Promoting parasitic wasps among Swiss lowland extensively managed meadows: positive effects of delaying mowing and leaving uncut grass refuges

Masterarbeit der Philosophisch-naturwissenschaftlichen Fakultät der

Universität Bern

vorgelegt von

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2015

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Promoting parasitic wasps among Swiss lowland extensively managed meadows: positive effects of delaying mowing and leaving uncut grass refuges

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Abstract

Intensification of agricultural practices is one of the main threats to farmland biodiversity. To alleviate the negative consequences of intensification, agri-environment schemes (AES) were established in Europe in the early 1990s. In Switzerland 13.5% of the utilized agricultural land are nowadays registered as AES (biodiversity promoting areas; BPA). The most common type of BPA are extensively managed meadows (EMM; about 50% of total land under BPA in Switzerland), which are considered as one of the species-richest habitats in Europe. The main goal of this study was to experimentally test if alternative mowing regimes (different from those required by the current Swiss prescriptions) within EMMs can promote parasitic wasps. Parasitic wasps were chosen as study model because they are important biological pest control agents and are good bioindicators of overall arthropod diversity in farmland. In 2010, 48 EMMs registered as BPA since at least 2004 were selected in 12 study areas across the Swiss Plateau. Within each study area, the following four mowing regimes were randomly assigned to four meadows: (1) first cut not before 15 June (standard for EMM according to Swiss regulations, C-meadow); (2) first cut not before 15 June and second cut not earlier than eight weeks after the first cut, with a maximum of two cuts per year (8w-meadow); (3) first cut not before 15 July (D-meadow, with D for delayed); (4) first cut not before 15 June but with 10–20% of the area left uncut serving as refuge (R-meadow). Parasitic wasps were sampled twice in 2014 (once before and once after 15 June) using a specially designed triangular sweepnet. One major result was that a cumulative effect was induced by the D-regime, i.e. measures implemented in 2010–2013 had carried-over effects discernable in 2014. Before mowing the abundance of parasitic wasps was, on average, as much as ten times higher in D- than in C-meadows. After mowing, family richness and genera richness were significantly greater in the uncut grass refuge compared to the mown area. This shows that the uncut refuge provides alternative habitat to parasitic wasps when the rest of the meadow has been mown. Similarly, after mowing, a combination of cumulative and immediate positive effects of D-meadows (compared to C-meadows) was observed in the abundance of Chalcidoidea, Eulophidae and Pteromalidae, as well as in terms of family and genus richness. This study demonstrates for the first time that delaying mowing from mid-June to mid-July and leaving uncut grass refuges at mowing can both enhance population abundances and taxonomic richness of parasitic wasps in EMMs. A systematic implementation of such measures across the agricultural matrix could secure and potentially increase the ecosystem service provided by this taxon.

Keywords: parasitic wasp, mowing, refuge, conservation, biodiversity, biodiversity promoting area, agri-environment schemes

Introduction

Intensification of land use has led to a severe decline of semi-natural habitats across Europe (Krauss, Bommarco et al. 2010), reducing both abundances and diversity of invertebrate groups (Batáry, Orci et al. 2007, orthopterans; Hoste-Danylow, Romanowski et al. 2010 & Kremen, 2002 , hymenopterans). About half of Europe's endemic species depend on semi-natural grasslands (Veen, Jefferson et al. 2009; Török, Vida et al. 2011); therefore their conservation is a priory. As a response to the biodiversity loss many EU countries have implemented agri-environment schemes (AES) that financially support farmers for modifying their farming practices so as to provide environmental benefits. The objectives of the AES usually reflect a combination of the main environmental, ecological and socio-economic problems associated with agriculture, as well as the political situation in each country (Kleijn and Sutherland 2003). In Switzerland, the main AESs available to farmers concentrate on wildlife and habitat conservation measures, they are called biodiversity promoting areas (BPAs) (Kleijn and Sutherland 2003; Aviron, Nitsch et al. 2009). Swiss farmers are obligated to set minimum 7% of their farmland as BPA, up to now BPAs covers 13.5% of the total Swiss utilized agricultural areas. At present farmers can choose among16 different types of such areas, with the most common one being extensively managed meadows (EMM) (Büchi 2002; Caillet-Bois, Weiss et al. 2015). The standard regulation for lowland EMM registered as BPA stipulates no fertilizer input and a first cut not before 15 June. The primary goal of these EMM is to restore and conserve the flora and fauna biodiversity typical of these habitats, yet, the benefits of these schemes for biodiversity are far from evident (Aviron, Nitsch et al. 2009).

In 2010, the Division of Conservation Biology at the University of Bern launched a long-term field-scale research project with the main objective to test new management regimes that can potentially improve the effectiveness of BPA EMM to restore and conserve farmland biodiversity for sustaining fundamental agro-ecosystem processes and services. Specifically, among lowland BPA EMMs, three alternative mowing regimes, plus the standard one, were experimentally manipulated at the field scale in order to increase spatio-temporal heterogeneity, which was hypothesized to be a key factor to restore biodiversity (Questad and Foster 2008; Buri, Arlettaz et al. 2013). After studying the effects of these alternative mowing regimes on wild bees in 2011 (Buri, Humbert et al. 2014), orthopterans in 2012 (Buri, Arlettaz et al. 2013), planthoppers, leafhoppers and spiders (2011-2012, Buri et al. in *prep*), as well as on butterflies in 2013 (Kühne, Arlettaz et al. 2015), parasitic wasps were investigated in 2014 (this paper). Parasitic wasps were chosen as study object because they are link to an important ecosystem service of pest control (Wilby and Thomas 2002; Fiedler, Landis et al. 2008), they are primary, secondary and hyper parasitoids typically occupying the third and fourth trophic levels in complex food webs (Godfray 1994). It has been shown that higher trophic level organisms often respond stronger to agricultural intensification (Hawkins 1994), almost 75% of all species of Apocrita (wasps, bees, ants) are, during the larval stage, parasitoids of other insects or spiders (Goulet and Huber 1993). The high diversity of the parasitic wasps and their ability to respond in a density-dependent manner to the population size of their hosts, make them essential to the maintenance of ecological balance (La Salle and Gauld 1992), so that the dynamic equilibrium within a community of pests and their biological control agents remain relatively stable. They control and mitigate the abundance of different pests, which makes them very important naturally occurring biological control agents, e.g. it has been shown that increasing the richness of the most important natural enemies (one is: parasitic wasp, *Aphidius ervi*) of pea aphids can reduce its density (Cardinale, Harvey et al. 2003; Petermann, Muller et al. 2010; Martin, Reineking et al. 2013). Furthermore, they are sensible to changes in their environmental conditions, making them good bioindicators to assess the general states of arthropod populations in agro-ecosystems (Anderson, McCormack et al. 2011).

