Low input meadow harvesting process and its impact on field invertebrates

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Low input meadow harvesting process and its impact on field invertebrates

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"Why not come and sing with me," said the Grasshopper to the Ant, *"instead of working so hard?"*

(Fable The Ant and the Grasshopper. Aesop, 600 B.C.)

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Abstract

There is currently considerable interest in developing agricultural strategies that minimize impacts on farm biodiversity, particularly as many species in agricultural landscapes have suffered dramatic declines in recent decades. An important element of the on-farm activities that directly impacts biodiversity, specifically grassland fauna community, is the harvesting process itself. As yet the direct effects, such as the mechanical impacts, of the cutting process on arthropods have rarely been differentiated from the indirect effects, such as changes in habitat.

This thesis assesses the direct impacts of the grass harvesting process on field invertebrates. Chapters 1 and 2 show that different mowing practices, using different types of machinery, are remarkably different in terms of their impacts. Hand bar mowers are slightly less damaging than rotary mowers, and adding a conditioner to a rotary mower increases impacts two to three folds. Furthermore, post-mowing harvesting interventions (i.e. tedding, raking and baling) also have considerable impacts, especially on less mobile species such as Orthoptera where about 60% of the individuals that survived mowing are subsequently killed (Chapter 3). Indeed, any benefits gained in terms of reduced grasshopper mortality by using a tractor-powered bar mower over a rotary mower are mostly lost by the cumulative impact of the subsequent harvesting stages. Finally, Chapter 4 demonstrates that leaving uncut grass refuges is a simple yet effective measure to mitigate the direct negative impact of the harvesting process.

Given the strong negative impacts on field fauna of harvesting practices we recommend, where conservation of field fauna is an objective, a reduction in the number of harvests per year to the strict minimum required to maintain the plant community (one or at most two). When harvesting the grass, no conditioner should be used and uncut refuges should be left for the fauna. The use of hand motor bar mowers is recommended over tractor-powered mowers. For field vertebrates, such as amphibians, a cutting height of 10 cm is recommended.

Résumé

L'intensification des pratiques agricoles d'après-guerre a exercé une forte pression sur la biodiversité, provoquant une chute dramatique des effectifs de nombreuses espèces typiques des paysages agricoles. Dès lors, depuis les années 1990, de considérables efforts sont déployés pour développer des pratiques plus respectueuses de l'environnement et de la biodiversité. Un élément important de l'activité agricole qui affecte la biodiversité, en particulier les communautés faunistiques des prairies, est le processus d'exploitation *per se*. Cependant, l'impact direct du processus d'exploitation sur les arthropodes, c'est-à-dire la mortalité due à l'utilisation des machines, a rarement été séparé des effets indirects du processus, tels que les effets dus aux changements de l'habitat.

Cette thèse répond à cette lacune en évaluant l'impact direct du processus d'exploitation des prairies extensives sur les invertébrés. Les Chapitres 1 et 2 montrent que différentes méthodes de fauche, employant différents types de faucheuses, sont remarquablement différentes en termes d'impacts. Les motofaucheuses à barre de coupe engendrent légèrement moins de dommages que les faucheuses rotatives, et ajouter un conditionneur à une faucheuse rotative double voire triple l'impact de la fauche. Les interventions post-fauches (i.e. pirouettage, andainage et bottelage) ont également un impact considérable, notamment sur les espèces peu mobiles, telles que les sauterelles et criquets pour lesquels environ 60% des individus qui ont survécu à la fauche sont ensuite tués (Chapitre 3). De ce fait, les gains en termes de réduction de la mortalité due à l'utilisation d'un tracteur avec une faucheuse à barre de coupe sont essentiellement perdus lors des étapes qui suivent. Finalement, le Chapitre 4 montre que laisser des zones refuges non-fauchées est une mesure, simple et efficace, qui réduit l'impact négatif du processus d'exploitation.

Etant donné le fort impact de la fenaison mécanique sur la faune, nous recommandons, dans les prairies où la préservation de la biodiversité fait partie des objectifs, que le nombre de coupes par année soit réduit au strict minimum nécessaire pour maintenir la communauté florale (une, ou deux au maximum). Les conditionneurs doivent être

abandonnés, et lors de la fauche, des zones non-fauchées doivent être laissées comme refuge pour la faune. Les motofaucheuses à barre de coupes sont recommandées par rapport aux autres types de faucheuses montées sur tracteur. Pour les vertébrés, tels que les amphibiens, une hauteur de coupe de 10 cm est recommandée.

General introduction

Context

Agricultural semi-natural grasslands are widespread throughout Europe, and the general impact of the intensification of such systems on biodiversity is relatively well known (Krebs et al. 1999; Robinson and Sutherland 2002). Grassland intensification interventions include increased fertilizer input, the application of pesticides (although often less than in arable fields) and reseeding, which results in increased grass production, allowing earlier and more frequent cuts or higher grazing intensity. These changes are, in general, detrimental to grassland biodiversity, with declining plant, bird and invertebrate populations attributed to grassland intensification (e.g. Benton et al. 2002; Donald et al. 2006; Hautier et al. 2009; Marini et al. 2008; Vickery et al. 2001; Walter et al. 2010; Wilson et al. 1999), a trend that is likely to continue if no appropriated land-use changes are made (Reidsma et al. 2006; Tilman et al. 2001). In view of this, initiatives in several European countries aim to restore the biodiversity of agricultural landscapes by promoting practices that are more favourable to biodiversity (Kleijn and Sutherland 2003; Swiss Federal Council 1998). Specifically for grasslands, more extensive forms of management and efforts, such as hay transfer from species rich grasslands to rehabilitation sites, are advocated to restore degraded systems (Edwards et al. 2007).

In Switzerland, the most important agri-environmental measure regarding biodiversity are the so-called Ecological Compensation Areas (ECA) that restrict fertilizers and pesticide applications, date of first cut, etc. Evaluations have shown ECA hay meadows are usually inhabited by a higher biodiversity than non ECA meadows (Aviron et al. 2009). However, for certain fauna groups and red listed species this is not the case, particularly in low land regions (Herzog and Walter 2005; Knop et al. 2006; Roth et al. 2008). The same applies for many European agri-environmental programs for which effectiveness about their ability to improve invertebrate diversity has been questioned (e.g. Kleijn et al. 2006; Taylor and

Morecroft 2009). Several factors have been advanced to explain the moderate success regarding improvement of invertebrate diversity Including, for example, limitation of the regional species pool (Knop et al. 2008), and fragmentation of the landscape (Tscharntke and Brandl 2004). Another possible factor is the intervention of modern harvesting methods that directly kill many organisms (Humbert et al. 2009).

Meadow harvesting process

Meadows require regular harvesting (cutting) to avoid vegetation succession, and which maintains high plant diversity (Grime 2001). Invertebrates, however, show opposite responses to cutting: there is usually a reduction in species diversity and abundance of most taxa (Gerstmeier and Lang, 1996; Morris, 2000). Responses vary among species and higher taxa (see Chapter 1 section 2), but attributing a causal basis to this is often difficult, as most studies have not separated direct effects, such as mortalities during the harvesting process, and indirect effects such as changes in the habitat characteristics.

Different harvesting processes exist, which involve different techniques and machines, and the direct effects of these different processes on the fauna might differ from one process to another. For example, we could expect differences if the grass is mown with a bar mower or a rotary mower, and if the grass is tedded before removal, though few studies have investigated this topic in any detail (see Chapter 1). This lack of knowledge has hindered the creation of effective empirically based management recommendations regarding the mowing of grasslands in ecological compensation areas where biodiversity conservation is an objective. Following strong interest from farmer and government stakeholder groups for clear recommendations and guidelines, this research has sought to quantify the direct effects of the different low input meadow harvesting processes on the field invertebrates, and to establish recommendations how to minimize these effects.

The meadow harvesting process, often referred to as “cutting” or “mowing” when used in a broad sense, includes several stages: 1) mowing the grass; 2) conditioning by crushing the grass; 3) drying by tedding the grass; 4) raking or windrowing the grass; 5) removing by baling or loading the grass. Not all these stages are necessarily present during the process, depending on the environment and type of meadow (see Chapter 1 section 3 for a complete description of the harvesting process).

Thesis outline

Here may be described the research gaps and uncertainties that are addressed in each chapter of the thesis:

- A synthesis of existing literature does not exist (Chapter 1).
- A comparison of different mowing techniques is not possible in satisfying manner (Chapter 2).
- No assessment of the impact of the whole harvesting process exists (Chapter 3).
- Influence of leaving uncut grass refuges is insufficiently known (Chapter 4).

Chapter 1 reviewed the available information on the direct mortality caused by the meadow harvesting process on vertebrate and invertebrate populations with the intention of raising the profile of this neglected area of research. Despite the limitations in the number and quality of the reviewed studies, the review provides some account of the broad impacts of harvesting on meadow fauna. One important conclusion that emerged is that population impacts following mowing can be substantial, and so it is surprising that this topic has received relatively little research attention and consideration in grassland conservation programs. A possible reason is that most of the research that has been completed was published in languages other than English, and therefore remained inaccessible to many in the scientific community.

Chapter 2 measure and compare the direct impact of four common mowing techniques on invertebrate wax-models and real *Pieris brassicae* butterfly caterpillars within experimental grass plots. While the results are in line with the conclusions from the earlier literature review (Chapter 1), the results additionally show the influence of the size of the organisms and their microhabitat, and point out the strong effect of the tractor wheels. The experiment also demonstrates the utility of invertebrate models as surrogates for live invertebrates, allowing for a future standardized approach for such studies.

Chapter 3 investigate the impacts of the whole meadow harvesting process on Orthoptera, disentangling the impacts of mowing, tedding, raking and baling, and other mowing associated operations. The results provide clear indications of substantial impact on less mobile species by the entire harvesting process, but also the potential, as well as the limitations, for reductions in such impact by adopting different combinations of harvesting techniques.

Chapter 4 investigate the influence of leaving a 10% uncut grass refuge in the centre of a 50 m diameter meadow plot when mowing on Orthoptera population. Because no practicable harvesting processes are damage free (Chapter 1 to 3), leaving uncut grass refuges is a simple and good practice that can benefit many organisms.

The thesis addresses the impact of harvesting on the numerical abundance of populations that comprise meadow communities, rather than on species richness. While this may be a simple surrogate for biodiversity, we nevertheless make the recommendation from the perspective that severe declines in population sizes of a wide variety of taxa is likely to alter biodiversity both directly, and indirectly through functional changes and trophic interactions.

References

Aviron S, Nitsch H, Jeanneret P, Buholzer S, Luka H, Pfiffner L, Pozzi S, Schupbach B, Walter T, Herzog F, 2009. Ecological cross compliance promotes farmland biodiversity in Switzerland. Front. Ecol. Environ. 7, 247-252.

Benton TG, Bryant DM, Cole L, Crick HQP, 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. J. Appl. Ecol. 39, 673-687.

Donald PF, Sanderson FJ, Burfield IJ, Van Bommel FPJ, 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. Agric. Ecosyst. Environ. 116, 189-196.

Edwards AR, Mortimer SR, Lawson CS, Westbury DB, Harris SJ, Woodcock BA, Brown VK, 2007. Hay strewing, brush harvesting of seed and soil disturbance as tools for the enhancement of botanical diversity in grasslands. Biol. Conserv. 134, 372-382.

Grime JP, 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Second edition. John Wiley, Chichester, UK.

Hautier Y, Niklaus PA, Hector A, 2009. Competition for Light Causes Plant Biodiversity Loss After Eutrophication. Science 324, 636-638.

Herzog F, Walter T, 2005. Evaluation des mesures écologiques, domaines biodiversité. Zurich. Les cahiers de la FAL 56. Agroscope Reckenholz-Tänikon Research Station ART, Zurich.

Humbert J-Y, Ghazoul J, Walter T, 2009. Meadow harvesting techniques and their impacts on field fauna. Agric. Ecosyst. Environ. 130, 1-8.

Kleijn D, Sutherland WJ, 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity. J. Appl. Ecol. 40, 947-969.

Kleijn D, Baquero RA, Clough Y, Diaz M, De Esteban J, Fernandez F, Gabriel D, Herzog F, Holzschuh A, Johl R, Knop E, Kruess A, Marshall EJP, Steffan-Dewenter I, Tscharntke T, Verhulst J, West TM, Yela JL, 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243-254.

Knop E, Kleijn D, Herzog F, Schmid B, 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. J. Appl. Ecol. 43, 120-127.

Knop E, Schmid B, Herzog F, 2008. Impact of regional species pool on grasshopper restoration in hay meadows. Restor. Ecol. 16, 34-38.
Krebs JR, Wilson JD, Bradbury RB, Siriwardena GM, 1999. The second silent spring. Nature 400, 611-612.
Marini L, Fontana P, Scotton M, Klimek S, 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. J. Appl. Ecol. 45, 361-370.
Reidsma P, Tekelenburg T, Van den Berg M, Alkemade R, 2006. Impacts of land-use change on biodiversity: An assessment of agricultural biodiversity in the European Union. Agric. Ecosyst. Environ. 114, 86-102.
Robinson RA, Sutherland WJ, 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157-176.
Roth T, Amrhein V, Peter B, Weber D, 2008. A Swiss agri-environment scheme effectively enhances species richness for some taxa over time. Agric. Ecosyst. Environ. 125, 167-172.
Swiss Federal Council, 1998. Ordonnance sur les paiements directs versés dans l'agriculture. RS 910.13.
Taylor ME, Morecroft MD, 2009. Effects of agri-environment schemes in a long-term ecological time series. Agric. Ecosyst. Environ. 130, 9-15.
Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D, 2001. Forecasting agriculturally driven global environmental change. Science 292, 281-284.
Tscharntke T, Brandl R, 2004. Plant-insect interactions in fragmented landscapes. Annu. Rev. Entomo. 49, 405-430.
Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK, 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647-664.
Walter T, Klaus G, Altermatt F, Ammann P, Birrer S, Boller B, Capt S, Eggenschwiler L, Fischer J, Gonseth Y, Grünig A, Homburger H, Jacot K, Kleijer G, Köhler C, Kohler F, Kreis H, Loser E, Lüscher A, Meyer A, Murbach F, Rechsteiner C, Scheidegger C, Schilperoord P, Schierscher B, Schmid H, Schnyder N, Senn-Irlet B, Suter D, Zbinden N, Zumbach S, 2010. 3 Landwirtschaft. In: Wandel der Biodiversität in der Schweiz seit 1900. Ist die Talsohle erreicht? Ed. by Lachat T, Pauli D, Gonseth Y, Klaus G, Scheidegger C, Vittoz P, Walter T, Bristol- Stiftung und Forum Biodiversität Schweiz. Haupt Verlag Bern (*in press*).
Wilson JD, Morris AJ, Arroyo BE, Clark SC, Bradbury RB, 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agric. Ecosyst. Environ. 75, 13-30.

Chapter I

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Meadow harvesting techniques and their impacts on field fauna

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Abstract

Meadows require regular harvesting (cutting) to avoid vegetation succession, and this is well known to promote high plant diversity. The impacts of the harvesting process on animal, and particularly invertebrate, abundance and diversity is not, however, well known, but is expected to be largely negative. This study reviews the available information on the direct mortality caused by the meadow harvesting process on vertebrate and invertebrate populations with the intention of raising the profile of this neglected area of research which is nevertheless important in the context of declining field fauna diversity. Collectively, the studies show a direct and often substantial impact of the harvesting process on the fauna, especially from the mowing stages, and that this impact depends on the techniques and equipment used, as well as the settings, the habitat and the ecology of each species. The post-mowing harvesting stages also have considerable relevance, especially grass removal (baling), which may first concentrate organisms in windrows before removing them from the field, but have been rarely studied. Differences among mowing techniques and equipment can amount to a threefold change in the scale of impact on field fauna, and therefore there is a potential to reduce direct harvesting impacts. According to the reviewed studies, the use of cutter bar mowers is recommended over rotary and flail mowers, as they cause half as much mortality. If a rotary mower is used, then an add-on conditioner should be avoided. However for less mobile species, it is still unclear if the benefit gain from friendly mowing techniques might be cancelled by subsequent harvesting stages, and this important point needs further investigation. Because no practicable harvesting processes are damage free, leaving uncut grass strips is a simple and good practice that will benefit many organisms.

Keywords: amphibians, conservation, cutting, field invertebrates, grasshoppers, grassland management, mowing

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Introduction

Meadow and pasture agricultural systems are widespread throughout Europe, and the general impact of the intensification of such systems on biodiversity in agricultural landscapes is relatively well known (Krebs et al. 1999; Robinson and Sutherland 2002). Grassland intensification interventions include increased fertilizer input, the application of pesticides (although often less than in arable fields) and reseeding, which results in increased grass production, allowing earlier and more frequent cuts or higher grazing intensity. These changes are, in general, detrimental to grassland biodiversity, with declining plant, bird and invertebrate populations attributed to grassland intensification (e.g. Benton et al. 2002; Donald et al. 2006; Marini et al. 2008; Vickery et al. 2001; Wilson et al. 1999), and this trend is likely to continue if no land-use changes are made (Reidsma et al. 2006; Tilman et al. 2001). In view of this, initiatives in several European countries aim to restore the biodiversity of agricultural landscapes by promoting practices that are more favourable to biodiversity (Kleijn and Sutherland 2003). Within agricultural landscapes, emphasis on the high biodiversity value of grassland (Bignal and Mccracken 1996; Vickery et al. 2001), has promoted more extensive forms of management and efforts to restore degraded meadow systems. However, scientific knowledge of the impacts on field fauna diversity of various agricultural techniques associated with cutting in more extensive systems is very limited. ‘Cutting’ or ‘mowing’ are terms referring often to the full meadow harvesting process and encompass several stages applied under different environmental conditions with different machines, and the response of organisms is likely to vary in response to these harvesting regimes. Therefore, to be able to advise farmers and land managers about appropriate harvesting techniques requires some knowledge of the impact of these on field fauna diversity as a whole, and on specific taxa of particular conservation or ecosystem function concern.

