Received: 24 March 2023 | Accepted: 11 September 2023
DOI: 10.1111/icad.12692

ORIGINAL ARTICLE

Insect Conservation and Diversity
Royal Entomological Society

Caterpillar loss through grassland harvest differs between two related butterfly species of conservation concern

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Funding information
Studienstiftung des Deutschen Volkes

Editor: Alan John Stewart and Associate Editor: Róbert Gallé

Abstract

1. Temperate, semi-natural grasslands emerged from traditional land use and are recognised for their outstanding biodiversity. However, these grasslands severely declined due to agricultural industrialisation. Accordingly, specialised species of nutrient-poor grasslands like the closely related butterflies Nickerls Fritillary *Melitaea aurelia* Nickerl, 1850 and Marsh Fritillary *Euphydyras aurinia* (Rottemburg, 1775) (Lepidoptera: Nymphalidae) have experienced strong declines in the last century due to grassland loss and deterioration. Here, we studied for the first time the effects of the complete harvest process in grasslands from mowing until the removal of the cut vegetation on the survival of their caterpillars.
2. To assess survival rates, we sampled larvae of both species and environmental conditions before and after the harvest process and analysed the results using generalised linear mixed-effects models.
3. Our study revealed that the harvest process in grasslands mown once by bar mowers resulted in substantial caterpillar loss influenced by (i) growth form of the host plants and (ii) timing of grassland harvest. Accordingly, the host plant of *E. aurinia*, *Succisa prantensis*, lost nearly half of its leaves during the harvest process, while late harvesting was especially harmful for caterpillars already commencing hibernation. Overall, *E. aurinia* had higher losses compared with *M. aurelia*, and these were most severe in late-mown moist meadows.
4. To increase the survival rate of *E. aurinia*, we recommend mowing before the beginning of hibernation using bar mowers. Complementary, or if mowing is done later, at least 20% of the meadow should be left as an untouched refuge in a spatially rotating manner.

KEYWORDS
biodiversity conservation, EU habitats directive, *Euphydryas aurinia*, *Melitaea aurelia*, mowing management, nutrient-poor grassland

INTRODUCTION

Temperate, semi-natural grasslands are among the most species-rich ecosystems on earth (Bonari et al., 2017; Feurdean et al., 2018). Throughout Europe, these grasslands are the outcome of centuries of traditional land use (Fartmann, 2023; Pärtel et al., 2005). However, due to the transition from pre-industrial farming to modern-day agriculture, particularly after World War II, the extent of semi-natural grasslands has greatly decreased. Nowadays, the remaining species-rich grasslands often suffer from habitat deterioration because of inappropriate management (Fartmann et al., 2021; Fumy et al., 2021; Poniatowski et al., 2018). Due to their significance for biodiversity conservation and high threat status, many of these grasslands are legally protected by the EU Habitats Directive (EC, 2007). To elucidate their value for biodiversity conservation, three fifths of the 436 native European butterfly species use dry calcareous grasslands and steppes as one of their main habitats (van Swaay et al., 2006).

Most European butterfly species exhibit highly specific habitat requirements (Scherer et al., 2021; Schwarz & Fartmann, 2021; Stefanescu et al., 2009). This is also true for grassland butterflies, which have strongly declined across Europe due to habitat loss and deterioration (Warren et al., 2021). To fulfil the high demands of specialised grassland butterflies, different management practices have been implemented to maintain their habitats and to prevent further losses (Goffart et al., 2014; Helbing et al., 2015; Schtickzelle et al., 2005). However, for many grassland butterfly species of conservation concern, our knowledge on the most suitable management techniques to foster their populations is still insufficient (Anthes & Nummer, 2006; Ghesini et al., 2018; Severns, 2011).

Nickerls Fritillary (*Melitaea aurelia*; Nickerl, 1850) and Marsh Fritillary (*Euphydyras aurinia*; Rottemburg, 1775) are closely related nymphalid butterfly species and specialised in nutrient-poor grassland habitats. They occur in nutrient-poor grasslands, in particular semi-dry calcareous grasslands, and *E. aurinia* can also be found in moist grasslands (Anthes, Fartmann, Hermann, & Kaule, 2003; Eichel & Fartmann, 2008; Konvicka et al., 2023; Scherer & Fartmann, 2022). The females of both species attach their egg batches to the underside of the host plants' leaves and prefer luxuriant plants for oviposition. After hatching, larvae form a silken web and feed gregariously on the leaves of their host plant. Mostly in September, caterpillars build a hibernaculum web where they overwinter in the fourth instar. However, growth forms of the main host plants of the two butterfly species differ and may result in a different sensitivity to grassland management. Hoary Plantain (*Plantago media*), the most important host plant of *M. aurelia* (Eichel & Fartmann, 2008), is a low-growing herb with a basal rosette (Grime et al., 2007). By contrast, Devil's-bit Scabious (*Succisa pratensis*), the primary host plant of *E. aurinia* (Anthes, Fartmann, Hermann, & Kaule, 2003; Eichel & Fartmann, 2008; Scherer & Fartmann, 2022), is much taller and has larger leaves (Grime et al., 2007). During the last century, both fritillary species have experienced strong declines due to grassland loss and deterioration (Anthes, Fartmann, & Hermann, 2003; Bräu et al., 2013; Brunbjerg et al., 2017; Fartmann et al., 2021; Fox et al., 2006). As a result, they are now considered endangered in the German Federal State of Bavaria (Voith et al., 2016). Additionally, *E. aurinia* is protected by the EU Habitats Directive (EC, 2007). To counteract the ongoing losses, both extensive mowing and grazing are used for conservation management (Bamann & Dittrich, 2017; Goffart et al., 2014; Smee et al., 2011). However, despite their threat status, there are still large knowledge gaps regarding the most favourable grassland management for *M. aurelia* and *E. aurinia* (Anthes & Nummer, 2006; Eichel & Fartmann, 2008).

