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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).

Colonies of *H. lucina* breed in two main habitat types throughout Europe: shrubby calcareous grasslands and clearings in ancient woodlands (Emmet & Heath 1989, Ebert & Rennwald 1991, Sparks *et al*. 1994, Bourn & Warren 1998, Oates 2000, León-Cortés *et al*. 2003, Fartmann 2004). The main larval host-plant is cowslip (*Primula veris*) (Heath *et al*. 1984, Emmet & Heath 1989), in woodlands oxlip (*Primula elatior*) and primrose (*Primula vulgaris*) (Emmet & Heath 1989, Ebert & Rennwald 1991, Sparks *et al*. 1994).

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 northwestern range limit in central Europe. I further summarize 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 suboceanic 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

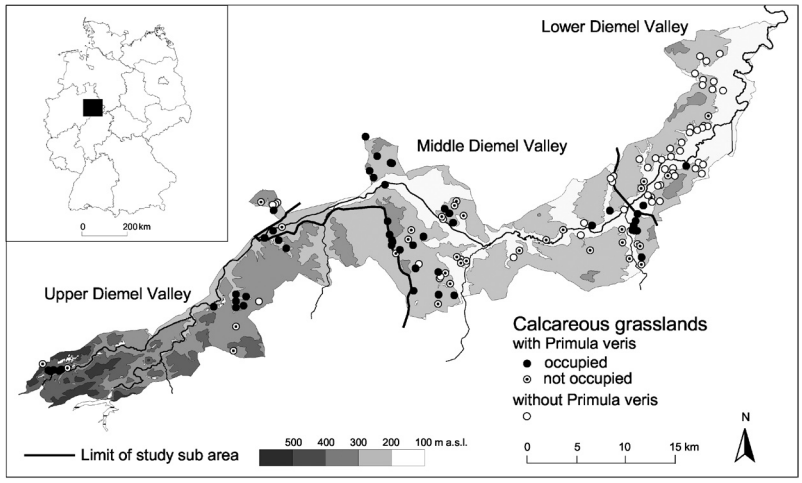

Fig. 1. Study area Diemel Valley in northwestern Germany (inlay) and patch occupancy of *Hamearis lucina* in the Diemel Valley between 1998 and 2000 (*N* = 145 surveyed sites).

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 *H. 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-Fiederzwenkenrasen')(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 categorised as high (luxuriant plants with huge leaves),

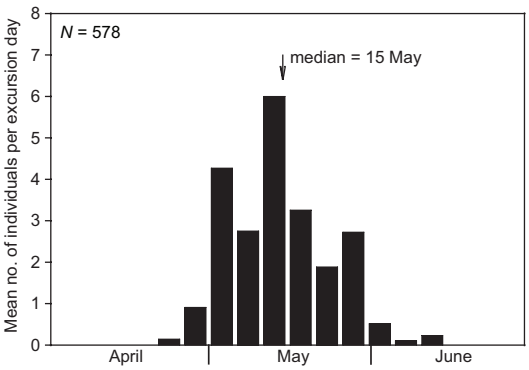

Fig. 2. Phenology of *Hamearis lucina* in the Diemel Valley between 1965 and 2000. Bars give 5-day means of observed adult individuals from April until June.

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

The current and past status of *Hamearis lucina* in Germany was assessed from local mapping schemes (Arten-Erfassungsprogramm Thüringer Landesanstalt für Umwelt und Geologie, T. Fritzlar pers. comm.; BLfU 2001, Ebert & Rennwald 1991; H. G. Joger pers. comm., P. Schmidt & C. Schönborn pers. comm., R. Thust pers. comm, R. Ulrich pers. comm.), local faunistic publications (Uffeln 1908, Bergmann 1952, Friese 1956, Retzlaff 1973, Harkort 1975, Hasselbach 1981, Stamm 1981, Kudrna 1988, Brockmann 1989, Ebert & Rennwald 1991, Kinkler *et al.* 1996, Schmitt 1998, Fartmann 2004) and the correspondence with 24 entomologists (*see* Acknowledgements).

