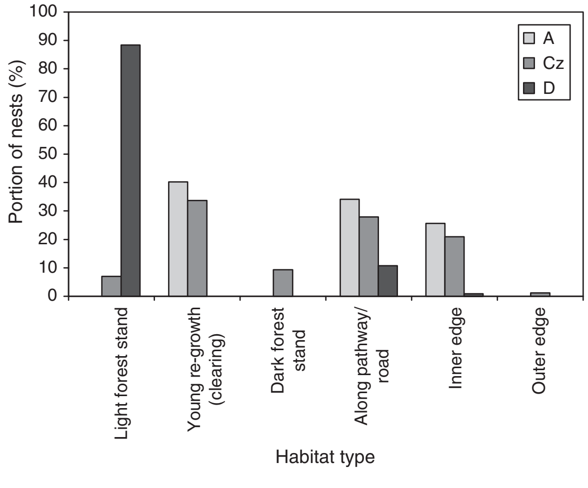

Figure 2 Comparison of habitat types used by larvae of *Euphydryas maturna* in Austria, the Czech Republic and Germany.

At Cz1, openings containing ($n = 12$) and not containing ($n = 41$) nests did not differ in cover of *F. excelsior* (Mann–Whitney $U = 168.5$, $Z = -1.65$, $P = 0.10$) or cover of *F. excelsior* in shrub layer ($U = 236.5$, $Z = 0.20$, $P = 0.84$). They also did not differ in Ellenberg's values for light, temperature, pH and nitrogen (all $P>0.1$), but the openings with nests attained higher values for moisture ($U = 121.0$, $Z = -2.66$, $P<0.01$).

Egg laying and distribution of autumn larvae

A majority of egg batches was located near the tips of ash leaves. The three terminal leaflets were used three times more frequently than all leaflets closer to the leaf base (Cz: $\chi^2_4 = 8.0$, $n = 17$, $P = 0.09$; D: $\chi^2_4 = 126.4$, $n = 208$, $P = <0.001$) and the pattern did not differ between D and Cz ($\chi^2_4 = 7.4$, $P = 0.12$).

The aspects of larval nests always differed from an equal distribution (A: $\chi^2_7 = 461.7$, $n = 211$, $P<0.001$; Cz: $\chi^2_7 = 51.2$, $n = 165$, $P<0.001$; D: $\chi^2_4 = 263.3$, $n = 317$, $P<0.001$). Availability of aspects was assumed to be equal as all trees can be reached from all sides. Prevailing (60–90%) aspects were those towards the south-east, south and south-west, whereas only one third or less of the nests were exposed to the west, east or north. Northern exposition was particularly rare (A: 0.0%; Cz: 3.6%; D: 2.8%). The orientation differed among countries ($\chi^2_{14} = 117.6$, $n = 693$, $P<0.001$): south and south-east orientation were more frequent in A, and west orientation prevailed in Cz. Within countries, sites did not differ in D ($\chi^2_{14} = 16.6$, $n = 316$, $P = 0.28$) and Cz ($\chi^2_7 = 6.5$, $n = 165$, $P = 0.48$), but the two sites in A differed ($\chi^2_5 = 23.4$, $n = 211$, $P<0.001$) because of a surplus of south-east orientation at A2.

The vertical positions of the nests ranged from 0.5 m (Cz) to 15 m (A), but the majority was located between 1.5 and 3.0 m (second + third quartile of the total data), the positions at A1 being higher than elsewhere (Fig. 3). The height of nest-bearing trees differed among the sites; the tallest trees were used at A1 and Cz1 and the shortest trees at A2 and D2 sites (Fig. 3). Despite this variation, the nests were situated at similar heights above ground in both D and Cz and there was no correlation between average heights of trees and average vertical positions of nest per site (Spearman rank: $k = 0.11$, $n = 7$, $P = 0.41$).