Meadows require regular harvesting (cutting) to avoid vegetation succession, and this is well known to promote high plant diversity (Grime 2001). However, the impacts of the harvesting process on animal, and particularly invertebrate, abundance and diversity is not well known, although is expected to be largely negative (Morris 2000). The increasing recognition of the value of invertebrates in ecosystem function, notably their role in key ecosystem processes such as herbivory, nutrient cycling and pollination belies the limited knowledge on their persistence in managed meadows, habitats that dominate agricultural landscapes in Europe (e.g. Brussaard et al. 2007; New 2005). Additionally, there has been much recent concern regarding invertebrate population declines, associated with a transformation and intensification of landscapes (Hendrickx et al. 2007). In the context of a metapopulation model of invertebrate persistence, it is not clear whether managed meadows represent source or sink populations. Understanding this will contribute to our understanding of the long term viability of invertebrate populations across anthropogenic landscapes. Further relevance of this topic relates to the incentives for low impact meadow management for the purpose of promoting biodiversity. Yet these biodiversity-rich extensively managed meadows are harvested using mechanised technology, the impact of which on invertebrate biodiversity is largely unknown. Here the available information on impacts of meadow harvesting on vertebrate and invertebrate biodiversity is reviewed with the intention of raising the profile of this neglected area of research which is nevertheless important in the context of declining field fauna populations.

This review will start with a brief section about the global effects of grassland management by cutting on meadow biodiversity. It will proceed with the main section, which reviews and synthesizes our current knowledge of the direct impact of different grassland harvesting techniques on the fauna of meadows. Finally, we will provide (i) recommendations about harvesting practices and techniques to minimize impacts on field fauna, and (ii) a foundation for effective targeted research to address areas of scientific uncertainty relevant to this field.

Meadow management by cutting

Grassland ecosystems depend on regular disturbances to prevent vegetation succession (Grime 2001; Huston 1994). Grassland disturbances include the grazing regime as well as management interventions and activities such as cutting and/or burning. Cutting is the most relevant and regular intervention for meadows that are managed for hay or silage production. The main objective of cutting is to provide winter cattle feed, but in recognition of high plant diversity on extensive meadows the cutting regime is also used to maintain natural habitats of conservation importance (e.g. Cattin et al. 2003). The objective of maintaining plant biodiversity is realised at the scale of the meadow itself, but it is not known whether plant diversity correlates with invertebrate diversity and abundance at the same scale and under the same management regime. Harvesting has also undergone changes in recent decades with a dramatic increase in mechanisation and the introduction of harvesting-associated activities such as conditioning. Invertebrate field organisms that were adapted to previously implemented 'traditional' hay systems may have become additionally vulnerable to current cutting techniques.

One or two cuts per year are beneficial to meadow plant diversity (Antonsen and Olsson 2005; Huston 1994). However, for grassland invertebrates, investigations have confirmed the usual responses to cutting: reduction in diversity and in abundance of most groups and species, with positive benefits to a few (Gerstmeier and Lang 1996; Morris 2000). For example, Coleoptera seems to be a robust group in its response to cutting treatments when compared to other more sensitive arthropods, such as Heteroptera (Gerstmeier and Lang 1996; Morris 1987). Butterflies and spiders are also sensitive taxa, and it has been shown that cutting has a drastic impact on their abundances and richness (e.g. Baines et al. 1998; Bell et al. 2001; Cattin et al. 2003; Johst et al. 2006).

The time and frequency at which meadows are cut are among the most important factors affecting field biodiversity, although appropriate timing for cutting regimes vary according to the taxon concerned (Morris 2000). For example grassland-nesting birds are mostly favoured by a summer cut to allow clutches to hatch (Müller et al. 2005; Tyler et al. 1998; Walter et al. 2007), while for spiders (Baines et al. 1998) and Hemiptera (Morris and Lakhani 1979) summer cuts are more detrimental than spring and/or autumn cuts. For butterflies, Feber *et al.* (1996) and Johst *et al.* (2006) recommended a spring and autumn cut over a summer cut, while Walter *et al.* (2007) argued that a spring cut should be avoided because it would affect the less mobile developmental-stages such as caterpillars. The type of the meadow is also an important feature dictating the time and frequency of the cut, as in wetlands, late mowing on a supra-annual cycle is recommended for the conservation of arthropods (Cattin et al. 2003; Wettstein and Schmid 1999).

It is not planned to review in detail the effect of timing here, but to emphasize that there is no ideal cutting time for all taxa, and therefore cutting will always occur at a critical period for some organisms. In addition, there is a wide literature on the subject, including reviews (e.g. Gerstmeier and Lang 1996; Morris 2000), and restriction on the first cutting date have already been implemented in some agri-environmental schemes. For instance, in Switzerland extensive meadows classified as Ecological Compensation Area (ECA) can not be mown before June 15th in lowland and first or 15th of July at higher elevations, and ECA wet meadows can not be mown before first of September (Swiss Federal Council 1998).

While the general negative impact of grass cutting on field invertebrates is relatively well known, few studies have investigated whether this negative impact is mainly due to direct effects, such as mechanical stresses during the harvesting process, or indirect effects, such as changes in habitat characteristic. As cutting is an essential requirement for the long term persistence of meadows, it is important to understand the impact of the cutting process itself on fauna diversity so that this impact can be minimized.

Impacts of harvesting on field fauna

Species abundance after a cut can change for at least three reasons (Kiel 1999; Thorbek and Bilde 2004). First, the fauna experience severe mechanical stresses during the harvesting process. Some organisms might be killed by the cutting operation itself or removed from the field when baling (e.g. Gerstmeier and Lang 1996; Oppermann et al. 2000). Second, there is a drastic change in the physical structure of the environment, as well as temperature, humidity, food availability and predation pressure (Bock et al. 1992; Gardiner and Hassall 2008; Guido and Gianelle 2001). Third, faunal changes occur as some species tend to move out of the habitat while others move in (Guido and Gianelle 2001; Thorbek and Bilde 2004). Responses to cutting may vary among species or among higher taxa, but attributing the causal basis to this is often difficult, as most studies have not examined separately each of the effects mentioned above (Morris 2000; Thorbek and Bilde 2004). All three probably contribute, but their importance is likely to vary among taxa.

The meadow harvesting process, often referred to as “cutting” or “mowing” when used in a broad sense, includes several stages:

1. Mowing the grass
2. Conditioning (crushing) the grass
3. Drying by tedding the grass
4. Windrowing (raking) the grass
5. Removing (baling or loading) the grass from the field

Not all these stages are necessarily present during the process, depending on the environment and type of meadow. In this review the term “mowing” restrictively refers to the actual cutting event (i.e. the first harvesting stage). Conditioning (stage two) is a recent practice that is used to accelerate the drying of the grass by crushing it after mowing. Most conditioners are directly fixed behind the mower (mower-conditioner), and perform a rolling or crimping mechanical action on the grass immediately after cutting. Drying (stage three) and its importance will primarily depend on the form in which the grass is to be stored, hay or silage. Silage, which is grass preserved in an anaerobic environment undergoing fermentation, can be made at a grass moisture content between 40 and 85% and will often require only one tedding event, while hay is baled when grass moisture content is less than 20% and therefore the drying stage is longer and will require more tedding (Dörfler 1978). Windrowing (stage four) consists in gathering the mown grass in lines to allow a baler or self-loading trailer to remove the harvest (stage five).

Direct impacts of mowing

The direct impacts of mowing on meadow fauna represent the physical damage caused by the cutting machinery. The initial interest in this impact arose out of concern for nesting birds (Labisky 1957; Norris 1947), as nest destruction and chick mortality often exceeded 50%, although mortality was typically reduced when the fields were mown from the centre towards the edge (e.g. Bollinger et al. 1990; Frawley and Best 1991; Green et al. 1997; Tyler et al. 1998). Along with the right mowing pattern (inward-outwards), the mowing date is the main factor affecting ground nesting bird vulnerability (Green et al. 1997).

Consequently, legally enforced restrictions on the first mowing date are implemented in many European agri-environmental schemes, allowing birds to fledge before any mowing activities are permitted (e.g. Swiss Federal Council 1998; Verhulst et al. 2007; Vickery et al. 2004). Because concern for birds is already incorporated in many agri-environmental schemes and supported by an extensive literature, the impact of mowing on birds is not considered any further here. The central aim of this review is to evaluate the impact of alternative mowing systems on other meadow fauna, for which information is less widely available.

Remarkably, only a single study has reported on the impact of meadow harvesting on small mammal populations. On a total of 5.2 ha, 27 dead mammals were found, the tendency being that rotary disc mowers with conditioner caused twice more mortality than double blade mowers (Oppermann et al. 2000). With a mammal density estimated to a few hundred individuals per ha, the authors concluded that the impact of mowing on small mammals is much less than on amphibians (see same study below). Another small study followed the fate of 30 wood turtles (*Glyptemys insculpta*) via radio-telemetry and found that six (20%) died as a results of harvesting, of which at least four because of impacts with rotary disc mowers (Saumure et al. 2007). Eight additional turtles were injured during the harvesting processes due to disc mowers, tedders and/or windrowers. No other studies examining meadow harvesting impacts on mammals or reptiles were found, while amphibians by contrast have been the focus of a number of studies.

Studies on amphibians have been stimulated out of concerns for birds that feed on them. For example, in Germany declining white stork populations was associated with declining numbers of amphibians following the widespread use of rotary mowers (Oppermann and Classen 1998). Indeed, mortality or injury has been reported to affect more than a quarter of the amphibian population following a single mowing event (Oppermann and Classen 1998). Damage, however, varied considerably according to the equipment used, the cutting height and amphibian body size. Mowing with finger cutter bar mowers, for example, impacted 10% of amphibians, but this figure rose almost three-fold (to 27%) when rotary (disc or drum) mowers were used (Classen et al. 1996; Oppermann and Classen 1998).

Interestingly, non-mechanised harvesting using a scythe had a higher impact (14% amphibian losses) than when plots were mown with finger cutter bars. This effect was linked to the lower cutting height of the scythe (5-7 cm) compared to the cutter bars (7-8 cm). Similarly, the damage caused by rotary mowers was strongly associated with cutting height: At a height of 7-8 cm losses were maximal at 27%, but this dropped to 19% at 10 cm height, and 5% at 12 cm (Classen et al. 1996; Oppermann and Classen 1998).

Additional work has confirmed differential impacts based on cutting equipment. A comparison of 16 0.2 ha plots (1635 amphibians recorded) in Germany revealed that double blade bar mowers impacted 13% of the amphibian population but 21% when meadows were mown with rotary disc mowers with conditioner (Oppermann et al. 2000; Oppermann 2007). This same study compared the sizes of affected animals, and concluded that larger amphibians were more vulnerable than smaller ones, with the same pattern observed for both mowing techniques. A similar pattern of impact was recorded in northern Poland, with damage increasing from 8.7% with finger cutter bar mowers for larger individuals (≥ 3 cm) to 11.4% with double blade bar mowers and reaching 14.1% with rotary drum mowers. These values were again much reduced for amphibians of lower body size: 3.6% with rotary drum mowers, 1.6% with double blade bar mowers, and 1.4% with finger cutter bar mowers (rotary mower damage was significantly different from bar mowers). The speed and height of mowing was also important (higher speed and higher cutting height caused less damage) (Oppermann et al. 2000).

Further confirmation that the type of equipment used is a major determinant of mowing impact is provided by a number of other studies on grasshoppers, beetles, honeybees, spiders and insect larvae, as well as models that simulate invertebrates (Blodgett et al. 1995; Classen et al. 1993; Frick and Fluri 2001; Gardiner 2006; Gardiner and Hill 2006; Hemmann et al. 1987; Kraut 1995; Löbbert et al. 1994; Oppermann et al. 2000; Wasner 1987; Wilke 1992). The results from these studies were obtained using different methodologies, and were derived from different taxa, but nevertheless revealed a consistent effect of mower type (Table 1): lowest impact was associated with bar mowers, and impact increased through rotary mowers, rotary mowers with conditioner to flail mowers which had the highest impact.

Most of these studies have been conducted on invertebrates, and particularly grasshoppers, which are relatively easy to assess and may be expected to be vulnerable to mowing by virtue of their size and comparatively limited mobility. Several studies demonstrated that grasshopper populations were reduced immediately after mowing. Nine percent of marked grasshoppers were killed or injured when plots were mown with double blade bar mower, 21% when mown with rotary drum mower with or without conditioner, and 34% when mown with a rotary disc mower with conditioner (Oppermann et al. 2000; Oppermann 2007). The differences observed among mowing equipment used were significant. As with amphibians, a significant effect of grasshopper body size and cutting height was recorded: small grasshoppers (< 11 mm) were hardly affected, while more than one third of larger grasshoppers (> 20 mm) were harmed, and lower cuts caused more damage than higher cuts. Other factors, such as wind, temperature and time of harvesting, and also the manner by which the hay was removed (loose hay or bale) did not significantly influence damage rates. While Oppermann *et al.* (2000) study was well replicated (with 30 experimental plots) other studies have been less well designed, but nevertheless provide data that support these conclusions. Consistent with Oppermann *et al.* (2000), a double blade bar mower was found to have less impact (5.6% damage at a cutting height of 6 cm) on grasshoppers than a rotary disc mower used at either 3 cm cutting height (30.4%) or 6 cm height (29.7%) (Wilke 1992), although this study was based on only two replicates and few individual insects. Even more dramatic reductions in some grasshopper species densities have been noted following mowing with a rotary ride-on mower, which resulted in a 59% reduction of *Chorthippus parallelus* adults, and 32% reduction of *Chorthippus spp.* nymphs (Gardiner 2006; Gardiner and Hill 2006). Unfortunately it is difficult to evaluate this result owing to the small size of the experimental plots (10 x 10 m) out of which grasshoppers may have escaped as the mower approached.

Other studies comparing different mower types have been flawed in other ways, limiting the value of results thereby obtained. Classen *et al.* (1993) attempted to compare the effect of rotary drum mowers (5 or 15 cm cutting heights), and a double blade bar mower (5 cm cutting height) in three meadows, each divided into three equal sized plots. However, they used pitfall traps to sample insects and found only nine injured insects, six ground beetles and three grasshoppers. From this they concluded that the direct effect of mowing with either mower was negligible, but failed to appreciate that pitfall traps are effective only in catching active invertebrates, and thereby are not a reliable measure of injured or dead invertebrates.

In addition to grasshoppers, studies undertaken on other insects reveal broadly similar patterns: bar mowers are generally less damaging to the field fauna than other types of mowing equipment, and the addition of conditioner usually increases damage. A sickle bar mower gave the lowest direct beetle mortality rate of all mowing equipment tested (Blodgett et al. 1995). Even highly mobile insects are affected: between 35% and 62% honeybees (*Apis mellifera*) were killed or injured in flowering phacelia (*Phacelia tanacetifolia*) and white clover (*Trifolium alba*) fields using rotary drum mowers with conditioner attached, but this figure dropped to only 5% when mown without a conditioner (Frick and Fluri 2001). Although these differences were presented as highly significant, only one trial was done without conditioner (in a white clover field), and three trials with conditioner (one in a phacelia field, and two in white clover fields), again limiting the value of the results. Damage to a known number of cotton bug (*Dysdercus intermedius*) larvae and adults, and meal beetle (*Tenebrio molitor*) adults, increased from the cutter bar (28% mean mortality), to the suction flail mower (47%) and was highest using a flail mower (63%) (Hemmann et al. 1987). Cotton bug adults (75% mean mortality across all mowing treatments) were more affected than cotton bug larvae (28%) and meal beetle adults (35%), because they were located in the herbaceous strata while the others were on the ground. The extreme damage caused by a suction flail mower is also illustrated by Wasner's (1987) study on insect and spider populations of road verges where none of the arthropods from the vegetation survived the suction flail mower, and even survival of the ground fauna was only 45%.

Invertebrate models to simulate either beetles or spiders have also been used to assess impacts, and the results from these studies are broadly similar to those on real invertebrates. Impacts of double blade bar mowers and rotary disc mowers were weak and not significantly different when the models were placed on the ground or at 20 cm height (damage range 1 to 7%), but when the models were located in the cutting horizon (5 – 10 cm above the ground), damage by rotary disc mowers increased to between 20 and 30%, but there was no damage increase using double blade bar mowers (Löbbert et al. 1994). Even so, both mowing techniques had an impact of between 10 to 40% mortality when using real fixed *Helicoverpa armigera* caterpillars at 5 to 10 cm height. However, for the models and caterpillars damages severely increased when mown with flail mowers (>50%, see Table 1) (Löbbert et al. 1994).

Finally, differences in impacts between various mowing techniques may be either absent, too small to be detectable given the experimental design, or overwhelmed by other variables. Impacts on spiders and insects over a three year experimental period were, for example, not significantly different among double bar mower (25%) and a rotary disc mower (25%) (Kraut 1995). Impact was higher, albeit not significantly, when fields were mown with a flail mower (33%). In this experiment, conducted in three wet meadows, there was a strong meadow, or habitat, effect based on different vegetation characteristics. Similarly, differences in management intensity between plots may confound results: Grosskopf (1988) claimed that a flail mower is less damaging to carabid beetles than the suction flail mower, but the roadside verges mown with a suction flail mower were more intensively managed. A lack of significant differences in some studies belies common sense and may be due to insufficient statistical power. For example, direct mortality of 15% of staphylinid beetles, 24% of spiders and 29% of carabid beetles appears substantial, but these values were apparently not significantly different from unmown control sites (Thorbek and Bilde 2004). In this study 3 out of 4 plots were mown with a Forage Plot Harvester (grass directly removed at harvest) and one plot with a rotary mower with conditioner (grass left to dry).

