



## Combining larval habitat quality and metapopulation structure – the key for successful management of pre-alpine *Euphydryas aurinia* colonies

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### Abstract

This study aims to analyse larval habitat preferences and landscape level population structure of the threatened Marsh Fritillary butterfly, *Euphydryas aurinia*, and discusses implications for the conservation and management of this strongly declining species in central Europe. Whereas current management strategies are mainly based on studies of habitat requirements of adult individuals, we intend to emphasise larval habitat quality and population processes at the landscape level as additional key factors. Microhabitat preference analysis of egg-laying females showed that eggs were predominantly laid on prominent large-sized host plant individuals. Additionally, when *Succisa pratensis* was used as a host plant (as opposed to *Gentiana asclepiadea*), host individuals in open vegetation structure were preferred. Optimal oviposition conditions were present in recently abandoned calcareous fen meadows and at the edges of such meadows currently in use. A two-year patch-occupancy study in the northern pre-alpine region of south-west Germany indicated that *E. aurinia* lives in a metapopulation. In a logistic-regression model, patch size, isolation, and habitat quality explained 82% of the observed patch-occupancy pattern in 2001. Our data suggest that a suitable conservation strategy must incorporate both the conservation of a network of suitable habitat patches, and efforts to maximise local habitat quality by ensuring that host plants can grow to a large size and are surrounded by sparse and low vegetation cover.

### Introduction

The Marsh Fritillary butterfly *Euphydryas aurinia* (Rottemburg 1775), listed in Annex II of the European Community Habitats and Species Directive (92/43/EEC), has suffered a severe decline in most European countries during the 20th century (van Swaay and Warren 1999; Asher et al. 2001). Stable populations are predominant only in the Mediterranean bio-geographic region (Warren et al. 1994; Munguira pers. comm.) and possibly eastern European countries (van Swaay,

pers. comm.). The German range of *E. aurinia* decreased by ~75% between 1950 and 2002 (based on a 10' × 6' geographic minute grid, Anthes et al. 2003) and the loss of colonies continues especially at the margins of the species' range. The former and current distribution in Germany is shown in Figure 1.

Management focusing on this species has mainly failed to reverse or slow down the negative trend. This might have been caused partly by inappropriate nature conservation strategies, which are still based on insufficient data. Most studies underlying

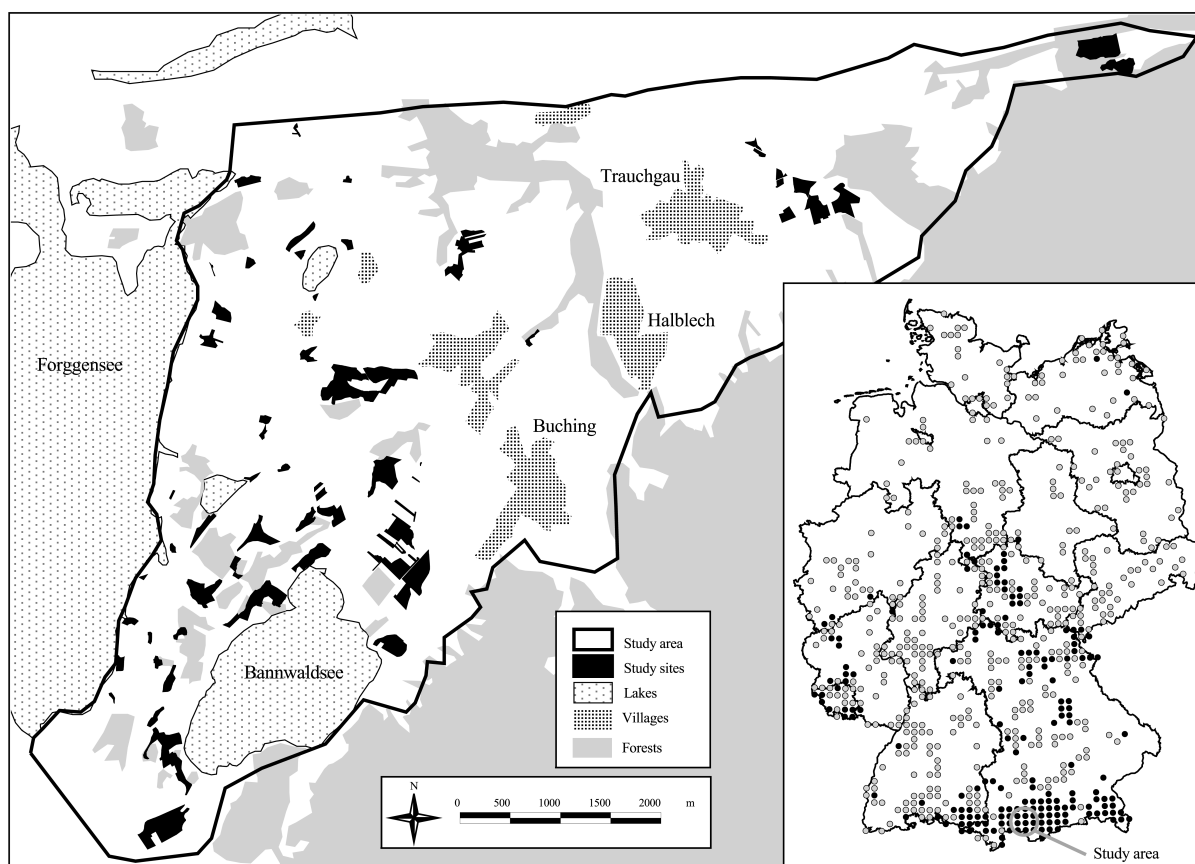


Figure 1. Study area in southern Bavaria, Germany. Names of the two major lakes and three villages are given. The inlay shows the former range (grey dots) and the maximum current distribution of *E. aurinia* in Germany based on data between 1996 and 2002 on a  $10' \times 6'$  geographic minute grid (black dots, data from Anthes et al. 2003).

current *E. aurinia* management have compared the presence or density of adults or larvae with the current land use on a patch level (e.g., Warren 1994; Dolek and Geyer 1997; Lewis and Hurford 1997). Dolek et al. (1999) concluded that mowing and grazing regimes were similarly suitable to support *E. aurinia* in southern German moorland. However, such studies do not consider two key factors which have been used to explain the high population extinction rates observed in many insect species in cultivated landscapes of Europe: (i) Changes of within-patch habitat quality (Thomas and Morris 1994), especially the larval habitat quality at the micro scale, and (ii) the inter-patch spatial structure of a metapopulation, mainly characterised by patch size and isolation (Hanski 1999). While previous metapopulation studies often lack a detailed analysis of habitat quality,

recent theoretical and empirical studies suggest that approaches including habitat quality enable a better understanding of metapopulation dynamics (Kuussaari et al. 1996; Dennis and Eales 1997; Boughton 1999; Thomas et al. 2001). In Germany the factors mentioned have only recently been included into conservation strategies (Fartmann et al. 2001) although they might be of crucial importance for *E. aurinia* conservation (Warren 1994; Wahlberg et al. 2002a,b).

