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A protracted phenology: Post-diapause larval development of a threatened butterfly

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Abstract

1. The Marsh Fritillary (*Euphydryas aurinia*, Rottemburg, 1758) is a grassland butterfly that has experienced severe population declines across Europe during the last century. Most studies on this species have focused on adults, oviposition or pre-diapause larvae. By contrast, knowledge on the time after diapause in spring is scarce.
2. Here, we studied phenology, developmental time, dispersal and feeding behaviour of post-diapause larvae of *E. aurinia* in montane grasslands in the Bavarian Alps (Central Europe).
3. Our study revealed that after diapause, larvae exhibited a strong variability in developmental time as well as pronounced differences in the dispersal and feeding behaviour between the three instars. Developmental time of post-diapause larvae to reach the 5th instar decreased with longer sunshine duration during January to March, higher litter cover and higher heat load index. In dry meadows, larvae reached the 5th instar in about 2 weeks after finishing diapause—nearly 2 weeks earlier than in wet grasslands in some cases. In contrast to the tiny 4th instar larvae, which stayed close to their hibernaculum web and primarily fed on *Succisa pratensis* leaves, larger 5th and 6th instar larvae increasingly dispersed and diversified their feeding behaviour.
4. We hypothesize that occupying a large environmental gradient, resulting in a protracted phenology of the different instars, helps *E. aurinia* to cope with the harsh climatic conditions in the study area and losses by specialized parasitoids like braconid wasps.

KEYWORDS
caterpillar phenology, climate, EU habitats directive, feeding behaviour, grassland ecosystem, habitat heterogeneity, litter layer, marsh fritillary (*Euphydryas aurinia*)

INTRODUCTION

Butterflies are very sensitive indicators of environmental alterations (Franzén et al., 2022; Krauss et al., 2010; van Swaay et al., 2006). Accordingly, during the last century, many butterfly species have heavily declined due to habitat loss and deterioration (Habel et al., 2016; Warren et al., 2021). In Europe, particularly grassland species have suffered strongly, comprising more than half of all threatened butterfly species (van Swaay, 2002; Warren et al., 2021). Within recent decades, grassland butterfly decline has mostly been explained by habitat deterioration (Habel et al., 2022). Especially the juvenile stages of butterflies often require high habitat quality for successful development, since they have a lower mobility and usually a longer life time than adults (García-Barros & Fartmann, 2009).

The Marsh Fritillary (*Euphydryas aurinia* (Lepidoptera: Nymphalidae), Rottemburg, 1758) is a grassland butterfly that has particularly experienced severe losses. During the last century, habitats and populations of the species have dramatically declined across Europe (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003; Asher et al., 2001; Stefanescu, 2019; van Swaay et al., 2006). Accordingly, the species is listed in Annex II of the EU Habitats Directive (Council Directive 92/43/EEC, 1992). However, recently there are contradicting population developments across Europe. van Swaay et al. (2025) published an uncertain trend for the species in the EU Grassland Butterfly Index, regarding data between 1991 and 2023, including short term gains. Yet, for Germany, but also other European regions like Catalonia the population trends for *E. aurinia* are still highly negative (Musche et al., 2025; Stefanescu, 2019).

Today, *E. aurinia* is mostly threatened by habitat deterioration through abandonment and eutrophication, but also by maladapted management, even in protected areas (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003; Brunbjerg et al., 2017; Stefanescu, 2019). The specialized butterfly species inhabits nutrient-poor dry or wet semi-natural grasslands, but also ecotones and glades of evergreen oak forests (Hula et al., 2004; Konvicka et al., 2023; Scherer & Fartmann, 2023; Stefanescu et al., 2006). Inappropriate or missing habitat management can result in cooler microclimates and reduced host plant abundance; both lead to a lower habitat quality (Braem et al., 2026; Brunbjerg et al., 2017; Tájek et al., 2023). Therefore, the species' persistence is tied to low-intensity land use practices and management schemes that reflect the requirements of the sensitive butterfly (Konvicka et al., 2008; Rada et al., 2019; Scherer & Fartmann, 2023; Warren et al., 2021).

After *E. aurinia* was protected at the EU level, studies on its ecology have experienced a boom (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003; Betzholtz et al., 2007; Botham et al., 2011; Bulman et al., 2007). However, most previous studies were conducted in late spring or summer and focused on adults, oviposition or pre-diapause larvae (Junker et al., 2023; Pielech et al., 2017; Scherer & Fartmann, 2022). By contrast, knowledge about the second half of larval development, the time between diapause and pupation in spring, is scarce (Anthes & Nunner, 2006). Especially diapause and the time shortly after are responsible for large losses of offspring of *E. aurinia* (Liu et al., 2006). However, for successful conservation management, it is crucial to understand the ecology during the full life cycle of the species (Anthes & Nunner, 2006).

Diapause is a very stressful period, where larvae have to minimize activity despite being exposed to substantial environmental stochastics (Koštál, 2006; Mansingh, 1971). As a state of arrested development, diapause requires specific and often complex cues for termination, which remain incompletely understood. Termination may be triggered by a combination of factors, including the exceedance of certain temperature and photoperiod thresholds and the passage of a defined time period (Koštál, 2006). If environmental conditions remain adverse following diapause termination, a subsequent post-diapause quiescent state may occur; this state is more readily reversible (e.g. by rising temperatures) and can be re-entered when unfavourable conditions return. Before diapause, larvae of *E. aurinia* feed gregariously in a communal web and stop feeding between August and September to spin a dense hibernaculum web (Porter, 1982). Inside the web, larvae moult to the 4th instar and start to rest. Usually, during March, diapause is completed (own observation). After diapause, larvae continue feeding gregariously despite heavily reduced host plant biomass. By contrast, larvae of the two last instars live solitary. For optimal metabolism, the larvae have to reach temperatures between 30 and 35°C, although ambient temperatures in early spring are much lower (Porter, 1982). This is facilitated by their black body colour and active basking. For their development the larvae need large amounts of host plant biomass. Franzén et al. (2022) hypothesize that high resource requirements are addressed by selecting oviposition sites with abundant host plants, thereby ensuring adequate food availability for post-diapause larvae in the following spring. Another strategy has been documented for closely related butterfly species. They increase their fitness during periods of limited resources by altering their diet from instar to instar (Arriens et al., 2021; Bernays & Chapman, 1994). Despite *S. pratensis* being the most relevant host plant in Western, Central and Northern Europe, Anthes and Nunner (2006) summarized reports of various other plant species the larvae used for feeding. Especially in the Alps and their surroundings, further species of Dipsacaceae and Gentianaceae could be of particular importance due to their high abundance and species richness (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003).

