

# **Effect of four different mowing regimes on ground-dwelling spiders in Swiss lowland extensively managed hay meadows**

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**Abstract**

1. Intensification of agricultural practices is the primary cause of the ongoing decline of farmland biodiversity. Agri-environment schemes (AES), which promote more biodiversity-friendly practices, have been implemented to counter this decline. Yet, AES measures applied in semi-natural grasslands were found to be only moderately effective in preserving biodiversity of invertebrates.
2. This study investigates if new alternative mowing regimes – new compared to current, conventional prescriptions for AES extensively-managed meadows – which aim at increasing habitat spatio-temporal heterogeneity can promote ground-dwelling spiders. A full-block design experiment - with treatments randomly assigned to meadows - was carried out in 12 replicated study areas across the Swiss lowlands. The four following mowing regimes were applied by contracted farmers, each in one of four meadows per study area: 1) mowing regime according to Swiss AES regulations for extensively-managed hay meadows, i.e. first cut not before 15 June (here used as control and therefore termed C-meadow); 2) first cut not before 15 July, i.e. mowing regime delayed by a month compared to C-meadow (here termed D-meadow); 3) first cut not before 15 June (as in C-meadow) but second cut not earlier than 8 weeks after the first cut (8W-meadow); 4) rotational refuge left on 10–20% of the area of the meadow at each cut (R-meadow). Spiders were sampled twice during the vegetation period, once before and once after mowing, using pitfall traps.
3. No statistically significant differences between the alternative mowing regimes (D-, 8W- and R-meadows) and the control mowing regime (C-meadow) or a discernable trend could be evidenced both for abundance and species richness.

*Synthesis and applications:* Although these alternative mowing regimes provide no benefits for ground-dwelling spiders, contrary to what we observed for other taxonomic groups (e.g. orthopterans and wild bees) they are not detrimental for them and can be applied with no restriction. Further, more detailed analysis should assess possible family-specific responses and to which extent the refuge regime might enhance spider survival.

**321 words**

**Keywords:** Araneae; Biodiversity; Conservation; Haying; Cutting

## Introduction

Extensively managed grasslands are one of the biodiversity richest habitats of Europe and are considered of high nature value as they harbour many rare plant and animal taxa (Pärtel *et al.* 2005; Pearce *et al.* 2005; Lange *et al.* 2011; Bock *et al.* 2013). These grasslands are nowadays under severe threat. Changes in agricultural practices during the 20<sup>th</sup> century have caused on the one hand conversion of grasslands into arable lands and, on the other hand, their intensification or abandonment (Tschardt *et al.* 2005; Öckinger *et al.* 2006). Grassland intensification includes increased fertilizer input, application of pesticides and earlier and more frequent cuts (Bock *et al.* 2013). In addition the improved mechanization and general expansion of field size caused a homogenization of the agricultural landscape with the corollary loss and fragmentation of the remaining semi-natural habitats (Robinson *et al.* 2002). These changes negatively impact grassland biodiversity, leading to a rapid decline of many plant, vertebrate and invertebrate species. This phenomenon is likely to continue unabated without profound changes in farming systems (Reidsma *et al.* 2006). To alleviate the negative consequences of intensified farming practices, agri-environment schemes (AES) were established across Europe. Despite the fact that these schemes have been devised to promote environmentally-friendly management practices, they have so far only moderately benefitted biodiversity (Kleijn *et al.* 2006; Knop *et al.* 2006; Aviron *et al.* 2009; Albrecht *et al.* 2010).

A common management practice in grassland is mowing, with the date of the first cut taking place earlier and earlier with time (Bock *et al.* 2013). While the impact of the timing and frequency of mowing on plants is well studied, its consequence on invertebrates has remained scarce until recently (Humbert *et al.* 2009; Humbert *et al.*

2012). The main aim of this study was to test, with a focus on spider abundance and species richness, novel alternative mowing regimes, fully compatible with the Swiss AES regulations, which could improve their effectiveness for biodiversity.

Spiders were chosen as a study model because they represent an important food source for other insectivorous organisms, both among the invertebrates and vertebrates, and play an important role in pest control (Nyffeler *et al.* 1987; Marc *et al.* 1999; Cizek *et al.* 2011). Their predation pressure on pest organisms can be especially high as spiders reduce prey not only by consumption, but also by dislodgment, superfluous killing and by-catch in webs (Sunderland 1999). In addition, grassland spider communities have been reported to be sensitive to the timing and frequency of mowing, to vegetation structure and both local and landscape heterogeneity, making them extremely valuable bioindicators (Uetz 1991; Gunnarsson 1996; Dennis *et al.* 1998; Marc *et al.* 1999; Sunderland *et al.* 2000).

To investigate the impact of different alternative mowing regimes on spider abundance and species richness, a field-scale experiment was carried out across the Swiss Plateau (lowlands between the Alps and the Jura mountains). Extensively-managed hay meadows, which form by far the majority of Swiss ecological compensations areas (ECA) and are typically included within many European AES, were selected given their great potential for promoting biodiversity. Prescriptions for Swiss ECA hay meadows stipulate: i) at least one cut per year at the earliest on 15 June (but without further restriction concerning the time and frequency of subsequent cuts); ii) prohibition of pesticide or fertilizer application; and iii) possible autumn grazing. Regarding mowing technique and machinery, there currently exists no federal prescription (Anonymous 1998).

Compared to conventional, high-intensity meadows, current prescriptions for ECA hay meadows do not seem to enhance spider abundance and species richness

(Knop *et al.* 2006), probably because they do not contribute to increasing vegetation structural heterogeneity while the timing of mowing remains too early (Knop *et al.* 2006; Jimenez-Valverde *et al.* 2007). We therefore decided to seek alternative mowing regimes that might contribute to increase spatio-temporal heterogeneity by: i) further delaying the date of the first cut by a month, by 15 July; ii) limiting the number of cuts per year to two, with at least eight weeks in-between; and iii) leaving an uncut grass refuge on a tiny fraction (typically 10-20% of the area) of a meadow when mowing.

