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Insect-friendly harvest in hay meadows – Uncut refuges are of vital importance for conservation management

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ABSTRACT

With ongoing industrialisation of farming practise, the area of species-rich temperate grasslands has strongly declined. Today, the remnants of these grasslands often suffer from habitat degradation due to unsuitable management. Here, we investigated the effects of the complete harvest process over the course of two harvest periods (mid-June and mid-August) on Orthoptera (hereinafter referred to as 'grasshoppers') in species-rich lowland hay meadows in southwestern Bavaria (Germany). We set up a randomised split-plot design including mown meadows (tractor-operated rotary-disc vs. double-bladed bar mower) and uncut refuges within grassland patches. Our study revealed that mower types did not differ in their effects on grasshopper mortality and that direct mortality through cutting was very low. By contrast, after mowing, on average 85–91 % of the individuals or biomass was lost by the end of the harvest process. However, in uncut refuges, grasshopper densities and biomass increased on average by 234–328 %. From the first to the second harvest period, an alignment in grasshopper densities and biomass between meadows and uncut refuges occurred. We explain the lack of direct cutting effects by the tall and dense vegetation of the hay meadows and, hence, the location of the grasshoppers far above the sphere of the mowers. Moreover, we assume that in particular emigration from the short and homogeneous meadows to uncut refuges or patch edges but also increased vertebrate predation were responsible for the severe grasshopper losses. Moreover, we hypothesise that grasshopper recolonization from the refuges to the meadows strongly contributed to the alignment in grasshopper densities from mid-June to mid-August. Hence, to protect abundant grasshopper populations in meadows in the long run, uncut refuges are of prime importance. Firstly, such refuges guarantee a continuity in (i) food resources, (ii) a balanced microclimate and (iii) shelter against predators and extreme weather events for the resident individuals. Consequently, they are not affected by any of the harvest-related losses. Secondly, they serve as an important refuge for the emigrants from the mown parts of the meadow.

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1. Introduction

Temperate grasslands rank among the most species-rich ecosystems on earth (Bonari et al., 2017; Feurdean et al., 2018). Across large parts of Europe, such grasslands have been characterised by a long history of low-intensity management (Pärtel et al., 2005; Fartmann, 2023). However, with ongoing industrialisation of farming practise, especially after World War II, the area of species-rich grasslands has strongly declined. Today, the remnants of these grasslands often suffer from habitat degradation because of unsuitable land use (Foley et al., 2005; Kleijn et al., 2009; Fartmann et al., 2021). Due to their importance for biodiversity conservation and high threat status, many of the species-rich grasslands, such as lowland hay meadows, are legally protected by the EU Habitats Directive (EC, 2013).

In meadow ecosystems, the type of mowing regime has a strong impact on the insect fauna (Humbert et al., 2010a; Van de Poel and Zehm, 2014; Bosshard, 2016; Schoof et al., 2023). Every harvest causes dramatic changes of the environmental conditions and severe losses of insects. Both direct (e.g., through cutting or tractor wheels) and indirect effects (e.g., through emigration or increased predation rates) contribute to these declines. Based on the current knowledge, particularly mowing by bar mowers is considered insect friendly (Humbert et al., 2010a; Van de Poel and Zehm, 2014; Schoof et al., 2023). However, due to economic reasons, bar mowers are nowadays rarely used (Hölzl, 2023). By contrast, mowers with conditioners have a strong negative impact on insects (Humbert et al., 2010a; Van de Poel and Zehm, 2014; Schoof et al., 2023). They roll and squeeze the grass directly after cutting to speed up drying and, hence, cause additional losses among insects. Today, rotary mowers are the most widely-used type of mowers (Schoof et al., 2023). Their direct effects on insects are usually in between those of the two other mentioned mower systems (Van de Poel and Zehm, 2014;

