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Oviposition preferences and larval survival of the marsh fritillary butterfly: The adverse impact of grazing

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Abstract

1. Species-rich semi-natural grasslands have been lost during the last century due to agricultural intensification. This has had large negative consequences for many specialised species, including grassland butterflies. To prevent further loss, management regimes in the remaining grasslands must maintain habitat quality over time, and we therefore need to understand the habitat preferences of specialised species and how different management regimes affect their survival.
2. We studied the egg-laying preferences of the threatened marsh fritillary butterfly in relation to host plant properties, microclimate and management (grazing) on Gotland, Sweden. Moreover, we followed the survival of eggs and larvae from 27 egg batches during a period of 8 months (from June 2020 to March 2021) in grazed and ungrazed areas.
3. We found 92 egg batches in total and the average number of eggs was 184.5. Egg-laying probability increased with increasing host plant size and abundance, and environmental variables associated with a warm microclimate (low grass cover, low vegetation height and south-facing edges). The 27 egg batches that were followed over time had on average 203 eggs in June. Roughly 28% of the eggs developed into larvae, and about 17% of these survived over the entire study period, resulting in an overall 4.7% survival. Egg survival was higher in ungrazed habitats compared with grazed; in March (post-hibernation), there were almost nine times more eggs in ungrazed habitats.
4. This study highlights the complex habitat ecology of specialised butterflies and underscores the detrimental impact of intense grazing, advocating for rotational grazing or mowing regimes.

KEYWORDS
calcareous grasslands, conservation strategies, egg-laying, *Euphydryas aurinia*, habitat preferences, host plant selection

INTRODUCTION

Global biodiversity loss is proceeding at an alarming rate (Dirzo et al., 2014; Newbold et al., 2015). A predominant factor causing this decline is the anthropogenic alteration of terrestrial areas, which directly affects various species and ecosystems (Foley et al., 2005). Semi-natural grasslands are important hotspots for biodiversity in agricultural landscapes (e.g., Duelli & Obrist, 2003; Feurdean

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et al., 2018), and the intensified use of agricultural land and abandonment of less productive land during the last century have led to a major loss and fragmentation of habitat for species associated with these grasslands (Cousins et al., 2015; Krauss et al., 2010; Wallis De Vries et al., 2002). Many grasslands rely on continuous management with grazing to remain open, and abandonment leads to succession that may have negative impacts on many grassland specialists (Luoto et al., 2003; Weiss, 1999). On the other hand, too intense grazing may also have negative impacts on the habitat quality of some species (Jerrentrup et al., 2014; Johansson et al., 2019; Kruess & Tscharntke, 2002). Despite targeted conservation measures, including the establishment of Natura 2000 sites (Bouwma et al., 2016), management regimes sometimes fail (Kindvall et al., 2022) and many species continue to experience population declines throughout much of Europe (Warren et al., 2021). Successful conservation strategies depend on a better understanding of species' habitat preferences and population dynamics (Thomas et al., 2011) and its relation to management.

Grassland butterflies are one species group that has experienced negative population trends due to the loss and changed management of semi-natural grasslands (Maes & Van Dyck, 2001; Warren et al., 2001). Almost a third of European butterflies are declining, mainly due to agricultural intensification and land abandonment (van Swaay et al., 2010). For species to persist in the remaining grasslands, it is important that habitat quality is maintained over time (Öckinger & Smith, 2007), and we therefore need to understand butterfly population dynamics in relation to, for example, host plant abundance, microclimate and management strategies (Curtis et al., 2015; Kindvall et al., 2022; Roy & Thomas, 2003). Although habitat preferences can be studied for all life stages, immature life stages are most often the critical phase, as adult resources are usually not as limited (e.g., Smee et al., 2011). Egg and larvae survival will ultimately determine next year's population and set the population trend. One important factor affecting the survival of immature life stages is female oviposition preferences (e.g., Bergman, 1999; Eilers et al., 2013; Thomas et al., 2011). Understanding oviposition preferences in relation to host plant abundance, microclimate and management, and how they in turn affect the survival of eggs and larvae is therefore key for successful conservation.

The marsh fritillary butterfly (*Euphydryas aurinia*) is a grassland specialist that is declining in most of the European countries within its geographical range (van Swaay et al., 2010). The species utilises different types of habitats such as moist to dry calcareous grasslands, hummocky meadows, heathy grasslands and forest clearings (e.g., Johansson et al., 2019; Konvicka et al., 2003; Saarinen et al., 2005; Scherer & Fartmann, 2022; Warren, 1994). It is monophagous in its larval stage, with the devil's bit scabious (*Succisa pratensis*) being its primary host plant in northern Europe (Betzholtz et al., 2007; Brunbjerg et al., 2017; Konvicka et al., 2003; Pschera & Warren, 2018). Not surprisingly, host plant size or abundance has been found to be an important predictor of larvae occurrence (Anthes et al., 2003; Botham et al., 2011; Brunbjerg et al., 2017; Ghidotti et al., 2018; Konvicka et al., 2003; Scherer & Fartmann, 2022; Smee et al., 2011; Tjørnløv et al., 2015). Declines in host plant abundance, for example, due to land use changes, overfertilization and extreme weather, has been suggested to be the major cause of marsh fritillary population declines in various studies (Brunbjerg et al., 2017; Johansson et al., 2019, 2020). Apart from host plant abundance, the occurrence probability of egg and larvae also seems to be affected by vegetation height, microclimate and management strategies (Franzén et al., 2022b; Johansson et al., 2019; Konvicka et al., 2003; Scherer & Fartmann, 2022; Smee et al., 2011). Low-intensity management is generally recommended for the marsh fritillary across Europe, with either light machine mowing or extensive cattle grazing (Munguira et al., 1997; Saarinen et al., 2005; Schtickzelle et al., 2005; Smee et al., 2011; Tájek et al., 2023), sometimes also with temporal retention strips (Scherer & Fartmann, 2024; Tájek et al., 2023). In contrast, high-intensity grazing, sheep grazing or intense mowing often have devastating consequences for the species (Hula et al., 2004; Kindvall et al., 2022; Saarinen et al., 2005; Scherer & Fartmann, 2024; Warren, 1994). Although oviposition preferences have been observed to vary depending on the region, a comprehensive understanding across multiple sites within the species' range remains elusive. However, extant literature offers limited insights into the survival rates of eggs and larvae through the post-hibernation stage and their interactions with different management practices. For the first time, we study larvae post-hibernation survival rates in relation to grazing management.