Impacts of other harvesting stages

In addition to the cutting stage of the harvesting process, subsequent treatments associated with the processing of the mown grass and its removal also potentially impact fauna that survive mowing itself. These impacts are less direct in that they may not kill the organisms directly but rather remove them from the field. Windrowing, for example, kills few grasshoppers, but concentrates most of them (80% of grasshoppers) in the windrows which are then removed in the baling process (Oppermann et al. 2000). 70% of field grasshoppers can be eliminated in this way. The process of hay removal therefore has a more severe impact on grasshopper populations than the more direct impact of mowing.

Averaged across all types of mowing equipment blister beetle (*Epicauta occidentalis*) mortality on experimental plots within alfalfa (*Medicago sativa*) fields was 20.2%, while recovery of live specimens was 44.3% (Blodgett et al. 1995). It was not possible to attribute the remaining 35.5% of unrecovered beetles to any certain fate, it seems likely that they either dispersed or were deposited beyond the sample area by the equipment (Blodgett et al. 1995). Subsequent wheel traffic over the mown grass increased mortality by 10-fold, resulting in significantly greater beetle mortality recovered from mown grass than the mortality caused by a combined mower-conditioner-windrower (all equipment fixed on one machine). By removing the conditioner from this equipment the mortality was reduced. To summarize, Blodgett *et al.* (1995) revealed three main sources of beetle mortality, ranked from most to least important: wheel traffic over mown grass before beetles could disperse, crimping (from conditioner), and finally the mowing stage itself.

The immediate impacts of the harvesting process need to be separated from delayed effects, which may be negative or positive depending on the nature of the harvesting process. Thus spider and beetle (staphylinid) richness and abundance are higher subsequent to the harvesting process when grass is left to dry *in situ* (Thorbek and Bilde 2004). This indicates that mown grass provides an appropriate refuge for the taxa post harvesting, although presumably refuge seeking organisms are then vulnerable to the collection of the hay during the bailing process.

In a grassland restoration investigation, collection of hay resulted in the removal of 11% of grasshoppers (*Metrioptera bicolor*), although almost half of these were considered still capable of reproduction when the hay was deposited in a nearby field (Wagner 2004). Nevertheless, in this particular study, the whole process from mowing to hay transfer still caused mortality of approximately 42% of grasshoppers.

In summer of 1997, Kiel (1999) monitored grasshopper population changes of *Chorthippus montanus*, *Chorthippus albomarginatus* and *Stethophyma grossum* in a wet meadow protected by nature conservation. Drastic declines in number of male singers (about 75%) occurred after the whole harvesting process (where a rotary mower was used for mowing) due to some direct mortality (estimated between 20% and 30%) and migrations to uncut adjacent grass strips.

Large temporal or site variation in impact of mowing complicates interpretation, particularly given that most studies are inadequately or insufficiently replicated. Population declines of *Chorthippus mollis* grasshoppers following the complete mowing (using a hand motor bar mower) and harvesting process, replicated annually over a five year period, varied between 4% and 67% of the pre-harvesting population (Thorens 1993). This wide variation between years was correlated with the weather: higher impacts were recorded when harvesting was followed by low temperature and rainfall.

Table 1 Percentage mortality or damage rates invertebrate models, due to different common mowing techniques on diverse taxa.

Taxa	Cutting height [cm]	% of damages							References [a]
		Scythe	Bar mowers	Rotary mowers	Rotary mowers with conditioner	Flail mowers	Suction flail mowers	Whole harvesting process	
Wood turtle (*Glyptemys insculpta*)				13				47	Saumure et al, 2007 PR
Amphibians	8		13		21				Oppermann et al., 2000 G
Amphibians	5-7	14							Classen et al., 1996 G, PR
Amphibians	7-8		10	27					Classen et al., 1996 G, PR
Amphibians	10			19					Classen et al., 1996 G, PR
Amphibians	12			5					Classen et al., 1996 G, PR
Mean for Amphibians		14.0	11.5±2	17.0±11	21.0				
Grasshoppers	7-10		9	21	34				Oppermann et al., 2000 G
Grasshoppers	7-10							80	Oppermann et al., 2000 G
Grasshoppers	6		6	30					Wilke, 1992 G
Grasshoppers	3			30					Wilke, 1992 G
Chorthippus parallelus (Ortho.)				59					Gardiner, 2006
Chorthippus spp. nymphs (Ortho.)				32					Gardiner, 2006
Metrioptera bicolor (Ortho.)								42	Wagner, 2004, PR
Grasshoppers								75	Kiel, 1999 G
Epicauta occidentalis (Coleo.)			4		21				Blodgett et al., 1995, PR
Tenebrio molitor (Coleo.)			16			60	30		Hemmann et al., 1987 G
Dysdercus intermedius (Hetero.) larva			17			41	26		Hemmann et al., 1987 G
Dysdercus intermedius (Hetero.)			52			88	84		Hemmann et al., 1987 G
Helicoverpa armigera (Lepido.) larva	5-10		18	16		77			Löbbert et al., 1994 G
Honey bees (*Apis mellifera*)					35				Frick and Fluri, 2001 G, PR
Honey bees (*Apis mellifera*)					50				Frick and Fluri, 2001 G, PR
Honey bees (*Apis mellifera*)				5					Frick and Fluri, 2001 G, PR
Insects and spiders			25	25		33			Kraut, 1995 G
Arthropods (9 groups)							55		Wasner, 1987 G
Mean for invertebrates			18.3±15	27.3±16	34.9±12	59.7±23	48.8±27	65.7±21	
Invertebrate models on the ground	5		7	2		49			Löbbert et al., 1994 G
Invertebrate models on the ground	10		2	2		8			Löbbert et al., 1994 G
Invertebrate models in the cut horizon	5		5	27		82			Löbbert et al., 1994 G
Invertebrate models in the cut horizon	10		4	24		52			Löbbert et al., 1994 G
Invertebrate models at 20 cm	5-10		1	5		81			Löbbert et al., 1994 G
Mean for invertebrate models			3.5±2	11.9±12		54.5±30			

[a] In the references column: "G" means that the publication is in German, and "PR" means that publications in this journal are usually peer-reviewed.
Mean values (±S.D., when possible) are given for amphibians, invertebrates, and invertebrate models.

Limitations of available information

In reviewing the impacts of meadow harvesting on fauna it becomes apparent that many publications that addressed this topic suffer from a number of experimental design deficiencies that limit confidence in the conclusions. Direct mortality due to the harvesting process is not always separated from other indirect causes of mortality associated with other stages of the harvesting process. Replication is often insufficient, confounded, or non-independent. Among the thirteen listed publications in Table 1, nine are journal articles (five of which were peer-reviewed), two were published as non-reviewed scientific reports, one is a diploma dissertation and one a PhD thesis. More than half were published in German. Many of these studies are therefore difficult to access and, being not peer-reviewed, of uncertain quality. Moreover, only six studies reported significant differences, and statistical power is uncertain in those studies that did not record significant effects.

Synthesis

Despite the limitations of the data sources, this review sought to consolidate the available information to provide some account of the broad impacts of harvesting on meadow fauna. One important conclusion that emerges is that population impacts following mowing can be substantial, often accounting for more than 50% mortality of invertebrates. Such a dramatic and sudden mortality event is likely to have profound changes to the meadow community, although our insights into this can be little more than speculation. Impacts on spiders and predatory beetles may have importance for prey communities, which are expected to be more resistant to harvesting processes as preys generally have smaller body size. Indeed the apparent differential impact by body size (Guido and Gianelle 2001; Oppermann et al. 2000; Saumure et al. 2007) suggests that predatory species will be more vulnerable to such impacts. Of course there is little data to support such speculation, yet the results of this review do suggest a number of hypotheses that have relevance to community structure and dynamics and ecosystem functions.

Another important outcome of this review is the consistent and often marked differences between different types or cutting equipment, and harvesting processes, in terms of mortality impacts. Comprehensive quantitative comparisons are not yet possible, but it appears clear that cutter bar mowers are least damaging. Averaging across all relevant studies, rotary mowers (disc or drum) generated about twice as much mortality as bar mowers. Adding conditioners increased mortality, often substantially: a conditioner added to rotary mowers resulted in three to four times as much damages as a bar mower. Flail and suction flail mowers caused the most damage, although it is difficult to distinguish between these two mower types owing to a limited number of studies and disagreement among them (see Grosskopf 1988; Hemmann et al. 1987).

Cutting height has a large influence on the degree of mowing impact, with a higher cut being less damaging, and sometimes considerably so (Classen et al. 1996; Löbbert et al. 1994; Oppermann et al. 2000). The height at which individual organisms are typically found in the vegetation is also therefore likely to be a factor in the amount of damage sustained by the population (Hemmann et al. 1987; Löbbert et al. 1994; Wasner 1987). Animals and invertebrates that occur relatively high in the meadow vegetation strata include many invertebrate larvae, folivorous invertebrates such as grasshoppers, flower-visiting insects such as bees and butterflies, and predators including spiders. Predominantly ground dwelling organisms (such as staphylinid and carabid beetles) are, conversely, less likely to be impacted, although even these organisms might be affected by wheel damage (Blodgett et al. 1995). Less mobile animals such as caterpillars may also be more vulnerable than more mobile or volant species.

The stages following mowing clearly have considerable impact also, especially the removal of the harvest (baling), which picks up most organisms taking refuge in the windrows. When summing the impacts of all stages grasshopper mortality can exceed 70% (Oppermann et al. 2000). No research has specifically looked at the effects of tedding and windrowing on the fauna mortality. Thus despite the limitations of each study, this review clearly shows that there is a direct and often substantial impact of the harvesting process on meadow fauna, especially from the mowing stages, and that this impact depends on the techniques and equipment used, as well as the settings, the habitat and the ecology of each species.

As the enhancement of biodiversity is a primary objective in many extensive meadow systems, for which farmers often receive remuneration, the results of our review allows some simple recommendations to be made by which the impact of mowing on field fauna might be minimized. We emphasise that the studies reviewed here do not directly address biodiversity in the sense of species richness and evenness, but rather the numerical abundance of populations that comprise meadow communities. While this may be a crude surrogate for biodiversity, we nevertheless make the recommendations from the perspective that severe declines in population sizes of a wide variety of taxa is likely to impact biodiversity both directly, and indirectly through functional changes and trophic interactions. These predictions remain to be tested.

The use of cutter bar mowers (finger or double blade) are recommended over rotary and flail mowers, because they cause around half as much mortality. When rotary mowers are used, then the add-on conditioner should be avoided. This applies to all arthropods, amphibians, turtles and small mammals. Cutting height should be set ideally at 10 cm or higher to preserve as much as possible the ground fauna. However, mowing is only the first stage of the harvesting process, and it is mostly unknown whether adopting such recommendations will actually deliver the intended benefits due to impacts from subsequent stages of the harvesting process. These include wheel traffic over mown grass and the removal of the grass (Blodgett et al. 1995; Oppermann et al. 2000). Additionally, the absolute reduction of damage using a double blade bar mower instead of a rotary drum mower without conditioner is relatively small: about 10% (e.g. Oppermann et al. 2000). Although these recommendations may have modest impact for these reasons, they are very easy to implement and require little more than a change to the equipment used. The processes of tedding, windrowing and baling are not so easily changed. Leaving time between harvesting stages might, on the other hand, allow some organisms to move to new and more favourable locations (Baines et al. 1998; Blodgett et al. 1995; Gardiner and Hassall 2008; Oppermann 2007; Thorbek and Bilde 2004), but organisms may also move in and become concentrated in the windrows (Oppermann et al. 2000) which are subsequently harvested. Leaving uncut grass strips is a simple and good practice that will benefit many organisms (Guido and Gianelle 2001; Kiel 1999; Oppermann 2007). Other issues of relevance include the timing and frequency of harvesting and the pattern of mowing, with centre to margin being recommended to avoid concentration of individuals in the centre and to facilitate escape (Green et al. 1997; Prochnow and Meierhöfer 2003; Saumure et al. 2007; Tyler et al. 1998). These recommendations may also be applied to the maintenance of field margins, an increasing ecological element of concern in agricultural land (Marshall 2002), and the management of wet meadows nature reserves (Cattin et al. 2003).

Effective management recommendations need to be based on an understanding of the outcome of the whole harvesting process in the context of local and wider dynamics of community interactions, immigration and metapopulations. From this perspective, we remain far from a comprehensive understanding, but it has not been the intention of this review to provide this. Instead, we have sought to identify the impacts of harvesting processes to serve as a basis for further enquiry relevant to wider issues in agroecosystem ecology and biodiversity. Thus the interaction among adjacent cut meadows and uncut refuges should be investigated to identify not only how management and planning of such refuges can be optimised for biodiversity, but also to understand the extent to which meadows serve as sinks that could potentially undermine the viability of populations within the refuges themselves.

The meadow harvesting process is an easily adapted farm practices, and so it is surprising that this topic has received relatively little research attention. The recent emphasis on biodiversity in agro-ecosystems makes it relevant to deliver clear guidance to farmers willing to adapt their farming practices for environmental gain, and the process needs to be considered in management plans of grassland reserves.

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References

Antonsen H, Olsson PA, 2005. Relative importance of burning, mowing and species translocation in the restoration of a former boreal hayfield: responses of plant diversity and the microbial community. J. Appl. Ecol. 42, 337-347.

Baines M, Hambler C, Johnson PJ, Macdonald DW, Smith H, 1998. The effects of arable field margin management on the abundance and species richness of Araneae (spiders). Ecography 21, 74-86.

Bell JR, Weater PC, Cullen RW, 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. J. Zool. 255, 377-387.

Benton TG, Bryant DM, Cole L, Crick HQP, 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. J. Appl. Ecol. 39, 673-687.

Bignal EM, McCracken DI, 1996. Low-intensity farming systems in the conservation of the countryside. J. Appl. Ecol. 33, 413-424.

Blodgett SL, Higgins RA, Millken GA, 1995. Blister beetle (Coleoptera: Meloidae) mortality evaluated during alfalfa harvest. J. Econ. Entomol. 88, 398-406.

Bock CE, Bock JH, Grant MC, 1992. Effects of bird predation on grasshopper densities in an Arizona grassland. Ecology 73, 1706-1717.

Bollinger EK, Bollinger PB, Gavin TA, 1990. Effects of hay-cropping on eastern populations of the bobolink. Wildl. Soc. Bull. 18, 142-150.

Brussaard L, de Ruiter PC, Brown GG, 2007. Soil biodiversity for agricultural sustainability. Agric. Ecosyst. Environ. 121, 233-244.

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. Biol. Conserv. 113, 179-188.

Classen A, Kapfer A, Luick R, 1993. Einfluss der Mahd mit Kreisel- und Balkenmäher auf die Fauna von Feuchtgrünland. Nat.schutz Landsch.plan. 25, 217-220.

Classen A, Hirler A, Oppermann R, 1996. Auswirkungen unterschiedlicher Mähgeräte auf die Wiesenfauna in Nordost-Polen. Nat.schutz Landsch.plan. 28, 139-144.

Donald PF, Sanderson FJ, Burfield IJ, Van Bommel FPJ, 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990-2000. Agric. Ecosyst. Environ. 116, 189-196.

Dörfler H, 1978. Der praktische Landwirt. Boden, Pflanze, Tier, Technik, Bauwesen. BLV Verlagsgesellschaft, München.

Feber RE, Smith H, Macdonald DW, 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. J. Appl. Ecol. 33, 1191-1205.

Frawley BJ, Best LB, 1991. Effects of mowing on breeding bird abundance and species composition in alfalfa fields. Wildl. Soc. Bull. 19, 135-142.

Frick R, Fluri P, 2001. Bienenverluste beim Mähen mit Rotationsmähwerken. Agrarforschung 8, 196-201.

Gardiner T, 2006. The Impact of Grassland Management on Orthoptera Populations in the UK. In: Faculty of Applied Science and Technology, Writtle College, University of Essex, Colchester, UK.

Gardiner T, Hill J, 2006. Mortality of Orthoptera caused by mechanised mowing of grassland. Br. J. Ent. Nat. Hist. 19, 38-40.

Gardiner T, Hassall M, 2008. Does microclimate affect grasshopper populations after cutting of hay in improved grassland? J. Insect Conserv. In press.

Gerstmeier R, Lang C, 1996. Beitrag zu Auswirkungen der Mahd auf Arthropoden. Z. Ökologie u. Naturschutz 5, 1-14.

Green RE, Tyler GA, Stowe TJ, Newton AV, 1997. A simulation model of the effect of mowing of agricultural grassland on the breeding success of the corncrake (*Crex crex*). J. Zool. 243, 81-115.

Grime JP, 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Second edition. John Wiley, Chichester, UK.

Grosskopf J, 1988. Die Aktivitätsstruktur der Carabiden (Col.) des Strassenrandes als Folge von Mulchen und Saugmähen. Nat. Landsch. 63, 511-516.

Guido M, Gianelle D, 2001. Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. Acta Oecol. 22, 175-185.

Hemmann K, Hopp I, Paulus HF, 1987. Zum einfluss der Mahd durch Messerbalken, Mulcher und Saugmäher auf Insekten am Strassenrand. Nat. Landsch. 62, 103-106.

