J Insect Conserv (2009) 13:77–87
DOI 10.1007/s10841-007-9128-z

ORIGINAL PAPER

Does prescribed burning mean a threat to the rare satyrine butterfly *Hipparchia fagi*? Larval-habitat preferences give the answer

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Received: 6 August 2007 / Accepted: 10 December 2007 / Published online: 9 January 2008

Abstract The ecological effects of fire management, especially regarding arthropods are poorly investigated. Burning in winter was assumed to pose a threat to butterfly species hibernating as larvae. To assess the impact of prescribed burning on population viability, we analysed larval-habitat preferences of the highly endangered, xerothermophilous butterfly *Hipparchia fagi* in vineyards of the Kaiserstuhl region (southern Germany). Microhabitat preference analyses for mature larvae and egg-laying females revealed a preference of *H. fagi* for *Bromus erectus*-dominated communities with sparse vegetation coverage and a distinct tuft growth of the host plant *B. erectus* on microclimatically benefited slopes. We explain the preference of *B. erectus* by a preference of vegetation structure. The grass tufts offer a suitable climatically buffered living space for larvae. Egg deposition took place on dry substrate at positions of high solar radiation, thus adapted to hot and dry microclimate. As the larval habitat was sparsely vegetated as well as generally legally protected, fire management was not applicable and therefore not affecting the populations. We think it is conceivable that *H. fagi*, occurring here at its northern range limit, might expand its larval habitat into denser, combustible *B. erectus* stands in the course of global warming. A change in habitat preferences would necessitate a re-evaluation of management options.

Keywords Dry grassland · *Bromus erectus* · Host-plant choice · Larval ecology · Fire management

Introduction

Butterflies belong to one of the highly threatened groups of species and are undergoing a substantial decline across Europe (van Swaay and Warren 1999; Thomas et al. 2004; van Swaay et al. 2006). They respond sensitively and more rapidly than other organisms to environmental changes (Thomas and Clarke 2004) and thus are considered to be good indicators for these changes (Watt and Boggs 2003; van Swaay et al. 2006). One of the main reasons for butterfly extinctions is habitat fragmentation and degradation (e.g. Thomas et al. 2004). Important threats are agricultural improvement but also abandonment and changing management of sites (van Swaay et al. 2006). Most butterfly species in Europe occur in man-made semi-natural habitats, in particular grasslands that depend on regular management (van Swaay et al. 2006). This means that an efficient conservation to maintain or to substitute traditional land use practices such as mowing and grazing is required in order to preserve such habitats.

Formerly managed slopes of vineyard terraces in the Kaiserstuhl region in south-west Germany contain a variety of grassland habitats and species, many of them highly endangered. A prescribed burning in winter was re-established during the last years to prevent succession on those slopes. Most of the studies dealing with the ecological effects of fire and fire management only address vegetation

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(c.f. Alfred Töpfer Akademie für Naturschutz 1997). Information dealing with the impact of burning on butterflies is scarce and it mainly covers species from other biogeographical regions (e.g. Swengel 1996; Schultz and Crone 1998; Fleishman 2000; Huntzinger 2003; Waltz and Covington 2004; Swengel and Swengel 2007). Surveys within an ecological monitoring of the Kaiserstuhl fire-management project provided indications that even closely related species showed different responses to burning: While populations of *Minois dryas* apparently declined with an increase of burnt slope area, populations of *Hipparchia fagi* showed no clear reaction (Hermann unpublished data). Both are satyrine species hibernating as larvae in grasslands on vineyard slopes and, thus, are generally considered sensitive to burning in winter. So how can this difference in response be explained?

The Kaiserstuhl is the last remaining breeding area in Germany for *H. fagi*, a highly endangered, xero-thermophilous satyrine species with a pontomediterranean distribution (SBN 1987; Ebert and Rennwald 1991; Settele and Reinhardt 1999), and also presently represents the northern range margin. Thus, special attention needs to be paid to the study and conservation of the population (Bourn and Thomas 2002). The very low population density of *H. fagi* makes it difficult to monitor population changes in comparison with the more abundant *M. dryas*. Furthermore, the low abundance of *H. fagi* causes its higher vulnerability towards environmental changes.

Knowledge of the *H. fagi* ecology and the species' distribution in the Kaiserstuhl area was sparse prior to this study (Ebert and Rennwald 1991) even though it is of crucial importance for the assessment and explanation of the effects of prescribed burning. The larval ecology is of particular interest: First of all, the species is present as larvae at the time of fire management. Second of all, immature stages usually have much more specific requirements than adult butterflies because of their immobility and long developmental period. A suitable larval habitat for butterflies is characterised by suitable conditions concerning microclimate, host plant availability (in sufficient quantity and quality), an adequate disturbance regime and other factors such as low predation and competition pressure (Fartmann and Hermann 2006; García-Barros and Fartmann submitted). Grass-feeding butterflies were generally thought to be unspecific in their host-plant and oviposition-site choice (Wiklund 1984; Bink 1985). The fact that most of the satyrine species have specific requirements concerning the quality of host plants and microhabitat structures was just recently discovered (e.g. Dennis 1983; Shreeve 1986; Bergman 1999, 2000; Steiner and Trusch 2000; Fartmann 2004; Leopold 2006a, b). There is still though a significant gap in knowledge on larval ecology features in this species group (Dennis et al. 2006; Fartmann and Hermann 2006).

The main objective of this study was to assess the microhabitat preferences of egg-depositing females and mature larvae for defining habitat quality for *H. fagi* within the vineyard slopes of the Kaiserstuhl. Based on this knowledge we will assess the impact of fire management in winter on larval habitat quality and survival.

