# Delayed mowing promotes planthoppers, leafhoppers and spiders in extensively managed meadows

PIERRICK BURI,[1,]* JEAN-YVES HUMBERT,[1,]* MARZENA STAŃSKA,[2] IZABELA HAJDAMOWICZ,[2] ELÉONORE TRAN,[1] MARTIN H. ENTLING[3] and RAPHAËL ARLETTAZ[1,4]    [1]Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland, [2]Department of Zoology, Siedlce University of Natural Sciences and Humanities, Siedlce, Poland, [3]Institute for Environmental Sciences, University of Koblenz-Landau, Landau/Pfalz, Germany and [4]Swiss Ornithological Institute, Sion, Switzerland

**Abstract.** 1. Biodiversity-rich grasslands have been severely impacted by agricultural intensification. Although agri-environment schemes (AES) have been launched partly to combat grassland biodiversity erosion, they could neither halt nor revert it, and this calls for alternative solutions.

2. We carried out controlled experiments on the effects of three mowing regimes on the arthropod biodiversity of extensively managed meadows, testing whether alternative mowing regimes can improve AES effectiveness: (i) mowing according to the Swiss AES prescriptions, i.e. first cut not before 15 June (control meadows); (ii) first cut not before 15 July (delayed mowing); (iii) refuge left uncut on 10–20% of the meadow area, otherwise first cut not before 15 June. Leaf- and planthoppers (Auchenorrhyncha) and spiders (Araneae) were sampled before and after mowing during 3 years, which enabled testing for immediate (within season) and carry-over (1 year to the next) effects.

3. Regarding immediate effects, Auchenorrhyncha and Araneae increased in abundance under the delayed mowing regime, with densities 3.5 and 1.8 times higher, respectively, than in control meadows. Furthermore, a positive carry-over effect was detected for Araneae density under the delayed mowing regime. The refuge mowing regime had no effect on abundance. Finally, no statistically significant changes were detected for species richness and diversity (Shannon index) after 2 years of manipulations.

4. We conclude that delaying the first cut in extensively managed meadows promotes these two taxa. It could be easily implemented by slight adjustments of the extant grassland AES.

**Key words.** Araneae, Auchenorrhyncha, biodiversity promotion areas, grassland management, pitfall traps, suction sampling.

## Introduction

Traditional farming practices have moulded Palaearctic landscapes for millennia, giving birth to some of the biodiversity richest open habitats in the world. Yet, since World War II, these practices have been progressively replaced by high-intensity management aimed at increasing food production. This shift was made possible by mineral fertiliser application, heavy mechanisation, enlarged fields, as well as a conversion from mixed farming to

Correspondence: Jean-Yves Humbert, Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH – 3012 Bern, Switzerland. E-mail: jean-yves.humbert@iee.unibe.ch

*These authors contributed equally to this work and should be considered co-first authors.

highly specialised, monoculture systems (Warren *et al.*, 2007). The well-known consequences are a strong uni-formisation of cultivated landscapes and a spatio-temporal homogeneisation of farming practices, which have led to dramatic losses of semi-natural habitats and the collapse of farmland biodiversity (Benton *et al.*, 2003; Tscharntke *et al.*, 2005; Vickery & Arlettaz, 2012).

To lessen the negative consequences of farming intensification, agri-environment schemes (AES) were established in the early 1990s with the objective of preserving and even restoring farmland biodiversity (Kleijn & Sutherland, 2003). Despite the high level of subsidies that flow into these schemes, most evaluation studies could only find weak evidence of benefits for biodiversity (Kleijn *et al.*, 2006; Aviron *et al.*, 2009), which questions the validity of these schemes and prompts calls for alternative, more effective options (Batáry *et al.*, 2011).

In 2010, we launched a research programme with the objective of testing for alternative management solutions compatible with current prescriptions for extensively managed hay meadows – one of the most widespread type of AES (Kleijn *et al.*, 2006) – that could improve their effectiveness. Investigated management options were deliberately inexpensive and easy to implement by farmers to ensure their potential future uptake. They consisted of different alternative mowing regimes: (i) delaying the first possible mowing date by approximately 1 month, to 15 July, in order to maintain undisturbed habitats at a time when most of the agricultural matrix has become void of protruding vertical stratified grass structures (Kőrösi *et al.*, 2012); and (ii) not mowing a fraction of the meadow otherwise mowed not before 15 June, i.e. leaving an uncut refuge that can provide field-scale continuity of food resources and shelter across the cultivated matrix (Dittrich & Helden, 2012; Humbert *et al.*, 2012a; Requier *et al.*, 2015). The biodiversity in meadows subject to the two experimental mowing treatments was compared to the biodiversity in meadows complying with the Swiss standard AES prescriptions for extensively managed meadows, which served as controls. Standard management of Swiss AES meadows consists of a first cut not before 15 June and no uncut refuge left behind. The experiments were conducted at the field scale, applying these three different mowing regimes during 3 years (2010–2012) in order to evaluate direct, immediate short-term effects (before vs. after the grass cut) and carry-over, cumulative effects (from 1 year to another).

Two groups of bioindicators that characterise grasslands were selected among arthropods: Auchenorrhyncha (Insecta: Hemiptera; plant- and leafhoppers) and Araneae (Chelicerata: Arachnida; Araneae). The former taxon feeds exclusively on plant sap, constituting an important part of the invertebrate community of grasslands (Nickel, 2003) and being an important food resource for many upper taxa such as birds (Helden *et al.*, 2014). The second taxon, Araneae, is a key component of farmland biodiversity: as pest predators, spiders provide an essential ecosystem service (Nyffeler & Benz, 1987; Sunderland, 1999).

We hypothesised that our alternative mowing regimes would have positive effects on the abundance and species richness of these two taxa through two mechanisms: first, by mitigating the direct negative mechanical impact (mortality) of the harvesting process (Humbert *et al.*, 2012a); and second, by prolonging the spatio-temporal availability of shelter, oviposition sites, microhabitat for web building, foraging grounds and prey, which otherwise abruptly disappear with mowing (Dittrich & Helden, 2012; Humbert *et al.*, 2012b).

