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Effects of mire type, land use and climate on a strongly declining wetland butterfly

Sarah Weking · Gabriel Hermann ·
Thomas Fartmann

Abstract Mires are characterised by highly specialised and threatened wildlife. One of these mire specialists that has severely declined is the Large Heath (*Coenonympha tullia*). However, detailed studies concerning the reasons for the dramatic population loss in central Europe are missing so far. In this paper: (1) we analyse the habitat preferences of adult *C. tullia* and oviposition site selection with respect to mire type and land use in one of the last German strongholds, and (2) we attempt to disentangle the impacts of land use and climate change on the decline of *C. tullia* on a national scale across Germany. Abundance of adult *C. tullia* was clearly affected by mire type and land use. It was highest on managed calcareous fens and lowest on unmanaged transition and raised bogs. The oviposition pattern of *C. tullia* females was best explained by (1) quantity of potential host plants (*Eriophorum latifolium*), (2) vegetation structure, and (3) microclimate. In Germany, *C. tullia* populations have become extinct in lowlands with a mild and relatively dry climate while most colonies in wet and cold mountain areas have survived. However, there is evidence that habitat loss and habitat deterioration, rather than climate change, are the drivers of the range retraction. To create low-growing vegetation rich in *E. latifolium,* traditional mowing late in the year and light grazing seem to be suitable management tools. In addition, conservation management should aim to maintain high water levels or restore them, especially to counteract effects of climate change in the future.

Keywords Bog · Calcareous fen · Conservation management · Global change · Habitat quality · Vegetation structure

S. Weking · T. Fartmann (✉)
Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Heisenbergstr. 2, 48149 Münster, Germany
e-mail: fartmann@uni-muenster.de

G. Hermann
Arbeitsgruppe für Tierökologie und Planung, Johann-Strauß-Straße 22, 70794 Filderstadt, Germany

T. Fartmann
Ecology Group, Department of Biology and Chemistry, University of Osnabrück, Barbarastr. 13, 49076 Osnabrück, Germany

Introduction

Peat-accumulating ecosystems have an extraordinarily high relevance for global carbon policy and biodiversity conservation (Parish et al. 2008) although only 3 % of the world's land surface is covered by mires (Rydin and Jeglum 2006). Mires are the most important carbon store in the terrestrial biosphere. In addition, they are characterised by a highly specific flora and fauna resulting in a high nature conservation value (Rydin and Jeglum 2006; Dierßen and Dierßen 2008; Parish et al. 2008).

Mires are mainly found in the northern hemisphere; at least 80 % of the global share occurs in this part of the world (Rydin and Jeglum 2006). Here these peatlands were originally widespread throughout the temperate and boreal zone. However, for centuries mires have been intensively modified by humans. They have been drained for peat cutting, agriculture and forestry resulting in a severe area loss (Joosten and Couwenberg 2001; Rydin and Jeglum 2006; Dierßen and Dierßen 2008). Particularly in central Europe, the decrease has been dramatic with only 1 % of the original mire area remaining (Joosten and Couwenberg 2001). Due to their role as a habitat for highly specialised

wildlife and the great threats they face, most European mire types are protected under the EC Habitats Directive (EC 2007).

Butterflies are characterised by a high host plant specificity (Munguira et al. 2009) and a narrow niche of the pre-adult stages (García-Barros and Fartmann 2009). In addition, they build metapopulations depending on a network of suitable habitats (Thomas et al. 2001; Anthes et al. 2003; Eichel and Fartmann 2008). Due to these very specific requirements, the decline of butterflies exceeds that of many other taxonomic groups (Thomas et al. 2004; Thomas 2005). Consequently, they are an important model group in ecology and conservation (Watt and Boggs 2003; Ehrlich and Hanski 2004) and among the most sensitive indicators for environmental change (Thomas and Clarke 2004; Thomas et al. 2004; Thomas 2005).

Across Europe, mires are the biotope with the highest proportion of threatened butterfly species; i.e. depending on the mire type, between 25 and 31 % of species are threatened (Van Swaay et al. 2006). One of these mire specialists that has severely declined is the Large Heath (Coenonympha tullia). Its distribution throughout Europe decreased by 20–50 % between 1970 and 1995 (Van Swaay and Warren 1999). In Europe, C. tullia is considered to be vulnerable (Van Swaay et al. 2010) and in Germany it is considered to be endangered (Reinhardt and Bolz 2011). The main threats for C. tullia have been identified as habitat loss and degradation as a consequence of drainage, intensification of agriculture and peat extraction (Bourn and Warren 1997; Dennis and Eales 1997, 1999; Asher et al. 2001; Beneš et al. 2002) as well as abandonment of traditional land use and afforestation (Trautner et al. 2004; Wainwright 2007). In addition, climate warming is assumed to be a further driver of the dramatic decline (Dennis 1993; Hill et al. 2003; Fox et al. 2006).

