Agriculture, Ecosystems and Environment 181 (2013) 22–30

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: Evidence drawn from field-scale experimentation

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ARTICLE INFO

Article history:
Received 20 March 2013
Received in revised form 2 September 2013
Accepted 4 September 2013

Keywords:
Biodiversity
Bush cricket
Conservation
Cutting
Grasshopper
Haying

ABSTRACT

Semi-natural grasslands are widely recognized for their high ecological value. They often count among the most species-rich habitats, especially in traditional cultural landscapes. Maintaining and/or restoring them is a top priority, but nevertheless represents a real conservation challenge, especially regarding their invertebrate assemblages. The main goal of this study was to experimentally investigate the influence of four different mowing regimes on orthopteran communities and populations: (1) control meadow (C-meadow): mowing regime according to the Swiss regulations for extensively managed meadows declared as ecological compensation areas, i.e. first cut not before 15 June; (2) first cut not before 15 July (delayed treatment, D-meadow); (3) first cut not before 15 June and second cut not earlier than 8 weeks from the first cut (8W-meadow); (4) refuges left uncut on 10–20% of the meadow area (R-meadow). Data were collected two years after the introduction of these mowing treatments. Orthopteran densities from spring to early summer were five times higher in D-meadows, compared to C-meadows. In R-meadows, densities were, on average, twice as high as in C-meadows, while mean species richness was 23% higher in R-meadows than in C-meadows. Provided that farmers were given the appropriate financial incentives, the D- and R-meadow regimes could be relatively easy to implement within agri-environment schemes. Such meadows could deliver substantial benefits for functional biodiversity, including sustenance to many secondary consumers dependent on field invertebrates as staple food.

1. Introduction

Extensively managed grasslands are among the most species-rich habitats of the Palaearctic, typifying its characteristic cultural landscapes. These low input grasslands are considered of high natural value, inhabited as they are by many threatened plant and animal taxa (Veen et al., 2009). Biodiversity-rich grasslands have suffered dramatically from the green revolution: they have been systematically converted into arable lands, improved (i.e. intensified), or simply abandoned (Poschlod and WallisDeVries, 2002; Torok et al., 2011). Grassland intensification interventions include an increase of fertilizer input, application of pesticides, and reseeding, all of which results in increased grass production, enabling earlier and more frequent cuts, or higher grazing intensity. Concurrently, mechanization improved, field sizes expanded, and farming practices temporally and spatially simplified the matrix, leading to a massive homogenization of the agricultural landscape (Robinson and Sutherland, 2002). Most changes linked to farming intensification negatively impact grassland biodiversity, by eliminating plant, invertebrate and vertebrate populations (e.g. Wilson et al., 1999; Vickery et al., 2001; Marini et al., 2008; Wesche et al., 2012). To counteract this, many European countries have implemented targeted grassland agri-environment schemes (AES). Despite these incentives for more environmentally friendly management practices, such as reduced, or no fertilizer application, these conservation schemes have so far had only limited success (e.g. Kleijn et al., 2006; Knop et al., 2006; Aviron et al., 2009).

Mowing is a common practice in extensively managed grasslands and is considered to be one of the most efficient management options to fulfil the needs of the field flora (Grime, 2001; Schaffers, 2002). Thus, it is not surprising that the influence of mowing on plant communities has been intensively studied by conservation biologists and restoration ecologists (e.g. Bakker et al., 2002; Cop et al., 2009; Torok et al., 2011; Valko et al., 2012). In comparison, the influence of mowing on field invertebrates has received relatively little research attention (Littlewood et al., 2012). It is only recently that the impact of the regime and technique of mowing on invertebrates has been properly quantified (Humbert et al., 2009, 2012b).

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http://dx.doi.org/10.1016/j.agee.2013.09.003

In 2010, we launched an ambitious research programme with a double objective: (1) to better appraise the influence of different mowing regimes on invertebrates, and (2) to propose management measures that can be easily implemented by farmers. A multidisciplinary group of experts was created at the beginning of the programme, which included, among others, representatives of local and national environment and agriculture offices. This early collaboration was intended to overcome the conventional gap that exists between science, policy and practice, by building, from the outset, a catalogue of pragmatic evidence-based management measures for effective public actions (Sutherland et al., 2004; Arlettaz et al., 2010; Braunisch et al., 2012; Caudron et al., 2012). The research programme took place on the Swiss Plateau in extensively managed meadows, declared as ecological compensation areas (ECA) by the Swiss AES (Swiss Federal Council, 1998). We focused on ECA meadows because they currently are, among the Swiss lowland grasslands, those that harbour the less impoverished biodiversity.

Orthopterans were selected as a model taxon because they are key components of food chains within grasslands; principally herbivores, they represent an important food source for many predators, such as insectivorous vertebrates (Arlettaz et al., 1997; Wilson et al., 1999; Baur et al., 2006). In addition, orthopterans are considered to be good indicators of grassland ecosystem health as they readily respond to management intensification, which negatively affects species richness and population density (Van Wingerden et al., 1992; Marini et al., 2008).

