



Within-habitat vegetation structure and adult activity patterns of the declining butterfly *Euphydryas aurinia*

Martin Konvicka^{1,2} · Vladimir Hula³ · Petr Vlasanek⁴ · Kamil Zimmermann⁵ · Zdenek Faltynek Fric²

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Abstract

Background *Euphydryas aurinia* is a declining butterfly inhabiting oligotrophic grasslands in Central and Western Europe. Despite numerous ecological studies, patterns of its adult activity have so far been rather neglected, although adult resource use contributes to resource-based understanding of insects' habitats.

Aim To relate *E. aurinia* adult activity patterns to within-habitat vegetation structures.

Methods (1) Timed adult activity observations along a transect crossing a colony site, analysed via partial ordination methods. (2) Activity records obtained during mark-recapture, analysed via binomial regressions.

Results Both methods, besides influences of weather, time of day (similarities between morning and late afternoon hours), and progression of season (mate locating replaced by maintenance activities), revealed consistent association of behaviours to vegetation structures. Of the two male mate-locating behaviours, perching occurred near shrubs and woodland edges, and patrolling over centres of inhabited meadows. Female activity concentrated in nectar-rich mid-height sward near host plants. Consequently, male and female activity were partly spatially separated.

Implications for conservation A habitat for *E. aurinia* should provide resources for all its activities in close proximity. Grasslands containing host plants should be dissected by structures such as shrubs, woodlot edges, or taller herbaceous vegetation, emphasising the importance of landscape heterogeneity for insect fauna.

Keywords Butterfly behaviour · Grassland conservation · Heterogeneity · Habitat architecture · Nymphalidae · Reserve management

Introduction

Preserving suitable habitats is the crucial condition for efficient conservation of invertebrates (Samways 2007) including butterflies (Settele et al. 2009; Warren et al. 2021). Increasingly detailed information on habitat requirements of increasing numbers of specialist butterflies (e.g. Kivinen et al. 2008; Turlure et al. 2011; Maes et al. 2014; Vrba et al. 2021) indicate that a habitat patch must contain all vital resources for diverse activities of the given species, including larval host plant and shelter, overwintering substrate, adult food and shelter, and substrates utilised for mate locating and copulation (Dennis 2010; Turlure et al. 2019). Such resources may exist syntopically (cf. Courtney and Duggan 1983) or disjunctly (cf. McKay 1991) in time and space, but they must be present within routine individual movements' distances of the species/developmental stages concerned (Dennis 2010). Consequently, the habitat of a butterfly species should not be viewed merely as a

✉ Martin Konvicka
konva333@gmail.com

¹ Faculty of Science, University South Bohemia, Branisovska 31, 37005 Ceske Budejovice, Czech Republic

² Institute of Entomology, Czech Academy of Sciences, Branisovska 31, 37005 Ceske Budejovice, Czech Republic

³ Department of Forest Ecology, Faculty of Forestry and Wood Technologies, Mendel University in Brno, 61300 Brno, Czech Republic

⁴ T. G. Masaryk Water Research Institute, P.R.I, Podbabská 2582/30, 16000 Prague, Czech Republic

⁵ Department of Environment, Agriculture and Forestry, Landscape Ecology and NATURA 2000, Regional Government Office, U Zimního Stadionu 1952/2, 37076 České Budejovice, Czech Republic

“vegetation community” containing the species’ larval host plant, or as a land cover category recognised, e.g., by geographers or landscape planners (Vanreusel and Van Dyck 2007). This distinction is crucial for managing reserves, biological restoration, and recovery programmes. For instance, the finding that behavioural responses to vegetation structure affect the reproductive fitness of individuals, quite accepted in vertebrate conservation (Caro 2007), implies that managing vegetation structure may enhance, or suppress, local populations of rare and endangered species (Shreeve and Dennis 2011; Turlure et al. 2011).

Euphydryas aurinia (Rottensburg, 1775; Nymphalidae: Nymphalinae) is a much-studied butterfly declining across Western and Central Europe and protected by the EU Habitat directive (van Swaay et al. 2012). It forms multiple genetic lineages across its large Palaearctic range (Tolman and Lewington 2009; Junker et al. 2015; Korb et al. 2016), utilises multiple larval host plants (Singer et al. 2002; Meister et al. 2015; Ghidotti et al. 2018), and inhabits diverse biotopes, from Mediterranean xeric scrub (Munguira et al. 1997; Junker and Schmitt 2010) to subalpine meadows (Junker et al. 2010). In Western and Central Europe, it mainly inhabits humid oligotrophic grasslands (Hula et al. 2004; Bulman et al. 2007; Pielech et al. 2017; Junker et al. 2021). Threats by habitat loss are augmented by gregarious larval development, linked to prominent abundance fluctuations (Schtickzelle et al. 2005; Bulman et al. 2007; Botham et al. 2011; Zimmermann et al. 2011a; Johansson et al. 2020), and vulnerability to inappropriate vegetation management, such as uniform cuts of the occupied meadows in autumn (Hula et al. 2004) or too intensive grazing (Johansson et al. 2019). In functioning metapopulation systems, local extinctions are compensated by a good dispersal ability, allowing recolonisation of sites over 10 km apart (Warren 1994; Zimmermann et al. 2011b; Junker et al. 2021).