A population of *E. aurinia* was studied in its German stronghold in pre-alpine litter meadows<sup>1</sup> in order to

- i. assess within-patch microhabitat and management preferences of egg depositing females.

<sup>1</sup>Litter' meadow: nutrient poor wet meadow mown in late summer or autumn. In the traditional farming systems the 'litter' was used to bed the cattle in stables.

This will enable to more specifically define habitat quality and assess the impact of different management types on larval stages.

- ii. classify the population structure on a landscape level based on a two-year patch-dynamic study.
- iii. estimate the explanatory power of habitat quality, isolation, and patch size on patch-occupancy in a single year.

Based on the results the combined implications of habitat quality and population structure for habitat management of the threatened *E. aurinia* are discussed.

## Materials and methods

### Study species

*Euphydryas aurinia* (Lepidoptera: Nymphalidae) is single brooded with adults flying from mid May to the beginning of July in the Bavarian pre-alpine region (about 800 m a.s.l.). The regionally often monophagous species feeds on at least 16 members of the families Dipsacaceae, Gentianaceae, and Caprifoliaceae over its range (e.g., Mazel 1984; Ebert and Rennwald 1991; SBN 1991; Warren 1994; Lewis and Hurford 1997; Munguira et al. 1997). All host plants contain seco-iridoid glycosides which are sequestered by the larvae to make them unpalatable (Wahlberg 2001). In the studied region batches of 220 (70–390) eggs are laid on two major host plants, *Succisa pratensis* (Dipsacaceae) and *Gentiana asclepiadea* (Gentianaceae). Each single female may lay more than one batch, with subsequently decreasing number of eggs per clutch (Porter 1992). Pre-hibernation larvae were recorded feeding on two members of families formerly unknown as hosts of the species: *Valeriana dioica* (Valerianaceae) and *Menyanthes trifoliata* (Menyanthaceae). The gregarious larvae spin a silken web in which they feed until they reach diapause in the 4th instar by early to mid September. Five to more than 50 larvae winter in a small silken web. It is usually constructed at the base of a host plant or neighbouring grasses, but occasionally 10–20 cm above ground. The species exhibits extreme fluctuations in population sizes (Ford and Ford 1930) which are mainly attributed to the influence of parasitoid wasps (Porter 1983).

### Study area and sites

The 38 km<sup>2</sup> study area is located in the northern foothills of the Alps east of the river Lech near Füssen in the southern federal state of Bavaria (Figure 1). In 2001 and 2002, 65 habitat patches considered as 'suitable' with a mean size of 2.14 ha (0.04–10.35, SD = 2.2 ha) were monitored during the flight season and pre-hibernation period in order to assess the landscape level population structure of *E. aurinia*. Results of previous mark-recapture studies that allow estimations of the species' mobility (Fischer 1997; Munguira et al. 1997; Wahlberg et al. 2002b) were used to define 'suitable' patches by grassland habitats containing the larval host plants that were separated from other such patches by at least 100 m of non-habitat (usually intensive pasture or uniform coniferous forests). Most patches were unimproved oligotrophic, calcareous fens, which are mown once a year between early September and early October (litter meadows, 'Streuwiesen'). Hence, larvae may be affected by mowing both before and after the start of hibernation. In both cases mowing can destroy webs completely, although the effect may be lower once diapause is reached (unpubl. data). Eight sites are remnants of formerly vast areas of common property extensively grazed by cattle and horses in a traditional regime called 'Allmende' (Scholle et al. 2002). Standard vegetation relevés (Dierschke 1994) indicated that most occupied habitats belonged to *Molinia*-dominated grassland (*Molinietum caeruleae*) and calcareous fen associations (*Primulo-Schoenetum*, *Caricetum davallianae*), but larval webs were also found in *Carex* swamps (*Magnocaricion*) and transitional bogs (*Caricion lasiocarpae* and *Caricion nigrae*) (see also Anthes et al. 2003). Both land use types, fen litter meadows ('Streuwiesen') and extensively grazed fens, receive a high priority in German and European nature conservation strategies as a stronghold for a number of endangered species restricted to extensively used oligotrophic wetlands including *E. aurinia*.

### Microhabitat and land use preferences

Nectar resources are abundant in calcareous fen meadows and are used in an opportunistic manner by *E. aurinia* (e.g., *Leontodon hispidus*, *Arnica montana*, *Ranunculus nemorosus* s.l.). This

indicates that the availability of suitable larval host plant resources may be the major factor controlling population density. Previous studies already indicated varying preferences on a regional scale, i.e., that large plant individuals in sunny exposition are preferred in some regions (Porter 1992; Lavery 1993; Warren 1994), small individuals in others (Lewis and Hurford 1997). Therefore, a detailed analysis of host preferences on a regional level is essential.

Larval host plants were systematically checked for egg batches (methods according to Hermann 1998) from 8 to 15 July 2001 in three habitat patches that were spatially separated by more than 500 m. The predominantly occupied host (>90%) was *S. pratensis* in two patches ( $n = 39$  and 35 batches, respectively) and *G. asclepiadea* ( $n = 12$ ) in one patch. For within-patch oviposition preference analysis seven host plant and habitat structure parameters at available and occupied host plants were measured. Forward stepwise logistic-regression was used to analyse which of these parameters best explain oviposition patterns. Host plants with several egg clutches (max. 3) were multiply included when clutch colours indicated different laying dates, hence independent egg deposition decisions of one or several females (Porter 1992). Available habitat structures were analysed at 100 randomly selected host plant individuals per site. We selected the host plant closest to a coloured stick thrown backwards in irregular intervals while walking the complete patch in circles. For each individual *Gentiana*, we measured total height and the number of single shoots, and for each *Succisa*, height, diameter, and the number of leaves in the rosette. Food availability was measured as the percentage host plant cover in a circle of 50 cm around the focal plant. Microhabitat structure was estimated by assessing the percentage horizontal herb cover in 10 cm height above soil surface (20 cm in depth, Hermann and Steiner 1997) and the average height of grasses surrounding the host plant (Oppermann 1987; Fartmann 1997; Sundermeier 1999).

