

# Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability

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**Abstract** Understanding the factors that determine habitat quality is vital to ensuring appropriate habitat management. The main objective of this study was to assess the microhabitat preferences of egg-depositing females of the Grizzled Skipper (*Pyrgus malvae*) in calcareous grasslands of the Diemel Valley (Central Germany) for defining habitat quality. Based on this knowledge, we make management recommendations for the conservation of this threatened species. *P. malvae* generally preferred open and warm oviposition sites. However, there were considerable differences in the environmental conditions, depending on the selected host plant. On the small *Potentilla tabernaemontani* plants that grew in sparse vegetation with low-growing turf, mostly only one egg was found per plant. In contrast, occupied *Agrimonia eupatoria* host plants were larger and more prominent, regularly having more than one egg, and grew at sites with a taller and denser vegetation. The observed oviposition pattern reflects a trade-off between microclimate and food availability: Usually, occupied *P. tabernaemontani* plants grow under favourable microclimatic conditions. However, during hot years the risk of desiccation is high, leading to food shortage. In contrast, *A. eupatoria* generally provides more biomass, thrives on deeper soils and the vegetation has a cooler microclimate: hence, food shortage is somewhat unlikely. To meet the described habitat requirements of *P. malvae*, traditional rough grazing by sheep and goats seemed to be the most appropriate land management strategy. The

re-introduction of coppicing in woodlands, particularly adjacent to calcareous grasslands, would also be beneficial.

**Keywords** Calcareous grassland · Habitat quality · Habitat requirements · Host plant selection · Oviposition · *Pyrgus malvae*

## Introduction

Butterflies exhibit a high host plant specificity (Munguira et al. 2009), the niches of the immature stages are often narrow (García-Barros and Fartmann 2009) and most species form metapopulations depending on a network of suitable habitats (Thomas et al. 2001; Anthes et al. 2003; Eichel and Fartmann 2008). Due to these complex requirements, the decline of butterflies exceeds those of many other taxonomic groups (Thomas et al. 2004; Thomas 2005). Thus, they are an important model group in ecology and conservation (Watt and Boggs 2003; Ehrlich and Hanski 2004) and function as sensitive indicators for environmental change (Thomas and Clarke 2004; Thomas et al. 2004; Thomas 2005).

Understanding the factors that determine habitat quality is vital to ensure appropriate habitat management (Thomas et al. 1998, 2001). Most studies on butterflies define habitat quality on the basis of the requirements of the immature stages (e.g. oviposition sites), because they are more specific than those of the adults (Thomas 1991; Clarke et al. 1997; Thomas et al. 1998, 2001; Bourn and Thomas 2002). This is due to low or absent mobility and the usually longer lifetime of the pre-adult stages (Fartmann 2004). Hence, the right choice of an oviposition site by the female is crucial for the survival of its offspring (García-Barros and Fartmann 2009).

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Generally, only a fraction of the total host plant population in a patch is suitable for oviposition (Dennis et al. 2006). Selection of a host plant often reflects a complex trade-off between several biotic and abiotic factors. Hence, a large body of research has dealt with environmental conditions influencing oviposition-site selectivity. Among these factors are plant size (Courtney 1982; Wiklund 1984; Küer and Fartmann 2005), plant quality (Bergström et al. 2006), plant phenology (Thomas and Elmes 2001), avoidance of parasitoids (Ohsaki and Sato 1994; Nieminen et al. 2001), occurrence of conspecifics (Courtney 1984; Sato et al. 1999) and microclimate (Shreeve 1986; Thomas et al. 1998; Roy and Thomas 2003). However, the relevance of each of these factors varies largely among species and regions.

Here we used the Grizzled Skipper (*Pyrgus malvae*) as a model system to study oviposition site selectivity in calcareous grasslands of the Diemel Valley (Central Germany). Although populations appear to be stable in many European countries (van Swaay and Warren 1999), declines have been observed, in particular in Northwestern Europe and northwestern Central Europe, and the species has disappeared in many regions (Asher et al. 2001; Bos et al. 2006). In the northern half of Germany, *P. malvae* is relatively rare and listed in the red data books of most of the Federal States (Reinhardt and Bolz in press). Most about the habitat requirements of the species is known from Great Britain (e.g. Brereton et al. 1998; Asher et al. 2001; Fox et al. 2006), while the knowledge base in Central Europe remains very scarce (Wagner 2006). Detailed information on the oviposition habitats is completely missing.