So far, studies targeting *E. aurinia* focused mainly on consequences of its metapopulation dynamics, i.e., modelling of colonisation/extinction probability (Wahlberg et al. 2002; Schtickzelle et al. 2005; Bulman et al. 2007; Zimmermann et al. 2011b), genetic population structure (Wang et al. 2003; Sigaard et al. 2008; Davis et al. 2021; Junker et al. 2021; Pertoldi et al. 2021), and larval habitat requirements (Anthes et al. 2003; Tjørnløv et al. 2015, Psechera and Warren 2018). The patterns of habitat use by adults remain rather neglected, despite existing evidence that the structuring of adult habitats influences multiple vital aspects of many Nymphalidae (e.g., Janz 2005; Swartz et al. 2015; Sielezniew et al. 2019; Vrba et al. 2021), including representatives of the *Euphydryas* genus. (Murphy et al. 1984; Bennett et al. 2014; Pennekamp et al. 2014).

Here, we explore the relations between vegetation structure and adult *E. aurinia* activity on humid grasslands

in Western Bohemia, Czech Republic. For several years, we surveyed the population using mark-recapture (Zimmermann et al. 2011a, b) supplemented by other methods targeting the species’ conservation requirements. This paper analyses two types of evidence: (a) observation of the butterfly activity, obtained during repeated timed walks along a fixed transect crossing a colony site; and (b) records of behaviour and substrate prior to the captures, recorded during marking the butterfly. Using these two approaches, we investigate adult temporal behavioural patterns and relationships between adult activity and structural features of its habitat. We predict that distinct behaviours will be associated with distinct habitat structures and that the association will be detectable despite activity changes due to weather conditions, time of day, and progressing season.

Material and methods

Study system

Field data originated from a network of humid seminatural grasslands near Karlovy Vary, Western Czech Republic (50° 9′ N, 13° 2′ E, altitude 650 m), on a hilly piedmont of the volcanic Doupovské Mts. We worked within a network of 28 ha humid meadow patches, separated one from another by ponds, shrubby hedges, and woodlots. In terms of vegetation, they are classified as intermittently wet *Molinia* meadows (association *Junco effusi-Molinietum caeruleae* Tüxen 1954; Fig. 1). The wider area represents a regional stronghold for humid grassland butterflies (Fric et al. 2010).

The population of *Euphydryas aurinia* develops solely on *Succisa pratensis* (Moench, 1794) on which the larvae feed gregariously until hibernation and solitarily in the spring. The adults emerge in late May and the emergence is protandrous, ♀♀ appear a few days after ♂♂. The flight period lasts about three weeks (Zimmermann et al. 2011a). While ♀♀ split their time between nectaring and egg laying, ♂♂ invest much time into mate-locating activities. Notably, they use two distinct mate-locating tactics, perching and patrolling (Wahlberg 2000; Wahlberg et al. 2001). The same ♂♂ individuals can alternate these two activities during their lifetime (unpublished data).

Transect observation of adult activity

In 2003, concurrently with marking the butterflies (carried out 28 May–17 June, cf. Zimmermann et al. 2011a), we set a fixed transect (total length: 970 m), crossing the meadows inhabited by *E. aurinia*. It was divided into 15 sections (mean length: 63 m ± 32.2 SD, range 20–150 m), separated