Hendrickx F, Maelfait JP, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Augenstein I, Billeter R, Bailey D, Bukacek R, Burel F, Diekotter T, Dirksen J, Herzog F, Liira J, Roubalova M, Vandomme V, Bugter R, 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. J. Appl. Ecol. 44, 340-351.

Huston MA, 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.

Johst K, Drechsler M, Thomas J, Settele J, 2006. Influence of mowing on the persistence of two endangered large blue butterfly species. J. Appl. Ecol. 43, 333-342.

Kiel E-F, 1999. Heuschrecken und Mahd, Empfehlung für das Pflegemanagement in Feuchtwiesenschutzgebieten. LOeBF-Mitteilungen 24, 63-66.

Kleijn D, Sutherland WJ, 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity. J. Appl. Ecol. 40, 947-969.

Kraut D, 1995. Schädigung der Kleintierfauna durch Mähwerke. Landtechnik 50, 138-139.

Krebs JR, Wilson JD, Bradbury RB, Siriwardena GM, 1999. The second silent spring. Nature 400, 611-612.

Labisky RF, 1957. Relation of hay harvesting to duck nesting under a refuge-permittee system. J. Wildl. Manage. 21, 194-200.

Löbbert M, Kromer K-H, Wieland CC, 1994. Einfluss von Mäh- und Mulchgeräten auf die bodennahe Fauna. In: Forschungsberichte "Integrative Extensivierungs- und Naturschutzstrategien", H. 15, 7-26.

Marini L, Fontana P, Scotton M, Klimek S, 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. J. Appl. Ecol. 45, 361-370.

Marshall EJP, 2002. Introducing field margin ecology in Europe. Agric. Ecosyst. Environ. 89, 1-4.

Morris MG, Lakhani KH, 1979. Responses of grassland invertebrates to management by cutting. I. Species diversity of Hemiptera. J. Appl. Ecol. 16, 77-98.

Morris MG, 1987. Abundance and diversity of the coleopterous fauna of a calcareous grassland under different cutting régimes. J. Appl. Ecol. 24, 451-465.

Morris MG, 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grassland. Biol. Conserv. 95, 129-142.

Müller M, Spaar R, Schifferli L, Jenni L, 2005. Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (*Saxicola rubetra*). J. Ornithology 146, 14-23.

New TR, 2005. Invertebrate Conservation and Agricultural Ecosystems. Cambridge University Press, Cambridge, UK.

Norris CA, 1947. Report on the distribution and status of the Corncrake. Br. Birds 40, 226-244.

Oppermann R, Classen A, 1998: Naturverträgliche Mähtechnik - Moderne Mähgeräte im vergleich -. Stuttgart: NABU Naturschutzbund Deutschland.

Oppermann R, Handwerk J, Holsten M, Krismann A, 2000: Naturverträgliche Mähtechnik für das Feuchtgrünland, Voruntersuchung für das E & E - Vorhaben. Bonn: ILN Singen.

Oppermann R, 2007. Auswirkungen landwirtschaftlicher Mähgeräte auf Amphibien. In: Die Amphibien und Reptilien Baden-Württembergs. Ed. by Laufer H, Fritz K, Sowig P, Ulmer, Stuttgart, 102-108.

Prochnow A, Meierhöfer J, 2003. Befahrmuster bei der Grünlandmahd: Faunaschonung und Aufwendungen. Landtechnik 58, 252-253.

Reidsma P, Tekelenburg T, Van den Berg M, Alkemade R, 2006. Impacts of land-use change on biodiversity: An assessment of agricultural biodiversity in the European Union. Agric. Ecosyst. Environ. 114, 86-102.
Robinson RA, Sutherland WJ, 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157-176.
Saumure RA, Herman TB, Titman RD, 2007. Effects of haying and agricultural practices on a declining species: The North American wood turtle, *Glyptemys insculpta*. Biol. Conserv. 135, 565-575.
Swiss Federal Council, 1998. Ordonnance sur les paiements directs versés dans l'agriculture. RS 910.13.
Thorbek P, Bilde T, 2004. Reduced numbers of generalist arthropod predators after crop management. J. Appl. Ecol. 41, 526-538.
Thorens P, 1993. Effets de la fauche sur une population du Criquet *Chorthippus mollis* (Charp.) (Orthoptera, Acrididae) dans une prairie du pied sud du Jura suisse. Bull. Soc. Ent. Suisse 66, 173-182.
Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D, 2001. Forecasting agriculturally driven global environmental change. Science 292, 281-284.
Tyler GA, Green RE, Casey C, 1998. Survival and behaviour of Corncrake *Crex crex* chicks during the mowing of agricultural grassland. Bird Stud. 45, 35-50.
Verhulst J, Kleijn D, Berendse F, 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. J. Appl. Ecol. 44, 70-80.
Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK, 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647-664.
Vickery JA, Bradbury RB, Henderson IG, Eaton MA, Grice PV, 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biol. Conserv. 119, 19-39.
Wagner C, 2004. Passive dispersal of *Metrioptera bicolor* (Phillipi 1830) (Orthopteroidea: Ensifera: Tettigoniidae) by transfer of hay. J. Insect Conserv. 8, 287-296.
Walter T, Schneider K, Gonseth Y, 2007. Schnittzeitpunkt in Ökowiesen: Einfluss auf die Fauna. Agrarforschung 14, 114-119.
Wasner U, 1987. Wirkung der Saugmahd auf den Insektenbestand am strassenrand. Mitteilungen der LÖLF 12, 34-39.
Wettstein W, Schmid B, 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J. Appl. Ecol. 36, 363-373.
Wilke, 1992. Beeinflussung von Heuschrecken durch Mahd und verschiedene Mahdsysteme in wechselfeuchten Wiesen norddeutscher Flussauen. In: Zoologisches Institut, Technischen Universität Braunschweig, Braunschweig.
Wilson JD, Morris AJ, Arroyo BE, Clark SC, Bradbury RB, 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agric. Ecosyst. Environ. 75, 13-30.

Chapter II

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Impact of different meadow mowing techniques on field invertebrates

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Abstract

Low-input meadows are now recognized for their high biodiversity value and form an integral element of many agri-environmental schemes in Europe. Meadow mowing techniques, however, have become highly mechanized in recent decades and scientific knowledge on the direct impacts of these techniques on field fauna is based on very few and often poorly replicated studies. Yet these studies, despite their limitations, suggest that such impacts can be considerable. With a view to providing a more comprehensive experimental assessment, we evaluated the direct impacts of four different mowing techniques (hand motor mower with cutter bar, rotary mower cut at 9 cm and rotary mower cut at 6 cm with and without a conditioner) on wax invertebrate models and real caterpillars. The size of the organisms, their microhabitat, the tractor wheel effect and the cutting height were also investigated as factors that could potentially affect mowing-caused mortality. Rotary mowers were found to be more damaging than motor bar mowers on caterpillars (37% versus 20%), but only on one type of invertebrate wax-model. Conditioners more than doubled damage to all wax-models in the vegetation (in average from 11% to 30%) and increased caterpillar mortality from 38% to 69%. Larger organisms were more vulnerable than smaller organisms and ground organisms were strongly impacted by tractor wheels. While conditioner should not be used in meadows where

conservation of the inhabiting fauna is of concern, we also recognize that there is no damage-free mowing technique. We therefore advocate the importance of leaving uncut areas as a refuge for invertebrates.

Keywords: butterfly, caterpillar, conservation, cutting, grassland, harvesting, insect

Introduction

Agricultural grasslands are disturbance-dependent habitats, and one or two cuts per year are usually considered beneficial to meadow plant diversity (Antonsen and Olsson 2005; Grime 2001; Huston 1994). On the other hand, the direct impacts of cutting can be substantially negative for field fauna, as has long been known for ground nesting birds (e.g. Labisky 1957; Tyler et al. 1998). More limited information suggests that this is also the case for arthropods although most of the few studies on this subject are limited in both their scope and experimental design (reviewed by Humbert et al. 2009). As yet the direct effects, such as the mechanical impacts, of the cutting process on arthropods have rarely been differentiated from the indirect effects, such as changes in habitat characteristic. The management of extensive meadows to promote conservation of plants and associated invertebrate diversity needs to be informed by both the direct and indirect impacts of mowing on the field invertebrate community. This becomes increasingly important when it is recognized that many invertebrates (including butterflies and bees) of agricultural landscapes in Europe have suffered dramatic declines in recent decades, and that vertebrates, particularly birds and small mammals many of which are also in decline, depend on the field invertebrate community for food (Churchfield et al. 1991; Vickery et al. 2001).

Meadow mowing techniques have advanced considerably through mechanization in recent decades including, among other developments, the introduction of new mowing-associated practices such as conditioning which mechanically crushes the freshly mown grass. In view of these developments, in recognition of declining meadow-associated invertebrate populations, and considering the limited number of well designed studies, we investigate the direct impacts of four alternatives but commonly used mowing techniques on wax invertebrate models and real *Pieris brassicae* butterfly caterpillars within experimental grass plots. Lepidopterans are a group of high conservation concern within Europe's agricultural landscape, particularly since the late 1940s when many of Europe's butterfly species, especially grassland specialists, have undergone dramatic declines associated with agricultural intensification (Robinson and Sutherland 2002; Van Swaay et al. 2006). Many studies on butterflies have focused only on the adult stage, but it is the caterpillars that are more habitat specific, and therefore conservation attention has shifted to a consideration of larval habitat requirements and impacts of agriculture on these resources (e.g. Eichel and Fartmann 2008; Johst et al. 2006; Schwarzwälder et al. 1997). Nevertheless, the direct impact of meadow harvesting on caterpillars has rarely been considered in any vulnerability assessment, and even when the impact is acknowledged as being harmful, no quantitative values are provided (e.g. Courtney and Duggan 1983; Erhardt 1985; Feber et al. 1996; Johst et al. 2006; Valtonen et al. 2006). Indeed, one recent review (Humbert et al. 2009) found only one small-scale experiment that investigated caterpillar mortality due to mowing impacts (Löbbert et al. 1994).

Here we provide quantitative values of the direct impact of mowing on caterpillars and invertebrates in general that will help field biologists to make management strategies for the conservation of biodiversity rich grassland.

Material and methods

We quantified the impacts of four different mowing techniques on cylindrical models of invertebrate made from bee wax (wax-models) and on real caterpillars of *Pieris brassicae.* The wax-models simulate invertebrates of two different sizes. They allow investigating the effect of the size, the stratum and their interaction. The real caterpillars allow us to test whether the wax cylinders are appropriate as models of caterpillars and invertebrates of this size and shape more generally. If this proves to be the case, then this technique would provide a basis for standardised comparative assessments among mowing techniques and locations. A randomized complete block design was adopted, where four treatments were applied within each meadow, the latter representing the blocks, such that treatment replicates were across meadows ensuring independence, while allowing for comparison across treatments within meadows. Nine meadows were used for the wax-models, and five for the caterpillar experiments.

Mowing techniques

Two different mowing machines were used: a hand-pushed motor mower with finger cutter bar (Rapid 505, Rapid Technic AG, 8956 Killwangen, Switzerland); and a tractor front rotary drum mower (CLAAS corto 3150F, CLAAS KGaA mbH, 33428 Harsewinkel, Germany). While the bar mower was used only for one treatment, the rotary mower was used for three treatments with different cutting heights and with or without a tractor rear flail conditioner (Kurmann Twin K618, Kurmann Technik AG, 6017 Ruswil, Switzerland). A conditioner is a machine that mechanically crushes the grass immediately after mowing; this damages the grass cuticle, thus accelerates the drying process. The four mowing treatments (with abbreviations) were:

1.	Bar Mower, cutting height 6-7 cm	BM6
2.	Rotary Mower, cutting height 9 cm, without conditioner	RM9
3.	Rotary Mower, cutting height 6 cm, without conditioner	RM6
4.	Rotary Mower, cutting height 6 cm, with Conditioner	RM6C

Invertebrate wax-models

We used two sizes of cylindrical invertebrate wax-models: ‘small’, 4 mm diameter x 20 mm length; and ‘big’, 8 mm x 40 mm. These sizes were chosen to reflect two body sizes (or life stages) of insects such as caterpillars, but also other similarly sized and shaped field invertebrates such as grasshoppers. Each of the four mowing treatments was applied to a 2.5 m long grass plot. The experimental plot width was determined by the functional width of the mowing machine, which is 2.5 m for the rotary mower and 1.7 m for the bar mower. Each plot contained 200 wax-models: 50 small and 50 big wax-models were regularly placed on the ground and 50 additional of each size were uniformly tied in the grass 20 to 30 cm above ground. A single replicate consisted of four plots in a single meadow (a block) with the four mowing treatments randomly allocated to the plots. All four treatments for any one replicate were completed in one day, so that time was included into the block effect. The experiment was replicated nine times in 2007 or 2008 in different meadows. All meadows were located in the vicinity of the research station Agroscope Reckenholz-Tänikon ART (8356 Ettenhausen, Switzerland) at about 550 m elevation. After mowing, the wax-models were recovered and returned to the lab for inspection of mechanical damage. Broken wax-models, as well as wax-models with an impact equivalent, or bigger, to a nail-thumb pressure were recorded as damaged. Mean recovery of wax-models was 91% for the small models and 96% for the big models.

After five replications it became clear that damage to the ground wax-models were mainly caused by the tractor wheels (the wax-models were run over). Therefore, to investigate specifically the impact of the tractor wheels a fifth treatment on a plot of 2.5 x 2.5 m where the grass was already mown was added (tractor wheels treatment, abbreviated TW). On this plot 50 small and 50 big wax-models placed on the ground were run over by the tractor. The tractor wheels treatment was replicated four times.

Caterpillars

The caterpillars used for the experiment were lab-raised *Pieris brassicae* final larval stage. *Pieris brassicae* was selected because it is a widespread indigenous species across Europe. The length of the final larva stage is about 40 mm, and therefore comparable to the big wax-models. The experimental design was the same as for the invertebrate wax-models experiment, with four grass plots within a single meadow to test the different mowing techniques. Each plot had 50 caterpillars placed on the ground and 50 in the vegetation (about 30 cm above ground). The caterpillars placed on the ground had been cooled in a portable cool box for 10 minutes before placement to limit their movement and so to ensure that they remained at ground level. Once placed on the ground the plot was directly mown. Although the caterpillars placed in the vegetation did move around slightly, they remained in the vegetation close to where they had been deposited (Humbert, pers. obs.). The time between the first caterpillar being released and the mowing treatment was always less than 10 minutes. The mowing treatments were randomly allocated to the plots and the experiment was replicated five times in 2008 (once in each of five different meadows, using the same meadows as in the wax-models experiments).

After mowing, the caterpillars were collected and inspected for injuries. Caterpillars that survived mowing were easy to see as they moved up the cut grass. In addition, the caterpillars were sprinkled with a coloured powder (randomly pink or orange for the ground or vegetation caterpillars) to distinguish between the two categories and to facilitate collection. The individuals that were not found were assumed to be dead. We make this assumption based on the high visibility of the survivors and because dead caterpillars were often crushed into the ground or fragmented. The proportion killed was compared with the proportion of damaged invertebrate wax-models.

Data analysis

Linear mixed-effects models were used (class "lme" in R) with the replicates (blocks) as random effect. Temporal differences are included into the block effects.

On the invertebrate wax-model data, five linear mixed models were performed. The first sought to test mowing, size and stratum effects, and interactions, but excluded the tractor wheels treatment. The four additional linear mixed models included only one type of wax-models (ground small, ground big, vegetation small, or vegetation big). These four analyses were done to test the influence of the mowing treatments on one type of wax-models independently of the other ones.

Similarly, on the caterpillar data one linear mixed model with all data was performed to test the mowing and stratum effects, and the interaction between both, and two additional linear mixed models were done to test the treatment effects on each category of caterpillar separately (ground or vegetation).

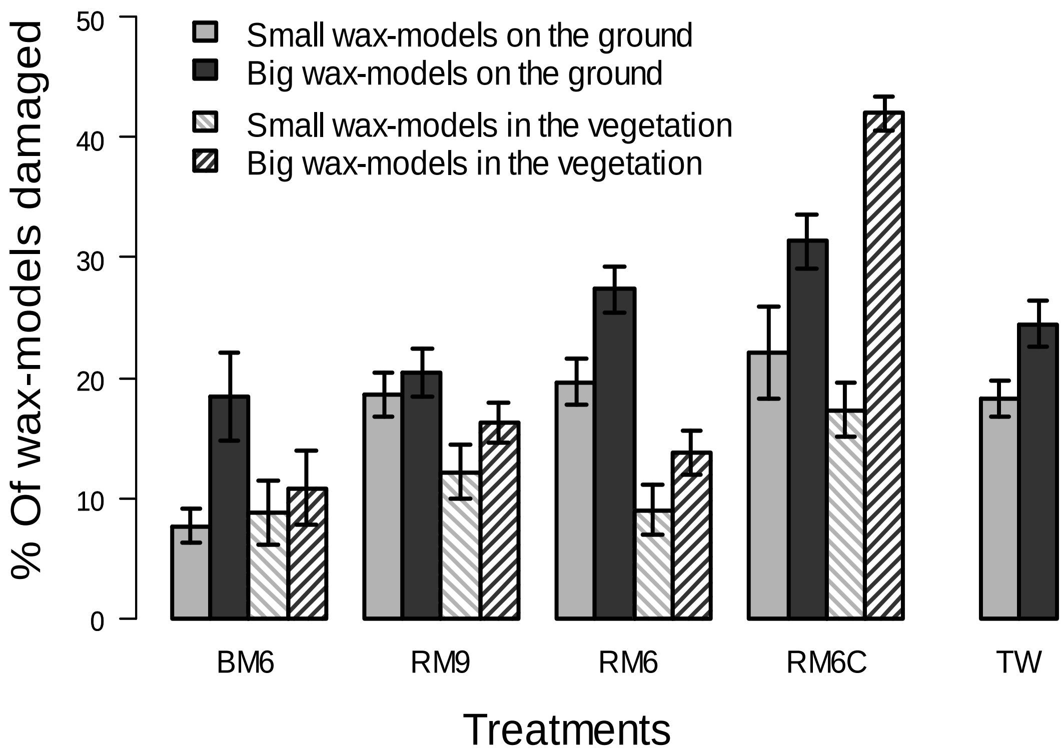
To test if the results of the invertebrate wax-models (percentage of damaged) reflect the same relative impact among the mowing treatments than the results of the caterpillars (percentage of killed), two chi-square tests were performed: one for comparisons among big wax-models and caterpillars located on the ground, and the next to compare among those located in the vegetation. All statistics analyses were performed with R version 2.8.1 (R Development Core Team 2008).