The main objective of this study was to assess the microhabitat preferences of egg-depositing females for defining habitat quality for *P. malvae*. Based on this knowledge we give management recommendations for the conservation of this threatened species.

## Materials and methods

### Study organism

The Grizzled Skipper *P. malvae* (Linnaeus, 1758) (Lepidoptera: Hesperiidae) has a Palearctic distribution ranging from the British Isles to Korea, and from the Mediterranean region to middle Finland (65°N) (Ebert and Rennwald 1991). The main habitats of *P. malvae* are woodland rides and clearings, unimproved grassland and abandoned industrial sites (Asher et al. 2001). In the Diemel Valley, *P. malvae* is still widespread and colonizes primarily nutrient-poor calcareous grasslands (Fartmann 2004). Adults are here on the wing in one generation from the end

of April to the end of June, with a peak in mid-May. Eggs are generally laid singly on the host plant (Asher et al. 2001). *Potentilla tabernaemontani* and *Agrimonia eupatoria* are the two main host plants in Central European calcareous grasslands (Wagner 2006). The caterpillars inhabit a twisted, slightly-spinned leaf in all stages (Ebert and Rennwald 1991). *P. malvae* hibernates as a pupa and emerges in spring.

### Study area

The Diemel Valley of about 390 km<sup>2</sup> 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). The climate is suboceanic and the majority of the region consists of limestone which maintains semi-dry grassland. It represents the largest area of calcareous grassland in the northern half of Germany (Fartmann 2006).

### Experimental design

In June 2009 we examined, in 30 person-days, seven randomly selected study sites in the calcareous grasslands of the Diemel Valley. The size of the patches ranged from 2.0 to 11.3 ha (mean value  $\pm$  SD = 7.9  $\pm$  2.9 ha). To avoid confusion with eggs of *Pyrgus serratalae*, the Lower Diemel Valley was left out of consideration in this study, as the sibling species occurs here sympatrically (Fartmann 2004). We systematically searched for eggs of all individuals on the two main host plants, *P. tabernaemontani* and *A. eupatoria* (cf. Wagner 2006), by pacing out each study site in sinuous lines with a distance of 5 m between each line. In a radius of 50 cm around each occupied plant, several environmental parameters were recorded (Table 1).

For comparing both occupied and the wider spectrum of available host plants, systematic samples were selected based on a 50  $\times$  50 m grid. Hence, the number of unoccupied plants studied per study site corresponded to the proportional area of each patch (Fartmann 2006). Samples were always taken at the next plant adjacent to the crossing points of the grid. In total, we selected 32 unoccupied plants for *P. tabernaemontani* and 33 for *A. eupatoria*. For each of the unoccupied plants we recorded the same parameters as for the occupied ones.

### Statistical analysis

Each host plant with eggs, regardless of the number of eggs, was treated as a single sample in our data set. Categorical variables were tested using Fisher's exact test.

To evaluate if environmental variables (response variables) differ between occupied and unoccupied host plants

**Table 1** Overview of parameters examined in generalized linear mixed-effects models (GLMMs) to explain host-plant occupancy

	Factor levels
Response variable	
Host-plant occupancy	2 <sup>g</sup>
Host-plant species	2 <sup>h</sup>
Predictor variable	
<i>Fixed effects</i>	
Climate	
Aspect (°) <sup>a</sup>	Metric
Inclination (°) <sup>a</sup>	Metric
Latitude (°) <sup>a</sup>	Metric
Potential daily sunshine duration (h) <sup>b</sup>	Metric
Habitat characteristics	
Land-use type <sup>c</sup>	3 <sup>i</sup>
Vegetation structure	
Field layer (%)	Metric
Shrub layer (%)	Metric
Litter layer (%)	Metric
Bare ground (%) <sup>d</sup>	Metric
Stony surface (%) <sup>d</sup>	Metric
Turf height (cm) <sup>e</sup>	Metric
Horizontal vegetation density (%) <sup>f</sup>	Metric
Host plant	
Height above ground (cm) <sup>e</sup>	Metric
Diameter (cm)	Metric
Egg	
Length and width of the occupied leaf (cm)	Metric
Oviposition height above ground (cm)	Metric
Location on the plant	3 <sup>j</sup>
<i>Random effect</i>	
Site	7

