For whom the bells toll: Demography of the last population of the butterfly *Euphydryas maturna* in the Czech Republic

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Abstract: The last surviving population of the scarce fritillary *Euphydryas maturna* (L., 1758) (Lepidoptera, Nymphalidae) in the Czech Republic was studied using mark-recapture methods in 2002 in order to assess adult population structure and mobility, and by annual censuses of larval nests since 2001. The population is restricted to clearings within an isolated lowland deciduous forest situated in a densely populated landscape. Modelling demography using constrained linear models revealed that adult survival was constant in time and lower in males than in females; catchability was equal in sexes and varied in time, while recruitment was constant in sexes and time. Total population size was extremely small, numbering less then 200 individuals. Mobility was well described by a negative exponential function. Less than 5 per cent of individuals are predicted to cross distances of 500 metres, and long distance movements were highly unlikely. We conclude that the butterfly persists as a dynamic metapopulation that tracks early successional woodland clearings. Under recent high-forest management, its long-term survival is highly unlikely and the only chance for preserving it in the long term is the re-establishment of traditional coppicing with standards, which should provide a more continuous supply of the butterfly's biotope.

Key words: Butterfly conservation, dynamic metapopulation, mark-release-recapture, dispersal, woodland management, linear modelling.

Introduction

The scarce fritillary, *Euphydryas maturna* (L., 1758) (Lepidoptera, Nymphalidae, Melitaeinae) in one of the most threatened butterflies in Europe. It has become extinct in two states and has strongly decreased in a further 12; it belongs among the species of European conservation concern (Van Swaay & Warren, 1999) and is protected by the EEC/EU Habitat Directive. Its situation seems to be stable only in Finland, the Baltic states, and parts of the Pannonian basin, whereas the decline in W and NC Europe has become apparent even on the coarse scale of continental distribution maps (Kudrna, 2002).

For two reasons, *E. maturna* remains an enigmatic representative of the otherwise well-studied tribe Melitaeini. First, it varies geographically in such traits as length of development, trophic range and habitat use (Wahlberg, 1998; Eliasson & Shaw, 2003). For in-

stance, some northern populations develop on herbaceous host plants and their life cycle exceeds one year (Wahlberg, 1998; Eliasson, 2001), whereas southern populations utilise woody hosts and develop within one year (Wahlberg, 2001; Eliasson & Shaw, 2003). Second, as nearly all populations in C and W Europe are small and declining, ecologists hesitate to study them in detail due to fear of harming the butterflies and reservations with investing effort into projects that can fail because lack of data. This causes the paradox that while sound ecological knowledge is available for the relatively safe northern populations (e.g., Eliasson, 1991, 2001; Komonen, 1997; Selonen, 1997; Wahlberg et al., 2002b), little is known about the immediately threatened populations in Central and W Europe.

This paper describes the demography of the last extant population of *E. maturna* in the Czech Republic where the butterfly has been recorded in 29 distribu-

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tion map cells during the 20th century (Beneš et al., 2002). In the mid-1990s, intensive surveys confirmed the presence of 3–4 local populations (Vrabec, 1994, 2001). The decline continued, and surveys organised after 2000 revealed that only one population still existed, while no new site had been discovered. The entire Czech distribution thus became limited to one isolated wood. Since the situation is no better in adjoining countries, including Germany, Austria, Poland and Slovakia (e.g., Schiller & Graul, 2000; Höttinger & Pennerstorfer, 1999; Freese et al., in litt.), the butterfly may soon be lost from a large part of C Europe.

Since 2001, the ecology of *E. maturna* has been studied at its last Czech site in order to devise a species conservation plan. Here, we present information on adult demography and mobility, based on a one-year mark-recapture study, and results of four years of monitoring of larval nests. We ask what are the long-term prospects of the population and discuss conservation implications of the demography findings.