The aim of this paper was to study how the different investigated mowing regimes affect orthopteran species richness and population sizes. The standard regulation for lowland ECA meadows stipulates a first cut not before 15 June. This practice is the most widely implemented AES option throughout Switzerland, covering 6.3% of the agricultural area (OFAG, 2012); it served as a control baseline in our experiments. It must be clear, however, that this measure is already considered to be an active management strategy aimed at promoting biodiversity in farmland. The following three management treatments were derived from the basic prescriptions of these control meadows. The first experimental mowing treatment stipulated delaying the first cut by one month. While the influence of delayed mowing on field invertebrates has been shown to be neutral or positive (reviewed in Humbert et al. (2012b)), its effects have never been specifically investigated on orthopterans. Predictions are thus not so easy to formulate. On the one hand, delaying mowing from 15 June to 15 July might have positive effects because it might give time to some orthopterans to reproduce before any mowing intervention. On the other hand, a summer cut may negatively impact the demography of larger organisms (including orthopterans) that typically have a longer developmental stage, i.e. a later phenology, compared to smaller organisms (Humbert et al., 2010b). The second experimental treatment limited the number of cuts to two per year, with a minimum of eight weeks in between. It has been established that reducing or limiting the number of cuts per year favours invertebrates (Helden and Leather, 2004; Marini et al., 2008), although it remains unclear if limiting the number of cuts to two provides better biodiversity outcomes than mowing regimes with non-prescribed number and frequency of cuts. The third experimental mowing treatment stipulated that each time the meadow was mown, an uncut grass area had to be left as a refuge. We hypothesized that this treatment would have a pronounced positive effect through basically two mechanisms: first, leaving uncut areas mitigate the directly negative mechanical impact of the harvesting process (Humbert et al., 2012a); second, uncut grass will enhance orthopteran fitness by providing continuity of shelter and food resources, which suddenly disappears over the area of the meadow which has been mown (Gardiner and Hassall, 2009).

The present study addresses these different issues through field-scale experiments, in which treatments consisted in specific targeted mowing regimes by farmers, with a given treatment being randomly attributed to a meadow. The major advantage of such an experimental approach, over a traditional correlational study, is that it better accounts for confounding factors, such as the influence of surrounding landscape features or the fact that AES are systematically applied in more marginal, i.e. less optimal agricultural land, thereby enabling firm, evidence-based recommendations to be drawn for meadowland management.

2. Materials and methods

2.1. Study sites

In 2010, 48 extensively managed hay meadows, registered as ECA since at least 2004 were selected in 12 study regions (with 4 meadows per region) across the Swiss Plateau (in the cantons of Vaud, Fribourg, Neuchâtel, Bern, Aargau and Basel-Landschaft; see Appendix A for exact coordinates). The meadows were situated between 390 and 833 m altitude. The four meadows in a single region were all located within 3.5 km radius, but were separated by a minimal distance of 440 m. The regions themselves were at least 5 km distant from each other (border to border). The average size of a meadow was 0.8 ha (range: 0.3–1.7 ha).

2.2. Experimental design

A randomized block design was adopted, where different management regimes were applied within each region, the latter representing the blocks, such that treatment replicates were across the regions, thus ensuring data independence. Within each region, the following management patterns (with abbreviations), consisting of different mowing regimes, were randomly assigned to the four meadows:

1. Extensively managed meadow with first cut not before 15 June, but with no restriction on the number and frequency of subsequent cuts (standards for ECA meadows according to Swiss regulations). These meadows constitute our baseline and are henceforth called control meadows (C-meadows) although they actually represented a specific management targeting biodiversity.
2. Extensively managed meadow with first cut not before 15 July, with again no restriction on the number and frequency of subsequent cuts (D-meadow, with D for delayed).
3. Extensively managed meadow with a maximum of two cuts per year and at least 8 weeks between the cuts, with first cut not before 15 June (8W-meadow, with 8W for eight weeks).
4. Extensively managed meadow with a rotational uncut refuge on 10–20% of the meadow area, meaning that a corresponding proportion of the area is left uncut each time the meadow is mown, with the location of the refuge being changed from time to time to avoid vegetation succession; otherwise first cut not before 15 June (R-meadows, with R for refuge).

Other management constraints included no fertilizer or pesticide application as well as grazing allowed only between 1 September and 30 November as specified in the present ECA regulations (Swiss Federal Council, 1998). The experiment started in spring 2010, with the random assignment of the different mowing regimes to the meadows; orthopterans were sampled in 2012.

Table 1
Summary of the mowing regimes. Mean ± standard deviation (and number of meadows) of the ordinal day the first and second cut occurred in 2010–2012. Not all meadows were cut a second time.

Treatment	2010		2011		2012	
	1st cut	2nd cut	1st cut	2nd cut	1st cut	2nd cut
Control	174.5 ± 5.4 (12)	239.4 ± 11.4 (9)	174.2 ± 2.8 (12)	242.5 ± 19.4 (8)	171.0 ± 4.7 (12)	235.7 ± 23.9 (12)
Delayed	200.0 ± 7.0 (12)	248.3 ± 20.3 (7)	209.3 ± 10.4 (12)	278.0 ± 34.6 (6)	204.9 ± 9.2 (11)	243.3 ± 19.3 (5)
Refuge	172.5 ± 2.8 (12)	234.4 ± 17.1 (12)	171.6 ± 3.3 (12)	233.5 ± 19.6 (12)	173.3 ± 9.7 (12)	225.1 ± 12.8 (11)
8W	172.3 ± 2.0 (12)	243.6 ± 19.7 (11)	175.6 ± 11.8 (12)	240.0 ± 14.6 (9)	174.9 ± 13.1 (12)	243.4 ± 21.2 (12)

2.3. Orthopteran sampling

The density of orthopterans (number of individuals per m^2) was measured using a biocenometer made of a net fastened around a strong circular wire so as to provide a total capture area of exactly 1 m^2. This technique is equivalent to the 1 m^2 box quadrat approved sampling methodology described by Badenhausser et al. (2009), except that our device was circular. The biocenometer was thrown into the field, and all trapped orthopterans belonging to the super families Tettigonioidea and Acridoidea (juveniles and adults) were recorded visually.