Most of what we know about the habitat requirements of C. tullia is from Great Britain: the main host plant in the British Islands is Eriophorum vaginatum (Melling 1984), larvae are sensitive to prolonged submersion (Joy and Pullin 1997), and patch occupancy depends on habitat quality, patch size and isolation (Dennis and Eales 1997, 1999). However, detailed studies of the oviposition sites of C. tullia are, as for most grass-feeding butterflies (Fartmann and Hermann 2006; García-Barros and Fartmann 2009; Beyer and Schultz 2010), lacking so far. For central Europe there is no empirical study analyzing the habitat preferences of adult butterflies.

In this paper: (1) we analyse the habitat preferences of adult C. tullia and oviposition site selection with respect to mire type and land use in one of the last German strongholds in the foothills of the Bavarian Alps (Fig. 1); (2) we attempt to disentangle the impacts of land use and climate change on the decline of C. tullia on a national scale across

Germany; and (3) we use these data to derive management recommendations for the conservation of C. tullia.

Materials and methods

Study species

The Large Heath (Coenonympha tullia) has a Holarctic distribution (Bink 1992; Bourn and Warren 1997). In Europe, it occurs from the British Islands across central and northern Europe (Kudrna 2002). C. tullia inhabits fens as well as transitional and raised bogs (SBN 1987). The usually univoltine species is on the wing from June until August (Ebert and Rennwald 1991; Thomas and Lewington 2010). In the far north, the life cycle is biennial (Melling 1989). In central Europe, the larvae hibernate in the third instar (Bink 1992). As for most grass-feeding butterfly species (Fartmann and Hermann 2006; García-Barros and Fartmann 2009), knowledge about host plants is rare (Ebert and Rennwald 1991; Rennwald 2007). The majority of the host plants mentioned in the literature are Cyperaceae: Eriophorum vaginatum is a well-documented host plant in Britain (Bourn and Warren 1997; Asher et al. 2001; Thomas and Lewington 2010). Eriophorum angustifolium is a further known host plant in Britain (Melling 1984) and also in central Europe (Bink 1992; Rennwald 2007). The use of Schoenus ferrugineus for oviposition has been documented several times in the foothills of the Alps (Trautner et al. 2004). In contrast, the role of Rhynchospora alba as a host plant has been discussed controversially (cf. Bourn and Warren 1997; Asher et al. 2001).