Material and methods

Study system
The only Czech site of *E. maturna* is a 100-hectare part of a lowland wood; we are keeping the precise location secret to safeguard it from collectors. The entire wood is over 10 km^2 large, but most of the area grows on acidic sandy substrates, whereas the portion inhabited by the butterfly is situated on base-rich and waterlogged soils. The wood is surrounded by arable lands and isolated from other such woods by > 10 km. It has a natural tree composition with *Quercus* spp., *Fraxinus excelsior* and *Carpinus betulus*, but some 20% of the area are stands of non-native trees (exotic oaks, *Pinus* sp., *Picea abies* and *Larix decidua*). Current management is commercial high-standard forestry with long (ca 120 years) turnover. Thus opened clearings (ca 10 ha in 2002) are subsequently replanted by oak and/or conifers. In addition, they naturally regenerate by diverse assemblages of woody species, including the butterfly's principal host plant *Fraxinus excelsior*, and richly flowering shrubs (e.g., *Ligustrum vulgare*, *Swida sanguinea*, *Viburnum opulus*) used as nectar sources. Both adults and larvae are restricted to these clearings, and to openings along forest roads.

The adult flight of *E. maturna* lasts from early June until late June/early July, depending on weather conditions. Males use perching tactics to attract females, which lay egg batches on underside leaves of sun exposed saplings, or low-hanging branches, of *Fraxinus excelsior* or (extremely rarely) *L. vulgare*. Pre-hibernation larvae feed communally in silk-woven nests, finish feeding in August, abandon the nests and hibernate in herbaceous vegetation. Spring larvae feed on *L. vulgare* and *Pulmonaria* spp. until flush of ash leaves, and then switch to feeding on ash foliage. Pupae, formed in May, are attached to tree trunks near the ground. Details on the ecology of pre-adult stages will be published elsewhere (Freese et al., in litt.).

The mark-recapture survey
Mark-recapture survey of adult butterflies was conducted in 2002, between June 2, when we observed the first individual, until the end of adult flight on June 20. The study was particularly labour intensive: each day (weather permitting), a minimum of three people did the marking, totalling 84 person-days in total. While marking, we walked regular routes that crossed all the clearings, road glades and forest meadows within the area. We marked all netted butterflies with unique numbers, recorded their sex and position of capture, and released them at the point of capture. As positions of capture, we used centroids of individual forest openings.

Survival, recruitment and population size
Adult demography parameters were estimated using constrained linear modelling (CLM), which applies the framework of generalised linear modelling to capture history matrices (Lebreton et al., 1992; Schwarz & Arnason, 1996). The approach was recently introduced to butterfly population studies (e.g., Schtickzelle et al., 2002, 2003; Baguette & Schtickzelle, 2003). Its advantages over more traditional analytical mark-recapture models (e.g., Pollock et al., 1990) include higher flexibility in treating of parameters, and the possibility of formal comparisons among models that differ in complexity using the quasi-likelihood Akaike values (cAICS).

We first employed the Jolly-Seber approach (cf. Williams et al., 2001) that estimates individual survival Φ and catchability p in open populations with births, deaths and migrations. Pradel (1996) modified the original Jolly-Seber approach to estimate the per capita rate of population change f via recursion of capture history matrices. Using the "Pradel survival and recruitment" module of the program MARK (White & Burnham, 1999; Cooch & White, 2001), we sought for the most parsimonious combination of the parameters Φ, p and f with respect to sex (s) and marking day (t). We modelled time as categorical (t), linear (t_{lin}) and polynomial ($t^2_{\mathrm{lin+lin}}$) effects, and checked for additive ($s + t$) and non-additive ($t * s$) effects of the variables. Later in the text, the most parsimonious model (with the lowest cAIC) is referred to as "Best", whereas models with ΔAIC < 2.0, which are still used for inference, are referred to as "supported models".