This study aims at proposing new management options to enhance the effectiveness of grassland AES. Such recommendations are especially timely, given the recent recognition that AES-subsidised grasslands represent the best instruments for the promotion of a greener European Common Agricultural Policy (Mouysset, 2014; Pe'er *et al.*, 2014). Within this same research programme, the effects of the mowing regimes have already been investigated on wild bees (Buri *et al.*, 2014), orthopterans (Buri *et al.*, 2013) and butterflies (Bruppacher *et al.*, 2016), however, this study further tackles a pressing but still poorly investigated issue: what is the best date for mowing hay meadows so as to maximise biodiversity benefits, in particular for invertebrates, and can a refuge area compensate for an otherwise earlier cut meadow (Humbert *et al.*, 2012b; Littlewood *et al.*, 2012).

## Materials and methods

### Study sites

In 2010, 36 extensively managed hay meadows registered as biodiversity promoting areas (previously known as ecological compensation areas) within the Swiss AES were selected across the Swiss Plateau (see Appendix S1; exact site coordinates in Appendix S2). The meadows retained for the experiments had to have been registered as biodiversity promoting areas since at least 2004 (range: 1993–2004) and had to have a minimal size of 0.3 ha (range: 0.3–1.7 ha). They were dispersed among 12 study areas, each ≥5 km distant from the other, between 390 and 833 m in altitude. Each study area comprised three meadows (one per mowing regime) that were distant from each other by at least 440 m (range: 440–6170 m) but encompassed within a radius of 3.5 km.

### Study design

A fully randomised block design was adopted, with the three different mowing regimes replicated within the study areas, the latter operating as experimental blocks, thus ensuring data independence. The following three mowing regimes were randomly assigned to the three meadows within a given study area:

1 Extensively managed meadow as declared under Swiss AES: first cut not before 15 June, but without further restrictions concerning the number and frequency of subsequent cuts. These meadows constitute our control meadows (C-meadows).

2 Extensively managed meadow with first cut 1 month later than the above AES regulation, i.e. not before 15 July, with no restriction on the number and frequency of subsequent cuts (D-meadows, with D for delayed).

3 Extensively managed meadow with a rotational uncut refuge on 10–20% of the meadow area, meaning that a corresponding proportion of the area was left uncut each time the meadow was mown, with the location of the refuge changing from one cut to the next to avoid vegetation succession; otherwise, first cut not before 15 June (R-meadows, with R for refuge).

Other management restrictions (neither fertiliser nor pesticide application; grazing permitted between 1 September and 30 November) were kept as specified in the extant AES regulations (Swiss Federal Council, 1998). The experimental treatments started in spring 2010.

*Sampling methods*

In 2010, 2011 and 2012, Auchenorrhyncha and Araneae were collected with a suction sampler (Stihl SH86; Stihl, Waiblingen, Germany). The device has an air flow rate of 770 $m^3$ $h^{-1}$ and an air suction velocity of 85 $m$ $s^{-1}$. This method is recognised as being efficient to collect the two above-mentioned taxa (Sanders & Entling, 2011). Each sample was vacuumed from inside a circular metallic tube enclosure of 0.51 m diameter (surface area 0.2 $m^2$) that prevented arthropods from escaping (Hossain *et al.*, 1999), thus enabling density estimates to be made (Bergthaler & Relys, 2002). Vacuum duration was not standardised because of variation in vegetation height, though it was minimum 20 seconds per sample of 0.2 $m^2$. Samples were collected twice a year: a first time before any mowing action occurred, i.e. between the end of May and mid-June (hereafter called June samples); and a second time around the beginning of July, after all but D-meadows had been mown (hereafter called July samples; for exact dates of collection see Appendix S2). Therefore, D-meadows were sampled both times before the first cut. A virtual cross with 6 m perpendicular branches was randomly placed in each meadow, where five samples were taken per visit and meadow, thus covering a total sampled area of 1 $m^2$ per visit. Samples were taken at the extremity of the cross branches and in the centre. Note that July samples for R-meadows were taken from the mown part of the meadow and not from the uncut refuge to avoid any bias. After collection, samples were transferred into plastic bags and stored in a deep freezer (−20 °C) before being categorised to main taxonomic groups and counted. Adult individuals collected in 2012 were identified to the species level, based on classical identification keys: Biedermann and Niedringhaus (2009) for Auchenorrhyncha; Almquist

(2005, 2006), Roberts (1985), and Nentwig *et al.* (2013) for Araneae.

In 2012, pitfall traps were additionally used for collecting ground-dwelling Araneae for a better assessment of Araneae communities. Traps were installed twice, for 1 week each time, a first time before and a second time after mowing, i.e. in parallel to the two suction sampling sessions (June and July). Three traps were set at each angle of an 11 m side virtual equilateral triangle centered on the virtual cross used for the suction sampling. Traps were plastic cups (9 cm in diameter, 15 cm deep) covered with a solid transparent plastic shield, to protect against rain (12 × 12 cm), nailed to the ground at 3 cm above its surface (Buchholz *et al.*, 2010). Traps were filled with 100 ml ethylene glycol mixed with water (1:3) to which we added 50 mg of sodium dodecyl sulphate to reduce surface tension (Jud & Schmidt-Entling, 2008). Collected Araneae were kept in 70% ethanol. The content of one randomly chosen trap per meadow and sampling session was identified.

*Statistical analyses*

Density data were computed per meadow and were analysed for each session separately (generating six different models per taxon) via linear mixed models (LMMs) with mowing regime as a main fixed effect and study areas as random intercept factor. Analyses of June sessions, before any mowing actions, were aimed at revealing the carry-over (from 1 year to another) effect of a mowing regime, while analyses of July samples were aimed at revealing a combination between carry-over and immediate effects of the mowing regime. Density data had to be log-transformed for Auchenorrhyncha, and were square rooted for the Araneae in order to achieve normal distribution of the residuals. To investigate the immediate effect of mowing (precisely the direct impact of the whole hay harvesting process, see Humbert *et al.*, 2010), the densities in July divided by densities in June were computed in all meadows, per year and for both taxa. Because both sampling sessions occurred before mowing in D-meadows but before and after mowing in C-meadows, the difference in relative changes between D- and C-meadows reflects the immediate effect of mowing. These relative changes (log-transformed) were analysed with the help of LMMs, with mowing regimes as fixed effect and year of sampling and study area as random intercept factors. Year was set as random factor to account for the multiple year samples and not as fixed effect, as the immediate impact of mowing is expected to be the same every year.

