Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany

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Analyses of phenology, oviposition preference and patch occupancy of *Hamearis lucina* were made in calcareous grasslands in the Diemel Valley (central Germany) at its northwestern latitudinal limit in continental Europe. Distribution and range dynamics in Germany are shown. The patch occupancy of *H. lucina* in calcareous grasslands could best be explained by oviposition-habitat preferences, adjacency of old woodland and isolation. *H. lucina* mainly colonised shrubby semi-dry calcareous grasslands with *Primula veris* and a high total vegetation coverage on west-facing slopes. The key factors determining the oviposition habitat are (i) the presence of the host plant and (ii) the vegetation structure and, partly interrelated with this, the meso-/microclimate. The spatial structure and the climate near ground drive the host plant availability. The colonies of *H. lucina* in calcareous grasslands showed a strong association with adjacent old woodlands, which suggests that the current distribution pattern still reflects the historical habitat shift from coppiced woods into calcareous grassland after abandonment of coppicing and grazing. The present study showed that *H. lucina* tolerates a wide range of grazing intensities in Germany. The most favourable tool is traditional rough grazing. Habitat heterogeneity could buffer populations against climate change. Therefore it is necessary to create and secure sites with a high structural and aspectual variety.

Introduction

Butterflies provide a well-studied model organism in animal ecology (Watt & Boggs 2003). They respond more rapidly to environmental changes than many other organisms and therefore serve as excellent indicators in conservation policies (Thomas & Clarke 2004, Thomas *et al.* 2004).

Three main factors have been found to determine the persistence of butterflies in cultivated landscapes: habitat quality within sites, isolation of habitat patches, and patch size (Dennis & Eales 1997, Fleishman *et al.* 2002, Fred &
Brommer 2003, J. A. Thomas et al. 2001, Anthes et al. 2003, WallisDeVries 2004). However, the type of metapopulation, and therefore the significance, of each of the three parameters differ considerably between species. As such, a detailed understanding of habitat quality as the basic unit for conservation measures (Dennis et al. 2003) is crucial for creating a network of suitable and sufficient habitat patches (Dennis et al. 2003, Shreeve et al. 2004, WallisDeVries 2004).

Shreeve et al. (2004) further stated that resources define the habitat and population structure. However, adequate habitat requires more than just a quantity of host plants. Since the habitat requirements of butterflies are often highly specific (Thomas 1991), detailed knowledge of autecology and synecology is indispensable for successful conservation (Shreeve et al. 2004). For example, the factors that determine the persistence of butterflies with low mobility in a landscape with widely distributed host plants are poorly understood. *Hamearis lucina* — the Duke of Burgundy — provides a good system to study such effects. This species is generally classified as a stress-tolerator with metapopulations of the Levins type and a low mobility (Dennis et al. 2004). It is the only European representative of the mostly tropical riodinid butterflies. *Hamearis lucina* has a rather sparse but widespread occurrence across Europe, from central Spain to southern Sweden, and east as far as central Russia (Emmet & Heath 1989, Ebert & Rennwald 1991).

Severe geographical and numerical decline has occurred throughout the northern half of its range (Sparks et al. 1994, León-Cortés et al. 2003). The species is listed as ‘near threatened’ in Europe as a whole (van Swaay & Warren 1999) and ‘threatened’ in Germany (Pretscher 1998). The main reasons for the decline are considered to be afforestation of grassland, decline of coppice management, extensive coniferisation of ancient woodland and, as a result of this, habitat fragmentation (Emmet & Heath 1989, Ebert & Rennwald 1991, Asher et al. 2001).


*Hamearis lucina* rarely uses nectaring flowers (Garling 1984) and nectar is not considered a limiting resource (Frohawk 1934, Oates 2000). As with many other butterfly species, the habitat requirements of the immature stages of *H. lucina* are more specific than that of the adults (Sparks et al. 1994, Oates 2000). While two studies documented larval habitats of *H. lucina* in Great Britain (Sparks et al. 1994, Oates 2000), there are only a few notes from continental Europe (Garling 1984, Ebert & Rennwald 1991, Weidemann 1995, Fartmann 2004). León-Cortés et al. (2003) combined habitat quantity and fragmentation in a metapopulation model. According to their study, extinction probability correlates positively with isolation and migration rate and negatively with habitat quantity.