Materials and methods

Study species

Hipparchia fagi occurs in southern and central Europe, from the north of Spain to the south of Russia. The northern distribution border crosses the south of the Czech Republic, south Germany and north-east France (SBN 1987; Ebert and Rennwald 1991; Bink 1992; Lafranchis 2000; Beneš and Konvička 2002; Kudrna 2002; García-Barros et al. 2004), where the species is generally declining (e.g. Switzerland, Germany, Austria, Czech Republic, Romania, Ukraine; van Swaay and Warren 1999). *H. fagi* is considered critically endangered on national level in Germany and is also a highest priority target species at the regional level (see summary in Settele and Reinhardt 1999). Little is known about the detailed ecological requirements of *H. fagi*. Habitats are hot and dry woodland edges and open woodlands as well as open and hot olive groves and orchards (SBN 1987; Ebert and Rennwald 1991; Stefanescu personal communication). In east Europe, disturbed steppes and forest steppes are used, likewise (Beneš and Konvička 2002). In the Kaiserstuhl, the species occurs in structurally diverse late-successional stages of dry and semi-dry grasslands within the nature reserves, as well as in the complexes of vineyards and vineyard slopes (Ebert and Rennwald 1991).

H. fagi is univoltine and, in the study area, on the wing from mid-June to the end of August or early September (Ebert and Rennwald 1991; own observations). Flight activity is low as adults are resting or thermoregulating in the canopy, on tree trunks, stones or on the ground most of the time (SBN 1987; Ebert and Rennwald 1991; Bink 1992; own observations). *H. fagi* females attach their eggs singly on dry substrate (SBN 1987). After hibernating in the third larval instar, *H. fagi* larvae feed by night from early spring on (SBN 1987). Pupation takes place in a chamber in the soil or grass tuft (SBN 1987; Lafranchis 2000) between mid-June and mid-August, with durations ranging from about 3 (Ebert and Rennwald 1991) to 5 weeks (37 [34–40] days; Bink 1992).

Detailed and reliable information about host plants is poor. For the study area, *Bromus erectus* was known as a host plant based on single records of few larvae (Ebert and Rennwald 1991) and *Brachypodium pinnatum* recorded once as an oviposition substrate (Hermann own observations).

Study area, study sites and fire management

The study area comprises the central and western part of the Kaiserstuhl (federal state of Baden-Württemberg, Germany), a 92 km^2 large volcanic mountain remain rising about 350 m above the southern Upper Rhine Valley between Freiburg and the Rhine (Wilmanns et al. 1974) (Fig. 1). Due to the geographic situation, the Kaiserstuhl benefits climatically from the invasion of warm air masses from southwest through the Belfort Gap and from rain shadow and foehn wind from the Vosges mountain range, resulting in exceptional warm and dry climatic conditions with low mean annual precipitation (700 mm for Oberrotweil), many hours of sunshine (1,424 h/year for Lilienthal near Ihringen), and a high annual mean temperature of 10.1°C (for Oberrotweil) with hot summers and mild winters (Wilmanns et al. 1974; Müller-Westermeier 1996). For about 85% of the area, the tertiary volcanic material is covered with a loess layer up to 30 m deep which determines the structure and development of the cultural landscape considerably (Geyer and Gwinner 1968; Wilmanns et al. 1974): for wine cultivation (the dominant agriculture for hundreds of years now), narrow and heterogeneous terraces were built. The small and steep slopes between terraces were used for haymaking until livestock keeping largely ceased after World War II. Thereafter, slopes were burnt to restrain the growth of bushes and trees until this practice was banned in 1970 by nature conservation law. Within the 1960s and 1970s, extensive land consolidations were implemented, and large terraces with steep slopes with a height of up to 40 m and an inclination of 45–50° were built, adding up to an area of about 4 km^2 (Fischer 1982). A prescribed burning in late winter was reintroduced during the last years in large-scale experiments for landscape and habitat management for both historical and meliorated vinery slopes. The aim of these measures was to prevent invasion of woody species and to maintain an open meadow-vegetation structure, to benefit both, vinery (avoiding shading trees) and nature conservation (habitat and species). Guidelines of fire management include the restriction to late winter (December to February), a temporal and spatial mosaic of burnt and unburnt patches (every 2nd or 3rd year, burnt sections are not longer than 40 m), technical questions (upslope fire) and weather (cold, calm weather). Legally protected vegetation types according to § 32 NatSchG BW (such as dry grasslands) and slopes close to forests, protected areas or urban areas are excluded from fire management.

Four of the studied sites comprise characteristic types of vineyards and vineyard slopes in the central (HB, LE) and western (KB, MH) part of the Kaiserstuhl, whereas one additional site (BB, search for larvae only) is situated within the dry grasslands of the nature reserve “Badberg” in the central Kaiserstuhl (Table 1, Fig. 1).

Microhabitat analyses

For gathering information on microhabitat use in *H. fagi*, two approaches were used: the first approach was searching at night for mature larvae in spring (end of April/first half of May 2005). The search was conducted success-oriented only on selected grass- and herb-dominated slopes with potential host plants and a high likelihood of finding larvae within all five study sites (HB, LE, KB, MH, BB). Therefore, all grasses especially tuft-building ones within every slope were illuminated by a torch light and checked for larvae. By checking only selected slopes that were expected to be inhabited, this approach, in contrast to the second one is somewhat biased towards inhabited sites and does not reflect selectivity in relation to the overall available sites, but only microsite selectivity within slopes. The second approach was observing ovipositing females (from at least 5 m distance) systematically five to seven times during the flight period (end of July to beginning of September 2005) over all slopes within the study site HB (intensively studied part, HBint). Oviposition points were marked.