Study area

The study area is located at the northern foothills of the Alps in southern Bavaria, Germany (Fig. 1), having a rather cool and wet climate (mean annual temperature: 6.0–7.0 °C, mean annual precipitation: 1,300–1,500 mm; German Weather Service, pers. comm.). The young moraine landscape is characterised by glacially formed hollows and valleys, where bogs evolved later on (Succow and Jeschke 1990). The "Murnauer Moos", "Staffelseemoore" and "Pfrühlmoos" are located at an altitude of about 650 m a.s.l., and the "Kochelfilz" and "Ettaler Weidmoos" at an altitude of about 850 m a.s.l. All study sites, except the Ettaler Weidmoos, contain mosaics of fens, transitional bogs and raised bogs. In the Ettaler Weidmoos solely calcareous fens occur. All study sites contain plots of litter meadows mown late in the year, in August or later, and unmanaged plots. In the traditional farming systems the litter was used to bed the cattle in stables. Only a few plots in the southern Murnauer Moos (Eschenloher Viehweide)
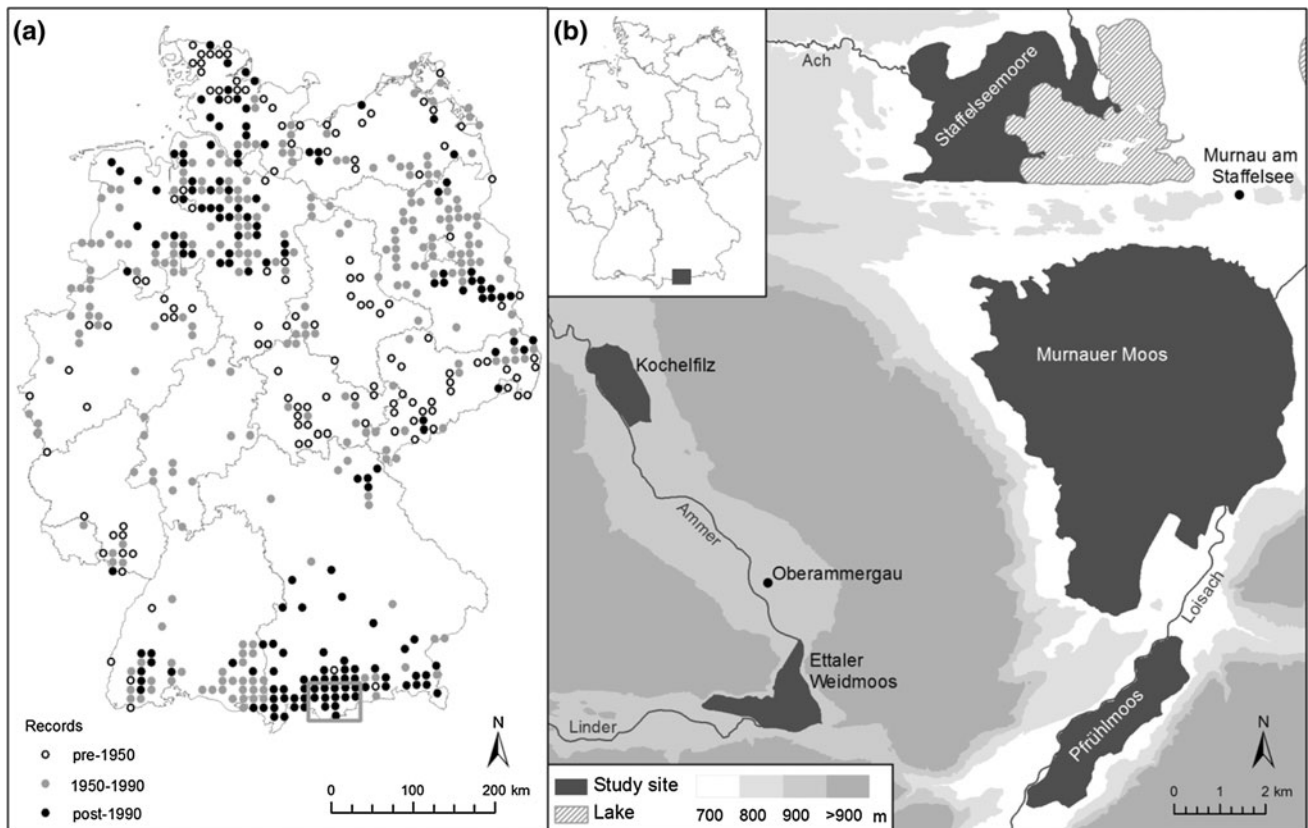
Fig. 1 a Recent and historical distribution of *C. tullia* in Germany. *Grey* framework = location of the study area. *Sources* Bayerisches Landesamt für Umweltschutz (2001), Ebert and Rennwald (1991), Engel (1987), Gelbrecht et al. (2003), Hafner (pers. comm), Harkort (1975), Karbiener (pers. comm.), Kolligs (2003, pers. comm.), Lange (pers. comm.), Meineke (1985), Niedersächsisches Landesamt für Ökologie (2001), Rennwald (2007), Reinhard (pers. comm.), Retzlaff (1973), Stamm (1981), Werno (2011). **b** Study area in Southern Bavaria with study sites

are grazed. The area of the study sites ranged from 80 to 2,355 ha (mean ± SE: 669 ± 426 ha). All five mires had a natural or near-natural water table. The Murnauer Moos and the Staffelseemoore are part of a prime butterfly area (Van Swaay and Warren 2003). In addition, the Murnauer Moos is the largest near natural bog ecosystem in Germany (Kaule 1974).

Sampling design

Adult habitat

Within the five study sites we sampled 58 randomly selected plots with a size of 500 m², 29 of these plots were located in calcareous fens, 14 were in transitional bogs and 15 were in raised bogs. The share of managed (mown: $N = 21$, grazed: $N = 9$) and unmanaged plots ($N = 28$) was nearly identical. Adult butterflies of *C. tullia* were counted using standardised transect walks (Pollard and Yates 1993). From June to August 2010, each plot was visited twice during suitable weather conditions (cf. Pollard

1977) for a period of 15 min (Krämer et al. 2012) and all individuals of *C. tullia* were counted. For statistical analyses the maximum abundance of the two counts was used (Streitberger et al. 2012).

Mire types were differentiated using character and differential plant species listed in Oberdorfer (1998) and Dierßen and Dierßen (2008). To characterise habitat quality we recorded several environmental parameters. Vegetation density was estimated using a 50 cm wide and 30 cm deep wire-framed box, which was open on all sides except the back. Horizontal wires on the front side of the box divided it into six layers (0–5, 5–10, etc. up to 25–30 cm). The cover of each layer was horizontally viewed against the bright back of the box (Poniatowski and Fartmann 2008). Vegetation density and height were sampled at three random points within the plot. The cover of total vegetation, shrubs, herbs, mosses, litter and potential host plants was estimated for the whole plot. Potential host plants comprised all *Eriophorum*, *Schoenus* and *Rhynchospora* species (cf. Melling 1984, 1989; Bourn and Warren 1997; Trautner et al. 2004) within the plot. The

potential daily sunshine duration during the flying period of *C. tullia* (June to August) was measured using a horizontoscope after Tonne (1954).

