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The Duke of Burgundy butterfly and its dukedom: larval niche variation in *Hamearis lucina* across Central Europe

Nils Anthes · Thomas Fartmann · Gabriel Hermann

Abstract In order to improve our understanding of habitat preferences and optimal management of open woodland insects, we analyse patch occupancy and oviposition electivity of the endangered Duke of Burgundy butterfly, *Hamearis lucina*, in three regions across German habitat types. Some newly available forest clearings created by a severe winter storm in the Schönbuch region were colonised within 2 years, whereas some suitable patches remained unoccupied for several years. We discuss how small population sizes, limited patch connectivity, and habitat quality may contribute to such an intermediate colonisation power. Across study regions, we document differences in oviposition site electivity. On calcareous grassland in the Diemeltal, shaded *Primula* plants on western slopes were preferentially used, probably to avoid desiccation of the natal food plant. To the contrary, sun-exposed *Primula* stands were preferred in forest clearings in the Schönbuch and calcareous fens in the Allgäu. In these regions, the risk of desiccation is low, but the overall cool and moist microclimate conditions may hamper larval development in shaded conditions, favouring oviposition at sites with maximum exposition to solar radiation. Optimal management strategies depend on the abiotic and biotic conditions and conservation priorities for the given region and habitat type, and we suggest management regimes that promise to sustain suitable *H. lucina* habitat at a landscape-level.

Keywords Butterfly conservation · Coppicing · Larval ecology · Metapopulation · Oviposition electivity

Introduction

Butterflies are an important system to study the effects of habitat degradation, fragmentation, and global warming on animal populations and communities (Thomas and Morris 1994; Parmesan 1996; Parmesan and Yohe 2003; Stefanescu et al. 2003; Thomas et al. 2004a, b). Butterflies are particularly suited for that kind of study because they often rapidly respond to changes in environmental conditions. In many species, this susceptibility to environmental fluctuations is associated with low mobility and pronounced habitat specificity of the larval life stages (Thomas et al. 2001; Anthes et al. 2003; Dennis et al. 2005a). Many species are constrained to use a single larval host plant genus or even species (monophagy; e.g. Wahlberg 2001; Dennis et al. 2004). Variation in intrinsic host plant quality among host plant individuals further renders a subset of these unsuitable for larval development and thus unacceptable for oviposition (Singer and Lee 2000). Egg and larval development is further sensitive to microclimatic conditions at the site of oviposition, such that intrinsically high quality larval host individuals growing in an unfavourable microhabitat may prove unsuitable. As a result, many butterfly species have evolved locally adapted host

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plant preferences (Thompson 1998) that allow optimising oviposition decisions in the natal habitat but may limit the ability to colonize new habitat that provides suitable but unfamiliar resources (Hanski and Singer 2001; Hanski and Heino 2003). The capacity of host plant specialists to compensate for habitat perturbations, e.g. by shifting host plants or habitats, may thus be limited (Singer 1983, 2003; Hellmann 2002; Dennis et al. 2004), in particular if restricted adult dispersal hampers compensatory spatial movements.

Understanding and defining larval habitat specificity is therefore crucial, but often non-trivial, for the conservation of endangered species. Abiotic and biotic conditions (e.g. climate, substrate, hydrology, or vegetation composition) will vary along temporal as well as large- and local scale environmental gradients, and so will the realised niches across a species' range. Such spatio-temporal variation may for example occur with respect to the occupied larval host plant species (Roy and Thomas 2003), the habitat management regimes that optimise larval or adult habitat (Hermann and Anthes 2003), or the microclimatic conditions that improve larval development (Davies et al. 2006). Successful species conservation thus requires up-to-date knowledge of habitat preferences at local scales across a species' range.

We here document larval habitats of an open woodland butterfly, the Duke of Burgundy *Hamearis lucina* L. 1758, across central European landscapes. *H. lucina* larvae are monophagous on the plant genus *Primula* (Ebert and Rennwald 1991; Sparks et al. 1994). Previous studies have shown that *Primula* stands under a closed forest canopy are usually ignored for oviposition such that only a subset of the natural host plant range is acceptable for the species (Sparks et al. 1994; Oates 2000; Fartmann 2006). Habitats range from dry to moist microclimate and soil conditions and include clearings in old woodland, forests under coppicing regimes, and adjacent calcareous grasslands and fens (Garling 1984; Ebert and Rennwald 1991; Warren 1993b; Sparks et al. 1994; Oates 2000; Fartmann 2006). Although some *H. lucina* females may cover distances of 250 meters or more (Bourn and Warren 1998; Oates 2000), the species is considered an inefficient disperser (Warren and Thomas 1992; Fartmann 2006) that can permanently persist even at small population sizes. Patch-turnover in *H. lucina* metapopulations is comparably slow (León-Cortés et al. 2003), indicating restricted between patch movements. In an analysis of patch occupancy in the Diemeltal (Fartmann 2006), the current distribution was best explained by the adjacency of old forests and low isolation from neighbouring patches, whereas neither patch size nor current habitat management significantly improved the prediction of patch occupancy. According to Fartmann (2006), this indicates that during the mid 20th century *H. lucina* colonised calcareous grasslands from nearby old

forests and persisted since then. Recolonisation of extinct patches with optimal larval habitat quality from distant grasslands occurred rarely.