Here, we studied phenology, developmental time, dispersal and feeding behaviour of post-diapause larvae of *E. aurinia* in montane grasslands in the Bavarian Alps (Central Europe). The research was conducted in semi-dry calcareous grasslands and three types of wet grasslands. In particular, we addressed the following research questions:

i. What drives post-diapause development, and does the developmental time differ among the studied grassland types?
ii. Does the dispersal differ among the three instars?
iii. Which host plants are used, and does the host plant spectrum differ among the three instars?

To answer these questions, we marked hibernaculum webs across the four grassland types in autumn and monitored the larvae from completing diapause until pupation. Based on our findings, we make management recommendations to favour this butterfly species of European conservation concern.

MATERIALS AND METHODS

Study species

The Marsh Fritillary (*Euphydryas aurinia*) is a nymphalid butterfly with Palearctic distribution, occurring from the British Isles throughout Europe to eastern Asia (Bräu et al., 2013). It is univoltine, and in Central Europe, adults are on the wing from mid-May to the beginning of

July. Here, the species predominantly colonizes wet grasslands with Devil's-bit Scabious (*S. pratensis*) as the primary host plant. However, *E. aurinia* also occurs in semi-dry calcareous grasslands, where the Small Scabious (*Scabiosa columbaria*) or Glossy Scabious (*Scabiosa lucida*) are the main host plants (Bräu et al., 2013; Scherer & Fartmann, 2022). In our study area, *E. aurinia* even inhabits both mentioned grassland types within short spatial distance. Nevertheless, although *Sc. lucida* is equally frequent in the calcareous grasslands, the butterfly predominantly utilizes *S. pratensis* (Scherer & Fartmann, 2022). Females of *E. aurinia* lay batches of 50–400 eggs on the underside of the leaves of prominent and easily accessible host plants (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003; Bräu et al., 2013). In our study area, besides *S. pratensis* and rarely *Sc. lucida*, Field Scabious (*Knautia arvensis*) and Willow Gentian (*Gentiana asclepiadea*) are also chosen for oviposition and as secondary host plants (own observation).

Study area

The study area in the Niederwerdenfelser Land covers an area of about 52 km^2 and an elevational range of 800–1350 m.a.s.l. It is located in the Northern Limestone Alps in Upper Bavaria (southern Germany), 100 km south of Munich (47°26′ N, 11°10′ E and 47°30′ N, 11°17′ E). Due to the elevation and its location in the Alps, which are affected by orographic rainfall, the climate is cold and wet with an annual average temperature of 7.1°C and a mean annual precipitation of 1378 mm (weather station: Mittenwald; long term mean: 1991–2020; German Weather Service, 2021). However, higher temperatures and periods of reduced precipitation are facilitated by foehn wind and rain-shelter effects caused by the Estergebirge in the north (Rösler, 1997). From late winter until the flight season of *E. aurinia*, the climate is often rough, with low temperatures—often below zero degrees—reoccurring periods of snow and, particularly in spring, periods of excessive rainfall (German Weather Service, 2021).

The study area is the most important stronghold of the so-called hummocky meadows ("Buckelwiesen") in Central Europe (~450 ha) (Embleton-Hamann, 2004; Gutser & Kuhn, 1998). Hummocky meadows are pre-Alpine calcareous grasslands with a geomorphological peculiarity: a microrelief consisting of regular pits and mounds. Due to the elevational gradient of the study area, a wide range of different aspects and slopes occur within the meadows. Accompanied by a strong microheterogeneity caused by the pits and mounds, but also trees at their margins, the meso- and microclimatic conditions may differ strongly between and within the grassland patches (Gutser, 1996). This results in a distinct variability in snow height and cover in winter and spring (Figure 1). *Scabiosa lucida* is widespread in these grasslands, but due to the high precipitation and microrelief, even species of wet grasslands such as *S. pratensis* regularly occur (Gutser & Kuhn, 1998). For hundreds of years, hummocky meadows have been used with low intensity, being mown once in summer. However, during the last century, either management has been intensified (including flattening of the microrelief and fertilization) or grasslands have become abandoned and afforested. As a result, the area of hummocky meadows has declined by 95% (Gutser & Kuhn, 1998). Today, the remaining hummocky meadows are scattered inside a diverse grassland-woodland mosaic but are still mostly well connected (Krämer et al., 2012; Löffler & Fartmann, 2017). For simplification, we refer to hummocky meadows hereinafter as dry meadows.

Besides the dry meadows, grasslands in the study area also comprise litter meadows. Here, *S. pratensis* has its main distribution and is the main host plant (Scherer & Fartmann, 2022). In contrast to the dry meadows, litter meadows are nutrient-poor, periodically wet grasslands mown in autumn to obtain bedding for livestock (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003; Schwarz et al., 2023). According to the Habitats Directive, both types of meadows are legally protected by the EU Habitats Directive (EC, 2007).

Study design

Study sites

To study the post-diapause larval development of *E. aurinia*, we selected eight patches of grasslands where *E. aurinia* and its main host plant, *S. pratensis*, frequently occurred (patch-occupancy data: Scherer & Fartmann, 2022; own observation). Patches varied in size between 0.7 and 5.1 ha (± 0.6 SE) and were composed of a mosaic of the four different grassland types used by *E. aurinia*. These were (i) dry meadows, mown in July, as well as litter meadows, which were subdivided into those that were (ii) mown in September (hereinafter mown litter meadows), (iii) characterized by regularly alternating fallows (hereinafter alternating fallows), meaning that they were unmown for up to 3 years according to the local conservation law and (iv) abandoned meadows for at least 10 years (hereinafter abandoned meadows). For more details about the distribution of the grassland types and host plants, see the Supporting Information.

Sampling of hibernaculum webs

In September 2020, we conducted standardized sinusoidal transect walks with a loop distance of 2 m at all locations of the patches, where potential host plants occurred to sample for larval hibernaculum webs (Fartmann, 2006; Krämer et al., 2012; occupancy data: Scherer & Fartmann, 2022). In total, we located 80 larval hibernaculum webs within the patches and marked them with magnets to be retrievable with a metal detector. The webs were distributed across the four grassland types as follows: (i) 29 webs in four dry meadows (ranging from 4 to 15 per patch), (ii) 25 webs in four mown litter meadows (ranging from 1 to 19 per patch), (iii) 10 webs in three alternating fallows (ranging from 2 to 6 per patch) and (iv) 11 webs in five abandoned meadows (ranging from 1 to 3 per patch). Furthermore, we recorded the distance to the next host plant and the host plant species.