<sup>a</sup> The ‘heat load index’ after McCune and Keon (2002) is used in GLMM

<sup>b</sup> Measured with a horizontoscope after Tonne (1954) for June, accuracy: ½ h

<sup>c</sup> Land-use type was not used for both GLMMs, because it is identic within one site

<sup>d</sup> The sum of bare ground and stony surface (gravel/stones/rocks) was used in the GLMM of *A. eupatoria*. In the GLMM of *P. tabernaemontani* it was excluded, because it was strongly correlated with horizontal vegetation density and field layer

<sup>e</sup> Prominence (the difference between host-plant height and vegetation height) was used in GLMM

<sup>f</sup> Measured within a frame of 30 cm depth and 50 cm width for different layers in 0–5, 5–10, ..., 25–30 cm height above ground (Poniatowski and Fartmann 2008), the mean of all layers is used in GLMM

<sup>g</sup> Occupied = 1, unoccupied = 0

<sup>h</sup> *P. tabernaemontani* and *A. eupatoria*

<sup>i</sup> Paddock grazing, rough grazing, unused

<sup>j</sup> Top side of the leaf, bottom side of the leaf, plant stem

as well as among occupied host plants, generalized linear mixed-effects models (GLMMs) (Bates et al. 2008) were conducted. For proportional data, cover data (such as field layer and bare ground), proportional binomial GLMMs were applied. In all other cases we used Poisson GLMMs. Moreover, two binomial GLMMs were applied to assess which environmental parameters possessed the highest explanatory power for host-plant occupancy (Table 1). To assess intercorrelations between predictor variables, Spearman’s correlation was used. Strongly intercorrelated parameters (Spearman correlation  $r_s > |0.7|$ ) were eliminated prior to regression analysis. Non-significant predictors were excluded from the final model by stepwise backward-selection ( $P > 0.05$ ). The significance of the predictor variables was assessed with likelihood ratio tests (Type III test). For all GLMMs, the variable *site* was set up as a random factor. Statistical analyses were performed using R-2.9.0 (R Development Core Team 2009) and SPSS 16.0 statistical packages.

## Results

In total, we found 265 eggs of *P. malvae* on 152 plants. Most of the eggs were deposited on *A. eupatoria* (220 eggs on 112 plants); less than one-fifth was found on *P. tabernaemontani* (45 eggs on 40 plants). Eggs were mainly placed on the underside of the leaf (88.4%), occasionally on the upperside (11.2%) and exceptionally on the stem (1.7%). In the vast majority of the cases, the leaves used for oviposition were directly located above a stony surface or bare ground (*P. tabernaemontani*: 78%; *A. eupatoria*: 57%).

Oviposition habitats of *P. malvae* were generally characterized by warm microclimatic conditions. Although occupied plants occurred in all aspects, the great majority (>80%) were found on south- or west-facing slopes (Table 2). For *A. eupatoria* the aspect of occupied plants significantly differed from that of unoccupied plants. Potential daily sunshine duration in June was generally high at occupied *P. tabernaemontani* and *A. eupatoria* plants (Table 3). Moreover, growing sites of occupied plants of both species had a sparse and open vegetation. Values for field-layer cover, turf height and horizontal-vegetation cover were significantly lower than at available sites (Fig. 1; Table 3). The cover of stony surface (*P. tabernaemontani*) and bare ground (*A. eupatoria*) were significantly higher at occupied plants. In one-third of the cases, *P. tabernaemontani* plants used for egg-laying grew directly on bedrock. Occupied individuals of *A. eupatoria* were often found at disturbed microsities with bare ground, such as path edges within the grasslands, or molehills.