For *M. aurelia*, there are no empiric data on the effects of grassland harvest on caterpillars at all. By contrast, for *E. aurinia*, in moist grasslands, there are observations that at least direct losses of larvae through cutting are low (Bamann & Dittrich, 2017; Bräu & Nummer, 2003). Here, we studied for the first time the effects of the complete harvest process in nutrient-poor grasslands from mowing until the removal of the cut vegetation on the survival of caterpillars of both endangered fritillary species. The study area, the Niederwerdenfelser Land in Upper Bavaria (southern Germany), comprises a mosaic of different grassland types rich in biodiversity. Our study was conducted in the two main habitats of the species: semi-dry calcareous and moist grasslands. In particular, we addressed the following research questions:

(i) Did the survival rates differ between the two fritillary species?

(ii) Did growth form of the host plant and timing of mowing affect survival rates?

(iii) What are the implications for the conservation of the endangered species?

MATERIALS AND METHODS

Study species

Nickerl's Fritillary (*M. aurelia*) and Marsh Fritillary (*Euphydryas aurinia*) are closely related nymphalid butterflies of the Palaearctic (Anthes, Fartmann, Hermann, & Kaule, 2003; Bräu et al., 2013; Eichel & Fartmann, 2008; Scherer & Fartmann, 2022). Both species are univoltine, colonise nutrient-poor grasslands, locally exhibit a high host-plant specificity and form metapopulations (Anthes, Fartmann, Hermann, & Kaule, 2003; Eichel & Fartmann, 2008; Ghidotti et al., 2018; Hula et al., 2004). The females attach their eggs as batches of 50–400 eggs to the underside of the host plants' leaves and prefer luxuriant plants for oviposition (Anthes, Fartmann, Hermann, & Kaule, 2003; Bräu et al., 2013; Eichel & Fartmann, 2008; Scherer & Fartmann, 2022). After hatching, larvae form a silken web and feed gregariously on the leaves of the host plant. The larval web protects the caterpillars to some extent against bad weather and invertebrate enemies. Mostly in September, caterpillars build a hibernaculum web where they moult and overwinter in the fourth instar. If a web is destroyed prior to hibernation (e.g., by mowing), the surviving pre-diapause larvae try to reconstruct the web on their former host plant or to build a new web on a suitable host plant in the vicinity. In spring, after hibernation, larvae resume foraging until they pupate in May.

M. aurelia has a smaller distribution range compared with *E. aurinia*. It occurs from Central Europe (eastern France) up to Central Asia (Bräu et al., 2013). In Central Europe, adults are on the wing from the beginning of June until the end of July (Bräu et al., 2013; Eichel & Fartmann, 2008). Here, *M. aurelia* mainly colonises semi-dry calcareous grasslands with Hoary Plantain (*P. media*) as the main host plant. *P. media* is a low-growing herb with a basal rosette (Grime et al., 2007). Prior to hibernation, third-instar larvae already start to feed in small groups or even solitarily and hibernate in the litter layer (own observation).

The range of *E. aurinia* extends from the British Isles to eastern Asia (Bräu et al., 2013). In Central Europe, adults are on the wing from mid-May to the beginning of July (Anthes, Fartmann, Hermann, & Kaule, 2003; Bräu et al., 2013; Scherer & Fartmann, 2022). Here, *E. aurinia* occurs mainly in two grassland types: (i) moist grasslands with Devil's-bit Scabious (*S. pratensis*) as the primary host plant and (ii) semi-dry calcareous grasslands with *S. pratensis*, Small Scabious (*Scabiosa columbaria*) or Shining Scabious (*Scabiosa lucida*) as the main host plants (Anthes, Fartmann, Hermann, & Kaule, 2003; Botham et al., 2010; Scherer & Fartmann, 2022). A peculiarity of our study area is that *E. aurinia* occurs in both mentioned grassland types and predominantly utilises *S. pratensis*, although *S. lucida* is equally available in calcareous grasslands (Scherer & Fartmann, 2022). *S. pratensis* is a semi-rosette herb with large leaves and tall flowering stems (up to 1 m height) (Grime et al., 2007). Larvae of *E. aurinia* feed gregariously prior to hibernation and in spring, directly after diapause. Afterwards, with the beginning of the fifth instar, larvae begin to live solitarily (Anthes, Fartmann, Hermann, & Kaule, 2003; Bräu et al., 2013; Scherer & Fartmann, 2022). The hibernaculum web is formed mostly between the leaves of the host plant and adjacent dead and vital plant material a few centimetres above the ground. When caterpillars are affected by the harvest process (e.g., displacement through cutting or raking), they try to regroup and either repair their former web or construct a new one. In contrast to earlier instars, displaced hibernating caterpillars are less mobile and rebuild hibernaculum webs regardless of the proximity to their former host plant and whether the web is located within the cut material or not (own observation).

Study area

The study area, the Niederwerdenfelser Land, covers about 52 km^2 and is located at the Northern Limestone Alps in Upper Bavaria (Germany), 100 km south of Munich (47°26′ N, 11°10′ E and 47°30′ N, 11°17′ E). The study sites are located at 800–1250 m a.s.l. Due to the elevation and its location in the Northern Limestone Alps, which are affected by orographic rainfall, the climate in the study area is cold and wet with a mean precipitation of 1437 mm and an annual mean temperature of 6.7°C (long-term mean: 1961–1990, DWD, 2022).