Across Europe, *H. lucina* has recently suffered considerable range retraction (van Swaay and Warren 1999) and climate-mediated range shifts (Parmesan et al. 1999; Oates 2000). Colony losses, which continue in the remaining strongholds, have mainly been attributed to grassland afforestation and the abandonment of coppice regimes in old forests (Ebert and Rennwald 1991; Warren 1993a; Asher et al. 2001). Yet, understanding the ultimate reasons for the ongoing decline in this butterfly requires more detailed knowledge of its larval habitat resources. While previous studies have focused on describing habitat utilisation within single regions and equivalent habitat types, we here compare larval habitats across the range of habitat types colonised in Central Europe. As a major aim, we analyse oviposition electivity per region by contrasting available habitat structures with those actually used by the butterfly for oviposition. We then compare the qualitative results of these within-region preferences between habitat types to derive information on larval habitat plasticity in *H. lucina*.

Study regions

We studied larval habitats of *Hamearis lucina* in three German regions that represent the most important habitat types colonised by this species (Fig. 1): The valley of the river Diemel (''*Diemeltal*'', 100–610 m a.s.l) forms the north-western range margin of *H. lucina* in continental Europe. A dense network of large calcareous grassland patches adjacent to old, dry forests provides the major habitat. The study in the Diemeltal focused on the host plant *Primula veris* (Cowslip), which grows abundantly in forests, open calcareous grasslands, and transitional vegetation. Oxlip (*Primula elatior*) also occurs in this region, but is restricted to forests with a closed canopy layer where even high-density stands are not occupied by the butterfly. Details of *H. lucina* patch-occupancy and larval habitats as studied in 1998–2000 have partly been published elsewhere (Fartmann 2006) and we refer to this study were applicable.

The ''*Schönbuch*'' (430–470 m a.s.l.) is a large nature park with old mesotrophic woodlands in southwestern Germany. *P. elatior* is common and widespread in woodland clearings and along forest tracks, although some clearings in particular on sandstone bedrock lack *P. elatior* or provide only few host plant individuals. *P. veris* is restricted to some calcareous grassland patches that have not been studied here. Larval habitats of *H. lucina* were studied in the year 2004 in forest clearings that either resulted from logging activity or had been deforested by the winter-storm ''Lothar'' in December 1999.

Fig. 1 Current distribution of
Hamearis lucina in Germany
(modified from Fartmann 2006)
and location of the three study
regions: 1—Diemeltal,
2—Schönbuch, 3—Allgäu
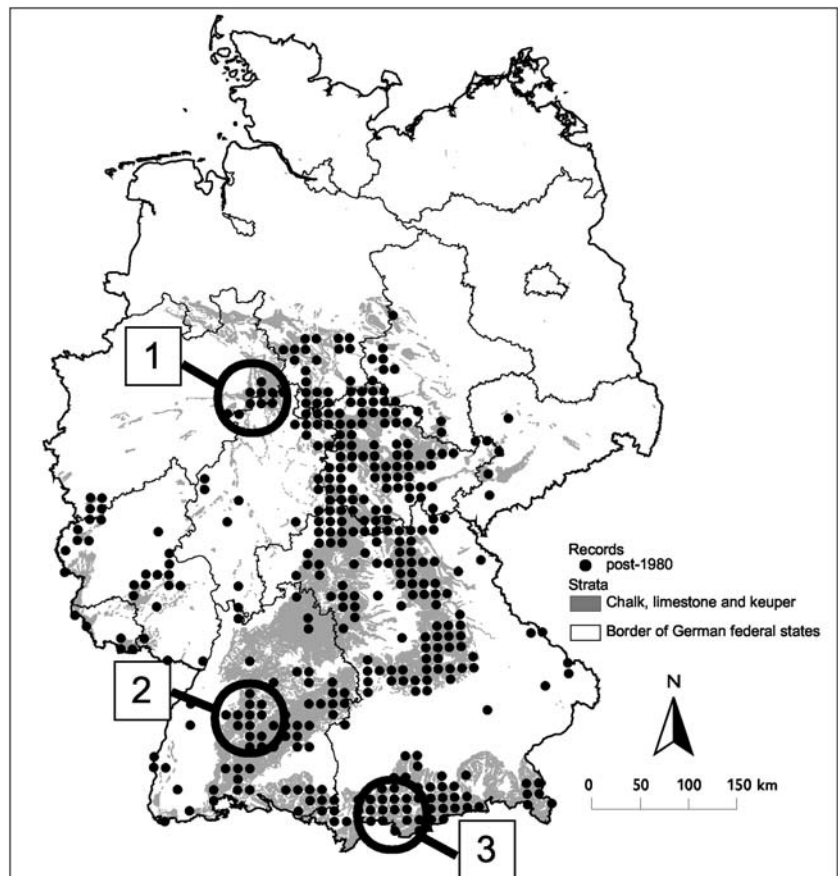
Our third study area, the Bavarian ''*Allgäu*'', is situated in the northern foothills of the Alps east of the river Lech near Füssen (800–900 m a.s.l.). The region is characterised by a highly diverse mosaic of oligotrophic limestone fens, bogs, coniferous forests (mostly *Picea*), and cattle-grazed pasture. *P. elatior*, which is the primary host plant of *H. lucina* in this region, is common in dense coverage within forests, in transitional vegetation along forest margins, and at lower densities in adjacent fen meadows and pasture. *H. lucina* inhabits moist forest edges flanking calcareous fens. Habitat preferences were studied in 2001 in an array of habitat types representing the species' distribution in the area, focusing on traditional cooperative cattle grazing regimes on common property (''Allmende'') in calcareous fens and litter meadows that are regularly mown in September or October (Scholle et al. 2002).