The aim of this study was to enhance our understanding of the oviposition preferences and survival of both eggs and larvae, in relation to host plant availability, microclimate conditions and grazing management practices in a substantial population of marsh fritillary on Gotland, Sweden.

METHODS

Study species and area

The marsh fritillary (*Euphydryas aurinia*) is protected within the European Union under Annex II in the 1992 Habitats and Species Directive (92/43/EEC) as well as Annex II of the Bern Convention. The species is declining in most of the European countries within its geographical range (van Swaay et al., 2010), and in Sweden it is classified as vulnerable (VU) (Artdatabanken, 2020). The species is univoltine, with adults flying from late May to late June in Sweden (Franzén et al., 2022a). The larvae are monophagous, with devil's bit scabious (*Succisa pratensis*) as host plant. Females mate once and lay large egg batches (usually 50–500 eggs/batch), under leaves of the host plant. After hatching, the larvae spin a silken nest around the host plant. Larvae feed and bask gregariously during sunny days until September, when they enter diapause in a collective conspicuous nest (larvae autumn nests). The larvae become active again in early spring and resume feeding and basking together before separating and pupating in the final sixth instar in April or May.

The study was conducted on the island of Gotland situated in the Baltic Sea, south-east Sweden (Figure 1). In the study area, the

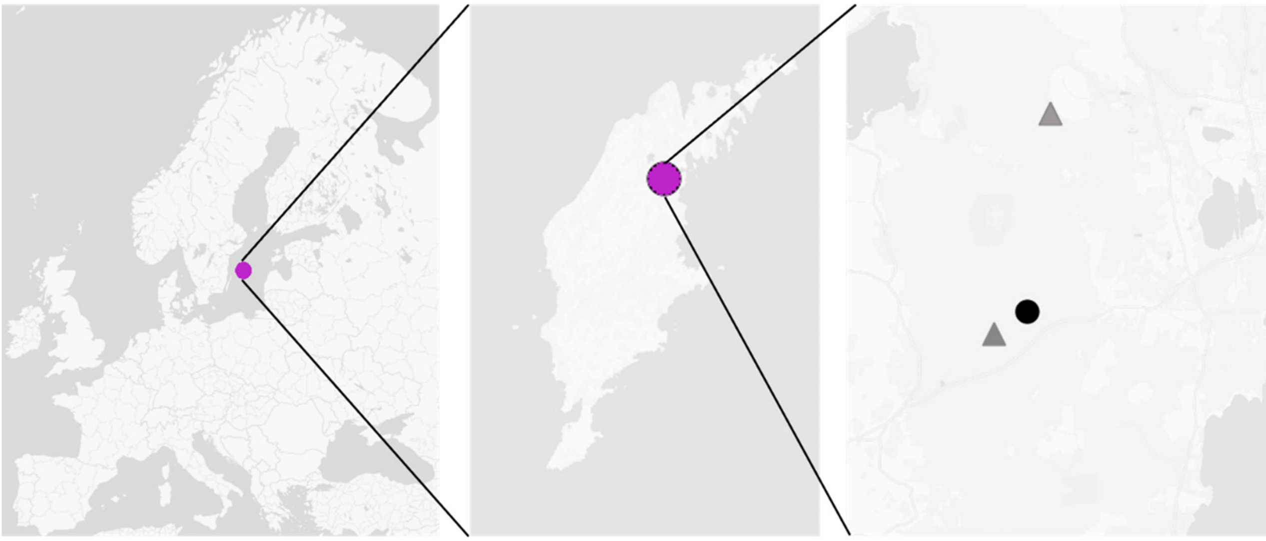

FIGURE 1 The study area on the island of Gotland in the Baltic Sea (purple dot) with grazed (black dots) and ungrazed (grey triangles) study sites.

TABLE 1 The explanatory variables used to analyse egg-laying probability, batch size and egg/larvae survival.

Variable	Description
Longest leaf length (cm)	The longest leaf among all host plants was measured (0.5 m^2)
Number of host plants	All host plants were counted (0.5 m^2)
Vegetation height (cm)	Vegetation height was measured using a 17-cm-wide sward ruler (the recorder stood 5 m in front of the ruler and noted the height where 50% of the width of the ruler was covered by vegetation) (0.5 m^2).
Tussock height (categorical)	1. No tussocks 2. Small tussocks (<15 cm in height), 3. Large tussocks (>15 cm)
Grass cover (%)	Estimation of percentage covered by grass (0.5 m^2)
Bush cover (%)—NE and SW	The cover of small trees and bushes (below 3 m) within 10 m divided into two directions: north-east (315–135°) and south-west (135–315°).
Tree cover (%)—NE and SW	Tree cover (trees higher than 3 m) within 10 m divided into two directions: north-east (315–135°) and south-west (135–315°).
South-facing edge	Bush cover NE − (Tree cover SW + Bush cover SW). A high value gives sun exposure from SW and wind protection from NE
Grazing (categorical)	Grazed or ungrazed hectare grid cell

marsh fritillary occurs in calcareous wet grasslands, and suitable habitat for the species has been mapped in previous studies in the area (Johansson et al., 2019, 2020). Roughly 30% of the study area is grazed by cattle (Angus and Charolais), with approximately 0.3 animals/ha, from late May to September. This is the yearly intensity required to receive EU subsidies (Kindvall et al., 2022). The remaining proportion has no current management. However, due to the poor soil and slow accumulation of humus, these grasslands remain naturally open for decades (Eliasson, 2008).