Species richness and diversity analyses (Shannon index) were based on 2012 samples only and sampling sessions were pooled, resulting in a single model per taxon. For the Aranea species, data collected with pitfalls and suction sampler were merged. Species richness was analysed via generalised linear mixed models (GLMMs) with mowing regime as a main fixed effect and study areas as random

intercept factor and the Poisson error distribution was used. Diversity data were analysed with LMMs with mowing regime as a main fixed effect and study areas as random intercept factor.

Other environmental descriptors that could influence Auchenorrhyncha and Araneae communities such as elevation, slope, mean ambient temperature, duration as extensively managed meadow as registered under Swiss AES, meadow size (ha), average growing season duration (days) and proportion of different land covers within a 250 m radius (forest; gravel pits; special crops, i.e. vineyards plus orchards; settlements; water bodies) were investigated in separate models, one for each taxon, covering all the sampling period (2010–2012). Land covers were extracted from the Vector 25 database of the Swiss Federal Office of Topography (Swisstopo, 2011) using QGIS (Quantum GIS Development Team, 2013) and SpatiaLite (Furieri, 2008) software. Due to the direct trophic link between plants and Auchenorrhyncha, which are sap suckers, initial plant species richness of the meadows (number of species recorded in 2010 in each meadow, see Appendix S3) was also included in the analysis for Auchenorrhyncha. These environmental descriptors were analysed in two steps to avoid over-parametrisation of GLMMs. The first step consisted of a non-metric multidimensional scaling analysis (NMDS), where empirical *P*-values of the NMDS factors were calculated with 999 permutations (Carré *et al.*, 2009). The NMDS significant factors (*P*-values ≤ 0.05) were selected for the second step that consisted of building several GLMMs with different combinations of the selected factors. A conventional AICc ranking procedure and the help of the *aictab* function of the package *AICmodavg* was therefore conducted in order to identify models with the best fits (Sugiura, 1978; Mazerolle, 2011). The variables included in the model with the lowest AICc for each taxon were then included in the above presented analyses. Further details on these model selections are presented in Appendix S3.

Moreover, specific analyses on several subgroups of the two taxa, defined by their taxonomic level and functional traits (Appendix S4), were also performed on data collected in 2012. Auchenorrhyncha were grouped into families and sub-families, and according to functional traits such as period of emergence (March, April, May, June, July or throughout the year), voltinism (number of generations per year, i.e. 1, 2 or 3), overwintering stage (egg, nymph or imago) and feeding habits (monophagous, limited to grass, oligophagous or polyphagous; Biedermann & Niedringhaus, 2009). Araneae subgroups consisted of families, hunting tactic (mobile hunters vs. web-users), type of web used (sheet-, space- or orb-webs), strata used (ground or plant dwelling), activity period (day or night), preference for shading and preference for moisture (Entling *et al.*, 2007; Cardoso *et al.*, 2011). Araneae rarity was also inferred from expected commonness among grasslands typical of the Swiss plateau (Hänggi, personal communication) and tested with regard of the three experimental mowing treatments. These models were run separately for June and July samples and also analysed using GLMMs with mowing regime as a fixed factor and study areas as random intercept factor. All analyses were performed with the statistical software R version 3.0.1 (R Core Team, 2015).

## Results

A total of 19 362 Auchenorrhyncha were collected in 2010, 2011 and 2012. From the 2012 samples, we identified 52 species out of 5707 individuals (Appendix S4). A total of 7175 Araneae were collected via suction sampling in 2010–2012. In 2012, we identified 72 species of Araneae from 2704 individuals collected via suction sampling, and 45 species from 1792 spiders collected with pitfall traps. In total, 89 species of Araneae were recognised, i.e. 28 species were collected with both sampling methods (Appendix S4). Numbers of individuals given above include all developmental stages.

### Mowing regimes

C-meadows (control) were mown, on average (mean for 2010–2012 ± standard deviation), 1.9 ± 0.5 times a year, with the first cut occurring on average on 22 June, and the second cut (if present) taking place at the end of August (exact dates in Appendix S2). R-meadows (refuge regime) were cut (except the refuge area), on average, 2.1 ± 0.4 times a year, with the first cut occurring, on average, on 21 June and the second cut on 19 August. D-meadows (delayed regime) were cut on average 1.6 ± 0.6 times a year, with the first cut taking place on average on 23 July and the second cut on 13 September. In spring 2012, one D-meadow was lost through unexpected conversion into a gravel pit.

### Auchenorrhyncha

Elevation and ambient temperature were removed from the list of variables considered with the help of the NMDS analysis for Auchenorrhyncha as they were autocorrelated with precipitation and the duration of the vegetation growing season. Regarding the selection of environmental variables, only forest (see Appendix S3 for detailed statistical outputs) was retained in the first step with NMDS. Model ranking (lowest AICc) in the second selection step retained a best model that did not include any environmental variable. Therefore, models containing only mowing regimes as fixed factor and study areas as random intercept effect were tested.

Before mowing (sampling sessions of June), Auchenorrhyncha densities did not differ between mowing regimes, with the exception of June 2010, where R-meadow density (mean ± standard error SE; 87.83 ± 20.94) was higher than in C-meadows (55.67 ± 3.13), indicating a difference

before the start of the experiment. In July, D-meadows harboured higher densities than C- and R-meadows for the three consecutive years (Fig. 1a and Table 1). Relative changes in densities from June to July in D- (multiplied by 1.37 ± 0.26) compared to C-meadows (multiplied by 0.57 ± 0.16) were significantly different (Table 2). In other words, there was a significant immediate negative impact of mowing on Auchenorrhyncha densities.