In this paper I determine for the first time the conditions that promote the persistence of *H. lucina* in calcareous grasslands at its north-western range limit in central Europe. I further summarise its phenology, oviposition preferences, patch occupancy and German distribution. Finally, I recommend revised management requirements for *Hamearis lucina*.

**Study area**

The study area (hereafter called Diemel Valley) of about 390 km² is located in central Germany along the border between the federal states of North Rhine-Westphalia and Hesse (51°22’N, 8°38’E and 51°38’N, 9°25’E) at an elevation of 100 to 610 m a.s.l. (Fig. 1). The climate is sub-oceanic and varies greatly with altitude (Müller-Wille 1981). The mountainous western Upper Diemel Valley (> 450 m a.s.l.) tends to be colder (mean annual temperature about 6.5 °C) and wetter (mean annual precipitation > 1000 mm). The Middle and Lower Diemel Valley (< 300 m a.s.l.) in the eastern part of the study area have
a relatively mild climate with less than 700 mm annual precipitation and an average annual temperature of up to 9 °C (Müller-Temme 1986, MURL NRW 1989, Fartmann 2004).

Until the mid-19th century the landscape of the Diemel Valley was characterised by nutrient-poor arable fields, large rough grazed meadows, and woodlands that were used as coppice or coppice-with-standards (Brökel 1984, Brohl 1990, Lucan & Eger 1996). Since then, the size of sheep pasture and coppiced woodland areas has decreased drastically. Following World War II coppicing nearly came to a standstill and many calcareous grasslands were left ungrazed and/or were afforested (Schubert 1989, Hozak & Meyer 1998, Fartmann 2004). This development closely matches that described for other parts of Europe (Buckley 1992, Quinger et al. 1994, Beinlich & Plachter 1995, Rossmann 1996, WallisDeVries et al. 2002).

Nowadays, calcareous grassland complexes, the only breeding sites of *Hamearis lucina* in the Diemel Valley, cover approximately 750 ha (approx. 2% of the total area). The most abundant vegetation type of the calcareous grassland is the *Gentiano-Koelerietum* (*Enzian-Fiederwiesenrasen*) (Fartmann 2004). Large parts of the Diemel Valley are proposed Sites of Community Interest (pSCI) (E. Schröder, German Federal Agency for Nature Conservation, pers. comm.) and the prime butterfly area *Diemeltal* is part of the study area (van Swaay & Warren 2003).

**Methods**

**Phenology**

To show the seasonal timing of various life-cycle stages of *Hamearis lucina* the study area was surveyed systematically between 1998 and 2000, aiming at visiting representative *H. lucina* patches for about three days every week from mid-April until the start of July. Furthermore, available data of local entomologists on adult individuals (H. Biermann, K. Gottschalk, H. Retzlaff, H.-J. Weigt pers. comm.) from the period between 1965 and 2000 were included.

**Oviposition habitats**

On the 47 occupied sites (cf. Patch occupancy), systematic samples of *Primula veris* on a 5 × 5 or 10 × 10 m grid were searched for eggs. Microhabitat structure was analysed in a radius of 50 cm around each of the 227 clutches based on the following parameters: coverage of shrub, herb/grass, moss/lichen and litter layers, horizontal vegetation coverage in 10, 20 and 30 cm (20 cm in depth) above ground (in 5% steps) (Anthes et al. 2003, Fartmann 2004). The number of eggs per batch was counted; egg-laying and host-plant height above ground level were measured.

Vitality of occupied host plants was categorized as high (luxuriant plants with huge leaves),
medium (‘normal’ plants) and low (small plants, sometimes wilting). The sites’ main vegetation was classified according to their characteristic and differentiating plant species (Dierschke 1994, Fartmann 2004). To examine the maximal average sunshine duration (in hours) and the time of the day of potential sunshine during population peak of *Hamearis lucina* (May), a horizontoscope (after Tonne 1954) was used. Both present and historical management of sites were ascertained by direct observation or through conversation with site managers and farmers. Slope aspect and inclination (both in degrees) were recorded by using a compass with inclinometer.