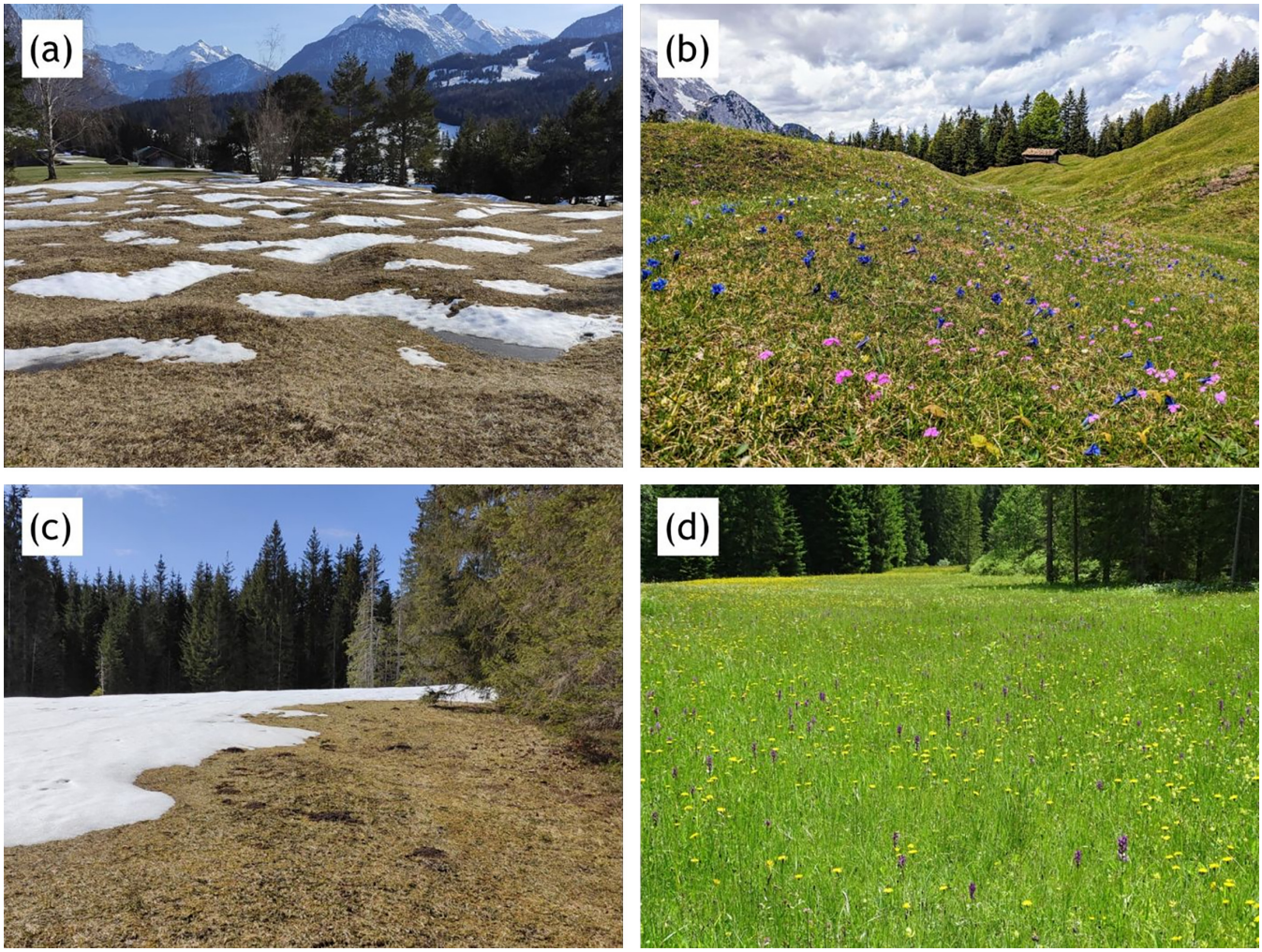

FIGURE 1 Typical habitats of *E. aurinia* in the pre-Alps. In semi-dry calcareous grasslands (a) March, (b) April. The expressed microheterogeneity significantly affects the snow melting process. Depressions and northern slopes were still partially covered by snow, while flat parts and south-facing slopes were free of snow (a). In wet grasslands (c) March, (d) May, in spring, heat accumulation was facilitated by trees. Faster melting of snow was caused by heat accumulation due to trees at the northern margin of grasslands (c).

Larval phenology and development

In 2021, between February and May, we revisited the locations of the marked hibernaculum webs every 3 to 5 days to survey larval activity. Resurveys were postponed when temperatures were below 5°C or days were characterized by rain- or snowfall. Diapause was recorded as completed when the first larvae were found feeding or when larvae were found outside their hibernaculum web and nearby host plants showed bite marks and excrements. At this point, we reviewed whether or not the closest host plant survived winter with vital leaves. Subsequently, we established 400 m^2 (20 × 20 m) plots around each hibernaculum web to standardize the search for larvae. To record the phenology of the larvae, we sampled all available larval instars inside the plot during each following visit by checking all available host plants for larvae. The survey ended at the 18th of May, when all larvae had reached the 6th instar or pupated.

To assess post-diapause larval development, for each marked hibernaculum web, we recorded the time between the first larvae completing diapause and the first larvae reaching the 5th instar. We chose to only monitor the 4th instar development in detail, as it is the last gregarious instar with a synchronized development. Furthermore, it is active during the most severe weather conditions in the entire life cycle of *E. aurinia*. At this stage, larvae not only experience suboptimal weather but, due to their limited mobility compared to later stages, are less able to relocate to more favourable microclimates and are easily traced. After the first active larvae were found, the cover of host plants and litter within a radius of 1 m around the hibernaculum were recorded. Furthermore, we assessed the mean of the potential daily sunshine duration (h) for the months January, February and March (second half of the diapause period; using a horizontoscope) (Scherer & Fartmann, 2022), elevation (m.a.s.l.; using a GPS) and heat load index calculated based on the slope and aspect of the location of

the former hibernaculum using a compass with inclinometer (McCune, 2007; McCune & Keon, 2002). For the calculation of the heat load index, we used Equation (3) described by McCune and Keon (2002) and updated by McCune (2007). When all larvae had completed diapause and patches were free of snow, we measured the surface temperature at the location of all previously marked hibernaculum webs using an infrared thermometer (accuracy ±0.5°C; Eventek Infrarot-Thermometer A60). Since the thermometer had a measurement radius of 1 cm, we sampled temperature at three randomly selected locations of the hibernaculum web. For further analyses, we used the mean of the three replications. Measurements were done on 28 April 2021 or 30 April 2021 between 12 pm and 1 pm. Both days where characterized by high solar radiation and at the time of the measurements a temperature of 10°C (German Weather Service, 2021).

To assess differences in surface temperature between basking larvae (4th instar) of *E. aurinia* and the upper side of vital host plant leaves (*S. pratensis*), we sampled larval aggregations and host plant leaves of the occupied host plant ($n = 15$, each) on a randomly selected patch using an infra-red thermometer as mentioned before. For each pair, we additionally sampled the current air temperature at a height of 1 m using a digital thermometer (accuracy ±0.5°C; Mebus digital thermometer 48,432). Sampled larval aggregations were selected closest to a randomly chosen coordinate within the patches using a digital raster within ArcGIS Pro 3.0. Locations had to be free of snow. All temperature measurements were conducted on 10 April 2021 between 12 pm and 1 pm. The day was sunny and air temperature was 9°C during the period of measurements (German Weather Service, 2021). Per sample, temperature of the basking larvae, the upper side of the leaf and at 1 m height was measured at the same time and in the same way as described above.