To cover the spectrum of available microhabitats, random data sets (the nearest grass tuft to a randomly thrown stick, Anthes et al. 2003) were sampled separately for each approach: 100 random points for the obtained 49 larvae points (only on those selected slopes checked for larvae, stratified by proportion of area) and 52 random points for 31 egg points (over all grass- and herb-dominated slopes of the study site HBint, stratified by vegetation type and proportion of area). For all microhabitat points (larva [L] and egg [E] points as well as random points [RL/RE]), microhabitat and environmental parameters (Table 2) were recorded on different scales: in 40 × 40 cm and in 1 × 1 m with the grass tuft as the centre as well as for the structure type (homogenous slope section) to which the microhabitat point belongs. As larvae points and larvae-random points are recorded on the same slopes, differences are supposed to occur mainly on smaller scales (40 × 40 cm and 1 × 1 m) but not for the structure-type scale.

The ‘structural combustibility’ was estimated by an ordinal scale with three categories (good, moderately and not combustible) for assessing the disposition for burning of a slope using the amount and size of the litter layer,

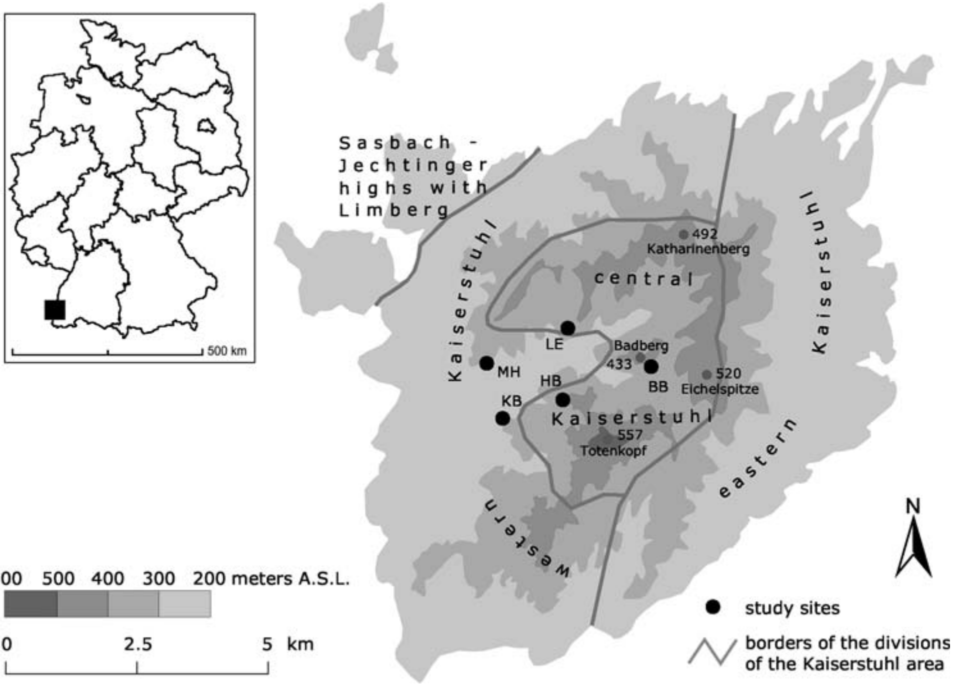

Fig. 1 Study area in southern Germany: divisions of the Kaiserstuhl and study sites (HB = "Hinterer Berg", LE = "Langeneck", KB = "Kunzenbuck", MH = "Mondhalde", BB = "Badberg"). The 200 m isoline corresponds with the border of the Kaiserstuhl area, approximately

Table 1 Characteristics of the five study sites

Study site		Habitat type	Site area (ha)	Slope area (ha)	Predominant exposure[a]
Hinterer Berg[b]	HB	Historical vinery slope	29.0	7.2	S–W
Langeneck	LE	Historical vinery slope	7.5	2.6	W, SO–SW
Kunzenbuck	KB	Meliorated vinery slope	61.4	14.6	(S–)W(–N)
Mondhalde	MH	Meliorated vinery slope	32.0	13.3	SO–S
Badberg[c]	BB	Dry grassland; nature reserve	0.1	–	S

[a] "S–W" meaning "south to west"; "W, ..." meaning "west and ..."; "(...)" meaning "partly"

[b] Intensively studied within HB (HBint): 11.5 ha site area, 4.1 ha slope area, S–W-facing; additionally adjacent nature reserve: +0.9 ha site area, S-facing, only adults

[c] Only larvae

vegetation structure and, where applicable, old traces of fire as traits. The 'legal combustibility' was derived from GIS, by categorising legally protected biotopes after § 32 NatSchG BW and nature reserves as well as areas close to them or to woodlands, houses or streets as not combustible. Slopes without egg or larva points but with suspicion of being used as larval habitat because of behavioural observations of females were included here as well to assure the most '*H. fagi*-friendly' estimation of fire management effects, meaning that potential negative fire effects are rather overestimated than underestimated.

Statistical analyses

To derive preferences from observed and expected values, mean values were compared for continuous variables (Mann–Whitney *U* test [MWU] for independent and Wilcoxon-signed-rank test [WSR] for dependent variables, respectively) and frequencies were compared by χ^2 test for categorical variables. Frequencies of 0 were set to 1 to allow χ^2 tests when categories were empty. Binary step-wise-forward logistic regression was applied to assess those parameters possessing the highest explanatory power for oviposition sites and larval habitat selectivity. Analyses were performed with SPSS 8.0 statistical package. Changing numbers of *n* between analyses originate from missing values for some variables.