Extant knowledge about the consequences of timing, frequency and schemes of mowing on spiders remains scarce. In general, higher frequency of mowings is thought to have long-term negative effects on spiders both due to increased direct mortality caused by machinery and to a reduction of vegetation structure that provide fewer ecological niches (Gunnarsson 1996; Bell *et al.* 2001). The species-specific vegetation strata used by different spider species, which relates to their hunting strategy, will also define which species are impacted by mowing. Two main groups of spiders are commonly distinguished: ground-dwelling and plant-dwelling spiders. The latter typically have been shown to be more affected by summer and late autumn cuts than spring cuts (Baines *et al.* 1998). In this study, however, we focus on ground-dwelling spiders, notably of the families Lycosidae, Gnaphosidae, Clubionidae, because they appear to be the most common in ECA hay meadows (Blick *et al.* 2008; Albrecht *et al.* 2010). These families are mostly stenochronous species, reproducing in spring or summer and overwintering as juveniles. Gnaphosidae and Clubionidae have moreover nocturnal habits and as such might be more affected by the drastic changes in habitat structure and food resources that follow mowing, than by the mowing operations themselves (Roberts 1996). Lycosidae, the most common family among the three, are most abundant from June

to August (Cordes 1991), benefitting from delayed mowing for completing their life cycle, yielding numerous overwintering juveniles. On this basis, we hypothesized a neutral or positive effect of i) further delaying the date of the first cut by a month, compared to extensively-managed ECA meadows that serve here as control, on ground-dwelling spiders. For ii) limiting the number of cuts per year to two, with at least eight weeks in-between, we did not predict any significant effect given that this measure did not, contrary to our expectations at the onset of the experiment, differ from control meadows as regards occurrence of the second mowing. As regards (iii) leaving an uncut grass refuge on a tiny fraction (10-20% of the area) of a meadow when mowing, we hypothesized a positive effect on ground-dwelling spiders, for three reasons essentially: firstly, because direct mortality due the harvesting process is reduced (Humbert *et al.* 2010a); secondly, because the uncut grass refuge will provide continuity of food resources and shelter; and, thirdly, because the refuge will serve as a overwintering site for spiders and facilitate subsequent recolonization of the mown area (Thorbek *et al.* 2004; Schmidt *et al.* 2008a; Cizek *et al.* 2011).

## **2. Material and Methods**

### *2.1 Study sites*

48 extensively managed hay meadows (Appendix 1) registered as ECA since at least 2004 were selected in 12 study areas across the Swiss Plateau (cantons of Aargau, Bern, Fribourg, Neuchatel, Vaud and Basel-Landschaft). The meadows were situated between 390 and 833 m altitude. Each study region consisted of 4 meadows occurring within 3.5 km radius, and with a minimal distance of 440 m between meadows.

A randomized block design was applied, in which, within each study region, the following different mowing regimes were randomly assigned to the four meadows, as detailed here:

- 1) Conventional extensively-managed hay meadow with the first cut not before 15 June and with no restriction on the number and frequency of subsequent cuts; this represents the standard for Swiss extensively-managed ECA hay meadows. These meadows serve as comparison baseline and are thereafter called control meadows (C-meadows).
- 2) As a conventional extensively-managed ECA hay meadow, but with the first cut not before 15 July and without any restriction on the number and frequency of subsequent cuts (D-meadow, with D for delayed).
- 3) As a conventional extensively-managed ECA hay meadow, but with a maximum of two cuts per year and at least 8 weeks between the cuts (8W-meadow, with 8W for eight weeks).
- 4) As a conventional extensively-managed ECA hay meadow, but with an annually rotated uncut refuge of 10-20% of the meadow area, (R-meadows, with R for refuge).

## *2.2 Spider sampling*

Spiders were sampled using pitfall traps consisting of white plastic cups of 15 cm height and 9 cm diameter (Brennan *et al.* 1999; Lange *et al.* 2011). A translucent plastic roof-cover measuring 12 x 12 cm was placed 3 cm above the pitfalls (Buchholz *et al.* 2010). Each trap was filled with 100 ml trapping fluid consisting of ethylene glycol mixed with water (ratio 1:3) with 0.5 g/l Sodium-Dodecyl Sulfate to reduce surface tension (Jud *et al.* 2008). Three traps were set up per meadow, at a randomly selected location, in a triangular arrangement, with an average distance



11.5 m between traps (Appendix 2). Traps were left open twice during one week, once before any mowing intervention (27 May–14 June) and once when C-meadows, 8W-meadows and R-meadows, but not D-meadows, had been mown (26 June–6 July). Spiders were stored in 70% ethanol. Adult and juvenile spiders of all samples per meadow were counted to assess mean relative abundance per meadow. One out of three samples per meadow and sampling session was then randomly chosen, from which adults were identified to species level using an online identification key ([www.araneae.unibe.ch](http://www.araneae.unibe.ch)) (Nentwig *et al.* 2013). Samples containing vertebrate by-catch (e.g. small rodents) were discarded as their content was biased (Pearce *et al.* 2005; Lange *et al.* 2011).

### 2.3 Covariables

In order to determine to which extent vegetation structure influences the diversity and abundance of spiders, sward height was measured in the field and included in all analyses as a covariate. It was assessed by measuring the tallest plant next to each pitfall trap.

In addition, the effects of presence of forest, gravel pits, settlements, water bodies, as well as experimental meadow age and size were also tested. These site-specific environmental variables were extracted from GIS databases, with estimates resulting from average pixel values of each meadow within a radius of 500 m (ESRI 2009). This reference radius has been shown to best reflect landscape factors for the most abundant spider species within this study (*Pardosa palustris*, *Pachygnatha degeeri*) (Schmidt *et al.* 2008b).

## 2.5 Statistical analysis

Analysis consisted of linear mixed effects models run with the *lmer* function of the *lme4* package for R (Bates *et al.* 2013). P-values were computed with 1 million Markov chain Monte Carlo (MCMC) iterations using the package *languageR* (Baayen 2011). The response variables were the total mean spider abundance and the mean adult spider abundance of all three samples per meadow and spider species richness of the one sample identified.