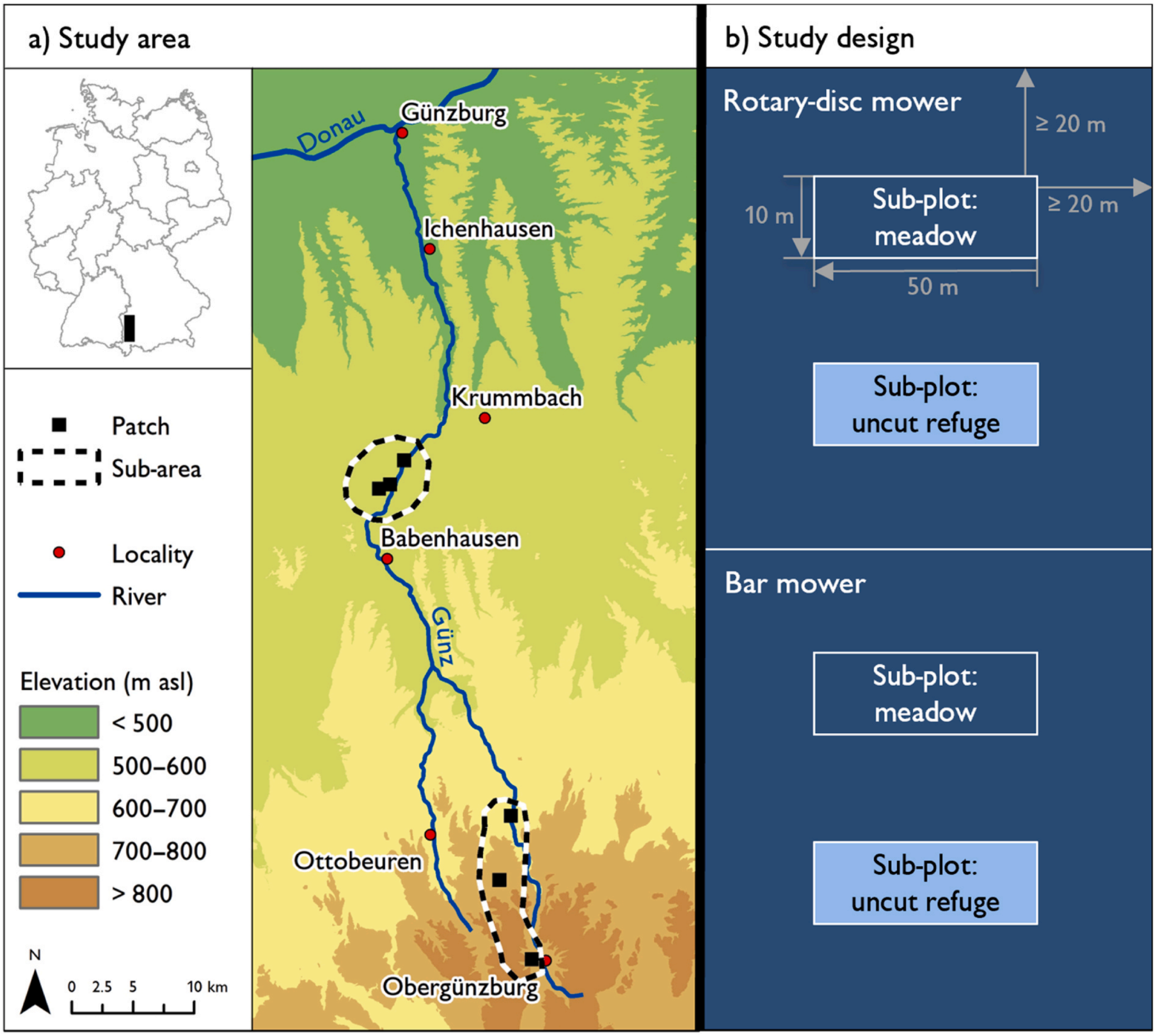

Fig. 1. Location of the study area in southwestern Bavaria (Germany) (a) and schematic illustration of the study design (b). For further information see 'Material and methods.

Schoof et al., 2023).

If bar mowers or rotary mowers without conditioners are applied, the insect declines following cutting are in fact usually much higher than the direct cutting effects (Kiel, 1999; Humbert et al., 2010b, 2012). The large extent of post-cutting losses can be explained by (i) the severe degradation of habitat suitability for grassland insects due to cutting, which increases mortality and emigration rates, and (ii) the impacts of the other working steps of the harvest process (Guido and Gianelle, 2001; Oppermann and Krismann, 2003; Humbert et al., 2010b; Schoof et al., 2023). However, if uncut areas are available at the patch edges or even in the meadows in fact they may serve as refuges and a source for the recolonization of the mown parts (Humbert et al., 2012; Schoof et al., 2023).