Oviposition habitat

To determine oviposition habitat requirements, egg-laying females were tracked during July and August in the plot with the highest adult abundance, a one-cut calcareous fen in the Murnauer Moos with the *Primulo-Schoenetum ferruginei* and *Caricetum davallianae* as the dominant plant communities (cf. Oberdorfer 1998; Dierßen and Dierßen 2008). In case of oviposition, the host plant was marked with adhesive tape and several environmental parameters were later recorded. We determined the host plant species, the oviposition height and the substrate (e.g. vital or dead part of the plant). To describe vegetation structure and microclimatic conditions, we recorded the same parameters as mentioned for the adult habitats in a radius of 30 cm around the host plant. If more than one egg was laid on a host plant, it was treated as a single sample in our data set. Additionally, we registered the same parameters for random sites ($N = 31$). To select a random site a stick was randomly thrown (Anthes et al. 2003) and the sample was taken from the next potential host plant adjacent to the stick.

Range retraction and climate

To detect potential climate effects on the range retraction of *C. tullia* in Germany, climatic parameters were related to historical and recent distribution data. The distribution data were classified into three categories reflecting the extinction history (pre-1950, 1951–1990, post-1990; cf. Fig. 1a). The historical and recent distribution of *C. tullia* was assessed according to the sources mentioned in Fig. 1a. Climate data comprised mean annual temperature, mean temperature for January and July, mean annual number of frost days (minimum daily temperatures below 0 °C), mean annual precipitation, mean precipitation for January and July and altitude (data for the period 1961–1990; German Weather Service, pers. comm.). Distribution and climate data were based on a 12.5 × 8.5 km grid.

Statistical analysis

Prior to Generalised Linear Mixed-effects Model (GLMM) and Generalised Linear Model (GLM) analyses (see below), all metric predictor variables were tested for inter-correlations by calculating Pearson's (r) correlation coefficients. In cases of high inter-correlation ($r > |0.7|$), a Principal Component Analysis (PCA) was carried out to summarise these parameters by a new factor (for further information, see Poniatowski and Fartmann 2011). As a result, for both predictor variables of the adult and egg data, three new factors representing independent principal components were created: (1) 'vegetation density upper herb layer' was positively correlated with vegetation height and vegetation density in the four different layers above 10 cm height (10–15, 15–20, 20–25, 25–30 cm); (2) 'vegetation density lower herb layer' was positively correlated with vegetation density in the two layers below 10 cm (0–5, 5–10 cm) and cover of herbs; and (3) 'sunshine duration' was positively correlated with potential daily sunshine duration in June, July and August. In all cases the predictor variables were positively correlated with the summarising factors; hence, they represent a gradient from light to dense vegetation (vegetation density lower and upper herb layer) and from low to high sunshine duration, respectively.

To evaluate whether adult *C. tullia* abundance is affected by bog and land use type, respectively, and which environmental parameters best explain adult *C. tullia* abundance, GLMMs (lmer, Bates et al. 2008) were conducted. For all GLMMs, the variable *study site* was set up as a random factor. The level of significance was set to 0.05 (cf. Crawley 2002), and the significance of each of the predictor variables was assessed with likelihood ratio tests (Type III test). Dunn's test was applied as a post hoc test.

Oviposition and random sites were compared using the *t* test, if the related model assumptions (i.e. normal distribution and heterogeneity of variances) were met, otherwise the Mann–Whitney *U* test was conducted. To assess important parameters for oviposition of *C. tullia*, a binomial GLM was obtained. A stepwise backward selection based on Akaike's information criterion was chosen to identify the combination of predictor variables with the highest explanatory power. An assessment of whether females adjust the egg-laying height to environmental conditions was made using a Poisson GLM with the oviposition height as the response variable and several predictor variables describing vegetation structure and microclimatic conditions; that is vegetation density lower and upper herb layer, cover of mosses and litter, and sunshine duration.

The potential effects of climate on the range retraction of *C. tullia* were analysed using a GLM with the number of the three extinction categories (1–3) as the response variable (Poisson error structure). All climatic parameters were strongly inter-correlated and were summarised by one variable using PCA. The new factor, hereafter called 'climate factor', was negatively correlated with mean annual temperature, and mean January and July temperature. In contrast, altitude, mean number of frost days per year, mean annual precipitation and mean January and July

precipitation were positively correlated. Thus, the climate factor represented a gradient from warm and dry to cold and wet climatic conditions of higher altitudes.

All GLMM and GLM analyses were performed using R-2.11.1 (The R Foundation for Statistical Computing 2010). Further statistical analyses were performed with PASW 18.