BPA meadows have the potential in providing parasitoids by a wider range of hosts and better nectar sources so that influencing their immigration and feeding behavior (Büchi 2002; Anderson, McCormack et al. 2011). This study wanted to investigate the following questions: what are the exact influences of different mowing regimes on the abundance of parasitic wasps and their family and genera richness, and if parasitoids actively use the uncut grass refuge when the rest of the meadow is mown. Our predictions were the following: (i): meadows with postponed mowing dates will have a greater diversity (abundance and richness) of parasitic wasps, since delaying mowing has either a positive or a neutral effect on invertebrate biodiversity (Humbert, Pellet et al. 2012). More specifically, before mowing we expect a positive carried over effect from the previous years (cumulative effect) of the delayed mowing regime for biodiversity of parasitoid Hymenoptera as it was already detected for orthopterans (Buri, Arlettaz et al. 2013); (ii) uncut refuges will serve as important food and host resources when the rest of the meadow is mown (Bianchi, Walters et al. 2015), thus representing higher diversity (abundance and richness) of parasitic wasps than the mown parts of the meadow; (iii) generally, families, that are less specialists, will occur in a higher number than species with a very narrow requirements (Kleijn, Berendse et al. 2001; Kleijn and van Langevelde 2006), they have a wider range of hosts available, so that even after mowing they can obtain easier suitable hosts; we expect Chalcidoidea, one of the most important hymenopteran biological agents, as the most widespread and most abundant group recorded from EMM, especially in D-meadows and after mowing in RR-meadows (Bouček 1988; Stephens, Schellhorn et al. 2006).

To the best of our knowledge, this study is the first to test alternative mowing regimes on parasitoid Hymenoptera in European lowland EMMs, it is urgent to study species on each trophic level of communities in a complex system to be able to maintain the biodiversity of agro-ecosystems.

Material and methods

Study sites

This study was carried out in 2014 in 47 EMMs registered as BPA since at least 2004. The meadows were selected in 2010 across the Swiss Plateau, they were arranged in 12 study regions with four meadows per region (except one region with only three meadows) and were situated between 390 and 833 m altitude (study sites coordinates and map are provided in Appendix1, 2 and 4). In a single region the four meadows were located within a 3.5 km radius, and with a minimal distance of 440 m between the meadows. The average size of a meadow was 0.8 ha (range: 03–1.7 ha).

In 2012, a D-meadow was converted into a gravel pit reducing the total number (48) of meadows to 47.

Experimental design

A randomized block design was used, where, within each study region the following four different mowing regimes were randomly assigned to the four meadows:

1) Extensively managed BPA hay meadows according to Swiss regulations, i.e. first possible cut not before 15 June with no restriction on the number and frequency of subsequent cuts. These meadows constituted our control meadows (hereafter abbreviated C-meadows).
2) Extensively managed BPA hay meadows where the first cut was not before 15 June and the maximum number of cuts per year was set to two with at least eight weeks between the cuts (8w-meadows).

3) Extensively managed BPA hay meadows with the first possible cut delayed by one month, i.e. not before 15 July and again no restriction on the number and frequency of subsequent cuts (D-meadows).
4) Extensively managed BPA hay meadows with a rotational uncut refuge of 10–20% of the meadow area left each time the meadow was mown (R-meadows). First cut was not before 15 June like in C-meadows and 8w-meadows.

Parasitic wasp sampling

Parasitic wasps were sampled using a special triangular net designed and recommended by Noyes (Noyes 2015), they were sampled once before 15 June (between 19 May and 8 June): hereafter referred to as the 'June' sample; and once after 15 June (between 20 June and 12 July): hereafter 'July' sample. On each meadow 2 x 30 net strokes were carried out along randomly chosen transects, tough the content of the net was emptied after each 10 net strokes using a mouth-aspirator. During the second session, i.e. after 15 June, additionally 2 x 30 net strokes were performed in the uncut refuge within the R-meadows, hereafter abbreviated RR-meadows. Sampling took place on sunny, dry days, from the morning to the early afternoon. After collection, specimens were transferred to 90% alcohol and kept in the freezer. Each individual was then determined to family level (Goulet and Huber 1993), furthermore the individuals of Pteromalidae were identified to genera level (Bouček, Rasplus et al. 1991).

Statistical analyses

To test the effects of the different mowing regimes the data were analyzed with linear mixed effects models using the *lmer* function of the *lme4* package for R (Bates, Maechler et al. 2014). Response variables were: 1) total abundance of parasitic wasps; 2) abundance of Chalcidoidea superfamily (Families: Aphelinidae, Calchididae, Encyrtidae, Eulophidae, Eurytomidae, Mymaridae, Ormyridae, Pteromalidae, Tetracampidae, Torymidae, Trichogrammatidae); 3) abundances of Braconidae, Eulophidae, Platygastridae and Pteromalidae (four most common families); 4) family richness of total parasitic wasps; and 5) genera richness of Pteromalidae. Fixed effects were the four mowing regimes (C, 8w, D and R) plus the uncut refuge within the R-meadows (RR) and sampling sessions (June or July) when appropriated, while regions (12 spatial replicates) were considered as a random effect. All analyses were performed using three seasonal datasets that regrouped sampling sessions, which gave three linear models (first model: June & July samples, second model: June sample only, third model: July sample only). All analyses were specified with Gaussian error distribution, when it was needed log-transformation was performed to meet model assumption of residual normality. All statistics were performed using RStudio, version 0.98.1028 (RStudio 2014).

Results

Overview

A total of 7’289 parasitic wasps, representing 21 families and 28 genera of the Pteromalidae family were collected during the whole sampling season. C- and 8w-meadows had very similar management regimes, from 2010 to 2014 they were both cut on average 1.9 times, R-meadows were cut on average 2.1 times and D-meadows were cut on average 1.5 times.

Parasitic wasp abundance

In pooled samples, i.e. June & July (Fig.1a), average parasitic wasp abundance varied between 43 and 150. Mean abundance ± standard error (SE) in D-meadows equaled 150 ± 31 and was significantly higher than C- (43 ± 6, $P < 0.001$), 8w- (53 ± 6, $P < 0.001$) and R-meadows (47 ± 8, $P < 0.001$). Detailed model outputs are provided in Table 1. Before mowing, in June (Fig.1b) the total abundances of parasitic wasp were significantly higher in D-meadows (239 ± 48) than in C- (53 ± 10), 8w- (52 ± 11) and R-meadows (67 ± 13, all $P < 0.001$). In July (Fig.1c), we sampled significantly higher number of parasitic wasps in D- (61 ± 14), than in C- (33 ± 5, $P = 0.012$) and R-meadows (27 ± 5, $P = 0.003$), while 8w-meadows (55 ± 7) did not differ significantly from it. 8w-meadows were significantly different from C-meadows ($P = 0.050$) and from R-meadows ($P = 0.015$). A trend of higher abundances (but no significant differences) could be shown in the uncut refuge (RR-meadows, 45 ± 9) compared to the rest of the meadows within the R-meadows (27 ± 5). To better understand the underlying processes we were running further abundance analyses with the Chalcidoidea superfamily (3’688 individuals) and with four parasite families sampled with the highest number above the other families, these were Braconidae (1’382 individuals), Eulophidae (2’078 individuals), Platygastridae (1’314 individuals) and Pteromalidae (1’108 individuals).