Orthoptera (hereinafter termed 'grasshoppers') often make up the largest proportion of arthropod biomass in grasslands and, thus, play a significant role in the food chain (Samways, 2005). Additionally, they are sensitive indicators of environmental conditions in general and land use in particular (Marini et al., 2009; Bazelet and Samways, 2012; Fartmann et al., 2012; Fumy et al., 2021). In contrast to other insect taxa, the effects of grassland harvest on grasshoppers have already gained some attention (Humbert et al., 2009; Van de Poel and Zehm, 2014; Schoof et al., 2023). However, often the available research does not distinguish between direct losses through cutting and further causes of decline during the course of the harvest process. Moreover, leaving uncut refuges within the grasslands is often recommended as a conservation measure, although, except the study of Humbert et al. (2012), its effects on grasshoppers had not been studied in detail. In fact, a study that analyses the role of such refuges over two consecutive harvest periods on grasshoppers was yet entirely absent.

Here, we investigated the effects of the complete harvest process over the course of two subsequent harvest periods (mid-June and mid-August) on grasshoppers in species-rich lowland hay meadows in southwestern Bavaria (Germany). We set up a randomised split-plot design including mown meadows (tractor-operated rotary-disc vs. double-bladed bar mower) and uncut refuges within grassland patches. We analysed the effects of (i) mower type, (ii) all working steps of the harvest process and (iii) uncut refuges on grasshopper densities and biomass. These data were used to assess the causes of insect declines through grassland harvest and to unravel the potential role of uncut areas as a refuge and also a source for recolonization of mown meadows. We hypothesised that bar mowers would be more insect friendly than the now widely used rotary-disc mowers. Nevertheless, we assumed that the losses occurring after mowing would be much more important for the strong overall decline of grasshopper densities and biomass by the end of the harvest process. Furthermore, we expected that uncut refuges would be of vital importance for the persistence of abundant grasshopper populations in the meadows. Based on our findings, we give recommendations to foster insect populations in meadow ecosystems.

2. Material and methods

2.1. Study area

The study was carried out in the Günz valley in the southwest of the German Federal State of Bavaria (Fig. 1a). The southern part of the valley belongs to the submontane and the northern part to the colline zone. Across this environmental gradient, mean annual temperatures increase from 7.7 to 9.2 °C and precipitation decreases from 1096–717 mm (meteorological stations: Kaufbeuren [716 m asl.] in the south and Günzburg [443 m asl] in the north, respectively; period: 1990–2020; German Weather Service, 2022). Today, the landscape is characterised by intensive agriculture; arable fields and improved grasslands dominate (BfN, 2012). However, there are still some species-rich grasslands such as only moderately fertilised lowland hay meadows, mown twice a year.

2.2. Sampling design

2.2.1. Study plots

In a previous study, we investigated the drivers of species richness of butterflies and grasshoppers in 39 randomly selected hay meadows across the study area (Fumy et al., 2023). From this set of patches, we chose those six meadows that were characterised by the highest grasshopper densities based on our field observations. The mean (± SE) size of the patches was 2.2 ± 0.3 ha. Three of the patches were located in the southern, submontane zone and another three patches in the northern, colline zone of the study area (Fig. 1a). In order to account for possible spatial autocorrelation, the two clusters of patches were considered as two different sub-areas in all analyses.

The characteristic plant community of the studied lowland hay meadows was the *Arrhenatherion elatioris,* but some plants of montane (*Triseto flavescentis-Polygonion bistortae*) and wet (*Molinietalia caeruleae*) meadows were usually also present (Fumy et al., 2023; for detailed descriptions of the plant communities see Burkart et al., 2004; Dierschke, 1997; Mucina et al., 2016). All meadows have been mown twice a year, in mid-June and mid-August, for at least the last three years (including the study year) (Fumy et al., 2023, own observation). Although all six hay meadows were characterised by a relatively high phytodiversity (own observation), they had a tall and dense vegetation. On average (± SE), in early-August (prior to the second harvest period), the grasslands had a vegetation height of 45.6 ± 4.0 cm, cover of grasses of 74.8 ± 3.4 % and cover of herbs of 31.0 ± 3.8 % (own unpublished data). The cover ratio between grasses and herbs was 2.6 ± 0.5.

To study the effects of the harvest process on grasshoppers in species-rich hay meadows, we established a randomised split-plot design at each patch: in order to assess the direct effects of the type of mower on grasshoppers, one half was cut by using a rotary-disc mower and the other half by a double-bladed bar mower (Fig. 1b). Both types of mowers were tractor-operated. Except the type of mower, all other aspects of the mowing process were kept constant: (i) the tractors with their attached mowers had a driving speed of ~10 km/h, (ii) the cutting height was ~7 cm and (iii) the working width was ~8 m.