The study area is located in one of the 30 German biodiversity hotspots (Ackermann & Sachteleben, 2012) and comprises the main distribution area of the hummocky meadows in Central Europe (extent: ~450 ha). Hummocky meadows (called 'Buckelwiesen' in Germany) are pre-alpine calcareous grasslands with a geomorphological uniquity—a microrelief consisting of regular pits and mounds creating a variety of different microhabitats (Gutser & Kuhn, 1998). Due to their pronounced microrelief as well as the dry and nutrient-poor soils, land-use intensity was always very low, dating back at least to 1406 (Gutser & Kuhn, 1998). However, during the last century, many patches have been improved (flattened and fertilised), afforested or abandoned. As a result, 95% of the former hummocky meadows have been lost (Gutser & Kuhn, 1998). The remaining hummocky meadows are scattered inside a diverse matrix of different biotopes and are still mostly well connected. Still today, they are mown annually in summer (July/August) for hay making. Historically, scythes were used for mowing. Now, however, manually operated bar mowers prevail. For simplification, we refer to hummocky meadows hereafter as dry meadows.

Litter meadows with *S. pratensis* are the second important habitat of *E. aurinia* within the study area. Litter meadows (hereinafter referred to as moist meadows) are nutrient-poor, periodically moist grasslands mown in autumn to obtain bedding for livestock (Anthes, Fartmann, & Hermann, 2003; Schwarz & Fartmann, 2021). Due to conservation law, moist meadows are mown in September. However, 20% of each patch is left untouched each year to secure successful development of species hibernating in the vegetation. Within the last century, agricultural improvement, afforestation and abandonment have also caused a severe loss of moist meadows in the study area (Gutser & Kuhn, 1998). Nevertheless, their decline was less dramatic than that described for dry meadows. Both meadow types are protected by the EU Habitats Directive (semi-natural dry grasslands [code 6210] and *Molinia* meadows [6410], respectively) (EC, 2007). In the study area, the complete harvest process within the grasslands follows the guidelines of the Bavarian conservation authorities.

Study design

Patch selection

We assessed the effects of mowing on the survival of caterpillars of *M. aurelia* and *E. aurinia* in annually mown meadows in 2020. For both fritillaries, we randomly selected meadow patches where the respective species and its host plant were present (patch-occupancy data: Scherer & Fartmann, 2022; own observation). Each grassland patch had to be characterised by a uniform type of land use. For *M. aurelia* and *E. aurinia*, 11 patches of dry meadows each were chosen. Since *E. aurinia* also occurs in moist meadows in our study area, additionally, five patches of this grassland type were selected. All studied patches were part of a Special Protection Area (SPA) of the EU Habitats Directive (EC, 2007). The size of the studied patches varied from 0.3 to 3.6 ha. Since patches were spatially clustered, we assigned them to four distinct subareas (cf. Scherer & Fartmann, 2022). In dry meadows, mowing took place within periods of sunny weather between July and August using manually operated bar mowers. Moist meadows were mown in the first half of September using tractor-operated bar mowers. However, 20% of each patch of moist meadows remained unmown (cf. Section 2.2). The mowing material was tedded, manually in dry meadows and using a tractor-operated tedder in moist meadows, respectively, and dried for 1 or 2 days. Afterwards, it was collected—in dry meadows through raking and in moist meadows mechanically using cutter wagons. In the following, the whole process from cutting up to the collection of the mowing material is referred to as the harvesting process.

Sampling design

Sampling of larval webs started 1 week prior to the date of mowing predefined by the land owners. For all patches, we conducted standardised sinusoidal transect walks with a loop distance of 5 m to search for larval webs. Overall, transect length was determined by patch size. For each web, the number of larvae was counted by steps of 10. Therefore, webs were partially opened with forceps to reduce the likelihood of larvae falling out of their webs. All samples were geotagged and marked with magnets in order to be retrievable via a metal detector. Additionally, we recorded the position height of the larval web, the larval instar inside the web and the number of leaves of the occupied host plant. Within a radius of 50 cm around the focal host plant, we measured the cover of all potential host plants. Accordingly, for *M. aurelia*, we recorded the cover of *P. media* and Ribwort (*Plantago lanceolata*) (Bräu et al., 2013; Eichel & Fartmann, 2008), and for *E. aurinia*, we recorded the cover of *S. lucida*, *S. pratensis*, Field Scabious (*Knautia arvensis*) and Gentian (*Gentiana* spp.) (Anthes & Nummer, 2006; Bräu et al., 2013). However, the two main host plants (*P. media* and *S. pratensis*) were by far the most abundant host-plant species within the studied patches (own observation). If mowing was postponed due to adverse weather, we revisited the webs and rerecorded all parameters 1 week before the next target date.

For each patch, we documented mowing date and measured mowing height. Because patches were characterised by a pronounced relief, we measured mowing height at three randomly chosen plots within the patch and averaged the values.

After mowing, we estimated the percentage loss of leaves through mowing for each of the host plants previously occupied by a larval web. The survival rate of the larvae was assessed 1 day after the end of the harvesting process to allow larvae to return or construct a new web. For each web, we counted the number of larvae using the same methods as described before. If webs were severely damaged or no larvae were found, we searched the whole area around the focal host plant within a radius of 2 m for larvae and new webs. If still no larvae were found, the search was repeated 1 week later to further allow larvae to reconstruct their webs.