Data collection

The egg batch survey was conducted in nine 1-hectare grid cells in marsh fritillary habitat from areas known to have high densities of adult butterflies (Franzén et al., 2022a; Johansson et al., 2022; Kindvall et al., 2022). Three of these were grazed and six were ungrazed (Figure 1). Egg batches were searched on all host plants along six randomly placed 1-m-wide and 20-m-long transects per hectare grid cell. When an egg batch was found, we recorded multiple environmental variables in and around a 0.5-m^2 circular plot (diameter = 80 cm) with the egg batch in the centre (Table 1). We also took a high-resolution picture of the egg batch that was used to count the number of eggs. Approximately 15 control points (14–18) were randomly chosen in the same hectare grid cells and the same variables were registered (Table 1). To increase the number of random points, we also included one extra grid cell. The total number of random points was 134.

To study larval survival, 27 egg batches were selected from the 9-hectare grid cells (8 in grazed habitat and 19 in ungrazed habitat). Each egg batch site was given a unique ID number and marked with a rock painted in red with a waterproof spray paint. We visited the egg sites four times from June 2020 to March 2021 and counted the eggs or larvae each time. The first visit was on 26 June 2020, the second was on 12 July 2020, the third on 1 August 2020 and the last on 30 March 2021.

TABLE 2 Standardised parameter estimates (with SE and statistical significance) for the generalised linear mixed-effects models (GLMMs) of the egg batch occurrence probability and batch size, and the change in AIC (ΔAIC) when removing the variable from the final models.

	Egg batch occurrence		Batch size	
	Parameter estimate	ΔAIC	Parameter estimate	ΔAIC
Intercept	−2.31 (0.65)***		5.12 (0.05)***	
Number of host plants	1.38 (0.33)***	23.5		
Longest leaf	1.65 (0.34)***	32.4	0.10 (0.05)*	2.4
Vegetation height:Grazing		16.4		
Ungrazed	−1.25 (0.41)**			
Grazed	1.35 (0.61)*			
Grass cover	−1.38 (0.36)***	16.2		
South-facing edge	0.82 (0.28)**	10.2		
Tussocks[a]		5.2		
Small	1.04 (0.59).			
Large	2.25 (0.78)**			

[a]Tussocks has two parameter estimates as the categories 'small' and 'large' are compared with the reference category 'No tussocks'.
*p < 0.05; **p < 0.01; ***p < 0.001.

Statistical analysis

We analysed the occurrence probability of egg batches in relation to the explanatory variables (Table 1) using a generalised linear mixed-effects model (GLMM), with a binomial distribution and hectare grid cell as random effect using the statistical software R, version 4.2.2 (R Core Team, 2022). The variable 'south-facing edge' was not tested together with its three components (bush cover NE, tree cover SW and bush cover SW) due to their correlation. For all variables, we tested the interaction with grazing (i.e., if the effect of a variable differs between grazed and ungrazed habitat). The final model was selected based on the lowest AIC. However, to avoid overparameterization, we only included variables that lowered the AIC with >2 in the final model. To analyse the number of eggs in an egg batch, we used the same model structure but with a negative binomial distribution (over-dispersed counts).

We analysed egg or larval survival based on the count of eggs or larvae from the four visits using a GLMM, with a negative binomial distribution and egg site identity nested in hectare grid cells as random effect. Explanatory variables were the date of the visit (a categorical variable with four levels, one for each visit) and the above-mentioned variables (Table 1) also including the interaction with grazing.

RESULTS

In total, we found 92 egg batches, and the number of eggs per batch ranged between 15 and 355 (mean = 184.5). The probability of egg batch occurrence increased with increasing number of host plants and the size of the longest leaf (Table 2, Figure 2), which also were the two most important variables for explaining the occurrence of egg batches (as judged by the change in AIC when removing them from the final model, Table 2). The interaction between vegetation height and grazing showed that vegetation height had a negative effect in ungrazed habitat and a positive effect in grazed habitat. Egg batch occurrence probability was higher on large tussocks (>15 cm in height), and it increased with increasing 'south-facing edge', while grass cover had a negative effect. The number of eggs in a batch increased with increasing size of the longest leaf (Table 2, Figure 3).

For the 27 egg batches that were followed over time, there were on average 203.1 (SE = 14.1) eggs in each batch when counted in June. The corresponding minimum numbers for larvae in July, August and March were 57.3 (SE = 8.8), 29.7 (SE = 4.9) and 9.6 (SE = 3.3), respectively. Hence, roughly 28% of the eggs developed into larvae, and about 17% of these survived over the entire study period, which constitute 4.7% of the eggs. The number of larvae decreased more in grazed areas based on the interaction between grazing and the different visits (Table 3, Figure 4). In March, the number of larvae was 8.9 times higher in ungrazed habitat compared with grazed according to model predictions. None of the other explanatory variables measured in June (Table 1) explained the number of larvae over time.

DISCUSSION

We show that marsh fritillary oviposition is explained both by host plant size and abundance, and by several factors associated with the microclimate. By following 27 egg batches from eggs to post-hibernating larvae, we also show a less than 5% survival rate overall and an almost nine times lower survival in grazed compared with ungrazed habitat.