Within each of the two plots mown by rotary-disc and double-bladed bar mowers, respectively, we installed two sub-plots, each with a size of 10 m × 50 m (Fig. 1b). In order to avoid edge effects (Schirmel et al., 2010), each sub-plot had a minimum distance of 20 m to the other sub-plot as well as to the border of the plot and patch, respectively. During each of the two harvest periods, one sub-plot per plot was harvested (hereinafter referred to as 'meadow sub-plot') and the other one was left as an uncut refuge. The mean (± SE) distance of the meadow sub-plots to the nearest patch edge was 30.6 m ± 6.9 m (range: 20–80 m). The grass verges at these patch edges had an average (± SE) width of 2.6 m ± 0.5 m (range: 1–5 m).

2.2.2. *Grasshopper assemblages*

In 2022, we studied the effects of the complete harvest process on grasshoppers. Harvest in hay meadows includes the following steps: (i) cutting of the vegetation, (ii) tedding of the cut vegetation until it is dry, (iii) windrowing of the dry hay and (iv) finally, the removal of the hay (Schoof et al., 2023). Usually, this process lasts for about two to three days. For each harvest period (mid-June, mid-August), grasshopper sampling was conducted at four times (hereinafter referred to as 'sampling events'): (i) on the day before cutting (hereinafter referred to as 'before cutting'), (ii) immediately after cutting ('after cutting'), (iii) two days after cutting, when the cut vegetation was drying ('during tedding'), and (iv) after hay removal, which was two to three days after cutting ('after removal'). Solely in the uncut refuges, we sampled grasshoppers only twice, during the first and last sampling event per harvest period (i.e., before cutting and after removal).

Grasshoppers were always sampled under favourable weather conditions (temperature > 15 °C, no rain) using a box quadrat (1.41 × 1.41 m) (Gardiner et al., 2005; Helbing et al., 2014; Löffler and Fartmann, 2017). We randomly placed the quadrat ten times per sub-plot (total area = 20 m^2) and counted all grasshoppers inside the quadrat—differentiated into nymphs and adults, the latter subdivided according to sex. Since all counted individuals during the second harvest period were adults, we calculated the live biomass of grasshoppers based on mean weights of males and females available for all detected species (Appendix 1, own unpublished results). The scientific nomenclature followed Fischer et al. (2020).

2.3. *Statistical analysis*

All statistical analyses were performed using R (R Development Core Team, 2023). To detect significant effects of the hay harvest (i.e., mower type and different working steps of the harvest process) and of the distance of the next patch edge on grasshopper densities and biomass, we calculated Generalized Linear Mixed-effects Models (GLMM) with negative-binomial error structure ('lme4′ package, Bates et al., 2015). To analyse the effect of mower type, grasshopper densities directly before and after cutting served as a response and mower type as a predictor variable. Since mower type had no effect on grasshopper densities, neither during the first nor the second harvest period, it was excluded from the subsequent analyses. To assess the effects of the different steps of the harvest process, densities (both harvest periods) and biomass (second harvest period) of grasshoppers were used as response variables and the sampling events or distance of the next patch edge as predictors. In all models, sub-plot nested in patch and patch nested in sub-area were used as random intercepts. The effects of mower type, different steps of the harvest process and distance to the next patch edge on the response variables (grasshopper density and biomass, respectively) were assessed by likelihood-ratio tests (comparison of full model and model without fixed factor). In the case of multiple comparisons (consideration of all four sampling events), significant differences were detected by Tukey's contrasts (glht function, 'multcomp' package, Hothorn et al., 2008). Possible inter-correlation between grasshopper density and biomass during the second harvest period was tested by Spearman rank correlation (r_s).