All analyses were fit a Gaussian error distribution. Mean total and mean adult abundance per sample were log-transformed to meet model assumptions of residual normality. Mean total abundance, mean adult abundance and species richness were analyzed using three seasonal datasets each, which gave three main models (first sampling session referred to as June, second sampling session referred to as July, and both sampling sessions pooled together). The analysis consisted first of a complex model containing all environmental variables and the experimental mowing treatment set as fixed effects, while the study area was a random effect. This model was then subjected to a model selection process where mowing treatment was never excluded as the impact of this variable was our focal interest. Environmental variables were excluded if they were not significant at an alpha rejection level of 0.05 and caused no change in deviance. Model selection also was based on the corrected Akaike Information Criterion (AICc) which is a measurement of goodness of fit and complexity (Zuur *et al.* 2009) and corrects for finite sample size and thus tends to avoid issues of over fitting (Bedrick *et al.* 1994). AICc were calculated using the package *AICmodavg* (Mazerolle 2013). In order to assess to which extent the mowing treatments of the final model differed in their effects, orthogonal comparisons were performed by removing C-, 8W- and D-treatments, respectively. All statistical analyses were performed using R version 3.0.0 (R Development Core Team 2011).

### 3. Results

#### 3.1 Overview

In total, 9'306 spiders were collected consisting of 6'807 adults and 2'499 juveniles. 2'529 adult spiders were identified resulting in 52 found species (Appendix 3). Twelve individuals could not be identified due to expanded pedipalps or destroyed epigynes. 31 samples contained vertebrate by-catch and were thus discarded due to the bias they may induce (Pearce *et al.* 2005; Lange *et al.* 2011).

#### 3.2 Model selection

The model selection showed that the most parsimonious model for *total spider abundance* in June and July pooled includes the variable sward height (MCMC mean = 0.0088; Lower 95% CI = 0.0053; Upper 95% CI = 0.0127; MCMC p-value = 0.0001). In June, the final model only included the effect of mowing regimes; in July only sward height was included in the final model (MCMC mean = 0.0083; Lower 95% CI = -0.0039; Upper 95% CI=0.0212; MCMC p-value = 0.191).

The most parsimonious model for *adult spider abundance* in June and July pooled again included the variable sward height (MCMC mean = 0.0099; Lower 95% CI =0.0055; Upper 95% CI=0.0142; MCMC p-value = 0.0001), but meadow age was also retained (MCMC mean = -0.048; Lower 95% CI = -0.091; Upper 95% CI = -0.0068; MCMC p-value = 0.0278). In June, the final model included only meadow size (MCMC mean = 0.4983; Lower 95% CI =0.0095; Upper 95% CI =0.9962; MCMC p-value = 0.0502), while in July it contained both sward height ( MCMC mean = 0.0058; Lower 95% CI = -0.0096; Upper 95% CI = 0.0216; MCMC p-value = 0.4692) and meadow age (MCMC mean = -0.0684; Lower 95% CI = -0.12; Upper 95% CI= .-0.004; MCMC p-value = 0.037).

The most parsimonious model for *spider species richness* in June and July pooled included the variable sward height (MCMC mean = 0.0119; Lower 95% CI = -0.002; Upper 95% CI = 0.0254; MCMC p-value = 0.0926). In June, the final model included only the effect of mowing regimes, while in July only sward height was included in the final model (MCMC mean = -0.0004; Lower 95% CI = -0.0451; Upper 95% CI = 0.0459; MCMC p-value = 0.9796).

### *3.3 Effect of management regimes*

No effect of any alternative management regime was found for total spider abundance, adult spider abundance and spider species richness when both sampling session (June + July) were pooled together and were compared to the control, or when the treatments were compared to each other (Table 1a, 2a, and 3a; Fig. 1A, 1D, and 1G). No effect was found in June for total spider abundance, adult spider abundance and spider species richness when compared to the control, or when treatments were compared to each other (Table 1b, 2b, and 3b; Fig. 1B, 1E, and 1H). No effect was found in July for spider abundance, adult spider abundance and spider species richness when compared to the control or when treatments were compared to each other (Table 1c, 2c, and 3c; Fig. 1C, 1F and 1I). Comparison between the two sampling sessions showed that total spider abundance and adult spider abundance decreased significantly over the season for all treatments (Table 4a, 4b; Fig. 2A-D and 2E-H). Species richness, however, did not differ significantly between the two sampling sessions (Table 4c; Fig. 1I-L).

#### 4. Discussion

This study is to our knowledge the first to investigate the potential benefits, for ground-dwelling spiders, of different management measures for improving the effectiveness of extensively-managed meadows registered within the Swiss agri-environment scheme. It could detect neither a positive nor negative effect of alternative mowing regimes on this taxonomic group. This confirms the findings obtained by (Kleijn *et al.* 2006; Knop *et al.* 2006) for spiders in general, but is at odd with the opposite conclusions reached by Baines *et al.* (1998) and Schmidt *et al.* (2008a) who found negative and positive effects, respectively, on spiders. The present results also contrast with the findings obtained with other groups of invertebrates, tested within the same experimental set up, which have been shown to benefit from delayed mowing and leaving an uncut grass refuge, such as wild bees and orthopterans (Buri *et al.* 2013). All in all, this suggests that responses might be both context-dependent and taxon-dependent.

The main findings of this study are based on the prevailing occurrence of two species *Pardosa palustris*, *Pachygnatha degeeri* belonging to the family of Lycosidae and Tetragnathidae, respectively. While reported to be common species in our types of meadows (Blick 1988) specific taxon-dependent responses are only detectable with a more extensive sampling scheme. The proposed sampling schemes require a considerable amount of workload regarding identification which was impossible to meet due to financial and logistical constraints. While the total number of 52 spider species found corresponds well with studies in swiss hay meadows (Duelli *et al.* 1999; Knop *et al.* 2006), the average number of species per trap was considerably low (mean $\pm$  standard error = 5.6  $\pm$ 2.3) and a more extensive sampling scheme can be achieved first by having more traps identified to the species

level. This will account for the differing spatial distribution of spider species in the meadow. Second, as phenologies of spider species vary, an extended sampling time is proposed. Duelli *et al.* (1999) recommend a sampling scheme which spans minimal six weeks of the season. The two mowing regimes might also be applied together as the increase of spatio-temporal heterogeneity is regarded as a key factor for increasing biodiversity (Benton *et al.* 2003). Furthermore sampling in the refuge is necessary to assess thorough the influence of leaving uncut grass areas for all families of ground-dwelling spiders.