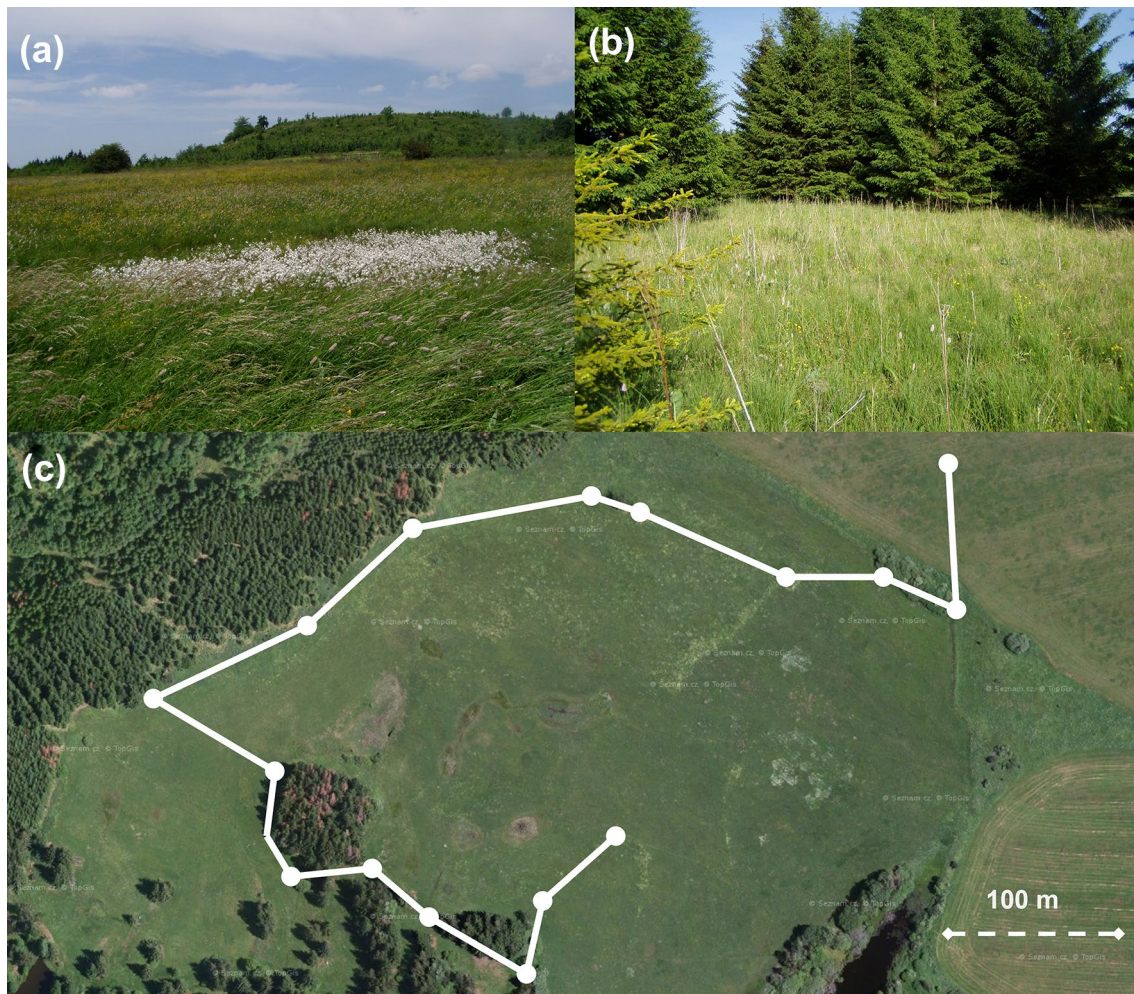


Fig. 1 Chart of the study area with (a), general view of part of the habitat (b), detailed view of a meadow edge with frequent perching records, and c position of the transect used to record *E. aurinia* activities

by distinct landmarks and characterised by vegetation physiognomy (Fig. 1).

For eight days spread across the flight period (30–31 May; 2, 5, 7–10 June), we repeatedly walked the transect between 8:30 a.m. and 17:30 p.m. (CEST), usually twice per hour but with some variation due to weather, summing up to 132 walks (mean per day: 16 ± 1.3 SD, range 12–18). During the walks, we recorded all *E. aurinia* individuals seen per walk and section as in standard Pollard transects (Pollard and Yates 1993) but considering a smaller distance to the recorder (an imaginary $3 \times 3 \times 3$ m cube), so that it was possible to record their behaviour.

The behaviours recorded, modified to fit the situation in *E. aurinia*, were, in ♂♂: Basking, Flight (direct, uninterrupted), Patrolling (gliding low over vegetation), Perching (settled at a prominent landmark, such as a tall grass blade or overhanging tree branch, at a sunny

spot, ready for take-off), Chasing (with another butterfly/insect), Mating, Nectaring, and Resting (wings closed, hidden position, usually in shade). In ♀♀, we recognised Basking, Flight, Oviposition, Chasing, Mating, Nectaring, and Resting.

Each walk was characterised by date, time of day (i.e., closest hour), and visit to each section by a set of predictors, which could vary with individual walks. (A) Weather: *Sky*, describing overall cloudiness, 1: overcast, 2: half-cloudy, 3: clear; *Sun*, describing the momentary insolation of the given section, 1: fully shaded, 2: partly shaded, 3: fully sunlit; *Wind*, ranked on a 1–4 scale, from none to strong; and *Dew*, 1 standing for wet and 0 for dry sward. (B) Habitat structures: *Host plant*: estimated visually, 1: absent, 2: a few scattered rosettes, 3: even distribution, or a few clumps along the section, 4: monodominant clumps covering > 10 m². *Nectar*: a ranked scale, 1: no flowers, 2: some flowers, 3:

richly flowered. Height of the sward, estimated as % of the given section and differentiating *Low sward*: < 25 cm; *Mid-height sward*: < 50 cm; 3: *Tall sward*: > 50 cm. *Shrubs*: estimated visually, 1: none, 2: a few small and short solitary shrubs, each with projected ground cover < 4 m², 3: larger clumps with projected cover > 4 m², but shorter than 3 m; 4: large rows of scrub taller than 3 m or high forest edges.

We analysed the data using canonical correspondence analysis (CCA), a unimodal ordination technique relating the composition of samples to external predictors, in CANOCO v.5 (Ter Braak and Smilauer 2012). Each section walk represented a sample, and the activity records were the multivariate dependent variables. Significances of the ordinations were tested using 999 Monte-Carlo permutations, accounting for the spatial (consecutive sections of the transect) and temporal (repeated walks) structure in the data by using a split-plot design, permuting the data as cyclic shifts on both whole-plot and split-plot levels. Because this permutation design does not allow “empty” samples, a small number (0.001) was added to each cell in the response data table.

Targeting the response of activities to vegetation, we first controlled for nuisance effects of transect length, hour, and serial day (cf. Vlasanek et al. 2018). We selected the best-fitting response to hour and day from linear, polynomial, and factorial codings, and used the coding explaining the highest amount of variation in response data (Var%). Next, we assessed the response to weather. Finally, we constructed a covariate model containing hours, day, and weather variables selected by forward selection, and vegetation variables as predictors.