Methods

Patch occupancy in the Schönbuch

An 8-year survey of patch occupancy documents the spatial dynamics of *H. lucina* in an 83.5 ha woodland (''Ketterlenshalde'') in the Schönbuch region. This small forest is surrounded by intensively mown Arrhenatherion-grassland. *H. lucina* inhabits natural and anthropogenic clearings of various ages, which are separated by 75 to 450 m of dense oak or spruce forest stands. Between 1997 and 2004, all available forest clearings were surveyed at least twice during the adult flight season in May / June and all available *Primula* plants were checked for the presence of egg clusters or larvae. Given the lack of more thorough definition of patch quality at the time of this study, we considered unoccupied clearings ''potential habitat'' when they contained (i) large-grown *Primula* stands that were not densely covered by shrubs or trees as well as (ii) flowering nectar plants during adult flight season. During the winter 1999/2000, the storm ''Lothar'' created several natural clearings that provided novel habitat for *H. lucina*.

Oviposition sites

We have observed that ovipositing females immediately turn away whenever other plants hamper their approach to a *Primula* leaf. This suggests that unhindered access to oviposition sites is an important criterion. Our characterisations of oviposition sites thus paid particular attention to the setting of host plant individuals within the surrounding vegetation.

We describe oviposition sites based on 227, 128, and 141 egg clusters in the Diemeltal, Schönbuch, and Allgäu, respectively. For each egg clutch we measured the oviposition substrate (plant species, total plant height, plant diameter, *n* leaves in the ground rosette), the position of the egg clutch on the plant (height above ground, length of the leaf, position of the clutch on the leaf [basal, mid, distal third]), the vegetation structure in a circle with 50 cm diameter around the host plant (% coverage of detritus, mosses, herbs, shrubs, trees; percentage horizontal vegetation cover [=vegetation density] in various heights above ground [5, 10, 20, 30 cm] estimated in a 50 cm wide × 20 cm deep enclose), turf height, the availability of further host plants as a larval food resource nearby (total number and coverage of *Primula* in a 50 cm circle around the host plant), the surrounding vegetation assemblage following the Braun-Blanquet system (Dierschke 1994), the hours of the day during which a host plant received direct sunshine during peak egg laying in June (measured with a horizontoscope, Tonne 1954), and slope aspect (°) and inclination (°). Deviations in sample sizes in figures and tables result from cases where the respective parameter could not be measured for a subset of clutches. Only some of the mentioned parameters were measured in each study area (see Table 2). In the Allgäu we further documented the development of 10 egg clutches in the field from egg-laying to hatching and measured survival until hatching as the proportion of hatching eggs for 34 freshly laid clutches that contained ≥4 eggs.

Oviposition electivity

In a second step we analysed oviposition electivity, i.e. the usage of host plants growing in particular conditions relative to their abundance (Singer 2000, 2004). Within each study region we contrasted plant architecture and surrounding vegetation structure of occupied host plant individuals with that of randomly selected host plants. The latter represented the relative frequencies in which host plant individuals were found in the different *H. lucina* habitats. Hence, they represent a random sample of host plant individuals and their surrounding vegetation structure available to ovipositing females. These available habitat structures were measured at 137 and 101 *Primula* plants in the Allgäu and Schönbuch, respectively, and derived from 47 vegetation relevées that contained *Primula veris* and represented all habitat types according to their area fraction in the region in the Diemeltal (Fartmann 2006). Note that a statistical comparison between regions is not possible because any difference in absolute values (e.g. plant sizes) may just be an effect of region or study year. Moreover, the measured variables were not identical between regions, making direct comparisons difficult. Instead, we used the

qualitative results on host plant electivity within each region to infer which aspects of oviposition ecology may differ between regions.

Statistical analysis

Mean values ± standard deviations are given unless otherwise stated. For comparisons between available and occupied host plants per region (i.e. oviposition electivity) we performed multiple stepwise forward logistic-regression analysis where at each step new parameters were entered at a probability below 0.05 and removed at a probability above 0.10. Categorical variables (tree cover and plant size in the Allgäu) were analysed separately using Chi-square tests. All statistical tests were performed using SPSS 11.01 statistical package.

Results

Patch dynamics in the Schönbuch

Our 8-year patch survey documents repeated colonisation and extinction of habitat patches in the Ketterlenshalde (Fig. 2). Most of the seven patches newly created by the storm ''Lothar'' (denoted I–P in Fig. 2) were in close proximity to other occupied patches. Three patches (L, M, and O in Fig. 2) were already colonised within 2 years. None of the remaining four patches was separated from the nearest occupied patch by more than 150 m of forest, indicating that colonisation of even nearby habitat is slow in *H. lucina*. Two formerly occupied patches (patches B and C) went extinct after the storm due to habitat restoration activities and were not recolonised thereafter despite providing suitable larval habitat. Although population sizes (number of adult butterflies) were not rigorously studied during the survey, it was striking that never more than six adults were found during a single survey. This indicates that, perhaps, dispersal and (re)colonisation in this study area were retarded by low population sizes. The only suitable habitat patch that has never been occupied during the study period (G in Fig. 2) was by far most isolated, being separated from the nearest occupied patch by 450 m of dense forest.