Dispersal and feeding behaviour

To assess the post-diapause mobility and feeding behaviour of the larvae of *E. aurinia*, we randomly selected five hibernaculum webs for each of the four occupied grassland types (see section: Study sites) in the beginning of April 2021. Hibernaculum webs had to be isolated by at least 20 m from other webs to minimize the probability of recording larvae originating from other hibernaculum webs. To sample larvae, we used the established plots as described above. During the 4th instar, we recorded all host plant species used until moulting to the 5th instar. This was also done if larval aggregations split up or changed host plants. We revisited the plots every 3 days and searched for larvae by walking in loops with a distance of 1 m between each loop across the plot, searching directly for the larvae and checking all potential host plants. The search was postponed if there was snowfall or rain and when air temperatures were below 5°C. When larvae were found shortly before or after moulting to the 5th instar (e.g. observation of small, pushed off head capsule or large yellow head capsule), we recorded the distance to the hibernaculum web in the centre of the plot with a measuring tape (cm). Afterwards, we repeated sampling for larvae of the 5th and 6th instar at least 1 week after we had found the first larvae of the respective instar within a plot. For 15 individually feeding larvae for each of the four grassland types ($n = 60$ larvae per instar), we recorded the distance to their hibernaculum web and the used host plant species. One larva was found near a plot with no other hibernaculum webs within range; we also recorded parameters for this larva. However, we did not sample larvae, when, in rare cases, we observed larvae between two plots. Finally, we assessed the cover of all available host plant species for all plots at the end of April.

Statistical analysis

All statistical analyses were conducted using the software R 4.3.1 (R Development Core Team, 2025). To determine differences between groups, we conducted generalized linear mixed-effects models (GLMM) with a Poisson (count data), gamma (interval-scaled data) or proportional-binomial (percentage data) error structure using the lme4 package (Bates et al., 2015) followed by Tukey contrasts for pairwise comparisons. To account for potential spatial autocorrelation, we used 'patch' as a random factor. This was done for the comparison (i) of the environmental parameters within the different grassland types occupied by *E. aurinia*, (ii) the dispersal range of the different larval instars and (iii) the proportion of the host plant species used by the different larval instars. All pairwise comparisons were made using the function 'glht()' in the multcomp package (Hothorn et al., 2008) and the default 'single-step' method to adjust the *P* values for multiple testing.

To test for temperature differences between basking larvae, host plant leaves and air within the studied patch, we used an analysis of variance (ANOVA) with Tukey test for pairwise comparisons. To evaluate larval developmental time, we conducted multivariable Generalized Linear Mixed Models (GLMM) with a negative binomial error structure using the *MASS* package (Venables & Ripley, 2002; Venables & Ripley, 2025) with 'patch' as a random factor. Within the models, time (days) larvae required to reach the 5th instar served as the response variable. It was recorded from the 18th of February 2021 onwards, when the first larvae were found emerging from diapause. The variables host plant cover, cover of litter, elevation, the potential daily sunshine for the months January–March and heat load index were used as fixed factors. We abstained from using surface temperature as a predictor, as it heavily depended on several of our other fixed factors. To test for intercorrelations between fixed factors, Spearman rank correlations (r_s; $|r_s| > 0.05$) and Variance Inflation Factors (VIFs) were calculated. However, none of the variables were intercorrelated. Spearman rank correlations are found in the Supporting Information. Multicollinearity was also low (VIF = 1–1.3). We also centred and squared the fixed factors to test for non-linear relationships, but we could not detect any. Prior to the analysis, fixed factors were centred and standardized to allow direct comparison of their estimates. In order to increase model robustness and to identify the most important environmental parameters, we conducted model

TABLE 1 Overview of the sampled environmental parameters (mean ± SE) at the four different grassland types occupied by *Euphydryas aurinia*.

		Litter meadow		
Parameter	**Dry meadow**	**Mown**	**Alternating fallow**	**Abandoned**
Host plant cover (%)	13.1 ± 0.8	14.0 ± 1.0	10.5 ± 0.9	10.0 ± 1.0
Cover of litter (%)	**68.1 ± 1.6^{bc}**	**43.4 ± 2.8^{a}**	**62.5 ± 5.6^{b}**	**79.5 ± 1.6^{c}**
Elevation (m)	1063.2 ± 14.1	1091.6 ± 9.8	942.0 ± 4.0	965.1 ± 15.4
Sunshine duration (h)	8.4 ± 0.1	7.9 ± 0.1	7.6 ± 0.4	7.6 ± 0.5
Heat load index	**0.90 ± 0.05^{b}**	**0.89 ± 0.04^{a}**	**0.91 ± 0.01^{b}**	**0.91 ± 0.06^{b}**
Surface temperature (°C)	31.4 ± 0.6	31.8 ± 1.2	26.5 ± 0.9	29.4 ± 1.1

Note: Sample size: Dry meadow—$n = 29$; litter meadow: Mown—$n = 25$, alternating fallow—$n = 10$, abandoned—$n = 11$. Comparisons between grassland types were done by generalized linear mixed-effects models (GLMM) with Poisson (count data), proportional-binomial (percentage data) or gamma (interval-scaled data) error structure followed by Tukey contrasts for pairwise comparisons. 'Patch' served as a random factor. Different letters indicate significant differences between grassland types ($p \leq 0.05$). Statistics of GLMM: The bold values indicates the cover of litter, $p \leq 0.001$, Heat load index $p \leq 0.01$.

selection using the "dredge" function (R package MuMIn; Barton, 2023) followed by model averaging based on an information-theoretic approach (Burnham & Anderson, 2004; Grueber et al., 2011). Model averaging only included top-ranked models within ΔAIC_C <3 (Grueber et al., 2011).

RESULTS

Environmental conditions in the four grassland types

Environmental conditions clearly differed between the four studied grassland types (Table 1). Especially abandoned meadows but also dry meadows had a higher cover of litter than mown litter meadows. By contrast, litter meadows with alternating fallows had an intermediate position. Additionally, mown litter meadows had a lower heat load index than the three other grassland types. All other environmental parameters did not differ significantly between the grassland types. Overall, dry meadows were not only characterized by a relatively high cover of litter and heat load index but also by the highest sunshine duration, a high surface temperature at noon and a high host plant cover.