**Table 2** Relative (%) and absolute frequencies of the nominal variables at occupied and unoccupied host plants of *Pyrgus malvae* in the study area

Parameter	<i>Potentilla tabernaemontani</i>				<i>Agrimonia eupatoria</i>			
	Occupied ( <i>N</i> = 40)		Unoccupied ( <i>N</i> = 32)		Occupied ( <i>N</i> = 112)		Unoccupied ( <i>N</i> = 33)	
	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>
Aspect	<i>P</i> = 0.155				<i>P</i> < 0.01			
North	2.5	1	9.4	3	7.1	8	9.1	3
East	2.5	1	0.0	0	4.5	5	6.1	2
South	55.0	22	43.8	14	43.8	49	36.4	12
West	40.0	16	37.5	12	37.5	42	27.3	9
Flat	0.0	0	9.4	3	7.1	8	21.2	7
Land use	<i>P</i> < 0.001				<i>P</i> < 0.001			
Paddock grazing	55.0	22	75.0	24	75.0	84	54.5	18
Rough grazing	7.5	3	12.5	4	17.9	20	27.3	9
Unused	37.5	15	12.5	4	10.4	8	18.2	6

Comparison of absolute frequencies between occupied and unoccupied host plants using Fisher's exact test

**Table 3** Mean values  $\pm$ SD of the numerical variables at occupied and unoccupied host plants of *Pyrgus malvae* in the study area

Parameter	<i>Potentilla tabernaemontani</i>			<i>Agrimonia eupatoria</i>			<i>P. vs. A.</i> <sup>a</sup>
	Occupied ( <i>N</i> = 40)	Unoccupied ( <i>N</i> = 32)	<i>P</i>	Occupied ( <i>N</i> = 112)	Unoccupied ( <i>N</i> = 33)	<i>P</i>	<i>P</i>
Oviposition							
Oviposition height (cm)	2.9 $\pm$ 2.3			8.7 $\pm$ 5.4			***
Host-plant characteristics							
Leaf length (cm)	2.1 $\pm$ 2.4			2.7 $\pm$ 0.9			***
Leaf width (cm)	1.0 $\pm$ 1.4			1.5 $\pm$ 0.4			***
Host-plant height (cm)	4.3 $\pm$ 2.7	5.5 $\pm$ 2.7	n.s.	12.5 $\pm$ 8.1	14.8 $\pm$ 8.9	n.s.	***
Host-plant diameter (cm)	6.0 $\pm$ 3.0	5.7 $\pm$ 2.8	n.s.	14.8 $\pm$ 6.4	14.4 $\pm$ 8.1	n.s.	***
Vegetation structure							
Field layer (%)	55.4 $\pm$ 26.2	71.9 $\pm$ 22.0	**	70.8 $\pm$ 21.4	83.12 $\pm$ 14.4	**	***
Shrub layer (%)	4.2 $\pm$ 11.6	5.3 $\pm$ 8.7	*	0.4 $\pm$ 1.3	4.8 $\pm$ 12.1	n.s.	**
Litter layer (%)	11.9 $\pm$ 12.0	20.2 $\pm$ 14.2	**	20.4 $\pm$ 16.6	17.4 $\pm$ 14.5	n.s.	***
Bare ground (%)	12.9 $\pm$ 15.6	10.6 $\pm$ 15.6	n.s.	10.9 $\pm$ 15.4	0.9 $\pm$ 1.5	***	*
Stony surface (%)	18.7 $\pm$ 24.7	2.1 $\pm$ 5.9	***	0.9 $\pm$ 5.8	0.3 $\pm$ 1.7	n.s.	*
Turf height (cm)	9.2 $\pm$ 7.5	13.2 $\pm$ 7.0	*	13.9 $\pm$ 8.1	21.9 $\pm$ 13.0	***	*
Microclimate							
Daily sunshine in June (h)	10.2 $\pm$ 2.1	10.2 $\pm$ 2.3	n.s.	10.3 $\pm$ 2.3	9.6 $\pm$ 3.0	n.s.	n.s.