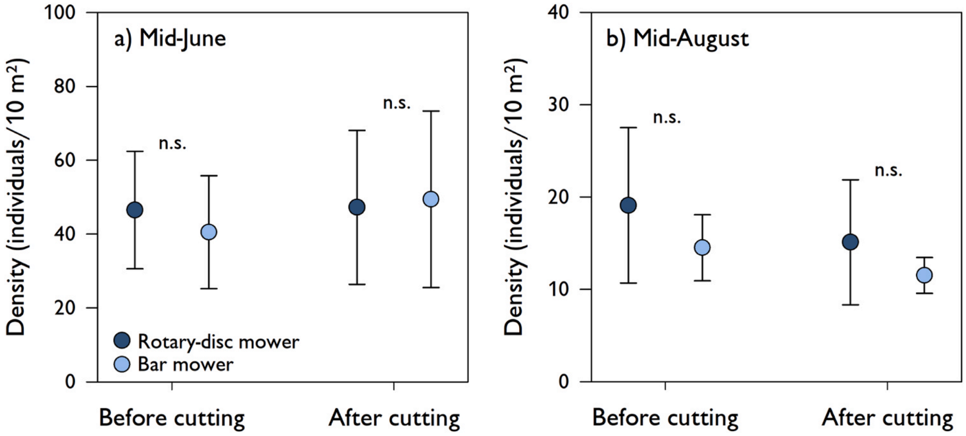

Fig. 2. Mean (± SE) grasshopper densities in meadow sub-plots mown with a rotary-disc ($n = 6$) and double-bladed bar ($n = 6$) mower, respectively, before and after mowing during the first (mid-June) (a) and second harvest period (mid-August) (b). Differences were analysed by using GLMMs with negative-binomial error structure. 'Meadow sub-plot' nested in 'patch' and 'patch' nested in 'sub-area' were used as random intercepts. For further information see 'Material and methods'. n.s. = not significant.

3. Results

In total, we recorded 8135 grasshopper individuals belonging to 15 species (Appendix 1). The most abundant ones were *Pseudochorthippus parallelus* and *Roeseliana roeselii*. Overall, 5635 (69.3 %) and 1849 (22.7 %) of the counted individuals, respectively, belonged to these two species. During the first harvest period, we observed 6570 individuals; the ratio between nymphs and adults was 4.3 : 1. During the second period, we counted 1565 individuals, all of which were adults.

During both harvest periods, grasshopper densities were similar before cutting in meadows that were subsequently mown by rotary-disc and bar mowers, respectively (Fig. 2). Even directly after cutting, there were no differences in grasshopper densities between meadows that were mown by the different types of mowers.

Grasshopper density and biomass (second harvest period) did not generally differ before cutting in sub-plots on meadows and uncut refuges (Figs. 3 and 4). Direct mortality through cutting was very low, since grasshopper densities and biomass (second harvest period) in meadow sub-plots did not differ before and directly after cutting. By contrast, within the two days following cutting (‘during tedding’), grasshopper densities and biomass (second harvest period) decreased sharply. Grasshopper density and biomass were strongly inter-correlated (second harvest period: $r_s = 0.98$, $N = 72$, $P \leq 0.001$). Additionally, during the first harvest period, we observed a further decline in grasshopper density until the hay had been removed (Fig. 3a). Overall, from the day before cutting until the end of the harvest process (‘after hay removal’), on average 91 % (first harvest period) and 85 % (second harvest period), respectively, of the grasshopper individuals had disappeared from the meadow sub-plots. Losses of grasshopper biomass amounted to 86 % (second harvest period).

By contrast, in uncut refuges, grasshopper density and biomass (second harvest period) strongly increased from the day before cutting until the end of the harvest process in the surrounding meadows (‘after removal’) (Figs. 3 and 4). By the end of the harvest process, grasshopper densities were on average 328 % (first harvest period) and 247 % (second harvest period), respectively, higher than before. Grasshopper biomass increased during the second harvest period by 234 %.

Despite the strong differences in grasshopper densities in meadow sub-plots compared to uncut refuges by the end of the first harvest period, there were no longer any differences before cutting in mid-August (Figs. 3 and 4). Grasshopper densities in meadow sub-plots had on average more than quadrupled during that time period but in uncut refuges it declined by more than 90 % (Figs. 2 and 3). The distance of the meadow sub-plots to the nearest patch edge had no effect on grasshopper densities (GLMM: estimate = –0.007847, $z = –0.794$, $P > 0.05$) and biomass (GLMM: estimate = –0.007574, $z = –0.\ 0.728$, $P > 0.05$) before the second cut.

4. Discussion

Surprisingly, our study revealed that tractor-operated rotary-disc and bar mowers did not differ in their effects on grasshopper mortality and that direct mortality through cutting was very low in the investigated hay meadows. By contrast, the vast majority of the individuals disappeared after cutting, especially during tedding but also after that, namely until the hay had been removed (only first harvest period). Overall, on average, 85–91 % of the individuals or biomass was lost by the end of the harvest process. By contrast, in uncut refuges, grasshopper densities and biomass increased on average by 234–328 % until the removal of the hay in the surrounding meadows, which lasted two to three days from cutting onwards. However, from the first harvest period in mid-June to the second one in mid-August, an alignment in grasshopper densities and biomass between meadow sub-plots and uncut refuges occurred.