Female marsh fritillary butterflies preferred to deposit eggs where host plants were larger and more abundant, which is in line with earlier studies of oviposition and larvae occurrence for the marsh fritillary (Anthes et al., 2003; Botham et al., 2011; Brunbjerg et al., 2017;

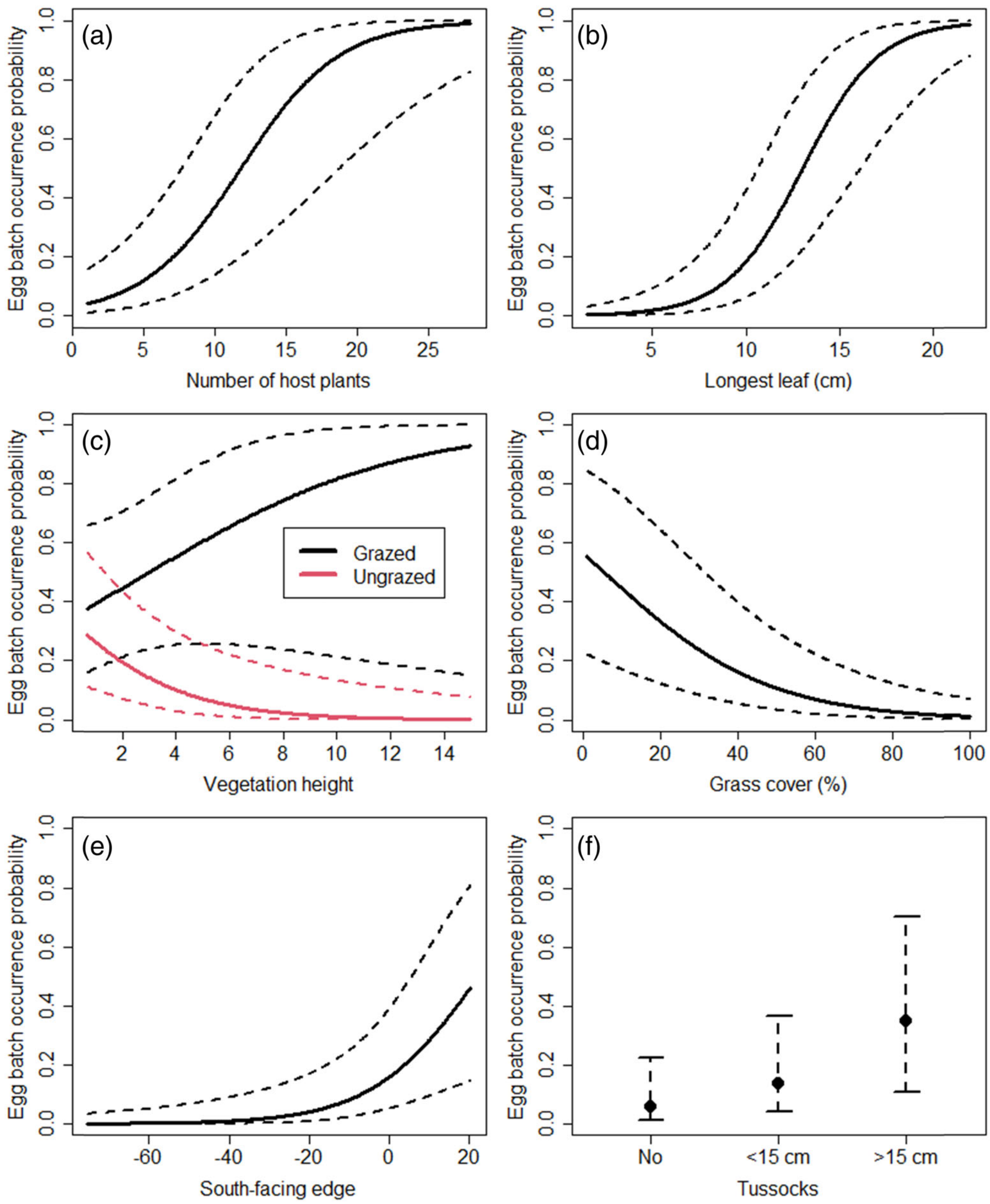

FIGURE 2 Egg batch occurrence probability in relation to (a) the number of host plants, (b) length of the longest leaf, (c) vegetation height, (d) grass cover, (e) 'south-facing edge' and (f) tussock height. Thick lines (and dot in f) are model predictions, with 95% confidence intervals (broken lines), from the final model based on 95 egg batches and 134 random points (parameter estimates in Table 1).

Ghidotti et al., 2018; Johansson et al., 2019; Konvicka et al., 2003; Scherer & Fartmann, 2022; Tjørnløv et al., 2015), as long as the sward is not too high for larval development (Konvicka et al., 2003). The importance of large and abundant host plants also agrees with egg-laying preferences of other lepidopterans (e.g., Albanese et al., 2008; Cohen & Brower, 1982; Zangerl & Berenbaum, 1992). Targeting spots with large and abundant host plants most likely reduces the risk of larvae starvation (Cohen & Brower, 1982; Pinzari et al., 2016) and the risk of forced movement. However, several other habitat factors also explained the female oviposition behaviour (Table 2), as shown also in other studies (Anthes et al., 2003; Eilers et al., 2013; Konvicka et al., 2023; Scherer & Fartmann, 2022). The preference for egg-laying in spots with potentially more south-facing edge, less surrounding grass cover, low vegetation height and large tussocks is most likely connected to the local microclimate. Increased solar exposure (and wind protection for south-facing edge) in such settings would facilitate thermoregulatory processes crucial for accelerating larval development (Porter, 1982) and increase larval survival (Radchuk et al., 2013). These results agree with studies emphasising the importance of factors related to a warm microclimate such as open and low vegetation (Anthes et al., 2003; Konvicka et al., 2003) and sun exposure (Pielech et al., 2017; Scherer & Fartmann, 2022) for the marsh fritillary. Interestingly, the effect of vegetation height was positive in grazed habitat, which could be a result of suitable (large) host plants only being found in spots where grazing has been less intense and the vegetation is higher. The preference for large tussocks could serve multiple ecological functions, besides possibly increasing sun exposure (see above). Tussocks may also aid in host plant detection and act as