Investigating for carry-over effects on subgroups based on the June 2012 samples, densities of Delphacidae (2.00 ± 0.52 in R- vs. 5.25 ± 1.72 in C-meadows), species emerging in April (0.67 ± 0.28 in R- vs. 5.25 ± 1.70 in C-meadows) and species overwintering as nymphs (2.00 ± 0.52 in R- vs. 5.25 ± 1.70 in C-meadows) were lower in R- compared to C-meadows. While considering the direct effect of mowing using July 2012 samples solely, higher densities were observed for many subgroups of Auchenorrhyncha in D-meadows (see Appendix S5). Furthermore, Deltocephalinae showed lower densities in R- (3.91 ± 0.76) compared to C-meadows (6.08 ± 2.30).

Finally, analyses of species richness (mean ± SE per meadow = 12.38 ± 0.48) and diversity (Shannon index: 1.74 ± 0.07) did not show any statistically significant difference between regimes and sampling sessions (Fig. 2a and Table 2).

## Araneae

As for Auchenorrhyncha, elevation and ambient temperature were removed with the help of the NMDS procedure as they correlated with other variables. Actually, the duration of registration of a meadow as extensively managed within the Swiss AES was the unique co-variable selected in the first step with the NMDS analysis (Appendix S3). As for Auchenorrhyncha, the second selection step retained as best model (lowest AICc) the one that included no co-variable at all. Therefore, models containing only mowing regimes as fixed factor and study areas as random intercept effect were tested.

Analysis for detection of carry-over effects (June samples) yielded no statistical difference between the mowing regimes, with a noticeable exception in June 2012, when Araneae density was higher in D- (35.82 ± 5.43) than in C-meadows (18.83 ± 3.17; see Fig. 1b and Table 1). Concerning the July samples, densities were always (i.e. in the 3 years) higher in D- compared to C- and R-meadows (Fig. 1b and Table 1). While densities from June to July increased in both D- and C-meadows, relative changes (respectively 2.53 ± 0.52 and 1.66 ± 0.30) were significantly different, indicating a significant immediate negative impact of mowing on Araneae densities too (Table 2).
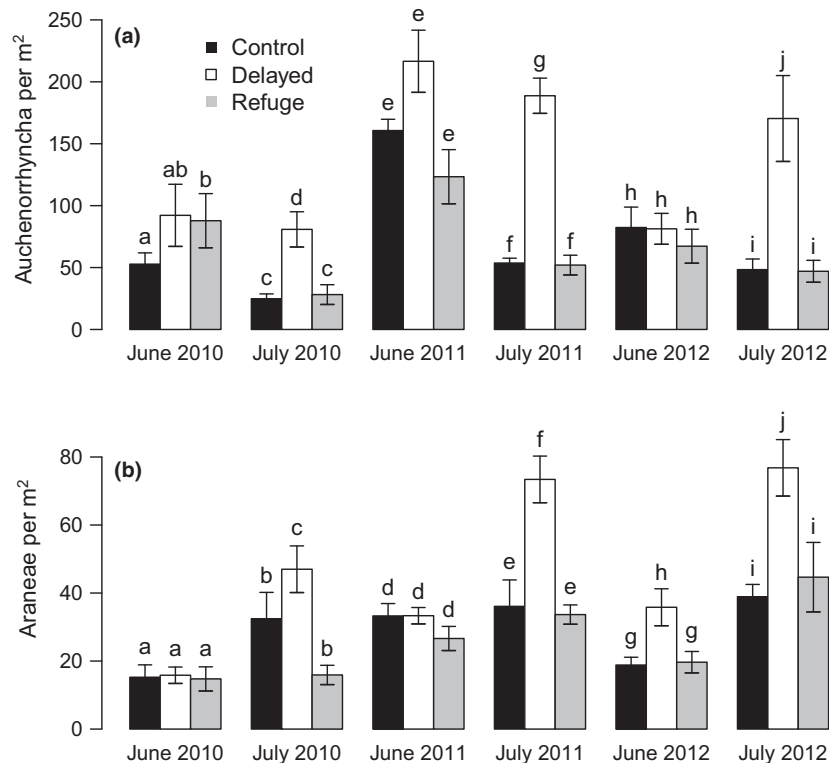


**Fig. 1.** Mean densities (individuals per m²) of (a) Auchenorrhyncha and (b) Araneae with respect to mowing regimes. Differences observed in the June sessions are due to carry-over effects, while differences evidenced in July sessions illustrate mostly the immediate effect of mowing. Error bars represent standard errors of the mean. Different letters indicate significant differences within sampling period (see Table 1 for statistical tests).

**Table 1.** Effects of mowing regimes on Auchenorrhyncha (log-transformed) and Araneae (square rooted) densities for each year and sampling session (June or July) separately.