Orthopteran density was measured five times between 20 May and 17 August: twice before any mowing intervention; once at the end of June – beginning of July, when C-meadows, 8W-meadows and R-meadows had been mown, but not D-meadows; and twice after 25 July when all meadows had been mown at least once. Sampling took place on sunny days between 9 am and 6 pm. In each meadow, 16 × 1 m^2 samples were regularly taken across the meadow, along 2–4 (depending on meadow shape) parallel transects at a distance of 10 m, but excluding a 10 m buffer zone around the meadow border in order to minimize edge effects (Knop et al., 2006). In R-meadows, during the last three sampling sessions, eight extra samples were taken from the uncut area of a meadow, in addition to the 16 samples collected in the mown area outside the refuges.

The mean orthopteran density per meadow was calculated over the 16 samples. However, the initial developmental stages (<1 cm body length) were not included in the datasets because the detectability of early nymphs may vary between cut and uncut meadows. Adult orthopterans were identified to species level while juveniles (nymphs) were simply classified into their suborder (Caelifera or Ensifera). In order to obtain a full picture of orthopteran species richness, two persons proficient at orthopteran identification carried out a 15 min qualitative visual and acoustic survey in each meadow during the three summer sampling sessions (3rd, 4th and 5th session). Species richness was then calculated as the addition of species found with the biocenometer and during the visual surveys.

2.4. Statistical analysis

Effects of mowing regimes were analyzed with generalized linear mixed models. Response variables were orthopteran density and species richness; they were analyzed with either Poisson (density) or Gaussian (species richness) error distribution. Fixed effects were the four mowing regimes (C, D, 8W and R) and, when necessary, the sampling sessions, while regions (12 spatial replicates) were considered as a random effect.

Density analyses were performed with three linear models, using three seasonal datasets that regrouped sampling sessions (first model: sessions 1 and 2; second model; session 3; third model: sessions 4 and 5). In order to better appraise the influence of the mowing regime on the reproductive segment of the orthopteran populations, the same statistical analyses were then performed on adult density only, i.e. discarding nymphs. As species from the suborder Ensifera are, on average, larger than species from the suborder Caelifera, and given that these two suborders differ in terms of mobility and ecology (Reinhardt et al., 2005), separate models on each suborder were run. We also investigated variation in species-specific responses, but only focusing on the most abundant ones. Finally, linear models were run with data from R-meadows only, testing whether, within these meadows, density in the uncut refuges differed from density in the cut area.

In order to asses to which extent mowing regimes differed in their effects, planned orthogonal comparisons were additionally conducted by removing the control, or the control and D-treatment from the dataset. Model assumptions were checked and met for each analysis. All statistics were performed using R version 2.15.3 (R Core Team, 2013).

3. Results

3.1. Mowing regimes

C-meadows (control) and 8W-meadows (8 weeks treatment) had very similar management regimes: they were both cut on average 1.9 ± 0.5 (mean 2010–2012 ± standard deviation) times per year, with the first cut occurring on average on 22 June, and the second cut (if present) taking place at the end of August (see Table 1 for all cutting dates per year and treatment). R-meadows (refuge treatment) were cut on average 2.1 (±0.4) times per year, with the first cut occurring on average on 21 June and the second cut on 19 August. D-meadows (delayed treatment) were cut on average 1.6 (±0.6) times a year, with the first cut occurring on average on 23 July and the second cut on 13 September. In spring 2012, one D-meadow was unfortunately lost through conversion into a gravel-pit extraction site.

3.2. Orthopteran density

Mean orthopteran densities varied from 0.6 to 16 individuals per m^2 and were clearly influenced by mowing regimes (Fig. 1a). Before mowing (first and second sampling sessions), mean orthopteran density was significantly higher in D-meadows (mean ± standard error, SE; 11.93 ± 3.34) and R-meadows (4.86 ± 1.10) than in C-meadows (2.33 ± 0.6) and 8W-meadows (3.30 ± 0.75; all $P < 0.001$, except for R-meadows vs. 8W-meadows $P = 0.002$; see Table 2a for detailed model outputs). There were also significantly more orthopterans in D-meadows than in R-meadows ($P < 0.001$), while 8W-meadows and C-meadows did not differ from each other ($P = 0.086$). During the third sampling session (i.e. after all meadows except D-meadows had been cut), orthopteran density was significantly higher in D-meadows (14.38 ± 3.20) compared to C-meadows (1.63 ± 0.76; $P < 0.001$), whereas densities in 8W-meadows (1.43 ± 0.39), R-meadows (1.80 ± 0.37) and C-meadows did not differ from each other. During the fourth and fifth sampling sessions, i.e. after all meadows had been cut, there were significantly fewer orthopterans per m^2 in D-meadows (0.89 ± 0.15) than in C-meadows (2.51 ± 0.66; $P < 0.001$), whilst densities in 8W-meadows (1.99 ± 0.42), R-meadows (2.31 ± 0.44) and C-meadows did not differ from each other (Table 2a).

When restricting the analysis to adult orthopterans, too few adult specimens were available from the first and second sampling sessions for any statistical testing (Fig. 1b). During the third sampling session, there were significantly more adults in D-meadows (3.56 ± 1.97) than in C-meadows (0.19 ± 0.08; $P < 0.001$; Table 2b). Densities in 8W-meadows (0.24 ± 0.08), R-meadows (0.30 ± 0.10) and C-meadows did not differ. During the last two sampling sessions, there were significantly fewer adults per m^2 in the D-meadows (0.61 ± 0.12) compared to C-meadows (1.20 ± 0.56; $P = 0.015$). Densities in 8W-meadows (1.04 ± 0.36), R-meadows (1.29 ± 0.31) and C-meadows did not differ.