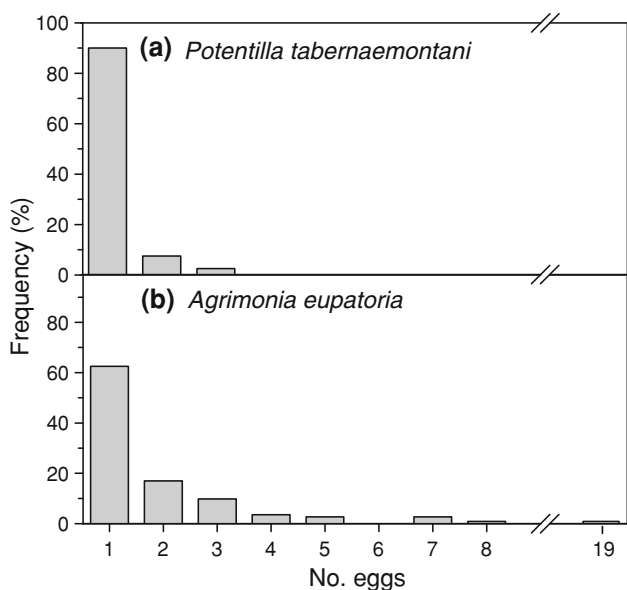
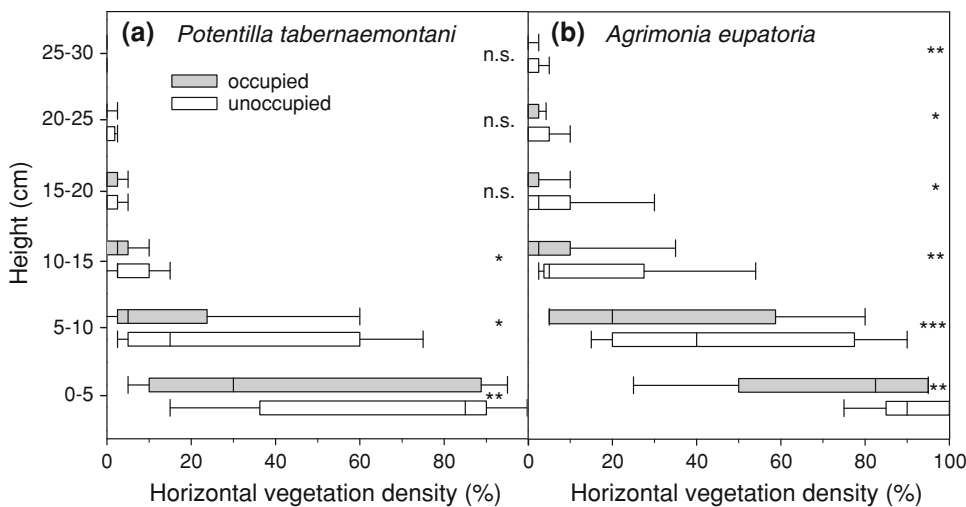
Comparison of values by generalized linear mixed-effects models (GLMMs); \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001, n.s. not significant

<sup>a</sup> Occupied *Potentilla tabernaemontani* and occupied *Agrimonia eupatoria* plants were tested against each other

Usually one egg per plant was found. However, particularly at *A. eupatoria*, higher egg numbers regularly occurred (Fig. 2). The number of eggs per host plant was significantly higher for *A. eupatoria* than for *P. tabernaemontani*. In general, occupied *A. eupatoria* provided more biomass than occupied *P. tabernaemontani*. Both leaves (length and width) and the whole plant (height and

diameter) were significantly bigger in *A. eupatoria* than in *P. tabernaemontani* (Table 3). *A. eupatoria* thrived in more dense and tall vegetation, while *P. tabernaemontani* grew in more open vegetation with short turf (Table 3; Fig. 3). Accordingly, the cover of bare ground and stony surface was significantly higher and the cover of litter was significantly lower at occupied *P. tabernaemontani* than at