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

1990s (1998–2000) (Fig. 2). The flight period lasts about four or five weeks each year. Typically, adult numbers peak by mid-May (median = 15 May, $N = 578$). Flight peak differed significantly between the predominantly cool seasons in 1965 to 1997 and the extraordinarily warm years of 1998–2000 (Mann-Whitney U-test: $U = 703.5$, $P < 0.001$). In 1965–1997 adults flew from 6 May until 11 June (median = 22 May, $N = 268$), and in 1998–2000 from 21 April until 5 June (median = 08 May, $N = 310$). Eggs were found from early May (3rd) until early July (4th, which was also the date of last data collection, $N = 262$). Empty eggshells ($N = 154$), larvae ($N = 7$) and the characteristic feeding damage ($N = 37$) on cowslip (*Primula veris*) were recorded from late May until early July (4th, also the date of last data collection).

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 were mostly elevated above the litter layer and therefore allowed the females to perch.

Oviposition sites of *H. lucina* were characterised by high total vegetation coverage (median: 100%), especially because of a more or less closed turf layer. More than three quarters of all clutches were found on places with more than 60% herb layer coverage (median = 100%). On relatively cool northwest-facing slopes or where tree or shrub coverage was high, sites with open turf were used as well. Usually, the coverage of mosses and lichens was low (median = 20%). However, where abundance of higher plants was low, up to 90% coverage was possible. There was always a certain amount of litter; mostly between 10% and 25% (median = 15%). Rocks, stones, gravel; bare ground and trees were of little significance in the egg-laying sites of *H. lucina*. A shrub layer often existed, but at low coverage (median = 10%).

Sward height at oviposition sites (median turf height = 20 cm, $N = 227$ clutches) was significantly greater than that at randomly chosen available plants (median turf height = 15 cm, $N = 47$ relevés, Mann-Whitney U-test: $U = 6693.0$, $P < 0.001$). Females usually laid their clutches about 10 cm (median = 11 cm above ground) below turf height.

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 ($\chi^2 = 17.1$, df = 4, $P < 0.005$) (Table 1), and even more so with that of plants used for oviposition ($\chi^2 = 107.4$, 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: $\chi^2 = 27.5$, df = 3, $P < 0.001$): While south- and southwest-facing oviposition habitats receive only about

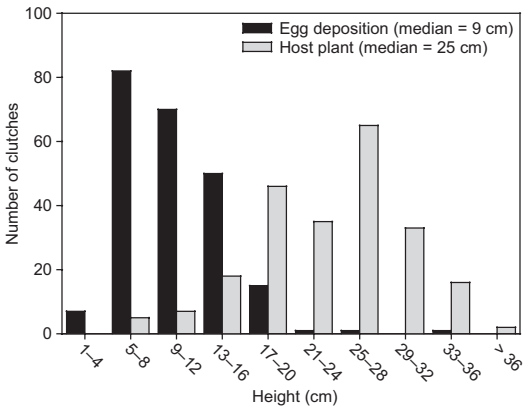

Fig. 3. Host-plant and egg-deposition height of *Hamearis lucina* in the Diemel Valley (*N* = 227 clutches).

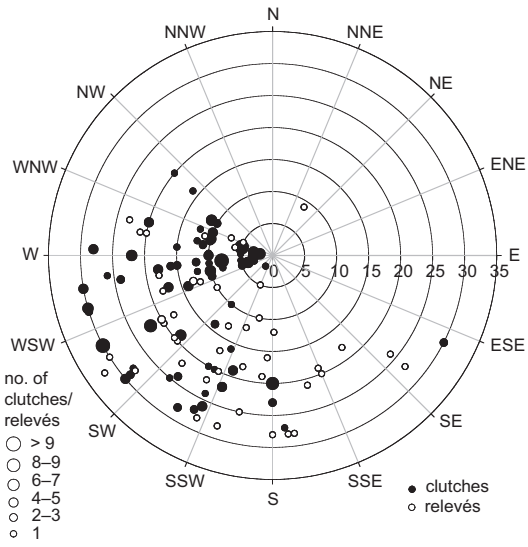

Fig. 4. Polarplot of the aspects and inclination of egg-laying sites of *Hamearis lucina* (*N* = 227 clutches) and representative relevés with *Primula veris* (*N* = 47) in the Diemel Valley.