Results

Invertebrate wax-models

The overall mean percentage of invertebrate wax-models damaged was 18.6%, ranging from 7.7% (ground small wax-models) when mowing with a bar mower, to a maximum of 42.0% (vegetation big wax-models) when mowing with a rotary mower with conditioner (fig. 1).

Figure 1 Percentages of invertebrate wax-models damaged for the four different mowing treatments (N=9) plus the tractor wheels treatment (N=4). Treatment abbreviations are: (BM6) motor bar mower, cutting height at 6-7 cm; (RM9) rotary mower, cutting height 9 cm; (RM6) rotary mower, cutting height 6 cm; (RM6C) rotary mower, cutting height 6 cm, with conditioner; (TW) tractor wheels impact. Mean values +/- SE are given.



The first analysis tested the influence of the mowing treatment, the size, the stratum (ground vs. vegetation) and the pairs' interactions on the percentage of wax-models damaged, and thus did not included the tractor wheels treatment (table 1). All factors and interactions were found to be significant, except the size:stratum interaction as the small wax-models of a stratum were always less damaged than the big ones in the same stratum whatever the treatment (see fig. 1). The significance of the mowing treatments means that at least one mowing technique significantly differed from another one, but the influence depends on the type of wax-models (size and stratum). Mean damage across all type of wax-models for BM6 was 11.4% and for RM6C 28.2%. While the rotary mowing techniques without conditioner cut at 9 cm or 6 cm had intermediate damage rates; mean damage for RM9 was 16.9% and for RM6 17.4%.

The results of the four analyses on each type of invertebrate wax-models (and caterpillars) are presented in table 2. The parameter estimates, which are the differences between mean percentages of wax-model damaged, and significances are given for all paired comparisons except for TW-BM6, because BM6 mowing treatment is not executed with a tractor and thus the comparison with the tractor wheel treatment make no practical sense.

Table 1 Anova table for the invertebrate wax-model analysis: Influence of the mowing treatment, the size (small vs. big), the stratum (ground vs. vegetation) and the pairs' interactions on the percentage of wax-models damaged.

Factor	Num df	Den df	F value	P-value
(Intercept)	1	123	293.4319	<0.0001
Mowing	3	123	38.1968	**<0.0001**
Size	1	123	51.6229	**<0.0001**
Stratum	1	123	15.1317	**0.0002**
Mowing:Size	3	123	7.2051	**0.0002**
Mowing:Stratum	3	123	7.4961	**0.0001**
Size:Stratum	1	123	0.4580	0.4998

Significant effects are highlighted in bold. Total d.f. = 144.

Table 2 Layout of the linear models outputs for each type of invertebrate wax-model and caterpillar: parameter estimates (differences between mean percentages of wax-model damaged or caterpillars killed) are given for the paired treatment comparisons.

Treatments	BM6	RM9	RM6	RM6C
Small wax-models on the ground:				
RM9	**10.9 ****			
RM6	**11.9 ****	1.0		
RM6C	**14.4 *****	3.5	2.5	
TW	-	-0.4	-1.4	-3.9
Big wax-models on the ground:				
RM9	2.0			
RM6	**8.0 ***	**7 ***		
RM6C	**12.9 *****	**10.9 ****	3.9	
TW	-	3.5	-3.5	-7.4
Small wax-models in the vegetation:				
RM9	3.4			
RM6	0.3	-3.1		
RM6C	**8.6 ****	5.2	**8.3 ****	
Big wax-models in the vegetation:				
RM9	5.4			
RM6	2.9	-2.5		
RM6C	**31.1 *****	**25.7 *****	**28.2 *****	
Caterpillars on the ground:				
RM9	**11.7 ****			
RM6	**16.0 *****	4.3		
RM6C	**22.1 *****	**10.4 ****	6.1	
Caterpillars in the vegetation:				
RM9	**21.9 *****			
RM6	**17.2 *****	-4.7		
RM6C	**48.4 *****	**26.5 *****	**31.2 *****	

Significant contrasts are highlighted in bold. Treatment abbreviations are: (BM6) motor bar mower, cutting height at 6-7 cm; (RM9) rotary mower, cutting height 9 cm; (RM6) rotary mower, cutting height 6 cm; (RM6C) rotary mower, cutting height 6 cm, with conditioner; (TW) tractor wheels impact (only on ground wax-models and the rotary mowing treatments). As the analyses are independent of each other, no p-value adjustment was performed.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Caterpillars

The mean percentage of caterpillar mortality was 37.3%, ranging from 19.5% on the ground caterpillars when mowing with a bar mower to a maximum of 69.2% mortality on the vegetation caterpillars when mowing with a rotary mower with conditioner (fig. 2).

The effects of the mowing techniques, the strata (ground vs. vegetation) and the interaction mowing:stratum on the percentage of caterpillars killed were all statistically significant (table 3). The two separate analyses on the ground caterpillars and on the vegetation caterpillars showed the same trend (table 2). For both categories of caterpillar, the three rotary mowing techniques caused significantly more mortality than the bar mower. RM6C also caused more mortality than the two rotary mower treatments without conditioner on the vegetation caterpillars. In contrast, the impact of RM9 did not differ from the impact of RM6.

Figure 2 Percentages of real caterpillars (*P. brassicae*) killed for the four different mowing treatments (N=5). For the treatment abbreviations, refer to figure 1. Mean values +/- SE are given.

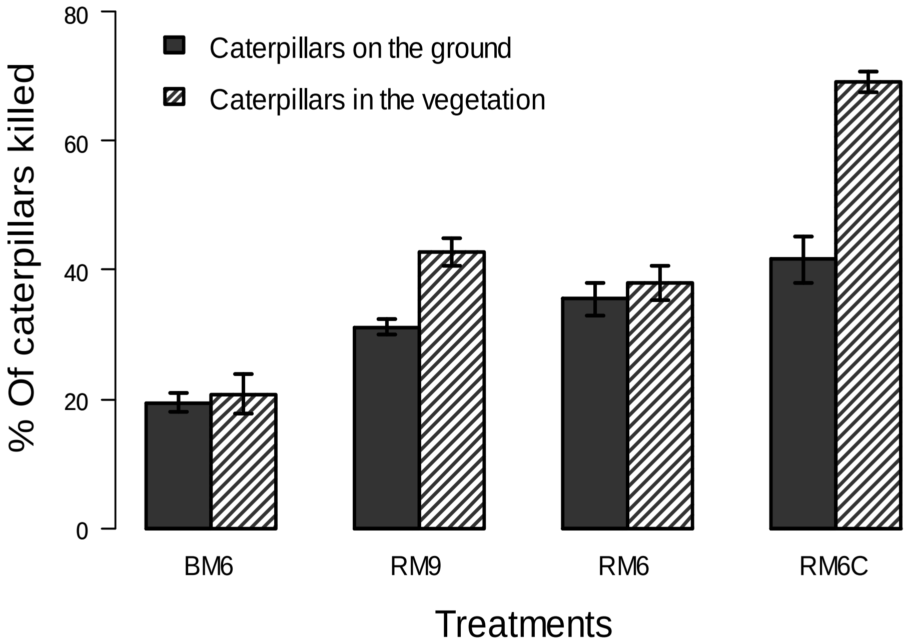


Table 3 Anova table for the caterpillar analysis: Influence of the mowing treatment, the stratum (ground vs. vegetation), and their interaction on the percentage caterpillars killed.

Factor	Num df	Den df	F value	P-value
(Intercept)	1	28	1700.4246	**<0.0001**
Mowing	1	28	40.9813	**<0.0001**
Stratum	3	28	73.8872	**<0.0001**
Stratum:Mowing	3	28	13.1184	**<0.0001**

Significant effects are highlighted in bold. Total d.f. = 40.

Invertebrate wax-models correlated with caterpillars

The chi-square test between the big wax-models placed on the ground and the caterpillars placed on the ground, as well the chi-square test between the big wax-models tied in the vegetation and the caterpillars in the vegetation were not significant.

Discussion

This study experimentally compared the direct impact of four common mowing techniques on field invertebrates in a controlled environment using both invertebrate wax-models of two sizes and real caterpillars. The damage and mortality rates estimated here apply mostly to less mobile species, but the relative impacts among treatments are expected to be valid for a wider range of invertebrates such as grasshoppers.

Regardless of mowing treatment and placement (ground or vegetation) small wax-models were consistently less vulnerable to damage than large wax-models, suggesting that larger invertebrates may be particularly susceptible to the direct physical impacts of mowing. These results are consistent with those of Oppermann et al. (2000) who showed that larger grasshopper individuals were more seriously impacted by mowing than smaller grasshoppers.

The wax-models and the caterpillars placed on the ground were impacted differently to those fixed in the vegetation (stratum influence), but the order of this influence differed between the mowing treatments. This is because the cause of damage differs between the strata; on the ground damage was mostly due to the machine’s wheels running over the invertebrates, while in the vegetation damage is largely due to the mowing machine, and the conditioner if used.

The cutting height (i.e., rotary mower cut at 6 cm versus rotary mower cut at 9 cm) did not affect the impact of mowing on caterpillars or wax-models at either ground level or in the vegetation stratum. Relatively small invertebrates (wax-models and caterpillars were 4 cm length in our study) may therefore escape mowing damage by simply being over in the vegetation, and below 6 cm there may be adequate refuges from either mowing height. This is unlikely to be the case for larger organisms, including amphibians and reptiles, where the cutting height has a strong influence on mortality (Oppermann 2007; Saumure et al. 2007). A cutting height of 8-10 cm is therefore recommended from the context of biodiversity conservation.

Conditioners have a strong impact on the fauna of the vegetation, as the grass is forced through flails that crush it as well as the attached organisms. When a conditioner was added to the rotary mower (treatment RM6C), damage to the wax-models and caterpillars placed in the vegetation significantly increased two to three times compared to RM6 (same cutting height but without a conditioner). The damages increased from 9% to 17% on vegetation small wax-models and from 14% to 42% on vegetation big wax-models, and mortality of the caterpillars in the vegetation increased from 38% (RM6) to 69% (RM6C). The use of conditioners has been shown to substantially impact honey bees (Frick and Fluri 2001), grasshoppers and amphibians (Oppermann et al. 2000). In our study, the use of the tractor rear-mounted conditioner also slightly increased ground caterpillar's mortality from. This may be due to the extra wheels of the conditioner or/and the suction effect of this machine.

While mowing with a hand motor bar mower caused almost half as much caterpillar mortality (20%) than a rotary mower without conditioner (RM9 and RM6, 37% in average), the difference was less clear with wax-models. Only the small wax-models on the ground were significantly less impacted by the hand motor bar mower than the rotary mowers without conditioner, and no clear differences appeared for the three other types of wax-models. A recent review (see Humbert et al. 2009) showed that mortality of amphibians and grasshoppers generally increases 1.5 times from bar mower (hand motor or tractor powered) to rotary mower. Hand motor bar mowers caused less ground damages than rotary mowers, presumably because they are considerably lighter and the wheels smaller than those of a tractor.

The main source of ground invertebrate mortality is the tractor wheels, which damaged about 20% of the ground wax-models in this experiment. The tractor wheels covered 46 cm of the 250 cm plot width (sum of the two tires width minus the spaces between the tread blocks), which corresponds to 18.4% of the plot surface. This can be considered as the baseline impact on the ground invertebrates. If the soil is moist the tractor will sink in the ground and more ground surface will be covered. In this experiment, the front rotary mower directly gathered the freshly mown grass in a line that fit between the tractor wheels; therefore the tractor did not run over the mown grass, and thus did not run over the invertebrates placed the vegetation.

Caterpillars

Our results demonstrate that invertebrate models can be used to assess mechanical damage on real caterpillars. While the absolute value of damages to wax-models did not reflect exactly the impacts on real caterpillars, it did reflect relative impacts among treatments.

Studies on the conservation of butterflies in agricultural landscapes often investigated the indirect effects of different grassland management systems including the frequencies and the time of the cuts, and usually spring or late summer cut are recommended over summer cut based on empirical counts of butterfly abundances (e.g. Feber et al. 1996; Valtonen et al. 2006). The direct impact of mowing on the caterpillar is rarely mentioned, or if it is then it is little more than presumption without quantitative data (e.g. Courtney and Duggan 1983; Feber et al. 1996; Johst et al. 2006). This study quantifies the direct impact of mowing on caterpillars: about 20% mortality when mowing with hand motor bar mower, about 40% mortality when mowing with a rotary mower (without conditioner), and up to 70% mortality to the caterpillars in the vegetation when mowing with a rotary mower with conditioner. These mowing mortalities should be considered as the minimum impact of the whole meadow harvesting process, because it is likely that further individuals will be killed by the subsequent harvesting stages (i.e. tedding, raking and baling the grass, see next section). This means that even if a meadow (or another grassland structure like a field margin) contains the host plant and that adults are observed in it vicinity, the meadow is not necessary an appropriate habitat, and can act more as a sink than a source population if mown with certain machinery at inappropriate times. Walter et al. (2007) showed that allowing earlier cuts of Swiss extensively used meadows (registered as ecological compensation areas) would negatively affect butterflies – in particular species already threatened – because mowing would take place during their most sensitive developmental stages (larva or pupa). Our study highlights that butterfly conservation research should include, in addition to the larva life cycle and their ecological requirements, the management of the habitat especially when mown (Feber et al. 1996).

Management recommendations

Our results confirm that conditioners should not be used in meadows where conservation of the inhabiting fauna is of concern. The results also imply that hand-pushed motor bar mowers causes less damage than rotary mowers, particularly on ground living invertebrates, due to the smaller weight and wheels of the machine. Hand motor bar mowers are therefore recommended over rotary mowers. However, if the bar mower is powered by a tractor, then the damage to the ground invertebrate will increase and the overall difference in damages compared to rotary mowers might not be significant anymore.

The impact of the tractor wheels on the ground fauna was emphasized in this study as an important factor affecting ground living invertebrates. Therefore constraining the number of passages on the meadow during the harvesting process will be beneficial for the field fauna. Altogether, the whole harvesting process includes usually four stages: mowing, drying by tedding the grass, raking, and finally baling or loading the hay. This requires a minimum of four passages on the field during which the ground fauna is exposed to the wheel traffic. In addition, the stages following mowing are executed with machines that will affect the fauna that survived mowing and did not leave the field, especially less mobile species. The impacts of those post-mowing stages on field fauna were observed to be high, although quantitative assessments are lacking (Humbert et al. 2009; Oppermann et al. 2000). To provide clear management recommendations, it is also important to understand the influence of all post-mowing stages, because if they have a strong impact on the invertebrate population, then the difference made during the mowing stage using a friendly mowing technique may be insignificant, and conservation efforts should then be re-orientated. Therefore further investigations on the impact of the post-mowing harvesting stages are needed.

For invertebrates that survived mowing, the availability of uncut grass strips in the meadows may provide refuges keeping them safe from the subsequent harvesting stages. The refuges will also provide structure, shelter, and food for many organisms after haying which highly reduced vegetation biomasses (Braschler et al. 2009; Broyer 2003; Gardiner and Hassall 2009; Morris 2000).

Mowing will inevitably affect the inhabited fauna of the meadow. However, mowing is required to maintain the habitat, thus a compromise between the plants and the different fauna groups should be found according to conservation objectives.

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References

Antonsen H, Olsson PA, 2005. Relative importance of burning, mowing and species translocation in the restoration of a former boreal hayfield: responses of plant diversity and the microbial community. J. Appl. Ecol. 42, 337-347.

Braschler B, Marini L, Thommen GH, Baur B, 2009. Effects of small-scale grassland fragmentation and frequent mowing on population density and species diversity of orthopterans: a long-term study. Ecol. Entomol. In press.

Broyer J, 2003. Unmown refuge areas and their influence on the survival of grassland birds in the Saone valley (France). Biodiversity Conserv. 12, 1219-1237.

Churchfield S, Hollier J, Brown VK, 1991. The effects of small mammal predators on grassland invertebrates, investigated by field exclosure experiment. Oikos 60, 283-290.

Courtney SP, Duggan AE, 1983. The Population Biology of the Orange Tip Butterfly Anthocharis-Cardamines in Britain. Ecol. Entomol. 8, 271-281.

Eichel S, Fartmann T, 2008. Management of calcareous grasslands for Nickerl's fritillary (Melitaea aurelia) has to consider habitat requirements of the immature stages, isolation, and patch area. J. Insect Conserv. 12, 677-688.

Erhardt A, 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. J. Appl. Ecol. 22, 849-861.