For comparing occupied and the spectrum of available host plants, 47 vegetation relevés of 16 m² with presence of *Primula veris* according to the Braun-Blanquet methodology were used. They represented all potential *H. lucina* habitat types corresponding to their area proportion in the Diemel Valley (Fartmann 2004). The explanatory power of nine predictor variables (cover [%] of trees, shrubs, herbs/grasses, litter, mosses/lichens, rocks/stones/gravel and bare ground as well as aspect [°] and vegetation height [%]) on oviposition was assessed using a stepwise-forward logistic regression.

### Patch occupancy in the Diemel Valley

In total, 145 calcareous grassland habitat patches were surveyed. Of those, 84 habitat patches with a mean size of 4.46 ha (0.08–21.32 ha; SD = 4.56 ha) were colonised by the host plant *Primula veris*. Occurrence of *H. lucina* in these patches was examined during the adult or immature stages. Stepwise-forward logistic regression was used to assess the relationship between presence or absence of the species on a patch on the one hand and the area, isolation (distance to the next populated patch, both ln-transformed to obtain normality), land-use types (abandoned pasture, rough grazing [sheep/goat], paddock [sheep/goat], mowing, cattle pasture) and presence or absence of adjacent woods (older and younger than 50 years) on the other hand. In the present study, a population is defined as a group of breeding individuals that is isolated from the nearest neighbouring group by over 50 m of woodland, improved grassland or arable fields.

### Distribution in Germany


Statistical analysis was performed using SPSS 8.0 statistical package. Because chi-square test does not allow empty categories, frequencies of 0 were conservatively set to 1.

### Results

#### Phenology

In the Diemel Valley *Hamearis lucina* has one generation per year, from early May to early June, but adults can emerge as early as the end of April (21st) in warm springs like in the late

![Fig. 2. Phenology of *Hamearis lucina* in the Diemel Valley between 1965 and 2000. Bars give 5-day means of observed adult individuals from April until June.](image-url)
Oviposition habitats

Females of *Hamearis lucina* were extremely selective about oviposition sites. Out of 227 clutches with 416 eggs or eggshells found, 226 were on *Primula veris*. Only 1 clutch was laid on *Sanguisorba minor* near *Primula veris*. Eggs were laid singly (49%), in groups of two (30%) or small batches of 3–4 (19%) up to 6 (2%) on the underside margin of host-plant leaves. In those cases where *Primula veris* was scarce, high concentrations of eggs per plant were possible, 12 eggs being the maximum per plant.

The great majority of clutches was found on medium-sized host plants (90%); only 9% were on large and 1% on small ones. Host plants with low vitality under warm and very dry conditions (e.g., in short open turf on south-facing slopes or on skeletal soil) were ignored. Occupied leaves (e.g., in short open turf on south-facing slopes or low vitality under warm and very dry conditions on large and 1% on small ones. Host plants with medium-sized host plants (90%); only 9% were from late May until early July (4th, also the date of last data collection, *Primula veris*) were recorded from early May (3rd) until early July (4th, also the date of last data collection).

Host plants with a shrub layer often existed, but at low coverage (median = 10%).

While the distribution of host-plant height is bell-shaped, the distribution of egg-deposition height is left-skewed, which indicates a preference for lower deposition heights between 5 and 16 cm above ground (median = 9 cm, range = 3–35 cm) (Fig. 3). The analysis of horizontal vegetation coverage at different heights above ground further showed that vegetation cover was very dense near the ground (5 cm height median = 80%, 1st to 3rd quartile: 50%–100%), but already drastically decreased at 10 cm above ground (median = 30%) and was negligible further up. When comparing the area of available *Primula veris* sites with that of occupied patches (χ² = 17.1, df = 4, P < 0.005) (Table 1), and even more so with that of plants used for oviposition (χ² = 107.4, df = 4, P < 0.001), westerly to southerly exposed slopes were predominantly used (Fig. 4).