Analyses on Chalcidoidea superfamily (Table 2) in samples June & July (Fig.1d) showed significantly higher abundances in D-meadows (93 ± 23) than C- (22 ± 4, $P = 0.002$), 8w- (19 ± 3, $P = 0.008$) and R-meadows (19 ± 5, $P < 0.001$). In June (Fig.1e) similarly, D-meadows (155 ± 38) harbored significantly higher abundances than C-meadows (34 ± 7, $P = 0.008$), 8w-meadows (21 ± 4, $P < 0.001$) and R-meadows (32 ± 7, $P = 0.010$). After mowing (i.e. in July; Fig.1f), there were significantly higher abundances in D-meadows (31 ± 6) than in C- (10 ± 2, $P = 0.037$) and R-meadows (6 ± 1, $P = 0.002$) but not when compared to 8w-meadows (17 ± 4). When R-meadows compared to RR-meadows (18 ± 3, $P = 0.031$), we could show significantly higher abundances in the uncut refuge. Analyses on Braconidae showed no significant effects of the different mowing regimes on abundance in June & July (Fig.2a) and in June (Fig.2b), but in July there were significantly higher abundances detected in D-meadows compared to R-meadows ($P = 0.028$; Fig.2c; Table 3). No difference was found in the RR-meadows compared to the R-meadows. In samples of June & July, Eulophidae abundances were significantly higher in D-meadows compared to any other mowing regime (all $P < 0.001$; Fig.2d; Table 4). Similar results could be shown on Pteromalidae, D-meadows had significantly higher abundances than C- ($P = 0.005$), 8w- ($P = 0.003$) and R-meadows ($P = 0.001$; Fig.2j; Table 6). Platygastridae abundances differed significantly only in D-meadows compared to C-meadows ($P = 0.013$; Table 5; Fig.2g). Before mowing (i.e. June) Eulophidae abundances of D-meadows, compared to C- ($P = 0.009$), 8w- ($P < 0.001$) and to R-meadows ($P = 0.007$; Fig.2e), were significantly higher, similarly, Platygastridae had significantly higher abundances in D-meadows than in C- ($P < 0.001$), 8w- ($P = 0.009$) just like in R-meadows ($P = 0.041$), besides, abundances of 8w-meadows ($P = 0.031$) and R-meadows ($P = 0.006$; Fig.2h) were significantly higher than in C-meadows. Pteromalidae abundances were significantly higher in D-meadows ($P = 0.016$; Fig.2k) than in 8w-meadows. In July, Eulophidae abundances were again significantly higher in D-meadows compared to C-meadows ($P < 0.001$), 8w-meadows ($P = 0.001$) and to R-meadows ($P < 0.001$), 8w-meadows had significantly higher abundances than R-meadows ($P = 0.022$). There were significant differences in the number of sampled wasps in RR-meadows compared to R-meadows ($P < 0.001$; Fig.2f). No significant differences detected between the different mowing regimes for Platygastridae (Fig.2i). Abundances of Pteromalidae showed significant differences when D-meadows compared to C- ($P = 0.002$), 8w- ($P = 0.012$) and to R-meadows ($P < 0.001$), likewise, RR-meadows compared to R-meadows were representing significantly higher abundances ($P < 0.001$; Fig.2l). See Fig.1 and Fig.2, Table 1-6 for detailed graphical and model outputs.

Parasitic wasp family richness

Overall, 21 families were recorded (i.e. in pooled samples of June & July; Fig. 3a). Numbers of families per meadow varied between 5 and 16, though no significant differences among mowing regimes were detected when the sampling sessions were pooled or in June alone. On the other hand, in July (Fig. 3c) family richness in D-meadows (10 ± 1) was significantly higher than in C- (8 ± 1, $P = 0.022$) and in R-meadows (7 ± 1, $P = 0.001$) but not in 8w-meadows (8 ± 1). 8w-, C- and R-meadows did not differ significantly from each other. Moreover, in RR-meadows (9 ± 1) the family richness of parasitic wasps were significantly higher than in R-meadows (7 ± 1, $P = 0.023$). See Table 7 for detailed model outputs.

Parasitic wasp genera richness of Pteromalidae

28 genera were found within family of Pteromalidae. In samples of June & July (pooled), there were significantly greater genera richnesses in D- (3 ± 0.4) than in C- (2 ± 0.3, $P = 0.045$) and in R-meadows (2 ± 0.3, $P = 0.003$) but not compared to 8w-meadows (3 ± 0.3). In June we did not find any significant differences between the alternative mowing regimes. In July there were significantly greater genera richnesses in D- (3 ± 0.6) compared to C- (2 ± 0.3, $P = 0.004$) and R-meadows (1 ± 0.5, $P < 0.001$), but not to 8w-meadows (2 ± 0.5).

Furthermore we could detect significant differences between R- and RR-meadows (3 ± 0.5, $P < 0.001$). See Table 8 for detailed model outputs. Genera list with the number of individuals per genera is provided in Appendix 3.

Discussion

This study investigated the effects of four different mowing regimes on the populations of parasitic wasps in Swiss lowland extensively managed meadows (EMMs). The results show that delaying the first possible mowing date by one moth (i.e. from 15 June to 15 July), or leaving uncut refuges on 10–20% of the meadow area when mowing promote parasitic wasp abundance, family- and genera richness. One of the major outcomes is that a tremendous cumulative effect could be demonstrated: before mowing the abundances of parasitic wasps were, on average, ten times higher in D- (first cut not before 15 July) than in C-meadows (first cut not before 15 June). After mowing, both, parasitic wasp family richness and Pteromalidae genera richness were higher in the uncut refuges compared to the cut area within the R-meadows (refuge meadows with first cut not before 15 June and with a rotational uncut refuge of 10–20% of the meadow), which demonstrates a direct positive effect of leaving uncut refuge. The finding that simple changes in the mowing regimes can enhance biodiversity of parasitic wasps in lowland EMMs is new and has, potentially, important implications to sustain organic and conventional food production (Cardinale, Harvey et al. 2003).

Parasitic wasp abundance

Considering all samples (i.e. June & July), results show that parasitic wasp abundances were, on average, six times higher in D-than in C-meadows. Abundances were also twice higher in 8w-meadows (8 weeks meadows with first cut not before 15 June and with a maximal number of two cuts per year) and in R-meadows compared to C-meadows. According to the prediction, Chalcidoidea were the most abundant superfamily (51% of all individuals), similar to a previous study on native and weedy plant species in agricultural landscapes (Stephens, Schellhorn et al. 2006). Their high number is probably a consequence of their greater range of biological diversity than any other superfamily of the parasitic Hymenoptera (Noyes 2015). As predicted, our modified local management measures promoted generalist families, which parasitize a diverse array of insects: Braconidae (Shaw and Huddleston 1991), Eulophidae (Noyes 2015), Platygastridae (Austin, Johnson et al. 2005) and Pteromalidae (Sureshan and Narendran 2003) with much higher abundances than e.g. the more specialized Tetracampidae, whose known hosts are associated with insects that mine in plants (Bouček and Askew 1968). When the two sampling sessions were pooled (i.e. June & July) Braconidae did not show any significant differences among the four mowing regimes, while Eulophidae, Platygastridae and Pteromalidae did have significantly higher abundances in D-meadows than in any others.

Before mowing (i.e. June) parasitic wasp abundances were, on average, ten times higher in D-meadows compared to C-meadows which reflect a cumulative effect, i.e. a carry-over effect from one year to the following. In other words it demonstrates that, in the long-term, delaying mowing increases the abundance (total number) of parasitic wasps at the population level. This cumulative effect of the D-meadows was also demonstrated for orthopterans sampled in 2012, i.e. two years after the implementation of the new mowing regime (Buri, Arlettaz et al. 2013). On average, seven times more chalcids were sampled in D-meadows than in C-meadows, which shows again a cumulative effect of the delayed mowing regime. Same effect of delayed mowing regime could be shown for Eulophidae and Platygastridae. Delaying mowing may promotes, in general, parasitic wasps longer, either with hosts or with suitable habitats, to reach adulthood and reproduce more, such a positive correlation between reproduction and survival was already showed in earlier studies (e.g. Bai and Smith 1993).