Activity records from mark-recapture

MR data originated from 2002 (24 May–28 June, 1141 behavioural records), 2003 (28 May–17 June, 2852 records), and 2004 (27 May–15 July, 2642 records). The marking was realized in a standard way: the butterflies were netted, marked with unique codes using alcohol-based pens, and released at points of capture. For every handling event, we also recorded the individual’s sex, time of capture (closest hour), weather (Sky and Wind, using the same system in the transect walks), and the butterfly’s behaviour prior to capture.

As above, we distinguished Resting, Basking, Nectaring, Flight, Patrolling, Reproduction (mating in ♂♂, mating plus oviposition in ♀♀), and Chasing. In addition, we recorded if the activity occurred at meadow *edge* (two-level categorical predictor), defined as located within approximately 3 m distance perpendicularly from a contiguous vertical wall of trees or shrubs, and near a *host plant* (again two categories, yes or no), again defined as approximately 3 m apart from

the closest host plant. *Edge* data were recorded in all three years, *host plant* data only in 2003 and 2004.

Regression models relating the occurrence of the activity patterns to habitat edge or host plant were constructed using the glm function with binomial distribution in R 3.6.2 (package stats, family “binomial”, link function “logit”). For each type of behaviour, separately for ♂♂ and ♀♀ and for each of the three years, the modelling followed the same routine. We first entered variables describing weather during the individual observation, influencing butterfly activity considerably and rapidly. Second, we entered the hour in linear or quadratic forms to account for systematic effects of diurnal activity rhythms. Third, we entered the effect of serial day, again in linear and quadratic form, to account for possible seasonal effects. We used ΔAIC (≤ 2.0) to decide which variables to retain in the respective model. To the thus constructed *covariate models*, we sequentially added *edge* (all three years) and *host plant* (2003 and 2004 only) effects, again using AIC-statistics to decide whether either of these two predictors, or their combination, improved the fit of the model in question.

Results

Transect monitoring of butterfly activity

We obtained 2194 ♂♂ and 376 ♀♀ activity records. The most frequent ♂♂ activities were chasing (598), perching (546), patrolling (552) and nectaring (323); those of ♀♀ were nectaring (118), flight (107), basking (79) and oviposition (39); there were 23 records of mating.

In the CCA analyses, all potential covariables influenced the distribution of records significantly (Table 1), although there were notable differences. Section length was a weak predictor, indicating that other circumstances were much more important. Section identity, in contrast, was the strongest of all predictors, clearly because the sections differed in vegetation structures, and butterfly activity reflected this. For weather (Fig. 2a), the distinction Sun plus Sky *versus* Dew represented the main gradient. In both sexes, basking, resting, and (less so) nectaring were positively associated with wet sward, low Sun and overcast Sky, while the opposite applied for chasing, ♂♂ patrolling and perching. On the secondary ordination gradient, resting of both sexes was often observed in windy conditions. Hour fitted the data best if coded as a category (Fig. 2b). The main gradient of variation was between mornings plus late afternoons, when both sexes mainly rested or nectared; and mid-days, when chasing, ♀♀ oviposition, and ♂♂ patrolling and perching peaked. Mating peaked in the afternoon hours. Ordination with day (Fig. 2c), again best coded as factor, revealed a difference between early and late flight period,

Table 1 Results of CCA ordinations relating the distribution of *Euphydryas aurinia* adult behaviour observed along a fixed transect route to characteristics of the route, time of day, seasonal time, and vegetation structures along the route

	Ax1	Ax2	Ax3	Ax4	Var%	<i>F</i> , <i>P</i> _(Ax1)	<i>F</i> , <i>P</i> _(all axes)
Effects of covariates							
Length	0.03				0.04	9.00*	
Section	0.205	0.047	0.040	0.034	4.96	4.8***	8.9***
Weather Length	0.110	0.018	0.012	0.005	1.96	8.2***	10.9***
Hour (factorial) Length	0.143	0.029	0.020	0.017	2.89	4.7***	7.5***
Hour (factorial) Length + Weather	0.102	0.028	0.018	0.015	2.24	3.4***	6.0***
Day (factorial) Length	0.069	0.039	0.015	0.009	1.77	2.9***	6.1***
Day (factorial) Length + Weather	0.0534	0.0361	0.0240	0.0090	1.69	2.3***	5.8***
Covariate model [†]	0.222	0.075	0.043	0.029	5.89	3.3***	7.2***
Effects of vegetation structures							
Vegetation	0.203	0.056	0.023	0.019	4.58	10.2***	15.8***
Vegetation Length	0.197	0.043	0.025	0.021	4.43	10.0***	15.2***
Vegetation Section	0.015				0.19	4.8**	
Vegetation Hour (factorial)	0.180	0.053	0.025	0.018	4.06	9.3***	14.9***
Vegetation Day (factorial)	0.194	0.050	0.022	0.016	4.13	9.9***	15.2***
Vegetation Weather	0.177	0.056	0.022	0.018	3.98	9.1***	14.6***
Vegetation Covariate model*	0.163	0.036	0.023	0.016	3.70	8.7**	13.5**

Ax1–Ax4 are eigenvalues of canonical axes 1–4

Var% is percentage of variation explained by the models, *F* and *P* are the Monte-Carlo test results (**p* < 0.05, ***p* < 0.01, ****p* < 0.001)

[†]Covariate model structure: ~ Day (factorial) + Hour (factorial) + Length + Wind + Sky + Dew

with ♂♂ prevailing in early and ♀♀ in late season. For ♂♂, the peak of patrolling seasonally preceded those of perching and nectaring; while for ♀♀, the peak of mating preceded that of nectaring and oviposition.