Feber RE, Smith H, Macdonald DW, 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. J. Appl. Ecol. 33, 1191-1205.

Frick R, Fluri P, 2001. Bienenverluste beim Mähen mit Rotationsmähwerken. Agrarforschung 8, 196-201.

Gardiner T, Hassall M, 2009. Does microclimate affect grasshopper populations after cutting of hay in improved grassland? J. Insect Conserv. 13, 97-102.

Grime JP, 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Second edition. John Wiley, Chichester, UK.

Humbert J-Y, Ghazoul J, Walter T, 2009. Meadow harvesting techniques and their impacts on field fauna. Agric. Ecosyst. Environ. 130, 1-8.

Huston MA, 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.

Johst K, Drechsler M, Thomas J, Settele J, 2006. Influence of mowing on the persistence of two endangered large blue butterfly species. J. Appl. Ecol. 43, 333-342.

Labisky RF, 1957. Relation of hay harvesting to duck nesting under a refuge-permittee system. J. Wildl. Manage. 21, 194-200.

Löbbert M, Kromer K-H, Wieland CC, 1994. Einfluss von Mäh- und Mulchgeräten auf die bodennahe Fauna. In: Forschungsberichte "Integrative Extensivierungs- und Naturschutzstrategien", H. 15, 7-26.

Morris MG, 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grassland. Biol. Conserv. 95, 129-142.

Oppermann R, Handwerk J, Holsten M, Krismann A, 2000: Naturverträgliche Mähtechnik für das Feuchtgrünland, Voruntersuchung für das E & E - Vorhaben. Bonn: ILN Singen.

Oppermann R, 2007. Auswirkungen landwirtschaftlicher Mähgeräte auf Amphibien. In: Die Amphibien und Reptilien Baden-Württembergs. Ed. by Laufer H, Fritz K, Sowig P, Ulmer, Stuttgart, 102-108.

R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robinson RA, Sutherland WJ, 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157-176.

Saumure RA, Herman TB, Titman RD, 2007. Effects of haying and agricultural practices on a declining species: The North American wood turtle, *Glyptemys insculpta*. Biol. Conserv. 135, 565-575.

Schwarzwälder B, Lörtscher M, Erhardt A, Zettel J, 1997. Habitat utilization by the heath fritillary butterfly, *Mellicta athalia* ssp. *celadussa* (Rott.) (Lepidoptera: Nymphalidae) in montane grasslands of different management. Biol. Conserv. 82, 157-165.

Tyler GA, Green RE, Casey C, 1998. Survival and behaviour of Corncrake *Crex crex* chicks during the mowing of agricultural grassland. Bird Stud. 45, 35-50.

Valtonen A, Saarinen K, Jantunen J, 2006. Effect of different mowing regimes on butterflies and diurnal moths on road verges. Anim. biodivers. conserv. 29, 133-148.

Van Swaay C, Warren M, Lois G, 2006. Biotope use and trends of European butterflies. J. Insect Conserv. 10, 189-209.

Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK, 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647-664.

Walter T, Schneider K, Gonseth Y, 2007. Schnittzeitpunkt in Ökowiesen: Einfluss auf die Fauna. Agrarforschung 14, 114-119.

Chapter III

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Hay harvesting causes high orthopteran mortality

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Abstract

Knowledge on the direct impact of the meadow harvesting process on field invertebrates has long been limited to studies that investigated impacts due to mowing. This study demonstrates that raking coupled with baling impacts orthopteran populations to a similar degree as mowing followed by tedding. At the end of the harvesting process, orthopteran surviving rate was 32% (SD = 14) when meadows were mown with rotary mowers without conditioner and lower, 18% (SD = 8), when mown with rotary mowers with conditioner. Conversely, given the strong impact of tedding, raking and baling, no evident advantages were found for the use of tractor bar mowers over rotary mowers without conditioner. Reduction in orthopteran densities observed after harvesting was slightly higher than the estimated mortality caused by the machineries, presumably because orthopteran reduction includes a small emigration and natural mortality. If conservation is the primary objective of the meadow, no conditioner should be used, uncut grass refuges should be left when mowing, and the number of time the meadow is harvested per year should be the minimum required to maintain the habitat.

Keywords: conservation, cutting, field invertebrates, grassland management, grasshopper, haying

Introduction

The relative influence of local vs. landscape factors is scale and species dependent, as taxa respond differently according to their trophic level, body size and habitat specialization (Tscharntke et al., 2005). For orthopterans specifically, local factors such as management intensity, vegetation structure and microclimate, appear to be more important than landscape factors with regard to abundance and species composition (e.g. Van Wingerden et al., 1992; Wettstein and Schmid, 1999; Gardiner et al., 2002; Marini et al., 2008). It is on this basis that Orthoptera are considered to be good indicators for habitat change (Baldi and Kisbenedek, 1997). Nevertheless, at scales of around 100 m, the proportion of woody vegetation adjoining a meadow increases orthopteran species richness presumably by providing a refuge when the meadow is mown (Marini et al., 2009a), and at larger scales (radius 500 m) urban elements in the surrounding landscape negatively affect orthopteran richness (Marini et al., 2008). Landscape pattern is therefore also important in determining patterns of grassland orthopteran richness and abundance.

Although orthopterans react negatively to grassland intensification, the underling mechanisms are not clear. For example Van Wingerden et al. (1992) argued that nitrogen input increases vegetation density and height which decrease temperatures near the soil surface where orthopteran eggs are usually located. Lower temperatures delay hatching and increase exposure of eggs to predation and mortality. Increase in vegetation biomass due to fertilizer input also allows more frequent harvests which have been shown to reduce orthopteran diversity, mostly due to mortality caused by the harvesting machines (e.g. Gardiner, 2006; Marini et al., 2008; Braschler et al., 2009).

Reductions in orthopteran density due to the direct impact of mowing ranges between 9–60% (Humbert et al., 2009). These results do not, however, disentangle mortality from emigration. Additionally, mowing is usually followed by tedding, raking and baling, with each operation likely to impact orthopterans that survived the initial mowing intervention (Humbert et al., 2009). Each harvesting step has a negative impact simply because of the tractor running over the field (Humbert et al., 2010a). Indeed it has been suggested that orthopteran mortality resulting from the whole harvesting process can exceed 70% (Oppermann et al., 2000).

To our knowledge, no quantitative assessments of orthopteran mortality caused by the whole meadow harvesting process exist. Therefore, the aim of this study was to investigate orthopteran mortality resulting from the sequential harvesting stages of mowing, tedding, raking and baling. Specifically, the mortality rates of each single or combined harvesting stage were measured, and then the total mortality was calculated. In addition different mowing techniques were compared; in particular we investigated the impact of rotary mowers with conditioner as there are evidences that conditioners have strong negative impacts on field invertebrates (Humbert et al., 2009; 2010a).

The meadow harvesting process, often referred to as "cutting" in the literature, includes several mechanized stages (in brackets are abbreviations used in this paper):

1.	Mowing the grass	(M)
2.	Conditioning the grass	(C)
3.	Tedding the grass for drying	(T)
4.	Raking the grass	(R)
5.	Baling or loading the grass	(B)

In this paper the term "mowing" restrictively refers to the actual mowing event (i.e. the first harvesting stage). Conditioning (stage two) is a recent practice used to accelerate the drying of the grass by crushing it after mowing. Conditioners, which are directly fixed on the mower (mower-conditioner) or attached behind the tractor, perform a rolling or crimping mechanical action on the grass immediately after cutting. Thus, if a conditioner is used, mowing and conditioning are executed simultaneously. We henceforth indicate this process as MC. Implementation of tedding (stage three) depends primarily on the form in which the grass is to be stored, hay or silage. Raking (stage four) consists in gathering the mown grass in lines to allow a baler or self-loading wagon to remove the harvest (stage five).

While our study addresses impacts on Orthoptera specifically, the results have relevance to far more than just Orthoptera biodiversity and conservation in an agricultural matrix. Orthopterans are an important food sources for farmland birds, many of which have undergone alarming declines in recent decades (Vickery et al., 2001). Further, it is likely that orthopterans are effective surrogates for many other grassland invertebrates of similar size and mobility, including many beetles, spiders and larval forms of Lepidoptera. Our results will also help the evaluation of agri-environment schemes, and improve the management of extensively used meadows, field margins or any other grassland elements to deliver conservation objectives.

Material and methods

Orthopteran mortality due to harvesting was measured using a capture-mark-resight technique, wherein the mortality of a group of individuals exposed to one or more harvesting stage(s) was compared to a control group (not exposed). We also assessed the impact of the whole harvesting process by summing the impacts across each harvesting stage. All experiments were carried on farms to catch the impact of “real” meadow harvesting processes.

Study sites

The experiments were carried out in summers 2008 and 2009. In total 14 fields located in seven different municipalities throughout Switzerland were used for the experiments: six in Aadorf (Aa1-Aa6); two in Doppleschwand (Do1 and Do2); one in Illnau-Effretikon (l1); two in Le Vaud (Le1 and Le2); one in Pfäffikon (Pf1); one in Villigen (Vi1); and one in Zürich (Zu1). All meadows were managed for hay production with sometime a late season grazing. Elevation ranged from 460–760 m.a.s.l. Four meadows were selected for the density investigations and eleven were used for the mortality experiments (see sub-sections below).

The fields in the different municipalities belong to different farmers. While tedding, raking and baling machines were similar across the experiments, the farmers used different mowing machines. Thus, the mowing machines were classified as rotary mower without conditioner, rotary mower with conditioner, or tractor powered bar mower.

Mortality experiments

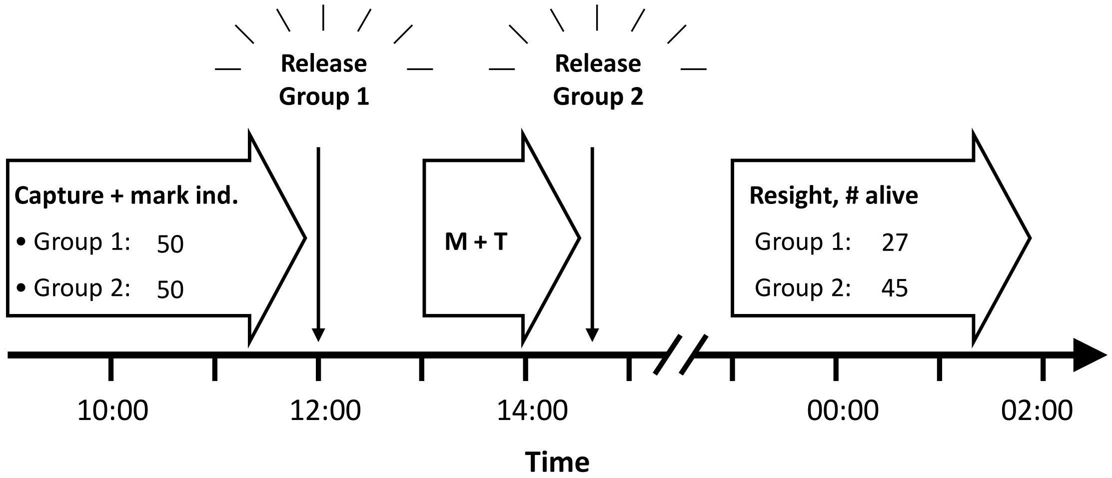
A capture-mark-resight method was used to measure orthopteran mortality. Two-three hours before mowing, tedding, raking or baling, 80 to 120 adult orthopterans of the same species were captured, marked and stored in net boxes. Orthopterans were captured with a sweep net and marked with RADGLO fluorescent pigments (Radiant Color NV, Europark 1046 B-3530, Houthalen Belgium) on their pronotum and wings using a small paint brush. The orthopterans were divided in two equal groups, a treatment and a control group marked with a different colour. All orthopterans were captured within the meadow used for the experiment or in its vicinity. Therefore, selection of the species was according to the species present in the meadow.

The first group of orthopterans (treatment group) was released about one hour before the start of the harvesting stage in the central zone (about 20 x 20 m) of a 50 x 50 m homogenous area of the meadow previously delimited. The second group (control) was released in that same zone just after the harvesting stage or the combined harvesting stages under investigation. The second group of orthopterans served as control for handling effects and refinding rate (cf. Figure 1).

During the following night, orthopterans were located using a black-light lamp (20W 230V tube). First the 50 x 50 m delimited plot was intensively searched by slowly turning the hay with a hayfork. Second, the area around the plot was inspected further and further away (20 to 50 m) until no more marked orthopterans where seen. Potential nearby refuges, such as uncut field margins, were also inspected. The individuals were recorded as dead or alive, and their fluorescent colour marking was noted. The mortality rate was calculated as follows: the number of resighted orthopterans alive from the control group minus the number of resighted orthopterans alive of the treatment group divided by the number of resighted orthopterans alive of the control group (Fig. 1).

Missing orthopterans of the treated group were assumed to be dead as they were often crushed, cut in pieces or packed in the bales, and were therefore not detectable using the methods described. Live orthopterans, by contrast, were easily located: mean resight rate of control group orthopterans across all experiments was 91.6%.

Figure 1 Chronology of the capture-mark-resight method used to measure orthopteran direct mortality due to harvesting. The figure shows a hypothetical example for mowing (M) plus tedding (T), but the same methodology applies for other combined or single harvesting stages. In this example, orthopteran mortality due to mowing + tedding = (45-27) / 45 = 40% (see text section 2.2.).



Rotary mower without conditioner

In fields mown with rotary mower without conditioner, the mortality rate due to mowing and tedding together was measured because these two harvesting stages took place one after another. In those cases the design followed exactly the example in Figure 1. The following day, raking and baling also took place one after another and thus the combined impact of R+B was estimated. The design also followed Figure 1, except that instead of "mowing + tedding" it was "raking + baling" and that different colours were used to avoid confusion with the orthopterans marked and released the day before. Nine replicates were performed.

In three fields (Aa5, Do2 and Le1) the hay was not baled, but removed with a self-loading wagon. The mechanism that removes the hay is the same for a baler or a self-loading wagon, therefore the two techniques were not differentiated in the analyses. For notation simplification in the tables and the text we talk only about baling, but imply the same for loading. Because of weather and logistic constraints, in two cases the impact of M+T and R+B had to be estimated in different fields (see Table 1). Some fields were used for more than one replicate. Though, we assume independence because the set of orthopterans were independent of each other.

Rotary mower with conditioner

In 2008, in Aadorf, the mortality rate due to mowing with a rotary mower with conditioner plus tedding was measured (four replicates). In those cases, an extra group of orthopterans marked with a third colour was released between mowing and tedding, which allowed also to estimate the separated impacts of mowing and tedding. The impact of raking and baling was not measured in those cases. Otherwise the methodology was the same as describe in section 2.2.

Similarly, in 2009, in Villigen, the impact of mowing with a conditioner was first measured. Then the impact of tedding plus raking was measured. In that case, tedding and raking were executed over a period of two days. And finally the impact of baling was measured. Three replicates were performed with different species.

Tractor bar mower

Using the same methodology, the impact of mowing (solely) with a bar mower powered by a tractor was investigated. Only one trial was done because only one farmer used that mowing technique.

Statistical analyses

The impact of the whole harvesting process was calculated by "adding" the impact of the different harvesting stages. The added impacts were calculated as follow: suppose mortality of M+T , and mortality of R+B , so that x and y are the surviving rates of M+T and R+B respectively, then the mortality of the whole harvesting process , which is one minus the multiplication of the surviving rates. The variance of is: .

To test if harvesting with a rotary mower without conditioner affected differently some species or group of species Wilcoxon rank sum tests were used. To test if harvesting with a rotary mower with or without a conditioner led to different mortalities at the end of the harvesting process (after baling), the following routine was done. First, the 2008 rotary mower with conditioner experiment (four first rows in Table 2) was completed with R+B mortality rates sampled with replacement from the rotary mower experiment. The mortality rates were sampled from Chorthippus spp. R+B values (five first rows Table 1). Second, the mortalities due to the whole harvesting process were calculated by adding MC+T and R+B as described before. This is possible because in Table 1 the mortality rates of R+B were independently measured from the mortality rates of M+T. Similarly in the field, the proportion of orthopteran killed during raking and baling is not influenced by the proportion killed before. We, therefore, assume the same impact of R+B whatever the mowing technique used. Finally, a t-test on arcsin square root transformed data was performed. With nine estimates for the mortality due to a harvesting process without using a conditioner (column M+T+R+B in Table 1) and seven estimates when a conditioner was used (columns MC+T+R+B in Table 2). This routine was repeated 10000 times to get all possible bootstraps, and the median of all p-values was used as final p-value.

Density experiment

Reduction in the abundance of orthopterans due to harvesting was investigated in three meadows both in 2008 and 2009. The density of orthopterans was measured two hours before the grass was mown and again just after baling using a biozoenometer. A biozoenometer is a one metre high canvas mesh attached to a solid circle of exactly 1 m2. The circle was thrown in the grass, and all trapped juvenile and adult orthopterans from the Tettigonioidea and Acridoidea super-families were counted (24 to 32 samples of 1 m2 regularly placed per meadow). This technique is equivalent to the 1 m2 box quadrat approved sampling methodology by Badenhausser et al. (2009), except that the biozeonometer is circular. Among the meadows, the harvesting processes differed in the number of times the grass was tedded, and the number of days between mowing and baling. Therefore, no harvesting-process-specific analyses were done, but all the data were combined to get an estimate of orthopteran density reduction during slightly different, but common meadow harvesting processes (Table 3).