Statistical analysis

All statistics were performed using R 4.0.3 (R Development Core Team, 2020). Altogether, we defined three treatments: (i) *M. aurelia*—dry meadow, (ii) *E. aurinia*—dry meadow, and (iii) *E. aurinia*—moist meadow. To identify significant differences between the three treatments, we conducted generalised linear mixed-effects models (GLMMs) with a Poisson (date of mowing) or gamma (height of mowing) error structure. For percentage data (cover of host plants and loss of leaves), we used proportional binomial GLMMs. The GLMMs were followed by Tukey contrasts for pairwise comparisons (glht function, R package multcomp; Hothorn et al., 2020). Regarding mowing and host-plant characteristics, we tested the parameters' date of mowing (measured from the 1st of July) and height of mowing on patch level and cover of the host plants and loss of leaves on host-plant level. Furthermore, we separately tested the height of larval webs and survival of larvae. In order to reduce overdispersion within the binomial GLMMs, observation-level random effects were added as a random factor (Harrison, 2014, 2015). To account for possible spatial autocorrelation, 'subarea' and 'patch' nested in subarea were also considered as random effects.

To assess the effects of environmental conditions on the survival of larvae, we fitted multivariable proportional binomial GLMMs for each of the three treatments. Survival of larvae served as a response variable and date of mowing, height of mowing, cover of host plants and loss of leaves served as predictors. To avoid model overfitting, we checked all predictors for intercorrelations using Spearman's rank correlation (r_S) and calculated variance inflation factors (VIFs). However, none of the parameters were intercorrelated ($|r_S| > 0.6$). To identify the most important predictors, model averaging based on an information-theoretic approach using the 'dredge' function (R package MuMIn; Barton, 2020) was conducted (Burnham & Anderson, 2004; Grueber et al., 2011). Only the top-ranked models within $\Delta AIC_C < 3$ were included (Grueber et al., 2011; Schirmel et al., 2016). To cope with overdispersion, we added observation-level random effects to increase model robustness (Harrison, 2014, 2015). Since these random effects inflate conditional R^2 despite having little ecological importance, we only displayed marginal R^2 in our models (Harrison, 2014; Nakagawa et al., 2017). 'Subarea' and 'patch' nested in subarea served again as random effects.

RESULTS

Environmental conditions

Date but not height of mowing differed between the dry and moist meadows (Table 1). Mowing occurred about 5 weeks earlier in dry than in moist meadows. In dry meadows, mowing on average took place on 4th August for *M. aurelia* and on 5th August for *E. aurinia*. By contrast, in moist meadows, the mean mowing date was 10th September. Cutting was conducted close to the soil surface. Mean mowing height ranged from 3.3 to 3.7 cm in the studied meadows.

Both the cover of further potential host plants around the occupied host plant and the loss of host-plant leaves through mowing differed between the *M. aurelia* treatment and the two treatments of *E. aurinia* (Table 1). In the vicinity of host plants occupied by larvae of *M. aurelia* in dry meadows, only slightly more than a tenth was covered by further potential host plants. By contrast, in the surrounding of host plants occupied by larval webs of *E. aurinia*, potential host plants covered on average more than a quarter (dry meadows) and nearly one third (moist meadows) of the area, respectively. The loss of host-plant leaves through mowing in the *M. aurelia* treatment was half as high as in the two *E. aurinia* treatments. For *M. aurelia*, *P. media* host plants lost on average 21% of the leaves, whereas for *E. aurinia*, on average 41% of the leaves disappeared.

TABLE 1 Mowing and host-plant characteristics of the three treatments.

	Melitaea aurelia		*Euphydryas aurinia*				
	Dry meadow		Dry meadow		Moist meadow		
Parameter	**Mean (±SE)**	**Min.–max.**	**Mean (±SE)**	**Min.–max.**	**Mean (±SE)**	**Min.–max.**	***p***
Patch level							
Date of mowing (days since 1st July)	35.6 ± 2.2^{a}	(9–68)	34.9 ± 2.7^{a}	(9–68)	71.8 ± 1.3^{b}	(57–81)	***
Height of mowing (cm)	3.3 ± 0.2	(2.3–4.0)	3.6 ± 0.2	(2.7–4.7)	3.7 ± 0.3	(2.3–4.7)	n.s.
Host-plant level							
Cover of host plants (%)	11.2 ± 0.6^{a}	(5–30)	26.5 ± 2.2^{b}	(7–60)	32.4 ± 4.0^{b}	(7–80)	***
Loss of leaves (%)	21.3 ± 3.2^{a}	(0–100)	40.8 ± 4.3^{b}	(0–100)	40.5 ± 6.5^{b}	(0–95)	**

Note: Patch level: *M. aurelia*—dry meadows ($n = 11$); *E. aurinia*—moist meadows ($n = 5$) and dry meadows ($n = 11$). Host-plant level: *M. aurelia*—dry meadows ($n = 66$); *E. aurinia*—moist meadows ($n = 22$) and dry meadows ($n = 42$). Significant differences between groups were assessed using generalised linear mixed-effects models (GLMMs) with a Poisson (count data), gamma (interval-scaled data) or binomial (percentage data) error structure followed by Tukey contrasts for pairwise comparisons. Subarea' and 'patch' nested in subarea served as random effects. For further details, see Section 2.3. Significant differences of pairwise comparisons are indicated by different letters ($p < 0.05$). n.s., not significant, **$p < 0.01$, ***$p < 0.001$.