**Fig. 1** Horizontal vegetation density for **a** occupied ( $N = 40$ ) and unoccupied ( $N = 32$ ) *Potentilla tabernaemontani* as well as **b** occupied ( $N = 112$ ) and unoccupied ( $N = 33$ ) *Agrimonia eupatoria*. Box-plots show 10th and 90th percentile (whiskers), 25th and 75th percentile (boundary of the box), and median (line); Mann-Whitney  $U$  test for significance ( $\alpha = 0.05$ ): \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , n.s. not significant



**Fig. 2** Number of eggs per plant on **a** *Potentilla tabernaemontani* ( $N = 40$ , mean  $\pm$  SD =  $1.1 \pm 0.4$ ) and **b** *Agrimonia eupatoria* ( $N = 112$ , mean  $\pm$  SD =  $2.0 \pm 2.2$ ). Comparison of absolute frequencies (three groups: 1, 2,  $>2$  eggs per plant) between the two host plants: Fisher’s exact test,  $P < 0.01$

occupied *A. eupatoria*. Occupied *A. eupatoria* plants were significantly more prominent than both unoccupied *A. eupatoria* and occupied *P. tabernaemontani* plants (Fig. 4). In contrast, the egg-laying decision of *P. malvae* females on *P. tabernaemontani* was not influenced by the prominence of the plant individuals. Oviposition heights on *A. eupatoria* and *P. tabernaemontani* also differed significantly. Eggs on *A. eupatoria* were mostly deposited 10 cm above the soil surface, while those on *P. tabernaemontani* were attached very close to the ground. While most occupied *A. eupatoria* plants were found in managed sites, this was only true for two-thirds of the occupied *P. tabernaemontani* plants (Table 2).

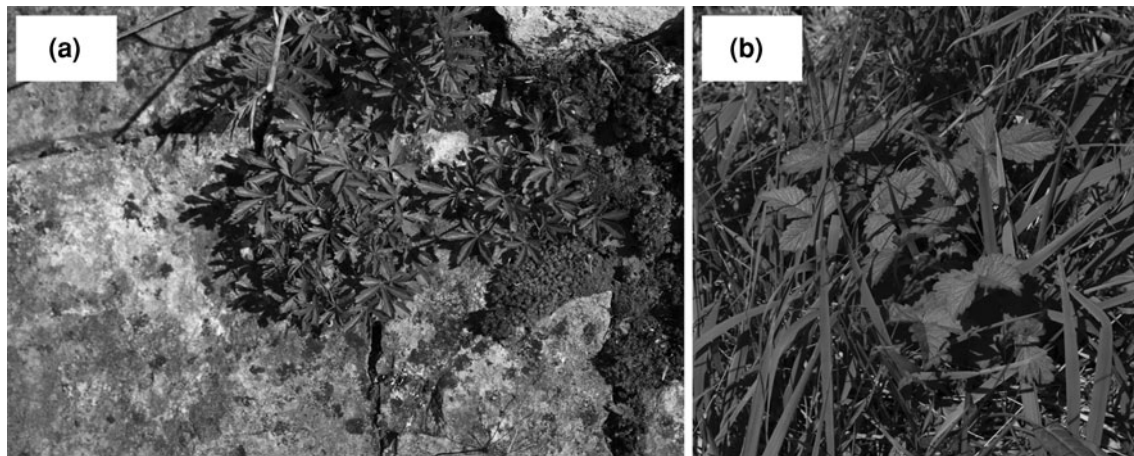
The GLMM analysis showed that the occurrence of eggs on *P. tabernaemontani* was best explained by a low horizontal vegetation density (Table 4). *A. eupatoria* plants were preferred for oviposition, if they were prominent and the growing sites had a low field layer cover, a high cover of bare ground/stony surface and high sunshine duration. The explanatory power of the models was generally high, with Pseudo  $R^2$  [Nagelkerke] values of 0.46 and 0.37 respectively.