| | | Auchenorrhyncha | | | | | | Araneae | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | June | | | July | | | June | | | July | | |
| | | Estimate | $t$ | $P$ | Estimate | $t$ | $P$ | Estimate | $t$ | $P$ | Estimate | $t$ | $P$ |
| 2010 | (Intercept) | 3.65 | 14.45 | **< 0.001** | 3.08 | 15.11 | **< 0.001** | 3.55 | 8.81 | **< 0.001** | 4.98 | 8.35 | **< 0.001** |
| | Delayed | 0.47 | 1.88 | 0.074 | 1.21 | 4.21 | **< 0.001** | 0.33 | 0.65 | 0.525 | 1.67 | 2.27 | **0.034** |
| | Refuge | 0.58 | 2.33 | **0.029** | −0.10 | −0.36 | 0.718 | 0.01 | 0.02 | 0.985 | −1.18 | −1.60 | 0.125 |
| | R versus D | 0.11 | 0.46 | 0.652 | −1.32 | −4.58 | **< 0.001** | −0.32 | −0.63 | 0.538 | −2.85 | −3.86 | **< 0.001** |
| | Random effect | 0.63 | | | 0.00 | | | 0.60 | | | 1.00 | | |
| 2011 | (Intercept) | 4.48 | 16.15 | **< 0.001** | 3.71 | 13.06 | **< 0.001** | 5.55 | 11.78 | **< 0.001** | 5.81 | 12.18 | **< 0.001** |
| | Delayed | 0.57 | 1.61 | 0.122 | 1.37 | 3.78 | **< 0.001** | 0.06 | 0.09 | 0.930 | 2.59 | 4.99 | **< 0.001** |
| | Refuge | 0.16 | 0.45 | 0.659 | −0.20 | −0.55 | 0.585 | −0.63 | −0.96 | 0.347 | −0.21 | −0.40 | 0.691 |
| | R versus D | −0.41 | −1.15 | 0.261 | −1.57 | −4.34 | **< 0.001** | −0.69 | −1.07 | 0.296 | −2.79 | −5.39 | **< 0.001** |
| | Random effect | 0.36 | | | 0.42 | | | 0.24 | | | 1.06 | | |
| 2012 | (Intercept) | 4.01 | 18.38 | **< 0.001** | 3.60 | 15.91 | **< 0.001** | 4.16 | 10.58 | **< 0.001** | 6.12 | 11.71 | **< 0.001** |
| | Delayed | 0.22 | 0.99 | 0.334 | 1.36 | 4.76 | **< 0.001** | 1.62 | 3.15 | **0.005** | 2.67 | 4.19 | **< 0.001** |
| | Refuge | 0.07 | 0.31 | 0.763 | 0.05 | 0.17 | 0.866 | 0.15 | 0.31 | 0.762 | 0.17 | 0.27 | 0.789 |
| | R versus D | −0.16 | −0.69 | 0.497 | −1.31 | −4.59 | **< 0.001** | −1.46 | −2.85 | **0.009** | −2.50 | −3.92 | **< 0.001** |
| | Random effect | 0.53 | | | 0.39 | | | 0.59 | | | 0.98 | | |

Significant *P*-values are highlighted in bold. Abbreviations are: D for delayed R for refuge. The intercept represents the control mowing regime. R versus D, represents estimate of R minus estimate of D. Random effect reports the estimated standard deviation for the random intercept effect (i.e. study area).

**Table 2.** Relative differences between July and June samples (densities in July divided by densities in June) as well as effects of mowing regimes on Auchenorrhyncha and Araneae species richness and diversity (Shannon index).

| | | July densities/June densities | | | Species richness | | | Shannon Wiener index | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Estimate | $t$ | $P$ | Estimate | $z$ | $P$ | Estimate | $t$ | $P$ |
| Auchenorrhyncha | (Intercept) | −0.57 | −2.09 | 0.064 | 2.41 | 26.94 | **< 0.001** | 1.72 | 12.01 | **< 0.001** |
| | Delayed | 0.88 | 4.61 | **< 0.001** | 0.15 | 1.28 | 0.200 | −0.11 | −0.54 | 0.592 |
| | Refuge | −0.31 | −1.62 | 0.108 | 0.14 | 1.18 | 0.239 | 0.04 | 0.17 | 0.863 |
| | Random effect (study area) | 0.63 | | | 0.08 | | | <0.001 | | |
| | Random effect (year) | 0.26 | | | − | | | − | | |
| Araneae | (Intercept) | 0.50 | 2.81 | **0.017** | 2.15 | 20.56 | **< 0.001** | 1.80 | 13.32 | **< 0.001** |
| | Delayed | 0.42 | 2.07 | **0.041** | 0.19 | 1.69 | 0.091 | −0.21 | −1.11 | 0.278 |
| | Refuge | −0.12 | −0.58 | 0.566 | 0.18 | 1.70 | 0.088 | 0.07 | 0.39 | 0.703 |
| | Random effect (study area) | 0.27 | | | 0.12 | | | <0.001 | | |
| | Random effect (year) | 0.12 | | | − | | | − | | |

Relative differences in densities were calculated on 3 years of data (2010–2012) and species richness and diversity data on samples collected in 2012. Significant differences are highlighted in bold. Random effect reports the estimated standard deviation for the respective random intercept effect.

When exploring the carry-over effects on subgroups from the June 2012 samples (the year with detailed taxonomic information), the species of spiders that build capture webs occurred at higher densities in D- (6.54 ± 1.64) than in C-meadows (3.75 ± 1.05). The same pattern occurred for mobile spider hunters (4.73 ± 1.27 in D- vs. 3 ± 0.64 in C-meadows). Interestingly, however, lower densities of Linyphiidae were also found in R- (4.67 ± 0.63) compared to C-meadows (6.92 ± 1.62). As per July 2012, the immediate effect of mowing increased the densities of many taxonomic subgroups in D- compared to C-meadows (Appendix S5).

Concerning the analysis of species richness (mean ± SE per meadow: 15.11 ± 0.61) and diversity (Shannon index: 1.77 ± 0.06) drawn from the high taxonomic resolution data obtained in 2012 (data from suction sampling and pitfall trapping pooled together), no difference between mowing regimes and sampling sessions was evident (Fig. 2b and Table 2).

## Discussion

This study shows that Auchenorrhyncha and Araneae inhabiting extensively managed meadows immediately
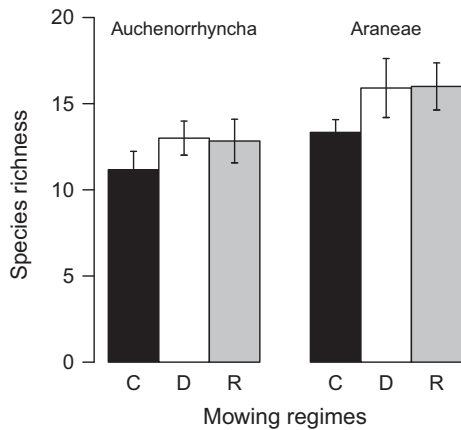
**Fig. 2.** Species richness of Auchenorrhyncha and Araneae with respect to mowing regimes. Error bars represent standard errors of the mean. Differences were not statistically significant in either Auchenorrhyncha or Araneae. Abbreviations of the mowing regimes are: C for control; D for delayed; and R for refuge.

benefit from delaying the first possible mowing date by a month (here from 15 June to 15 July). The density of Auchenorrhyncha in July, before D-meadows had been mown, was, on average, 3.5 times higher in D- than in C-meadows (mown in June), while that of Araneae was about 80% higher in D- than in C-meadows. The present results are in line with our findings from previous studies using the same experimental set up where densities of orthopterans and butterflies were, respectively, five and two times higher in D-meadows than in C-meadows, but mainly due to carry-over effects (Buri *et al.*, 2013; Bruppacher *et al.*, 2016). Here, this carry-over effect was evident only in 2012 for Araneae, additionally to other immediate effects. These results also support the conclusion of a recent systematic review on the mostly positive effects of delayed mowing on plant and invertebrate communities (Humbert *et al.*, 2012b). To the best of our knowledge and according to Humbert *et al.* (2012b), this is the first study that experimentally investigated the question on Araneae. Our findings thus provide new arguments in favour of delayed mowing as a measure to improve the effectiveness of grassland AES. By extension, these recommendations also apply to the management of other types of extensive grassy habitats such as wetlands, stream and canal banks, and road verges (Schmidt *et al.*, 2008; Noordijk *et al.*, 2009; Veen *et al.*, 2009).