Vegetation alone explained second-highest proportion of variation in the behavioural records after section identity, and retained its significant effect if controlled for hour, day, and weather, and even section, and in a complex covariate model (Table 1). The ordination diagrams, both without control for covariates (not shown) and after filtering their effects (Fig. 2d) showed that the first ordination gradient distinguished between mid- to tall sward with rich nectar and a high host plant representation, and conditions with shrubs and short sward. The tertiary gradient (not shown) distinguished short sward from mid- and tall sward. ♀♀ oviposited, basked, nectared, and rested near the host plants, though resting occurred in taller sward than the other activities. ♂♂ rested most frequently in tall sward near shrubs, perched and chased other insects near shrubs at shorter sward, and patrolled, nectared, and basked at short to medium sward, independently of host plant abundance. It follows that some ♂♂ activities, especially those associated with mate locating, were spatially separated from spots with high host plant cover, where ♀♀ performed most of their activities.

Activity records from mark-recapture

We obtained a total of 1251 behaviour records for 2002 (♂♂/♀♀: 876/375), 1624 for 2003 (1060/564), and 2639 for 2004 (2400/239). Across years, the most frequently recorded ♂♂ activities were patrolling (*n* = 1290), followed by perching (969), chasing (593), nectaring (495), basking (415), flight (396), resting (116), and reproductive activities (62). In ♀♀, the ordering was flight (414), basking (336), nectaring (259), resting (99), and reproductive behaviours (88). The higher number of reproductive behaviours, the majority of which concerned pairs marked *in copula*, was due to ♀♀ captured and marked during oviposition.

Results of the binomial regressions (Tables 2, 3), despite some inconsistencies among years, agreed with the established knowledge of adult butterfly activities. For instance, ♂♂ basking decreased with sunny weather (all three years), ♀♀ mating decreased (2003, 2004) and nectaring increased (♂♂: 2003 and 2004, ♀♀: 2004) with flight period duration, and ♂♂ perching followed domed patterns, indicating peaks in the middle of the adult period (all 3 years).

Regarding the within-habitat structures, the results were consistent across the three years for ♂♂ perching and patrolling. Perching prevailed near edges in all three years, plus outside of host plant patches in 2003. Patrolling consistently prevailed over centres of