Oviposition sites

Eggs were predominantly laid on the larval food plants *Primula elatior* and *P. veris* in all regions. Only in the Allgäu, however, did we systematically examine non-host plants for egg clutches. This survey revealed that oviposition on non-hosts is more common than previously thought (Table 1). Oviposition on non-host plants was also

Fig. 2 Temporal patch-dynamics of *H. lucina* in the "Kettelenshalde" in the Schönbuch region. Open boxes: patch classified "non-habitat". Grey boxes: unoccupied habitat patches. Black boxes: occupied habitat patches. The vertical bar indicates the storm "Lothar", which provided new patches during the following 2 years

Patch	Size [ha]	N Primula	Nearest patch ID	Distance [m]	1997	1998	1999	2000	2001	2002	2003	2004
A	0.6	1–10	H	80	■	■	■	□	□	■	■	▨
B	0.7	1–10	E	90	■	■	■	▨	▨	▨	▨	▨
C	1	1–10	D	80	■	■	■	■	■	▨	▨	▨
D	0.4	11–20	C	80	■	■	■	■	■	■	■	■
E	1	1–10	B	90	■	■	■	■	■	■	■	■
F	0.8	1–10	K	115	▨	▨	▨	▨	▨	▨	▨	▨
G	0.5	1–10	O	450	▨	▨	▨	▨	▨	▨	▨	▨
H	0.8	> 20	A	80	□	□	■	▨	▨	■	■	■
I	1.3	1–10	E	95	□	□	□	▨	▨	▨	■	▨
K	2.2	1–10	F	115	□	□	□	▨	▨	■	■	■
L	0.7	11–20	M	100	□	□	□	□	□	■	■	■
M	1.3	1–10	L	100	□	□	□	■	■	■	■	■
N	1	1–10	P	75	□	□	□	□	▨	▨	■	■
O	1.6	> 20	C	150	□	□	□	□	▨	■	■	■
P	0.4	1–10	N	75	□	□	□	□	□	▨	▨	■

confirmed in the Diemeltal (a single clutch on *Sanguisorba minor*, 0.5% of all clutches) and in the Schönbuch (two clutches on *Lysimachia nummularia*, 1.6%), thus likely being a common but previously overlooked phenomenon across regions. In the Allgäu, oviposition heights above ground increased with average host plant height (Table 1, Spearman rank correlation $r_S = 0.98$, $N = 9$, $P < 0.001$). Importantly, taller host plant species were preferentially occupied in transitional vegetation types (*Molinion* fallows with dense coverage by *Molinia caerulea* tussocks, Table 2) where the leaf rosettes of *Primula* where not directly accessible for ovipositing females. Among occupied *Primula* plant individuals, we also found significant covariation between vegetation height, individual plant height, and oviposition height in the Diemeltal and Schönbuch (Table 3; respective data not available for the Allgäu).

Detailed characteristics of occupied host plants and the surrounding vegetation structure are given in Table 4. We did not statistically compare these characteristics between regions, because any difference may simply reflect regional climate or soil conditions and principal differences between the two host plant species, *P. elatior* and *P. veris*. Rather, this information serves as a background for the within-region electivity analysis provided in the next section.

Oviposition occurred in a wide range of vegetation types (Table 2). Although nutrient-poor grassland communities (*Molinion*, *Caricion davallianae*, *Bromion*) apparently dominated in the Diemeltal and Allgäu, these figures basically represent the distribution of *Primula* across vegetation types in the study areas. Importantly, however, forest communities were rarely accepted, although dense

Table 1 Oviposition substrates of *H. lucina* in the Allgäu

Plant species	N	%	Oviposition height (cm)		Ø Host plant height (cm)
			Ø ± SD	Min–Max	
Aegopodium podagraria	1	0.7		8	15.0
Angelica sylvestris	5	3.6	24.2 ± 1.8	23–27	25.0
Filipendula ulmaria	2	1.4	25.0 ± 5.7	21–29	27.5
Galium mollugo	1	0.7		27	28.0
Gentiana asclepiadea	13	9.2	26.8 ± 6.2	20–39	41.5
Mercurialis perennis	1	0.7		17	20.0
Paris quadrifolia	3	2.1	15.7 ± 6.4	11–23	17.3
Primula elatior	114	80.9	6.7 ± 3.7	2–23	9.7
Prunus padus	1	0.7		17	24.0

Systematic counts on non-food plants were restricted to a subset of sites, indicating that their proportions given here may even be an underestimate

Table 2 Characterisation of *H. lucina* oviposition sites, based on vegetation assemblages (Dierschke 1994)

Vegetation type	N clutches	Nectar	*Primula*
Diemeltal (N = 227)			
Calcareous grassland			
Gentiano-Koelerietum	160	++	+
Brachypodium pinnatum D	13	+	+
Bromus erectus D	10	+	−
Mesotrophic grassland			
Arrhenatheretalia	18	++	+
Forest and other vegetation types			
Prunus spinosa shrubs	10	++	+
Carici-Fagetum	13	+	+
Forest	2	−	+
ruderal land	1	+	−
Schönbuch (N = 126)			
Forest seams			
Querco-Fagetea	12	+	+
Querco-Fagetea / Epilobietea	89	++	+
Grassland vegetation types			
Molinietalia / Arrhenatheretalia	25	++	+
Allgäu (N = 141)			
Fen meadows / pasture			
Molinion	**13	++	+
Molinion (fallow)	**16	+	+
Caricion davallianae	48	++	+
Mesotrophic grassland types			
Magnocaricion	10	+	−
Filipendulion	2	++	−
Mentha longifolii-Juncetum inflexi	7	+	−
Calthion	6	+	−
Cynosurion	2	+	−
Forests and their seams			
Alnion	3	+	+
Picea forest seam with *Juncus inflexus*	21	+	++
Picea forest seam (dry)	10	+	++
Other	3	+	+

''D'' indicates dominance stands of the particular grass species. Box shadings indicate the proportional use per study region: 1–5% (white), 6–10% (pale grey), 11–50% (dark grey), 51–100% (black), based on the number (N) of clutches. Nectar resources during the flight period were almost absent (−), scattered (+), or very abundant (++). We further indicate the abundance of the host plants, being scarce and dispersed (−), common (+), or very abundant in often high-density stands (++)

** > 66% of clutches on non-host plant species, cf. Table 1

stands of *Primula* often grow under the closed forest canopy. Only in the Schönbuch were forest communities frequently occupied. However, these oviposition sites were always in forest clearings (which still compose a ''forest plant community'') or in marginal vegetation types, but not under a closed canopy.