#### *4.1 Impact of mowing treatments on spiders*

Indeed the families of Gnaphosidae, Clubionidae, belonging to ground-dwelling spiders, are reported to respond positively to availability of a refuge (Schmidt *et al.* 2008a). These groups rely on litter provided by refuges for shelter from harsh climatic changes during overwintering (Uetz 1979). This partly explains the absence of a cumulative effect i.e alternative management implemented in 2010 and 2011 had no discernable effects in the samples collected in June 2012, as our main families are Lycosidae and Tetragnathidae, which rely not as heavily on litter (Uetz 1979). Leaving a refuge after mowing event was also thought to reduce direct mortality and facilitate recolonization of unmown areas. The absence of positive effect in July after the mowing event is possibly due to spiders staying in the refuge and only later migrating to the mown area after becoming more suitable (Thorbeck *et al.* 2004).

The absence of a cumulative effect of the delayed mowing on abundance of ground-dwelling spiders contrasts with the negative effect observed by Baines for plant-dwelling spiders (Baines *et al.* 1998). A possible explanation for this difference is that the majority of ground-dwelling spiders in Swiss extensively-managed ECA meadows are members of the family Lycosidae, the abundance of which mostly

peaks in May and June (Cordes 1991; Albrecht *et al.* 2010), which is definitely the case of the two most common species at our study sites: *Pardosa palustris* (Lycosidae) and *Pachygnatha degeeri* (Tetragnathidae) (Blick 1988; Szymkowiak *et al.* 1998). *Pardosa palustris* females bearing an egg sac are most abundant in May beginning of June, indicating that the majority of the population can complete its life cycle before any mowing operation (Cordes 1991). In addition the results indicate that the effect depends on hunting strategy and ground –dwelling spiders might not be as affected as plant-dwelling spiders due to their ground-living situation (Bell *et al.* 2001; Humbert *et al.* 2010b). Absence of immediate effect of a delayed mowing event on spider abundance confirms again findings of Szymkowiak (1998) indicating that abundance decreases to the same extent in the unmown as in mown meadows.

The lack of both cumulative and immediate effect after mowing event on *spider species richness* caused by the alternative mowing regimes merely confirms that extensifying meadows management from conventional, high-intensity management to low-intensity (ECA) meadows management has no effect on this taxonomic group (Knop *et al.* 2006; Aviron *et al.* 2009). Several authors have argued that this non-response is due to the fact that spiders rely more on prey abundance and vegetation structure than vegetation *per se* (Uetz 1991; Baines *et al.* 1998; Bell *et al.* 2001). In other terms, the changes in vegetation structure triggered by our experimental manipulation may have been too shallow to enhance spider diversity significantly.

The age of a meadows negatively affected adult spider abundance during the whole season, which contrast with the findings that positive effects should increase with longer term extensification (Herzog *et al.* 2005). For plants the major changes were found to develop during the first five years after onset of specific treatment (Gaisler *et al.* 2013). As our meadows were under ECA prescription for much longer

(mean $\pm$  standard error =15 $\pm$ 4.15) it is likely that the effect of a changed vegetation structure abated before the start of our project and the effect is an artefact.

Sward height positively affected ground-dwelling spider abundance and adult spider abundance over the whole season, which reflects the impact of the mowing and confirms the importance of vegetation structure even for spiders having mostly a terrestrial ecology (Uetz 1991; Dennis *et al.* 1998). This is most certainly due to the fact that over-arching vegetation heavily influences the conditions faced at ground level (Bell *et al.* 2001).

#### *4.2 Synthesis and application*

Within lowland intensively-used agricultural landscapes, semi-natural hay meadows often offer the last refuges for biodiversity, providing population reservoirs for beneficial organisms such as pollinators and pest predators (Duelli *et al.* 2003; Öckinger *et al.* 2007). Maintaining or restoring these semi-natural meadows is thus a high, but challenging priority. In our field-scale experiments, we could not evidence any significant effect of alternative mowing regimes on ground-dwelling spiders. As there was furthermore no clearly discernable trend in our data, we can conclude that in contrast to plant-dwelling spiders, ground-dwelling spiders cannot be promoted by alternative mowing practices, probably because they are less vulnerable to mowing and/or less dependent on vegetation structure (Humbert *et al.* 2010b). As a corollary, however, we can affirm that these alternative mowing regimes have no detrimental effects on ground-dwelling spiders. As these mowing regimes have been previously shown to promote if not boost other groups such as leaf- and plant-hoppers, solitary wild bees and orthopterans (Buri *et al.* 2013; Humbert *et al.* 2012, unpublished data), they can be deployed without restriction.