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° to the horizontal were classified as flat (Warren 1993).

Aspect	Sites with *Primula veris* (*N* = 84)		Occupied patches (*N* = 47)		Used plants (*N* = 227)	
	Area (ha)	Proportion (%)	Area (ha)	Proportion (%)	No. of plants	Proportion (%)
N	38	10	30	13	0	0
E	40	11	12	5	2	1
S	106	29	70	31	41	18
W	106	29	82	36	125	55
Flat	77	21	33	15	59	26
Total	374	100	229	100	227	100

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).

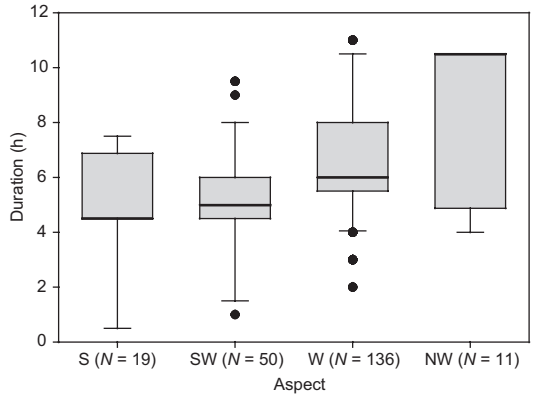

Fig. 5. Maximum daily direct insolation duration in May and aspect at egg-laying sites of *Hamearis lucina* in the Diemel Valley (N = 216 clutches). Box plots show outliers, maximum, minimum, interquartile range, and median duration (h).

Presence or absence of *H. lucina* at the patch level was furthermore not influenced by land use ($\chi^2 = 3.63$, df = 4, $P = 0.458$; Table 4). However, both adult and egg densities seemed to be very high on fallow land or at sites that are grazed late in the season. The colonies of *H. lucina* were

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).

Independent variable	Parameter (B)	SE	Wald	*P*	*R*
Cover (%)					
Shrubs	0.06	0.02	6.00	< 0.05	0.13
Litter	0.05	0.02	10.39	< 0.01	0.18
Bare ground	–0.06	0.03	4.82	< 0.05	–0.11
Aspect (°)	0.03	0.01	27.46	< 0.001	0.32
Constant	–4.14	1.16	19.64	< 0.001	
Model χ^2 = 65.05, d.f. = 4, P < 0.001, Correctly classified 84.62%					

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).

Independent variable	Parameter (B)	SE	Wald	*P*	*R*
Constant	2.21	1.56	2.00	n.s.	
Old woodland (0/1)	2.05	0.54	14.27	< 0.001	0.33
Distance (ln m)	–1.18	0.54	4.79	< 0.05	–0.16
Model χ^2 = 28.57, d.f. = 2, P < 0.001, Correctly classified 77.38%					