Survival of larval webs

Survival rate of larval webs was generally high. Larvae successfully emerged after diapause from 75 (94%) out of 80 marked hibernaculum webs. Three lost webs were located beneath cross-country ski trails, another web on a vole track and one had disappeared due to unknown reasons. Out of the remaining 75 webs, 70 (93%) were located at or close to *S. pratensis* and 5 (7%) at *G. acaulis*, which very likely represented the host plants used last before diapause. Most of these plants had survived winter with vital leaves remaining. This was true for 60 (86%) plants of *S. pratensis* and all 5 plants of *G. acaulis* (100%). Although some host plants had died, hibernaculum webs were mostly within a very close proximity to the next vital host plant with a mean (± SE) distance of 2.4 ± 0.7 cm. The maximum distance was 40 cm.

Larval phenology and development

Post-diapause larval development started on the 18th of February with the first 4th instar larvae beginning to feed in dry meadows and abandoned meadows. In mown litter meadows, first feeding larvae were observed on the 11th of March and in alternating fallows a day later, on the 12th of March. Larval development ended in mid-May with 6th instar larvae pupating (Table 2). However, larvae were seen outside their hibernaculum web basking even earlier but returned afterwards without feeding. After finishing diapause, larvae aggregated in large groups and basked before seeking host plants. The 4th instar larvae stayed gregariously either in one large group or split up into smaller groups until moulting to the 5th instar. Within groups, moulting to the 5th instar was largely synchronized and occurred aggregated in a loose web. On the 2nd of March, first 5th instar larvae were seen in dry meadows and abandoned meadows. Later, first moulting larvae in mown litter meadows were found on the 28th of March and in alternating fallows on the 5th of April. With the beginning of the 5th instar, no new webs were observed. Yet, larvae were often still feeding gregariously at the beginning of the 5th instar. Afterwards, as larvae searched for new host plants, 5th and 6th instar larvae dispersed solitarily. The 6th instar was first recorded in dry meadows on the 2nd of April, while larvae in abandoned meadows now took longer – up to the 9th of April. Interestingly, on the same day we also found the first 6th instar larvae in mown litter meadows. The last larvae freshly moulted to the 6th instar were found in alternating fallows on the 20th of April.

Overall, developmental time of post-diapause larvae varied strongly (Table 2). While 4th instar larvae were recorded up until the 29th of April, the first 6th instar larvae were found as early as the 2nd of April. Accordingly, in April, 4th, 5th and 6th instar larvae were

TABLE 2 Post-diapause larval phenology of *Euphydryas aurinia*.

	February			March						April						May			
Instar	IV	V	VI	I	II	III	IV	V	VI	I	II	III	IV	V	VI	I	II	III	IV
4																.	.	.	.
5	.	.	.	.														.	.
6	.	.	.	.	.	.	.	.											

Note: Each roman number is equal to the length of one sixth of the respective month. Grey = all instars occurred at the same time in specific patches.

recorded simultaneously within some of the patches. By the 9th of May, all detected larvae had reached the 6th instar and larval density strongly decreased due to larvae dispersing and pupating underneath litter or large leaves (e.g. *S. pratensis*). After the 18th of May, no larvae were observed any longer. Developmental time of post-diapause larvae to reach the 5th instar decreased the longer the sunshine duration, the higher the cover of litter and the higher the heat load index was (Figure 2, Table A1). By contrast, elevation and cover of host plants had no effect on developmental time.

The developmental time of post-diapause larvae to reach the 5th instar strongly differed between the four studied grassland types (Figure 3). In dry meadows, larvae reached the 5th instar in the mean in about 2 weeks (range: 10 to 25) after the end of the diapause and therefore earlier than in wet grasslands. Here, larval development often took twice as long (mown–range: 17 to 38; alternating fallow–range: 24 to 38; abandoned–range: 10 to 28).

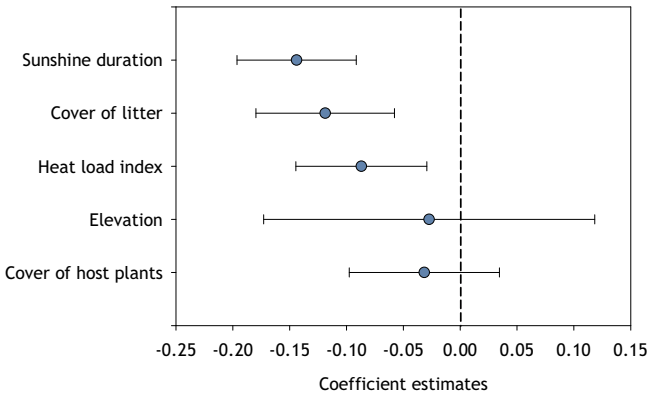

FIGURE 2 Standardized estimates (± 95% confidence intervals) of environmental predictors of the developmental time of post-diapause larvae of *E. aurinia* ($N = 75$) to reach the 5th instar (for details and GLMM statistics see Table A1). Confidence intervals of significant predictors ($p < 0.05$) do not cross x = 0. Parameters with a significant negative effect reduce the developmental time.

Effects of basking

The gregariously basking black 4th instar larvae were often found on dry leaves in the vicinity of their host plants. They were able to warm up much stronger than the upper side of the host plant leaves and the air temperature at 1 m height (Figure 4). In early April at noon, larvae bodies had a mean (± SE) temperature of 30.3 ± 1.1°C, exceeding leaf-surface temperatures (18.9 ± 1.0°C) by over 11°C and air temperature (8.3 ± 0.9°C) by more than 22°C.

Dispersal and feeding behaviour

From the 4th to 6th instar, the dispersal range of the larvae strongly increased (Figure 5). The 4th instar larvae mostly stayed within half a metre of their hibernaculum web and often returned to their host plant which had been used in the previous year. With the beginning of the solitary 5th instar, larvae moved much further. Larvae searched for host plants within a mean radius of about 3 m around their hibernaculum web. The 6th instar larvae were mostly found within a mean radius of more than 6 m around their hibernaculum web, while single individuals were even detected up to 50 m away from the next hibernaculum.

Succisa pratensis, the primary host plant, remained the main food source throughout the post-diapause larval development (Figure 6).

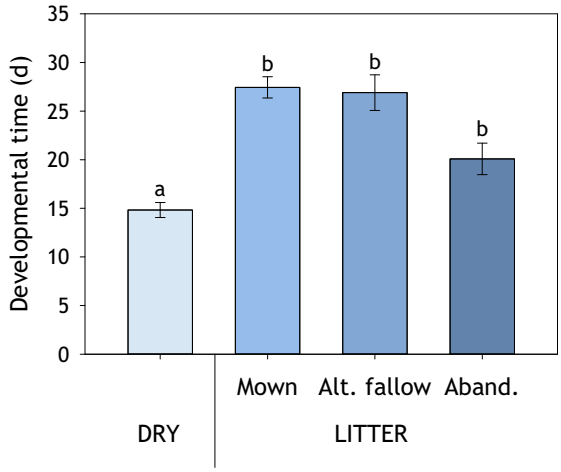

FIGURE 3 Mean (±SE) developmental time of post-diapause larvae until the 5th instar was reached at four different grassland types occupied by *Euphydryas aurinia*. Sample size: dry meadow—$n = 29$; litter meadow: mown—$n = 25$, alternating fallows (Alt. fallow)—$n = 10$, abandoned (Aband.)—$n = 11$. Comparisons between grassland types were done by generalized linear mixed-effects models (GLMM) with a Poisson error structure followed by Tukey contrasts for pairwise comparisons. 'Patch' served as a random factor. Different letters indicate significant differences between grassland types ($p \leq 0.05$).