Analyses on Caelifera and Caelifera adults only (Fig. 1c and d; Table 2c and d) showed exactly the same responses as overall orthopterans, i.e. the same statistical differences between regimes appeared. Analyses on Ensifera and Ensifera adults only (Fig. 1e and f; Table 2e and f) showed responses that were broadly the same, but not all comparisons were significant (at $P = 0.05$ level). For example, no differences were found among regimes in sessions four and five. Note that Ensifera were at relatively

Table 2

Effect of mowing regimes on orthopteran densities (individuals m^{-2}). Table refers to, and follows the same layout as Fig. 1. Density analyses were performed with generalized linear mixed models, using three seasonal datasets that regrouped sampling sessions (first model: sessions 1 and 2; second model; session 3; third model: sessions 4 and 5). Parameter estimates (differences between expected mean densities on log scale) are given for the paired regime comparisons and significant contrasts are highlighted in bold. Abbreviations are: (C) C-meadows: control meadows with first cut not before 15 June; (D) D-meadows: mowing delayed by a month, i.e. after 15 July; (8W) 8W-meadows: as C-meadows, but minimum of 8 weeks between first and second cut; (R) R-meadows: as C-meadows, but uncut refuge left over 10–20% of meadow area.

Model (sampling session) and comparison	(a) All			(b) Adults only		
	Estimate	SE	$P(>\lvert z\rvert)$	Estimate	SE	$P(>\lvert z\rvert)$
Model 1 (session 1 & 2)						
D vs. C	1.547	0.141	**<0.001**	–	–	–
8W vs. C	0.288	0.168	0.086	–	–	–
R vs. C	0.719	0.155	**<0.001**	–	–	–
8W vs. D	−1.270	0.126	**<0.001**	–	–	–
R vs. D	−0.839	0.108	**<0.001**	–	–	–
R vs. 8W	0.431	0.142	**0.002**	–	–	–
Model 2 (session 3)						
D vs. C	2.178	0.243	**<0.001**	2.984	0.703	<0.001
8W vs. C	−0.130	0.332	0.696	0.267	0.901	0.767
R vs. C	0.103	0.313	0.741	0.477	0.863	0.581
8W vs. D	−2.320	0.258	**<0.001**	−2.733	0.625	<0.001
R vs. D	−2.087	0.233	**<0.001**	−2.522	0.569	<0.001
R vs. 8W	0.233	0.326	0.474	0.210	0.785	0.789
Model 3 (session 4 & 5)						
D vs. C	−1.104	0.268	**<0.001**	−0.804	0.332	0.015
8W vs. C	−0.228	0.197	0.248	−0.160	0.266	0.546
R vs. C	−0.139	0.193	0.471	−0.037	0.257	0.887
8W vs. D	0.852	0.277	**0.002**	0.618	0.337	0.067
R vs. D	0.940	0.274	**0.001**	0.742	0.331	0.025
R vs. 8W	0.089	0.205	0.664	0.124	0.268	0.644

	(c) Caelifera only			(d) Caelifera adults only		
	Estimate	SE	$P(>\lvert z\rvert)$	Estimate	SE	$P(>\lvert z\rvert)$
Model 1 (session 1 & 2)						
D vs. C	1.603	0.154	**<0.001**	–	–	–
8W vs. C	0.359	0.181	0.058	–	–	–
R vs. C	0.789	0.168	**<0.001**	–	–	–
8W vs. D	−1.255	0.134	**<0.001**	–	–	–
R vs. D	−0.826	0.115	**<0.001**	–	–	–
R vs. 8W	0.430	0.150	**0.004**	–	–	–
Model 2 (session 3)						
D vs. C	2.125	0.246	**<0.001**	2.906	0.738	**0.000**
8W vs. C	−0.151	0.337	0.653	0.141	0.972	0.885
R vs. C	0.102	0.316	0.746	0.455	0.909	0.617
8W vs. D	−2.289	0.264	**<0.001**	−2.782	0.697	**0.000**
R vs. D	−2.035	0.236	**<0.001**	−2.468	0.605	**<0.001**
R vs. 8W	0.254	0.331	0.443	0.314	0.854	0.713
Model 3 (session 4 & 5)						
D vs. C	−1.128	0.272	**<0.001**	−0.834	0.339	**0.014**
8W vs. C	−0.216	0.198	0.275	−0.139	0.268	0.605
R vs. C	−0.157	0.195	0.419	−0.066	0.263	0.802
8W vs. D	0.888	0.281	**0.002**	0.669	0.344	0.052
R vs. D	0.947	0.279	**0.001**	0.742	0.340	**0.029**
R vs. 8W	0.059	0.206	0.775	0.073	0.272	0.789

	(e) Ensifera only			(f) Ensifera adults only		
	Estimate	SE	$P(>\lvert z\rvert)$	Estimate	SE	$P(>\lvert z\rvert)$
Model 1 (session 1 & 2)						
D vs. C	1.237	0.360	**0.001**	–	–	–
8W vs. C	−0.163	0.464	0.725	–	–	–
R vs. C	0.273	0.417	0.513	–	–	–
8W vs. D	−1.405	0.385	**<0.001**	–	–	–
R vs. D	−0.969	0.327	**0.003**	–	–	–
R vs. 8W	0.436	0.432	0.314	–	–	–
Model 2 (session 3)						
D vs. C	3.476	1.660	0.036	3.582	2.344	0.127
8W vs. C	0.606	2.030	0.765	1.099	2.667	0.680
R vs. C	0.154	2.225	0.945	0.693	2.829	0.806
8W vs. D	−2.870	1.243	**0.021**	−2.483	1.393	0.075
R vs. D	−3.322	1.541	**0.031**	−2.888	1.682	0.086
R vs. 8W	−0.452	1.934	0.815	−0.406	2.108	0.848
Model 3 (session 4 & 5)						
D vs. C	0.000	1.670	1.000	0.000	1.670	1.000
8W vs. C	−2.485	4.163	0.551	−2.485	4.163	0.551
R vs. C	0.734	1.405	0.601	0.734	1.405	0.601
8W vs. D	−2.485	4.178	0.552	−2.485	4.178	0.552
R vs. D	0.734	1.447	0.612	0.734	1.447	0.612
R vs. 8W	3.219	4.079	0.430	3.219	4.079	0.430