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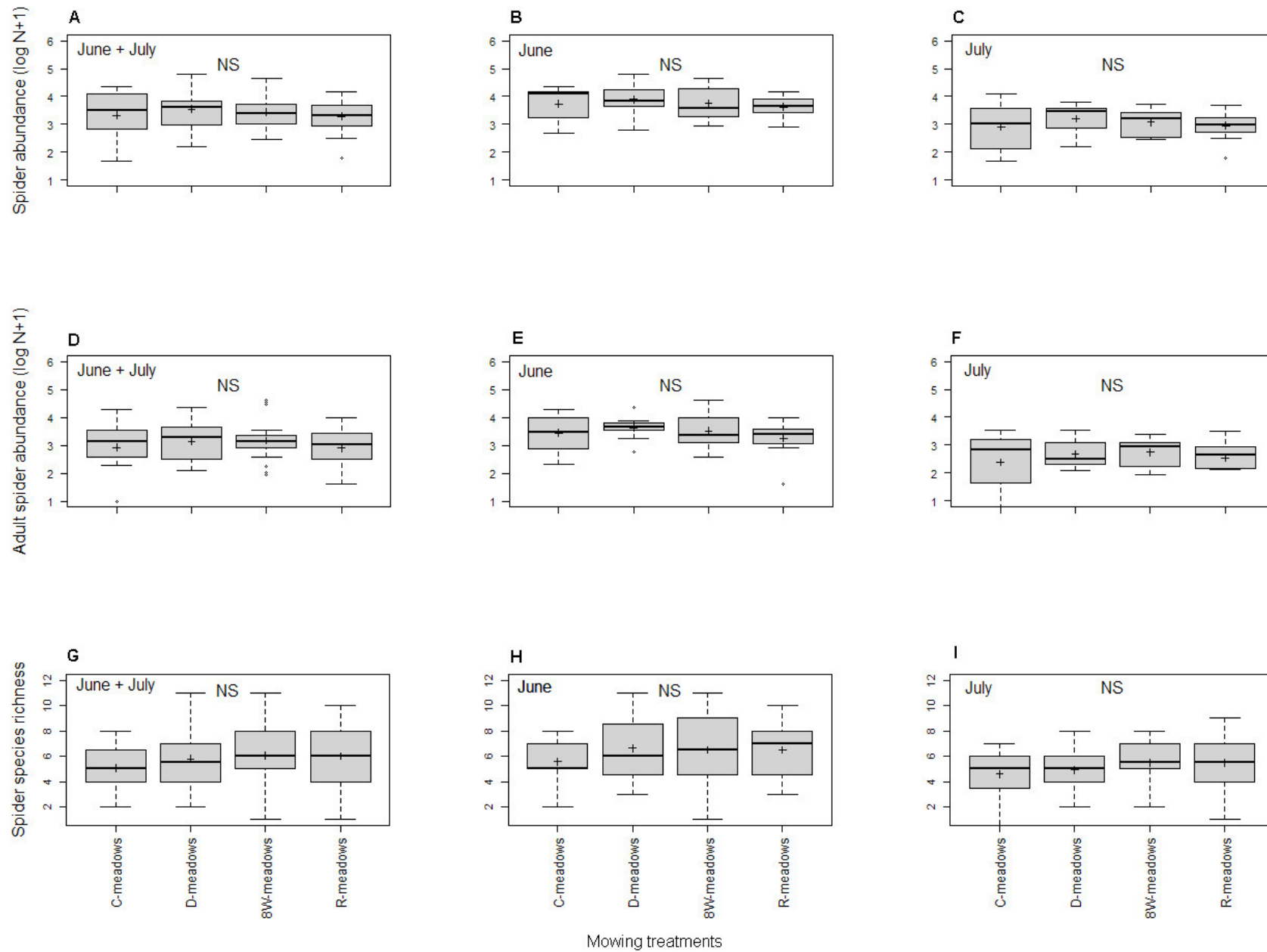
## Figure Legends

**Figure 1.** Linear mixed effects models for spider abundance, adult spider abundance and spider species richness in relation to mowing regime, with June and July samples pooled and separated. Spider abundance and spider species richness of June and July pooled together (A and G) includes sward height as a co-factor. Adult spider abundance of June and July pooled together (D) includes sward height and meadow age as a co-factor. Adult spider abundance in July (F) includes meadows age as co-factor.

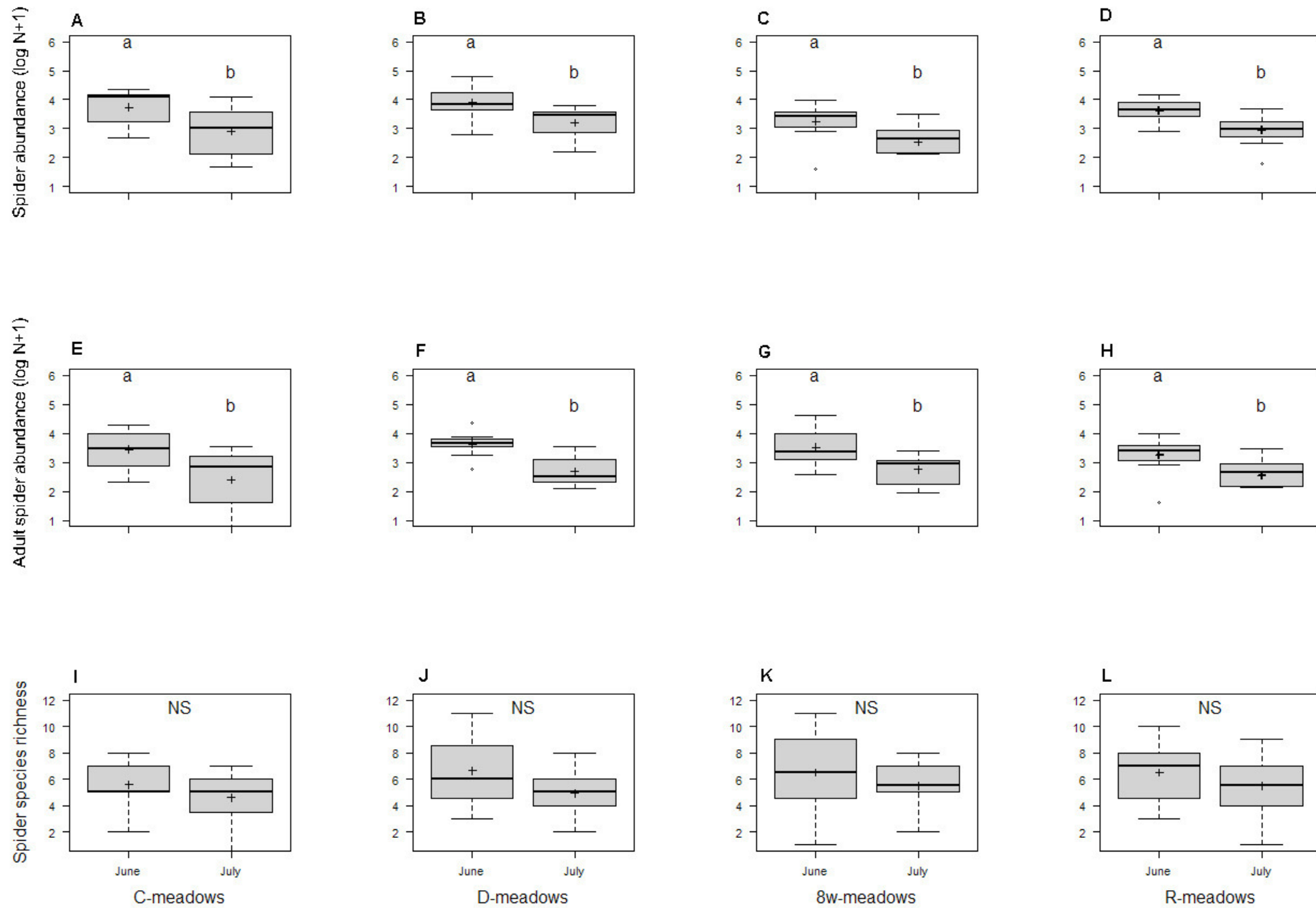
No statistical (NS) differences among treatments were found. Note the logarithmic scale for spider abundance and adult spider abundance. C-meadows: control meadows; D-meadows: meadows with delayed mowing; 8W-meadows: second mowing not earlier than 8 weeks after first mowing; R-meadow: grass refuge left uncut on 10-20% of meadow area). Detailed characteristics of mowing regimes and statistical treatment are given in Material and Methods.