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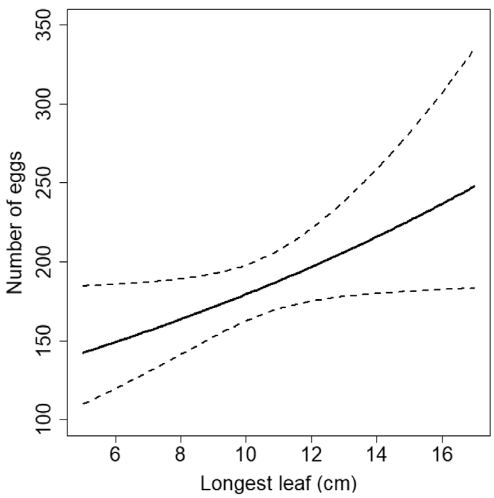

FIGURE 3 The number of eggs in a batch in relation to the length of the longest leaf. Thick lines are model predictions, with 95% confidence intervals (broken lines).

TABLE 3 Parameter estimates (with SE and statistical significance) for the generalised linear mixed-effects models (GLMMs) of the number of eggs or larvae over time, and the change in AIC (ΔAIC) when removing the variable from the final models.

	Parameter estimate	ΔAIC
Intercept	5.60 (0.53)***	
Date[a]		64.6
July 12	−3.52 (0.71)***	
August 1	−4.66 (0.71)***	
March 31	−5.72 (0.75)***	
Interaction with grazing		13.5
June 26:Ungrazed	−0.08 (0.61)	
July 12:Ungrazed	2.20 (0.77)**	
August 1:Ungrazed	2.65 (0.77)***	
March 31:Ungrazed	2.27 (0.81)**	

[a]Date has three parameter estimates as the categories ‘July 12’, ‘August 1’ and ‘March 31’ are compared with the reference category ‘June 26’. Positive interaction terms mean that the number of larvae is higher in ungrazed habitat compared with grazed.
**$p < 0.01$; ***$p < 0.001$.

flood deterrents (Betzholtz et al., 2007). Based on our results and earlier work, it is evident that females engage in a complex decision-making process for oviposition, integrating both host plant and surrounding microhabitat features in an apparent strategy to augment offspring survival.

EGG AND LARVAL SURVIVAL

We show that the survival of egg and larvae is clearly linked to management as the difference in the survival of eggs and larvae between grazed and ungrazed areas was clearly visible already in July. In March,

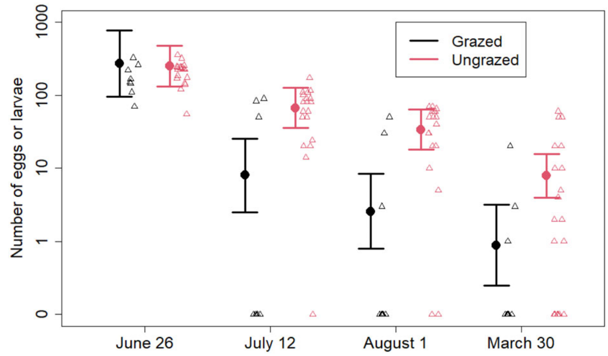

FIGURE 4 The number of marsh fritillary eggs or larvae over time in grazed (black) and ungrazed (red) habitat. Filled circles show model predictions with 95% confidence interval (vertical lines), and triangles show the raw data used to fit the model (with a small scatter to improve visualisation). Notice the log10 scale on the *y*-axis.

the number of larvae was almost nine times higher in ungrazed habitat compared with grazed based on model predictions. We have earlier shown that ungrazed habitat harbours almost five times more larvae nests based on autumn counts (Johansson et al., 2019). If only comparing the number of larvae in nests that survived until August (which is closest to the count in Johansson et al., 2019), ungrazed habitat had 1.7 times more larvae in March, which taken together suggests that ungrazed habitat should produce over eight times more larvae compared with grazed. This difference may also further accelerate during years with droughts (Kindvall et al., 2022). These results align with existing literature on the deleterious effects of high grazing pressure on the marsh fritillary (Hula et al., 2004; Saarinen et al., 2005; Smee et al., 2011) and other grassland butterflies (Ellis, 2003; Johansson et al., 2017; Schtickzelle et al., 2007; van Noordwijk et al., 2012) elsewhere, as well as on other grassland insects (Jerrentrup et al., 2014; Kruess & Tscharntke, 2002). For the occurrence probability of larvae nests, one explanation could be smaller and less abundant host plants in grazed habitat (Johansson et al., 2019; Schtickzelle et al., 2007), which here also were the two most important variables for the occurrence of egg batches. However, once deposited, the survival of eggs and larvae was not explained by host plant size or abundance (or any other variables that explained the occurrence of nests). Even if it is difficult to determine the exact mechanism leading to lower survival in the present study, it is likely that butterfly eggs and larvae are damaged or eaten by grazing animals (van Noordwijk et al., 2012).