Results

Larval host plants and oviposition sites

Forty-nine out of 50 mature larvae of *H. fagi* found in the field were staying or feeding on *B. erectus*, only one larva

Table 2 Parameters examined for microhabitat analyses and used in logistic regression

	Type	Scales[a]	Used in[b]
Vegetation structure			
Coverage of different layers[c]	[%]	40, 1, st	logReg[c]
Mean height of herb/grass layer	[cm]	40, 1, st	logReg
Height of litter layer	[cm]	40, 1, st	
Vegetation coverage in 0–5, 5–10,..., 25–30 cm height above ground[d]	[%]	40	logReg[d]
Climate			
Aspect (‘southness’, ‘westness’)[e]	[°]	40	logReg
Inclination	[°]	40	
Potential daily sunshine duration[f]	[h]	40	logReg[f]
Available grasses[g]			
Coverage of *Bromus erectus*	[%]	40, 1, st	logReg
Coverage of *Brachypodium pinnatum*	[%]	40, 1, st	logReg
Habitat characteristics			
Vegetation type	Nominal	st	
Host plant[h]			
Species	Nominal		
Height	[cm]		
Larva/egg			
Height above ground	[cm]		
Position on the plant (plant component; exposure)	Nominal		
Condition of the substrate (dry/fresh)	Nominal		
Combustibility			
‘Structural combustibility’[i]	Categorical	40, 1, st	
‘Legal combustibility’[j]	Categorical	40, 1, st	

[a] Scales: 40 = 40 × 40 cm, 1 = 1 × 1 m with the grass tuft as the centre, st = structure type (homogenous slope section)

[b] logReg: parameter used in a binary stepwise-forward logistic regression

[c] Categories: total vegetation, shrub, herb/grass, moss/lichen, litter, bare ground, gravel/stones/rock; thereof categories used in logReg: herb/grass, litter, bare ground, gravel/stones/rock

[d] Within a frame of 20 cm depth and 40 cm width (Anthes et al. 2003; Fartmann 2006); vegetation coverage in 10–15 cm height is used in logReg

[e] Conversion of aspect by sinus and cosinus into ‘westness’ and ‘southness’ (westness = 0 and southness = 1 meaning 180°, westness = 1 and southness = 0 meaning 270°)

[f] Measured with a horizontoscope after Tonne (1954) for each month from March to September, accuracy ½ h; the sum of all months (March to September) is used in logReg

[g] Only the most frequent and dominating species

[h] For eggs not laid on *B. erectus*, the *B. erectus* tuft closest to the actual host plant was recorded additionally to the actual host plant

[i] Categories: good, moderately, not combustible

[j] Categories: protected, not protected

was resting on a leaf of *B. pinnatum* amongst *B. erectus*. Occupied *B. erectus* tufts were higher than randomly chosen tufts (L 27 ± 7 cm, RL 22 ± 16 m, MWU $U = 824.5$, $P \leq 0.001$). In comparison to random points, vegetation coverage in all layers above 5 cm above soil surface was disproportionately higher at larvae points, likewise (e.g. for 10–15 cm height: L 32 ± 24%, RL 20 ± 21%, MWU $U = 1664.5$, $P \leq 0.001$).

Thirty-four egg depositions were observed, with eggs attached singly on plant material. Females showed an affinity for dry plant material (litter, dry leaves or dry inflorescences) as an oviposition substrate (74%, $n = 25$) and for *B. erectus* tufts (68%, $n = 23$) or places close to them (mean distance = 9.8 ± 2.5 cm to the next *B. erectus* specimen, for substrates different from *B. erectus*) (Fig. 2). Substrates different from *B. erectus* included fine-structured and hairy surfaces, primarily. For oviposition, high-growing *B. erectus* tufts were preferred (E 20 ± 7 cm, RE 15 ± 6 cm, MWU $U = 282.0$, $P = 0.004$). When oviposition took place on substrates different from *B. erectus*, the oviposition plant overtopped random *B. erectus* tufts, likewise (E 25 ± 12 cm, RE 15 ± 6 cm, MWU $U = 209.5$, $P \leq 0.001$).

Egg deposition height ranged between 0 and 38 cm (14 ± 10 cm) and could be explained to a high degree by mean herb layer height (at 40 × 40 cm) in a linear regression (31% for all samples, 57% for *B. erectus* only) (Fig. 3). Horizontal vegetation coverage was low in heights of egg deposition (15 ± 11%), but increased significantly in the subjacent 5 cm layer (28 ± 20%) (WSR $Z = -3.836$, $P \leq 0.001$; $n = 22$) and the denser the vegetation, the greater the difference between density in egg deposition height and the next layer beneath (Fig. 4). Below 10 cm above ground, egg deposition only took place if horizontal vegetation coverage was below 30% (one exception with 40%) (Fig. 5).

Habitat and microhabitat

Egg-laying sites of *H. fagi* ($n = 33$) were confined to slopes with mostly sparse to very sparse vegetation, belonging mainly to *B. erectus*-dominated communities or fragmentary types of *Xerobrometum* and *Mesobrometum* communities (91%). Oviposition-site plant communities differed significantly from available plant communities ($\chi^2 = 130.5$, $P \leq 0.001$). Slopes with high coverage of grass or herb layer (13% proportion of total area in the study site HBint) as well as those with sparse vegetation without *B. erectus* or with very fine and small *B. erectus* plants (13%) and slopes with dominant tall forbs and polycormic species or trees and shrubs (48%) were not used as larval habitat.

Egg-laying and larvae sites of *H. fagi* were predominantly steep (E 37.0 ± 11.3°, L 42.4 ± 9.6°), south- to south-west-exposed slopes (E 194.3 ± 26.1°, L 210.0 ± 25.9°) receiving about 11 h of potential daily sunshine in August (E 10.8 ± 0.9, L 10.5 ± 1.2). More southerly exposed slopes ('southness', MWU E $U = 562.5$, $P \leq 0.05$; L $U = 1627.0$, $P \leq 0.01$) were preferred.