After mowing (i.e. July), D-meadows still had significantly higher abundances of total parasitic wasp, Chalcidoidea, Eulophidae and Pteromalidae. Within the R-meadows, mean abundances of parasitic wasps collected in the uncut refuges (RR-meadows) were higher than those from mown areas (R-meadows), but the difference was not significant. Similarly to our findings, in previous studies higher density and diversity of parasitoids were found in floral strips than in the mown areas (Landis, Wratten et al. 2000; Rebek, Sadof et al. 2005; Dib, Libourel et al. 2011). Abundances of Chalcidoidea superfamily, Braconidae, Eulophidae and Pteromalidae families collected from RR-meadows were higher than those from mown areas. Remnant vegetation may provide overwintering sites, food resources, access to hosts, they could serve as major habitats for the conservation of parasitoids, maintaining refuges allow parasitoid populations to build up and move into adjacent, younger plantings (Schellhorn, Harmon et al. 2000; Tscharntke 2000; Bianchi, Walters et al. 2015). We could not detect any significant differences between the different mowing regimes on Platygastridae.

In July, surprisingly, seeing the results on total abundance of parasitic wasps and abundances of Chalcidoidea, Braconidae and Eulophidae, 8w-meadows seemed to be very similar to D-meadows; they both differed significantly from R-meadows. It is hard to find a biological explanation for that pattern and we argue that it may comes from the fact that, even if the mowing regimes were randomly assigned to the four meadows within each region, 8w-meadows were on average slightly bigger (0.94 ± 0.12 ha) than the other meadows (0.77 ± 0.05 ha), which is usually beneficial for biodiversity in general (e.g. Oertli, Auderset Joye et al. 2002).

Parasitic wasp family richness

Out of the 21 sampled families, 11 belonged to Chalcidoidea that has 19 described families up to now (Noyes 2015). Before mowing, we did not see any cumulative effect on family richness. We detected only small non-significant differences between the mowing regimes; also C-meadows appeared with the lowest value. After mowing compared to our D-meadows, C-, 8w- and R-meadows turned out as family poor meadows. Uncut refuges shown a significantly higher family richness than the mown areas within the R-meadows, this suggests that refuges may be providing an important reservoir of hosts for parasitic wasps when the rest of the meadow is mown allowing parasitoids to occur and persist with a greater family richness within an extensively managed agricultural system. Similar findings on orthopteran species richness were already shown (Buri, Arlettaz et al. 2013).

Pteromalidae genera richness

Pteromalidae has about 588 genera and 3506 described species worldwide (Noyes 2015). About 98% of them develop as parasites of various stages of insects or, rarely, of spiders, therefore they play an enormous role, by controlling and mitigating a diverse array of pests, in agriculture (Bouček, Rasplus et al. 1991; Sureshan and Narendran 2003). In June a trend of greater genera richnesses in D-meadows could be detected, in a longer-term delaying mowing could make significant differences. In July genera richnesses were significantly higher in D-meadows compared to C- and R-meadows, which is an immediate positive effect of the delaying mowing regime. At the same time RR-meadows were also having significant greater genera richnesses than C- or R-meadows, as we expected, uncut refuges seem to boost Pteromalidae genera richness. D- and 8w-meadows did not show significant differences, we assume this comes again from the fact, that 8w-meadows were bigger than the others.

Conclusions and management recommendations

This study found that allowing the vegetation of delayed meadows to stand one month longer can significantly increase biodiversity (abundance) of parasitic wasp communities. Similar to previous findings, that in general terms insect diversity and abundance can be increased by delaying the first mowing date from early to mid-summer (e.g. Marini, Fontana et al. 2008; Humbert, Ghazoul et al. 2012; Humbert, Pellet et al. 2012; Buri, Arlettaz et al. 2013). Furthermore we found that leaving uncut refuge when the rest of the meadow is mown has an immediate positive significant effect on the abundance, family- and genera richness of parasitoids.

Based on these findings, we can highly recommend to postpone the first mowing dates and to leave uncut refuges after the first mowing date to support the diversity (abundance, family and genera richness) of parasitic wasps. We recommend further investigation of combinations of different mowing regimes (mainly: delaying mowing and leaving uncut refuges), to be able to define the optimum size of mown areas and the degree of fragmentation of unmown areas, so that we could determine whether increasing the amount of D-meadows or the % of uncut refuges increases parasitoid abundance and diversity in a long-term. A systematic implementation of this measure within extensive hay meadows across the agricultural matrix in Swiss lowland and in European plains might efficiently boost parasitic wasp and many other insect populations and communities. As parasitic wasps have a wide range of hosts, increasing their diversity may enhance also the potential to control larger scale of pests.

Acknowledgements

We are grateful to the team of the Divison of Conservation Biology and Marc Neumann for the helpful comments and inputs, to the Natural History Museum of Bern for the materials. We thank to the farmers for their collaboration. Special thanks go to Andreas Boeriis for his valuable suggestions and support. This study was financially supported by the Swiss National Science Foundation (grant. no. 31003A 149656/1 to R. Arlettaz), Federal Offices for Environment and Agriculture, and the following Swiss cantons (Aargau, Bern, Basel-Landschaft, Fribourg, Graubünden, Neuchâtel, Valais and Vaud).

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Table 1. Output of linear mixed effects models for parasitic wasp abundance in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.1.

	Estimate	SE	P-value
a)			
8w vs. C	10.33	22.02	0.640
D vs. C	107.18	22.52	**<0.001**
R vs. C	4.25	22.02	0.847
D vs. 8w	96.85	22.52	**<0.001**
R vs. 8w	-6.08	22.02	0.783
R vs. D	-102.93	22.52	**<0.001**
b)			
8w vs. C	-1.17	34.03	0.973
D vs. C	187.04	34.80	**<0.001**
R vs. C	14.17	34.03	0.680
D vs. 8w	187.21	34.80	**<0.001**
R vs. 8w	15.33	34.03	0.655
R vs. D	-171.87	34.80	**<0.001**
c)			
8w vs. C	21.83	10.81	**0.050**
D vs. C	29.10	11.08	**0.012**
R vs. C	-5.67	10.81	0.603
D vs. 8w	7.27	11.08	0.515
R vs. 8w	-27.50	10.81	**0.015**
R vs. D	-34.77	11.08	**0.003**
8w vs. RR	9.750	10.81	0.372
D vs. RR	17.02	11.08	0.132
C vs. RR	-12.08	10.81	0.270
R vs. RR	-17.750	10.81	0.108

Table 2. Output of linear mixed effects models for Chalcidoidea abundance in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.1.

	Estimate	SE	P-value
a)			
8w vs. C	0.14	0.26	0.587
D vs. C	0.87	0.27	**0.002**
R vs. C	-0.19	0.26	0.476
D vs. 8w	0.72	0.27	**0.008**
R vs. 8w	-0.33	0.26	0.211
R vs. D	-1.05	0.27	**<0.001**
b)			
8w vs. C	-0.40	0.43	0.356
D vs. C	1.23	0.44	**0.008**
R vs. C	0.03	0.43	0.937
D vs. 8w	1.63	0.44	**<0.001**
R vs. 8w	0.43	0.43	0.317
R vs. D	-1.20	0.44	**0.010**
c)			
8w vs. C	0.44	0.23	**0.059**
D vs. C	0.51	0.23	**0.037**
R vs. C	-0.26	0.23	0.261
RR vs. C	0.25	0.23	0.282
D vs. 8w	0.06	0.23	0.795
R vs. 8w	-0.70	0.23	**0.004**
RR vs. 8w	-0.20	0.23	0.398
R vs. D	-0.77	0.23	**0.002**
RR vs. D	-0.26	0.23	0.280
R vs. RR	-0.51	0.23	**0.031**

Table 3. Output of linear mixed effects models for abundances of Braconidae in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.2.