Estimates of total size of open populations are laden with intrinsic difficulties. However, even if our population was *opened* in terms of births and deaths, it was *closed* in the sense that no immigrants entered it from outside, and no butterflies lived beyond one season. Therefore, total recruitment equals the sum of births between individual sampling days,

$$\hat{N} = \hat{B}_0^* + \cdots + \hat{B}_{s-2}^* + \hat{B}_{s-1}^* \qquad (1)$$

adjusted, as proposed by Schwarz et al. (1993), for survival during the periods

$$B_i^* = B_i \frac{\log \phi_i}{\phi_i - 1} \qquad (2)$$

To obtain daily numbers of births B_i, we used the full Jolly-Seber analytical model in POPAN (Arnason et al., 1998), with time heterogeneity in the probability of captures. We then computed two adjustments, one based on daily-specific ϕ_is (from POPAN), the other using the sex-specific but time constant $\Phi(sex)$ (from MARK). Both estimates were computed separately for males and females.

Table 1. Overview of population size and mobility data on the last Czech population of the butterfly *Euphydryas maturna*, collected during mark-recapture survey in June 2002.

Marking	Individuals captured	Individuals recaptured	Proportion recaptured	Recapture events	Max. residence (days)
Males	57	22	38.6%	32	12
Females	79	33	41.8%	89	10

Mobility	Patch-to-patch movements	Mean distance moved	Modal indiv. distance	Maximum single move	Maximum total distance
Males	17	275 m (SD 191)	150 m ($n = 6$)	850 m	950 m
Females	25	250 m (SD 177)	100 m ($n = 12$)	500 m	1050 m
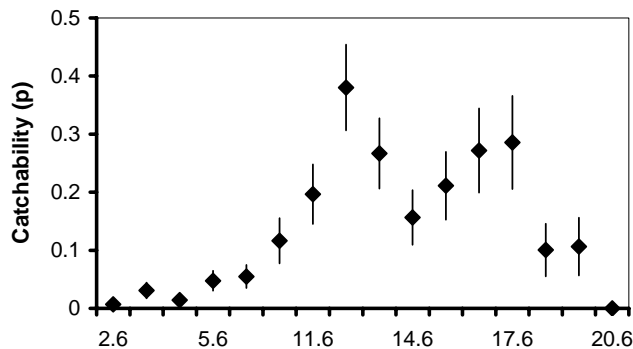
Fig. 1. Capture probabilities of *E. maturna* butterflies, and their standard errors, according to Best Pradel survival and recruitment model (parameter $p(t)$ in Tab. 3), plotted against marking days.

Mobility
For butterflies re-captured at least once, we fitted observed movement distances using two regression-based functions that describe dispersal kernels of mobile organisms and allow predicting movements beyond distances covered by mark-recapture designs (HILL et al., 1996; BAGUETTE et al., 2000; VANDEWOESTIJNE & BAGUETTE, 2004; CIZEK & KONVICKA, in press). The negative exponential function (NEF), expresses the probability density I of movements to distance D, measured in kilometres, as,

$$I_{\text{NEF}} = a \cdot e^{-k \cdot D} \qquad (3)$$

The fatter-tailed inverse power function (IPF) again expresses the probability density of movements to certain distances,

$$I_{\text{IPF}} = C \cdot D^{-n} \qquad (4)$$

To estimate the parameters a, k, C and n, natural logarithms of cumulative fractions of individuals moving to certain or higher distances ($\ln I$) are regressed against linearised expressions of the distances, i.e., $\ln a - kD$ for (Eq. 1); and $\ln C - n(\ln D)$ for (Eq. 2). We fitted both functions, separately for males and females, to dispersal data for all individuals recaptured at least once. We then compared the fits of the models to the data by regressing, separately for the two functions and sexes, the predicted values of I against observed cumulative proportions of movements. To select between models, we used the decrease in values of the Akaike information criterion (Δ AIC) relative to the values for regressions of observed values against unity. The computing was done S-plus v. 4.5 (S-PLUS 2000, 1999).

Yearly counts of larval nests
From 2002 onwards, we searched the entire inhabited area for conspicuous late-summer (August) larval nests. We always followed an identical procedure, starting from roads, glades, clearings and forest edges and gradually covering the entire forest. Each located nest was tagged to avoid accidental re-counting and to facilitate a parallel study of larval survival. Every year, the census took 10–14 person days.