CONCLUSIONS AND CONSERVATION IMPLICATIONS

Our results highlight the complex habitat selection of specialised grassland butterflies, which is key knowledge for efficient conservation planning and management (Thomas et al., 2011). Preserving habitat with high densities of large host plants in warm microclimates is of utmost importance for successful conservation of the marsh fritillary. Intense grazing has clear negative impacts on egg and larval survival rates, as well as densities of larval nests (Johansson et al., 2019) and the abundance of adult butterflies (Kindvall et al., 2022) for the marsh fritillary in our study area. It is therefore clear that the marsh fritillary habitat in our study area must be managed with lower intensity. This agrees with management recommendations for different habitat types across Europe where either light machine mowing or extensive cattle grazing is suggested (e.g., Munguira et al., 1997; Saarinen et al., 2005; Schtickzelle et al., 2005; Smee et al., 2011; Tájek et al., 2023). How to achieve 'low-intensity' management, however, will depend on soil moisture and productivity, and it is therefore important that the management regime is adapted to the local conditions (Johansson et al., 2019; Tájek et al., 2023). Temporal retention patches ensure that high-quality habitat is available each year (Scherer & Fartmann, 2024; Tájek et al., 2023), which should decrease local extinction risks and maintain sources for re-colonisation (Anthes et al., 2003; Johansson et al., 2019; Schtickzelle et al., 2005). Given the slow recovery rate of nutrient-poor grasslands, we therefore suggest rotational grazing or mowing with low intensity, especially in areas featuring larger and more abundant host plants. Rotational management also possibly creates more habitat heterogeneity, which may be important for surviving in a changing climate (Oliver et al., 2010).

AUTHOR CONTRIBUTIONS

Victor Johansson: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; visualization; formal analysis; supervision; data curation. **Demieka Seabrook Säwenfalk:** Investigation; writing – original draft; formal analysis. **Karl-Olof Bergman:** Conceptualization; writing – original draft; methodology; supervision. **Oskar Kindvall:** Conceptualization; investigation; writing – original draft; methodology. **John Askling:** Conceptualization; methodology. **Markus Franzén:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; formal analysis.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author on request.

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REFERENCES

Albanese, G., Vickery, P.D. & Sievert, P.R. (2008) Microhabitat use by larvae and females of a rare barrens butterfly, frosted elfin (Callophrys irus). *Journal of Insect Conservation*, 12(6), 603–615. Available from: https://doi.org/10.1007/s10841-007-9097-2

Anthes, N., Fartmann, T., Hermann, G. & Kaule, G. (2003) Combining larval habitat quality and metapopulation structure – the key for successful management of pre-alpine Euphydryas aurinia colonies. *Journal of Insect Conservation*, 7(3), 175–185. Available from: https://doi.org/10.1023/A:1027330422958

Artdatabanken. (2020) Rödlistade Arter i Sverige 2020.

Bergman, K.-O. (1999) Habitat utilization by Lopinga achine (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. *Biological Conservation*, 88(1), 69–74. Available from: https://doi.org/10.1016/S0006-3207(98)00088-3

Betzholtz, P.-E., Ehrig, A., Lindeborg, M. & Dinnétz, P. (2007) Food plant density, patch isolation and vegetation height determine occurrence in a Swedish metapopulation of the marsh fritillary Euphydryas aurinia (Rottemburg, 1775) (lepidoptera, Nymphalidae). *Journal of Insect Conservation*, 11(4), 343–350. Available from: https://doi.org/10.1007/s10841-006-9048-3

Botham, M.S., Ash, D., Aspey, N., Bourn, N.A.D., Bulman, C.R., Roy, D.B. et al. (2011) The effects of habitat fragmentation on niche requirements of the marsh fritillary, Euphydryas aurinia, (Rottemburg, 1775) on calcareous grasslands in southern UK. *Journal of Insect Conservation*, 15(1), 269–277. Available from: https://doi.org/10.1007/s10841-010-9344-9

Bouwma, I., Liefferink, D., Apeldoorn, R.V. & Arts, B. (2016) Following old paths or shaping new ones in natura 2000 implementation? Mapping path dependency in instrument choice. *Journal of Environmental Policy & Planning*, 18(2), 214–233. Available from: https://doi.org/10.1080/1523908X.2015.1070334

Brunbjerg, A.K., Høye, T.T., Eskildsen, A., Nygaard, B., Damgaard, C.F. & Ejrnæs, R. (2017) The collapse of marsh fritillary (Euphydryas aurinia) populations associated with declining host plant abundance. *Biological Conservation*, 211, 117–124. Available from: https://doi.org/10.1016/j.biocon.2017.05.015

Cohen, J.A. & Brower, L.P. (1982) Oviposition and larval success of wild monarch butterflies (lepidoptera: Danaidae) in relation to host plant size and cardenolide concentration. *Journal of the Kansas Entomological Society*, 55(2), 343–348.

Cousins, S.A.O., Auffret, A.G., Lindgren, J. & Tränk, L. (2015) Regional-scale land-cover change during the 20th century and its consequences for biodiversity. *Ambio*, 44(1), 17–27. Available from: https://doi.org/10.1007/s13280-014-0585-9

Curtis, R.J., Brereton, T.M., Dennis, R.L.H., Carbone, C. & Isaac, N.J.B. (2015) Butterfly abundance is determined by food availability and is mediated by species traits. *Journal of Applied Ecology*, 52(6), 1676–1684. Available from: https://doi.org/10.1111/1365-2664.12523

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, 345(6195), 401–406. Available from: https://doi.org/10.1126/science.1251817

Duelli, P. & Obrist, M.K. (2003) Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic and Applied Ecology*, 4(2), 129–138. Available from: https://doi.org/10.1078/1439-1791-00140

Eilers, S., Pettersson, L.B. & Öckinger, E. (2013) Micro-climate determines oviposition site selection and abundance in the butterfly Pyrgus armoricanus at its northern range margin. *Ecological Entomology*, 38(2), 183–192. Available from: https://doi.org/10.1111/een.12008

Eliasson, C.U. (2008) *Åtgärdsprogram för väddnätfjäril 2008–2012 (5920)*. Stockholm, Sweden, Naturvårdsverket.