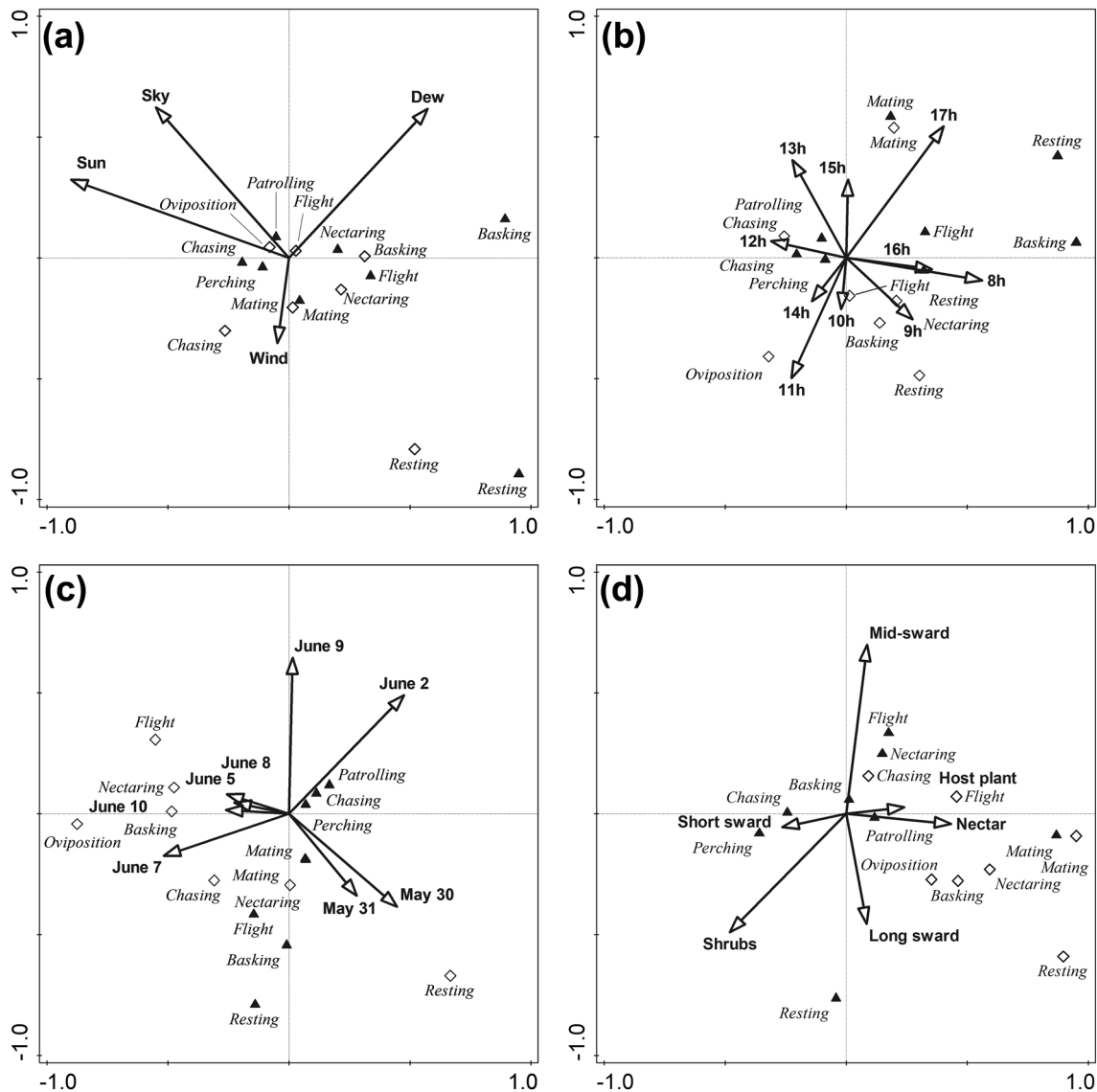


Fig. 2 CCA ordination biplots (first—vertical and second—horizontal axes) showing *Euphydryas aurinia* activity records collected along a fixed transect route across a colony site (cf. Fig. 1). Black triangles are males, empty diamonds are females. **a** Effects of Weather, with section length as covariate (~Weather | Length). **b** Effects of categorical Hour, with length and

weather as covariates (~Hour | Length+Sun+Sky+Dew). **c** Effects of categorical Day, with length and weather as covariates (~Day | Length+Sun+Sky+Dew). **d** Effects of Vegetation structures, with forward-selected covariates (~Vegetation | Day+Hour+Length+Wind+Sky+Dew). See Table 1 for relevant statistics of the models

grasslands, i.e., further from woody edges. Patterns of ♂♂ chasing were inconsistent, prevailing at edges and in the centres depending on the year. Results for ♀♀ were also inconsistent, probably due to considerably lower sample sizes, but suggested that basking prevailed in the centres (2002, 2004) and near host plant (2003), while basking and nectaring prevailed outside the host plant patches (both 2003).

Discussion

Using two alternative approaches, timed observation of activities along a fixed transect and analysis of capture circumstances during mark-recapture, we linked within-habitat vegetation structures to adult activity patterns of the *Euphydryas aurinia* butterfly. Out of two mate-locating behaviours of ♂♂, perching was closely associated with meadow edges, i.e., with trees, woodland margins, lines of shrubs, or just unmanaged tall herbaceous vegetation surrounding regularly mown grasslands containing the host

Table 2 Results of binomial regressions of *Euphydryas aurinia* adult ♂♂ behaviour records obtained during mark-recapture campaigns in 2002–2004

	2002*			2003			2004		
	Model terms	DF resid	AIC	Model terms	DF resid	AIC	Model terms	DF resid	AIC
Basking ~		875	480.2		1059	200.4		2399	1913
I	↓sky ↑wind	873	445.5	–	–	–	↓sky	2398	1893
II	↑↓hour	871	441.3	↓↑hour	1057	185.1	↓↑hour	2396	1889
III	–	–	–	–	–	–	↓day	2395	1757
IV	–	–	–	Centre, near HP	1055	128.4	–	–	–
Flight ~		875	694.5		1059	533.5		2399	1403
I	↑wind	874	684.8	↑wind	1058	525.9	↓sky ↑wind	2397	1350
II	–	–	–	↑↓hour	1056	509.9	↑↑hour	2395	1341
III	–	–	–	↓↑day	1054	499.9	↓↑day	2393	1324
IV	–	–	–	Centre	1053	491.9	Centre, outside HP	2391	1306
Chasing ~		875	751.5		1059	837		2399	1876
I	–	–	–	–	–	–	↑sky	2398	1847
II	↑↓hour	273	743.3	↓↓hour	1057	833.4	↓↓hour	2396	1806
III	↓day	272	739.2	↑↑day	1055	827.0	–	–	–
IV	Edge	271	737.5	Centre, near HP	1053	810.9	Edge	2395	1772
Perching ~		875	1032.6		1059	1394		2399	1960
I	↑sky↓wind	873	1002.0	–	–	–	↑sky↓wind	2397	1930
II	↑↓hour	871	992.4	↑↓hour	1057	1389	↑↓hour	2395	1907
III	↓↑day	869	964.9	↓↑day	1055	1367	↓↓day	2393	1888
IV	Edge	868	950.0	Edge, outside HP	1053	1325	Edge	2393	1857
Patrolling ~		875	698.2		1059	1254		2399	3153
I	↑sky	874	696.0	↑sky	1058	1249	↑sky	2398	3124
II	–	–	–	–	–	–	↓hour	2397	3109
III	–	–	–	↓day	1057	1237	↓day	2396	3095
IV	Centre	873	685.7	Centre	1056	1225	Centre	2395	3075
Reproduction ~		875	153.8		1059	200.4		2399	214.0
I	–	–	–	↓wind	1058	194.9	–	–	–
II	–	–	–	↑↑hour	1056	183.8	–	–	–
III	–	–	–	↓↓day	1054	181.1	↓↓day	2397	210.0
IV	–	–	–	Centre	1053	180.4	Near HP	2396	206.5
Resting ~		875	296.1		1059	105.8		2399	720.0
I	↓sky ↑wind	873	229.4	–	–	–	↑wind	2398	562.2
II	–	–	–	–	–	–	↑↑hour	2396	548.6
III	–	–	–	–	–	–	↑day	2395	538.6
IV	Edge	872	227.9	–	–	–	–	–	–
Nectaring ~		875	791.4		1059	725.7		2399	1540
I	–	–	–	–	–	–	–	–	–
II	–	–	–	–	–	–	–	–	–
III	–	–	–	↓↑day	1057	725.5	↑day	2398	1533
IV	–	–	–	Outside HP	1056	724.9	Centre	2397	1529