	Estimate	SE	P-value
a)			
8w vs. C	0.25	0.25	0.323
D vs. C	0.44	0.25	0.085
R vs. C	0.05	0.25	0.852
D vs. 8w	0.20	0.25	0.442
R vs. 8w	-0.20	0.25	0.422
R vs. D	-0.40	0.25	0.123
b)			
8w vs. C	-1.92	3.67	0.604
D vs. C	4.89	3.75	0.199
R vs. C	1.08	3.67	0.769
D vs. 8w	6.81	3.75	**0.076**
R vs. 8w	3.00	3.67	0.418
R vs. D	-3.81	3.75	0.315
c)			
8w vs. C	9.33	4.62	**0.049**
D vs. C	7.50	4.73	0.120
R vs. C	-3.25	4.62	0.485
RR vs. C	0.92	4.62	0.844
D vs. 8w	-1.84	4.73	0.700
R vs. 8w	-12.58	4.62	**0.009**
RR vs. 8w	-8.42	4.62	0.075
R vs. D	-10.75	4.73	**0.028**
RR vs. D	-6.58	4.73	0.172
R vs. RR	-4.17	4.62	0.371

Table 4. Output of linear mixed effects models for abundances of Eulophidae in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.2.

	Estimate	SE	P-value
a)			
8w vs. C	-0.13	0.34	0.714
D vs. C	1.26	0.35	**<0.001**
R vs. C	-0.27	0.34	0.433
D vs. 8w	1.39	0.35	**<0.001**
R vs. 8w	-0.14	0.34	0.675
R vs. D	-1.53	0.35	**<0.001**
b)			
8w vs. C	-0.41	0.51	0.419
D vs. C	1.41	0.52	**0.009**
R vs. C	-0.05	0.51	0.926
D vs. 8w	1.83	0.52	**<0.001**
R vs. 8w	0.37	0.51	0.474
R vs. D	-1.46	0.52	**0.007**
c)			
8w vs. C	0.16	0.27	0.558
D vs. C	1.14	0.28	**<0.001**
R vs. C	-0.50	0.27	0.081
RR vs. C	0.54	0.27	**0.055**
D vs. 8w	0.98	0.28	**0.001**
R vs. 8w	-0.65	0.27	**0.022**
RR vs. 8w	0.38	0.27	0.175
R vs. D	-1.63	0.28	**<0.001**
RR vs. D	-0.60	0.28	**0.040**
R vs. RR	-1.03	0.27	**<0.001**

Table 5. Output of linear mixed effects models for abundances of Platygastridae in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.2.

	Estimate	SE	P-value
a)			
8w vs. C	0.48	0.35	0.169
D vs. C	0.91	0.36	**0.013**
R vs. C	0.50	0.35	0.157
D vs. 8w	0.43	0.36	0.233
R vs. 8w	0.01	0.35	0.967
R vs. D	-0.41	0.36	0.249
b)			
8w vs. C	0.82	0.36	**0.031**
D vs. C	1.86	0.37	**<0.001**
R vs. C	1.06	0.36	**0.006**
D vs. 8w	1.04	0.37	**0.009**
R vs. 8w	0.24	0.36	0.509
R vs. D	-0.80	0.37	**0.041**
c)			
8w vs. C	0.15	0.29	0.616
D vs. C	-0.03	0.30	0.910
R vs. C	-0.07	0.29	0.818
RR vs. C	0.21	0.29	0.471
D vs. 8w	-0.18	0.30	0.548
R vs. 8w	-0.21	0.29	0.465
RR vs. 8w	0.06	0.29	0.825
R vs. D	-0.03	0.30	0.911
RR vs. D	0.24	0.30	0.415
R vs. RR	-0.28	0.29	0.343

Table 6. Output of linear mixed effects models for abundances of Pteromalidae in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.2.

	Estimate	SE	P-value
a)			
8w vs. C	-0.04	0.31	0.897
D vs. C	0.91	0.32	**0.005**
R vs. C	-0.15	0.31	0.625
D vs. 8w	0.95	0.32	**0.003**
R vs. 8w	-0.11	0.31	0.719
R vs. D	-1.06	0.32	**0.001**
b)			
8w vs. C	-0.28	0.41	0.498
D vs. C	0.79	0.42	0.070
R vs. C	0.18	0.41	0.674
D vs. 8w	1.08	0.42	**0.016**
R vs. 8w	0.46	0.41	0.275
R vs. D	-0.62	0.42	0.157
c)			
8w vs. C	0.20	0.30	0.497
D vs. C	1.00	0.30	**0.002**
R vs. C	-0.48	0.30	0.116
RR vs. C	0.83	0.30	**0.008**
D vs. 8w	0.80	0.30	**0.012**
R vs. 8w	0.80	0.30	0.116
RR vs. 8w	0.62	0.30	**0.041**
R vs. D	-1.48	0.30	**<0.001**
RR vs. D	-0.17	0.30	0.581
R vs. RR	-1.31	0.30	**<0.001**

Table 7. Output of linear mixed effects models for Family richness of parasitic wasps in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.3.

	Estimate	SE	P-value
a)			
8w vs. C	0.58	0.85	0.497
D vs. C	1.20	0.87	0.178
R vs. C	-0.50	0.85	0.560
D vs. 8w	0.61	0.87	0.486
R vs. 8w	-1.08	0.85	0.211
R vs. D	-1.70	0.87	0.060
b)			
8w vs. C	0.33	1.02	0.745
D vs. C	0.54	1.04	0.605
R vs. C	0.25	1.02	0.807
D vs. 8w	0.21	1.04	0.841
R vs. 8w	-0.08	1.02	0.935
R vs. D	-0.29	1.04	0.780
c)			
8w vs. C	0.50	0.81	0.542
D vs. C	1.98	0.83	**0.022**
R vs. C	-0.92	0.81	0.266
RR vs. C	1.00	0.81	0.226
D vs. 8w	1.48	0.83	0.084
R vs. 8w	-1.42	0.81	0.088
RR vs. 8w	0.50	0.81	0.542
R vs. D	-2.89	0.83	**0.001**
RR vs. D	-0.98	0.83	0.249
R vs. RR	-1.92	0.81	**0.023**

Table 8. Output of linear mixed effects models for Genera richness of Pteromalidae in relation to mowing regime in: a) June & July (pooled data), b) June only and c) July only. For mowing regime abbreviations see legend of Fig.4.