Host plants of spring larvae

The most complete data originated from A, for both April ($n = 83$) and May ($n = 75$), that is before and after the foliation of ash trees. The most frequently used early spring host was *Plantago lanceolata*, followed by *Valeriana dioica* and *L. vulgare*, and all larvae switched to *F. excelsior* in May (Fig. 4). In Cz, 15 larvae were located in early May, shortly before ash leaves began unfolding. One was on *L. vulgare*, two restlessly crawled on the ground obviously searching for food, and the rest basked on bare ash branches. Moreover, several *Ligustrum* shrubs showed signs of recent larval feeding and identical signs were found on 12 plants of *Pulmonaria officinalis*. In D, we located only two caterpillars in April. One fed on *Viburnum opulus*, and one, observed for 3 h, searched for food without success on an ash tree (buds still completely closed) and on the ground, testing all available herbs. Later in spring, when the ash leaves flushed, caterpillars fed exclusively on *F. excelsior* ($n = 21$).

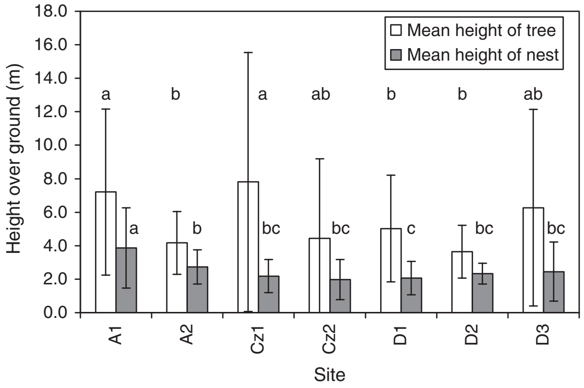

Figure 3 Vertical positions of larval nests of *Euphydryas maturna*, and heights of nest-bearing ash trees. Means and standard deviations are shown. Different letters indicate significant differences [Kruskal–Wallis ANOVA, nests: $H_{(6\ \mathrm{d.f.})}=127.8$, $n=724$, $P=<0.001$; trees: $H_{(6\ \mathrm{d.f.})}=46.1$, $n=722$, $P=<0.001$; both tests followed by HSD *post hoc* test for unequal *n*].

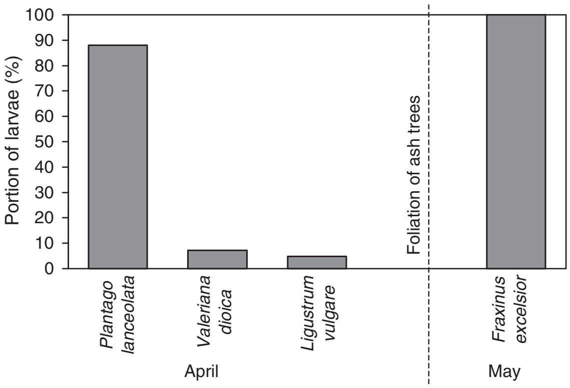

Figure 4 Use of food plants by spring larvae of *Euphydryas maturna* before and after the foliation of *Fraxinus excelsior* in Austria [n(April) = 83; n(May) = 75].

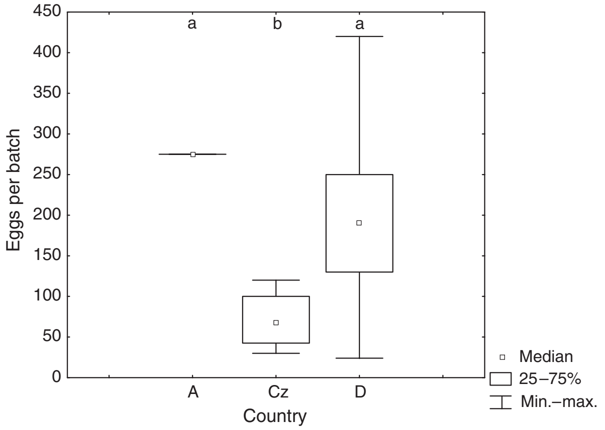

Figure 5 Comparison of numbers of *Euphydryas maturna* eggs per egg batch in Austria, the Czech Republic and Germany. Different letters indicate significant differences [Kruskal–Wallis ANOVA: $H_{(2\ \mathrm{d.f.})}=46.1$, $n(\mathrm{A})=4$, $n(\mathrm{Cz})=16$, $n(\mathrm{D})=130$, $P=<0.001$; followed by HSD *post hoc* test for unequal *n*].