Results

Individual survival and population size
We marked 136 individuals and obtained 121 recaptures distributed among 55 individuals (Tab. 1). The capture sex ratio did not deviate from an equal representation of sexes ($P > 0.1$), but females were recaptured more often than males ($\chi^2 = 7.1$, $P < 0.01$). For both sexes, the distributions of captures per individual were markedly left-skewed (males: maximum = 4, mean = 1.6, median = 1; females: maximum = 9, mean = 2.1. median = 1).

The captures were very low for marking effort. Altogether, we made 2,036 visits to individual patches (mean per patch = 74.0, SD = 34.6), but mean captures per patch and visit were as low as 0.13. This suggested an extremely low density of individuals.

The Best Pradel model for survival and recruitment (Tab. 2) showed that survival was constant in time but lower for males than females (0.74 ± 0.035 SE vs. 0.85 ± 0.033 SE), the catchability varied in time but was equal for sexes (Fig. 1), and recruitment was fixed in time and sexes (0.12 ± 0.038). The lower survival of males was retained in all supported models. However, one supported model suggested a slight difference in catchability between sexes (higher in males), whereas alternative model pointed to a polynomial trend in catchability.

Figure 2 shows daily estimates of population sizes. There was no marked indication of protandry, and peak population size was higher for females than for males. Subsequent estimation of total recruitment using (Eq. 3) and (Eq. 4) resulted into 75 males/115 females (time-varying values of ϕ_i from POPAN), or, alternatively, 84 males/118 females (time-invariant values of $\Phi(sex)$ from MARK). The former estimate was female biased ($\chi^2 = $
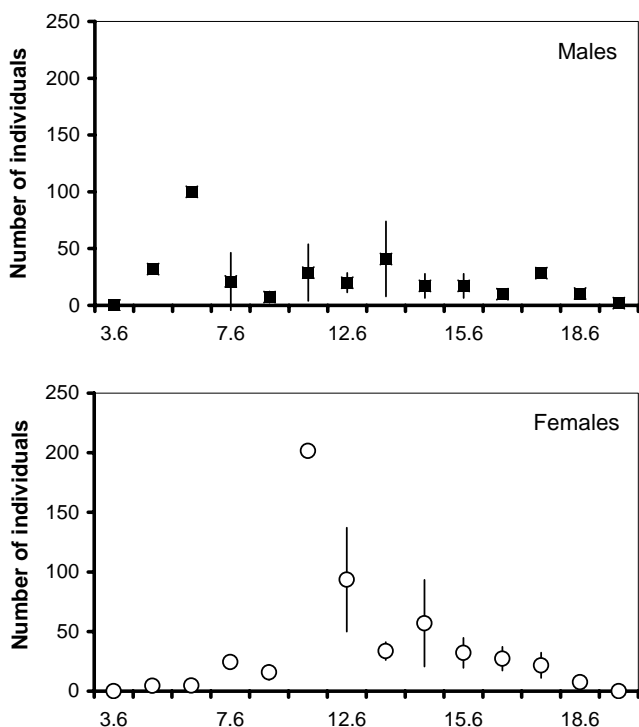
Fig. 2. Daily numbers of *E. maturna* adults present in the last population of the species in the Czech Republic.
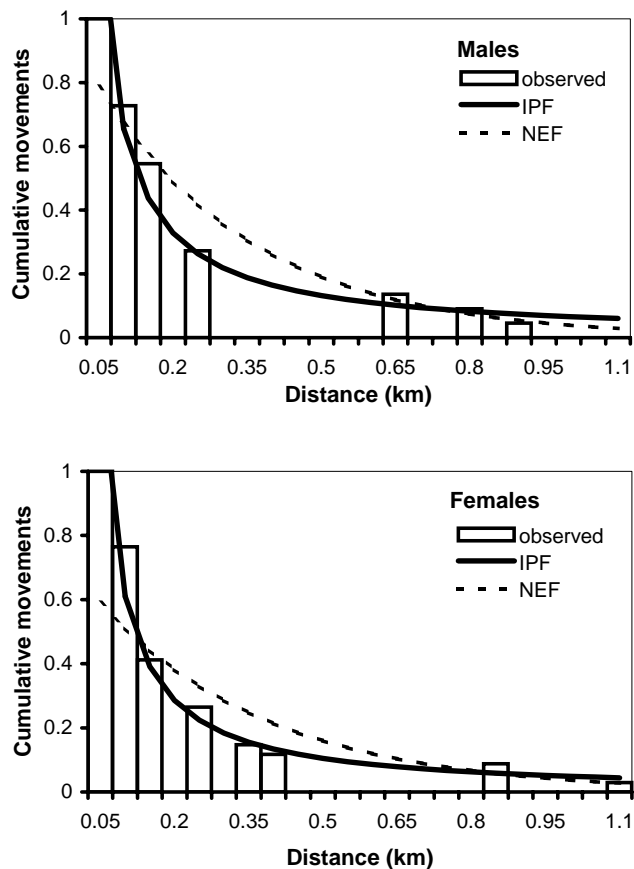