Mowing by bar mowers is usually assumed to be less harmful for insects than the application of rotary mowers (Oppermann and

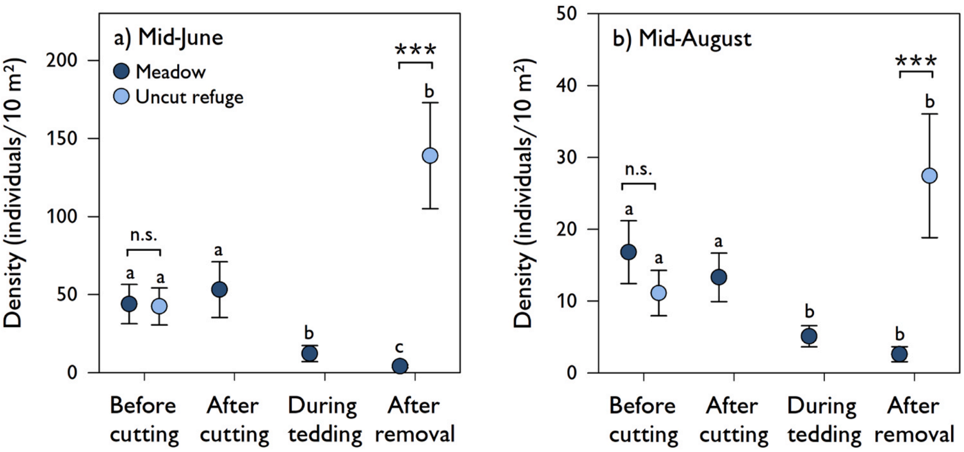

Fig. 3. Mean (± SE) grasshopper densities in sub-plots on meadows ($n = 12$) and uncut refuges ($n = 12$) before and after cutting, during tedding and after hay removal during the first (mid-June) (a) and second harvest period (mid-August) (b). Differences were analysed by using GLMMs with negative-binomial error structure. In case of multiple comparisons, significant differences were detected by Tukey’s contrasts. ‘Sub-plot’ nested in ‘patch’ and ‘patch’ nested in ‘sub-area’ were used as random intercepts. For further information see ‘Material and methods’. Different letters indicate significant differences in case of multiple comaprisons ($P < 0.05$). n.s. = not significant, ***$P < 0.001$.

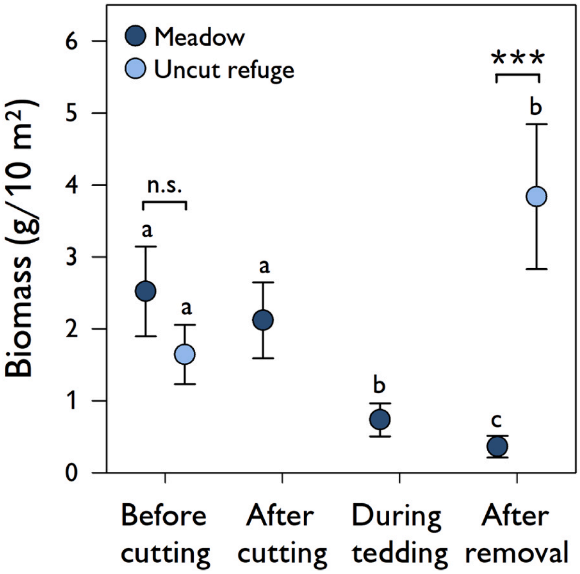

Fig. 4. Mean (± SE) grasshopper biomass in sub-plots on meadows ($n = 12$) and uncut refuges ($n = 12$) before and after cutting, during tedding and after hay removal during the first (mid-June) (a) and second harvest period (mid-August) (b). Differences were analysed by using GLMMs with negative-binomial error structure. In case of multiple comparisons, significant differences were detected by Tukey's contrasts. 'Sub-plot' nested in 'patch' and 'patch' nested in 'sub-area' were used as random intercepts. For further information see 'Material and methods'. Different letters indicate significant differences in case of multiple comaprisons ($P < 0.05$). n.s. = not significant, ***$P < 0.001$.