Oviposition sites were flat (≤ 5° inclination) in the Schönbuch with a slight predominance of northern slope aspects. In both Allgäu and Diemeltal, slope inclination at oviposition sites ranged between 2° and 30°. However, W and SW aspects (80%) clearly dominated over southern aspects (10%) in the Diemeltal, but less so in the Allgäu (51% and 30%, respectively).

Clutches usually contained only one or two eggs, but regularly up to five eggs in all three study sites (Fig. 3). Larger clutches were only recorded once in the Diemeltal, rarely in the Schönbuch, and most abundantly in the Allgäu. In the latter region, the largest clutch contained

Table 3 Covariation between heights (in cm) of the herb layer, the occupied host plant individual, and oviposition sites on *Primula veris* in the Diemeltal (upper right sector, $N = 226$) and on *P. elatior* in the Schönbuch (lower left sector, $N = 126$)

	Herb layer	Host plant	Oviposition
Herb layer	–	0.350	0.389
Host plant	0.501	–	0.437
Oviposition	0.505	0.749	–

The table gives Spearman rank correlation coefficients rho, with all $P < 0.0001$

22 eggs. In consequence, median clutch size was larger in the Allgäu as compared to the other two regions, and larger in the Schönbuch as compared to the Diemeltal (Median Test $\chi^2 = 12.75$, df = 2, $P = 0.002$). In none of the three regions were clutch sizes correlated with host plant size or density (Spearman rank correlations, all $P > 0.3$).

Larvae from 10 freshly laid clutches in the Allgäu hatched after 13 to 28 days (20.2 ± 4.7 days). Survival until hatching was rather equally distributed between 0 and 100% in 34 clutches ($47.7 \pm 38.7\%$), with 10 clutches (18.9%) being completely lost before hatching for unknown reasons.

Oviposition electivity

In the Diemeltal, oviposition preferentially occurred at sites with comparably few mosses and shrubs and above-average herb cover (Fartmann 2006), indicating that the proximity to hedgerows or forest seams was preferred. Note, however, that for this region no information was available to assess electivity with respect to individual host plant characteristics, horizontal vegetation structure, or insolation (Fartmann 2006).

In the Schönbuch, occupied host plant individuals had a smaller diameter but more leaves than the average available host plant (Table 5). Vegetation structure was characterised by an elevated coverage of the herb layer and close proximity to the nearest tree. Turf height and host plant coverage did not contribute significantly to the model. The analysis further indicated that host plants with elevated total insolation duration (Table 5, Fig. 4) were disproportionately occupied. In concord with these results, we found that eggs were predominantly laid on plants without tree shading, whereas plants under full tree coverage were avoided (χ^2-test $\chi = 38.9$, df = 2, $P < 0.001$).

In the Allgäu (Table 5), occupied *Primula* plants grew in comparably sparse vegetation density (measured as the horizontal herb cover in 10 cm above ground). Similar to

Table 4 Characteristics of host plants and oviposition sites of *H. lucina*

| Parameter	Diemeltal (*P. veris*, $N = 227$)		Schönbuch (*P. elatior*, $N = 128$)		Allgäu (*P. elatior*, $N = 141$)	
	Mean ± SD	min–max	Mean ± SD	min–max	Mean ± SD	min–max
Host plant characteristics						
Diameter [cm]	n.a.	n.a.	22.4 ± 9.9	2–52	12.2 ± 6.7	3–40
N leaves	n.a.	n.a.	15.0 ± 14.2	2–62	6.0 ± 4.2	1–20
Plant height [cm]	23.6 ± 6.6	6-40	18.3 ± 6.2	7–35	13.9 ± 11.1	3–60
Food availability (50cm circle)						
Primula cover [%]	n.a.	n.a.	6.3 ± 4.7	1–25	8.3 ± 7.8	0–50
Primula abundance	n.a.	n.a.	3.1 ± 2.2	1–11	9.7 ± 6.3	0–40
Vegetation cover [%]						
Moss	29.0 ± 25.6	0–90	1.0 ± 2.7	0–20	47.5 ± 28.3	0–100
Herb	73.8 ± 21.7	10–100	53.0 ± 23.7	5–100	55.2 ± 18.1	10–90
Shrub	18.4± 21.2	0–100	7.6 ± 13.4	0–80	3.5 ± 12.0	0–80
Vegetation density [%]						
5 cm above ground	71.0 ± 29.3	10–100	n.a.	n.a.	52.4 ± 22.6	5–95
10 cm above ground	37.1± 27.0	0–90	n.a.	n.a.	24.2 ± 17.8	2–80
20 cm above ground	4.9± 7.8	0–40	n.a.	n.a.	6.9 ± 8.2	0-40
30 cm above ground	0.3± 1.5	0–10	n.a.	n.a.	2.1 ± 3.1	0–20
Turf height [cm]	22.1± 6.5	9–40	26.7 ± 10.3	10–80	n.a.	n.a.
Daily sun exposure in June [h]	6.5 ± 2.6	0.5–11.5	7.0 ± 2.7	0–13	6.7 ± 2.6	1–13.5
Oviposition above ground [cm]	10.4± 4.4	3–35	12.9 ± 5.9	4–31	10.0 ± 8.1	2–39
N eggs/clutch	1.8± 1.0	1–6	2.2 ± 1.6	1–11	2.8 ± 2.6	1–22