Results

Rotary mower without conditioner

Mowing with a rotary mower without a conditioner plus tedding killed on average 42% orthopterans (Table 1). Assuming 27% mortality due to tedding, the mortality due to mowing solely is then equal to 21%. Raking and baling together killed 46% of the orthopterans. This does not correspond to 46% of the initial population, but 46% of the orthopterans present before raking. The impact of R+B is independent of the impact of

M+T. The cumulative impact of (M+T) + (R+B) was on average 68% (last column, Table 1).

Table 1 Orthopteran mortality rates for mowing with a rotary mower plus tedding (M+T) and for raking plus baling (R+B). The last column (M+T+R+B) show the calculated cumulative mortality rates of R+B added to M+T. Mean values ± SD are given.

		% mortality		
Meadow and year	**Species**	**M+T**	**R+B**	**Calculated M+T+R+B**
Do2 2008	*C. parallelus*	30	72	80
Le1 2008	*C. parallelus*	40	32	59
Aa5 2009	*C. parallelus*	39	40	63
Aa6 2009 / Ie2 2009	*C. parallelus*	52	30	67
Aa6 2009 / Il1 2009	*C. biguttulus*	37	22	51
Le1 2009	*S. lineatus*	24	34	50
Do2 2008	*M. roeselii*	58	78	91
Le1 2008	*M. roeselii*	44	57	76
Le1 2009	*M. roeselii*	50	48	74
	Mean	**42 ± 11**	**46 ± 20**	**68 ± 14**

Rotary mower with conditioner

In 2008, the rotary mower with a conditioner killed 53, tedding alone 27, and the combined stages 66% orthopterans (Table 2). Note that the MC+T mortalities presented in Table 2 are the mortalities measured in the fields, not the calculated values from T added to MC. Since the impact of R+B was not measured in those fields, values bootstrapped from Table 1 were used to calculate the impact of the whole harvesting process (MC+T+R+B). One bootstrap consists of sampling with replacement (Table 1 Chorthippus spp.) an R+B value for each four replicates. In 2009, the rotary mower with conditioner killed 62, tedding plus raking plus baling 59, and baling itself (not shown in Table 2) 27% orthopterans.

The overall mortality of mowing with a rotary mower with conditioner across all replicates was 57%. The mean mortality of the whole harvesting process (MC+T+R+B) was 82%; this value and its associated SD were from the 10000 bootstraps.

Table 2 Mortality rates for mowing with a rotary mower with conditioner (MC), tedding (T) and both combined (MC+T), or mowing with a rotary mower with conditioner (MC) and tedding plus raking plus baling (T+R+B). The last column (MC+T+R+B) show the calculated cumulative mortality rates. Mean values ± SD are given.

		% mortality				
Meadow and year	**Species**	**MC**	**T**	**MC+T**	**T+R+B**	**Calculated MC+T+R+B**
Aa1 2008	*C. parallelus*	57	13	63		**
Aa2 2008	*C. biguttulus*	66	30	76		**
Aa3 2008	*C. para. + C. bigu.**	56	46	76		**
Aa4 2008	*C. para. + C. bigu.**	35	21	49		**
Vi1 2009	*M. bicolor*	53			66	84
Vi1 2009	*P. albopunctata*	69			63	88
Vi1 2009	*S. lineatus*	65			49	82
	Mean	**57 ± 12**	**27 ± 14**	**66 ± 13**	**59 ± 09**	**82 ± 8**

* Here *C. parallelus* and *C. biguttulus* had to be pooled because there were not enough individuals of a single species to do the experiment.

** R+B values were sampled with replacement from Table 1, species *C. parallelus* and *C. biguttulus* (see statistical analyses section).

Tractor bar mower

In 2009, in field Il1, mowing with a bar mower powered by a tractor engendered a mortality of 13% on Chorthippus biguttulus population. To this mowing mortality, if we add an impact of T = 27 ± 14% (from Table 2), and an impact of R+B = 46 ± 20% (from Table 1), then the mortality of the whole harvesting process when mowing with a tractor bar mower adds to 66 ± 14%.

Statistical analyses

Orthopteran species were pooled in the analyses for two reasons. First, the data did not support any difference between species or groups of species. For example, mortality rates of M+T, R+B and M+T+R+B (Table 1), did not significantly differ between C. parallelus and M. roeselii (all Wilcoxon rank sum test outputs equal: W = 2, P = 0.229), and between Ensifera and Caelifera (all Wilcoxon rank sum test outputs equal: W = 2, P = 0.095). Additionally, no differences between mobile (C. parallelus and C. biguttulus) and less mobile species (Stenobothrus lineatus and M. roeselii) — mobility classes according to Reinhardt et al. (2005) — were found (Wilcoxon rank sum tests for M+T and M+T+R+B: W = 2, P = 0.557; for R+B: W = 4, P = 0.191). Finally, no qualitative interactions were observed, i.e. all species reacted in the same way to the different harvesting stages and mowing techniques.

The impact of the whole harvesting process when mowing with a rotary mower (M+T+R+B) is equal to 68 ± 14% (Table 1). The impact of the whole harvesting process when mowing with a rotary mower with conditioner (MC+T+R+B) is 82 ± 8% (Table 2). To test if these two harvesting processes led to different mortalities, a t-test was done for each single bootstrap. The median of the 10000 p-values obtained from all t-tests is 0.035. Thus, mowing with a rotary mower with conditioner led to a significantly higher mortality rate at the end of the harvesting process than mowing with a rotary mower without conditioner (Fig. 2).

Among 1642 marked orthopterans of the treatment groups, 86 were resighted outside the meadow, correcting for recovery rate (91.6%), it shows that 5.7% of the marked orthopterans moved out the meadow during the harvesting process (5.6% were Caelifera and 6% Ensifera).

Density experiment

Orthopteran population density before mowing varied between meadows and years, and ranged between 1.7 and 16.5 individuals per m2. All populations experienced strong declines during harvesting; density after baling ranged between 0.3 and 0.6 orthopteran per m2 (Table 3). Average orthopteran population reduction was 88.7 ± 5.9%. Values include all individuals found of the Tettigonioidea and Acridoidea super-families. The grass was tedded one or two times and the harvesting processes lasted two or four days.

Figure 2 Mean orthopteran population densities with standard error bars through the meadow harvesting process (data from Table 1 and 2).

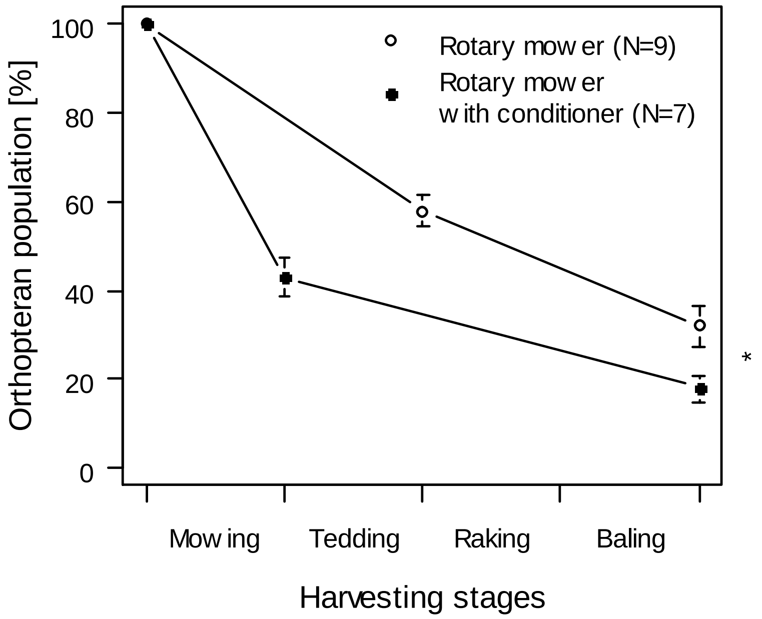


Table 3 Densities of orthopterans before mowing and after baling, and their associated reduction. All meadows were mown with rotary mower without conditioner. Mean reduction ± SD is given.

Meadow and year	Tedding events	Days for harvesting	[Orthopterans / m^2] Before mowing	After baling	% reduction
Pf1 2008	2	4	5.63	0.47	91.7
Le1 2008	1	2	3.09	0.47	84.8
Do1 2008	2	2	16.45	0.50	97.0
Pf1 2009	2	4	6.66	0.56	91.5
Le1 2009	1	2	1.71	0.33	80.5
Zu1 2009	1	2	2.56	0.34	86.6
		Mean			**88.7 ± 5.9**

Discussion

The results show that, overall, the meadow harvesting process caused a direct mortality of 65–85% orthopterans. The variability was largely due to the different mowing machines adopted for the mowing stage. These results demonstrate the very substantial impact of the mechanical harvesting process on field invertebrates, a factor that has been largely overlooked by management policies that aim to enhance the biodiversity of meadow fauna.

This is important for many European agri-environmental programs for which effectiveness has been questioned, especially regarding their ability to improve invertebrate diversity (Kleijn et al., 2006; Roth et al., 2008). In addition to agricultural grasslands, some open nature reserves and hotspots are also mown as a management strategy (e.g. Cattin et al., 2003). When conservation is the primary goal of such management, the harvesting techniques used should be considered carefully in the light of our results.

Mortality due to mowing

Mowing with rotary mowers killed about 21% of the orthopterans, while adding a conditioner increased mortality by almost three times (57%). These estimates are similar to other studies that used insect models (Humbert et al., 2010a), or orthopterans (Oppermann et al., 2000). While only adult orthopterans were used in this study, Oppermann et al.'s study showed that juveniles are less affected than adults. Our results also provide further evidence that for orthopterans, tractor bar mowers are slightly less damaging than rotary mowers (Oppermann et al., 2000). For larval butterfly, Humbert et al. (2010b) found no differences between tractor bar mowers and rotary mowers without conditioner.

Mortality due to the whole harvesting process

Mortality due to the mowing machines has usually been assumed to be the most damaging of meadow harvesting impacts on field fauna. Our results demonstrate that post-mowing interventions such as raking coupled with baling impact orthopteran populations to a similar degree as mowing followed by tedding (Table 1). Indeed, any benefits gained in terms of reduced orthopteran mortality by using a tractor-powered bar mower relative to a rotary mower are mostly lost by the cumulative impact of the subsequent harvesting stages (see also Oppermann et al., 2000). These results underline the need to consider the entire harvesting process for a complete assessment of harvesting impacts on field invertebrates.

Conditioner increased Orthoptera mortality to such an extent that at the end of the harvesting process, after baling, the cumulative mortality (82%) is significantly higher compared to harvesting without conditioner (68% mortality, see Fig. 2).

The variability found in the results may be due to different species mixtures among trials. While no significant differences were found between C. parallelus and M. roeselii, or between Ensifera and Caelifera or between mobile (C. parallelus and C. biguttulus) and less mobile species (S. lineatus and M. roeselii), the literature suggests that some differences may exist between species (Oppermann et al., 2000; Humbert et al., 2010a). Note that a power analysis indicates that the sample size (N = 5) does not allow detection of differences smaller than 20% between species or group of species. Additionally, different machine brands were used. For example, tedders might vary in their visibility to orthopterans, and tractor wheels, which can influence the impact of the process, might differ in size. The speed at which the tractors move across the field might also affect rates of mortality.

Across all six meadow harvesting processes using rotary mowers without conditioner, orthopteran population density decreased by 88.7% on average (Table 3). As expected, this value is higher than the mortality rate calculated for similar harvesting processes (68%), because this decrease represents the proportion of orthopteran missing after harvesting, and includes the ones that were killed by the harvesting machines, the ones that naturally died, as well as the ones that moved out the meadow. Emigration during harvesting is believed to be low. Daily movement and dispersal capacities of orthopterans are usually smaller than 10 m, although species specific (Reinhardt et al., 2005), and higher in unsuitable habitat (Hein et al., 2003; Berggren, 2004). During the mortality experiment, 5.7% of 1642 marked orthopterans moved out the meadows when harvesting. Whereas this proportion is linked to the size and form of the meadow, it gives a good daily emigration estimate for our 1 ha average size meadows. Daily adult natural mortalities haven been reported for several species in Grant et al. (1993) and range between 3 and 4%. In the density experiments, average harvesting process length was 2.7 days, thus average natural mortality can be estimated around 10%. Subtracting the emigration rate and natural mortality from the overall density reduction leads to the following: 88.7 – 5.7 – 10 = 73.0%, which correspond to the estimated proportion of orthopteran killed by the harvesting machines. While this is a rough estimation, it is nevertheless close to the mortality measured using the capture-mark-resight methodology and confirms the strong impact of the harvesting process.

Management recommendations

While the impact of harvesting is considerable whatever the type of process, it appears that using a conditioner significantly increases the total mortality. Therefore we recommend not using conditioner where biodiversity is of concern.

Our single replicate using a tractor bar mower corresponds with previous results that indicate bar mowers as being less damaging than rotary mowers (Humbert et al., 2009). Nevertheless, given the strong impact of tedding, raking and baling, the difference between tractor bar and rotary mowers at the end of the harvesting process is small. Therefore, there is no clear advantage to using tractor bar mowers over rotary mowers over the whole harvesting process.

Given the strong negative impact of harvesting, reducing the number of harvests per year, and considering the date of harvesting are probably the major issues. Where faunal abundance is a primary objective, we recommend that the number of cuts is reduced to the minimum required to maintain the plant community. In Europe, this is usually one or, at most, two cuts per year according to meadow location and conditions (Parr and Way, 1988; Jantunen et al., 2007). Harvesting late in the season, when most species have completed reproduction is also an option (Wettstein and Schmid, 1999). For Alpine meadows, Marini et al. (2009b) even recommended supra-annual mowing regimes of once every 3-5 years to reduce mortality of Orthoptera. Providing nearby refuges such as uncut grass strips is also likely to be important, as such refuges could act as source populations for recolonization of the meadow after the harvesting process, though the effectiveness of such refuges remains to be explored.

Acknowledgements

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References

Badenhausser, I., Amouroux, P., Lerin, J., Bretagnolle, V., 2009. Acridid (Orthoptera: Acrididae) abundance in Western European Grasslands: sampling methodology and temporal fluctuations. J. Appl. Entomol. 133, 720-732.

Baldi, A., Kisbenedek, T., 1997. Orthopteran assemblages as indicators of grassland naturalness in Hungary. Agric. Ecosyst. Environ. 66, 121-129.

Berggren, A., 2004. Impact of grazing on individual male movement in Roesel's bush-cricket Metrioptera roeseli: one possible clue to species range expansion. J. Insect Behav. 17, 419-429.

Braschler, B., Marini, L., Thommen, G.H., Baur, B., 2009. Effects of small-scale grassland fragmentation and frequent mowing on population density and species diversity of orthopterans: a long-term study. Ecol. Entomol. 34, 321-329.

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. Biol. Conserv. 113, 179-188.

Gardiner, T., 2006. The Impact of Grassland Management on Orthoptera Populations in the UK. Unpublished PhD thesis, University of Essex, Colchester, UK.

Gardiner, T., Pye, M., Field, R., Hill, J., 2002. The influence of sward height and vegetation composition in determining the habitat preferences of three Chorthippus species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. J. Orthoptera Res. 11, 207-213.

Grant, A., Hassall, M., Willott, S.J., 1993. An alternative theory of grasshopper life-cycles. Oikos 66, 263-268.

Hein, S., Gombert, J., Hovestadt, T., Poethke, H.J., 2003. Movement patterns of the bush cricket Platycleis albopunctata in different types of habitat: matrix is not always matrix. Ecol. Entomol. 28, 432-438.

Humbert, J.-Y., Ghazoul, J., Sauter, G.J., Walter, T., 2010a. Impact of different meadow mowing techniques on field invertebrates. J. Appl. Entomol. 134, 592–599.

Humbert, J.-Y., Ghazoul, J., Walter, T., 2009. Meadow harvesting techniques and their impacts on field fauna. Agric. Ecosyst. Environ. 130, 1-8.

Humbert, J.-Y., Richner, N., Sauter, G.J., Ghazoul, J., Walter, T., 2010b. Graslandernte-Prozesse und ihre Wirkung auf die Fauna. ART Report 724. Agroscope Reckenholz-Tänikon Research Station ART, Zurich.

Jantunen, J., Saarinen, K., Valtonen, A., Saarnio, S., 2007. Flowering and seed production success along roads with different mowing regimes. Appl. Veg. Sci. 10, 285-292.

Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243-254.

Marini, L., Fontana, P., Battisti, A., Gaston, K.J., 2009a. Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach. Insect Conserv. Diver. 2, 213-220.

Marini, L., Fontana, P., Battisti, A., Gaston, K.J., 2009b. Response of orthopteran diversity to abandonment of semi-natural meadows. Agric. Ecosyst. Environ. 132, 232-236.

Marini, L., Fontana, P., Scotton, M., Klimek, S., 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. J. Appl. Ecol. 45, 361-370.

Oppermann, R., Handwerk, J., Holsten, M., Krismann, A., 2000. Naturverträgliche Mähtechnik für das Feuchtgrünland, Voruntersuchung für das E & E - Vorhaben. ILN Singen, Bonn, p. 236.
Parr, T.W., Way, J.M., 1988. Management of roadside vegetation: the long-term effects of cutting. J. Appl. Ecol. 25, 1073-1087.
Reinhardt, K., Kohler, G., Maas, S., Detzel, P., 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography 28, 593-602.
Roth, T., Amrhein, V., Peter, B., Weber, D., 2008. A Swiss agri-environment scheme effectively enhances species richness for some taxa over time. Agric. Ecosyst. Environ. 125, 167-172.
Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol. Lett. 8, 857-874.
Van Wingerden, W.K.R.E., van Kreveld, A.R., Bongers, W., 1992. Analysis of species composition and abundance of grasshoppers (Orth. Acrididae) in natural and fertilized grasslands. J. Appl. Entomol. 113, 138-152.
Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647-664.
Wettstein, W., Schmid, B., 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J. Appl. Ecol. 36, 363-373.