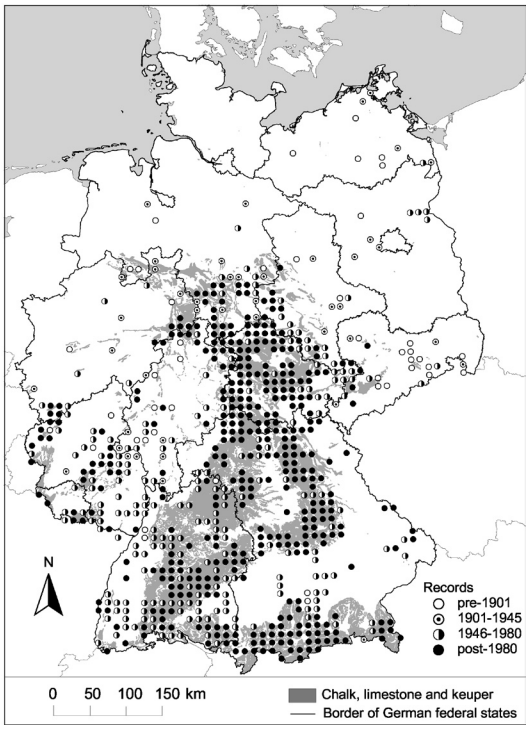

Fig. 6. Past and present distribution of *Hamearis lucina* in Germany, indicating the distribution of chalk, limestone and keuper strata as an indicator of calcareous grassland. Plotted by 10 × 6 geographic minute grid.

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.

Management regime	Surveyed sites (N = 84)		Occupied sites (N = 47)	
	Area (ha)	Proportion (%)	Area (ha)	Proportion (%)
Abandoned pasture	172	46	90	39
Rough grazing (sheep/goat)	89	24	56	24
Paddock (sheep/goat)	55	15	51	22
Mowing	7	2	5	2
Cattle pasture	51	14	28	12
Total	374	100	229	100

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-Agrimonietum*) and initial shrub communities (*Prunо-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 south-west-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 alciphron*, 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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References

Anthes, N., Fartmann, T., Hermann, G. & Kaule, G. 2003: Combining larval habitat quality and metapopulation structure — the key for successful management of pre-alpine *Euphydryas aurinia* colonies. — *Journal of Insect Conservation* 7: 175–185.

Asher, J., Warren, M., Fox, R., Harding, P., Jeffcoate, G. & Jeffcoate, S. 2001: *The millenium atlas of butterflies in Britain and Ireland*. — Oxford University Press, Oxford.

Beinlich, B. & Plachter, H. (eds.) 1995: Schutz und Entwicklung der Kalkmagerrasen der Schwäbischen Alb. — *Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg* 83: 1–520.

Belling, H. 1928: Einiges vom Frühlingsscheckenfalter, *Nemobius lucina* L. — *Internationale Entomologische Zeitschrift* 22(10): 105–109 + 437–439.

Bergmann, A. 1952: *Die Großschmetterlinge Mitteldeutschlands. 2. Tagfalter. Verbreitung, Formen und Lebensgemeinschaften*. — Urania-Verlag, Jena.

BLfU (Bayerisches Landesamt für Umweltschutz) 2001: *Artenschutzkartierung Bayern: Arbeitsatlas Tagfalter*. — Augsburg.

Bourn, N. & Warren, M. S. 1998: *Species action plan — Duke of Burgundy Hamearis lucina*. — Butterfly Conservation, Dorset.

Brockmann, E. 1989 *Schutzprogramm für Tagfalter in Hessen (Papilionoidea und Hesperioidea)*. — Reiskirchen.

Brohl, E. 1990: Ein Feldlager bei Erlinghausen. — *Marsberg* 90: 174–178.

Brökel, G. 1984: *Erlinghausen, eine Dorfgeschichte*. — Erlinghausen.

Buckley, G. P. 1992: *Ecology and management of coppice woodlands*. — Chapman & Hall, London.

BUTT (Butterflies Under Threat Team) 1986: The management of chalk grassland for butterflies. — *Focus on Nature Conservation* 17: 1–80.

de Lattin, G. 1957: Die Lepidopteren-Fauna der Pfalz. I. Teil. — *Mitteilungen der Pollichia* 3(4): 51–167.

Dennis, R. L. H. (ed.) 1992: *The ecology of butterflies in Britain*. — Oxford University Press, Oxford.

Dennis, R. L. H. & Eales, H. T. 1997: Patch occupancy in *Coenonympha tullia* (Müller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. — *Journal of Insect Conservation* 1: 167–176.

Dennis, R. L. H., Shreeve, T. G. & van Dyck, H. 2003: Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. — *Oikos* 102: 417–426.