	Estimate	SE	P-value
a)			
8w vs. C	0.21	0.47	0.661
D vs. C	0.98	0.48	**0.045**
R vs. C	-0.50	0.47	0.293
D vs. 8w	0.78	0.48	0.112
R vs. 8w	-0.71	0.47	0.138
R vs. D	-1.48	0.48	**0.003**
b)			
8w vs. C	-0.42	0.72	0.564
D vs. C	0.19	0.73	0.797
R vs. C	-0.42	0.72	0.564
D vs. 8w	0.61	0.73	0.413
R vs. 8w	-0.00	0.72	1.000
R vs. D	-0.61	0.73	0.413
c)			
8w vs. C	0.83	0.58	0.157
D vs. C	1.78	0.59	**0.004**
R vs. C	-0.58	0.58	0.320
RR vs. C	1.50	0.58	**0.013**
D vs. 8w	0.95	0.59	0.117
R vs. 8w	-1.42	0.58	**0.018**
RR vs. 8w	0.67	0.58	0.256
R vs. D	-2.36	0.59	**<0.001**
RR vs. D	-0.28	0.59	0.639
R vs. RR	-2.08	0.58	**<0.001**

Figure legends

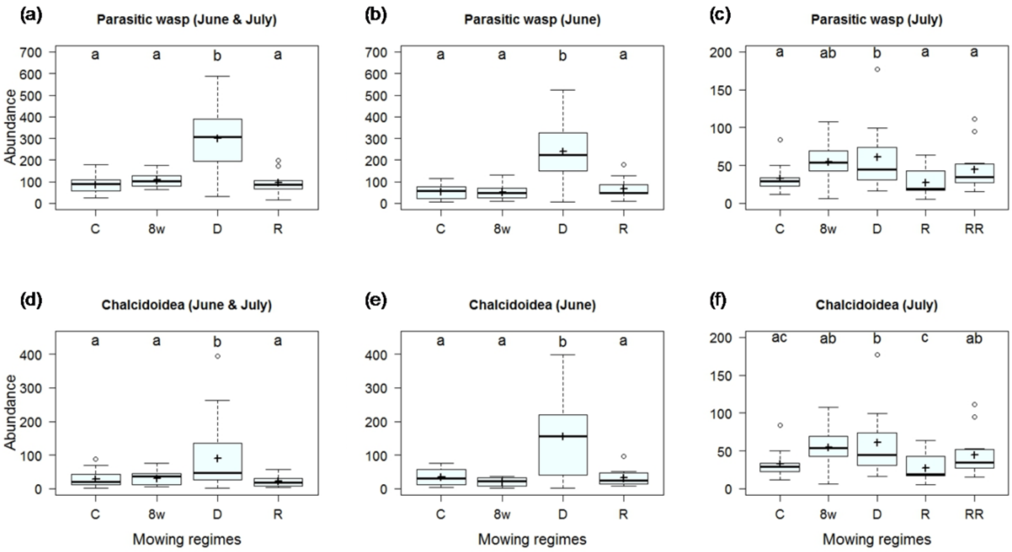
Fig.1. Abundances of parasitic wasp and Chalcidoidea superfamily, in response to the four different mowing regimes. The figure is divided in six parts according to the sampling sessions (June & July, June or July only, in columns) and the different response variables in rows: (a), (b), (c), (d), (e) and (f). Mowing regimes are: 8w (8 week meadows), first cut not before 15 June with a minimum of 8 weeks between first and second cut; C (control meadows), first cut not before 15 June; D (delayed meadows), first cut not before 15 July; and R (refuge meadows), first cut not before 15 June with un uncut refuge of 10-20% of meadow area. Additionally for the July sampling session RR (uncut refuge within the refuge meadows) were sampled. Different letters indicate significant differences among regimes at an alpha-rejection level of 0.05. See Table 1-2 for statistical analyses.

Fig.2. Abundance of parasitic wasp families in response to the four different mowing regimes. The figure is divided in twelve parts according to the sampling sessions (June & July, June or July, in columns) and the different response variables in rows: (a), (b), (c), (d), (e), (f), (g), (h), (i), (j), (k) and (l). For mowing regime abbreviations see legend of Fig. 1. Different letters indicate significant differences among regimes at an alpha-rejection level of 0.05. See Table 3-6 for statistical analyses.

Fig.3. Parasitic wasp family richness in response to the four different mowing regimes. The figure is divided in three parts according to the sampling sessions (June & July, June or July, in columns) and the different response variables in rows: (a), (b), (c) and (d). For mowing regime abbreviations see legend of Fig. 1. Different letters indicate significant differences among regimes at an alpha-rejection level of 0.05. See Table 7 for statistical analyses.

Fig.4. Pteromalidae genera richness in response to the four different mowing regimes. The figure is divided in three parts according to the sampling sessions (June & July, June or July, in columns) and the different response variables in rows: (a), (b), (c) and (d). For mowing regime abbreviations see legend of Fig. 1. Different letters indicate significant differences among regimes at an alpha-rejection level of 0.05. See Table 8 for statistical analyses.

Fig.1.



(a)
Parasitic wasp (June & July)
Abundance
C 8w D R
a a b a
(b)
Parasitic wasp (June)
a a b a
(c)
Parasitic wasp (July)
a ab b a a
C 8w D R RR
(d)
Chalcidoidea (June & July)
a a b a
(e)
Chalcidoidea (June)
a a b a
(f)
Chalcidoidea (July)
ac ab b c ab
Mowing regimes

Fig.2.