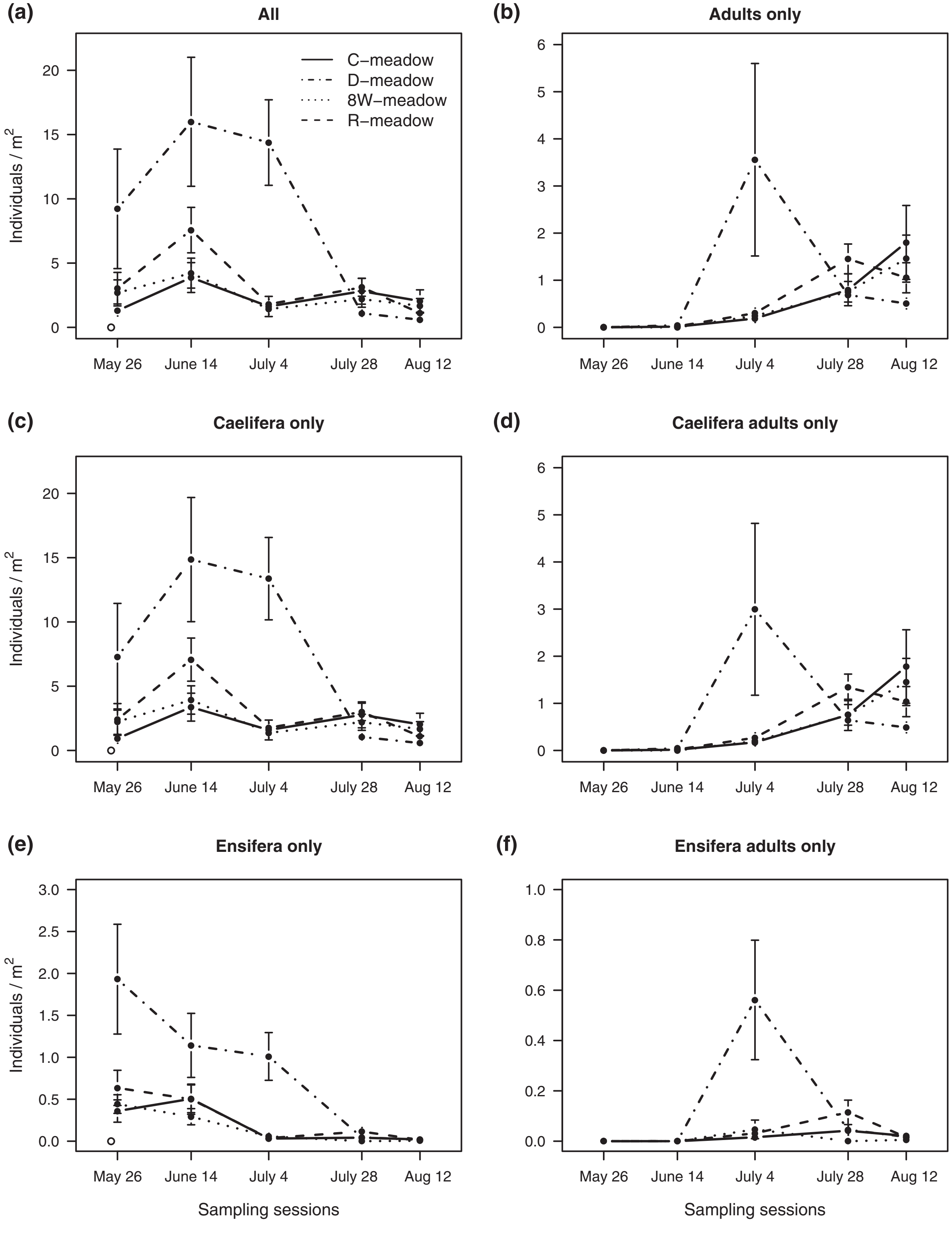

Fig. 1. Seasonal (May–August 2012) density (mean ± standard error) of orthopterans in response to the four different mowing regimes. Each sampling session is represented by a single date that corresponds to the average of the 4–12 days needed to complete the session. The figure is divided in six parts according to orthopteran suborder(s) and developmental stage: (a) all individuals (nymphs and adults of both Caelifera and Ensifera); (b) adults only; (c) Caelifera only; (d) Caelifera adults only; (e) Ensifera only; (f) Ensifera adults only. C-meadows: control meadows (first cut not before 15 June); D-meadows: mowing delayed by a month, i.e. after 15 July; 8W-meadows (as C-meadows, but minimum of 8 weeks between first and second cut); R-meadows: as C-meadows, but uncut refuge left over 10–20% of meadow area. See Table 2 for statistical analyses.

low densities compared to Caelifera, which limited power in the analyses of the former taxon.

The even more restricted analyses of species-specific responses to mowing regimes retained the following seven dominant species (number of meadows out of 47 harbouring the species): *Chorthippus parallelus* (47), *Chorthippus biguttulus* (46), *Metrioptera roeselii* (41), *Mecostethus parapleurus* (28), *Tettigonia viridissima* (25), *Chorthippus brunneus* (23), *Gomphocerippus rufus* (15). Analyses were limited to sampling sessions three, four and five because nymphs recorded in sampling sessions one and two were not identified to species level. Species-specific responses showed the same trends as with all orthopterans pooled, but significant differences