**Discussion**

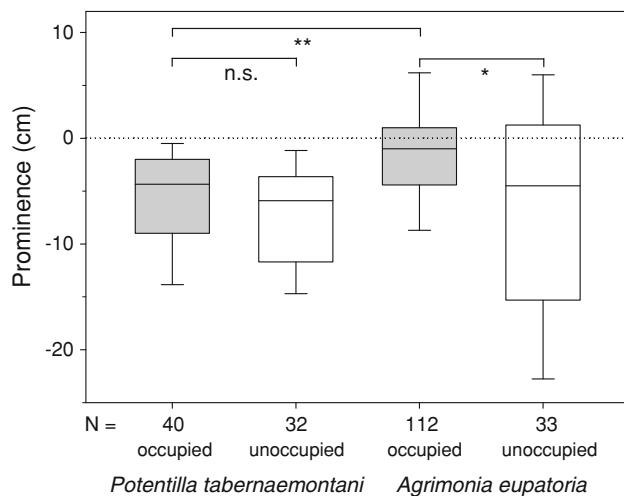
In this study, *P. malvae* generally preferred open and warm oviposition sites within calcareous grasslands. However, there were considerable differences in the environmental conditions depending on the selected host plant. On the small *P. tabernaemontani* plants that grew in sparse vegetation with low-growing turf, often on bedrock, mostly only one egg was found. In contrast, occupied *A. eupatoria* host plants were larger and more prominent, regularly having more than one egg. The vegetation at the growing sites of occupied *A. eupatoria* plants was higher and more closed. Oviposition heights also differed; while eggs on *P. tabernaemontani* were mostly found close to the ground, eggs on *A. eupatoria* were deposited clearly above the soil surface ( $\sim 10$  cm).

Although oviposition habitats on both host plants are characterized by a warm microclimate (that is, south- and west-facing slopes, low and sparse vegetation), conditions at the *P. tabernaemontani* sites are clearly more extreme. On sunny days, temperatures become much higher in sparsely vegetated sites near the ground than at the radiation surface in denser vegetation (Stoutjesdijk and Barkman 1992). Warm microclimatic conditions generally speed up larval development (Weiss et al. 1988; Roy and





**Fig. 3** Characteristic oviposition habitats of *Pyrgus malvae* in the study area. **a** host plant *Potentilla tabernaemontani* and **b** host plant *Agrimonia eupatoria*



**Fig. 4** Prominence of occupied and unoccupied host plants. Prominence was calculated as the difference between host-plant height and turf height. The *dotted line* indicates the turf height (see also Fig. 1)

**Table 4** Statistics of GLMM: relationship between host-plant occupancy of (a) *Potentilla tabernaemontani* (binomial response variable: presence [ $N_{\text{plots}} = 40$ ] versus absence [ $N_{\text{plots}} = 32$ ]) and (b) *Agrimonia eupatoria* (binomial response variable: presence [ $N_{\text{plots}} = 112$ ]

Variable	Estimate	SE	Z	P
<b>(a) <i>Potentilla tabernaemontani</i></b>				
Horizontal vegetation density	-0.174	0.039	-4.513	<0.0001
Pseudo $R^2$ [Nagelkerke's] = 0.46				
<b>(b) <i>Agrimonia eupatoria</i></b>				
Field layer	-0.032	0.014	-2.331	<0.05
Sunshine duration	0.061	0.029	2.101	<0.05
Prominence	0.069	0.028	2.466	<0.01
Cover of bare ground and stony surface	0.195	0.080	2.453	<0.001
Pseudo $R^2$ [Nagelkerke's] = 0.37				

Non-significant predictors were excluded from the final model by stepwise backward-selection ( $P > 0.05$ )

Thomas 2003). However, in combination with the low water content of the often very shallow soils, the risk of desiccation for *P. tabernaemontani* increases. In line with this, we regularly observed wilting *P. tabernaemontani* plants on bedrock and shallow soils during hot summers, but never desiccating *A. eupatoria* plants.

It is a common phenomenon that females choose conspicuous host plant individuals for oviposition (Porter 1992; García-Barros and Fartmann 2009). One measure for optical conspicuousness is the prominence of the host plants; that is, the difference between host plant height and vegetation height (Küer and Fartmann 2005; Eichel and Fartmann 2008). In our study, more prominent *A. eupatoria* plants were significantly preferred for oviposition. Although prominence had no influence on the decision to lay eggs on *P. tabernaemontani*, we have to be careful about assuming that visibility of this host plant is negligible. When examined more closely, we see that

versus absence [ $N_{\text{plots}} = 33$ ]) with several environmental parameters (predictor variables) (heat load index, sunshine duration, vegetation structure and host plant characteristics; for details see Table 1)

*P. tabernaemontani* host plants are also very apparent for the females because they usually form bigger cushions in the sparsely covered and low vegetation (Fig. 3a).