Dennis, R. L. H., Hodgson, J. G., Grenyer, R., Shreeve, T. G. & Roy, D. B. 2004: Host plants and butterfly biology. Do host-plant strategies drive butterfly status? — *Ecological Entomology* 29: 1–16.

Dierschke, H. 1994: *Pflanzensoziologie*. — Ulmer Verlag, Stuttgart.

Dolek, M. & Geyer, A. 2001: Der Violette Feuerfalter (*Lycaena alciphron,* Rottemburg, 1775): Artenhilfsprogramm für einen wenig bekannten Tagfalter. — *Schriftenreihe des Bayerischen Landesamtes für Umweltschutz* (*Beiträge zum Artenschutz* 23) 156: 341–354.

Ebert, G. & Rennwald, E. 1991: *Die Schmetterlinge Baden-Württembergs. Band 2, Tagfalter II*. — Verlag Eugen Ulmer, Stuttgart.

Emmet, A. M. & Heath, J. (eds.) 1989: *The moths and butterflies of Great Britain and Ireland, 7, part 1: Hesperiidae to Nymphalidae*. — Harley Books, Colchester.

Fartmann, T. 2004: Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales. Biozönologie von Tagfaltern und Widderchen in einer alten Hudelandschaft. — *Abhandlungen aus dem Westfälischen Museum für Naturkunde* 66: 1–256.

Fleishman, E., Ray, C., Sjörgen-Gulve, P., Boggs, C. L. & Murphy, D. D. 2002: Assessing the roles of patch quality, area and isolation in predicting metapopulation dynamics. — *Conservation Biology* 16: 706–716.

Fred, M. S. & Brommer, J. E. 2003: Influence of habitat quality and patch size on occupancy and persistence in two populations of the Apollo butterfly (*Parnassius apollo*). — *Journal of Insect Conservation* 7: 85–98.

Friese, G. 1956: Die Rhopaloceren Nordostdeutschlands (Mecklenburg und Brandenburg). Mit zoogeographischen Erörterungen und einem vergleichenden Überblick über die Nachbargebiete. — *Beiträge zur Entomologie* 6(3/4): 403–442.

Frohawk, F. W. 1934: *The complete book of British butterflies*. — London.

Fuller, R. J. & Warren, M. S. 1992: *Coppiced woodlands: their management for wildlife*. — British Trust for Ornithology, Norfolk.

Garling, B. 1984: *Hamearis lucina* L., der Braune Würfelfalter: Lebensraum, Flugzeiten und Entwicklungsdaten (Lep.: Riodinidae). — *Entomologische Zeitschrift* 94: 321–336.

Harkort, W. 1975: Schmetterlinge in Westfalen (ohne Ostwestfalen): Fundortkarten und Fundortlisten (Stand: Ende 1974). — *Dortmunder Beiträge zur Landeskunde: Naturwissenschaftliche Mitteilungen* 9: 33–102.

Hasselbach, W. 1981: Bestandsentwicklung der Tagfalter Rheinhessens in den Jahren 1966–1980. — *Mainzer Naturwissenschaftliches Archiv* 19: 139–220.

Heath, J., Pollard, E. & Thomas, J. A. 1984: *Atlas of butterflies in Britain and Ireland*. — Viking, Harmondsworth.

Hozak, R. & Meyer, C. 1998: Konzepte zur Wiederbelebung der Hüteschäferei auf Kalkmagerrasen und Heiden. — *LÖBF-Mitteilungen* 4: 22–28.

Kinkler, H., Kwiatkowski, I., Kwiatkowski, H. & Bosselmann, J. 1996: Die Tagschmetterlinge des Landkreises Mayen-Koblenz und der angrenzenden Gebiete. — *Pflanzen und Tiere in Rheinland-Pfalz*, Sonderheft 3: 1–111.

Kudrna, O. 1988: *Die Tagschmetterlinge der nördlichen Hohen Rhön*. — Bonn.

León-Cortés J. L., Lemmon, J. J. & Thomas, C. D. 2003: Ecological dynamics of extinct species in empty habitat networks. 1. The role of habitat pattern and quantity, stochasticity and dispersal. — *Oikos* 102: 449–464.