Land use or management type (extensive grazing, intensive grazing, yearly cut litter meadow, or abandoned meadow) was recorded for each site to calculate the proportion of occupied patches in each land use class. Additionally, this simplified patch-level management classification was com-

pared with the exact within-patch position of all recorded egg batches or larval webs. Thus, within a patch classified as 'litter meadow' egg batches can be situated at an un-mown ditch and will thus be classified as 'abandoned' on the microhabitat level.

#### *Population structure at the landscape level*

At the landscape level, population structure and dynamics were assessed using presence-absence-data for all surveyed habitat patches in 2001 and 2002. Patches were classified 'occupied' when either adults or larvae were present. To be classified 'unoccupied' patches had to be surveyed unsuccessfully twice, during the adult flight period (June) and the conspicuous 3rd instar larval period (August).

To explain patch-occupancy we measured total patch size  $a$  and isolation  $i$  for each patch and habitat quality  $h$  for a subset of 46 patches in 2001. Isolation  $i$  was measured as the mean distance to the next three habitat patches, irrespective whether or not they were occupied (according to Thomas et al. 2001). As such 'simple' isolation measures have been questioned recently (Moilanen and Hanski 2001) we reanalysed our data using the more complex connectivity index  $S_i$  introduced by Hanski (1994), where

$$S_i = \sum_{j \neq i} p_j \exp(-\alpha d_{ij}) A_j$$

with  $p_j$  the incidence of *E. aurinia* in patch  $j$  (0 in case of absence, 1 in case of presence in 2001),  $\alpha$  as a constant of survival rate on migration (set to 1),  $d_{ij}$  as the distance between patches  $i$  and  $j$ , and  $A_j$  the area of patch  $j$ .

Habitat quality  $h$  was quantified as the density of suitable larval host plants. 'Suitable' host plants were defined on the basis of female oviposition preferences (cf. Thomas et al. 2001; Wahlberg et al. 2002a) measured in the previous section as large host plant individuals in sunny exposure with unrestricted access to leaves.

The explanatory power of the three independent predictor variables on patch occupancy in 2001 was assessed using a forward stepwise multiple logistic-regression.

The number of larval webs per patch as a representation of population size was surveyed once per site in mid August 2001. Small patches were

Table 1. Egg deposition preference analysis for *E. aurinia* with respect to host plant and microhabitat characteristics. Forward stepwise logistic-regression was used to compare accepted host plants ( $n = 39, 35,$  and  $12$  at sites I, II, and III, respectively) with available structures at 100 randomly selected host plants per site. n.s.=not significant.

| Parameter                 | Site I: <i>Succisa</i>              |        | Site II: <i>Succisa</i>            |        | Site III: <i>Gentiana</i>          |        |
|---------------------------|-------------------------------------|--------|------------------------------------|--------|------------------------------------|--------|
|                           | Coefficient <i>B</i>                | Sig.   | Coefficient <i>B</i>               | Sig.   | Coefficient <i>B</i>               | Sig.   |
| Constant                  | -4.904                              | 0.007  | -9.651                             | <0.001 | -4.431                             | <0.001 |
| Plant height (cm)         | 0.312                               | 0.002  | 0.323                              | <0.001 | 3.491                              | n.s.   |
| <i>n</i> leaves/shoots    | 0.585                               | <0.001 | 1.042                              | <0.001 | 0.337                              | <0.001 |
| Diameter (cm)             | 1.522                               | n.s.   | 1.732                              | n.s.   | –                                  | –      |
| Grass height (cm)         | -0.075                              | 0.05   | 0.074                              | n.s.   | 1.088                              | n.s.   |
| <i>Succisa</i> cover (%)  | 0.001                               | n.s.   | 0.079                              | n.s.   | 3.596                              | n.s.   |
| <i>Gentiana</i> cover (%) | 0.227                               | n.s.   | 0.003                              | n.s.   | 1.870                              | n.s.   |
| Horizontal herb cover (%) | -0.071                              | 0.002  | -0.068                             | 0.001  | 0.647                              | n.s.   |
| Model summary             | $\chi^2 = 109.3, df = 4, P < 0.001$ |        | $\chi^2 = 95.8, df = 3, P < 0.001$ |        | $\chi^2 = 35.4, df = 1, P < 0.001$ |        |
| Correctly classified      | 92.8%                               |        | 88.9%                              |        | 92.9%                              |        |

Table 2. Parameter values of host plant and microhabitat structures at available and accepted host plants. Mean values are given  $\pm$  SD (standard deviation). For sample sizes and statistical analysis see Table 1.

| Parameter                 | Site I: <i>Succisa</i> |                 | Site II: <i>Succisa</i> |                 | Site III: <i>Gentiana</i> |                 |
|---------------------------|------------------------|-----------------|-------------------------|-----------------|---------------------------|-----------------|
|                           | Accepted               | Available       | Accepted                | Available       | Accepted                  | Available       |
| Host plant parameters     |                        |                 |                         |                 |                           |                 |
| <i>n</i> leaves/shoots    | 11.3 $\pm$ 4.2         | 6.5 $\pm$ 2.1   | 9.8 $\pm$ 5.7           | 5.5 $\pm$ 1.5   | 15.1 $\pm$ 8.5            | 3.0 $\pm$ 3.3   |
| Height (cm)               | 17.0 $\pm$ 5.4         | 10.5 $\pm$ 4.1  | 17.5 $\pm$ 4.3          | 10.3 $\pm$ 4.5  | 55.7 $\pm$ 9.3            | 33.2 $\pm$ 14.1 |
| Diameter (cm)             | 20.7 $\pm$ 6.5         | 15.6 $\pm$ 4.9  | 21.0 $\pm$ 5.2          | 16.0 $\pm$ 5.7  | –                         | –               |
| Grass height (cm)         | 25.1 $\pm$ 9.4         | 36.8 $\pm$ 11.5 | 39.4 $\pm$ 16.3         | 39.3 $\pm$ 11.6 | 32.5 $\pm$ 7.2            | 34.0 $\pm$ 11.0 |
| <i>Succisa</i> cover (%)  | 1.2 $\pm$ 1.9          | 1.1 $\pm$ 2.4   | 8.1 $\pm$ 7.8           | 3.6 $\pm$ 6.7   | 0.3 $\pm$ 0.9             | 0.1 $\pm$ 0.4   |
| <i>Gentiana</i> cover (%) | 0                      | 0.3 $\pm$ 1.2   | 0.1 $\pm$ 0.5           | 0.04 $\pm$ 0.2  | –                         | –               |
| Horizontal herb cover (%) | 26.2 $\pm$ 20.4        | 47.4 $\pm$ 20.2 | 33.7 $\pm$ 19.4         | 52.8 $\pm$ 16.9 | 54.2 $\pm$ 14.4           | 48.2 $\pm$ 19.6 |