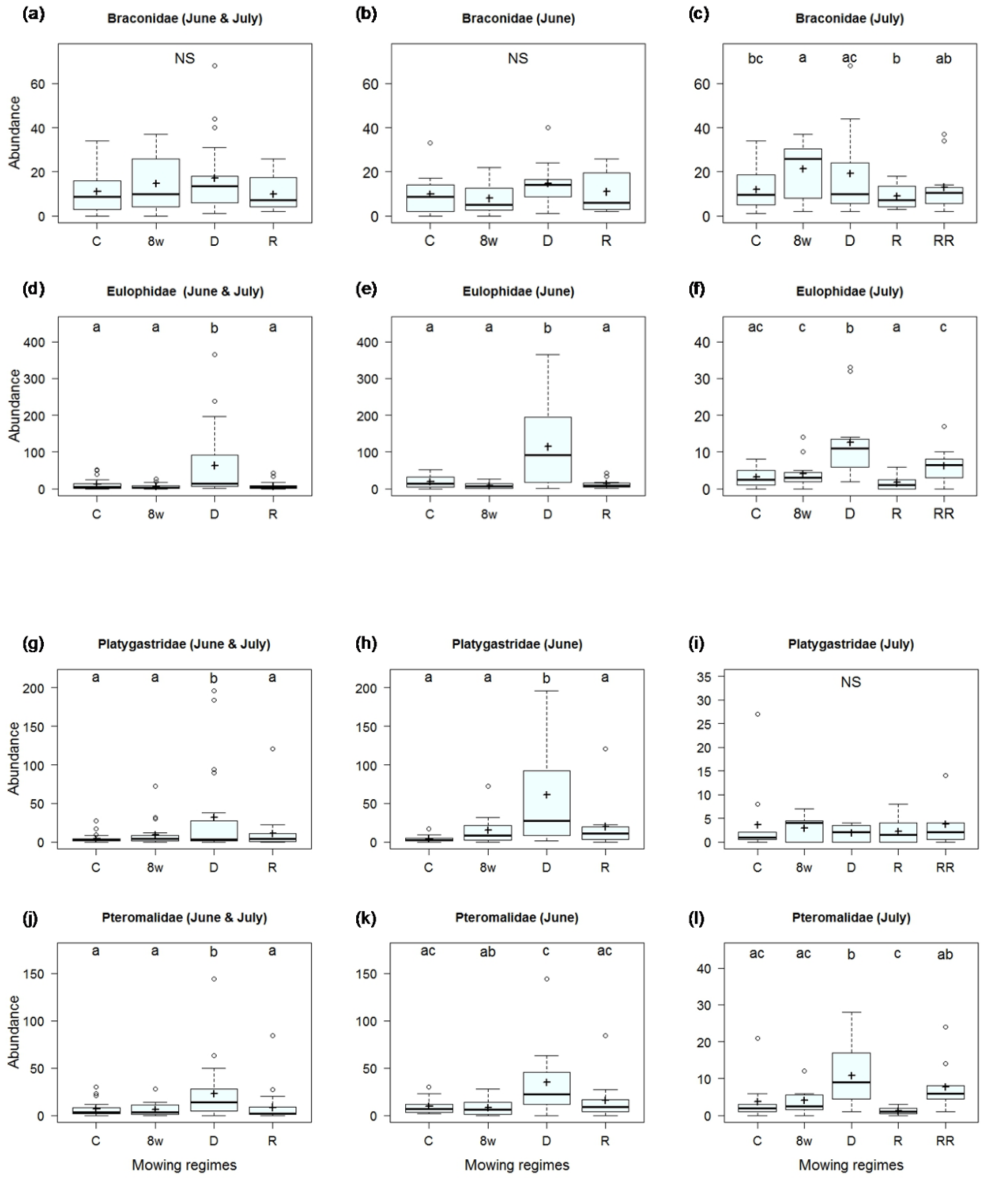

(a)
Braconidae (June & July)
NS
Abundance
C
8w
D
R
(b)
Braconidae (June)
NS
(c)
Braconidae (July)
bc a ac b ab
RR
(d)
Eulophidae (June & July)
a a b a
(e)
Eulophidae (June)
a a b a
(f)
Eulophidae (July)
ac c b a c
(g)
Platygastridae (June & July)
a a b a
(h)
Platygastridae (June)
a a b a
(i)
Platygastridae (July)
NS
(j)
Pteromalidae (June & July)
a a b a
(k)
Pteromalidae (June)
ac ab c ac
(l)
Pteromalidae (July)
ac ac b c ab
Mowing regimes

Fig.3.

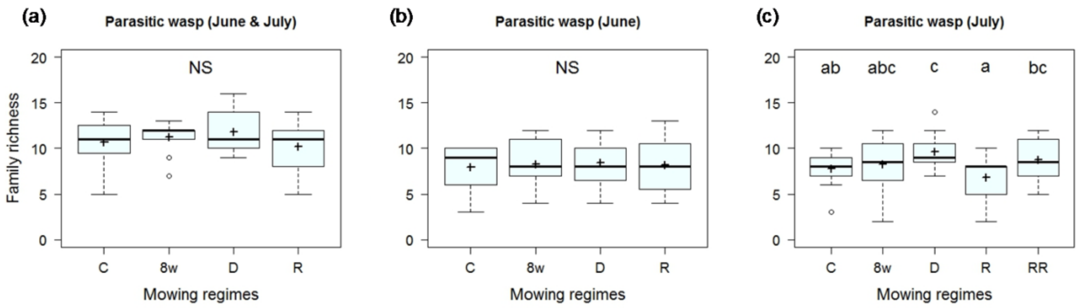
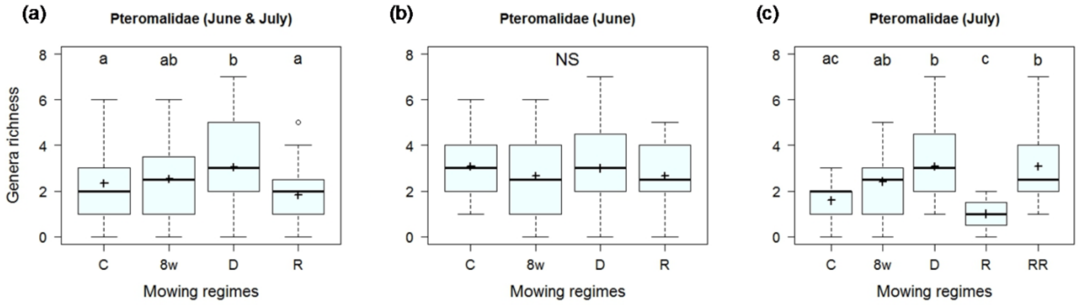

(a)
Parasitic wasp (June & July)
NS
Family richness
Mowing regimes
C
8w
D
R
(b)
Parasitic wasp (June)
NS
(c)
Parasitic wasp (July)
ab
abc
c
a
bc
RR

Fig.4.


(a)
Pteromalidae (June & July)
a
ab
b
a
Genera richness
0
2
4
6
8
C
8w
D
R
Mowing regimes
(b)
Pteromalidae (June)
NS
0
2
4
6
8
C
8w
D
R
Mowing regimes
(c)
Pteromalidae (July)
ac
ab
b
c
b
0
2
4
6
8
C
8w
D
R
RR
Mowing regimes

Appendix 1. List of meadows with their respective management regime, geographic coordinates and total number of sampled parasitic wasps per meadow (June & July samples).

Landscape Unit	Canton	Mowing regime	WGS_X°	WGS_Y°	Total number of sampled parasitic wasp
Nyon	VD	Control	6°13'9.4"	46°24'53.2"	65
Nyon	VD	Delayed	6°11'45.4"	46°22'42.4"	76
Nyon	VD	8 weeks	6°11'9.4"	46°22'43.5"	100
Nyon	VD	Refuge	6°15'15.6"	46°24'27.7"	102
Orbe	VD	Control	6°30'11.6"	46°42'37.5"	92
Orbe	VD	Delayed	6°29'30.5"	46°42'2.9"	376
Orbe	VD	8 weeks	6°28'52.7"	46°41'52.3"	87
Orbe	VD	Refuge	6°29'54.3"	46°43'2.8"	173
Avenches	VD	Control	7°0'28.4"	46°55'27.9"	53
Avenches	VD	Delayed	7°3'22.1"	46°56'20.3"	587
Avenches	VD	8 weeks	7°0'8.5"	46°55'23.6"	101
Avenches	VD	Refuge	7°3'35.3"	46°56'35.4"	65
Cousset	FR	Control	6°58'50.8"	46°49'23.4"	111
Cousset	FR	Delayed	6°58'23.7"	46°49'26.3"	401
Cousset	FR	8 weeks	6°58'33.7"	46°49'10.5"	127
Cousset	FR	Refuge	7°0'8.3"	46°49'51.8"	98
Coffrane	NE	Control	6°51'42.3"	47°0'5.6"	24
Coffrane	NE	8 weeks	6°51'12.2"	47°0'43.1"	66
Coffrane	NE	Refuge	6°50'58.2"	47°0'29.3"	105
Wohlen	BE	Control	7°22'40.8"	46°59'59.2"	177
Wohlen	BE	Delayed	7°25'29.5"	46°59'51.0"	33
Wohlen	BE	8 weeks	7°24'53.6"	46°58'58.5"	155
Wohlen	BE	Refuge	7°23'22.4"	46°58'11.9	76
Grossaffoltern	BE	Control	7°22'35.5"	47°3'54.0"	59
Grossaffoltern	BE	Delayed	7°22'29.9	47°4'31.9"	536
Grossaffoltern	BE	8 weeks	7°20'4.8"	47°4'39.3"	176
Grossaffoltern	BE	Refuge	7°20'52.1"	47°3'49.6"	68
Belp	BE	Control	7°30'38.2"	46°52'56.6"	140
Belp	BE	Delayed	7°28'26.6"	46°54'52.0"	236
Belp	BE	8 weeks	7°30'56.3"	46°53'20.6"	125
Belp	BE	Refuge	7°31'2.2"	46°53'45.8"	199
Hindelbank	BE	Control	7°33'12.0"	47°3'26.4"	95
Hindelbank	BE	Delayed	7°32'51.3"	47°1'27.4"	362
Hindelbank	BE	8 weeks	7°48'53.2"	47°5'32.3"	81
Hindelbank	BE	Refuge	7°51'10.9"	47°6'32.3"	104
Huttwil	BE	Control	7°50'42.5"	47°6'1.6"	27
Huttwil	BE	Delayed	7°49'21.4"	47°6'37.7"	306
Huttwil	BE	8 weeks	7°49'3.0"	47°25'30.3"	118
Huttwil	BE	Refuge	7°49'57.6"	47°26'18.8"	67
Diegten	BL	Control	7°49'17.5"	47°25'6.6"	104
Diegten	BL	Delayed	7°49'1.2"	47°24'52.6"	172
Diegten	BL	8 weeks	8°11'45.9"	47°26'51.3"	63
Diegten	BL	Refuge	8°11'15.1"	47°26'35.2"	15
Lupfig	AG	Control	8°11'45.9"	47°26'51.3"	85
Lupfig	AG	Delayed	8°11'15.1"	47°26'35.2"	219
Lupfig	AG	8 weeks	8°11'38.0"	47°26'29.7"	81
Lupfig	AG	Refuge	8°13'0.2"	47°26'39.8"	62