**Figure 2.** Linear mixed effects models for within-treatment seasonal comparison (June vs July) of total spider abundance (A-D), adult spider abundance (E-H) and species richness (I-L). Different letters indicate significant differences between sampling session at an alpha rejection level of 0.05. Characteristics of mowing regimes and statistical treatment are given in the main text; abbreviations as in Fig. 1

**Fig. 1**



**Fig. 2**



**Table S1.** Outputs of linear mixed effects models for spider abundance in relation to mowing treatment. a) June +July, b) June and c) July. For treatment abbreviations see legend of Fig.1.

	MCMC mean	Lower 95% CI	Upper 95% CI	MCMC <i>P</i> -value
<b>a)</b>				
D vs. C	0.0576	-0.3176	0.4436	0.7640
8W vs. C	0.1125	-0.2485	0.4873	0.5450
R vs. C	0.0376	-0.3152	0.3792	0.8232
8W vs. D	0.0392	-0.3375	0.3927	0.8212
R vs. D	-0.0529	-0.4108	0.3107	0.7802
R vs. 8W	-0.0874	-0.3947	0.2386	0.5738
<b>b)</b>				
D vs. C	0.1646	-0.2783	0.6225	0.4638
8W vs. C	0.0004	-0.4106	0.4500	0.9980
R vs. C	-0.1231	-0.5400	0.3065	0.5678
8W vs. D	-0.1231	-0.5400	0.3065	0.5678
R vs. D	-0.2836	-0.7270	0.1492	0.1970
R vs. 8W	-0.1254	-0.5314	0.2897	0.5378
<b>c)</b>				
D vs. C	-0.1279	-1.0247	0.7283	0.7750
8W vs. C	0.2440	-0.2845	0.7612	0.3590
R vs. C	0.2038	-0.2868	0.7000	0.4104
8W vs. D	3.9058	-13.2040	19.9030	0.6406
R vs. D	3.2247	-15.1180	20.1978	0.7110
R vs. 8W	-0.0390	-0.5393	0.4577	0.8662



**Table S2.** Outputs of linear mixed effects models for adult spider abundance in relation to mowing treatment. a) June +July, b) June and c) July. For treatment abbreviations see legend of Fig. 1.

	MCMC mean	Lower 95% CI	Upper 95% CI	MCMC <i>P</i> -value
<b>a)</b>				
D vs. C	0.0152	-0.4127	0.4715	0.9506
8W vs. C	0.1698	-0.2760	0.6052	0.4444
R vs. C	0.0901	-0.3421	0.5086	0.6654
8W vs. D	0.1417	-0.2802	0.5694	0.5070
R vs. D	-0.0033	-0.4497	0.4305	0.9834
R vs. 8W	-0.1164	-0.5658	0.2919	0.5804
<b>b)</b>				
D vs. C	0.0886	-0.3788	0.5457	0.6996
8W vs. C	-0.0582	-0.5136	0.3910	0.7950
R vs. C	-0.2146	-0.6569	0.2288	0.3220
8W vs. D	-0.1343	-0.5886	0.2878	0.5420
R vs. D	-0.2628	-0.7431	0.1637	0.2460
R vs. 8W	-0.1189	-0.6166	0.3775	0.6404
<b>c)</b>				
D vs. C	0.0322	-1.1276	1.1621	0.9470
8W vs. C	0.3678	-0.3037	1.0719	0.2798
R vs. C	0.3841	-0.2484	1.0532	0.2358
8W vs. D	0.2142	-0.8224	1.1977	0.6542
R vs. D	0.1237	-0.9660	1.1837	0.8176
R vs. 8W	-0.0659	-0.7859	0.6619	0.8428

**Table S3.** Outputs of linear mixed effects models for spider species richness in relation to mowing treatment. a) June +July, b) June and c) July. For treatment abbreviations see legend of Fig. 1.

	MCMC mean	Lower 95% CI	Upper 95% CI	MCMC <i>P</i> -value
<b>a)</b>				
D vs. C	0.6961	-0.6695	2.165	0.3258
8W vs. C	0.9659	-0.346	2.3108	0.1582
R vs. C	1.0617	-0.2491	2.4048	0.1098
8W vs. D	0.2176	-1.2365	1.6964	0.7752
R vs. D	0.3142	-1.1861	1.823	0.6680
R vs. 8W	0.0647	-1.3757	1.5964	0.9328
<b>b)</b>				
D vs. C	1.1106	-0.737	2.948	0.2326
8W vs. C	0.9205	-0.8492	2.749	0.3088
R vs. C	0.9225	-0.967	2.699	0.3058
8W vs. D	-0.2157	-2.051	1.761	0.8070
R vs. D	-0.2199	-2.216	1.66	0.8076
R vs. 8W	0.0134	-2.112	2.142	0.9812
<b>c)</b>				
D vs. C	0.8796	-2.5274	4.0692	0.5962
8W vs. C	1.0933	-0.8292	3.1071	0.2642
R vs. C	1.1587	-0.785	2.9682	0.2162
8W vs. D	-0.5751	-3.9527	2.7261	0.7338
R vs. D	-0.6016	-4.2974	2.9036	0.7434
R vs. 8W	-0.1429	-2.459	2.142	0.8958