To a null model for each activity (coded 0/1) * year combination, we sequentially added (I) weather variables, (II) hour, (III) serial day since start of the marking, and (IV) information on a meadow centre vs edge, and near vs outside larval host plant (HP). Terms that decreased the model's fit by AIC by ≥ 2 were retained in the respective model. Models containing the variables describing within-habitat structures are in bold. The darts indicate linearly positive (\uparrow), negative (\downarrow) or polynomial ($\uparrow\downarrow$, $\downarrow\uparrow$, $\uparrow\uparrow$ or $\downarrow\downarrow$) depending on the shape of the fitted polynomial relationships

*Only information on meadow centre vs. edge was recorded in this year

Table 3 Results of regression analysis of *Euphydryas aurinia* adult ♀♀ activity records obtained during mark-recapture campaigns in 2002–2004

	2002			2003			2004		
	Model terms	DF resid	AIC	Model terms	DF resid	AIC	Model terms	DF resid	AIC
Basking ~		375	422.9		563	622.8		238	300.9
I	↓sky	374	420.2	↑sky ↑wind ↑sky*wind	560	610.2	–	–	–
II	–	–	–	↑hour	559	605.4	–	–	–
III	–	–	–	–	–	–	↑day	237	293.6
IV	Centre	373	418.2	Near HP	558	443.4	Centre	236	292.6
Flight ~		375	417.6		563	755.5		238	315.4
I	↑sky	374	407.7	–	–	–	↑sky ↑wind	237	302.9
II	–	–	–	–	–	–	↓↑hour	235	300.5
III	–	–	–	–	–	–	↓day	234	297.3
IV	–	–	–	Near HP	562	750.5	–	–	–
Chasing ~		375	79.43		563	125.7		238	14.95
I	–	–	–	–	–	–	–	–	–
II	–	–	–	–	–	–	–	–	–
III	↓day	374	75.81	–	–	–	–	–	–
IV	Edge	373	73.39	–	–	–	–	–	–
Reproduction** ~		375	216.1		563	315.9		238	134.7
I	–	–	214.1	↑sky	561	311.8	–	–	–
II	↑hour	374	214.1	↓hour	560	303.8	–	–	–
III	↓day	373	210.6	↓↓day	558	277.1	↓day	237	128.7
IV	–	–	–	–	–	–	–	–	–
Resting ~		375	243.8		563	242.1		238	157.8
I	↓sky ↑wind	372	200.5	–	–	–	↑cloud	237	137.5
II	–	–	–	–	–	–	–	–	–
III	–	–	–	–	–	–	–	–	–
IV	–	–	–	Outside HP	562	239.9	–	–	–
Nectaring ~		375	461.7		563	569.8		238	162.2
I	↑sky ↓wind	373	447.9	↓wind	562	562.4	–	–	–
II	↓hod	372	443.4	↓hour	561	559.6	–	–	–
III	–	–	–	–	–	–	↑↑day	237	159.3
IV	–	–	–	Outside HP	560	551.4	–	–	–

See Table 2 for description of the modelling procedure

*Only information on meadow centre v. edge was recorded in this year

**Combines mating and oviposition records

plants, *Succisa pratensis*. Patrolling, on the other hand, tended to occur at open short- to mid-sward grassland patches. Females concentrated at transect sections with high concentrations of host plants and nectar, which in turn caused a spatial separation of sexes. For conservation management of *E. aurinia* sites, it follows that in addition to efforts to maintain high host plant concentrations, the sites should contain some shrubs, edges, taller-sward and similar structures. The latter advice is sometimes mentioned as “heterogenous management” (e.g. van Swaay et al. 2012), but to our knowledge, until recently it lacked a quantitative support for *E. aurinia*.

Both our approaches produced complementary results and both withstood robust controls for short-term weather conditions and temporal aspects of adult flight. While the behavioural patterns due to weather (resting in windy overcast conditions, basking when the sward was wet by morning dew or after rains, behaviours associated with movements in sunny conditions) were rather trivial, the diurnal and the seasonal patterns displayed clear structuring. Interestingly, morning and late afternoon hours shared many similarities. The prevailing activities in 8:00–10:00 in the morning and 16:00–17:00 in the afternoon were basking, nectaring, and resting. This was arguably connected to the intake of energy, both thermal (cf. Franzen et al. 2022)

and nutritional (cf. Botham et al. 2011) for commencing daily activities in the mornings, and to replenish the energy before night rest in the evenings (cf. Vlasanek et al. 2018). The energy demanding activities such as male perching (with frequent conspecific and heterospecific chases) and patrolling, and female oviposition, culminated in 11:00–14:00, i.e., around noon. Franzen et al. (2022) described peaks of *E. aurinia* activity in early afternoons, attributing it to the thermal requirements of this early-season species, and showed that activity tends to decline under extremely hot temperatures.