Krismann, 2003; Humbert et al., 2009; Steidle et al., 2022). In contrast to bar mowers, in particular rotary-tube but also rotary-disc mowers are known to have a suction effect on insects (Oppermann and Claßen, 1998; Schoof et al., 2023). Accordingly, rotary mowers may not only kill insects that are directly located at the cutting height but also those from the immediate surrounding. Hence, direct mortality through cutting also depends on the preferred strata above ground of the considered taxa (see overview in Schoof et al., 2023). Except the two ground-dwelling *Tetrix* species, which accounted for only 0.4 % of all observed individuals (Appendix 1), all other detected grasshoppers are inhabitants of the herbaceous layer (Detzel, 1998; Schlumprecht and Waeber, 2003). Within this stratum, they are usually located in the upper part, where solar irradiation is highest. This is especially true for dense grasslands exhibiting a cooler microclimate near the ground (Stoutjesdijk and Barkman, 2014). The investigated hay meadows in our study had a tall and dense vegetation (see 2.1 Study area). Mean vegetation height prior to the second harvest in mid-August was 46 cm but the average mowing height was around 7 cm. Hence, we suspect that during cutting nearly all grasshoppers were located far above the sphere of the mowers, even of the sucking effects of the rotary-disc mower, explaining the lack of both mower type effects (Fig. 2) and direct cutting effects in general (Figs. 3, 4).

Despite the absence of clear direct cutting effects on grasshoppers in the studied hay meadows, we observed severe losses in grasshopper density and biomass after cutting by the end of the harvest process (Figs. 3, 4). Comparably alarming declines during the harvest have also been observed in former studies (Kiel, 1999; Humbert et al., 2010b, 2012). Each cutting event causes severe changes in environmental conditions and, hence, in habitat quality. For grassland insects, cutting implies (i) the removal of the vast majority of the food resources, (ii) an abrupt change in the microclimate, leading to less balanced, warmer and drier conditions that may increase the risk of drying out, and (iii) the disappearance of shelter against vertebrate predators (such as insectivorous birds or mammals like the Red fox [*Vulpes vulpes*]) and extreme weather events (Guido and Gianelle, 2001; Fartmann et al., 2021; Schoof et al., 2023). Due to these adverse environmental conditions in mown grasslands, insects are known to search actively, in dependence of their mobility, for habitats in the vicinity offering a suitable habitat quality (Kiel, 1999; Guido and Gianelle, 2001; Schoof et al., 2023). Moreover, the further working steps of the harvest process following cutting may also cause direct mortality. This has especially been shown for the effects of tractor wheels during harvest on ground-dwelling organisms and of the baling process on grasshoppers (Oppermann and Krismann, 2003; Humbert et al., 2010a). In mown meadows lacking any shelter, grasshoppers usually gather on the windrows and many of them are killed by baling (Oppermann and Krismann, 2003). The authors showed that more than 50 % of all losses during the complete harvest process were regularly attributed to mortality through baling.

Our data do not allow an exact quantification of the impact of each of the potential drivers of density and biomass loss in the studied meadows. Nevertheless, we assume that (i) in particular emigration from the short and homogeneous meadows to uncut refuges or patch edges but also (ii) increased vertebrate predation were responsible for the severe decline. The doubling or even tripling of the grasshopper densities in the uncut refuges until the hay had been removed provides clear evidence for the prior. Since we regularly observed groups of Carrion crows (*Corvus corone*) and White storks (*Ciconia ciconia*) foraging directly after cutting on the meadows, the latter seems also be very likely. By contrast, due to the short time period of the harvest process, increased mortality due to food shortage and extreme weather would be a rather unlikely explanation for the severe declines. During the first harvest period, baling was very likely another cause of loss since we observed another decline in grasshopper densities from 'during tedding' to 'after removal'. In contrast to mid-August, when we only counted adults, in mid-June, nymphs strongly dominated (ratio nymphs to adults: 4.3 : 1). Nymphs are less mobile than adults (Ingrisch and Köhler, 1998). Hence, possibly a higher share of them was not able to reach the uncut refuges and especially patch edges within the short time period of the harvest process. Consequently, they may have used the windrows as shelter and have been killed by baling (cf. Oppermann and Krismann, 2003).

Two months after the first harvest (mid-August), there were no longer any differences in grasshopper densities between meadow sub-plots and uncut refuges (Fig. 3). This alignment coincided with an on average more than fourfold increase of the densities in meadows and a simultaneous decline by more than 90 % in uncut refuges. Consequently, we assume that grasshopper recolonization from the refuges to the meadow sub-plots, which were 20 m away, strongly contributed to these changes. By contrast, immigration from grassland verges at the patch edges seemed to play a minor role in our study. They were much smaller (mean width: 2.6 m) and further away from the meadow sub-plots (mean distance: 31 m) than the uncut refuges. Accordingly, we did not detect an effect of the distance of the nearest patch edge on grasshopper densities and biomass in the meadow sub-plots before the second harvest. An increase in grasshopper densities in the meadow sub-plots due to newly hatched individuals can also largely be excluded. The vast majority of the detected grasshopper species hatches usually before mid-June (Ingrisch and Köhler, 1998).