Results

Adult habitat

The maximum abundance of *C. tullia* varied from 1 individual per 500 m^2 in an unmanaged raised bog to 20 individuals per 500 m^2 in a mown calcareous fen. Calcareous fens had the highest abundance and significantly differed from transition and raised bogs (Fig. 2). Within calcareous fens, abundance was significantly higher on managed (mown) than on unmanaged plots. In contrast, in transition bogs, abundance did not differ between managed (grazed) and unmanaged plots.

Abundance of adult *C. tullia* was best explained by a combination of land use type and the cover of certain potential host plant species (Table 1). Abundance was positively correlated with mown plots and a high cover of *Eriophorum latifolium*. In contrast, unmanaged plots with a high cover of *Rhynchospora alba* negatively affected
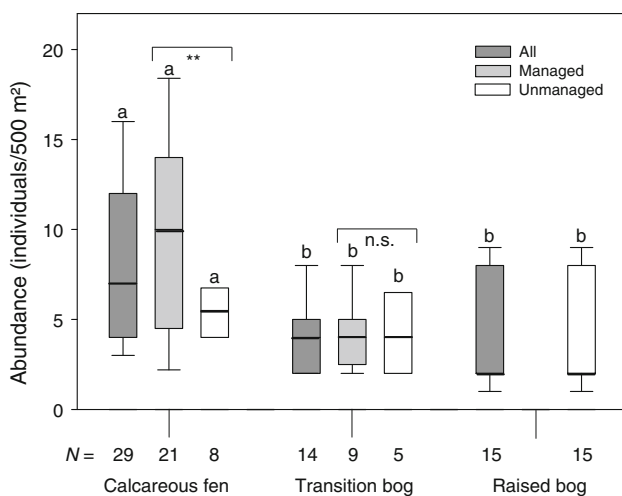
abundance. The explanatory power of the model was very high with a pseudo R^2 [Nagelkerke] value of 0.73.

Oviposition habitat

We observed a total of 71 ovipositions at 41 oviposition sites. In most cases, females laid their eggs singly (19 cases, 46 %). However, in one third of the cases a second (14, 34 %) and infrequently a third egg (8, 20 %) was laid within a few centimeters of the previous one. Three quarters (75 %) of the eggs were deposited on vital parts of grasses, especially on scrawny stems or leaflets near to the ground. The remaining quarter (25 %) of the eggs were attached on dry parts of a plant or litter. Occupied grass plants were, in order of frequency of use, *Schoenus ferrugineus* (27 %), *Carex davalliana* (24 %), *E. latifolium* (20 %) and *Molinia caerulea* (4 %).

The oviposition sites were characterised by a high potential daily sunshine duration, high vegetation cover, some litter, short turf and low vegetation density (Table 2). Potential sunshine duration in July and the cover of litter were significantly higher at oviposition sites than at random sites. In contrast, vegetation height and vegetation density of the upper herb layer were significantly lower. The oviposition pattern of *C. tullia* was best explained by the quantity of potential host plants, vegetation structure and microclimate (Table 3a): A high cover of *Eriophorum latifolium* and litter as well as a high sunshine duration promoted oviposition. In contrast, the likelihood of a site being accepted for oviposition decreased with vegetation density of the upper herb layer. The females adjusted the oviposition height to vegetation structure and consequently to microclimate: the higher the cover of litter and the

Fig. 2 Abundance of *C. tullia* individuals per 500 m^2 in all managed and unmanaged plots of calcareous fens, transition bogs and raised bogs. All managed calcareous fens were mown and all managed transition bogs were grazed. *Letters* at the *top* of the *bars* indicate significant differences between the mire types for each land use type revealed by Dunn's test ($\alpha = 0.05$) (a priori test: GLMM, random factor: *study site*, Poisson error structure). Differences in land use within a mire type were tested using a GLMM (Poisson error structure) with *study site* as a random factor. **$P < 0.01$, *n.s.* not significant

Table 1 Statistics of GLMM (Poisson error structure): relationship between abundance of *C. tullia* (individuals per 500 m^2) and environmental parameters

Parameter	Estimate	SE	Z	P
Land use type				**
Unmanaged	−0.0725	0.3218	−0.225	
Mown	0.4196	0.3369	1.245	
Cover of *Eriophorum latifolium* (%)	0.0150	0.0070	2.159	*
Cover of *Rhynchospora alba* (%)	−0.0117	0.0058	−2.001	*
Pseudo R^2 [Nagelkerke] = 0.73				

The following variables were included in the model: bog-type (categories: fen, transitional bog, raised bog), type of land use (categories: unmanaged, mown, grazed), cover of shrubs, moss, litter, vegetation density lower herb layer, vegetation height and density upper herb layer, potential sunshine duration in June, July and August. Non-significant predictors were excluded from the final model by stepwise backward-selection ($P < 0.05$). The five study sites were entered as random factor. $N = 58$. * $P < 0.05$; ** $P < 0.01$

denser the vegetation near ground was, the higher the females of *C. tullia* laid their eggs (Table 3b). The explanatory power of both GLMs was high with a pseudo R^2 [Nagelkerke] value of 0.45 and 0.37, respectively.