Reproduction and mortality

Egg batches in Cz were significantly smaller than in A or D (Fig. 5: the few counts from A still confirm the ability of females to lay large batches). The largest batch in Cz (120 eggs) was smaller than the mean in size in D (191 eggs). The combined mortality of eggs and autumn larvae was close to 70% in both Cz [$69 \pm 32.0\%$, $n(2003) = 29$] and D [$74 \pm 18.4\%$, $n(2000+2003) = 70$]. No difference was found between years in D (Kruskal–Wallis ANOVA: $H_2 = 1.59$, $P = 0.45$) and between countries (Mann–Whitney $U = 1000$, $Z = -0.11$, $P = 0.91$). Larval survival was negatively correlated with all indices of solar energy for the 20 nests studied using the horizontoscope (Table 3), revealing that increasing duration of sunshine led to smaller nests.

Comparing imaginal and larval distribution

At the Cz1 site, the numbers of adults observed at individual clearings were positively associated with nectar availability, cover of *F. excelsior*, covers of shrub and herb layer, and the percentage of clearings per site perimeter. Negative predictors included openness and the percentage of open land per perimeter (Table 4). Rich nectar and dense cover of *F. excelsior* saplings were positively associated with high numbers of larval nests in both 2002 and 2003; a negative predictor was openness. The multiple regressions (Table 5) corroborated the importance of windproof position, rich nectar (adults and nests 2002 models) and high cover of *F. excelsior* saplings (adults and nests 2003 models).

Discussion

Habitat requirements

Euphydryas maturna exhibits a highly exacting biotope requirement. Pre-hibernation larvae develop on *F. excelsior* growing in open canopy, but sheltered and humid conditions, 1.5–3 m above the ground. This was already noted by earlier authors (e.g. Kühnert, 1967; Weidemann, 1985, 1988; Settele, Feldmann & Reinhardt, 1999) and our results support these observations by quantitative data.

The underlying causes of the requirements seem to be microclimatic. Open canopy ensures that pre-diapause larvae receive enough solar radiation (cf. Porter, 1984; Weiss, Murphy & White, 1988; Osborne & Redak, 2000). However, too much solar energy decreases larval survival, suggesting an upper limit of suitable insolation. Microclimatic requirements also explain the variation of nest placement among the populations, such as the relatively high vertical positions of nests in A, where the pre-alpine slopes receive high rainfall (1500 mm year^{-1}), or the frequent western orientation in Cz, where foresters prefer east–west orientation of clearings to provide maximum light for young trees.

Table 3 Duration of sunshine and amount of solar energy received per day by nests of *Euphydryas maturna*, and correlation with final nest size

	Sunshine per day (min)	Sunshine and half-shadow per day (min)	Solar energy per day (W m^{-2})
Mean	360.0	513.2	229.8
SD	96.7	121.0	84.5
Minimum	225	330	98.2
Maximum	570	720	373.1
Spearman rank correlation with nest size	$k=-0.36$ $P=0.07$	$k=-0.52$ $P<0.05$	$k=-0.64$ $P<0.01$

All correlations are based on 20 nests; the theoretical maximum duration of sunshine is 925 min per day in July; the maximum solar energy on a normal area is *c.* 520 W m^{-2}.

Another limiting factor may be the floristic composition of the herb layer. Spring larvae depend on non-ash hosts, and the range seems to depend on the composition of local plant communities. For instance, *P. lanceolata*, the most frequent spring host in A, is rare at both Czech and German sites. Still, there was a pattern in the use of non-ash plants. They either (1) were taxonomically close to *F. excelsior* (i.e. *Ligustrum*) or (2) shared with *Fraxinus* the content of iridoid glycosides (*Plantago*, *Pulmonaria*). Host choice in Melitaeinae is driven by plant chemistry (Wahlberg, 2001*b*), but it remains unknown whether individual populations of *E. maturna* prefer specific non-ash hosts, or whether they feed on whatever plant is available, provided that it contains the right chemicals. Interestingly, the females do not seem to discriminate egg-laying sites according to floristic composition at the ground. In Cz, some nests were located on ashes within stands of exotic *Quercus rubra*, which were completely devoid of herb and shrub layers. The requirements of adults, particularly that for high nectar supply, further narrows the extent of sites with suitable conditions.