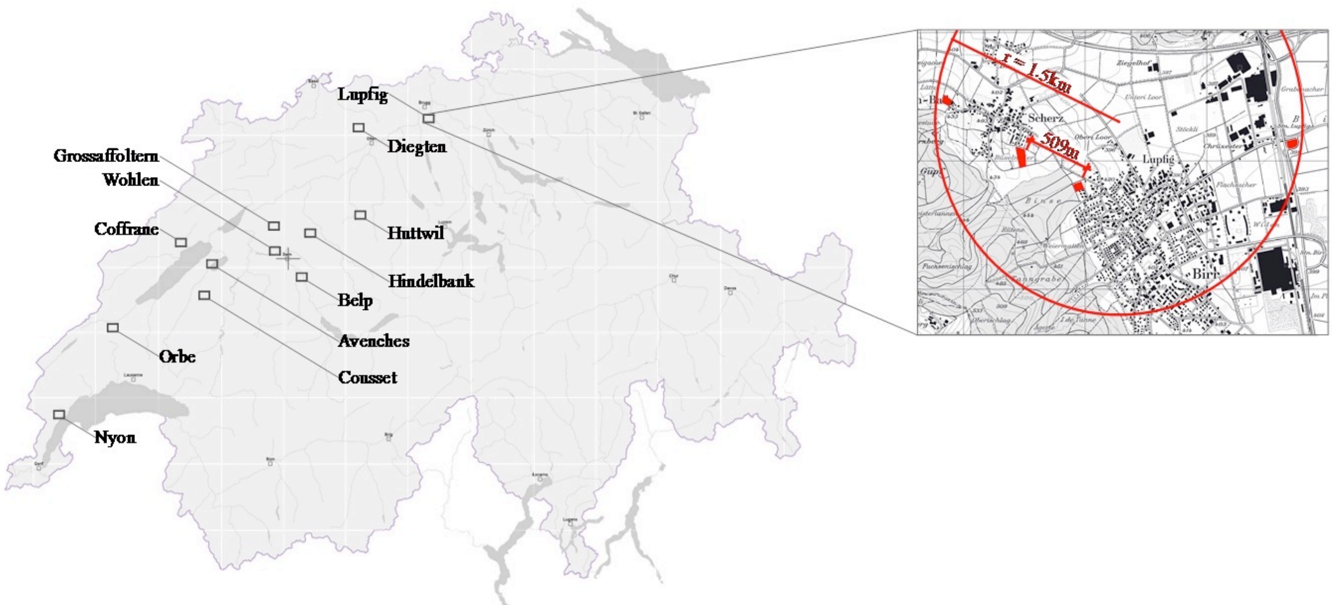
Appendix 2. List of RR-meadows with their geographic coordinates and number of sampled parasitic wasps per meadow (July samples).

Landscape Unit	Canton	Mowing regime	WGS_X°	WGS_Y°	Total number of sampled parasitic wasp
Nyon	VD	RefugeRefuge	6°15'15.6"	46°24'27.7"	32
Orbe	VD	RefugeRefuge	6°29'54.3"	46°43'2.8"	95
Avenches	VD	RefugeRefuge	7°3'35.3"	46°56'35.4"	29
Cousset	FR	RefugeRefuge	7°0'8.3"	46°49'51.8"	43
Coffrane	NE	RefugeRefuge	6°50'58.2"	47°0'29.3"	111
Wohlen	BE	RefugeRefuge	7°23'22.4"	46°58'11.9	53
Grossaffoltern	BE	RefugeRefuge	7°20'52.1"	47°3'49.6"	51
Belp	BE	RefugeRefuge	7°31'2.2"	46°53'45.8"	26
Hindelbank	BE	RefugeRefuge	7°51'10.9"	47°6'32.3"	38
Huttwil	BE	RefugeRefuge	7°49'57.6"	47°26'18.8"	28
Diegten	BL	RefugeRefuge	8°11'15.1"	47°26'35.2"	18
Lupfig	AG	RefugeRefuge	8°13'0.2"	47°26'39.8"	15

Appendix 3. List of genera within family of Pteromalidae, with number of individuals found per genera.

Family	Genera	Number of individuals
Pteromalidae	Asaphes	3
	Coruna	1
	Chlorocytus	3
	Coelopisthia	1
	Cyrtogaster	10
	Diglochis	2
	Gastrancistrus	26
	Halticoptera	5
	Homoporus	6
	Macroglenes	286
	Merismus	1
	Mesopolobus	344
	Micradelus	3
	Norbanus	1
	Psilocera	2
	Pteromalus	37
	Rhicnocoelia	3
	Seladerma	53
	Semiotellus	1
	Spintherus	141
	Sphegigaster	2
	Stenomalina	23
	Stictomischus	2
	Systasis	1
	Thinodytes	25
	Toxeuma	46
	Trichomalopsis	4
	Trichomalus	76

Appendix 4. Map (schweizerische Landeskarten 1:1'000'000, Hintergrundkarte hydrol. Daten) with the 12 study regions across the Swiss Plateau. Lupfig (schweizerische Landeskarten 1:10'000, Hintergrundkarte SW) as an example for a single region with the 4 meadows, which were located within a 3.5 km radius (actual radius = 1.5 km) and with a minimal distance of 440 m (actual distance = 509 m) between the meadows.



Erklärung

gemäss Art. 28 Abs. 2 RSL 05

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Matrikelnummer:	13-108-410
Studiengang:	Master of Science in Ecology and Evolution with special qualification in Animal Ecology and Conservation, Universität Bern
	Bachelor ☐ Master ☐ Dissertation ☐
Titel der Arbeit:	Promoting parasitic wasps among Swiss lowland extensively managed meadows: positive effects of delaying mowing and leaving uncut grass refuges
Leiter der Arbeit:	Dr Jean-Yves Humbert, Hannes Baur und Prof Dr Raphaël Arlettaz

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe r des Gesetzes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist. Ich gewähre hiermit Einsicht in diese Arbeit.

Ort/Datum Unterschrift