Ovipositing females showed strong preferences for sites with low herb layer coverage (E 41 ± 13%, for the structure type), which was significantly lower than at randomly chosen available sites (RE 57 ± 23%; MWU $U = 471.0$, $P \leq 0.001$). Larvae points were characterised by low herb layer coverage (L 36 ± 14%), likewise, but did not differ from random points (see above for sampling design) (RL 42 ± 20%; MWU $U = 2051.0$, $P = 0.104$). Bare ground, rocks, stones and gravel, in return, played an important role at habitat sites and accounted for 46 ± 18% (E) and 54 ± 20% (L) of the surface area, respectively. Contrary to random points, the great majority of larvae and eggs were

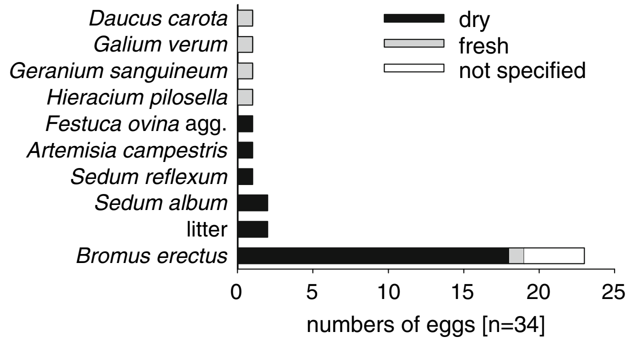

Fig. 2 Oviposition substrates of eggs of *Hipparchia fagi* ($n = 34$) and conditions of the substrate (dry $n = 25$, fresh $n = 5$, not specified $n = 4$)

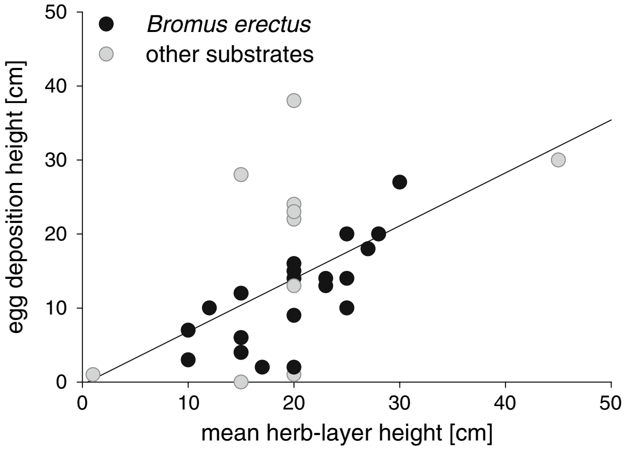

Fig. 3 Relation between egg deposition height and mean herb-layer height (at 40 × 40 cm around the egg). For all substrates: $n = 30$, $r = 0.560$, $r^2 = 0.313$, $P < 0.001$, $y = -0.332 + 0.715 * x$; for *B. erectus* only: $n = 20$, $r = 0.753$, $r^2 = 0.567$, $P < 0.001$, $y = -5.356 + 0.858 * x$

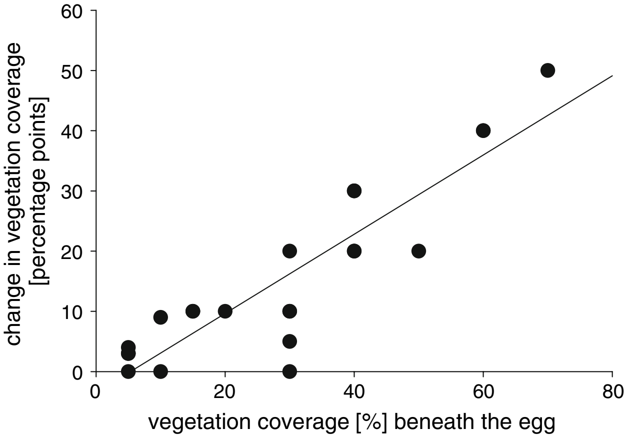

Fig. 4 Relation between the vegetation coverage at the layer beneath egg deposition and the change in vegetation coverage towards egg deposition layer (difference in vegetation coverage at egg deposition height and vegetation coverage in the layer beneath). $n = 23$, $r = 0.893$, $r^2 = 0.797$, $P < 0.001$, $y = -3.497 + 0.658 * x$

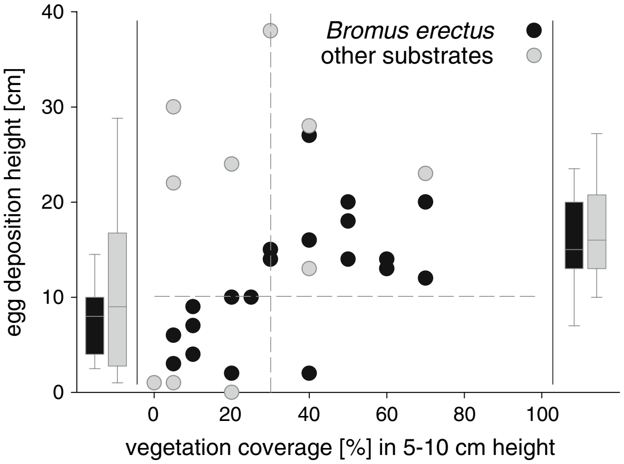

Fig. 5 Relation between egg deposition height ($n = 30$) and vegetation coverage in 5–10 cm height. The horizontal dashed line clarifies the upper limit of the considered height (10 cm), the vertical dashed line clarifies the border between low vegetation coverage ($\leq 30\%$) and high vegetation coverage ($>30\%$). Boxplots show the distribution of egg deposition heights with low (left) and high (right) coverage, respectively. Mann–Whitney U test: for all substrates: $U = 65.5$, $P = 0.059$, for *B. erectus* only: $U = 16.5$, $P = 0.011$

found at points with medium to high litter height (≥ 5 cm height, E 85%, $\chi^2 = 32.396$, $P \leq 0.001$; L 96%, $\chi^2 = 12.937$, $P \leq 0.01$).