surveyed completely. In large patches we calculated the number of larval webs as the fraction of the patch surveyed times the number of webs found on this fraction. Numbers were then classified in five arbitrary categories (cf. Figure 3).

To assess the influence of patch quality on *E. aurinia* density the effect of local host plant density on the density of larval webs and egg batches in 24 occupied patches was analysed using linear regression. Larval web/egg batch densities were calculated according to Boughton (1999). First, we counted suitable host plants in 5–13 randomly distributed 25 m<sup>2</sup> plots. Second, we estimated the fraction of suitable host plants supporting a larval web or egg batch by checking 100–300 randomly selected host individuals (methods see above). The larval web density  $R$  was then calculated as

$$R = (n_G/n_W) \times \rho_D$$

where  $n_W$  is the number of checked host plants,  $n_G$  is the number of larval webs, and  $\rho_D$  is the mean host plant density in the surveyed plots.

All statistical analysis was performed with SPSS 11.0 statistical analysis package.

## Results

### *Egg deposition preferences*

Oviposition pattern at *S. pratensis* was best explained by a combination of host plant and microhabitat parameters (Table 1, absolute parameter values at available and accepted host plants are given in Table 2). The probability of a host plant being accepted for oviposition increased with plant size (height and number of leaves), but decreased with vegetation density. Additionally, height of surrounding grasses contributed with

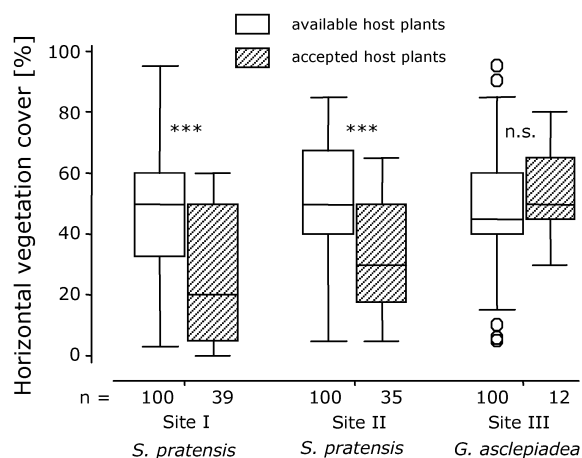


Figure 2. Horizontal vegetation cover in 10 cm height above soil surface at available and accepted host plants. Box-plots show minimum, maximum, interquartile range, and median coverage (%) per site. Open dots indicate outliers. \*\*\* $P < 0.001$ . n.s.: not significant, Mann–Whitney  $U$  Test. Compare Tables 1 and 2 for statistics.

low significance to the model at site I. In *G. asclepiadea*, plant size (number of shoots) already explained most of the variation in oviposition positions and no further parameters were included in the model. In contrast to *Succisa*, accepted *Gentiana* grew in similar microstructure situations compared to available plants (Figure 2, Tables 1 and 2). Food availability did not significantly influence egg deposition decisions. To explain the observed differences in vegetation structural preferences between occupied *Succisa* and *Gentiana*, we recorded egg deposition heights on both hosts. On *Succisa*, eggs were mainly laid at ground rosette leaves less than 20 cm above ground. In contrast, egg deposition heights on *Gentiana* ranged between 13 and 70 cm and were significantly higher than those on *Succisa* ( $t$ -test,  $F_{86,18} = 27.82$ ,  $P < 0.001$ ).

#### Land use

On the patch-level, the fraction of occupied patches on grazed, mown, and abandoned sites did not differ from a random distribution ( $\chi^2$ -Test,  $\chi^2 = 3.15$ ,  $P = 0.21$ ,  $df = 2$ ; Table 3a). Considering the position of larval webs within occupied patches separately, however, revealed a strong bias towards abandoned areas (either abandoned plots or unmown edges of regularly cut patches), whereas

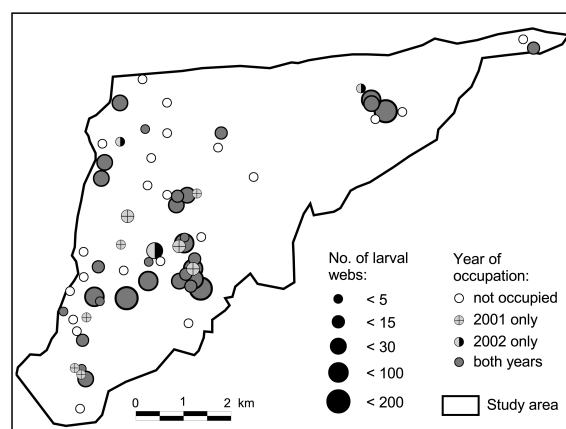


Figure 3. Two-year spatial dynamics of *E. aurinia* in the study area. Patches with either adult or larval webs were considered as occupied. The number of larval webs per site is given in five arbitrary categories for the first year of occupation (usually 2001; 2002 in the three colonised patches).

mown and grazed sites were largely under-represented (Table 3b).

#### Population parameters

In 2001 and 2002, 40 (62%) and 35 (49%) patches were occupied by either adult or larval stages of *E. aurinia* with a strong variation in the number of larval webs between sites in 2001 (Figure 3). Extinctions were recorded at eight patches (20%). In 2001 larval webs were still present in four of those, while four patches were considered ‘occupied’ only due to observations of one to four adult butterflies. Colonisations were recorded for three patches in 2002 (9%). In two of these, 3 and 10 larval webs were found, while the third was occupied by more than 15 adult butterflies. All these small patches were unsuccessfully checked for larval webs on 100% of the area in 2001. Surrounded by intensive pasture and forests, they are separated from the next *E. aurinia* colony by 200, 250, and 550 m.