Lucan, V. & Eger, W. 1996: Der Einfluss des Menschen auf die Pflanzendecke. — In: Becker, W., Frede, A. & Lehmann, W. (eds.), *Pflanzenwelt zwischen Eder und Diemel. Flora des Landkreises Waldeck-Frankenberg mit Verbreitungsatlas Naturschutz in Waldeck-Frankenberg* 5: 46–53. Bing, Korbach.

Max, W. 1977: Die Tagfalter des Harzes. — *Naturwissenschaftlicher Verein Goslar*, 125 Jahre: 61–97.

Müller-Temme, E. 1986: *Niederschläge in raum-zeitlicher Verteilung*. — Geographisch-landeskundlicher Atlas II, Lieferung 6. Geographische Kommission für Westfalen, Münster.

Müller-Wille, W. 1981: *Westfalen. Landschaftliche Ordnung und Bindung eines Landes*. 2. Aufl. — Aschendorffsche Verlagsbuchhandlung, Münster.

MURL NRW (Minister für Umwelt, Raumordnung und Landwirtschaft des Landes Nordrhein-Westfalen) (ed.) 1989: *Klima-Atlas von Nordrhein-Westfalen*. — Landesamt für Agrarordnung, Düsseldorf.

Oates, M. R. 2000: The duke of Burgundy — conserving the intractable. — *British Wildlife* 2: 250–257.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennant, J., Thomas, J. A. & Warren, M. S. 1999: Poleward shifts in geographical ranges of butterfly species associated with regional warming. — *Nature* 399: 579–583.

Pretscher, P. 1998: Rote Liste der Großschmetterlinge (Macrolepidoptera). — *Schriftenreihe für Landschaftspflege und Naturschutz* 55: 87–111.

Quinger, B., Bräu, M. & Kornprobst, M. 1994: *Lebensraumtyp Kalkmagerrasen. 1. und 2. Teilbd. Landschaftspflegekonzept Bayern, Bd. II.1*. — Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen (StMLU) und Bayerische Akademie für Naturschutz und Landschaftspflege (ANL), München.

Retzlaff, H. 1973: Die Schmetterlinge von Ostwestfalen-Lippe und einigen angrenzenden Gebieten Hessens und Niedersachsens (Weserbergland, südöstliches Westfälisches Tiefland und östliche Westfälische Bucht). I. Teil. — *Berichte des Naturwissenschaftlichen Vereins Bielefeld* 21: 129–248.

Rossmann, D. 1996: *Lebensraumtyp Nieder- und Mittelwälder. Landschaftspflegekonzept Bayern, Bd. II.13*. — Bayerisches Staatsministerium für Landesentwicklung und Umweltfragen (StMLU) und Bayerische Akademie für Naturschutz und Landschaftspflege (ANL), München.

Schmitt, T. 1998: Tagfalterbeobachtungen in rheinland-pfälzischen Naturschutzgebieten. — *Mainzer Naturwissenschaftliches Archiv* 36: 217–251.

Schubert, W. 1989: Kiefern kontra Knabenkräuter — Entstehung, Gefährdung, Schutz und Pflege der Marsberger Kalkhalbtrockenrasen. — *Marsberg* 89: 84–87.

Shreeve, T. G., Dennis, R. L. H. & van Dyck, H. 2004: Resources, habitats and metapopulations — whither reality? — *Oikos* 106(2): 404–408.

Sparks, T. H, Porter, K., Greatorex-Davies, J. N., Hall, M. L. & Marrs, R. H. 1994: The choice of oviposition sites in woodland by the Duke of Burgundy butterfly *Hamearis lucina* in England. — *Biological Conservation* 70: 257–264.

Stamm, K. 1981: *Prodomus der Lepidopteren-Fauna der Rheinlande und Westfalens*. — Selbstverlag, Solingen.

Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M. & Conradt, L. 2001: Ecological and evolutionary processes at expanding range margins. — *Nature* 411: 577–581.