The aggregated distribution of larval nests was expected in A and Cz, where the butterfly dwells on clearings, but unexpected in the coppiced woods in D. It suggests that coppicing does not provide equal conditions across entire forests. It ensures the basic requirement of open canopy, but even coppiced woods contain places with too dense and/or too high understorey, or areas without *F. excelsior*.

The highly exacting requirements for larval development explain why the butterfly never occupies solitary *F. excelsior* trees outside of woodlands. Our results indicate that large, even-aged clearings typical for high forests, exposed to

Table 4 Single-term regressions of numbers of adults and larval nests of *Euphydryas maturna* recorded at individual openings at the Cz1 site during a mark–recapture study in 2002 (adults) and during searches for larval nests

	Adults 2002				Nests 2002				Nests 2003			
	dir.	d.f.	AIC	*P*	dir.	d.f.	AIC	*P*	dir.	d.f.	AIC	*P*
Null model		69	1112.3			69	137.1			69	443.5	
Visit	+	1, 68	551.8	***								
Area	+	2, 67	511.3	*		1, 68	131.7	NS		1, 68	456.4	NS
Biotope		3, 66	557.8	NS	[a]	2, 67	121.2	*		2, 67	464.0	NS
Nectar	+	2, 67	326.4	***	+	1, 68	104.5	***	+	1, 68	290.1	***
Cover of *Fraxinus*	+	2, 67	515.0	***	+	1, 68	118.1	**	+	1, 68	399.3	**
Cover of canopy		2, 67	574.4	NS		1, 68	146.6	NS		1, 68	464.0	NS
Cover of shrubs	+	2, 67	524.1	*		1, 68	142.9	NS		1, 68	447.7	NS
Cover of herbs	+	2, 67	498.8	*	+	1, 68	133.2	NS	+	1, 68	372.4	***
Openness	–	2, 67	409.4	***	–	1, 68	104.2	***	–	1, 68	397.7	**
Open per perimeter	–	2, 67	519.9	*	–	1, 68	111.3	**	–	1, 68	402.4	*
Forest per perimeter		2, 67	575.0	NS	+	1, 68	108.4	***		1, 68	455.8	NS
Clearing per perimeter	+	2, 67	517.6	*		1, 68	145.8	NS		1, 68	436.7	NS

[a] Clearing > road/glade > edge.

Percentage variables (i.e. covers and perimeters) were arcsine transformed before the analysis. See Methods for a description of variables.

dir., direction of the relationship; AIC, Akaike information criterion weighting explained variance against model complexity; *P*, significance of *F*-comparison against model containing covariate visit (for adults), and against null models (for larvae).

*$P<0.05$; **$P<0.01$; ***$P<0.001$.

Table 5 Multiple regression models of numbers of adults and larval nests of *Euphydryas maturna* recorded at individual openings at the Cz1 site during a mark–recapture study in 2002 (adults) and during searches for larval nests

Model		d.f.	AIC	*P*	% variance
Adults	+ visits + cover of *Fraxinus* – openness – forest perimeter + nectar	5, 64	197.6	***	69.1
Nests 2000	+ cover of *Fraxinus* – openness	2, 67	51.9	***	67.2
Nests 2003	+ nectar – openness + cover of herbs	3, 66	290.1	***	47.9

Percentage variables (i.e. covers and perimeters) were arcsine transformed before the analysis. See Methods for description of variables.

P, significance of *F*-tests computed against respective null models; % variance, variance explained by fitted model; AIC, Akaike information criterion.

***$P<0.001$.

winds and lacking enough humidity, are less suitable than the fine-grained mosaics typical for coppicing.

Viability of the populations

All populations of *E. maturna* in Central Europe are small. The mark–recapture study at the Cz1 site, 2002, estimated <200 adults (Konvicka *et al.*, 2005) corresponding to 31 larval nests in the same year (Table 1). A comparison with nest counts from other populations documents that none is large enough to be considered safe (cf. Warren, 1987; Hellmann *et al.*, 2003).