A slight asynchrony of local population dynamics was indicated in 2001 by mean larval hatching dates being earlier on site III (18 July,  $n = 13$ , main host *Gentiana*) than on site II (22 July,  $n = 34$ , main host *Succisa*) ( $t$ -test,  $t = -2.4$ ,  $P = 0.02$ ).

Patch-occupancy in 2001 was best explained by a combination of all three predictor variables in a logistic-regression model: patch size, isolation,

Table 3. Management regimes (a) on a patch-level and (b) on the larval web level in the immediate surroundings of larval groups or egg batches.

| Management regime         | a: patch level |                   |                | b: larval web level                    |                |
|---------------------------|----------------|-------------------|----------------|--|----------------|
|                           | Surveyed sites | <i>n</i> occupied | Proportion [%] | <i>n</i> egg batches/<br>larval groups | Proportion [%] |
| Extensively cattle grazed | 8              | 7                 | 17.5           | 3                                      | 1.2            |
| Intensively cattle grazed | 2              | 0                 | 0              | 0                                      | 0              |
| Yearly mown litter meadow | 38             | 20                | 50.0           | 36                                     | 14.1           |
| Abandoned litter meadow   | 17             | 13                | 32.5           | 216                                    | 84.7           |

Table 4. Logistic-regression model of the occurrence of *E. aurinia* in a set of 65 habitat patches in 2001. In (a), isolation was measured as the ln mean distance to the next three suitable habitat patches, in (b) as connectivity *S* according to Hanski (1994).

| Independent variable                      | Coefficient <i>B</i> (SE)                         | Odds ratio<br>(95% confidence intervals) | Model improvement |          |
|---|---|--|-------------------|----------|
|   |   |  | $\chi^2$          | <i>P</i> |
| (a)                                       |   |  |                   |          |
| Constant                                  | 25.55 (8.65)                                      |  |                   |          |
| Patch size (ha)                           | 2.67 (1.03)                                       | 14.50 (1.94–108.37)                      | 11.74             | 0.001    |
| Isolation (m)                             | –8.69 (3.10)                                      | 0.0002 (0.00–0.07)                       | 11.55             | 0.001    |
| Host plant density (ind./m <sup>2</sup> ) | 1.24 (0.45)                                       | 3.45 (1.43–8.38)                         | 12.80             | <0.001   |
| Model summary                             | $\chi^2 = 36.1$ , <i>df</i> = 3, <i>P</i> < 0.001 |  |                   |          |
| Correctly classified                      | 83.0%   |  |                   |          |
| (b)                                       |   |  |                   |          |
| Constant                                  | 0.61 (0.86)                                       |  |                   |          |
| Patch size (ha)                           | 1.40 (0.52)                                       | 4.07 (1.46–11.37)                        | 11.74             | 0.001    |
| Host plant density (ind./m <sup>2</sup> ) | 1.04 (0.36)                                       | 2.82 (1.40–5.69)                         | 8.92              | 0.003    |
| Connectivity                              | 0.17 (0.09)                                       | 1.19 (0.99–1.43)                         | 4.51              | 0.034    |
| Model summary                             | $\chi^2 = 25.2$ , <i>df</i> = 3, <i>P</i> < 0.001 |  |                   |          |
| Correctly classified                      | 85.1%   |  |                   |          |

and habitat quality (Table 4a). The probability of a patch being occupied increased with patch size and host plant density, but decreased with isolation from neighbouring suitable patches (Table 4a, Figure 4). Odds ratios indicate the quantitative effects of each variable on the probability of a patch being occupied by *E. aurinia* (Table 4a). Thus, the increase in logarithmic patch size by one unit (e.g., from 2.7 to 7.4 ha when increasing the natural logarithm (ln) of patch size from 1 to 2) increases the probability of occupancy 15-fold. The probability of *E. aurinia* being present increases by 0.02% when isolation is reduced by 100 m, and increases 3.5-fold when increasing the density of suitable host plants by one. Although odds ratio values should not be overinterpreted (large confidence intervals, Table 4) they may give an impression of the magnitude of the effect that each parameter has on the presence of *E. aurinia*.

Qualitative results of the regression analysis were robust when using connectivity *S<sub>j</sub>* instead of mean distance to the next three habitat patches as a measure of isolation (Table 4b).

Density of suitable host plants explained about 44% of the variation in larval web density in 24 patches in a linear regression model (Figure 5). This confirms that host plant density is an important factor in determining habitat quality.

## Discussion

### *Microhabitat preferences and land use*

Our data strongly suggest that both host plant size and vegetation structure influence female egg deposition decisions and thus determine larval habitat quality for *E. aurinia*. Vegetation structure

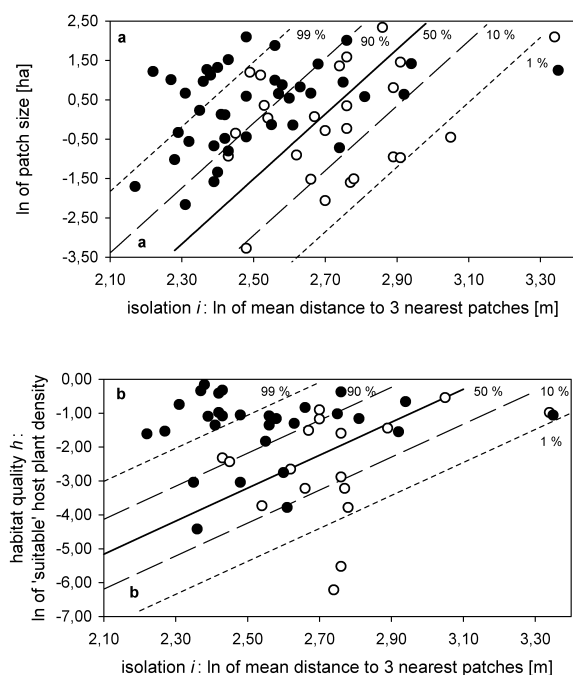


Figure 4. Distribution of occupied (solid circles) and unoccupied (open circles) habitat patches in relation to isolation and (a) patch size and (b) habitat quality (definitions see text). Lines indicate the predicted probabilities of a patch to be occupied based on the logistic-regression model (coefficients and statistics see Table 4a). (a)  $\log(P/(1 - P)) = 14.78 - 5.51i + 0.67a$ . (b)  $\log(P/(1 - P)) = 14.22 - 4.50i + 0.93h$ .