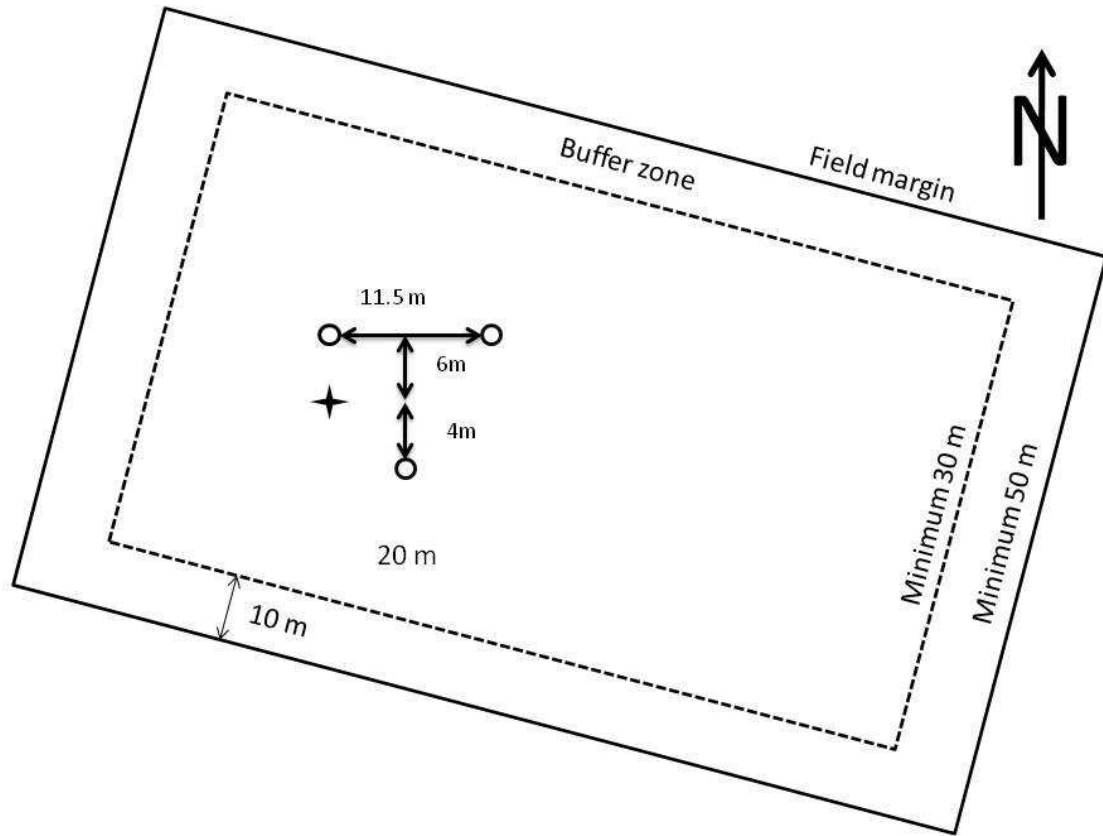
**Table S4.** Outputs of linear mixed effects models for within-treatment seasonal comparison (June vs July) of spider (a) total abundance, (b) adult abundance and (c) species richness. Significant contrasts are highlighted in bold. For the definition of treatment abbreviations see legend of Fig. 1.

		Lower 95% CI	Upper 95% CI	MCMC <i>P</i> -value
<b>a)</b>				
C-meadows	-1.063	-1.786	-0.3706	<b>0.006</b>
D-meadows	-0.7006	-1.144	-0.2507	<b>0.005</b>
8W-meadows	-0.6617	-1.131	-0.1684	<b>0.011</b>
R-meadows	-0.6618	-1.024	-0.308	<b>0.002</b>
<b>b)</b>				
C-meadows	-0.8232	-1.388	-0.2723	<b>0.005</b>
D-meadows	-0.9603	-1.348	-0.5741	<b>0.000</b>
8W-meadows	-0.778	-1.339	-0.271	<b>0.005</b>
R-meadows	-0.7133	-1.237	-0.1758	<b>0.011</b>
<b>c)</b>				
C-meadows	-1.002	-2.639	0.5915	0.221
D-meadows	-1.711	-3.477	0.2127	0.068
8W-meadows	-1.724	-3.562	0.1505	0.069
R-meadows	-0.9978	-2.906	0.853	0.293

**Appendix S1.** List of meadows with their respective treatment, geographic coordinates and number of adult and juveniles spiders found per meadow.