Aspect and inclination are linked with maximal potential daily sunshine at the egg-laying sites. Most clutches were found at sites with 4–8 hours of sunshine in May (median = 6 h, range = 0.5–11 h). The majority of clutches was found at sites that potentially receive direct insolation between 09:00 and 17:00. A general feature of the oviposition habitats of *H. lucina* is sunshine during only a part of the day, mostly in the afternoon. However, insolation at egg-laying sites further varied significantly according to their aspect (Fig. 5, Kruskal-Wallis test: χ² = 27.5, df = 3, P < 0.001): Whilesouth- and southwest-facing oviposition habitats receive only about
4.5 and 5 h direct insolation in May, it was 6 and 10.5 h on west- and north-facing slopes, respectively.

Herb coverage and maximal daily sunshine in May did not correlate significantly at oviposition sites on south and southwest-facing slopes (south: $r_s = 0.24, N = 19, P = 0.34$; southwest: $r_s = -0.15, N = 50, P = 0.29$), but did so on both west-facing ($r_s = 0.29, N = 136, P < 0.01$) and even stronger on northwest-facing slopes ($r_s = 0.77, N = 11, P < 0.01$).

Egg-laying sites mostly occurred on semi-dry grasslands of the Gentiano-Koelerietum trifolietosum, the seams of the Trifolio-Agrimonietum and initial forms of the shrub community Pruno-Ligustretum. Furthermore, nutrient-poor grassland types like the Arrhenatherum elatius meadows (Arrhenatheretum), the Lolio-Cynosuretum pastures, swards of Brachypodium pinnatum and Bromus erectus, clear cuts, and light forest communities like calcareous beech forests (Carici-Fagetum) and scotch pine forests on limestone (Erico-Pinion) were used for egg-laying.

In the Lower and Middle Diemel Valley oviposition habitats were mostly near shrubs or forest edges, while in the cooler and wetter Upper Diemel Valley the distances to shrub groups were up to 10 m.

Oviposition pattern at Primula veris was best explained by a combination of vegetation structure parameters and aspect (Table 2). The likelihood of a host plant being accepted for oviposi-

**Table 1.** Aspects of surveyed habitat patches, patches occupied by Hamearis lucina and used plants for oviposition in the Diemel Valley between 1998–2000. Slopes of less than $10^\circ$ to the horizontal were classified as flat (Warren 1993).

<table>
<thead>
<tr>
<th>Aspect</th>
<th>Sites with Primula veris ($N = 84$)</th>
<th>Occupied patches ($N = 47$)</th>
<th>Used plants ($N = 227$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area (ha) Proportion (%)</td>
<td>Area (ha) Proportion (%)</td>
<td>No. of plants Proportion (%)</td>
</tr>
<tr>
<td>N</td>
<td>38 10</td>
<td>30 13</td>
<td>0 0</td>
</tr>
<tr>
<td>E</td>
<td>40 11</td>
<td>12 5</td>
<td>2 1</td>
</tr>
<tr>
<td>S</td>
<td>106 29</td>
<td>70 31</td>
<td>41 18</td>
</tr>
<tr>
<td>W</td>
<td>106 29</td>
<td>82 36</td>
<td>125 55</td>
</tr>
<tr>
<td>Flat</td>
<td>77 21</td>
<td>33 15</td>
<td>59 26</td>
</tr>
<tr>
<td>Total</td>
<td>374 100</td>
<td>229 100</td>
<td>227 100</td>
</tr>
</tbody>
</table>
tion increased with aspect (°) and coverage of shrubs and litter, but decreased with coverage of bare ground.

**Patch occupancy**

The distribution of *Hamearis lucina* in the Diemel Valley is clumped and can, in the first instance, be explained by the presence of *Primula veris* on calcareous grasslands (Fig. 1). However, *H. lucina* occurred only in 47 (56%) out of 84 surveyed habitat patches with the host plant present, suggesting that further patch characteristics determine its distribution. In a logistic-regression model, 77% of the patch occupancy could correctly be predicted by the presence of woodland older than 50 years adjacent to chalk grassland and the distance to the next populated patch (Table 3). Patch size did not further improve the model: The mean size of the occupied patches was 4.87 ha (0.1–21.3 ha, SD = 4.51 ha), the mean distance to the nearest occupied patch 597 m (63–1900 m, SD = 589 m).

**Table 2.** Binary logistic-regression analysis on nine predictor variables at available (N = 47 relevés) and occupied host plants (N = 227 clutches) of *Hamearis lucina* in the Diemel Valley. Several variables entered into the regression were not significant: cover (%) of trees, herbs/grasses, mosses/lichens, rocks/stones/gravel and vegetation height (cm).