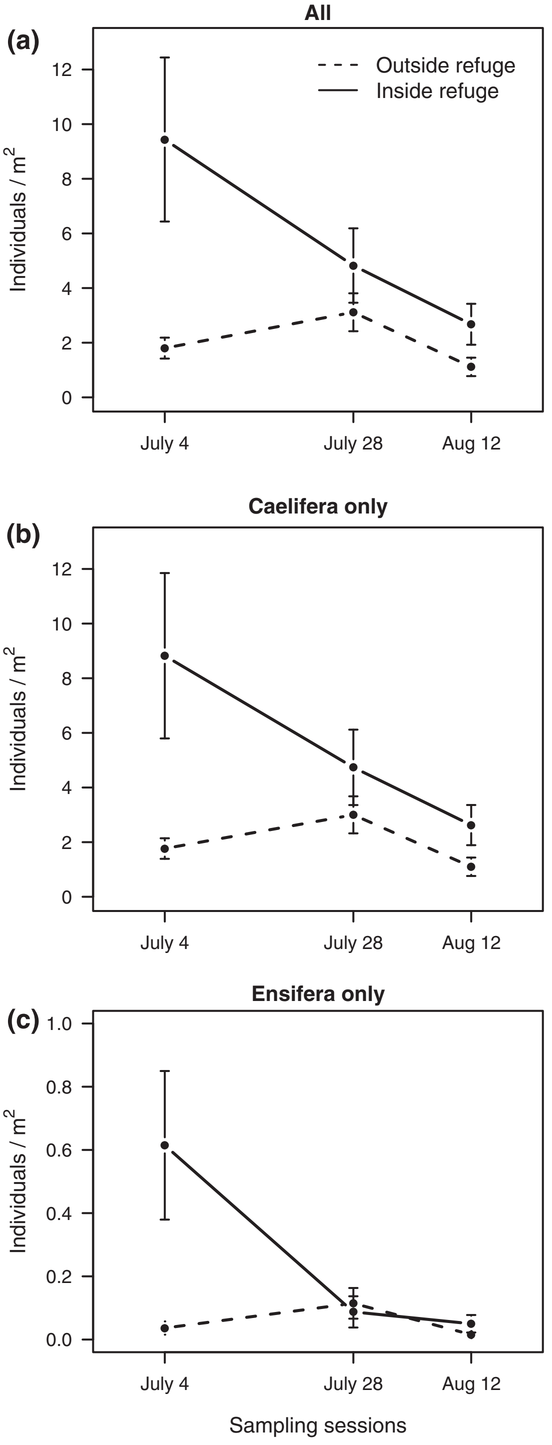

Fig. 2. Seasonal density (mean ± standard error) of orthopterans within R-meadows after the initiation of mowing operations (sampling sessions 3–5). Shown are the densities inside and outside (area of the meadow submitted to mowing) the uncut refuge. See Table 3 for statistical analyses.

Table 3
Paired comparisons of orthopteran densities (individuals m^{-2}) inside vs. outside (area of the meadow submitted to mowing) the uncut refuge within R-meadows after the initiation of mowing operations (sampling sessions 3–5). Table refers to, and follows the same layout as Fig. 2. Density analyses were performed with generalized linear mixed models on each sampling session separately. Parameter estimates (differences between expected mean densities on log scale) are given for the paired comparisons and significant contrasts are highlighted in bold.

Suborder(s), and sampling session	Estimate	SE	$P(>\|z\|)$
(a) All			
Session 3	1.656	0.235	**<0.001**
Session 4	0.350	0.222	0.116
Session 5	0.867	0.346	**0.012**
(b) Caelifera only			
Session 3	1.609	0.239	**<0.001**
Session 4	0.368	0.226	0.103
Session 5	0.860	0.349	**0.014**
(c) Ensifera only			
Session 3	2.825	1.556	0.070
Session 4	−0.270	1.368	0.844
Session 5	1.163	2.708	0.668

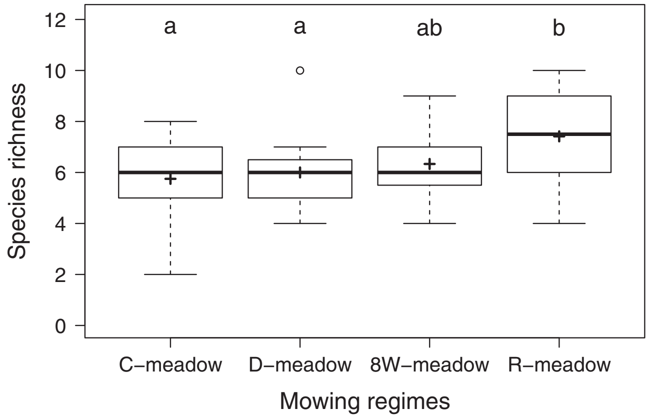

Fig. 3. Orthopteran species richness with respect to mowing regime (median: bold line; mean: cross; first and third quartiles: box borders; interquartile distance multiplied by 1.5: whiskers; and open circles: outliers). Different letters indicate significant differences among regimes at an alpha rejection level of 0.05. For abbreviations, see legend of Fig. 1, for statistical analyses see Table 4a.

were detected only for *C. parallelus:* during the third sampling session, the density in D-meadows was significantly higher than in C-meadows, 8W-meadows and R-meadows ($P < 0.001$ for all tests).

After the first cut (samples from the third, fourth and fifth sessions), densities of orthopterans differed between uncut and cut areas within R-meadows (Fig. 2a). While density inside uncut grass refuges (9.44 ± 3.00) was significantly higher compared to density outside them (1.80 ± 0.38; $P < 0.001$, Table 3a) during the third sampling session, the difference vanished during the fourth sampling session (mean ± SE density inside and outside refuge was 4.83 ± 1.24 and 3.11 ± 0.69, respectively), reappearing only during the fifth sampling session, with density inside uncut grass refuges being higher (2.68 ± 0.68) than outside refuges (1.11 ± 0.34; $P = 0.012$; Table 3a). The same significant differences appeared when analysing Caelifera only, but no differences were detected when analysing Ensifera only (Fig. 2b and c; Table 3b and c).