The presence of *B. erectus* was an important factor for females to oviposit, whereas sites with high proportions of *B. erectus* were notably favoured (coverage on 1 × 1 m only for sites with presence of *B. erectus* on the slope section: E 26 ± 15%, RE 16 ± 17%, MWU $U = 389.5$, $P \leq 0.01$; L 23 ± 14%, RL 15 ± 10%, MWU $U = 1515.5$, $P \leq 0.01$). Sites with high coverage of *B. pinnatum* were avoided by the immature stages of *H. fagi* (for 1 × 1 m: E 1 ± 3%, RE 11 ± 19%, MWU $U = 458.0$, $P \leq 0.001$; L 1 ± 4%, RL 4 ± 12%, MWU $U = 2289.0$, $P = 0.432$; not significant for larvae because of sampling design, e.g. slopes with high coverage of *B. pinnatum* were not searched for larvae; see above).

The oviposition pattern was best (to 74%) explained by a combination of vegetation-structure and host-plant coverage (Table 3a). The likelihood of a site being accepted as oviposition habitat increased with the coverage of *B. erectus* and decreased with increasing herb layer coverage. Occurrence of mature larvae was best explained by a combination of host plant coverage and aspect (Table 3b): The likelihood of a site being accepted increased with host plant coverage and with more southerly aspect.

Fire management

The structural combustibility of the vegetation has only been classified as being 'good' for 7% of all larval and egg points ($n = 87$), while 72% of all points are laid on slopes being classified as not combustible (Table 4). Ninety percent of all larvae and egg points are situated on slopes that are legally protected from fire management. Thus, for 94% of all larvae and egg points, fire management is not applicable in the study area because of vegetation structure or legal protection. For the slope sections with egg points, combustibility differs significantly from available sites (Fig. 6). It does not for larvae points because of sampling design (see above).

Discussion

The crucial parameters within habitat requirements of larvae and ovipositing females of *H. fagi* in the vinery slopes of the Kaiserstuhl are vegetation structure and microclimate as well as host plant availability and host plant structure. Microhabitat preferences explain the lack of effects of fire management on the population.

Habitat requirements

Larval habitats at the northern species' range margin in Europe are characterised by sparse vegetation coverage and high proportions of bare ground, rocks, stones and gravel, relatively high amounts of litter and the tuft growth of the host plant *B. erectus*. Typical habitats are *B. erectus*-dominated communities and fragmentary forms of *Xerobrometum* and *Mesobrometum* communities. In addition to the generally warm climatic situation of the Kaiserstuhl, slopes with larval habitats are microclimatically hot due to their southern aspect and the absence of shading groves.

Our results clearly show that *B. erectus* is the only important host plant of *H. fagi* within the study area. High coverage of *B. erectus* is an important explanatory parameter for larval and egg presence (Table 3). The preference of satyrine butterflies for a single host plant species is not always obligatory but often linked to vegetation structure and host plant quality as well as to the synchronisation of host plant and butterfly life cycle (Bink 1985). On the one hand, the preference of *H. fagi* for *B. erectus* can most likely be explained by a preference for sparse vegetation on south-facing slopes linked with a warm and dry microclimate, and on the other hand by a preference for tuft-growing grasses. Larvae are most likely to be found in tall and sturdy tufts with high amounts of litter that are beneficial for two reasons. First, such tufts ensure food availability for the larva with limited mobility. Second, the tuft is used as living space, both for the small, hibernating larva, and for the large, nocturnal larva in spring and early summer. A sturdy tuft offers security

Table 3 Binary stepwise-forward logistic regression analysis on 11 variables at available sites (random sites) and sites occupied by *Hipparchia fagi*

	B	SE	Wald	*P*	R	Exp (B)	95% CI for Exp (B)	
							Lower	Upper
(a) Oviposition sites[a]								
Coverage herb layer	−0.591	0.0211	7.8766	<0.001	−0.2315	0.9426	0.9045	0.9823
Coverage *B. erectus*	0.0660	0.0194	11.5810	<0.001	0.2955	1.0682	1.0284	1.1096
Constant	0.5727	0.6880	0.6929	0.4052				
Model $\chi^2 = 23.512$, df = 2, $P < 0.001$, correctly classified 73.49%								
(b) Larvae sites[b]								
Coverage *B. erectus*	0.0447	0.0168	7.0669	<0.01	0.1638	1.0457	1.0118	1.0807
Southness	1.6833	0.5377	9.7996	<0.01	0.2033	5.3831	1.8764	15.4428
Constant	−2.6184	0.5196	25.3955	<0.001				
Model $\chi^2 = 26.635$, df = 2, $P < 0.0001$, correctly classified 69.80%								

(a) Oviposition sites ($n = 31$) and random points ($n = 52$), (b) larvae sites ($n = 49$) and random points ($n = 100$)

CI = confidence interval

[a] Variables entered into the regression that were not significant: coverage (%) of litter, bare ground, gravel/stones/rock, vegetation coverage in 10–15 cm height, mean herb layer height, coverage *Brachypodium pinnatum*, westness, sum of potential daily sunshine duration (March–September)

[b] Variables entered into the regression that were not significant: coverage (%) of herb layer, litter, bare ground, gravel/stones/rock, vegetation coverage in 10–15 cm height, mean herb layer height, coverage *Brachypodium pinnatum*, westness, sum of potential daily sunshine duration (March–September)

Table 4 Structural and legal combustibility of larval habitats (see chapter "Microhabitat analyses" for definition in terms of combustibility) of *Hipparchia fagi* ($n = 87$)

Structural combustibility	Legal combustibility				Σ	
	Protected		Not protected			
Good	**4**	**5%**	2	2%	6	7%
Moderately	**15**	**17%**	3	3%	18	21%
Not	**59**	**68%**	**4**	**5%**	63	72%
Σ	78	90%	9	10%	87	100%

Not-combustible sites are highlighted in bold figures

against predators and could serve as a climatic buffer (Brakefield et al. 1992; García-Barros and Fartmann submitted; García-Barros personal communication). Depending on weather conditions, larvae are able to translocate their position between the edge of the tussock with more extreme temperatures (warmer during day, colder during night) and the more balanced microclimate inside the tuft.