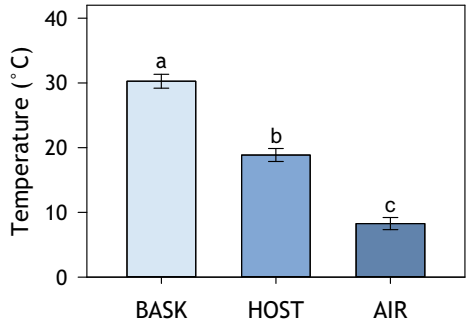

FIGURE 4 Mean temperature (±SE) of basking larvae (4th instar) of *Euphydryas aurinia* (BASK), the upper side of vital leaves of the host plant *S. pratensis* (HOST) and the air temperature (AIR) on a sunny day at 12 pm in early April (10/04/2021) (in each case $N = 15$). Differences between groups were analysed by ANOVA. Pairwise comparisons were done using a Tukey test. Different letters indicate significant differences between the groups ($p \leq 0.05$). Statistics of ANOVA: $^{***}p \leq 0.001$.

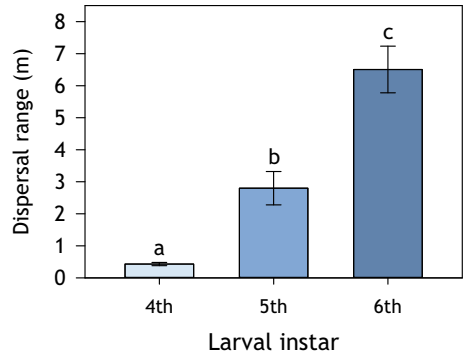

FIGURE 5 Dispersal range of 4th ($n = 43$), 5th ($n = 60$) and 6th ($n = 60$) instar larvae of *Euphydryas aurinia* from their hibernaculum web. Differences between groups were analysed by generalized linear mixed-effects models (GLMM) with a gamma error structure and Tukey's contrasts. Patch served as a random factor. Different letters indicate significant differences between the groups ($p \leq 0.05$).

However, all available plant species of the families Caprifoliaceae and Gentianaceae present on occupied patches were also observed to be consumed by the larvae. Larvae of the 4th and 5th instar predominantly fed on *S. pratensis* and rarely on early flowering *Gentiana* species (*Gentiana acaulis*, *G. clusii*, *G. verna*) and *Scabiosa lucida*. The gregarious 4th instar larvae even completely defoliated their host plants. When in the second half of April the vegetation began to grow, host plant abundance and biomass strongly increased. *Succisa pratensis*, *Sc. lucida* and *Valeriana dioica* rapidly increased biomass, and *Gentiana* species as well as *V. dioica* started to grow floral buds and inflorescences. At that time, most larvae reached the 5th and 6th instar. Both instars were often recorded feeding on leaf buds in the centre of the rosettes of *S. pratensis* and *Sc. lucida*. Interestingly, 5th and 6th instar larvae also started to feed exclusively on reproductive parts of *Gentiana* species while avoiding their leaves. By contrast, 6th instar larvae consumed all parts of *V. dioica* plants. Overall, the spectrum of consumed host plants of the 6th instar larvae strongly reflected the availability of host plant species on the patches.

DISCUSSION

Our study in montane grasslands in the Bavarian Alps revealed that after diapause, *E. aurinia* larvae exhibited a strong variability in developmental time as well as pronounced differences in the dispersal and feeding behaviour between the three instars. Developmental time of post-diapause larvae to reach the 5th instar decreased the longer the sunshine duration from January to March, the higher the cover of litter and the higher the heat load index was. In dry meadows, larvae reached the 5th instar in about two weeks after finishing diapause, which was in some cases almost two weeks earlier than in litter meadows. In contrast to the tiny 4th instar larvae, which stayed close to their hibernaculum web and primarily fed on *S. pratensis* leaves that had persisted through winter,

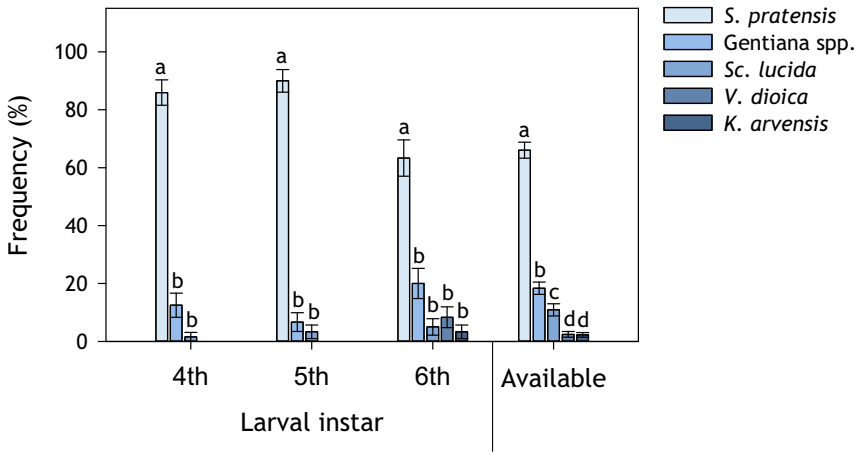

FIGURE 6 Frequency in host plant use of 4th ($n = 43$), 5th ($n = 60$) and 6th ($n = 60$) instar larvae of *Euphydryas aurinia* and the proportion of available host plants in mid-April. Differences between groups were analysed by generalized linear mixed-effects models (GLMM) with a proportional-binomial error structure and Tukey's contrasts. Patch served as a random factor. Different letters indicate significant differences between the groups ($p \leq 0.05$).

larger 5th and 6th instar larvae increasingly dispersed and diversified their feeding behaviour.

Drivers of larval developmental time

There is large evidence that warmer microhabitats increase development rate and larval survival of *E. aurinia* and closely related species, in particular at higher elevations (Curtis & Isaac, 2015; Franzén et al., 2022; Johansson et al., 2024; Porter, 1982; Weiss et al., 1988). All three sampled predictors of larval developmental time that were closely related to the microclimate had an impact on larval developmental time.

The most important predictor of larval developmental time was sunshine duration, which is a mesoclimatic parameter. In our study area, particularly shading through mountain peaks and hills but also trees limited sunshine duration, which resulted in slower warming up and longer periods of snow cover (own observation; see also Stoutjesdijk & Barkman, 2014).