also determines whether *Succisa* or *Gentiana* is the preferred host plant species on a specific site. In both host species, female *E. aurinia* predominantly deposit their eggs on exceptionally large plants. Females probably prefer large host plants because they provide sufficient food resources for the larval group to survive until hibernation (4th instar). This strategy potentially eliminates danger to the larvae, as moving to a neighbouring plant after defoliation exposes them to both predators and unpredictable weather conditions outside their larval web. Indeed only five out of 182 surveyed larval groups moved to a neighbouring host plant before late 3rd instar stage at the end of August. These were the only groups that had already completely defoliated their natal plant.

Vegetation structure surrounding the occupied host is of particular importance only in *Succisa*. Females chose plants in open vegetation structures fully exposed to the sun ( $12-14 \text{ h d}^{-1}$ ). Under such microclimate conditions larvae may be able to

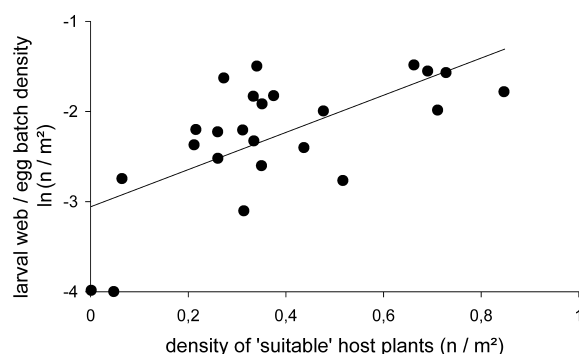


Figure 5. Effect of host plant density on larval web density in *E. aurinia* colonies. Data were analysed for 24 occupied patches. Linear regression equation:  $y = 2.06 \times x - 3.1$ . Model  $R^2 = 0.44$ ,  $F_{1,22} = 17.3$ ,  $P < 0.001$ .

grow comparably fast even in cool, but sunny weather (sun basking, Porter 1982). This has been suggested as an important factor to reduce the infection rate with parasitoid braconid wasps (*Cotesia* spp.) after diapause (Porter 1983). Secondly, host plants in open vegetation structure are easily accessible for egg-depositing females, which is not the case in large host plants that are overgrown by *Molinia* or *Carex* tussock grasses (represented by horizontal vegetation cover greater than 50%, cf. Figure 2, Table 2). In June, when eggs are laid, *Succisa* leaves are only present in a rosette close to the ground. In contrast to *Succisa*, several year old *Gentiana* plants already protrude above the surrounding vegetation by June. Hence, as *E. aurinia* deposits egg batches in the upper portion of *Gentiana*, vegetation structure neither hinders female access to the plants, nor does it affect the daily sun exposure duration.

These factors partly explain the differential use of within-patch habitat structures by different life cycle stages of *E. aurinia*. While adult butterflies spend considerable time feeding on the abundant nectar resources in grazed or yearly mown parts, these areas hardly provide suitable habitat for larval development. In contrast, ideal breeding conditions are often found nearby at edges of current management units and ditches or larger-sized abandoned litter meadows. Highest larval habitat quality in pre-alpine litter meadow complexes is probably reached after 2-3 years of abandonment. Here, host plants can grow to a large size while plant succession on the oligotrophic, low



productive soils is still suppressed such that host plants are easily accessible. In later fallow stages (>5 years) *Succisa* is subsequently overgrown by tussock grasses and becomes unsuitable for egg-laying, while *Gentiana* may remain suitable to very late succession stages until shrubs and trees like *Frangula alnus* and *Betula pubescens* displace this host species (cf. Lavery 1993).

Grazing is the most typical land use type in damp or dry calcareous grassland in most parts of the species' range (Fischer 1997; Lewis and Hurford 1997; Munguira et al. 1997; Asher et al. 2001). In contrast, within our study area, a detailed analysis of the locations and density of larval webs shows that extensively cattle-grazed fens support only few larval groups (cf. Dolek et al. 1999). We suppose that this mainly results from the lack of suitable microhabitat structures: grazed fens are characterised by a combination of heavily grazed sites on mineral soils, and wet and marshy, often minerotrophic parts which are only seldom grazed in late summer. At the former, *Succisa* grows in very small and thus unsuitable individuals (Bühler and Schmid 2001), while at the latter dense *Carex*-, and *Molinia*-stands overgrow ground rosette leaves of even large sized *Succisa* plants. Intermediate sites (ecotones) and transition stages are rare.

#### *Landscape scale population structure*

Although long-term studies are necessary to properly assess the spatial dynamics of butterfly populations (see discussion in Reich and Grimm 1995; Lewis et al. 1997) the studied *E. aurinia* population shows characteristics of a metapopulation structure similar to that described for British (Warren 1994) and Finnish populations (Wahlberg et al. 2002b). Our two-year survey shows that at least small colonies both close to neighbouring colonies and isolated by more than 500 m of non-habitat are subject to extinction and colonisation events. As shown by Munguira et al. (1997) and Wahlberg et al. (2002b) the dispersal ability of *E. aurinia* is comparably low, indicating that the exchange between populations is far too low to define the situation as a spatially structured population. This is supported by the comparably low extinction and colonisation rates in this study that correspond with the figures obtained by Wahlberg et al. (2002a). Various authors defined different

conditions for a metapopulation structure. According to Settele (1998) a metapopulation is sufficiently defined by occasional extinction and recolonisation of local populations at a low dispersal rate, which we can already show by the data mentioned above. Other authors add asynchrony of dynamics between populations as a condition (e.g., Reich and Grimm 1995; Hanski 1999), although this is not necessary for a metapopulation structure *per se*, but for long-term persistence of the metapopulation (Settele, pers. comm.). Our data is not sufficient to demonstrate asynchronic dynamics. However, variation in hatching dates between colonies at least indicates a potential for independent dynamics due to phenological variation.