Host-plant choice of the ovipositing female should reflect the requirements of larvae (Porter 1992). As the larvae prefer sturdy tufts, the females prefer to oviposit on or near high and strong *B. erectus* tufts. The texture of the substrate seems to be (at least partly) decisive for the female's selection for egg attachment. Egg deposition substrates other than those from *B. erectus* are, to a certain degree similar to dry *B. erectus* leaves. They are fine and usually dry (*Artemisia campestris*, *Galium verum*, dry inflorescences of *Sedum album* and *S. reflexum*) or hairy (*Hieracium pilosella*, *Geranium sanguineum*, *Daucus carota*). A preference for dry substrates in oviposition is also recorded for other xero-thermophilous satyrines [Steiner and Trusch (2000) for *H. stalinius*; Leopold (2001) for *Chazara briseis*; Leopold (2006b) for *H. semele*] and many alpine *Erebia* species (Fartmann and Hermann 2006). Dry plant biomass provides drier and warmer environments than green plants do (WallisDeVries and van Swaay 2006). Due to evapotranspiration the temperature of green leaves is comparable to that of the ambient air temperature, whereas dry plants rapidly warm up in the sun over ambient temperature (Stoutjesdijk and Barkman 1992). Hairiness of the dry plant material enhances the warming up of the substrates due to the creation of a boundary layer with lower air circulation close to the surface (Porter 1992). The eggs of *H. fagi* are small enough to fit into this boundary layer.

Although egg deposition positions seem to be diverse at the first sight, analysis of the vegetation structure reveals that females consistently attach their eggs at positions that receive high solar radiation, i.e., more precisely, on the 'local radiation surface'. At low vegetation densities near the ground, eggs are laid close to the ground. By contrast, at high vegetation densities near the ground, egg deposition takes place significantly higher (Fig. 5). Though a decrease of vegetation density with height is to be expected as a rule, the denser the vegetation the higher the difference between

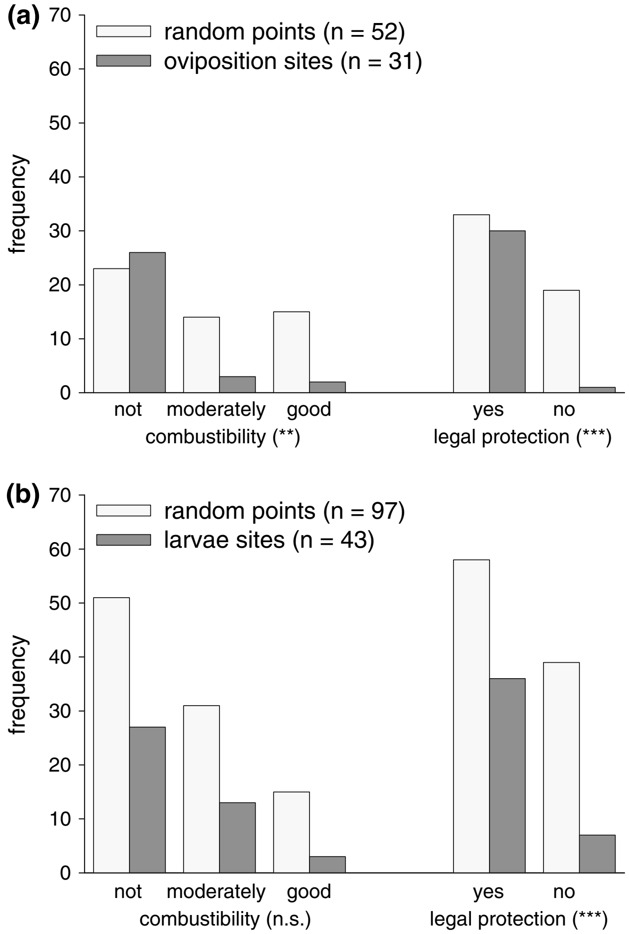

Fig. 6 Combustibility of (**a**) oviposition and (**b**) larvae sites of *Hipparchia fagi* and of random sites, respectively. χ^2 test: (**a**) structural combustibility $\chi^2 = 12.745$, $P = 0.002$, legal combustibility $\chi^2 = 11.784$, $P = 0.001$, (**b**) structural combustibility $\chi^2 = 2.255$, $P = 0.342$, legal combustibility $\chi^2 = 7.731$, $P = 0.005$. ns = not significant, ** = $P \leq 0.01$, *** = $P \leq 0.001$

vegetation density at deposition height and vegetation density in the layer underneath. Egg deposition at such dry and exposed positions should assure successful egg development.