Landscape Unit	Canton	Mowing regime	WGS_X°	WGS_Y°	Juveniles	Adults	Total
Nyon	VD	Control	6°13'9.4"	46°24'53.2"	56	105	161
Nyon	VD	Delayed	6°11'45.4"	46°22'42.4"	26	137	163
Nyon	VD	8 weeks	6°11'9.4"	46°22'43.5"	161	63	224
Nyon	VD	Refuge	6°15'15.6"	46°24'27.7"	99	128	227
Orbe	VD	Control	6°30'11.6"	46°42'37.5"	114	224	338
Orbe	VD	Delayed	6°29'30.5"	46°42'2.9"	30	167	197
Orbe	VD	8 weeks	6°28'52.7"	46°41'52.3"	11	143	154
Orbe	VD	Refuge	6°29'54.3"	46°43'2.8"	41	118	159
Avenches	VD	Control	7°0'28.4"	46°55'27.9"	12	217	229
Avenches	VD	Delayed	7°3'22.1"	46°56'20.3"	0	0	0
Avenches	VD	8 weeks	7°0'8.5"	46°55'23.6"	14	280	294
Avenches	VD	Refuge	7°3'35.3"	46°56'35.4"	17	134	151
Cousset	FR	Control	6°58'50.8"	46°49'23.4"	14	17	31
Cousset	FR	Delayed	6°58'23.7"	46°49'26.3"	294	160	454
Cousset	FR	8 weeks	6°58'33.7"	46°49'10.5"	29	144	173
Cousset	FR	Refuge	7°0'8.3"	46°49'51.8"	25	102	127
Coffrane	NE	Control	6°51'42.3"	47°0'5.6"	40	35	75
Coffrane	NE	Delayed	6°51'11.9"	47°0'5.4"	84	177	261
Coffrane	NE	8 weeks	6°51'12.2"	47°0'43.1"	86	86	172
Coffrane	NE	Refuge	6°50'58.2"	47°0'29.3"	48	19	67
Wohlen	BE	Control	7°22'40.8"	46°59'59.2"	78	246	324
Wohlen	BE	Delayed	7°25'29.5"	46°59'51.0"	75	193	268
Wohlen	BE	8 weeks	7°24'53.6"	46°58'58.5"	62	142	204
Wohlen	BE	Refuge	7°23'22.4"	46°58'11.9"	24	210	234
Grossaffoltern	BE	Control	7°22'35.5"	47°3'54.0"	33	219	252
Grossaffoltern	BE	Delayed	7°22'29.9"	47°4'31.9"	163	315	478
Grossaffoltern	BE	8 weeks	7°20'4.8"	47°4'39.3"	12	91	103
Grossaffoltern	BE	Refuge	7°20'52.1"	47°3'49.6"	22	141	163
Belp	BE	Control	7°30'38.2"	46°52'56.6"	22	140	162
Belp	BE	Delayed	7°28'26.6"	46°54'52.0"	27	147	174
Belp	BE	8 weeks	7°30'56.3"	46°53'20.6"	0	57	57
Belp	BE	Refuge	7°31'2.2"	46°53'45.8"	32	100	132
Hindelbank	BE	Control	7°36'4.2"	47°2'19.2"	191	166	357
Hindelbank	BE	Delayed	7°33'12.0"	47°3'26.4"	153	169	322
Hindelbank	BE	8 weeks	7°32'51.3"	47°1'27.4"	18	175	193
Hindelbank	BE	Refuge	7°34'3.0"	47°1'50.2"	74	104	178
Huttwil	BE	Control	7°48'53.2"	47°5'32.3"	95	166	261
Huttwil	BE	Delayed	7°51'10.9"	47°6'32.3"	11	85	96
Huttwil	BE	8 weeks	7°50'42.5"	47°6'1.6"	14	390	404
Huttwil	BE	Refuge	7°49'21.4"	47°6'37.7"	70	61	131
Diegten	BL	Control	7°49'3.0"	47°25'30.3"	8	37	45
Diegten	BL	Delayed	7°49'57.6"	47°26'18.8"	7	42	49
Diegten	BL	8 weeks	7°49'17.5"	47°25'6.6"	10	88	98
Diegten	BL	Refuge	7°49'1.2"	47°24'52.6"	32	165	197
Lupfig	AG	Control	8°11'45.9"	47°26'51.3"	4	98	102
Lupfig	AG	Delayed	8°11'15.1"	47°26'35.2"	11	143	154
Lupfig	AG	8 weeks	8°11'38.0"	47°26'29.7"	37	343	380
Lupfig	AG	Refuge	8°13'0.2"	47°26'39.8"	13	118	131

**Appendix S2.** Hypothetical meadow showing the set-up of the three pitfall traps positioned in a triangular manner. The randomly chosen GPS location is indicated by a star.



**Appendix S3.** Species list with number of individuals found per species.

Family	Species	Number of individuals
Agelenidae	<i>Histoipona torpida</i>	1
Atypidae	<i>Atypus affinis</i>	1
Corinnidae	<i>Phruolithus festivus</i>	2
Dictynidae	<i>Asagena phalerata</i>	9
	<i>Dictyna unicata</i>	1
Gnaphosiidae	<i>Halodrassus signifer</i>	12
	<i>Micaria pulicaria</i>	5
	<i>Zelotes latreilli</i>	2
	<i>Zelotes lutentianus</i>	3
	<i>Zelotes praeficus</i>	16
	<i>Zelotes pusillus</i>	60
Hahniidae	<i>Hahnina nava</i>	4
Lycosidae	<i>Alopecosa cuneata</i>	6
	<i>Alopecosa pulverulenta</i>	55
	<i>Arctosa leopardus</i>	94
	<i>Arctosa lutetiana</i>	1
	<i>Aulonia albimania</i>	5
	<i>Pardosa agrestis</i>	33
	<i>Pardosa agricola</i>	1
	<i>Pardosa amentata</i>	19
	<i>Pardosa lugubris</i>	6
	<i>Pardosa paludicola</i>	1
	<i>Pardosa palustris</i>	1113
	<i>Pardosa pratigava</i>	1
	<i>Pardosa proxima</i>	10
	<i>Pardosa pullata</i>	43
	<i>Trochosa ruricola</i>	136
	<i>Trochosa terricola</i>	1
	<i>Xerolycosa miniata</i>	17
	<i>Xerolycosa nemoralis</i>	5
Lyniiphidae	<i>Cnephalocotes obscurus</i>	4
	<i>Dicymbium nigrum</i>	7
	<i>Diplostyla concolor</i>	6
	<i>Erigone dentipalpis</i>	112
	<i>Meioneta rurestris</i>	28
	<i>Mermessus trilobatus</i>	31
	<i>Oedothorax apicatus</i>	19
	<i>Oedothorax fuscus</i>	48
	<i>Pelecopsis paralella</i>	67
	<i>Pocadicnemis juncea</i>	1
	<i>Tiso vagans</i>	17
	<i>Trichoncyboides simoni</i>	2
Salticidae	<i>Euophrys thorelli</i>	1
	<i>Phlegra fasciata</i>	3
	<i>Synageles venator</i>	1
	<i>Talavera aquipes</i>	1
Tetragnathidae	<i>Pachygnatha degeeri</i>	445
Thomisidae	<i>Ozyptilla simplex</i>	8
	<i>Xysticus acerbus</i>	1
	<i>Xysticus crisatus</i>	9
	<i>Xysticus kochi</i>	41
Zodariidae	<i>Zodarium italicum</i>	2

# Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname: .....

Matrikelnummer: .....

Studiengang: .....

Bachelor       Master       Dissertation

Titel der Arbeit: .....

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LeiterIn der Arbeit: .....

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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.

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Ort/Datum

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Unterschrift