Range retraction and climate

Coenonympha tullia once occurred in all German Federal States and was widespread in the northern lowlands and the foothills of the Alps in southern Germany (Fig. 1a). Thus far, it has been recorded in 555 12.5×8.5 km grid cells across Germany. Until 1990, *C. tullia* had disappeared from 72 % of its previously occupied cells and 5 of the 16 German Federal States. Nowadays, the strongholds are the moorlands and bogs in Lower Saxony and Schleswig–Holstein as well as the fens and bogs in the Bavarian foothills of the Alps. The GLM revealed that the likelihood of extinction of *C. tullia* was positively correlated with the climate factor (Table 4). Hence, survival of *C. tullia* populations was higher in regions with lower temperatures (annual, January, July), higher precipitation (annual, January, July), more frost days per year, and higher altitudes. However, the explanatory power of the model was very low with a pseudo R^2 [Nagelkerke] value of 0.06.

Discussion

Habitat preferences in the foothills of the Bavarian Alps

Abundance of adult *C. tullia* was clearly affected by mire type and land use. It was highest on mown plots with a high cover of *Eriophorum latifolium* (calcareous fens) and lowest on unmanaged plots with a high cover of *Rhynchospora alba* (transition and raised bogs). The oviposition pattern of *C. tullia* females was best explained by (1) the quantity of potential host plants, (2) vegetation structure and (3) microclimate: oviposition was promoted by a higher cover of *E. latifolium* and litter as well as a high sunshine duration. In contrast, the likelihood of a site being accepted for oviposition decreased with vegetation density of the upper herb layer.

For a long time, without information on the reproduction sites being available, *C. tullia* has been considered to be a species that preferentially occurs in bogs (=tyrphophilous species) in the northern foothills of the Alps (Meineke 1985; Bräu 1995) and all over central Europe (Ebert and Rennwald 1991; Beneš et al. 2002; Bos et al. 2006). In contrast, in our study the abundance of adult *C. tullia* was significantly higher in calcareous fens than in transitional bogs and raised bogs. In addition, calcareous fens were

Table 2 Mean values ± SE (range) of habitat characteristics at oviposition sites ($N = 41$) and random sites ($N = 31$)

Parameter	Mean ± SE (min–max)				Test
	Oviposition sites ($N = 41$)		Random sites ($N = 31$)		
No. eggs	1.7 ± 0.1	(1–3)	–	–	–
Oviposition height (cm)	5.0 ± 0.3	(1.5–13)	–	–	–
Sunshine duration (h)					
June	13.9 ± 0.1	(12–16)	13.5 ± 0.2	(11–15)	t[n.s.]
July	12.5 ± 0.1	(11–15)	12.0 ± 0.2	(10–13.5)	t*
August	9.9 ± 0.1	(8.5–13)	10.0 ± 0.2	(9–12.5)	U[n.s.]
Cover (%) of					
Total vegetation	99.9 ± 0.1	(95–100)	100 ± 0	–	U[n.s.]
Herb	87.0 ± 1.3	(70–100)	90.3 ± 0.8	(80–95)	U[n.s.]
Moss	74.5 ± 3.6	(20–100)	74.5 ± 4.8	(15–95)	U[n.s.]
Litter	11.6 ± 1.7	(1–50)	6.7 ± 0.9	(1–20)	U*
Eriophorum latifolium	6.7 ± 0.8	(1–15)	5.1 ± 0.7	(0.1–15)	U[n.s.]
Rhynchospora alba	0.4 ± 0.3	(0–10)	0.4 ± 0.3	(0–10)	U[n.s.]
Schoenus ferrugineus	30.8 ± 2.1	(0.1–55)	27.4 ± 2.5	(1–55)	t[n.s.]
Vegetation height (cm)	21.5 ± 0.6	(14–30)	24.0 ± 0.8	(19–36)	t**
Vegetation density (%) in					
0–5 cm	95.2 ± 0.9	(80–100)	97.6 ± 0.5	(90–100)	U[n.s.]
5–10 cm	65.7 ± 2.9	(20–90)	72.9 ± 3.4	(25–95)	t[n.s.]
10–15 cm	18.0 ± 1.9	(5–75)	24.7 ± 2.7	(5–80)	U**
15–20 cm	6.4 ± 1.2	(1–50)	11.1 ± 1.6	(2.5–45)	U***
20–25 cm	2.2 ± 0.4	(0–15)	5.0 ± 0.9	(1–20)	U***
25–30 cm	0.5 ± 0.1	(0–2.5)	2.0 ± 0.4	(0–10)	U***