Ellis, S. (2003) Habitat quality and management for the northern brown argus butterfly Aricia artaxerxes (lepidoptera: Lycaenidae) in north

East England. *Biological Conservation*, 113(2), 285–294. Available from: https://doi.org/10.1016/S0006-3207(02)00376-2

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S.M. & Hickler, T. (2018) Biodiversity-rich European grasslands: ancient, forgotten ecosystems. *Biological Conservation*, 228, 224–232. Available from: https://doi.org/10.1016/j.biocon.2018.09.022

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. et al. (2005) Global consequences of land use. *Science*, 309(5734), 570–574.

Franzén, M., Francioli, Y., Askling, J., Kindvall, O., Johansson, V. & Forsman, A. (2022a) Differences in phenology, daily timing of activity, and associations of temperature utilization with survival in three threatened butterflies. *Scientific Reports*, 12(1) Article 1, 7534. Available from: https://doi.org/10.1038/s41598-022-10676-0

Franzén, M., Francioli, Y., Askling, J., Kindvall, O., Johansson, V. & Forsman, A. (2022b) Yearly weather variation and surface temperature drives the spatiotemporal dynamics of a threatened butterfly and its host plant. *Frontiers in Ecology and Evolution*, 10, 917991. Available from: http://urn.kb.se/resolve?urn=urn:nbn:se:liu:diva-189950

Ghidotti, S., Cerrato, C., Casacci, L.P., Barbero, F., Paveto, M., Pesce, M. et al. (2018) Scale-dependent resource use in the *Euphydryas aurinia* complex. *Journal of Insect Conservation*, 22(3), 593–605. Available from: https://doi.org/10.1007/s10841-018-0088-2

Hula, V., Konvička, M., Pavlicko, A. & Fric, Z. (2004) Marsh fritillary (Euphydryas aurinia) in The Czech Republic: monitoring, metapopulation structure, and conservation of an endangered butterfly. *Entomologica Fennica*, 15(4), 4. Available from: https://doi.org/10.33338/ef.84226

Jerrentrup, J.S., Wrage-Mönnig, N., Röver, K.-U. & Isselstein, J. (2014) Grazing intensity affects insect diversity via sward structure and heterogeneity in a long-term experiment. *Journal of Applied Ecology*, 51(4), 968–977. Available from: https://doi.org/10.1111/1365-2664.12244

Johansson, V., Kindvall, O., Askling, J. & Franzén, M. (2019) Intense grazing of calcareous grasslands has negative consequences for the threatened marsh fritillary butterfly. *Biological Conservation*, 239, 108280. Available from: https://doi.org/10.1016/j.biocon.2019.108280

Johansson, V., Kindvall, O., Askling, J. & Franzén, M. (2020) Extreme weather affects colonization-extinction dynamics and the persistence of a threatened butterfly. *Journal of Applied Ecology*, 57, 1068–1077. Available from: https://doi.org/10.1111/1365-2664.13611

Johansson, V., Kindvall, O., Askling, J., Säwenfalk, D.S., Norman, H. & Franzén, M. (2022) Quick recovery of a threatened butterfly in well-connected patches following an extreme drought. *Insect Conservation and Diversity*, 15(5), 572–582. Available from: https://doi.org/10.1111/icad.12574

Johansson, V., Knape, J. & Franzén, M. (2017) Population dynamics and future persistence of the clouded apollo butterfly in southern Scandinavia: the importance of low intensity grazing and creation of habitat patches. *Biological Conservation*, 206, 120–131. Available from: https://doi.org/10.1016/j.biocon.2016.12.029

Kindvall, O., Franzén, M., Askling, J., Forsman, A. & Johansson, V. (2022) Subsidized common agricultural policy grazing jeopardizes the protection of biodiversity and natura 2000 targeted species. *Animal Conservation*, 25(5), 597–607. Available from: https://doi.org/10.1111/acv.12773

Konvicka, M., Hula, V. & Fric, Z. (2003) Habitat of pre-hibernating larvae of the endangered butterfly Euphydryas aurinia (lepidoptera: Nymphalidae): what can be learned from vegetation composition and architecture? *European Journal of Entomology*, 100(3), 313–322. Available from: https://doi.org/10.14411/eje.2003.050

Konvicka, M., Hula, V., Vlasanek, P., Zimmermann, K. & Faltynek Fric, Z. (2023) Within-habitat vegetation structure and adult activity patterns of the declining butterfly *Euphydryas aurinia*. *Journal of Insect Conservation*, 27, 335–346.

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R., Helm, A., Kuussaari, M. et al. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, 13(5), 597–605. Available from: https://doi.org/10.1111/j.1461-0248.2010.01457.x

Kruess, A. & Tscharntke, T. (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology*, 16(6), 1570–1580. Available from: https://doi.org/10.1046/j.1523-1739.2002.01334.x

Luoto, M., Pykälä, J. & Kuussaari, M. (2003) Decline of landscape-scale habitat and species diversity after the end of cattle grazing. *Journal for Nature Conservation*, 11(3), 171–178. Available from: https://doi.org/10.1078/1617-1381-00052

Maes, D. & van Dyck, H. (2001) Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation*, 99(3), 263–276. Available from: https://doi.org/10.1016/S0006-3207(00)00182-8

Munguira, M.L., Martín, J., García-Barros, E. & Viejo, J.L. (1997) Use of space and resources in a Mediterranean population of the butterfly *Euphydryas aurinia*. *Acta Oecologica*, 18, 597–612.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A. et al. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, 520(7545) Article 7545, 45–50. Available from: https://doi.org/10.1038/nature14324

Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44(1), 50–59. Available from: https://doi.org/10.1111/j.1365-2664.2006.01250.x

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T. & Thomas, C.D. (2010) Heterogeneous landscapes promote population stability. *Ecology Letters*, 13(4), 473–484. Available from: https://doi.org/10.1111/j.1461-0248.2010.01441.x