In summary, our study highlighted that (i) the vast majority of the severe grasshopper losses during the harvest process occurred after cutting and that (ii) uncut refuges play a vital role for the recolonization of mown meadows. We explain the lack of both mower-type and generally direct cutting effects by the tall and dense vegetation of the studied hay meadows, and, hence, the location of the grasshoppers far above the sphere of the mowers. Moreover, we assume that in particular emigration from the short and homogeneous meadows to uncut refuges or patch edges but also increased vertebrate predation were responsible for the severe losses in grasshopper density and biomass after cutting by the end of the harvest process. However, two months after the first harvest, these differences in grasshopper densities between meadow sub-plots and uncut refuges had already been counterbalanced. We hypothesise that grasshopper recolonization from the refuges to the meadow sub-plots, which were 20 m away, strongly contributed to this alignment.

5. Conclusion

Every cutting event, irrespective of the applied mower type, causes dramatic changes in environmental conditions and, hence, also in insect assemblages of grasslands (Schoof et al., 2023; this study). Loss rates in grasshoppers and many other insects usually exceed 70 % until the end of the harvest process, but are mostly higher (Humbert et al., 2010a; Schoof et al., 2023; this study). However, direct mortality through cutting by tractor-operated bar mowers and even rotary mowers is usually only responsible for a small part of the overall losses.

Due to the aforementioned and as stressed by our study, uncut refuges are of prime importance to secure abundant grasshopper populations in meadows in the long run. Firstly, such refuges guarantee a continuity in (i) food resources, (ii) a balanced microclimate and (iii) shelter against predators and extreme weather events for the resident individuals. Consequently, they are not affected by any of the harvest-related losses. Secondly, they serve as an important refuge for the emigrants from the mown parts of the meadow. As our study showed, with ongoing regeneration of the grassland vegetation, the formerly cut areas can successfully be recolonized from the refuges. Many other groups of animals, such as other arthropods or vertebrates, have been shown to benefit from uncut refuges (see overview in Schoof et al., 2023). To avoid negative effects of long-term abandonment on grassland vegetation (Moog et al., 2002; Schüle et al., 2023) but also on animal assemblages (Fartmann et al., 2021), the refuges should spatially vary from one mowing event to another (Scherer et al., 2023). As long as empirical evidence is missing, we recommend leaving 5–20 % of uncut refuges during each mowing event (see also Oppermann and Krismann, 2003; Humbert et al., 2010a; Scherer et al., 2023; Schoof et al., 2023). These refuges should be evenly distributed across the grassland patches. In our study, refuges had a size of 10 m × 50 m and grasshoppers were able to successfully recolonize mown parts 20 m apart from the refuges within two months. Accordingly, these values can be used as a further guidance for the implementation of the refuges within the meadows.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix

Table 1

Absolute number and proportion (%) of counted individuals as well as the mean body weight of living adult males and females of the detected grasshopper species in this study. Data on body weight are based on 10 samples for each sex and species (own unpublished results). Data for Leptophyes punctatissima are not shown since we only detected nymphs.

Species	Individuals		Weight (g)	
	Absolut	Proportion (%)	♂♂	♀♀
Chorthippus albomarginatus	46	0.6	0.07	0.21
Chorthippus biguttulus	66	0.8	0.09	0.18
Chorthippus dorsatus	414	5.1	0.10	0.20
Conocephalus fuscus	25	0.3	0.13	0.18
Euthystira brachyptera	17	0.2	0.09	0.30
Gomphocerippus rufus	2	0.0	0.10	0.20
Leptophyes punctatissima	5	0.1	.	.
Omocestus viridulus	4	0.0	0.11	0.30
Phaneroptera falcata	7	0.1	0.22	0.34
Pholidoptera griseoaptera	12	0.1	0.40	0.46
Pseudochorthippus parallelus	5635	69.3	0.10	0.20
Roeseliana roeselii	1849	22.7	0.29	0.48
Tetrix subulata	23	0.3	0.02	0.04
Tetrix undulata	5	0.1	0.03	0.05
Tettigonia viridissima	25	0.3	1.67	2.17
Sum	**8135**	**100**		

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