Whereas diel activity patterns displayed a similarity between mornings and evenings, seasonal patterns were linear, reflecting the changing proportion of sexes and changing status of the individuals along the flight period. Perching and patrolling peaked early in season, when ♂♂ prevailed in the studied colony (Zimmermann et al. 2011a) and were later followed by the peak of “maintenance activities”, especially nectaring. Vlasanek et al. (2018) observed this pattern for multiple temperate species with distinct generations. Notably, perching and patrolling were not segregated temporarily. Regarding ♀♀, besides later seasonal peaks of all activities attributable to protandry (Schitzckzelle et al. 2005; Zimmermann et al. 2011a), the ordination analysis showed that oviposition and nectaring were postponed relative to mating. A female must evidently have mated to oviposit, and intake of nectar presumably increases the number of egg batches produced (O’Brien et al. 2004).

The relationships between behaviours and vegetation structures remained apparent after considering the above weather and temporal effects. The most robust patterns concerned mate-locating activities. The association of perching with shrubs near short sward (ordination) and with edges (regressions) conforms with the classic (Scott 1974; Dennis and Shreeve 1998; Rutowski 1991; Wickman 1992) concept of perches as conspicuous landmarks in wind-shielded locations provided by edges of taller vegetation, but with good oversight of the habitat. Perches may occur at host plant patches (as in the skipper *Carterocephalus palaemon* (Pallas, 1771): Ravenscroft 1994, or the satyrine *Coenonympha pamphilus* (Linnaeus, 1758): Wickman 1985) or at patches of other critical resources, notably nectar (as in the copper *Lycaena hippothoe* (Linnaeus, 1761): Fischer and Fiedler 2001; Turlure and Van Dyck 2009). In our case, both the ordination and regressions suggested that the location of perches was independent of host plants distribution. Patrolling, on the other hand, occurs over mid-sward with a good supply of nectar, in the central parts of individual meadows (regressions) and rather close to host plants (ordination). Such a setting allows patrolling males to spot freshly hatched virgin females and at the same time, the unmated females to approach perching males. The

latter consideration may deserve further attention, because Pinzari et al. (2019) observed that a fraction of females of *Euphydryas aurinia provincialis* (Boisduval, 1828) mate a few days after emergence. The location of perches away from host plants indicates that perching males unlikely harass females seeking for oviposition, a situation described for *L. hippothoe* by Turlure and Van Dyck (2009), but does not exclude potential harassment of females by patrolling males.

The whole situation with perches situated near edges independently of host plants distribution, and males alternating perching with patrolling over host plants patches suggests that an ideal *E. aurinia* habitat would be finely structured, with shorter and taller swards, leeward edges, and host plant patches alternating at small scales of routine within-habitat movements. In such a setting, host plants with increased activity of females would naturally occur near edges with male perches. In traditional landscapes (cf. Loos et al. 2014; Perovic et al. 2015), and presumably in naturally patchy landscapes of prehistory (cf. Fahrig 2017), proximity of open short sward patches and edges of all types was probably a rule, and restoring highly heterogeneous conditions, e.g., by forest grazing (Saarinen et al. 2005), could boost *E. aurinia* populations. Several authors across the *E. aurinia* range disclosed “heterogeneity” as a positive correlate of its presence and density (Munguira et al. 1997; Scherer and Fartmann 2021), while others warned against uniformising management (Johansson et al. 2019). It is not unlikely that mate-seeking ♂♂, in contrast to ovipositing ♀♀, cannot recognise host plant patches, which may occasionally cause establishment of perches too far from females’ activity; such a situation was described in a patrolling butterfly, *Parnassius mnemosyne* (Linnaeus, 1758) (Konvička et al. 2007).

From a more general insect conservation perspective, detailed understanding of *E. aurinia* adult activity provides further evidence that large uniformly managed land units exceeding in size routine within-habitat movements (cf. Baguette and Van Dyck 2007), even if containing abundance of some resources (e.g., larval host plants), will always be inferior to patchily heterogeneous environment (cf. Liu et al. 2006). This knowledge, increasingly accepted by the conservation community over the past decades (Rundlöf and Smith 2006; Kivinen et al. 2008; Lebeau et al. 2015; Perovic et al. 2015; Schwarz and Fartmann 2022) gradually transferred into reserve management on small scales, including our study system. The practices applied to conserve grassland insects may include patchy mowing, retention of uncut fallows, or grazing via small panels. Regretfully, diversifying grasslands’ management remains difficult at large scales and beyond protected areas, including the matrix separating *E. aurinia* occupied

sites in the western Czech Republic (Junker et al. 2021), although evidence is accumulating that much can be gained by relatively cheap measures, such as dissecting vast management units by temporary fallows or hedgerows (Buri et al. 2013; Bruppacher et al. 2016; Salek et al. 2018).

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Declarations

Competing interests The authors declare no competing interests.

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