Larval webs

Altogether, we recorded 66 larval webs of *M. aurelia* on *P. media* (only in dry meadows) and 64 webs of *E. aurinia* on *S. pratensis* (42 in dry meadows and 22 in in the mown parts of moist meadows). For *M. aurelia*, 1 week before mowing, the average number (±SE) of larvae within a web was 100 ± 8 (range: 9–310). In the early-mown dry meadows, none of the caterpillars were already hibernating before mowing, all belonged to the first to third instar (Figure 2). For *E. aurinia*, prior to mowing, the mean number (±SE) of larvae per web was 169 ± 7 on dry (range: 60–320) and 165 ± 10 (range: 80–240) on moist meadows. In the early-mown dry meadows, only 7% of the *E. aurinia* larvae were already hibernating (fourth instar) before mowing. By contrast, 82% of the *E. aurinia* caterpillars in the late-mown moist meadows had reached hibernation prior to mowing. The remaining larvae in dry and moist meadows belonged to the second or third instar.

Web height at host plants differed between *M. aurelia* and *E. aurinia* (Figure 1). On average (±SE), webs of *M. aurelia* were located at a height of 2.7 ± 0.5 cm above ground and those of *E. aurinia* at 4.1 ± 0.2 cm and 5.0 ± 0.3 cm, respectively. Accordingly, in dry meadows, webs of *M. aurelia* were situated below and those of *E. aurinia* slightly above mean mowing height. By contrast, in wet meadows, *E. aurinia* webs were located clearly above cutting height.

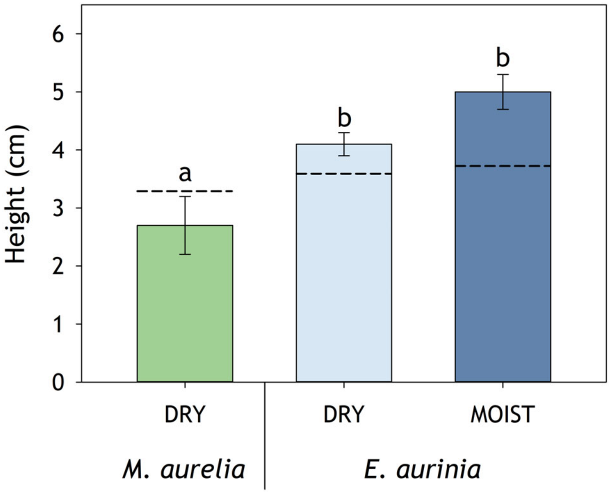

FIGURE 1 Mean (±SE) height of larval webs in the three treatments. *M. aurelia*: dry meadows ($n = 66$); *E. aurinia*: moist meadows ($n = 22$) and dry meadows ($n = 42$). Dashed line = mean mowing height (cf. Table 1). Significant differences between groups were assessed using generalised linear mixed-effects models (GLMMs) with a gamma error structure followed by Tukey contrasts for pairwise comparisons. 'Subarea' and 'patch' nested in subarea served as random effects. For further details, see Section 2.3. Significant differences of pairwise comparisons are indicated by different letters ($p < 0.05$).

Response of larvae to mowing

Overall, the harvesting process resulted in at least partial destruction of most larval webs and in strong losses of fritillary larvae (Figures 2 and 3). However, web destruction and survival differed between the two species and among the instars of *E. aurinia* but not of those of *M. aurelia*. For *M. aurelia*, 48 (73%) of the 66 larval webs showed signs of damage through the harvesting process. By contrast, all 64 larval webs of *E. aurinia* exhibited at least some damage. Accordingly, caterpillar survival was much higher for *M. aurelia* than for *E. aurinia*. On average (±SE), 73.1 ± 4.3% of the larvae of *M. aurelia* and 46.8 ± 4.3% of those of *E. aurinia* survived mowing (Figure 2). For *E. aurinia*, survival rates did not differ between dry and moist meadows (Figure 3). By contrast, mean survival of the third-instar larvae was more than two times higher than those of the fourth-instar caterpillars (63.4 ± 8.5% vs. 28.2 ± 6.7%) (Figure 2). Survival of second-instar larvae (47.5 ± 5.9%) did not differ from those of the two other instars.

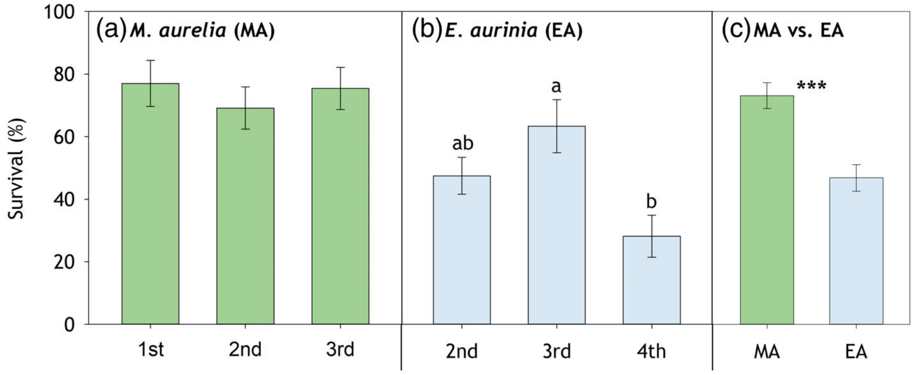

FIGURE 2 Mean (±SE) survival of larvae across the different instars of *M. aurelia* (a) and *E. aurinia* (b) as well as at both species (c). *M. aurelia*: first instar ($n = 22$), second instar ($n = 30$) and third instar ($n = 14$); *E. aurinia*: second instar ($n = 27$), third instar ($n = 20$) and fourth instar ($n = 17$). Significant differences between groups were assessed using proportional binomial generalised linear mixed-effects models (GLMM). GLMMs regarding instars were followed by Tukey contrasts for pairwise comparisons. Subarea' and 'patch' nested in subarea served as random effects. For further details, see Section 2.3. Significant differences of pairwise comparisons are indicated by different letters ($p < 0.05$). ***$p < 0.001$.