Statistical comparison was made using the *t* test in the case of a normal distribution and homogeneity of variances, otherwise a Mann–Whitney *U* test was used ($\alpha = 0.05$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, *n.s.* not significant

Table 3 (a) Statistics of GLM (binomial): relationship between oviposition of *C. tullia* and environmental parameters. The following variables were included in the model: cover of litter, moss, *Eriophorum latifolium*, *Schoenus ferrugineus*, vegetation density lower herb layer, vegetation height and density upper herb layer, potential sunshine duration in June, July and August. Backward model selection was used to remove non-significant predictor variables. The best model was assessed using Akaike's information criterion (AIC; cf. Zuur et al. 2009). Occupied sites: $N = 41$, random sites: $N = 31$. (b) Statistics of GLM (Poisson): relationship between oviposition height and microhabitat parameters. Variables included in the model were: cover of moss, litter, vegetation density lower herb layer, vegetation height and density upper herb layer, potential sunshine duration in June, July and August. $N = 61$

Parameter	Estimate	SE	Z	P
(a) Oviposition sites				
Cover of litter	0.0866	0.0503	1.721	0.06
Cover of *Eriophorum latifolium*	0.1167	0.0693	1.685	0.08
Sunshine duration	0.9097	0.3664	2.483	*
Vegetation density upper herb layer	−1.7572	0.5201	−3.378	***
Pseudo R^2 [Nagelkerke] = 0.45				
(b) Oviposition height				
Cover of litter	0.0104	0.0041	2.552	*
Vegetation density lower herb layer	0.2453	0.0664	3.691	***
Pseudo R^2 [Nagelkerke] = 0.37				

$* P < 0.05$; $*** P < 0.001$

Table 4 Statistics of GLM (Poisson): relationship between last observation of *C. tullia* (categories: pre-1950, 1951–1990, post-1990) and climate factor

Parameter	Estimate	SE	Z	P
Climate factor	0.08306	0.02775	0.00276	**
Pseudo R^2 [Nagelkerke] = 0.06				

Strongly intercorrelated climatic parameters were summarised by PCA into one factor (negatively correlated with mean annual temperature, mean temperature in January and July, number of frost days, altitude; positively correlated with mean annual precipitation, mean precipitation in January and July) based on a 12.5×8.5 km grid survey. $** P < 0.01$

regularly used for oviposition. In mire ecosystems west of our study area, Trautner et al. (2004) also observed that while raised bogs had very low densities of *C. tullia,* calcareous fens had strong populations with ovipositing females.

Traditional management of calcareous fens (mowing late in the year) favoured adult densities and created suitable oviposition sites for *C. tullia* in our study area. Whether light grazing of calcareous fens is as beneficial as mowing for *C. tullia* cannot be confirmed based on our data because all grazed plots ($N = 9$) were located in transition bogs that generally had low *C. tullia* densities. However, direct loss of eggs through grazing seems to be relatively unlikely because eggs were deposited close to the ground. In line with this, observations of Trautner et al. (2004) showed that grazing of calcareous fens is at least as beneficial as mowing for *C. tullia*. For British populations, Wainwright (2007) also pointed out that low-intensity grazing has positive effects on *C. tullia* populations.

Our study shows that oviposition sites are characterised by low-growing vegetation and a high sunshine duration resulting in warm microclimatic conditions (cf. Stoutjesdijk and Barkman 1992). To preserve these structures in calcareous fens, low-intensity management is necessary, otherwise dead plant litter would accumulate leading to floristic homogenisation and high-growing stands (Quinger et al. 1995). However, some litter seems to have positive effects as females preferred sites with a higher cover of litter (~ 12 %) for oviposition. A certain amount of litter affects microclimatic conditions and possibly favours successful development of the immature stages. Measurements confirmed that on sunny days, the surface temperatures of dead plants (litter) exceed those of green plants and air temperature (WallisDeVries 2006). In addition, litter is able to store humidity (Stoutjesdijk and Barkman 1992; cf. Fartmann 2006) which is a crucial factor for wetland butterflies in general (Settele et al. 2009) and *C. tullia* in particular (Dennis and Eales 1997). Besides this, litter may function as a climatic buffer (cf. Möllenbeck et al. 2009; Turlure et al. 2010). Depending on weather conditions, larvae are able to translocate their position between the litter surface with more extreme temperatures (warmer during the day, colder during the night) and the more balanced microclimate inside the litter.

In this study, oviposition height increased with the cover of litter and the density of the lower herb layer which may also reflect an adaptation to microclimatic conditions. Möllenbeck et al. (2009) observed that *Hipparchia fagi* adapts oviposition height to the height of the local radiation surface to maximise heat absorption. The same might be true for *C. tullia*. In addition, oviposition near the vegetation and litter surface, respectively, will guarantee sufficient humidity (cf. Eggelsmann 1990) for egg development.