Fig. 3. Cumulative proportions of movements of *E. maturna* adults against movement distances, and fitted dispersal kernel functions describing the observed movements. NEF – negative exponential function; IPF – inverse power function.

4.26, $P < 0.05$), whereas the latter was not ($\chi^2 = 4.88$, $P = 0.09$).

Mobility
Observations of mobility are summarised in Table 1. The proportions of animals recaptured outside of their original patches did not differ between males and females ($P > 0.96$), and there was no difference in total distances moved per individual (Mann-Whitney $U = 351.5$, $Z = 0.38$, $P = 0.70$).

For both sexes, the negative exponential function achieved a better fit than the inverse power function (Tab. 3). The (linearised) NEF lines did not differ between sexes (slopes: $t_{11} = 0.42$, *ns*, elevations: $t_{11} = 0.92$, *ns*), suggesting essentially identical mobility. Shapes of the functions (Fig. 3, Tab. 3) indicated (i) relatively high mobility up to ca 300 m, followed by steep decrease; (ii) even within the wood, the mobility in distances to ca 1 km becomes very low; and (iii)

the probability of movements becomes negligible in distances exceeding 1 km.

Yearly counts of larval nests
Numbers of larval nests fluctuated widely during four consecutive years: the counts were 34 (2001), 31 (2002), 139 (2003) and 138 (2004), with coefficient of variation = 0.62. Dividing adult population in 2002 by nest count gave the ratio 6.1. Recalculating annual adult populations for the four years using this admittedly crude coefficient led to estimates ranging from ≈190 to ≈850 butterflies, with harmonic mean ≈320 individuals.

Table 2. Best supported models of survival and recruitment of adults of *Euphydryas maturna*, 2002, modelled using Pradel survival and recruitment models. See Material and methods for explanations of symbols.

Model	AIC	ΔAIC	Model likelihood	Number of parameters	Deviance
$\Phi(s)p(t)f(.)$	1173.4	0.00	1.00	19	244.7
$\Phi(s)p(t^2_{\text{lin+lin}})f(.)$	1175.1	1.66	0.44	6	276.0
$\Phi(s)p(s+t)f(.)$	1175.3	1.93	0.38	20	244.5

Key: Φ – individual survival; p – catchability; f – rate of population change (= recruitment).

Table 3. Regression equations, and predicted movements to selected distances, for the negative exponential functions (NEF) and the inverse power functions (IPF) that express probability density *I* of movements of *E. maturna* individuals to distances *D*. Fits of the regressions were compared by fitting values predicted by the functions against real data, the test criterion was the decrease in values of the Akaike information criterion (ΔAIC: higher values indicate better model) between the fitted and null model. Better-fitting models are in bold.