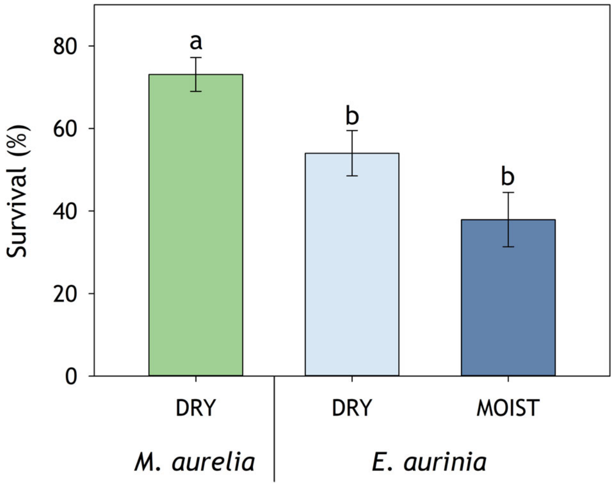

FIGURE 3 Mean (±SE) survival of larvae in the three treatments. *M. aurelia*: dry meadows ($n = 66$); *E. aurinia*: moist meadows ($n = 22$) and dry meadows ($n = 42$). Significant differences between groups were assessed using proportional binomial generalised linear mixed-effects models (GLMMs) followed by Tukey contrasts for pairwise comparisons. 'Subarea' and 'patch' nested in subarea served as random effects. For further details, see Section 2.3. Significant differences of pairwise comparisons are indicated by different letters ($p < 0.05$).

The loss of host-plant leaves through mowing was the most important predictor of larval survival (Table 2, Figure 4). Across all three treatments, survival rates decreased with leaf loss. If 60% or more of the leaves were lost, larval survival in all three treatments was below 15% (Figure 4). For *M. aurelia*, no larvae survived under such conditions. Additionally, in moist meadows, web height above ground had a negative effect on the survival of *E. aurinia* larvae (Table 2, Figure 4).

TABLE 2 Results of proportional binomial generalised linear mixed-effects models: predictors of larval survival in the three treatments.

Parameter	Estimate	SE	Z	p
Melitaea aurelia				
(a) Dry meadow ($R^2_m = 0.68–0.69$)				
Intercept	5.62	1.37	4.05	***
Leaf loss	−1.01	0.23	6.3	***
Euphydryas aurinia				
(b) Dry meadow ($R^2_m = 0.28 - 0.32$)				
Intercept	2.3	3.67	0.62	n.s.
Leaf loss	−0.32	0.09	3.42	***
(c) Moist meadow ($R^2_m = 0.21–0.45$)				
Intercept	2.44	3.04	0.78	n.s.
Leaf loss	−0.19	0.08	2.16	*
Web height	−0.97	0.44	2.06	*

Note: *M. aurelia*: dry meadows ($n = 66$); *E. aurinia*: moist meadows ($n = 22$) and dry meadows ($n = 42$). Subarea' and 'patch' nested in subarea served as random effects. For further details, see Section 2.3. R^2_m = variance explained by fixed effects (Nakagawa et al., 2017). n.s., not significant; *$p < 0.05$; ***$p < 0.001$.

DISCUSSION

Our study revealed that the harvesting process in nutrient-poor grasslands mown once by bar mowers resulted in substantial caterpillar loss for two endangered butterfly species. However, survival differed between species and among the larval instars of *E. aurinia*. On average, more than a quarter of the larvae of *M. aurelia* and more than half of the larvae of *E. aurinia* disappeared by the end of the harvest process. For *E. aurinia*, the immobile caterpillars in the hibernaculum web