*Impact of mowing regimes on Auchenorrhyncha*

Compared to other global analyses, such as Humbert *et al.* (2012b), where the distinction between immediate or carry-over effects is rarely performed, this study yields detailed results. For example, we showed that Auchenorrhyncha densities severely dropped from June (before any meadows were mown) to July (when all but D-meadows

had been mown) in C-meadows but increased in D-meadows. This supports the view that mowing has an immediate negative impact on this taxon (Morris, 1981). Postponing mowing was also found to be beneficial for bivoltine species that emerge between April and June (e.g. *Javesella pellucida* or *Philaenus spumarius*, two typical inhabitants of early-succession habitats). Delaying the first possible cut additionally decreased the yearly frequency of mowing operations, i.e. overall disturbance of biodiversity. In effect, the mean number of cuts per year was 1.6 in D- versus 1.9 in C-meadows. Despite this reduction in mowing pressure (Everwand *et al.*, 2014), and its positive effect on Auchenorrhyncha density, few specialised species were recorded altogether. Of note is that the positive effect of lower cutting frequency found in Everwand *et al.* (2014) on leafhopper species richness is probably due to the stronger contrast in their management treatments, from 3× to 1× cut per year, compared to ours. Conversely, Everwand *et al.* (2014) found a positive effect of higher cutting frequency on leafhopper abundance, but as stated by the authors, this might be indirectly due to improved performance of graminoid plants under more frequent cutting. In this study, plant assemblage did not differ among mowing regimes (unpublished data). Altogether, this might explain the general absence of carry-over effects of the mowing regime and the absence of statistically significant effects on species richness and diversity (see also Blake *et al.*, 2011).

The refuge treatment had only a moderate impact on Auchenorrhyncha overall, and even a negative impact on the density of Delphacidae in June, before any mowing operation. This group consists of species that overwinter as nymphs and are therefore likely to seek extensive vegetation cover as winter refuges (Nickel, 2003). Yet, we measured their density only in the mown part of the meadows and not in the very refuge of the R-meadows. This pattern could be explained if an active search for a refuge took place, causing a population drop in the non-refuge fraction, as we observed in orthopterans (Buri *et al.*, 2013) and butterflies (Kühne *et al.*, 2015).

*Impact of mowing regimes on Araneae*

Spiders roughly showed a similar response to the mowing regimes as Auchenorrhyncha. Overall densities in D-meadows were, on average, 40% higher than in C-meadows, with the higher density in D-meadows mainly driven by the July samples. These results corroborate the principal findings reviewed (Nyffeler, 2000): undisturbed grasslands generally harbour 10–50% greater densities of Araneae than mown meadows. In addition to the observed immediate beneficial effects of delaying mowing, the almost doubling of Araneae density detected in June 2012 in D-meadows is indicative of carry-over effects of a given management treatment from the first 2 years of the experiment to the third year (2010–2012). Such a carry-over effect was mainly observed in the species relying on a

capture web for hunting, such as *Agyneta rurestris* or *Tenuiphantes tenuis*. Species that have an active, mobile hunting strategy such as *Erigone dentipalpis* were also favoured by delayed mowing. The relatively small body size of such Linyphiidae species allows them to settle in relatively dense sward.

Lower abundances of Linyphiidae were observed in R-meadows. As observed with Delphacidae, one explanation could be that individuals aggregate in the uncut area serving as a refuge. Moreover, as farmers have the tendency to set the uncut refuges recurrently at the same place, some spatio-temporal continuity in refuge availability might favour these spiders. As for Auchenorrhyncha, this hypothesis needs to be confirmed.

Web-building spiders were somewhat advantaged by the grassy stratified structure of the D-meadows. Araneae are in fact so sensitive to mechanical disturbance (Cattin *et al.*, 2003) that only very delayed mowing regimes would permit the accomplishment of their life cycle (Baines *et al.*, 1998). As for plant- and leafhoppers, the spider communities sampled at our study sites comprise mostly generalist species. The restoration of diverse Araneae communities in extensively managed meadows seems thus to require further management options that provide more permanent grassy habitats throughout the vegetation period.

## Conclusions and management recommendations

Although Auchenorrhyncha and Araneae belong to different trophic levels, both responded similarly to our experimental mowing regimes: in July, densities were systematically higher in D-meadows than in C- and R-meadows, when only the former were still unmown, thus evidencing the negative immediate effects of any mowing action (Humbert *et al.*, 2009). This confirms the advantageous effect exerted upon biodiversity by delayed grass mowing. Furthermore, a cumulative positive carry-over effect of the delayed mowing regime over the years was also evidenced for Araneae, as previously demonstrated for orthopterans and butterflies in particular (Buri *et al.*, 2013; Bruppacher *et al.*, 2016). Our extensification treatments showed no significant effect on species richness and diversity, maybe due to the fact that they were too similar to the control regime to elicit any diversification (Cattin *et al.*, 2003; Everwand *et al.*, 2014). Our species richness results are based only on the samples of 1 year and thus a survey covering a larger time period might be necessary to detect a shift in the community. Although increases in species richness and diversity were not evident here, the strong increases observed in population densities are likely to elicit cascading effects along the food chain, contributing to reinstatement of more integral communities and ecosystem functionalities (Arlettaz *et al.*, 2010).