Pielech, R., Zając, K., Kadej, M., Malicki, M., Malkiewicz, A. & Tarnawski, D. (2017) Ellenberg's indicator values support prediction of suitable habitat for pre-diapause larvae of endangered butterfly *Euphydryas aurinia*. *PLoS One*, 12(6), e0179026. Available from: https://doi.org/10.1371/journal.pone.0179026

Pinzari, M., Pinzari, M. & Sbordoni, V. (2016) Egg laying behaviour, host plants and larval survival of *Euphydryas aurinia* provincialis (lepidoptera Nymphalidae) in a Mediterranean population (central Italy). *Bollettino Della Società Entomologica Italiana*, 148(3) Article 3, 121–140. Available from: https://doi.org/10.4081/BollettinoSEI.2016.121

Porter, K. (1982) Basking behaviour in larvae of the butterfly Euphydryas aurinia. *Oikos*, 38(3), 308–312. Available from: https://doi.org/10.2307/3544670

Pschera, J. & Warren, J.M. (2018) Microhabitat selection by ovipositing females and pre-diapause larvae of a Welsh population of Euphydryas aurinia (lepidoptera: Nymphalidae). *Journal of Insect Conservation*, 22(3), 571–579. Available from: https://doi.org/10.1007/s10841-018-0086-4

R Core Team. (2022) R: a language and environment for statistical computing. (4.4.2) [Computer software]. R Foundation for Statistical Computing. http://ftp.sunet.se/pub/lang/CRAN/, http://www.R-project.org

Radchuk, V., Turlure, C. & Schtickzelle, N. (2013) Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, 82(1), 275–285. Available from: https://doi.org/10.1111/j.1365-2656.2012.02029.x

Roy, D.B. & Thomas, J.A. (2003) Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia*, 134(3), 439–444. Available from: https://doi.org/10.1007/s00442-002-1121-3

Saarinen, K., Jantunen, J. & Valtonen, A. (2005) Resumed forest grazing restored a population of Euphydryas aurinia (lepidoptera: Nymphalidae) in SE Finland. *European Journal of Entomology*, 102, 683–690.

Scherer, G. & Fartmann, T. (2022) Occurrence of an endangered grassland butterfly is mainly driven by habitat heterogeneity, food availability, and microclimate. *Insect Science*, 29(4), 1211–1225. Available from: https://doi.org/10.1111/1744-7917.12975

Scherer, G. & Fartmann, T. (2024) Caterpillar loss through grassland harvest differs between two related butterfly species of conservation concern. *Insect Conservation and Diversity*, 17, 77–87.

Schtickzelle, N., Choutt, J., Goffart, P., Fichefet, V. & Baguette, M. (2005) Metapopulation dynamics and conservation of the marsh fritillary butterfly: population viability analysis and management.

Schtickzelle, N., Turlure, C. & Baguette, M. (2007) Grazing management impacts on the viability of the threatened bog fritillary butterfly Proclossiana eunomia. *Biological Conservation*, 136(4), 651–660. Available from: https://doi.org/10.1016/j.biocon.2007.01.012

Smee, M., Smyth, W., Tunmore, M., Ffrench-Constant, R. & Hodgson, D. (2011) Butterflies on the brink: habitat requirements for declining populations of the marsh fritillary (Euphydryas aurinia) in SW England. *Journal of Insect Conservation*, 15(1), 153–163. Available from: https://doi.org/10.1007/s10841-010-9334-y

Tájek, P., Tenčík, A., Konvička, M. & John, V. (2023) Vegetation changes at oligotrophic grasslands managed for a declining butterfly. *Nature Conservation*, 52, 23–46.

Thomas, J.A., Simcox, D.J. & Hovestadt, T. (2011) Evidence based conservation of butterflies. *Journal of Insect Conservation*, 15(1), 241–258. Available from: https://doi.org/10.1007/s10841-010-9341-z

Tjørnløv, R.S., Kissling, W.D., Barnagaud, J.-Y., Bøcher, P.K. & Høye, T.T. (2015) Oviposition site selection of an endangered butterfly at local spatial scales. *Journal of Insect Conservation*, 19(2), 377–391. Available from: https://doi.org/10.1007/s10841-014-9747-0

van Noordwijk, C.G.E., Flierman, D.E., Remke, E., WallisDeVries, M.F. & Berg, M.P. (2012) Impact of grazing management on hibernating caterpillars of the butterfly Melitaea cinxia in calcareous grasslands. *Journal of Insect Conservation*, 16(6), 909–920. Available from: https://doi.org/10.1007/s10841-012-9478-z

van Swaay, C., Cuttelod, A., Collins, S., Maes, D., López Munguira, M., Šašic, M. et al. (2010) European red list of butterflies. https://portals.iucn.org/library/node/9511

Wallis De Vries, M.F., Poschlod, P. & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, 104(3), 265–273. Available from: https://doi.org/10.1016/S0006-3207(01)00191-4

Warren, M.S. (1994) The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary Eurodryas aurinia. *Biological Conservation*, 67, 239–249.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B. et al. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414(6859), 65–69. Available from: https://doi.org/10.1038/35102054

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., Dyck, H.V., Bourn, N.A.D. et al. (2021) The decline of butterflies in Europe: problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences*, 118(2), e2002551117. Available from: https://doi.org/10.1073/pnas.2002551117

Weiss, S.B. (1999) Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology*, 13(6), 1476–1486. Available from: https://doi.org/10.1046/j.1523-1739.1999.98468.x

Zangerl, A.R. & Berenbaum, M.R. (1992) Oviposition patterns and hostplant suitability: parsnip webworms and wild parsnip. *The American Midland Naturalist*, 128(2), 292–298. Available from: https://doi.org/10.2307/2426463

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