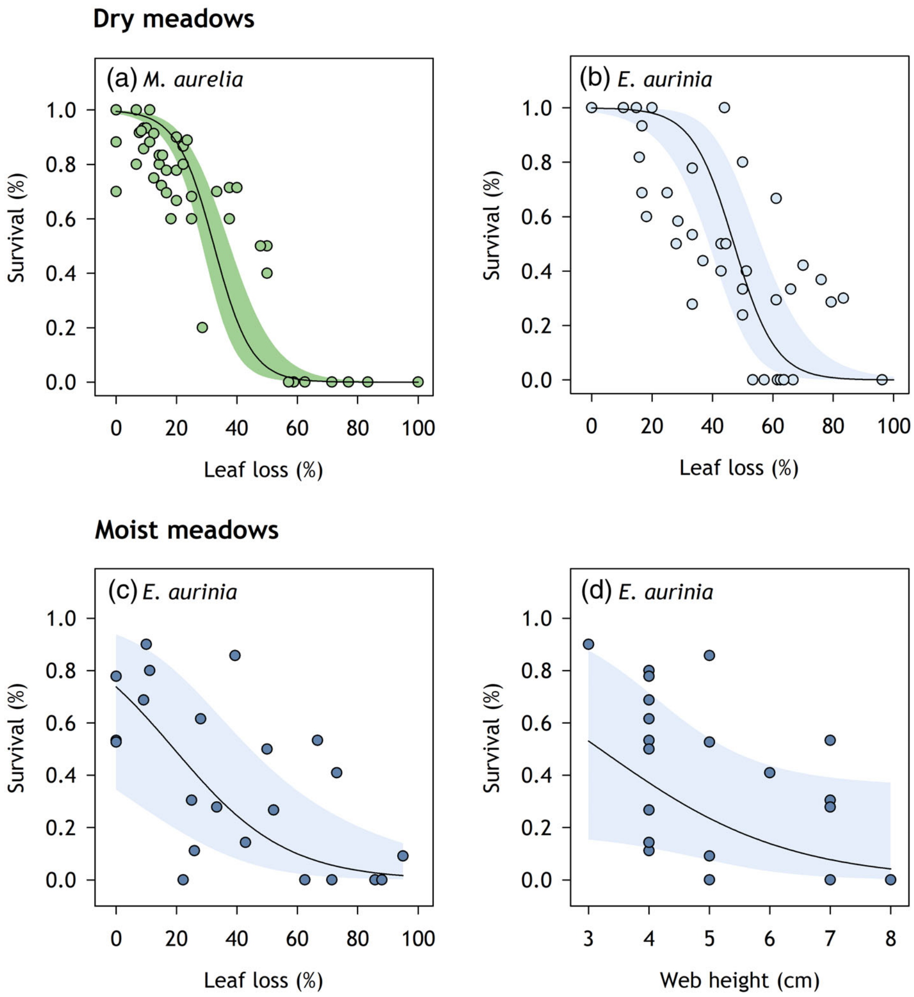

FIGURE 4 Results of proportional binomial generalised linear mixed-effects models (GLMMs): significant predictors of larval survival in the three treatments. Regression curves ± CI are shown. See Table 2 for detailed GLMM statistics.

(fourth larval instar) suffered the most; just slightly more than one third of these larvae survived. Overall, in both species, the loss of host-plant leaves through mowing was the main predictor of caterpillar survival.

As larvae of both butterfly species feed prior to hibernation gregariously on their host plants (*M. aurelia* at least until the third instar), they depend on sufficient plant biomass to avoid food shortage (cf. Section 2.1). As a result, we identified loss of host-plant leaves through mowing as the major driver of caterpillar disappearance across both fritillary species and meadow types. In dry and moist meadows, cutting was conducted at the same height close to the soil surface (~3.5 cm above ground). However, the mean loss of leaves on host plants of *M. aurelia* (21%) was half as high as at those of *E. aurinia* (41%). *P. media*, the host plant of *M. aurelia*, has a basal rosette and is low-growing (Grime et al., 2007). By contrast, *S. pratensis*, the host plant of *E. aurinia*, is a semi-rosette herb with large leaves. Accordingly, we explain the strong variation in biomass loss through mowing by the differences in the growth form of the two species of host plants. At least for larvae of *E. aurinia* in dry grasslands, we assume that food shortage was an important cause of caterpillar loss. Shortly before mowing, webs were still large and contained on average 165 larvae. Moreover, more than 90% of the caterpillars had not yet reached the fourth instar and, hence, had to forage.

However, plant growth form affected not only the loss of leaves but also the height of the larval webs above ground. In both fritillary species, the larval webs are usually located on those parts of the plant where leaf biomass is high (Anthes, Fartmann, Hermann, & Kaule, 2003; Eichel & Fartmann, 2008; Scherer & Fartmann, 2022). Larval webs of *M. aurelia* are situated at the basal rosette of the host plant, which was in our study below the average mowing height. By contrast, webs of *E. aurinia* on the generally taller *S. pratensis* host plants were located above the mean cutting height as these plants exhibited larger leaves in dry and particularly in moist grasslands, which contained very luxuriant host plants (own observation). Accordingly, larval webs of *M. aurelia* on *P. media* were relatively safe from direct negative effects of mowing. In line with this, we explain the twofold higher loss of *E. aurinia* larvae than those of *M. aurelia* not only by a stronger depletion of host-plant leaves and possible food shortage but also by a higher sensitivity of the *E. aurinia* webs to direct mowing effects due to their position above ground.

If webs are within the cutting height, cutting may (i) directly kill caterpillars, (ii) destroy webs partially or totally and (iii) displace larvae. We assume that direct mortality through cutting was of minor importance for the overall loss of the tiny caterpillars. First, the application of bar mowers ranks among the least harmful mowing techniques for grassland insects (Humbert et al., 2010; Schoof et al., 2023). Second, the likelihood of direct killing by mowers is much lower in small insects than in larger ones (Humbert et al., 2010; Schoof et al., 2023). Third, even when webs were heavily damaged by mowing, we rarely found any dead remains of larvae directly after mowing (own observation). Bamann and Dittrich (2017) made similar observations in litter meadows in southwestern Germany and also supposed a low direct mortality.

Among the larvae of *E. aurinia*, the hibernating fourth-instar caterpillars suffered the most. We explain this pattern by the different capabilities of the more mobile pre-diapause and the relatively immobile hibernating larvae (see Section 2.1) to respond to web destruction and displacement. Hibernating caterpillars merely repaired damaged webs but did not search actively for new vital host plants. By contrast, we regularly observed pre-diapause larvae constructing new webs on the remaining vital parts of the original host plant but also on host plants further away after mowing. In a similar way, we explain the negative relationship between the survival rate of larvae and web height in moist meadows. Due to the late mowing date in moist meadows, 82% of the *E. aurinia* caterpillars had already reached hibernation prior to mowing. As a result, only those webs of hibernating larvae that were situated close to the ground were able to repair damaged webs on the remaining vital part of the host plant. By contrast, larvae of webs that were located higher above ground reconstructed their webs in the cut vegetation (own observation). Hence, later removal of hay containing the attached hibernation webs was very likely an important cause for the high caterpillar loss. The further steps of the harvest process (e.g., tedding or raking) may result in further web destruction and displacement having the same effects as described above. If a displaced larvae of *E. aurinia* becomes completely separated from its siblings, its basking efficiency is strongly reduced, and successful hibernation of solitary larvae has not yet been documented (Porter, 1982). Other studies also highlighted that timing of grassland management strongly affects survival rates in specialised butterfly species and that immobile stages usually suffer more than mobile ones (Johst et al., 2006; Konvicka et al., 2008; Van Noordwijk et al., 2012).