Egg batches in Cz were considerably smaller than in A, D, and other regions for which data are available (Wahlberg, 1998; Eliasson, 2001). Small batches could indicate sub-optimal habitat, decreased individual fitness, or both. Females of cluster-laying butterflies should invest in selecting the best possible oviposition sites (Porter, 1992). If such sites are not available, they might lay smaller batches in order to spread the risks associated with sub-optimal conditions. Alternatively, the Czech butterflies may exhibit decreased fecundity, perhaps as a consequence of inbreeding (cf. Saccheri *et al.*, 1998). Smaller batch size could also be related to lower feeding rates of females, perhaps because of poorer climate or nectar scarcity (O'Brien, Boggs & Fogel, 2004) or possibly host use of spring larvae.

The combined mortality of eggs and young larvae was nearly identical both in D and in Cz, and similarly high values apply to a population in Sweden (Eliasson, 2001; Eliasson & Shaw, 2003). In the field it is not possible to assess the mortality of separate larval instars. First-instar larvae build their nests just above the egg batch, and counting of later gregarious stages would intolerably damage entire broods. Regardless, the mortality is high and, as in related species (Ford & Ford, 1930; Ehrlich, 1984; Schtickzelle *et al.*, 2005), it likely contributes to remarkable oscillations in abundance. At the Czech sites, numbers of larval groups varied with coefficient of variation of 0.62 during just 3 years (Konvicka *et al.*, 2005). Such strong fluctuations necessarily diminish genetically effective population size and enhance the risks of stochastic extinctions. We cannot offer advice on how to battle these fluctuations at this time: it is not even known whether they are driven by dynamics of colony sites (e.g. management) or by such factors as cycles of parasitoids or diseases (for mortality risks of *E. maturna*, see Dolek *et al.*, in press). Regardless, any sensible conservation strategy should focus on (1) increasing the abundance of local colonies via purposeful habitat management and (2) establishment of new colonies in the vicinity of existing ones. The latter measure should reduce extinction risks via asynchronous dynamics of individual populations connected by interchange of individuals, and rescues of crashed populations by immigration (Hanski, 1999).

Forestry and conservation

Although all the studied populations of *E. maturna* exhibit similar resource requirements, the available biotopes are subject to dramatically differing forestry practices. Coppicing with standards sustains fine-grained mosaics of sheltered sunny patches, high humidity and rich vegetation. Because of much longer harvest rotation, there are always less open structures in high forests than in coppices (Warren & Key, 1991; Buckley, 1992), rendering *any* high forests effectively 'smaller' for the butterfly compared with a coppice of equal area. Practically all historical localities of *E. maturna* were coppiced several decades ago (cf. Höttinger & Pennerstorfer, 1999; Benes *et al.*, 2002), but the historically widespread technique now occurs in only 1% of German forests (BMELF, 1998) and in less than 0.1% of Czech forests (Ministerstvo zemedelstvi CR, 2000). Although it remains a matter of debate how 'natural' biotopes of *E. maturna* were structured, there is an emerging consensus that disturbances such as fires, large animals, water logging and pest outbreaks would have kept European woods more open throughout most of the Holocene than under recent high forest management (Warren & Key, 1991; Vera, 2000; Bakker *et al.*, 2004; Birks, 2005). Transfers of coppices to high forests, carried out by foresters for most of the 20th century, have brought to the verge of extinction, together with *E. maturna*, numerous other species associated with open-canopy woodlands (e.g. Trautner, 1996; Höttinger & Pennerstorfer, 1999; Konvicka & Kuras, 1999; Liegl & Dolek, in press).

To safeguard *E. maturna* in Central Europe, urgent action is absolutely necessary. Exact measures to maintain the butterfly at its present sites must differ between countries. In A, where the traditional management had been woodland pasture and litter harvest, the high precipitation seems to contribute to suitability of relatively large areas for the butterfly. Immediate measures should include cessation of woodland drainage, maintaining the semi-open state of litter meadows, and ultimately restoring traditional forest pasture. In Cz, where the management is unsuitable and the inhabited area is critically small, it is necessary to restore coppicing with standards at the inhabited sites and in the neighbouring vicinity. German sites, unlike the Czech ones, enjoy more favourable management, but are, unlike the Austrian ones, restricted in extent. Hence, maintaining and expanding the management is a logical first step.