n.a. = no data available
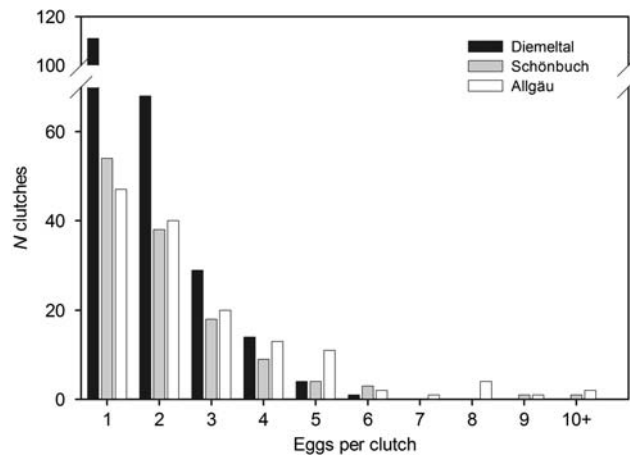
Fig. 3 Frequency distribution of *H. lucina* clutch sizes

the Schönbuch, we found a preference for host plants with above-average total insolation duration. Interestingly, insolation was the first parameter to be added to the model in the stepwise regression procedure in both regions. Note that for the Allgäu we could not analyse individual host plant characteristics.

The distribution of insolation across the time of day shown in Fig. 4 indicates that plants with elevated insolation during late morning hours were preferred in the Allgäu. In the Schönbuch, average insolation was higher on occupied than on available host plants during all times of the day (Fig. 4). Average total insolation durations of

occupied *Primula* plants did not differ between study regions (ANOVA $F_{2,478} = 1.40$, $P = 0.25$; Fig. 4), but this does not exclude that differences in the total solar radiation experienced by the plants do occur.

Discussion

Our study documents differences in qualitative oviposition electivity of *H. lucina* between regions. Based on our data we identify three factors that likely mediate this variation.

(i) Solar radiation and humidity

Optimal embryonic development in butterflies requires a compromise between sufficient humidity to avoid egg and host plant desiccation and elevated solar radiation to speed up larval development (Weiss et al. 1988; Roy and Thomas 2003). Assuming that, in *H. lucina*, the optimal compromise, in absolute terms, is roughly constant between regions, the realised ecological niches that provide these conditions may substantially differ. Depending on factors such as elevation a.s.l., the dominant slope aspects, humidity (in particular near ground), or vegetation structure, *H. lucina* eggs may develop optimally in sun-exposed localities in some regions but shaded localities in others. Although we lack direct measurements of solar radiation, our measurements are in agreement with this hypothesis:

Table 5 Oviposition preference analysis based on available and occupied *Primula* host individuals using forward stepwise logistic-regression

Parameter	Schönbuch ($N = 277$)	Model improvement		Allgäu ($N = 250$)	Model improvement	
	Coef. B ± SE	χ^2	P	Coef. B ± SE	χ^2	P
Constant	–2.25 ± 0.70		0.001	1.08 ± 0.51		0.034
Plant parameters						
Plant height (cm)			n.s.			n.a.
Plant diameter (cm)	–0.13 ± 0.03	0.41	0.002			n.a.
N leaves (log)	1.79 ± 0.83	4.90	0.027			n.a.
Vegetation characteristics						
Moss cover (%)			n.a.			n.s.
Herb cover (%)	0.02 ± 0.01	5.76	0.016			n.s.
Shrub cover (%, log)			n.a.			n.s.
Turf height (cm)			n.s.			n.a.
Tree distance (m; log)	–2.16 ± 0.75	7.25	0.007			n.s.
Primula cover (%; log)			n.s.			n.s.
Vegetation density 10cm above ground (%; log)			n.a.	–1.73 ± 0.41	43405.00	0.001
Microclimate						
Insolation (h)	0.56 ± 0.08	83.67	<0.001	0.17 ± 0.04	17.56	<0.001
Model summary	$\chi^2 = 110.9$, df = 5, $P < 0.001$			$\chi^2 = 28.7$, df = 2, $P < 0.0001$		
Correctly classified	81.10%			64.00%		