3.3. *Orthopteran species richness*

Overall, 22 orthopteran species were recorded, of which six are red listed (Appendix A). Average (±SE) number of species per meadow was 6.38 ± 0.26 (Fig. 3). There were significantly more species in R-meadows (7.42 ± 0.56) than in C-meadows (5.75 ± 0.49; $P = 0.018$) and D-meadows (6.00 ± 0.50; $P = 0.048$), but not than in 8W-meadows (6.33 ± 0.47; $P = 0.142$; Table 4a). Species richness in C-meadows, D-meadows and 8W-meadows did not differ significantly. Additional analyses on species richness of Caelifera and Ensifera separated showed similar trends, but significant differences were detected only for Ensifera with more species in R-meadows (2.67 ± 0.43) than in C-meadows (1.58 ± 0.23; $P = 0.022$; Table 4b and c; figures not shown).

4. Discussion

This study shows that relatively slight changes in grassland management practices, such as delaying mowing or leaving uncut grass refuges, can make a significant difference for biodiversity. Compared to our control meadows (C-meadows; first cut not before 15 June, no grass refuge left), orthopteran density in the spring and early summer two years after the introduction of these alternative management measures were, on average, five times higher in

Table 4
Orthopteran species richness in relation to mowing regime. Table shows results for all orthopteran species (including both Caelifera and Ensifera), Caelifera species, and Ensifera species only. Data were analyzed with linear mixed models, p-values and 95% confidence intervals (CI) were computed with 1 million Markov chain Monte Carlo (MCMC) iterations. MCMC mean parameter estimates (differences between expected mean densities) are given for the paired regimes comparisons and significant contrasts are highlighted in bold. For abbreviations, see legend of Table 2.

Suborder(s) and comparison	MCMC mean	Lower 95% CI	Upper 95% CI	MCMC *P*-value
(a) All				
D vs. C	0.242	−1.147	1.642	0.727
8W vs. C	0.584	−0.798	1.930	0.391
R vs. C	1.667	0.301	3.026	**0.018**
8W vs. D	0.334	−1.074	1.761	0.633
R vs. D	1.409	0.026	2.802	**0.048**
R vs. 8W	1.085	−0.407	2.554	0.142
(b) Caelifera				
D vs. C	0.017	−0.913	0.891	0.975
8W vs. C	0.166	−0.720	1.056	0.724
R vs. C	0.585	−0.296	1.493	0.191
8W vs. D	0.152	−0.783	1.056	0.749
R vs. D	0.567	−0.325	1.518	0.209
R vs. 8W	0.412	−0.535	1.379	0.377
(c) Ensifera				
D vs. C	0.235	−0.682	1.198	0.618
8W vs. C	0.416	−0.509	1.347	0.369
R vs. C	1.086	0.199	2.061	**0.022**
8W vs. D	0.175	−0.815	1.235	0.735
R vs. D	0.846	−0.137	1.922	0.102
R vs. 8W	0.667	−0.366	1.660	0.192

meadows in which mowing was delayed by a month (D-meadows), and twice as high in meadows where an uncut refuge was maintained during mowing operations (R-meadows). Furthermore, we were able to show that, after just two years of this targeted management, leaving uncut grass refuges also promotes species richness among orthopterans. Delaying mowing, or leaving small patches of the grassland area uncut does not require extra work by farmers and would thus be readily implementable in extant agri-environment schemes (AES). The different experimental mowing regimes were readily implemented by the farmers, suggesting that these could be well-accepted measures providing financial compensation were made available for the reduction in hay production and nutritive value (Cop et al., 2009).

These findings provide clear advice not only for improving biodiversity in extensively managed meadows or field margins under AES (e.g. Kleijn et al., 2006; Badenhausser and Cordeau, 2012), but also for the management of high natural value grasslands beyond AES, buffer zones of wetland nature reserves, river and canal embankments, and road verges (Noordijk et al., 2009; Veen et al., 2009). By providing additional resources to upper trophic levels, all these measures will contribute to re-instating integral, functional food chains within modern agro-ecosystems.

4.1. Impact of mowing regimes on orthopteran density

A first major outcome of our experimental manipulation of mowing regimes is the demonstration of a so-called “cumulative” effect, namely that measures implemented in 2010 and 2011 had carried-over effects discernable in 2012. In fact, we observed tremendously increased densities of orthopterans on the first two sampling sessions in 2012, i.e. in spring prior to any mowing operation. A five times higher orthopteran density in spring 2012 in D-meadows, compared to baseline control C-meadows, means that massively increased egg production took place the previous year, due either to a larger number of reproducers and/or to a higher individual reproductive success (Grant et al., 1993). Definitely, delaying the first possible cut until 15 July (D-meadows) allowed many more orthopterans to reach adulthood and to reproduce, thanks to both continuous food supply and no mortality induced by the mowing operation itself before the first cut (68–82% mortality according to Humbert et al., 2010a). In fact, in D-meadows during the third sampling session (ca. 4 July) there were 3.6 adult orthopterans per m^2 which is more than what was recorded at any other time of the season, and more than in any other mowing regimes. Delaying the first cut to 15 July in turn led to delaying the second cut to mid-September, when reproduction is over for most orthopterans (Baur et al., 2006), while it additionally contributed to fewer mean number of cuts per year in that treatment. The positive effect of the uncut grass refuge principally results from the same mechanisms as for delaying mowing. An earlier experiment has established that leaving 10% of the area of a meadow uncut can reduce orthopteran mortality by 30–35% (Humbert et al., 2012a).

Later in the season (at the fourth and fifth sampling sessions), when all mowing operations are finished, any observed differences among mowing regimes mirror the combined immediate and cumulative effects of the various mowing patterns. D-meadows had significantly lower densities than the other mowing regimes, which contrasts with the mass densities they harboured until mid summer, but values in all regimes were extremely low compared to the situation from spring to midsummer. This dramatic decrease to a few orthopterans per m^2 we observed confirms the overall severe negative impact of mowing on orthopterans (Humbert et al., 2010a).