Although *P. tabernaemontani* is far more widespread within the calcareous grasslands of the Diemel Valley (Fartmann 2004), we found three times more occupied *A. eupatoria* plants and five times more eggs on them. The growing sites of *P. tabernaemontani* in these grasslands range from dense and high-growing stands to sites with a high cover of rocks or bare ground (Fartmann 2004). Except in open stands, the tiny plants are usually overgrown by higher plants, and are neither visible to the females nor grow under the favoured warm microclimatic conditions. Accordingly, most of *P. tabernaemontani* plants are unsuitable for oviposition.

Sufficient food is of crucial importance for successful larval development. Consequently, the higher egg load on *A. eupatoria* might be explained by its higher biomass in combination with the very low risk of desiccation. Hence, food availability is generally higher and more predictable for the larvae. Anthes et al. (2008) also found a relationship between egg-load on the host plants and food quantity in *Hamearis lucina*.

In conclusion, we found that the observed oviposition pattern of *P. malvae* in calcareous grasslands of the Diemel Valley reflects a trade-off between microclimate and food availability. Usually, occupied *P. tabernaemontani* grow under favourable microclimatic conditions (Fig. 3a). However, during hot years the risk of desiccation is high, leading to food shortage (cf. Roy and Thomas 2003; Piessens et al. 2009). In contrast, *A. eupatoria* generally provides more biomass, thrives on deeper soils and the vegetation has a cooler microclimate, and so food shortage is more unlikely (Fig. 3b). Due to the differences in food availability, the egg load is low on *P. tabernaemontani* and high on *A. eupatoria*. The regular use of two such different oviposition habitats should generally strongly decrease the risk of extinction due to adverse weather conditions, regardless of whether too hot or too cool.

### Implications for conservation

The key factor limiting the distribution and abundance of *P. malvae* is the preferred breeding vegetation (Brereton et al. 1998). Oviposition sites require a sparse vegetation with bare ground, bedrock or litter to provide a warm microclimate for larval development.

Although occupied *P. tabernaemontani* were significantly more often found on unmanaged sites than unoccupied plants, this does not reflect a real preference for abandoned sites but rather for specific site conditions. The unmanaged sites were the only sites where a higher share

of bedrock, one of the preferred breeding habitats, occurred naturally. However, *P. tabernaemontani* cushions on bedrock are only suitable for oviposition as long as they do not become overgrown by tall plants.

Thus, maintaining suitable habitats for *P. malvae* requires an appropriate management strategy that creates early successional habitats (cf. Brereton et al. 1998; Asher et al. 2001). To meet these demands, traditional rough grazing with sheep and goats seems to be the most appropriate. It has already been recommended as a strategy to preserve the habitats of other threatened insect species of calcareous grasslands in the Diemel Valley (Fartmann 2006; Eichel and Fartmann 2008; Poniatowski and Fartmann 2010). If rough grazing is not appropriate due to different constraints (economic or logistic, for instance), paddock grazing might be an alternative. In addition to a suitable grazing system, the active creation of oviposition habitats might be a possibility. Slater (2007) describes how the construction of low dry-stone walls in herb-rich grasslands in England created additional egg-laying habitats for *P. malvae*. However, due to the high costs of such manual activities, a sustainable grazing management of the whole landscape should have priority.

As shown for Great Britain, *P. malvae* does not only react positively to the restoration of grazing, but also to coppicing (Warren and Thomas 1992; Asher et al. 2001). Coppiced woodlands were formerly widespread in the Diemel Valley, but the practice was abandoned during the last century (Fartmann 2006). The reintroduction of this forest management technique in woodlands, particularly adjacent to calcareous grasslands, would be beneficial for *P. malvae* and other threatened butterfly species of open woodlands (e.g. *Hamearis lucina*: Fartmann 2006; Anthes et al. 2008).

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