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Parameter (B)</th>
<th>SE</th>
<th>Wald</th>
<th>P</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cover (%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrubs</td>
<td>0.06</td>
<td>0.02</td>
<td>6.00</td>
<td>&lt; 0.05</td>
<td>0.13</td>
</tr>
<tr>
<td>Litter</td>
<td>0.05</td>
<td>0.02</td>
<td>10.39</td>
<td>&lt; 0.01</td>
<td>0.18</td>
</tr>
<tr>
<td>Bare ground</td>
<td>−0.06</td>
<td>0.03</td>
<td>4.82</td>
<td>&lt; 0.05</td>
<td>−0.11</td>
</tr>
<tr>
<td>Aspect (°)</td>
<td>0.03</td>
<td>0.01</td>
<td>27.46</td>
<td>&lt; 0.001</td>
<td>0.32</td>
</tr>
<tr>
<td>Constant</td>
<td>−4.14</td>
<td>1.16</td>
<td>19.64</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>Model χ² = 65.05, d.f. = 4, P &lt; 0.001, Correctly classified 84.62%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 3.** Binary logistic-regression analysis on presence and absence of *Hamearis lucina*. The analysis included all 84 calcareous grassland patches with presence of *Primula veris* in 1998–2000 in the Diemel Valley. n.s.: parameter not significant; land-use type: abandoned pasture, rough grazing (sheep/goat), paddock (sheep/goat), mowing and cattle pasture. Several variables entered into the regression were not significant: area (ln ha), young woodland (0/1), land use type (5 categories).

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Parameter (B)</th>
<th>SE</th>
<th>Wald</th>
<th>P</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>2.21</td>
<td>1.56</td>
<td>2.00</td>
<td>n.s.</td>
<td></td>
</tr>
<tr>
<td>Old woodland (0/1)</td>
<td>2.05</td>
<td>0.54</td>
<td>14.27</td>
<td>&lt; 0.001</td>
<td>0.33</td>
</tr>
<tr>
<td>Distance (ln m)</td>
<td>−1.18</td>
<td>0.54</td>
<td>4.79</td>
<td>&lt; 0.05</td>
<td>−0.16</td>
</tr>
<tr>
<td>Model χ² = 28.57, d.f. = 2, P &lt; 0.001, Correctly classified 77.38%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
found in altitudes between 140 and 520 m a.s.l., representing almost the full altitudinal range of the study area (100–610 m a.s.l.).

**Distribution in Germany**

*Hamearis lucina* has thus far been recorded in 683 10 × 6 geographic minute grid squares across Germany. Only for the northern German federal states Schleswig-Holstein, Hamburg, Berlin and Bremen records are lacking (Fig. 6). During the 19th and the early 20th centuries colonies occurred in the mountain areas and to a lesser extent in the lowlands; high mountain ranges were never colonised. Since then the Duke of Burgundy has declined in the lowlands, while the populations in low mountain ranges have remained more or less stable. Now the Duke of Burgundy is extinct in the whole northern lowland including the German federal states Mecklenburg-Western Pomerania and Brandenburg. On the distributional basis the species has declined by about 13% since recording started. Nowadays, the strongholds of *H. lucina* are the low limestone mountain ranges in central and southern Germany.

**Discussion**

The patch occupancy of *Hamearis lucina* in the calcareous grasslands of the Diemel Valley can best be explained by: (i) oviposition preferences, (ii) adjacency of old woodland and (iii) isolation.

In the study area and in all other calcareous grasslands in central and northern Europe, the Duke of Burgundy is restricted to a narrow ecological niche, defined by the larval host-plant resource (Warren & Thomas 1992, Sparks et al. 1994, Oates 2000, Fartmann 2004). The results presented here indicate that *H. lucina* requires shrubby semi-dry calcareous grasslands with presence of *Primula veris* and a high total vegetation coverage on west-facing slopes. Vegetation was

**Table 4.** Management regimes of surveyed habitat patches and those occupied by *Hamearis lucina* in the Diemel Valley between 1998–2000.