The cover of the litter layer was the second most important predictor. On sunny days, litter warms up much faster than living green plant material or constantly moist soil surfaces (Porter, 1982; Stoutjesdijk & Barkman, 2014; WallisDeVries, 2006). Moreover, a thick litter layer with a heterogeneous surface may regularly provide some spots that are sheltered from wind (own observation), which additionally favours heating (Stoutjesdijk & Barkman, 2014). In line with this, basking larvae were mainly observed on dry litter in the vicinity of their host plants, but not on vital parts of the host plants themselves. For an optimal metabolic rate, feeding larvae require a body temperature of about 30 to 35°C (Porter, 1982). Due to their basking strategy and black colour, this threshold was effectively reached by the larvae despite low ambient temperature. In early April at noon, the larvae had a temperature of more than 30°C, which was exceeding leaf-surface temperatures by over 11°C and air temperature by more than 22°C.

The third important parameter was the heat load index. Similar to litter, a higher heat load index facilitates a warmer microclimate based on the amount of sunshine the patch is exposed to (McCune & Keon, 2002). By choosing south-facing edges (high heat load index) Johansson et al. (2024) found females of *E. aurinia* to choose warmer microclimates for oviposition, which is reflected by the overall high values for the heat load index (means ≥0.89) in our study. Consequently, it is very likely that differences in the heat load index also affect the developmental time of the larvae of the butterfly. Furthermore, we assume that particularly the strong relief, but also wind shelter effects (south-facing mound or pit slopes, Figure 1a; trees at the northern margins of grasslands, Figure 1c) and general differences in slope had a strong effect on surface temperature and therefore played an important role in within-patch or within-hibernaculum variation of larval development in the 5th and 6th instar.

Regarding grassland types, dry meadows were characterized by a unique combination of relatively high litter cover and the highest sunshine duration, which have been proven in our study to foster larval developmental time. By contrast, in the three types of litter meadows, which were often located in depressions (own observation), in each case, at most one of the predictors of larval developmental time reached high figures. In abandoned meadows and those with alternating fallows, this was true for litter cover. Consequently, in dry meadows, larvae reached the 5th instar in about 2 weeks after the end of the diapause, which was in some cases almost 2 weeks earlier than in each of the three types of litter meadows.

Larval phenology

Interestingly, although diapause duration differed drastically, larvae emerged from nearly all hibernaculum webs and commenced feeding. Compared to other studies, the survival rate we encountered was very high, especially compared to captive breeding (Johansson et al., 2024; Klapwijk & Lewis, 2014). Reasons can probably be found in the prolonged snow cover, which is hard to imitate in captive breeding and in the overall low temperatures, reducing the chances of interruptions during diapause (Stuhldreher & Fartmann, 2014). However, larval survival rate after emergence was not recorded.

Due to the high environmental heterogeneity in the studied montane grasslands, which resulted in strong meso- and microclimatic differences (see above), phenology of post-diapause larvae varied strongly across the grassland types (see above) and microhabitats. For example, in April, 4th, 5th and 6th instar larvae were recorded simultaneously within some of the studied patches. In late spring and early summer, in the Bavarian Alps and pre-Alps, females of *E. aurinia* prefer to oviposit on host plants that grow under warm microclimatic conditions (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003; Scherer & Fartmann, 2022). However, as our study showed, meso- and microclimatic conditions can highly vary within these microhabitats in late winter and early spring resulting in strong differences in the duration of diapause and the developmental time of larvae of the same instar.

From late winter until the flight season of *E. aurinia*, the climate in the study area is often characterized by low temperatures (often below zero degrees), reoccurring periods of snow and, particularly in spring and early summer, periods of excessive rainfall (see Section 2.2). Females of *E. aurinia* do not only prefer to oviposit on host plants that grow under warm microclimatic conditions, but also prefer large host plants (Anthes, Fartmann, & Hermann, 2003; Anthes, Fartmann, Hermann, & Kaule, 2003; Scherer & Fartmann, 2022). Yet, the expression of these preconditions is strongly dependent on the characteristics of the occupied habitat (i.e. dry vs. wet grasslands). Consequently, the large environmental gradient females chose for reproduction in the study area could just be a result of stochastics, due to which microhabitats are available in the respective patches. However, occupying different habitats in close proximity might enable *E. aurinia* to cope with the harsh climatic conditions. Combined with the metapopulation structure *E. aurinia* exhibits generally and in the study area (Junker et al., 2023; Scherer & Fartmann, 2022; Tájek et al., 2023), this behaviour may ensure that larval, but possibly also adult populations later

on due to an extended flight period, can survive extreme weather events (for the closely related *Euphydryas editha* (Boisduval, 1852) see also Weiss et al., 1987, 1988, 1993) and host plant shortages (Rytteri et al., 2021). In times of climate change, this incident might become more and more important (Johansson et al., 2020; WallisDeVries & van Swaay, 2006). Moreover, the protracted phenology of the different instars could also play a crucial role in avoiding losses by specialized parasitoids like braconid wasps (Braconidae). Klapwijk et al. (2010) observed that parasitism is less effective when emerging post-diapause braconid wasps are heavily desynchronized with the larvae of their host *E. aurinia*.

We observed that prolonged snow cover and shaded post-diapause habitats can substantially delay larval development in our study area. At the northern range limit of *E. aurinia*, as well as in other related species, larvae have been shown to prolong development by adding an extra larval instar (Eliasson & Shaw, 2003; Saastamoinen et al., 2013; Ravenscroft, 2021). Specifically, *E. aurinia* larvae were found to re-enter diapause after moulting to the 6th instar when development was delayed and to complete a 7th instar in the following spring (Ravenscroft, 2021). In contrast, *Melitaea cinxia* (Linnaeus, 1758) was observed to undergo an 8th instar (typically seven) within the same spring, thereby prolonging its flight period (Saastamoinen et al., 2013). Interestingly, despite extensive searches conducted between February and May, we did not observe similar developmental plasticity in our studied population, although it appeared plausible based on environmental conditions. This may reflect strong differences in the expression of development-related genes compared to populations inhabiting colder regions (Saastamoinen et al., 2013). The genetic basis of these differences requires further investigation, particularly incorporating populations that do not experience prolonged snow cover (WallisDeVries & van Swaay, 2006). In our case, larvae with delayed development appeared to partially catch up in May, potentially at the cost of reduced body mass and fitness, in order to avoid a substantial delay in flight period. Nonetheless, this hypothesis requires further investigation.

Dispersal and feeding behaviour

Gregariously feeding butterfly species, like *E. aurinia*, require a high host plant biomass during their development (Scherer & Fartmann, 2022). To avoid food shortage, *E. aurinia* larvae diapaused close to their perennial host plants, predominantly *S. pratensis*, providing vital leaves even when larvae complete diapause in February. However, after the first host plant was quickly defoliated by the larvae, they started to search for new plants. The 4th instar larvae are relatively immobile due to their small size (Weiss & Murphy, 1988). However, due to the former snow cover, dead and vital vegetation was flattened (own observation), favouring their dispersal.