Thomas, J. A. 1983a: The ecology and status of *Thymelicus acteon* (Lepidoptera: Hesperiidae) in Britain. — *Ecological Entomology* 8: 427–435.

Thomas, J. A. 1983b: The ecology and conservation of *Lysandra bellargus* (Lepidoptera: Lycaenidae) in Britain. — *Journal of Applied Ecology* 20: 59–83.

Thomas, J. A. 1991: Rare species conservation: case studies of European butterflies. — In: Spellerberg, I. F., Goldsmith, F. B. & Morris, M. G. (eds.), *The scientific management of temperate communities for conservation*: 149–197. Blackwell Scientific, Oxford.

Thomas, J. A. & Clarke, R. T. 2004: Extinction rates and butterflies. — *Science* 305: 1563–1564.

Thomas, J. A., Bourn, N. A. D., Clarke, R. T., Stewart, K. E., Simcox, D. J., Pearman, G. S., Curtis, R. & Goodger, B. 2001: The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. — *Proceedings of the Royal Society of London B* 268: 1791–1796.

Thomas, J. A., Telfer, M. G., Roy, D. B., Preston, C. D., Greenwood, J. J. D., Asher, J., Fox, R., Clarke, R. T. & Lawton, J. H. 2004: Comparative losses of British butterflies, birds, and plants and the global extinction crisis. — *Science* 303: 1879–1881.

Tonne, F. 1954: *Besser Bauen mit Besonnungs- und Tageslicht-Planung*. — Hofmann, Schorndorf.

Treiber, R. 2003: Genutzte Mittelwälder — Zentren der Artenvielfalt für Tagfalter und Widderchen im Südelsass. — *Naturschutz und Landschaftsplanung* 35(1): 50–63.

Uffeln, K. 1908: Die Grossschmetterlinge Westfalens mit besonderer Berücksichtigung der Gegenden von Warburg, Rietberg und Hagen. — *Jahresberichte der zoologischen Sektion des Westfälischen Provinzial-Vereins für Wissenschaft und Kunst*, Beih.: 1–158.

van Swaay, C. & Warren, M. 1999: Red data book of European butterflies (Rhopalocera). — *Nature and Environment* 99, Strasbourg, France.

van Swaay, C. & Warren, M. (eds.) 2003: *Prime butterfly areas in Europe: priority sites for conservation*. — National Reference Centre for Agriculture, Nature and Fisheries, Ministry of Agriculture, Nature Management and Fisheries, The Netherlands.

WallisDeVries, M. F. 2004: A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. — *Conservation Biology* 18(2): 489–499.

WallisDeVries, M. F., Poschlod, P. & Willems, J. W. 2002: Challenges for the conservation of calcareous grasslands in Northwestern Europe: integrating the requirements of flora and fauna. — *Biological Conservation* 104: 265–273.

Warren, M. S. 1993: A review of butterfly conservation in central southern Britain: II. Site management and habitat selection of key species. — *Biological Conservation* 64: 37–49.

Warren, M. S. & Thomas, J. A. 1992: Butterfly responses to coppicing. — In: Buckley, G. P. (ed.), *The ecological effects of coppice management*: 249–270. Chapman and Hall, London.

Warren, M., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., Roy, D. B., Telfer, M. G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S. G., Greatorex-Davies, J. N., Moss, D. & Thomas, C. D. 2001: Rapid responses of British butterflies to opposing forces of climate and habitat change. — *Nature* 414: 65–68.

Watt, W. B. & Boggs, C. L. 2003: Synthesis: butterflies as model systems in ecology and evolution — present and future. — In: Boggs, C. L., Watt, W. B. & Ehrlich, P. R. (eds.), *Butterflies. Ecology and evolution taking flight*: 603–613. The University of Chicago Press, Chicago and London.

Weidemann, H. J. 1995: *Tagfalter: beobachten, bestimmen*. 2. Aufl. — Naturbuch-Verlag, Augsburg, Germany.