<table>
<thead>
<tr>
<th>Management regime</th>
<th>Surveyed sites (N = 84)</th>
<th>Occupied sites (N = 47)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area (ha)</td>
<td>Proportion (%)</td>
</tr>
<tr>
<td>Abandoned pasture</td>
<td>172</td>
<td>46</td>
</tr>
<tr>
<td>Rough grazing (sheep/goat)</td>
<td>89</td>
<td>24</td>
</tr>
<tr>
<td>Paddock (sheep/goat)</td>
<td>55</td>
<td>15</td>
</tr>
<tr>
<td>Mowing</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Cattle pasture</td>
<td>51</td>
<td>14</td>
</tr>
<tr>
<td>Total</td>
<td>374</td>
<td>100</td>
</tr>
</tbody>
</table>
particularly dense in the first 5 cm above ground. Together with a certain amount of litter this may serve to store humidity and therefore prevent eggs and host plants from desiccation. Eggs are usually deposited singly or in small batches on medium-sized Primula veris plants 10 cm above soil surface. Primula veris is the only host plant of H. lucina in the Diemel Valley, although Primula elatior is common in the region as well, but it typically grows in locations that are too shady to be used by the butterfly. The main occupied vegetation types include semi-dry grasslands (Gentiano-Koelerietum trifolietosum), seams (Trifolio-Agri monietum) and initial shrub communities (Pruno-ligustretum) no farther away than 10 m from shrubs or woodland. The key factors determining the oviposition habitat are (i) the presence of the host plant and (ii) the vegetation structure and, partly interrelated with this, the meso-/microclimate. The spatial structure and the climate near ground drive the host plant availability.

Why does H. lucina prefer west-facing slopes in the Diemel Valley? It appears very likely that southern aspects are usually too hot and dry in May and June, so that host plants are prone to desiccation. Furthermore, a higher humidity could be necessary for the development of the eggs. Egg-laying on the undersides of leaves, as opposed to the top, and the dense layers of herbs, mosses and litter that are able to store humidity are in line with this hypothesis. Eastern aspects, in contrast, are rarely used, presumably because they do not warm up sufficiently to enable egg development.

Apparently, females use south- and southwest-facing slopes for egg-laying only in cases where direct insolation and heat stress are restricted due to the screening-off of the horizon. On west and northwest aspects, in contrast, egg-deposition sites are chosen only when the sites are characterised by extended insolation, possibly enabling a faster egg development.

The oviposition habitat characterisation given here fits previous remarks (Ebert & Rennwald 1991, Dennis 1992, Sparks et al. 1994, Warren & Bourn 1998, Oates 2000). The preference for west- and north-facing slopes as well as the avoidance of south facing slopes except at sites where scrub is abundant to provide some taller areas and shade was reported from Britain (Warren 1993). Herrmann (as cited in Ebert & Rennwald 1991) reported that H. lucina avoids the hottest sites in the ‘Kaiserstuhl’ in Baden-Württemberg and Ebert and Rennwald (1991) emphasised that egg-laying sites receive sunshine in the afternoon.

The strong association between presence of H. lucina and adjacent old woodlands could indicate two things: (i) a shift from woods into calcareous grasslands and (ii) a low mobility of the species. As in Great Britain (Frohawk 1934, Emmet & Heath 1989) the Duke of Burgundy was formerly a species of open woodland in most parts of its German range (Belling 1928, Bergmann 1952, de Lattin 1957, Max 1977, Hasselbach 1981, Brockmann 1989).

Occurrence in calcareous grasslands at the beginning of the 20th century was not reported. Apparently, woodlands became too shaded when traditional coppice management and grazing were successively abandoned. Optimal conditions are the early successional stages of coppiced woodland in the first 2–4 years after cutting (Warren & Thomas 1992). In the Alsatian Hardt, H. lucina is a typical species of the seam and shrub phase of coppice-with-standards (Treiber 2003).

Almost simultaneously with the neglect of forest habitats after World War II, many calcareous grasslands in the Diemel Valley became abandoned because of decreasing sheep numbers (Fartmann 2004). This provided new, suitable habitat to H. lucina, since successional stages of formerly grazed grasslands structurally resemble coppiced woodland. Whether this coincides with a decrease of rabbit populations due to the spread of myxomatosis and the relaxation of rabbit grazing, as recorded in Great Britain (BUTT 1986, Warren & Thomas 1992, Sparks et al. 1994) cannot be said.