Due to rising temperatures and larger bodies, which are able to absorb more solar radiation, the need for gregarious basking diminished in the 5th instar. As a consequence, these larvae started dispersing solitarily and further away from their former hibernaculum web, even though it was mostly located in areas rich in host plants. Consequently, separation across larger spatial scales by 5th and 6th instar larvae is mainly considered a strategy to decrease losses by predators and parasitoids (Stefanescu et al., 2009). In contrast to 4th instar larvae that defoliated host plants completely, 5th instar larvae were recorded feeding more selectively, yet still focusing on *S. pratensis*. Interestingly, larvae fed on single leaves or distinct plant parts, like leaf buds and inflorescences, before leaving the host plant for resting, basking or dispersal.

This pattern was even more pronounced in the 6th instar. In contrast to most other populations of *E. aurinia* in Western, Central and Northern Europe and in contrast to laboratory experiments (Meister et al., 2015; Pschera & Warren, 2018; Thoss, 2004), we regularly observed 6th instar larvae feeding on various different host plant species besides *S. pratensis*. Moreover, feeding of 5th and 6th instar larvae was no longer restricted to host plant leaves. We often detected larvae using leaf buds (*S. pratensis*, *Sc. lucida*), exclusively reproductive parts (*Gentiana* species) or the entire plant (*V. dioica*) as a food source. The selection of nutrient-rich plant parts like leaf buds and inflorescences has been shown to increase growth rates and fitness in butterflies (Burghardt & Fiedler, 1996; Smallegange et al., 2007). Furthermore, diversifying the diet also enhances fitness during periods of limited resources (Arriens et al., 2021; Bernays & Chapman, 1994). According to Arriens et al. (2021), the diet in the post-diapause larvae of the related *Euphydryas phaeton* (Drury, 1773) is more driven by food availability than by preferences for certain species. This is in line with our study, since the available and used host plants of the families Gentianaceae and Caprifoliaceae were quite similar.

Limitations

The main limitation of this study was its short sampling period of just one year. In particular, weather variability could reduce the comparability of our results. Between February and May in spring 2021, the weather was rather cold. The mean temperature was 3.8°C (± 0.5 SE) compared to the mean temperature of the period between 2011 and 2021 of 4.7°C (± 0.3°C SE; range: 3.0–7.5°C) (German Weather Service, 2021). Though the snow cover of 6.3 cm (± 1.0 SE) in 2021 was slightly below the mean height of 10.2 cm (± 3.1 SE; range: 1.7–47.9 cm) in the period between 2011 and 2021 (German Weather Service, 2021). However, as no prolonged periods of extreme weather occurred and all of our predictors were weather independent, our models should be robust. Furthermore, we did not investigate population trends and only sampled a fixed amount of hibernaculum webs with a standardized sampling design. Therefore, we think that our results are well comparable. Yet, the spatial limitation to one region must also be taken into account, especially when comparing to lowland populations of the focal species.

Hence, we sampled mobile larvae inside fixed transects; a further limitation of our study could be found in an underestimation of the actual dispersal range of 5th and 6th instar larvae of *E. aurinia*. If

larvae left our plots, they were not sampled. Accordingly, older larvae might even be more mobile.

Conclusions

To sum up, developmental time of post-diapause larvae to reach the 5th instar in montane grasslands in the Bavarian Alps was driven by (i) meso- (sunshine duration) and (ii) microclimate (heat load index, cover of litter). The high habitat heterogeneity in the grasslands has led to strong differences in meso- and microclimatic conditions and thus in the phenology of post-diapause larvae across the grassland types and microhabitats. In dry meadows, the unique combination of a high sunshine duration, relatively high litter cover and a high heat load index explained why the time to reach the 5th instar was much shorter than in the three types of litter meadows. We hypothesize that occupying such a large environmental gradient, resulting in a protracted phenology of the different instars, helps *E. aurinia* to cope with the harsh climatic conditions in the study area and losses by specialized parasitoids like braconid wasps. Due to rising temperatures and larger bodies, which are able to absorb more solar radiation, the need for gregarious basking diminished from the 5th instar onwards. As a consequence, larvae started dispersing solitarily and further away from their former hibernaculum web, even though it was mostly located in areas rich in host plants. This could be a further strategy to avoid losses by predators and parasitoids. Throughout the post-diapause larval development, *S. pratensis* remained the main food source. However, from the 5th instar onwards, larvae started to feed not only on leaves but also on leaf buds or reproductive plant parts. Finally, 6th instar larvae fed on all available species of the families of Gentianaceae and Caprifoliaceae in the studied grasslands.

AUTHOR CONTRIBUTIONS

Gwydion Scherer: Conceptualization; investigation; funding acquisition; writing – original draft; data curation; formal analysis; methodology; validation; visualization; software; project administration. **Thomas Fartmann:** Conceptualization; funding acquisition; writing – review and editing; supervision; resources; methodology; validation; project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at https://doi.org/10.26249/FK2/XMQOUV (Scherer & Fartmann, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supplementary Table S1. Overview of the study plots and the proportion of four grassland types occupied by *Euphydryas aurinia*. Host plant species are abbreviated as follows: *Succisa pratensis* = SP, *Gentiana* spp. = GS, *Scabiosa lucida* = SL, *Valeriana dioica* = VD, *Knautia arvensis* = KA.

Supplementary Table S2. Statistics of the Spearman rank correlations between the environmental parameters used in the GLMMs. n.s. not significant, $^{*}p < 0.05$, $^{**}p < 0.01$.

Supplementary Table S3. Proportion of host plant species used by different larval instars of *E. aurinia* in the four sampled grassland types.

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APPENDIX A

TABLE A1 Statistics of the negative binomial GLMM (model averaging): Environmental predictors of the developmental time of post-diapause larvae of *E. aurinia* ($N = 75$) to reach the 5th instar.

Parameter	Estimate	SE	Z	*p*
Intercept	3.01	0.09	30.56	**0.001**
Sunshine duration[a]	−0.14	0.02	5.38	**0.001**
Cover of litter	−0.12	0.03	3.82	**0.001**
Heat load index[b]	−0.08	0.03	2.96	**0.003**
Cover of host plants	−0.03	0.07	0.37	0.349
Elevation	0.05	0.03	1.46	0.713

Note: Range of marginal and conditional R^2 values across all top-ranked models selected via model averaging (ΔAICC <3): R^2GLMMm = 0.30–0.32, R^2GLMMc = 0.71–0.73. Bold = significant difference.

[a]Mean of hours of potential daily sunshine for January, February and March measured with a horizontoscope (Scherer & Fartmann, 2022).

[b]Conversion of aspect, slope and latitude to the heat load index according to McCune and Keon (2002) and McCune (2007).