The four grass species used for oviposition by *C. tullia* females in our study were, in order of their frequency, *Schoenus ferrugineus*, *Carex davalliana*, *Eriophorum latifolium* and *Molinia caerulea*. With the exception of *E. latifolium*, all species have been confirmed as oviposition plants by other authors (cf. Trautner et al. 2004; Marthaler 2010). However, feeding observations from the field do not exist for any of the four plant species. Nevertheless, we believe that *E. latifolium*, a character species

of calcareous fens (Oberdorfer 2001), is an important host plant for *C. tullia* in the study area. Two other closely related *Eriophorum* species have already been detected as host plants: *E. vaginatum* is the main host plant in Britain (Melling 1984; Bourn and Warren 1997; Asher et al. 2001) and feeding larvae have been found on *E. angustifolium* in south-western Germany (Rennwald 2007). In addition, the cover of *E. latifolium* was a predictor of both adult densities and oviposition sites. Due to the high number of eggs deposited on the two other Cyperaceae, *Schoenus ferrugineus* and *Carex davalliana*, we assume that they are also used for feeding by the larvae of *C. tullia*.

Drivers of the decline throughout Germany

The decline of *C. tullia* was positively correlated with higher temperatures (annual, January, July), lower precipitation (annual, January, July), fewer frost days per year and lower altitudes. More generally speaking, *C. tullia* populations have become extinct in lowlands with a mild and relatively dry climate while most colonies in wet and cold mountain areas have survived. However, we have to take into consideration that the explanatory power of the model was very low.

Apart from the low model accuracy, there is further evidence that directs us towards the assumption that habitat loss and habitat deterioration, rather than climate change, are the drivers of the range retraction of *C. tullia* in Germany: (1) the lowlands are not only characterised by a mild climate with warm winters; they are also the areas where agricultural intensification and the loss of mires has been greatest (Ellenberg and Leuschner 2010); (2) the vast majority of the extinctions occurred prior to 1990 (Fig. 1) and hence, before the beginning of the strong temperature increase (IPCC 2007); and (3) there are still strong populations of *C. tullia* in areas having mild winters and relatively low precipitation, e.g. in the north-western German lowland. Franco et al. (2006) reported similar findings for Britain and attributed the decline of the species to habitat degradation rather than climate change. In line with this, Thomas and Lewington (2010) described the current distribution of *C. tullia* in Britain as a probable reflection of the distribution of its habitats rather than any intrinsic need for a cooler climate.

However, if global warming proceeds as predicted, the water balance in central Europe will increasingly become negative during summer (IPCC 2007). *C. tullia* is known to be very sensitive to a lowering of the water level (Dennis and Eales 1997). Consequently, climate change probably becomes a future threat for the species (cf. Dennis 1993; Fox et al. 2006).

Implications for conservation

Studies of Dennis and Eales (1997, 1999) have shown that *C. tullia* builds meta-populations. Hence, patch occupancy depends on (1) habitat quality, (2) habitat area, and (3) isolation. So far, very sparse data concerning the habitat quality of *C. tullia* were available for central Europe. Of special relevance for the conservation of *C. tullia* at the northern foothills of the Alps are based on our study calcareous fens, especially managed ones. The traditional mowing late in the year as well as light grazing seem to be suitable management tools for creating low-growing vegetation rich in *E. latifolium*. Regular management is particularly necessary as the cessation of land use under the cold and wet climate in the study area favours the development of ombrotrophic conditions and, hence, of transition and raised bogs (Wagner 2000) having a lower habitat quality for *C. tullia*. In general, low-intensity management can be recommended for mire systems that are colonised by *C. tullia* (Beneš et al. 2002; Trautner et al. 2004; Wainwright 2007). In contrast, overgrazing can cause severe population declines (Asher et al. 2001; Wainwright 2007).

Another crucial factor for determining habitat quality in *C. tullia* is a high water level at or just below the surface (Dennis and Eales 1997). Consequently, conservation management should aim to maintain high water levels or restore them, where drainage systems have caused desiccation of the mires. Blocking of drainage channels in the Czech Republic induced spectacular population increases of *C. tullia* (Settele et al. 2009). However, re-wetting has to be done with caution because the larvae are sensitive to prolonged submersion (Joy and Pullin 1997). Hence, host plants should never be totally submerged. In general, stabilisation of the water level will increasingly become important in the future to counteract the effects of climate change.

All plots in this study lay in large mire systems containing strong *C. tullia* populations. Conservation management should first focus on these large mires which have a high habitat quality. They are less sensitive for edge effects, e.g. nitrogen depositions from adjacent agriculture, and large populations have a lower risk of extinction due to environmental fluctuations. Due to the low mobility of *C. tullia* (Ebenhard 1995; Wainwright 2007) restoration of habitats for the species should take place in close vicinity of the existing core populations.

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