AES have been launched to conserve and restore biodiversity in farmland, yet these highly subsidised schemes have delivered only moderate benefits so far, which calls for new valuable AES options (Kleijn *et al.*, 2006). This has been the over-arching objective of our field-scale experimentation of alternative mowing regimes. Our study was carried out in Switzerland only, however, our results have clear management implications beyond its borders. Delaying the first possible grass cut until mid-July appears to be a legitimate option to enhance the efficacy of grassland AES, as it increases Auchenorrhyncha and Araneae densities but also other taxa such as Orthoptera. Such a measure might, however, require a higher financial incentive for farmers to adopt it, as the reduction of mowing activity will not only diminish the hay yield but also the hay quality due to the late first cut (Isselstein *et al.*, 2005).

As some subgroups had lower abundances in R- (at least in the cut area) than C-meadows, this research confirms that reinstating spatio-temporal management heterogeneity within agricultural matrices is key to the preservation and restoration of farmland biological diversity (Benton *et al.*, 2003; Batáry *et al.*, 2011; Diacon-Bolli *et al.*, 2012; Rösch *et al.*, 2015). These two readily implementable options (delaying mowing or leaving uncut refuges) would probably benefit from being applied in concert, in the form of two alternative, complementary measures to be incorporated into future grassland AES, though the benefits of such a conjunction still need to be demonstrated.

## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12186:

**Appendix S1.** Location of the study sites on Google Earth (Buri_appendix_1.kml).

**Appendix S2.** Exact coordinates of the study sites,

sampling dates, number of individuals collected for Auchenorrhyncha and Araneae, and mowing dates.

**Appendix S3.** Selection of the environmental co-variables.

**Appendix S4.** Species list of the Auchenorrhyncha and Araneae identified per study area.

**Appendix S5.** Results of the subgroup (trait-based) analyses for Auchenorrhyncha and Araneae sampled in 2012.

# References

Almquist, S. (2005) Swedish Araneae, part. 1 families Atypidae to Hahniidae (Linyphiidae excluded). *Entomologica Scandinavica Supplementum*, **62**, 1–284.

Almquist, S. (2006) Swedish Araneae, part 2: families Dictynidae to Salticidae. *Insect*, **63**, 285–601.

Arlettaz, R., Krähenbühl, M., Almasi, B., Roulin, A. & Schaub, M. (2010) Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. *Journal of Ornithology*, **151**, 553–564.

Aviron, S., Nitsch, H., Jeanneret, P., Buholzer, S., Luka, H., Pfiffner, L., Pozzi, S., Schüpbach, B., Walter, T. & Herzog, F. (2009) Ecological cross compliance promotes farmland biodiversity in Switzerland. *Frontiers in Ecology and the Environment*, **7**, 247–252.

Baines, M., Hambler, C., Johnson, P.J., Macdonald, D.W. & Smith, H. (1998) The effects of arable field margin management on the abundance and species richness of Araneae (spiders). *Ecography*, **21**, 74–86.

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society of London B: Biological Sciences*, **278**, 1894–1902.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182–188.

Bergthaler, G.J. & Relys, V. (2002) Suction sampling in alpine habitats: experiences and suggestions. In European Arachnology 2000: 19th European Colloquium of Arachnology, Aarhus, Denmark, 17-22 July 2000, pp. 291. Aarhus Universitetsforlag.

Biedermann, R. & Niedringhaus, R. (2009) *The Plant-and Leafhoppers of Germany: Identification Key to all Species*. WABV Fründ, Scheeßel, Germany.

Blake, R.J., Woodcock, B.A., Ramsay, A.J., Pilgrim, E.S., Brown, V.K., Tallowin, J.R. & Potts, S.G. (2011) Novel margin management to enhance Auchenorrhyncha biodiversity in intensive grasslands. *Agriculture, Ecosystems & Environment*, **140**, 506–513.

Bruppacher, L., Pellet, J., Arlettaz, R. & Humbert, J.-Y. (2016) Simple modifications of mowing regime promote butterflies in extensively managed meadows: evidence from field-scale experiments. *Biological Conservation*, **196**, 196–202.

Buchholz, S., Jess, A.-M., Hertenstein, F. & Schirmel, J. (2010) Effect of the colour of pitfall traps on their capture efficiency of carabid beetles (Coleoptera: Carabidae), spiders (Araneae) and other arthropods. *European Journal of Entomology*, **107**, 277.

Buri, P., Arlettaz, R. & Humbert, J.-Y. (2013) Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: evidence drawn from field-scale experimentation. *Agriculture, Ecosystems & Environment*, **181**, 22–30.

Buri, P., Humbert, J.-Y. & Arlettaz, R. (2014) Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees. *PLoS ONE*, **9**, e85635.

Cardoso, P., Pekár, S., Jocqué, R. & Coddington, J.A. (2011) Global patterns of guild composition and functional diversity of spiders. *PLoS ONE*, **6**, e21710.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M. & Rodet, G. (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture, Ecosystems & Environment*, **133**, 40–47.

Cattin, M.-F., Blandenier, G., Banašek-Richter, C. & Bersier, L.-F. (2003) The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. *Biological Conservation*, **113**, 179–188.

Diacon-Bolli, J., Dalang, T., Holderegger, R. & Bürgi, M. (2012) Heterogeneity fosters biodiversity: linking history and ecology of dry calcareous grasslands. *Basic and Applied Ecology*, **13**, 641–653.

Dittrich, A.D.K. & Helden, A.J. (2012) Experimental sward islets: the effect of dung and fertilisation on Hemiptera and Araneae. *Insect Conservation and Diversity*, **5**, 46–56.

Entling, W., Schmidt, M.H., Bacher, S., Brandl, R. & Nentwig, W. (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography*, **16**, 440–448.

Everwand, G., Rösch, V., Tscharntke, T. & Scherber, C. (2014) Disentangling direct and indirect effects of experimental grassland management and plant functional-group manipulation on plant and leafhopper diversity. *BMC ecology*, **14**, 1.

Furieri, A. (2008) SpatiaLite-A complete spatial DBMS in a nutshell.