The strong decline of H. lucina took place in woodland and nutrient-poor grassland until the mid-19th century and until the 1980s, respectively. In the last two decades the populations of H. lucina in the Diemel Valley (Fartmann 2004) and most calcareous grasslands in Germany seemed to be stable or decreasing slowly (G. Hermann pers. comm., J.-U. Meineke pers. comm., R. Thust pers. comm.).

While males defend small territories and are sedentary, females can disperse over distances
of 250 m or more (Oates 2000). Moreover, a number of colonisations reaching as far as 5 km from the sources have been documented in well studied parts of Britain (Bourn & Warren 1998). In contrast to these findings, Kirtley (1995, 1997 as cited in Bourn & Warren 1998) documented a low mobility and Oates (2000) pointed out the paucity of new colonisations. The present study is in line with the latter cases; otherwise more calcareous grasslands with adjacent young woods or forests would have been colonised. Furthermore, the populations of *H. lucina* in the Diemel Valley, even small and isolated ones, seem to have a high persistence.

**Conservation management**

For conservation of many butterfly species it is crucial to provide a continuity of preferred egg-laying sites (Thomas 1983a, 1983b, Thomas et al. 1986, Sparks et al. 1994). Of particular relevance to the Duke of Burgundy is (i) the vegetation structure within the host plant communities and (ii) sufficient food for the larvae.

The present study shows that *Hamearis lucina* tolerates all kinds and intensities of grazing that are found in the calcareous grasslands of the Diemel Valley. All sites are characterised by a certain amount of shrub. The elimination of colonies through overgrazing, e.g. in Great Britain (Oates 2000), was not recorded in the Diemel Valley. Nevertheless, the highest population densities seemed to occur at sites grazed late in summer or in fallow land. The key to successful management of *H. lucina* in calcareous grasslands in Germany is keeping the sites open and free of invading scrub. The most favourable tool is traditional rough grazing (BUTT 1986), but some other grazing regimes are tolerable as well. Grazing must be practiced with special care only at small and isolated sites with low scrub cover.

Because resources to manage sites are scarce, cheap management tools are needed. In Germany *H. lucina* occurs at mostly small sites in the Diemel Valley often co-occurring with another threatened butterfly *Maculinea rebeli* (Fartmann 2004). An easy way of creating new habitats would be cutting down parts of the adjacent forests, often pine forests. This would allow populations to expand for a couple of years without any other management activities.

Where habitat conditions allow, some butterflies are able to respond rapidly to climate change (Warren et al. 2001). Recently, *H. lucina* extended northwards at its northern boundary and retreated northwards at the southern range limit due to global change (Parmesan et al. 1999). It is possible that this process may lead to a shift in larval habitat requirements as reported in other species (e.g. *Aricia agestis* and *Hesperia comma*, C. D. Thomas et al. 2001; *Lycaena alci-phron*, Dolek & Geyer 2001).

In case of predicted future climate change, shifts of the oviposition microhabitats of *H. lucina* seem necessary, due to the sensitivity to drought during the egg and larval stage. While the species currently prefers west-facing slopes, it may be expected to shift onto flat or north-facing slopes and cooler areas. For the Diemel Valley (own data) or parts of southern Germany (G. Hermann pers. comm.) this could mean that there will be insufficient habitat patches with these aspects to preserve the current populations. Furthermore, it seems obvious, due to the low mobility of *H. lucina*, that not all northern aspects or flat sites can be colonised. Therefore it is necessary to create and secure sites with a high structural and aspectual variety. Habitat heterogeneity could buffer populations against climate change (Oates 2000).

Due to the low mobility of *H. lucina* and the high persistence of the populations, metapopulation aspects play a minor role in the Duke of Burgundy in comparison with those in other butterfly species (cf. Discussion). Nevertheless, a conservation strategy should include a network of suitable habitat patches. Due to the low colonisation power, potential sites in a circle < 600 m around occupied patches are of special significance. Optimisation and creation of these patches should have priority.

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