It has been stated that *E. aurinia* population structure mostly resembles the 'mainland-island' or 'source-sink' type, simply because of the great variation of local population sizes (Lewis and Hurford 1997). However, this might lead to the false conclusion that conservation measures should mainly focus on the large populations considered as 'mainlands'. In fact, a long-term study of *Plebejus argus* (Thomas et al. 2002) has shown that even in cases where short-term population dynamics do not affect regional strongholds, long-term dynamics may also lead to extinction of the largest local populations in a metapopulation patch network. Hence, fluctuations of patch-occupancy are not restricted to small and peripheral patches, but also include populations considered as unaffected 'mainlands'. In such situations ephemeral populations may facilitate the recolonisation of a core habitat after a stochastic extinction event (Sternberg 1995).

#### *Combining habitat quality and population structure for conservation purposes*

Our study demonstrates that the evaluation of patch quality and suitability of management regimes based on a single life cycle stage may be misleading for insect species with a complex life cycle like *E. aurinia*. Previous studies based on standardised transect counts indicate a similar habitat suitability of extensively grazed pasture and litter meadows in pre-alpine southern Germany (Dolek and Geyer 1997; Dolek 2000). By considering larval habitat quality, however, we can show that suitable vegetation structures are

mainly restricted to litter meadows. Extensive pasture is primarily used by nectar feeding adults and may thus be an important habitat component. Within litter meadows, uncut edges and recently abandoned areas are essential for successful larval development. Hence, a conservation strategy that aims to fix a single management regime, e.g., a single cut per year in late autumn, will almost certainly accelerate the decline and extinction of *E. aurinia* in small patches. Successful management has to include both, cut or grazed parts as nectar and patrolling habitat, and uncut/abandoned areas for larval development, best established by some sort of rotational mowing. It should be noted, however, that our data do not show whether or not mowing is detrimental for *E. aurinia* webs. To test this further studies are urgently needed.

As larval density is correlated with host plant density, it appears possible to increase population size by increasing the availability of suitable host plants within a patch.

A management exclusively focusing on optimising within patch habitat quality might increase local environmental capacity and thus decrease the local extinction probability, but it will not alter the principle dynamics of the entire metapopulation. Our results show that a conservation strategy for *E. aurinia* should also include a network of suitable habitat patches, whether or not currently occupied. Similar conclusions have been drawn for other threatened butterfly species with low colonisation power (e.g., *Lycaena helle*, Fischer et al. 1999). In cases where the current spatial pattern of *E. aurinia* colonies does not allow an exchange between local populations, as is the case in several parts of Germany, the restoration of former habitats close to currently occupied habitats should have priority. Artificial reintroduction of mated females into formerly occupied habitats that are part of a habitat network may also be considered. However, previous reintroduction attempts in England had very low success (Oates and Warren 1990) and far more experience would be necessary to establish such measures.

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### References

- Anthes N., Hermann G. and Fartmann T. 2003. Wie lässt sich der Rückgang des Goldenen Scheckenfalters (*Euphydryas aurinia*) in Mitteleuropa stoppen? Erkenntnisse aus populationsökologischen Studien in voralpinen Niedermoorgebieten und der Arealentwicklung in Deutschland. *Naturschutz und Landschaftsplanung* 35: 279–287.
- Asher J., Warren M., Fox R., Harding P., Jeffcoate G. and Jeffcoate S. 2001. The millenium atlas of butterflies in Britain and Ireland. Oxford University Press.
- Boughton D.A. 1999. Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. *Ecology* 80: 2727–2739.
- Bühler C. and Schmid B. 2001. The influence of management regime and altitude on the population of *Succisa pratensis*: implications for vegetation monitoring. *J. Appl. Ecol.* 38: 689–698.
- Dennis R.L.H. and Eales H.T. 1997. Patch occupancy in *Coenonympha tullia* (Muller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. *J. Insect Conserv.* 1: 167–176.
- Dierschke H. 1994. Pflanzensoziologie, Ulmer Verlag, Stuttgart.
- Dolek M. 2000. Der Einsatz der Beweidung in der Landschaftspflege: Untersuchungen an Tagfaltern als Zeigergruppe. *Laufener Seminarbeiträge* 4/2000: 63–77.
- Dolek M. and Geyer A. 1997. Influence of management on butterflies of rare grassland ecosystems in Germany. *J. Insect Conserv.* 1: 125–130.
- Dolek M., Radlmair S. and Geyer A. 1999. Der Einfluss der Nutzung (Weide, Mahd, Brache) voralpiner Mooregebiete auf die Insektenfauna (Tagfalter, Heuschrecken). *Schriftenreihe des Bayerischen Landesamts für Umweltschutz* 150: 133–140.
- Ebert G. and Rennwald E. 1991. Die Schmetterlinge Baden-Württembergs. Band 1, Tagfalter I. Verlag Eugen Ulmer, Stuttgart.
- Fartmann T. 1997. Biozöologische Untersuchungen zur Heuschreckenfauna auf Magerrasen im Naturpark Märkische Schweiz (Ostbrandenburg). *Arbeiten aus dem Institut für Landschaftsökologie, Westfälische Wilhelms-Universität Münster* 3: 1–62.
- Fartmann T., Hafner S. and Hermann G. 2001. Skabiosen-Scheckenfalter (*Euphydryas aurinia*). In: Fartmann T., Gunnemann H., Salm P. and Schröder E. (eds), Berichtspflichten in Natura-2000-Gebieten. Empfehlungen zur Erfassung der Arten des Anhangs II und Charakterisierung der Lebensraumtypen des Anhangs I der FFH-Richtlinie (= Angewandte Landschaftsökologie, Heft 42), Bundesamt für Naturschutz, Bonn, pp. 363–368.