Helden, A.J., McKenzie, R., Cobbold, G., Grice, P.V., Anderson, G.Q.A. & MacDonald, M.A. (2014) Field-based grassland management for cirl buntings (Emberiza cirlus L.) and its effect on plant- and leafhoppers (Hemiptera: Auchenorrhyncha). *Insect Conservation and Diversity*, **8**, 272–281.

Hossain, Z., Gurr, G.M. & Wratten, S.D. (1999) Capture efficiency of insect natural enemies from tall and short vegetation using vacuum sampling. *Annals of Applied Biology*, **135**, 463–467.

Humbert, J.-Y., Ghazoul, J., Richner, N. & Walter, T. (2010) Hay harvesting causes high orthopteran mortality. *Agriculture, Ecosystems and Environment*, **139**, 522–527.

Humbert, J.-Y., Ghazoul, J., Richner, N. & Walter, T. (2012a) Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. *Biological Conservation*, **152**, 96–101.

Humbert, J.-Y., Ghazoul, J. & Walter, T. (2009) Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems & Environment*, **130**, 1–8.

Humbert, J.-Y., Pellet, J., Buri, P. & Arlettaz, R. (2012b) Does delaying the first mowing date benefit biodiversity in meadowland. *Environmental Evidence*, **1**, 1–9.

Isselstein, J., Jeangros, B. & Pavlu, V. (2005) Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe–a review. *Agronomy Research*, **3**, 139–151.

Jud, P. & Schmidt-Entling, M.H. (2008) Fluid type, dilution, and bitter agent influence spider preservation in pitfall traps. *Entomologia experimentalis et applicata*, **129**, 356–359.

Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., Esteban, J.D., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A. & Jöhl, R. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.

Kőrösi, Á., Batáry, P., Orosz, A., Redei, D. & Báldi, A. (2012) Effects of grazing, vegetation structure and landscape complexity on grassland leafhoppers (Hemiptera: Auchenorrhyncha) and true bugs (Hemiptera: Heteroptera) in Hungary. *Insect Conservation and Diversity*, **5**, 57–66.

Kühne, I., Arlettaz, R., Pellet, J., Bruppacher, L. & Humbert, J.-Y. (2015) Leaving an uncut grass refuge promotes butterfly abundance in extensively managed lowland hay meadows in Switzerland. *Conservation Evidence*, **12**, 25–27.

Littlewood, N.A., Stewart, A.J. & Woodcock, B.A. (2012) Science into practice – how can fundamental science contribute to better management of grasslands for invertebrates? *Insect Conservation and Diversity*, **5**, 1–8.

Mazerolle, M.J. (2011) AICcmodavg: model selection and multi-model inference based on (Q) AIC (c). R package version, 1.

Morris, M.G. (1981) Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorrhyncha. *Journal of Applied Ecology*, **10**, 7–123.

Mouysset, L. (2014) Agricultural public policy: green or sustainable? *Ecological Economics*, **102**, 15–23.

Nentwig, W., Blick, T., Gloor, D., Hänggi, A. & Kropf, C. (2013) Spiders of Europe. Version 2013, 11. < http://www.araneae.unibe.ch > 31 July 2013.

Nickel, H. (2003) The leafhoppers and planthoppers of Germany (Hemiptera, Auchenorrhyncha): patterns and strategies in a highly diverse group of phytophagous insects.

Noordijk, J., Delille, K., Schaffers, A.P. & Sýkora, K.V. (2009) Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, **142**, 2097–2103.

Nyffeler, M. (2000) Ecological impact of spider predation: a critical assessment of Bristowe's and Turnbull's estimates. *Bulletin of the British arachnological Society*, **11**, 367–373.

Nyffeler, M. & Benz, G. (1987) Spiders in natural pest control: a review1. *Journal of Applied Entomology*, **103**, 321–339.

Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Baldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Shwartz, A., Sutherland, W.J., Turbe, A., Wulf, F. & Scott, A.V. (2014) AGRICULTURE POLICY EU agricultural reform fails on biodiversity. *Science*, **344**, 1090–1092.

Quantum GIS Development Team (2013) *Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project.* < http://qgis.osgeo.org > 1 October 2013.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2012. ISBN 3-900051-07-0.

Requier, F., Odoux, J.-F., Tamic, T., Moreau, N., Henry, M., Decourtye, A. & Bretagnolle, V. (2015) Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecological Applications*, **25**, 881–890.

Roberts, M.J. (1985) *The Spiders of Great Britain and Ireland*. pp. 1–458. Brill Archive, Leiden, The Netherlands.

Rösch, V., Tscharntke, T., Scherber, C. & Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*, **179**, 209–222.

Sanders, D. & Entling, M.H. (2011) Large variation of suction sampling efficiency depending on arthropod groups, species traits, and habitat properties. *Entomologia experimentalis et applicata*, **138**, 234–243.

Schmidt, M.H., Rocker, S., Hanafi, J. & Gigon, A. (2008) Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows. *Biodiversity and Conservation*, **17**, 3003–3012.

Sugiura, N. (1978) Further analysts of the data by akaike's information criterion and the finite corrections: further analysts of the data by akaike's. *Communications in Statistics-Theory and Methods*, **7**, 13–26.

Sunderland, K. (1999) Mechanisms underlying the effects of spiders on pest populations. *Journal of Arachnology*, **27**, 308–316.

Swiss Federal Council (1998) *Verordnung über die Direktzahlungen an die Landwirtschaft*. Bundesrat, Bern, Switzerland.

Swisstopo (2011) *Vector25*. Federaol Office for Topography, Wabern, Switzerland.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, **8**, 857–874.

Veen, P., Jefferson, R., Smidt, J.D. & Straaten, J. (2009) *Grasslands in Europe of High Nature Value*. pp. 1–320. KNNV, Zeist, The Netherlands.

Vickery, J. & Arlettaz, R. (2012) The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes. *Birds and Habitat: Relationships in Changing Landcapes* (ed. by R.J. Fuller), pp. 177–204. Cambridge University Press, Cambridge.

Warren, J., Lawson, C. & Belcher, K. (2007) *The Agri-Environment*. Cambridge University Press, Cambridge.