Hill et al. (1999) postulated that climate and habitat availability will determine distribution patterns of butterflies at their range margins in the 21st century. As a xerothermophilous and pontomediterranean species, *H. fagi* should profit from global warming at the northern range limit. In northern and central Europe, many butterfly species reach their northern range limit and they are frequently depending on unusual warm microhabitats (Thomas 1993; Thomas et al. 1999; Bourn and Thomas 2002; Fartmann 2004; Fartmann and Hermann 2006; Eichel and Fartmann 2007). As shown above, oviposition and larval habitat niches of *H. fagi* are very specific and characterised by a certain vegetation structure and microclimate. The habitat niches are usually narrower at the range margin than that at the distribution core (Thomas 1993; Bourn and Thomas 2002). An expansion into denser *B. erectus* stands as a larval and oviposition habitat due to warmer summers and more moderate winters in the future seems to be conceivable in the Kaiserstuhl. Potential habitats fulfilling these conditions are numerous in the region.

On the other hand, WallisDeVries and van Swaay (2006) recently indicated a microclimatic cooling in spring due to an earlier start of plant growth in oceanic climates resulting from climate change and anthropogenically increased nitrogen input. This microclimatic cooling will first affect butterflies with actively sun-basking caterpillars in spring (e.g. *Euphydryas aurina* or *Melitaea cinxia*). For *H. fagi*, the process of microclimatic cooling due to eutrophication is most likely of low significance since there is no evidence for sun-basking of the larvae.

Fire management

Larval-habitat analyses clearly explain why winter burning has no noticeable effect on populations of *H. fagi* within vineyard slopes in the Kaiserstuhl. Sites that serve as a larval habitat are nearly exclusively found on slopes that are, as a result of sparse vegetation structure, not or almost not combustible. The *B. erectus*-dominated vegetation is too sparse and tufted and does not provide the necessary fuel biomass for complete and effective winter burning. Moreover, the majority of larval habitats are legally protected vegetation units (dry and semi-dry grassland, § 32 NatSchG BW) and/or are excluded from fire management because of their vicinity to forests. The fact that hardly any mature larvae are found on slopes that are combustible cannot be explained by the theory that, on those slopes, hibernating larvae died due to the fire: Only a small proportion of combustible slopes is actually burnt every winter, depending on weather conditions and fire management regulations.

Although the direct impact of fire on individual larvae could not be tested, the results of combustibility analyses of larval habitats lead to the conclusion that a direct impact of fire management on *H. fagi* larvae, and hence the population, does not occur in the Kaiserstuhl. Observations made on *M. dryas*, in return, explain why this species apparently suffers from fire management: Potential larval habitats of *M. dryas* in vineyard slopes are abandoned dry grasslands and *B. pinnatum*-dominated communities that have a very good combustibility (c.f. Ebert and Rennwald 1991; own observations). Larvae hibernating in the dense grass vegetation probably die due to the heat or suffer from indirect effects of burning (e.g. changes in microclimate or predators).

An indirect impact of fire management on *H. fagi* populations by changes in adult habitat quality could not be observed. Also adults show a preference for slopes with sparse vegetation ($\chi^2 = 230.0$, $P \leq 0.001$ for $n = 26$, standardised observations within HBint; data not shown here), predominantly for resting and thermoregulation. Sites experiencing fire management (slopes with dense grass and herb layers) are utilised very rarely by adults (only 6% of adult observations on good combustible slopes; $n = 160$; not standardised observations within all study sites; data not shown here), mainly for nectar foraging or as resting site.

Within the current legal regulation and with respect to the observed current habitat preferences, larval habitats of *H. fagi* in the study area are not essentially affected by fire management. But if the habitat preferences of *H. fagi* expand or shift into more densely vegetated slopes in the course of global warming, a higher percentage of larval habitats might be combustible and the impact of fire management might be different and would need a re-evaluation.

Management options

Fire is used as one possible management tool in the vineyard slopes within the Kaiserstuhl area and as shown above it is not applicable to the larval habitats of *H. fagi*. Nevertheless, habitat management is needed. Some few slopes that are very steep and sparsely vegetated probably stay stable because of their exposure and dry soil conditions or because of land slides (c.f. Ebert and Rennwald 1991). But most larval habitats are threatened by invasion of polycormic species such as *Solidago gigantea* and overgrowth of species such as *Clematis vitalba*, *Vitis* spec. and *Rubus fruticosus* agg. Slopes that are characterised by expanding thermophilous forb species of forest margins and increasing vegetation coverage are too dense and not optimal for *H. fagi* larval development, likewise. Here, occasional mowing is probably the only feasible option to keep larval habitats open, although this is a rather expensive method with considerable practical problems due to the steepness of the slopes. Mowing annually in June proved to be most effective to preserve dominant stands of *B. erectus* (Kahlert et al. 2005), and mowing regimes were also shown to be effective in reducing the dominance of *B. pinnatum* in abandoned chalk grasslands (Bobbink and Willems 1993). Non-intensive grazing with goats could be another appropriate management option as recent results from the study site Badberg indicate (Hofmann and Hafner personal communication; own observations). Disturbance by trampling and grazing creates gaps which is probably rather beneficial for larval habitat quality (c.f. Bolz and Geyer 2001 for *H. alcyone*). In contrast, creating new potential habitats for *H. fagi* by burning of biomass-rich sites is unlikely, because winter fires usually promote polycormic species (e.g. *B. pinnatum*) and *B. erectus* will be repressed (Moog et al. 2002; Kahlert et al. 2005; Kohler et al. 2005).

Acknowledgements The investigations have been carried out in the framework of the research project “Ecological monitoring of the integration of prescribed fire in the management of vineyard slopes in the Kaiserstuhl area” on behalf of the Emmendingen Landscape Conservation Association (Landschaftserhaltungsverband Emmendingen), with financial support by the Ministry for Food and Rural Area Baden-Württemberg and the municipalities of the study area. We are very grateful to Norbert Hölzel for valuable comments that considerably improved the manuscript and to Lillian Harris for help with the English language.

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