Within R-meadows, orthopteran density remained spatially heterogeneous for a while after the first cut. If a high density in the uncut refuge just after mowing is not surprising (Müller and Bosshard, 2010; Humbert et al., 2012a), a discernable effect until two weeks (ca. 4 July) after mowing is reported for the first time. Uncut refuges thus not only enable orthopterans to avoid being mechanically eliminated by mowing, but they also provide shelter and food resources until the re-colonisation of the mown fraction of the meadow is again possible (see also Gardiner et al., 2002).

A second important outcome is that both suborders, Caelifera and Ensifera, responded in the same way to the mowing regimes, i.e. they were both more abundant in the D- and R-treatments, and inside the uncut refuge area, showing that even if they have some different ecological requirements, these management measures can favour both suborders. Data were limited regarding species-specific conclusions, and only *C. parallelus* was sufficiently abundant and widespread to detect a positive effect of

D-treatment on its population. Nevertheless, the impact of mowing regime on orthopteran density depends on the identity and environmental requirements of the dominant species, which were in this study mainly generalists (Reinhardt et al., 2005).

Finally, the observation that orthopteran communities and population sizes did not differ between the 8W-meadows and the C-meadows is due to unexpectedly very similar mowing practices in these two regimes: actually, the average number of weeks between the first and second cut was 9.7 weeks in 8W-meadows and 9.4 weeks in C-meadows, demonstrating that such a mowing prescription is meaningless.

4.2. Impact of mowing regimes on orthopteran species richness

There were, on average, 23% more species ($n = 7.4$) in R-meadows compared to C-meadows ($n = 5.8$), while the other two treatments did not increase species numbers. Knop et al. (2006) already found significantly more orthopteran species in Swiss extensively managed ECA hay meadows compared to conventionally managed, improved meadows. Here we demonstrate that, among extensively managed ECA hay meadows, species richness can be further increased if uncut grass refuges are left uncut when mowing. Leaving uncut areas increases local-scale habitat and sward heterogeneity, offering a broad palette of ecological niches that boost invertebrate diversity including orthopterans (Guido and Gianelle, 2001). Ensifera benefitted more than Caelifera from the measure (see also Braschler et al., 2009), which is easily explained by a general preference of the former for denser, more structured habitats (Baur et al., 2006).

4.3. Conclusions and management recommendations

This study provides strong evidence that, among extensively managed hay meadows, delaying the first mowing date from early to mid summer boosts orthopteran density, while leaving uncut grass refuges is an efficient measure favouring orthopteran species diversity and abundance. While landscape factors must be considered in agri-environmental conservation planning for most components of farmland biodiversity, this research suggests that specific conservation and restoration action for orthopterans inhabiting meadowland can be achieved by simple measures implemented at the field scale (see also Poniatowski and Fartmann, 2010).

We recognize that these outcomes are not totally new. Delayed, and in particular partial or rotational mowing have already been recommended, not only for orthopterans (e.g. Guido and Gianelle, 2001; Marini et al., 2008; Braschler et al., 2009; Gardiner and Hassall, 2009; Müller and Bosshard, 2010; Humbert et al., 2012a), but also for several other grassland invertebrates that are sensitive to mechanized mowing, such as butterflies (both larvae and adults), bees and spiders (e.g. Buri et al., in prep; Baines et al., 1998; Dover et al., 2010; Humbert et al., 2010b; Cizek et al., 2012). This study, however, is the first that actually proves positive, immediate and cumulative (over three years) effects of such measures on an essential component of grassland food chains. Although it remains to be experimentally established to what extent other taxa of the upper trophic levels benefit from these measures, it is likely that an increased abundance of orthopterans will have positive effects on agro-ecosystem functioning and food web integrity given that this taxon constitutes a staple commodity for a great variety of insectivorous predators (e.g. Arlettaz et al., 1997; Vickery et al., 2001; Kovacs-Hostyanszki et al., 2011). We also stress that the exact responses of orthopterans to the different mowing regimes might depend on the weather conditions of the previous and current years which, in turn, influence the phenological development of the species (Thorens, 1993; Gardiner and Hassall, 2009). In Switzerland, 2011 was the hottest year since the climatic records began in 1864, and it was also rather dry. Spring 2012 was relatively hot and sunny too, which may have advanced orthopteran development, while June and July were cooler and wetter than usual.

Based on our principal findings, we formulate the following recommendations for improving agri-environmental measures, within the Swiss scheme and beyond. A fraction of extensively managed meadows should have their earliest possible mowing date postponed until mid summer (ca 15 July), while another fraction of these extensive meadows should maintain, including over winter, an uncut grass refuge on typically 10–20% of the grassland area (see also Schmidt et al., 2008). If implemented in concert across the matrix, these two measures are likely to produce additional positive effects through the increase of spatial habitat heterogeneity at the landscape scale (Benton et al., 2003). We believe that these rather simple measures could pave the way towards more efficient AES and sustainable agricultural management in the future.

Acknowledgements

We thank our colleagues at the Division of Conservation Biology and the members of the accompanying group for valuable inputs, logistical support, and field assistance, with a special credit to Laura Bruppacher and Nadia Bianco. Thanks to the farmers who collaborated in this project, allowing us to work in their fields and applying the management we prescribed. We are grateful to the Swiss National Science Foundation (grant no. 31003A_125398/1 to R. Arlettaz), the Federal Office for the Environment, and several Swiss cantons (Aargau, Bern, Basel-Landschaft, Fribourg, Graubünden, Neuchâtel and Vaud) for their financial support. Many thanks to Markus Fischer and Jérôme Pellet for co-initiating this project, and to Aliki Buhayer who assisted with the English.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.09.003.

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