Humbert et al. (2010) showed that running over of invertebrates by wheels of tractors or cutter wagons can also be an important cause of invertebrate mortality during the harvest process in meadows. In our study, dry grasslands were mown by a manually operated bar mower, and all consecutive steps of the harvest processes were also conducted manually (cf. Section 2.3). By contrast, in moist meadows, all harvesting measures were tractor-operated. Accordingly, the surface that was driven on by heavy machinery was considerably greater on moist than on dry meadows (see also Figure 5). Bamann and Dittrich (2017) observed that caterpillars of *E. aurinia* may survive an overrun by wheels of heavy vehicles on the soft peat soils of moist meadows. Nevertheless, we believe that the intensive driving on the moist meadows may have also contributed to caterpillar losses in moist meadows.

To sum up, in contrast to *E. aurinia*, *M. aurelia* was less affected by grassland harvest and seemed to be well adapted to mowing once

FIGURE 5 Moist meadow mown in mid-September after finishing the harvest process. The wheels of the tractor and cutter wagon had heavily disturbed the soft peaty soil. The inlay depicts a strongly defoliated plant of *S. pratensis* through cutting.

per year. The difference in caterpillar loss between the two fritillary species was mainly explained by (i) growth form of the host plants and (ii) timing of grassland harvest. The larval webs of *M. aurelia* were situated on the basal rosette of its low-growing host plant *P. media*, and hence below the average mowing height. By contrast, webs of *E. aurinia* in dry and particularly in moist grasslands on the much taller *S. pratensis* host plants were located on the larger leaves above the mean cutting height. The different growth forms of the host plants were responsible for a twofold lower loss of host-plant leaves for *M. aurelia* compared with *E. aurinia*. At least for the larvae of *E. aurinia* in the early-mown dry grasslands, we assume that food shortage caused by leave loss was an important driver of caterpillar depletion. Moreover, the different growth forms of the host plants explained the variation in height of the larval webs above ground and, therefore, the sensitivity of the caterpillars against direct mowing effects. Consequently, in particular, the webs of *E. aurinia* suffered from partial or total destruction and displacement of larvae. In contrast to the mobile pre-diapause larvae that search for new host plants, the immobile hibernating larvae only repaired their webs, usually within the cut vegetation. In the later-mown moist grasslands, nearly all larvae of *E. aurinia* were already hibernating. Hence, their webs were removed within the hay from the grassland, explaining the high losses among these caterpillars due to the harvest process.

Implications for conservation

In both studied meadow types, the harvest process followed the guidelines of the Bavarian conservation authorities (cf. Section 2.1). Nevertheless, only one of the two butterfly species of conservation concern, *M. aurelia*, exhibited low caterpillar losses. Webs of *M. aurelia* were located below the cutting height at the basal rosette of its low-growing host plant *P. media*. Accordingly, both the host-plant leaves and the caterpillars were relatively well protected against direct negative effects of mowing in early August by bar mowers.

By contrast, for *E. aurinia*, the leaves of the host plant *S. pratensis* were taller and, hence, the webs were located higher above ground. Consequently, both the leaves and webs were within the cutting height and suffered severe losses. This was particularly true for moist meadows that were mown in early September, when the vast majority of larvae were already hibernating. Accordingly, we recommend mowing of moist meadows in the beginning of August. To counteract potential losses of species hibernating in the vegetation, leaving 20% of a patch untouched when mowing is already mandatory as per Bavarian guidelines for conservation management in litter meadows (cf. Section 2.1). The location of the refuges varies spatially from year to year to avoid negative long-term effects of abandonment, that is, the accumulation of litter and the expansion of a few tall competitive plants at the expense of many less competitive ones (cf. Schoof et al., 2023). Therefore, complementary to mowing earlier, or if harvesting cannot be rescheduled, we believe that partially mowing by bar mowers in early September and leaving the rest as an untouched refuge in a spatially rotating manner are another suitable tool to foster long-term survival of *E. aurinia* on a patch despite the caterpillar losses caused by the harvest process. To compensate as well for the strong caterpillar losses of *E. aurinia* in dry grasslands mown in early August, we recommend the integration of a similar share of uncut refuges. Nowadays, there is increasing evidence that many other invertebrate species including *M. aurelia* also benefit from such temporary refuges within nutrient-poor grasslands (Eichel & Fartmann, 2008; Fartmann, 2023; Humbert et al., 2010; Schoof et al., 2023).

AUTHOR CONTRIBUTIONS

Gwydion Scherer: Conceptualization; data curation; writing – review and editing; writing – original draft; formal analysis. **Thomas Fartmann:** Conceptualization; writing – review and editing.

ACKNOWLEDGEMENTS

We are grateful to Wolfgang Krauss of the Sachgebiet Naturschutz of the federal state authority of Garmisch-Partenkirchen for helpful information on land-use history in the study area. We would also like to thank all the land owners for the access to their property and the insights in traditional land-use practices. This study was funded by a PhD scholarship of the Studienstiftung des Deutschen Volkes. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: Scherer, G. & Fartmann, T. (2024) Caterpillar loss through grassland harvest differs between two related butterfly species of conservation concern. *Insect Conservation and Diversity*, 17(1), 77–87. Available from: https://doi.org/10.1111/icad.12692