n.s. = parameter not significant, n.a. = data not avaliable. The preference analysis for the Diemeltal is provided in Fartmann (2006) and not repeated here
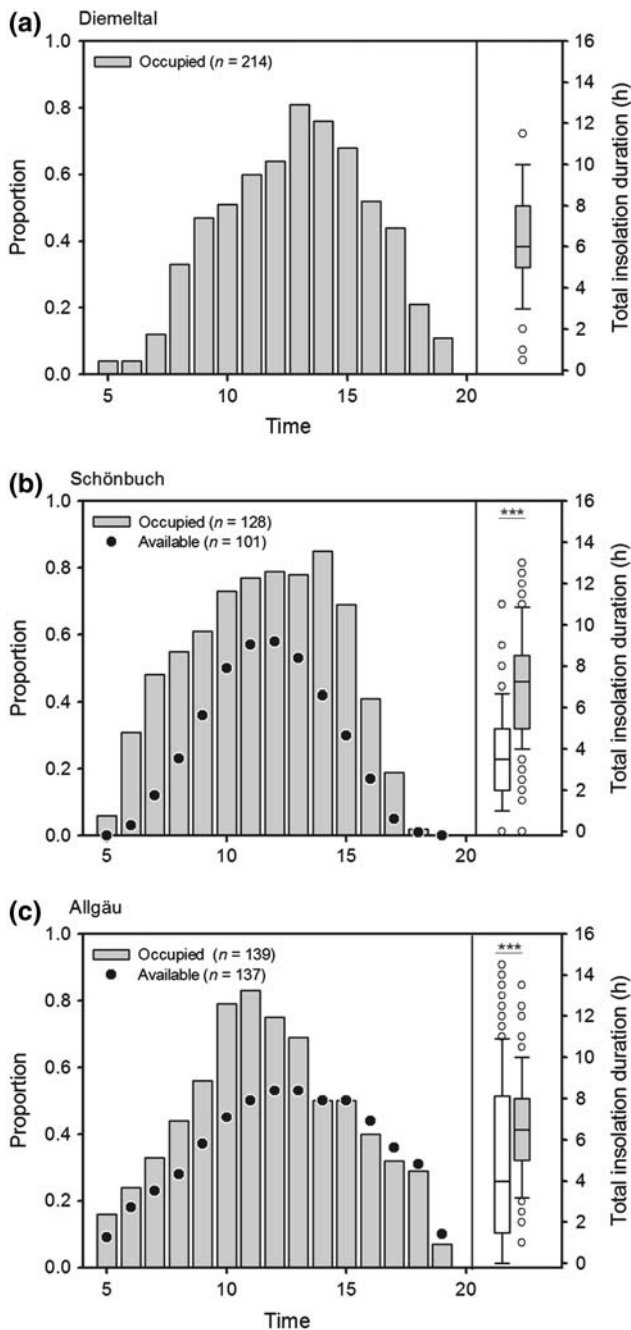
Fig. 4 Insolation of *H. lucina* egg clutches. In each graph the left panel shows the proportion of host plants that are exposed to direct sunlight at a given time (hour) in June. The right panel gives the total daily insolation duration for randomly selected (white) and occupied (grey) host plants. (**a**) Diemeltal (no data on available insolation), (**b**) Schönbuch, Mann-Whitney $U = 2194$, $P < 0.001$. (**c**) Allgäu, Mann-Whitney $U = 6799$, $P < 0.001$

In the Diemeltal, where south-facing slopes with open vegetation cover experience high solar radiation and rapid desiccation, *H. lucina* preferably oviposits in shaded conditions with elevated vegetation cover and on western rather than southern slopes such that direct insolation is restricted to the afternoon (Fartmann 2006). In contrast, oviposition sites in the comparably moist and cool regions Schönbuch and Allgäu were characterised by an elevated exposure to solar radiation (Fig. 4). Interestingly, egg developmental durations in the Allgäu were considerably retarded in comparison to both laboratory studies (larvae hatching after 6–10 days; Goltz 1978; Garling 1984) and earlier field studies (hatching after 7–21 days; Emmet and Heath 1989). Perhaps, even longer exposition to the sun could further speed up larval development in this region.

The necessity to receive sufficient radiation for embryonic development may also contribute to the occurrence of egg-laying on non-host plants in dense vegetation. Here, *Primula* ground rosettes receive shading from surrounding perennial plants such that microclimatic conditions may not be optimal for larval development.

(ii) Larval food quantity

Selecting host plant individuals that provide sufficient food for the larvae to survive until pupation is of vital importance for ovipositing females. Although *H. lucina* clutches usually contain less than five eggs, food quantity can be a limiting factor. We have observed that *H. lucina* larvae occasionally defoliated their natal *Primula* plant prior to hibernation and evaded to find a new host individual. Food quantity may therefore be relevant in regions where local climatic or soil conditions restrict *Primula* growth. Host plant desiccation occurs frequently in the Diemeltal (Fartmann 2006; similar reports from *H. lucina*'s UK range, M. Oates, pers. comment), indicating that later in the season, when larvae approach hibernation, larvae hatching on withering plants face the risk of starvation more than larvae from clutches deposited on non-withering plants (e.g. in shaded conditions). This may also explain why clutches contained fewer eggs, on average, in the Diemeltal than in both other regions. In regions with an elevated risk of plant withering, females may benefit from spreading their eggs across more individual plants and laying only a single or two eggs per plant. In contrast, desiccation is restricted to exceptionally dry springs and summers in the moist microclimatic conditions in both the Schönbuch and the Allgäu. Therefore, single *Primula* plants may more reliably provide sufficient food even for larger clutches. Additionally, different *Primula* species may vary in their nutritional value (food quality) such that *P. elatior* allows faster growth than *P. veris*. Partitioning the effects of food quantity and food quality on clutch-size regulation, however, is difficult in field based studies and would require controlled laboratory studies (Singer 2004), perhaps comparable to those previously performed in the pipevine swallowtail *Battus philenor* (Fordyce and Nice 2004) or the comma butterfly *P. c-album* (Bergström et al. 2006).

(iii) Host plant accessibility

We have observed that *H. lucina* females immediately terminated oviposition attempts when any other plant hindered access to *Primula* leaves. Differences in vegetation structure may therefore explain why we found eggs on *Primula* leaves only at localities with low vegetation densities and turf heights. With increasing vegetation density and height (e.g. in fallow land), the proportion of clutches found on larger plant species that protrude over the surrounding vegetation increased. In the latter case, 1st instar larvae need to locate a *Primula* plant immediately after hatching. This likely exposes the offspring to an elevated risk of both predation and starvation, indicating that fallow land with high vegetation density—even under low-nutrient conditions where *Primula* can persist after abandonment—may provide only suboptimal larval habitat.