- Fischer K. 1997. Zur Ökologie des Skabiosen-Scheckenfalters *Euphydryas aurinia* (Rottemburg, 1775) (Lepidoptera: Nymphalidae). Nachr. Entomol. Ver. Apollo 18: 287–300.
- Fischer K., Beinlich B. and Plachter H. 1999. Population structure, mobility and habitat preferences of the violet copper *Lycaena helle* (Lepidoptera: Lycaenidae) in Western Germany: implications for conservation. J. Insect Conserv. 3: 43–52.
- Ford H.D. and Ford E.B. 1930. Fluctuation in numbers, and its influence on variation in *Melitaea aurinia*, Rott. (Lepidoptera). Trans. Entomol. Soc. Lond. 78: 345–351.
- Hanski I. 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63: 151–162.
- Hanski I. 1999. Metapopulation Ecology, 1st edn, Oxford University Press.
- Hermann G. 1998. Erfassung von Präimaginalstadien bei Tagfaltern – Ein notwendiger Standard für Bestandsaufnahmen zu Planungsvorhaben. Naturschutz und Landschaftsplanung 30: 133–142.
- Hermann G. and Steiner R. 1997. Eiablage- und Larvalhabitat des Komma-Dickkopffalters (*Hesperia comma* Linné 1758). Carolinea 55: 35–42.
- Kuussaari M., Nieminen M. and Hanski I. 1996. An experimental study of migration in the glenville fritillary butterfly *Melitaea cinxia*. J. Anim. Ecol. 65: 791–801.
- Lavery T.A. 1993. A review of the distribution, ecology and status of the marsh fritillary *Euphydryas aurinia* Rottemburg, 1775 (Lepidoptera: Nymphalidae) in Ireland. Ir. Nat. J. 24: 192–199.
- Lewis O.T. and Hurford C. 1997. Assessing the status of the marsh fritillary butterfly (*Eurodryas aurinia*): an example from Glamorgan, UK. J. Insect Conserv. 1: 159–166.
- Lewis O.T., Thomas C.D., Hill J.K., Brookes M.I., Crane T.P.R., Graneau Y.A., Mallet J.L.B. and Rose O.C. 1997. Three ways of assessing metapopulation structure in the butterfly *Plebejus argus*. Ecol. Entomol. 22: 283–293.
- Mazel R. 1984. Trophisme, hybridation et Speciation chez *Eurodryas aurinia* Rottemburg (Lepidoptera – Nymphalidae). PhD thesis, University of Perpignan, France.
- Moilanen A. and Hanski I. 2001. On the use of connectivity measures in spatial ecology. Oikos 95: 147–151.
- Munguira M.L., Martin J., Garcia-Barros E. and Viejo J.L. 1997. Use of space and resources in a Mediterranean population of the butterfly *Euphydryas aurinia*. Acta Oecologica 18: 597–612.
- Oates M.R. and Warren M.S. 1990. A Review of Butterfly Introductions in Britain and Ireland. World Wide Fund for Nature, Godalming.
- Oppermann R. 1987. Tierökologische Untersuchungen zum Biotopmanagement in Feuchtwiesen. Ergebnisse einer Feldstudie an Schmetterlingen und Heuschrecken im württembergischen Alpenvorland. Natur und Landschaft 62: 235–241.
- Porter K. 1982. Basking behaviour in larvae of the butterfly *Euphydryas aurinia*. Oikos 38: 308–312.
- Porter K. 1983. Multivoltinism in *Apanteles bignelli* and the influence of weather on synchronisation with its host *Euphydryas aurinia*. Ent. exp. & appl. 34: 155–162.
- Porter K. 1992. Eggs and egg-laying. In: Dennis R.L.H. (ed.) The ecology of butterflies in Britain, Oxford University Press, pp. 46–72.
- Reich M. and Grimm V. 1995. Das Metapopulationskonzept in Ökologie und Naturschutz: Eine kritische Bestandsaufnahme. Z. Ökologie u. Naturschutz 5: 123–139.
- SBN(Schweizer Bund für Naturschutz), 1991. Tagfalter und ihre Lebensräume. Arten, Gefährdung, Schutz. Band 1. Fotorotar, Basel.
- Scholle D., Hofmann C., Kaule G., Lederbogen D., Rosenthal G., Thumm U. and Trautner J. 2002. Co-operative grazing systems ('Allmende'): An alternative concept for the management of endangered open and semi-open landscapes. In: Redecker B., Fink P., Härdtle W., Riecken U. and Schröder E. (eds), Pasture Landscapes and Nature Conservation, Springer, Berlin, pp. 387–398.
- Settele J. 1998. Metapopulationsanalyse auf Rasterdatenbasis. Teubner Verlagsgesellschaft, Stuttgart.
- Sternberg K. 1995. Populationsökologische Untersuchungen an einer Metapopulation der Hochmoor-Mosaikjungfer (*Aeshna subarctica elisabethae* Djakonov, 1922) (Odonata, Aeshnidae) im Schwarzwald. Z. Ökologie u. Naturschutz 4: 53–60.
- Sundermeier A. 1999. Zur Vegetationsdichte der Xerothermrassen nordwestlich von Halle/Saale – Erfassungsmethoden, strukturelle Vegetationstypen und der Einfluß der Vegetationsdichte auf das reproduktive Potential von Xerothermrassenarten. Dissertationes Botanicae 316: 1–192.
- Thomas C.D., Wilson R.J. and Lewis O.T. 2002. Short-term studies underestimate 30-generation changes in a butterfly metapopulation. Proc. R. Soc. Lond. B 269: 563–569.
- Thomas J.A., Bourn N.A.D., Clarke R.T., Stewart K.E., Simcox D.J., Pearman G.S., Curtis R. and Goodger B. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc. R. Soc. Lond. B 268: 1791–1796.
- Thomas J.A. and Morris M.G. 1994. Patterns, mechanisms and rates of decline among UK invertebrates. Phil. Trans. R. Soc. Lond. B 344: 47–54.
- van Swaay C. and Warren M. 1999. Red data book of European butterflies (Rhopalocera). In: Council of Europe, Nature and Environment, No. 99, Strasbourg, France.
- Wahlberg N. 2001. The phylogenetics and biochemistry of host-plant specialization in Melitaeine butterflies (Lepidoptera: Nymphalidae). Evolution 55: 522–537.
- Wahlberg N., Klemetti T. and Hanski I. 2002a. Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography 25: 224–232.
- Wahlberg N., Klemetti T., Selonen V. and Hanski I. 2002b. Metapopulation structure and movements in five species of checkerspot butterflies. Oecologia 130: 33–43.
- Warren M.S. 1994. The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary (*Eurodryas aurinia*). Biol. Conserv. 67: 239–249.
- Warren M.S., Munguira M.L. and Ferrin J. 1994. Notes on the distribution, habitats and conservation of *Eurodryas aurinia* (Rottemburg) (Lepidoptera: Nymphalidae) in Spain. Entomologists' Gazette 45: 5–12.