Crude estimates of a minimum area necessary for the butterfly could be derived from the Czech population (Konvicka *et al.*, 2005). Its size fluctuates around a geometric mean of 300 adults per *c.* 10 ha of clearings at present. A permanent supply of 17 ha is necessary to obtain 500 adults a year, and 170 ha to obtain 5000 adults a year (minimum viable populations resilient to demographic and environmental stochasticity, respectively; Reed *et al.*, 2003). Because the area of the inhabited wood is near 100 ha, the entire forest should be managed via coppicing with standards, and an additional *c.* 100 ha should be added in nearby woodlands. At German sites, the woodland area is 320 ha, but the coppice rotation cycle of 35 years provided yearly coppiced areas of 9 ha, leading to 126 ha of stands (assuming 14 years of suitability; M. Dolek *et al.*, unpubl. data) in appropriate age *at any given time*. Very recently (2005), the cycle has been shortened to about 30 years (about 11 ha cut per year), providing 154 ha of suitable stands. Neither this suffices in a long term, however, because the wood is not suitable for *E. maturna* across its entire area.

As a next step, the currently limited distribution will have to be extended via expansion of appropriate management beyond the recently occupied sites, either within dispersal limits of the butterfly (*c.* 10 km from occupied sites; Konvicka *et al.*, 2005) or supplemented by re-introductions. This might be facilitated by the fact that many potentially suitable sites are publicly owned or enjoy legal protection. The development is already well under way in D, where a general procedure for conservation in forests used as coppice with standards, based on indicator species, has been developed (Liegl & Dolek, in press). The programme ['Vertragsnaturschutzprogramm (VNP) Wald'; for an overview of these programmes in D, see Häusler *et al.*, in press] has been in force since 2005 and now allows maintenance and improvement of the management of our German sites via payments to the users. Large adjoining areas are managed as high forest, and suggestions for an improved management are currently being developed. In Cz, there are *c.* 800 ha of potentially suitable woods in a wider vicinity of the current site, and the species action plan for *E. maturna* (currently in review process) proposes managing half of their area for the butterfly. Currently, the major hindrances include unresolved strategy of payments.

Economic aspects will be crucial in efforts to safeguard the species. Although exact situations vary from area to area, managing forests for the butterfly incurs two major costs. The first is increased labour compared with high forests, which is not balanced by fuelwood prices. A standard solution seems to be subsidies, which may not be too prohibitively high. For instance, one estimate of annual loss incurred by the owner of the Czech site was about 10 000 Czech crowns ha^{-1} (or 300 Euro) annually, which is comparable to subsidies paid to farmers managing orchid meadows. Nevertheless, this estimate is much higher than the introduced subsidies on German sites, which are variable and do not reach 100 Euro ha^{-1} annually (see Liegl & Dolek, in press). In D municipalities owning coppiced forests discuss, over many years, the use of wood heating systems (e.g. wood pellets) in communal buildings. This was so far prevented by easily available and cheap energy, but the rising oil and gas prices are shifting the balance. In future, this might decrease the dependency on subsidies.

A more serious problem seems to be opportunity cost associated with transfers of already established high forests back to coppicing (especially important for Cz). Although this may be paid for by selling the harvested timber, the transfer requires that the money is not re-invested into planting new high forest, but consumed by managing the coppices instead. What is worse, the current practice of paying subsidies annually places owners at constant risk of losing their money if governments policy changes or if fuelwood prices drop. A solution might be longer term, perhaps decennial, payments, which might capitalize for the benefit of forest owners. These should be accompanied by supporting investments that would increase the value of coppice products, whether they are heating wood facilities for local communities or machinery for the production of such commodities as wood pellets.

By propelling the restoration of open woodlands, *E. maturna* may become a flagship for a whole range of organisms threatened across Europe because of the current preference of foresters for high forests (compare the general strategy in Bavaria; Liegl & Dolek, in press). A shift of emphasis towards coppicing, forest pasture, and such additional measures as maintenance of wide margins and open rides is absolutely necessary if the forestry profession is to meet its commitment towards biodiversity conservation. As some of the last localities of open-canopy woodlands adjoin political boundaries (see Fig. 1; a few nests of *E. maturna* were found in Germany next to the Austrian sites), the change of emphasis may be propelled by international collaboration, as this study indeed documents.

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