Population structure and management

Although *H. lucina* females have been found to covering distances of 250 m (Oates 2000) and colonising patches as far as 5 km from the nearest existing colony (Bourn and Warren 1998) in England, our 8-year survey of patch-occupancy in the Schönbuch highlights that (re)colonisation of empty habitat—despite some documented patch-turnover—can be a rather slow process. This coincides with Fartmann (2006), who found the current distribution in the Diemeltal best explained by long-term persistence in small habitat patches without much spatial patch dynamics. The extent, however, to which dispersal ability is linked with regional differences in climate, landscape structure, and population size or density warrants further study. The combination of retarded metapopulation-like dynamics in transitional habitats with long-term within-patch persistence indicates that management of *H. lucina* must maintain within-site habitat quality within a suitable network of occupied and empty habitat patches. Maintaining transitional habitats is not only difficult and cost-intensive, but may often proove impossible (e.g. Sparks et al. 1994; Bourn and Warren 1998; Oates 2000; Fartmann 2006). Therefore, large-scale regimes that generate the required network of transitional habitats as a side effect are likely to provide the most effective management. The regime of choice further depends on a combination of the local abiotic and biotic conditions (such as soil characteristics and vegetation), regional land-use history, and conservation priorities. With reference to our study regions, on calcareous grasslands, short-term benefit for *H. lucina* could be maximised with moderate autumn sheep grazing (Fartmann 2006; M. Oates, pers. comment), which maintains *Primula veris* growth (Ehrlen et al. 2005) and allows recruitment and long-term persistence of *P. veris* populations

(Brys et al. 2004). Such a scenario, however, poses two problems. First, moderate grazing will also favour the recruitment of fast-growing competitors of *P. veris*, such as Tor-grass (*Brachypodium pinnatum*) and Blackthorn (*Prunus spinosa*), being counter-productive for the management of *H. lucina*. Second, management strategies on calcareous grassland need to put particular emphasis on habitat-specialists such as *Hesperia comma* (Hermann and Steiner 1997; Fartmann and Mattes 2003; Davies et al. 2005; Davies et al. 2006) or *Maculinea arion* (Thomas et al. 1998), which require open habitat structures and thus rather intensive grazing combined with occasional coppicing. Given that also these regimes will always provide forest seams and hedgerows that facilitate *P. veris* growth, maintenance of *H. lucina* under the 'umbrella' of the top conservation species should nevertheless be possible.

In large-scale calcareous fen-regions, our study indicates that moderate cattle-grazing (Scholle et al. 2002) combined with occasional clearance of birch or pine growth ('Schwenden', Lederbogen et al. 2004) can provide and maintain the most suitable habitats for *H. lucina*. Large-scale grazing regimes have the advantage that grazing intensities vary with soil substrate and moisture, providing spatially heterogeneous patches with suitable *Primula* stands at any time (see Oates 2000). Note, however, that here again studies on a range of high-priority species are equivocal in their evaluation of the ability of large-scale grazing to sustain suitable habitats (e.g. Hermann and Anthes 2003; Lederbogen et al. 2004).

Given the historical importance of woodland as *H. lucina* habitat, we believe that management should particularly target this ecological niche. Here, spatially and temporarily dynamic coppice regimes, perhaps combined with occasional deliberate clearing (Buckley 1992; Warren and Thomas 1992) are likely to provide the most effective conservation strategy. In contrast to the previous two habitat types, such a management regime would also coincide well with the requirements of other high-priority butterfly species in woodland conservation such as *Lopinga achine* (Bergman 2001) or *Euphydryas maturna* (Freese et al. 2006).

Perspectives

Our study will help to improve future definitions of habitat quality for this endangered butterfly species. Yet, at the within-patch level, two determinants of patch quality merit further attention. First, intensive inspection of host plant individuals by egg-laying females indicated that subtle quality-differences between plant individuals, perhaps in nutritional value, chemical composition, or leaf structure, may affect oviposition decisions. Second, although nectar feeding has previously not been considered a limiting

resource for *H. lucina* (Garling 1984; Oates 2000), we found that ovipositing females frequently visit nectar plants between subsequent oviposition events (Diemltal: *Fragaria viridis*, *Potentilla tabernaemontani*; Schönbuch: *Fragaria vesca*; Allgäu: *Aster bellidiastrum, Berberis vulgaris, Menyanthes trifoliata, Primula farinosa, Vaccinium uliginosum, Valeriana dioica*). Hence, nectar resources may contribute to the quality of oviposition sites (Dennis et al. 2005b). Our study also urges investigations to what extent the differences in host plant electivity between regions are the result of genetically manifested variation in oviposition behaviour or simply the consequence of applying identical cues in different landscapes. Such knowledge would greatly help to adjust management strategies accordingly.

Future studies further need to improve our understanding of long-term persistence of *H. lucina* at a landscape-level. We lack assessments of the effects of habitat turnover on metapopulation dynamics. Such studies should be complemented by direct measurements of patch connectivity in relation to characteristics of the landscape matrix. Here, new developments in (satellite) tracking of small insects (Cant et al. 2005; Wikelski et al. 2006) open a suite of new methodological possibilities. Moreover, local population sizes, which were not included in our assessment of patch occupancy, may strongly affect dispersal and colonisation ability (Hanski 1999). Finally, the susceptibility of *H. lucina*—as that of other insects inhabiting temperate microclimates—to current climate change remains poorly understood. In order to evaluate management strategies, we clearly need to improve or abilities to predict large-scale population dynamics under future environmental variation.

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