Model	Equation[1]	ΔAIC	300 m	500 m	1 km	5 km	10 km
NEF ♂♂	$\ln I = -0.08(\pm 0.158) - 3.15(\pm 0.298) \cdot D$	**1.983**	**0.358**	**0.191**	**0.039**	$\approx 10^{-7}$	$\approx 10^{-14}$
NEF ♀♀	$\ln I = -0.38(\pm 0.251) - 2.91(\pm 0.467) \cdot D$	**2.271**	**0.286**	**0.160**	**0.037**	$\approx 10^{-7}$	$\approx 10^{-13}$
IPF ♂♂	$\ln I = -2.72(\pm 0.186) - 1.00(\pm 0.110) \cdot \ln D$	1.279	0.220	0.132	0.066	0.013	0.007
IPF ♀♀	$\ln I = -3.01(\pm 0.172) - 1.09(\pm 0.105) \cdot \ln D$	1.517	0.183	0.105	0.049	0.008	0.004

Key: [1]NEF: $\ln a - kD$; IPF: $\ln C - n(\ln D)$.

Discussion

The last Czech population of *E. maturna* numbered less then 200 adults during the year when the mark-recapture study was carried out. The species depends on a few hectares of clearings within one isolated wood, it widely fluctuates in numbers, and its chances for colonising novel sites are negligible.

Demography and mobility

All supported models attained by the constrained linear modelling agreed that adult survival was lower in males than in females. This seems fairly common in butterflies (e.g., FRIC & KONVIČKA, 2000; PETIT et al. 2001; SCHTICKZELLE et al., 2002), and might be attributable to more risky behaviour during mate locating efforts, such as contests for perches in *E. maturna* (KEMP & WIKLUND, 2001). A less expected pattern was the equal catchability of both sexes, as more conspicuous males are often more catchable for butterflies. Perhaps it was explicable by relatively high marking intensity combined with low density of the butterflies. Under high densities of studied animals, researchers tend to optimise their effort by concentrating on the more conspicuous sex. This was not the case in our study, as the butterflies were so sparse that we literally had to search for them. Still, the model with higher catchability of males passed as one of the supported models. Another unexpected pattern was recruitment independent on time. Recruitment is frequently convex in butterflies with non-overlapping generations (SCHTICKZELLE et al., 2002). We also did not observe any sign of protandry, although it occurs in populations of *E. maturna* in Sweden (ELIASSON, 2001). Possibly, the population size was too low to allow detecting time-related patterns in recruitment.

Although we detected only 42 patch-to-patch movements, this represents the largest existing data set on movements of *E. maturna*. The larger sample explains why our maximum movement distances (close to 1 km) exceeded those found by SELONEN (1997) and WAHLBERG et al. (2002b), who based their analysis on 27 movements. However, our mean distances were close to those reported by them.

For the shape of dispersal kernel, the negative exponential model achieved a better fit than the inverse power model. However, BAGUETTE (2003) observed, in a study of movements of the fritillary *Boloria aquilonaris* (Stichel, 1908), that rare long-distance movements may easily switch the relative fits of the two models. In any case, since the probability of dispersal to long distances depends on population size, the chances that *E. maturna* would colonise novel woodlands remains unrealistically low regardless of the exact shape of dispersal function.

The counts of larval nests demonstrated wide fluctuations of butterfly numbers among years. This is a well-known phenomenon in other *Euphydryas* butterflies (e.g., MCLAUGHLIN et al., 2002a; HELLMAN et al., 2003), the fluctuation being driven by weather (MCLAUGHLIN et al., 2002b), parasitoids (JOYCE & PULLIN, 2003) and perhaps predators (VRABEC & JINDRA, 1998). Another driver of the changes may be habitat quality: KUDRNA (2001) observed a marked increase of a population of *E. maturna* inhabiting a wood defoliated by a gypsy moth outbreak, followed by a bust when the outbreak was over. However, habitat quality did not markedly improve at our site during the four years, which suggests that the post-2002 increase was unlikely to be a sign of recovery. It was more likely a short-time boom, as a period of "high adult density" was actually observed at our site in mid-1990s by V. VRABEC (personal communication to authors).

Conservation

Prospects of survival of *E. maturna* in the study region depend on increasing its population size. It is now clearly below a threshold for long-term viability, which is generally considered to be near 500 individuals to buffer deleterious genetic effects and closer to 5000 individuals to buffer environmental stochasticity (REED et al., 2003).

The demography data presented here, the dependency of autumn larvae on sun exposed ash saplings, and the requirements of spring larvae for forest floor plants (cf. FREESE et al., in litt.) all suggest that the population is suppressed by small area, isolation, and the poor quality of its biotope. The general requirements of *E. maturna* are thus akin to other threatened butterflies inhabiting early successional patches within

European woodlands. Examples include *Lopinga achine* (L., 1763) in Sweden (Bergman & Landin, 2002), *Parnassius mnemosyne* (L., 1758) in C Europe (Konvička & Kuras, 1999), *Melitaea athalia* (Rottemburg, 1775), *Argynnis adippe* (Dennis et Schiffermüller, 1775) and *Hamearis lucina* (L., 1758) in Britain (Warren, 1987; Sparks et al., 1994) and *Euphydryas aurinia* (Rottemburg, 1775) in Finland (Wahlberg et al., 2002a). All these species require frequent establishment of short-lived early successional sites. Wahlberg et al. (2002a) coined the term dynamic metapopulations for such situations, and showed that both dynamics of the species and dynamics of their habitats should be considered in conservation planning (see also Johnson, 2000; Ellner & Fussmann, 2003).

In principle, two strategies may be employed to provide suitable woodland openings. The static approach maintains selected openings in perpetually blocked successional stages (e.g., Bergman & Kindvall, 2004), whereas the dynamic approach allows individual openings to disappear due to succession while perpetually creating new ones by management (e.g., Wahlberg et al., 2002a). The static approach seems unsuitable for *E. maturna*, whose post-hibernation larvae utilise forest floor herbs, since an opening maintained for the long-term would gradually lose forest vegetation.

The principal problem of the dynamic approach is limited space. Consider that although the occupied wood covers some 100 hectares, only about 10% are clearings. Assuming that effective population size (estimated, crudely, as harmonic mean from population sizes during the four years) is about 300 individuals, the perpetual supply of 15 ha of clearings would be necessary for 500 individuals and 150 ha for a safe population of 5000 individuals. It is simple arithmetic that enough clearings available at any given time cannot be provided by the ongoing high forest management which has a turnover time of 120 years.

Importantly, high forest management is a relatively new phenomenon in lowlands of C Europe. Various forms of coppicing, coppicing with standards and pasture woodlands, had been widespread in the region some one hundred years ago. Under these management practices, short rotation of cuts provides more early-successional sites at any given time, and forests attain an open savannah-like appearance favourable for heliophilous organisms. Not surprisingly, most of the still surviving populations of *E. maturna* in C Europe inhabit coppices with standards (Höttinger & Pennerstorfer, 1999; Van Swaay & Warren, 2003; Freese et al., in litt.).

It follows that the only chance to conserve the Czech population of *E. maturna* is reestablishment of traditional short-rotation coppicing. It should be reestablished at the present site, as well as in selected woods in wider surroundings, and measures facilitating re-colonisation of the additional woods, including rein-

troductions, should be undertaken. Both measures are proposed in the species action plan, recently in review. The proposal bears considerable risks, as reestablishment of coppicing with standards will likely meet opposition from forestry professionals. It cannot fully guarantee that the butterfly will ultimately be saved: there is still much uncertainty regarding its population dynamics; our conclusions are based on a relatively short-term survey, and species so depressed in numbers may well become extinct before the management comes into operation. However, the critical state of the population does not allow any procrastinating, because the possibility of extinction whilst taking action must be considered with respect to certain extinction if no action is taken.

Acknowledgements

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