Manuscript

Leaving uncut grass refuges when mowing benefits grasshoppers

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Abstract

Recent studies have shown that haying has a severe direct negative impact on grasshoppers and other field invertebrates. In view of this, leaving uncut grass areas as refuge has often been recommended, yet no studies have proved it. Therefore, in this study we investigated the influence of leaving a 10% uncut grass refuge in the center of 50 m diameter meadow plots when mowing on Orthoptera population. Final grasshopper population size was about 60% higher in plot with refuge compared to without. The results demonstrate that providing refuges is a simple and good measure to mitigate the direct negative impact of the harvesting process. In addition, we show that at the landscape scale, nature reserves with a late harvesting date (after 1st of September) can be valuable grasshopper source populations.

Keywords: conservation, cutting, grassland management, haying, Orthoptera

Introduction

Meadow harvesting techniques and their impacts on field fauna have been reviewed by Humbert et al. (2009). The review shows that grass harvesting has a direct and often substantial impact on the field fauna, especially the mowing process, and that this impact depends on the techniques and machines used, as well as the settings, the habitat and ecology of each species. Further research on the influence of mowing confirms the strong direct impact of the machineries on field invertebrates and highlights the differences between mowing techniques, especially regarding the two fold increase in damages when a conditioner is added to a rotary mower (Humbert et al. 2010). On the other hand, post-mowing harvesting stages have received relatively little attention; only one recent study quantitatively assessed the impact of the whole harvesting process on grasshoppers (Humbert et al. 2010). Their results demonstrate that post-mowing interventions such as raking coupled with baling impact grasshopper populations to a similar degree as mowing followed by tedding. While collectively, all above cited studies show that impact can be reduced using the appropriate mowing technique, they recognized that the impact of the whole harvesting process remains yet important. Thus all recommend that when mowing, uncut grass areas should be left as a refuge for the fauna.

Evidence about the benefit of uncut refuges for Orthoptera exists. For example, Guido and Gianelle (2001) showed a shift in the distribution patterns of four Orthoptera species when haying, suggesting that some grasshoppers actively moved in the adjacent undisturbed microhabitats during the process. Similarly, in northeast Italy mountain region, meadow Orthoptera species richness is correlated with the proportion of woody vegetation adjoining the meadow, presumably because it provides refuges when meadows are mown (Marini et al. 2009). Other recent studies on the influence of local management types and intensities on Orthoptera recommend that undisturbed areas should be left as refuge when harvesting (e.g. Braschler et al. 2009; Gardiner and Hassall 2009; Marini et al. 2008; Van Wingerden et al. 1991). Despite these studies and recommendations, no study has investigated the direct influence of uncut refuges on Orthoptera populations during the harvesting process (i.e. if Orthoptera actually retreat in the uncut areas during harvesting). The present study sought to test this refuge hypothesis.

At the field scale, grasshopper populations densities were measured in plots were a refuge was left when harvesting and compared to plots with no refuge left. In addition, grasshopper population phenology was investigated in four wet-meadows that were not harvested before September to see if those meadows could act as refuge at the landscape scale.

Material and methods

Study sites

The study was carried out in 2008 and 2009 in ECA extensively used meadows (Ecological Compensation Area; with no fertilizer application and a first cut not before June 15th or July 1st according to site elevation). Two meadows were located in the municipality of Illnau ZH, (Il1) and (Il2), at about 580 elevation. These meadows were used in 2008 and 2009. A third meadow was located in the municipality of Pfäffikon ZH, elevation 550 m (Pf1), and a fourth meadow in the municipality of Doppleschwand LU (Do1), elevation 730 m with first possible cut not before July 1st. All meadows were at least 115 x 60 m big, mostly flat and homogenous. Their vegetations communities were associated between Arrhenatherion and Mesobromion alliances. All experiments were carried one between the 17th of June and 3rd of July, which was the first annual cut of the meadow. Except in meadow Il2 in 2008, the experiment took place during the second harvest between August 26th and 28th.

Sampling method

The density of grasshoppers (i.e. number of individuals / m^2) was measured using a one meter square biozoenometer. This technique is equivalent to the 1 m^2 box quadrat approved sampling methodology by Badenhausser et al. (2009), except that the biozeonometer is circular. The biozoenometer was thrown in the grass, and all trapped grasshoppers from the Tettigonioidea and Acridoidea super-families (juveniles and adults) were recorded. This was repeated 12 to 16 times and averaged.

Experimental design

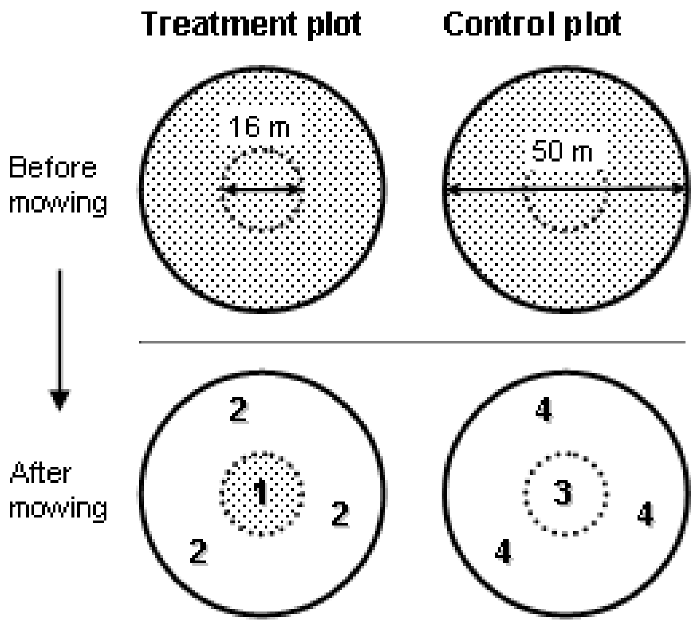
To investigate the influence of leaving uncut grass refuge on Orthoptera during the haying process, a randomized block design was adopted with two 50 m diameter plots set per meadow; a treatment and a control plot (see Fig. 1). When mowing the treatment plot, a circle of 16 m diameter was left uncut in the center (the refuge). While the whole control plot was mown, a same size central zone was delimited for comparison. Mowing machines were tractor bar mowers for the fields located in Illnau (Il1 and Il2) and rotary mowers (without conditioner) for fields Do1 and Pf1. The mowing direction was from outside inward in both plots to push the grasshoppers in the central zone. Tedding, raking and baling were executed linearly, parallel to meadow length, but the refuge was left untouched during the whole harvesting process. A minimum five meters buffer zone was left between the plots. Meadows Il1 and Il2 were used twice (once in 2008 and once in 2009). However, independence is recognized because the experimental unit is not the field, but the haying event.

Grasshopper densities were measured two to three hours before mowing in both plots. Before mowing 16 samples were taken per plot where density was assumed homogenous within plots. After mowing grasshopper density was not homogenous anymore and measured separately in all four zones described in figure 1. Twelve samples were regularly taken in the uncut refuge (zone 1 fig. 1) and 16 samples were regularly taken around the refuge (zone 2). Similarly, in the control plot, 12 samples were regularly taken in the central zone (zone 3) and 16 samples were taken around it (zone 4). This was repeated once again after baling (when the whole harvesting process was finished). First developmental stage larvae (< 5 mm) were not included in the analyses because detectability may vary between cut and uncut zones.

The literature suggests that grasshoppers may exhibit directional movements, however which factors influence movements and how is not well understood (Narisu et al. 1999). The sun, the wind, as well as the surrounding landscape elements may all influence. Therefore, a circle design was adopted to avoid any grasshopper directional movement effects across replicates. Indeed, in the treatment plot if grasshoppers move more in a specific direction, the proportion that will reach the refuge will be the same whatever the direction.

Treatment effects were analyzed with a generalized linear model with a quasipoisson family to account for overdispersion (Crawley 2007). The response variable was grasshopper density after baling (number of individuals / m^2). To account for differences in initial population densities, grasshopper density before mowing was included as co-factor. A separated generalized linear model was used to test if the density of grasshoppers within the uncut refuge changed after mowing and after baling. All statistics analyses were performed with R version 2.8.1 (R Development Core Team 2008).

Figure 1 Design for the refuge experiment. Grasshopper densities were measured before mowing, after mowing and again after baling. Before mowing grasshopper densities were assumed homogenous within plots. Numbers 1 to 4 corresponds to sampling zones for after mowing and after baling.



Grasshopper phenology in wet meadows

Four wet meadows were selected to study grasshopper population phenology; two in Greifensee south shore nature reserve (canton ZH) and two in Schmerikon nature reserve (canton SG). Meadows were classified as litter meadow (Molinion alliance) and were part of an agri-environment scheme with no fertilizer application allowed and a late first cut not before September 1st. Within nature reserve, meadows were at least 500 m apart. Grasshopper densities were measures in all meadows from spring to fall 2009, about every two weeks. Using a biozoenometer, 16 samples per meadow were taken each time between 10:00 and 17:00 on warm sunny days. All grasshopper developmental stages were recorded.

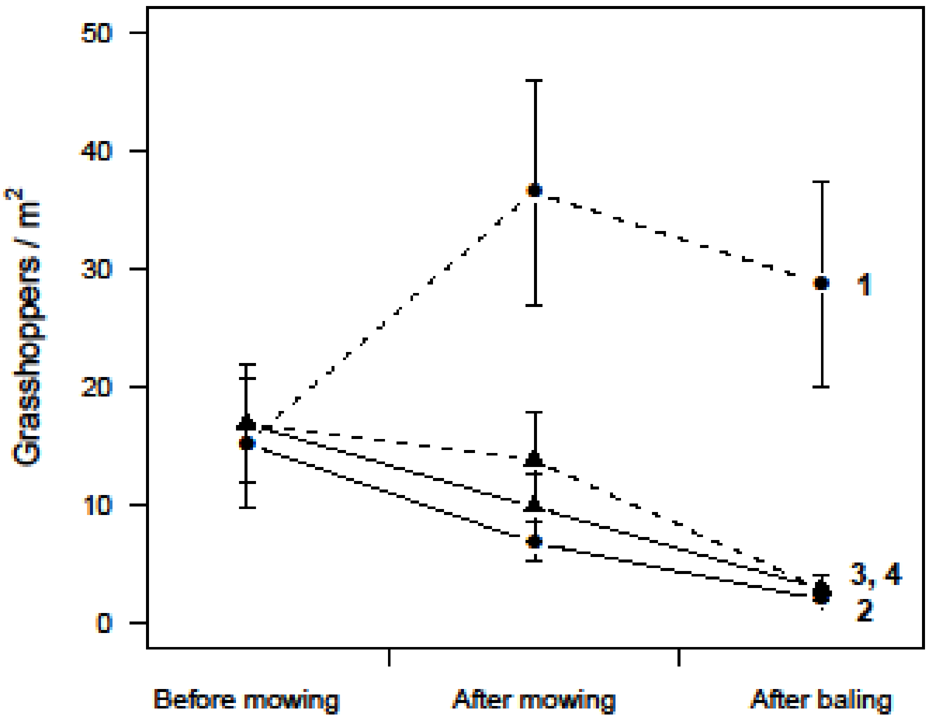
Results

Refuge experiment

Grasshopper densities before mowing varied across meadows and ranged between 3.5 and 39.5 individuals per m^2 (6 replicates). Densities were on average 15.2 for treatment plots and 16.9 for control plots (Fig. 2). After mowing density within the refuge (zone 1) was

36.5 ind. / m^2, while densities in all other zones were lower than before mowing. After baling, the density in the refuge, 28.7 ind. / m^2, was significantly higher than the density around the refuge (zone 2), 2.0 ind / m^2 ($t = 5.86$, $df = 19$, $P < 0.0001$). Which corresponds to 3525 grasshoppers around the refuge and 5773 in the refuge (total = 9298). In the control plots, after baling grasshopper density was homogenous and averaged 2.9 ind. / m^2 in zones 3 and 4, and was significantly lower than the density within the refuge (Fig. 2: zone 1 versus 3, $t = 6.36$, $df = 19$, $P < 0.0001$; zone 1 versus 4, $t = 5.42$, $df = 19$, $P < 0.0001$). Therefore a total of 5727 grasshoppers in the control, corresponding to 62% less than in the treatment plot. On the other hand densities in zones 2, 3 and 4 were not significantly different from each other (Fig. 2: zone 2 versus 3, $t = 0.63$, $df = 19$, $P = 0.5378$; zone 2 versus 4, $t = 0.66$, $df = 19$, $P = 0.5173$; zone 3 versus 4, $t = 0$, $df = 19$, $P = 1$). Within the uncut refuge the density of grasshoppers after baling was significantly higher than before mowing ($z = 4.9$, $P < 0.0001$), but significantly lower than after mowing ($z = 2.34$, $df = 10$, $P = 0.0195$).

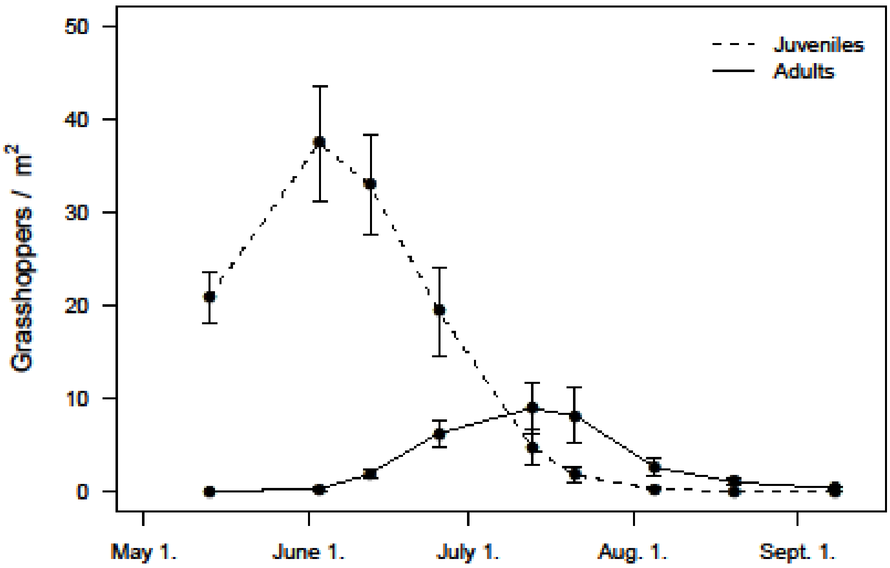
Figure 2 Mean grasshopper densities before mowing, after mowing and after baling with SE bars. Numbers correspond to the four different zones shown in figure 1. Solid circles are for the treatment plots and triangles for the control plots, while dashed lines are for the densities in the central zone 1 (uncut refuge) and central zone 3 (cut). After baling, only the density in zone 1 significantly differed from the other zones.



Grasshopper phenology in wet meadows

Grasshopper phenology during summer 2009 is shown in figure 3. On May 14th, juvenile density was about 20 ind. / m^2. First adults appeared on the third of June, but adult maximum densities were observed mid-July. All population densities were below 1 ind. / m^2 at the time of harvesting (September 8th). On June 25th, 10 White storks (*Ciconia ciconia*) were observed preying on grasshoppers in one of study site located at Greifensee.

Figure 3 Grasshopper phenology in four wet-meadows (summer 2009). Dashed lines are for juvenile densities and solid lines for adult densities. The last point corresponds to the timing of the cut. Mean values +/- SE are given.



Discussion

Recent studies have proved that haying has a severe direct negative impact on grasshoppers and other field invertebrates (see Humbert et al. 2009; Humbert et al. 2010; Humbert et al. 2010). In view of this, leaving uncut grass areas as refuge have often been recommended, yet no studies have proved it. Our results demonstrate that providing uncut grass refuges is a simple and good measure to mitigate the direct negative impact of the harvesting process on grasshoppers. This is important for many grassland agri-environmental programs such as extensive meadows and field margins, that seek to enhance both flora and fauna diversity. Additionally, we show that at the landscape scale, nature reserves with a late harvesting date (after 1st of September) can be valuable grasshopper source populations. Especially when nearby intensive meadows are extensified to promote the return of a biodiversity lost.

Refuge at local scale

The results show that when mowing, leaving an uncut grass refuge benefits Orthoptera by reducing their exposure to harvesting machineries. Not only the individuals already present in the refuge benefit from it, but additional grasshoppers move in the refuge during – or just after – the mowing process, thus safe from the post-mowing harvesting stages (Fig. 2). The density in the refuge after baling is about two times higher than before mowing. For a refuge equivalent to 10% of the area, it means that at least 20% of the grasshopper initial population survived the meadow harvesting process. An additional 12% was found around the refuge.

In Humbert et al. (2010) capture-mark-resight experiment, grasshopper capacity to move out the meadow was found to be low. While they recognized that this is influenced by the size and form of the meadow, on average only 5.6% of the marked grasshoppers were resighted outside the meadow. In this experiment, the maximum distance between the refuge hedges and the treatment plot border was 17 m, though only 10 to 15% of the grasshoppers moved in the refuge during or just after mowing. This confirms grasshopper low dispersal capacity even in the presence of disturbance.

During the post-mowing harvesting stages, grasshopper density slightly decreased within the refuge. This pattern may be explained by a kind of maximum density threshold exceeded within the refuge after mowing, with strong interspecific competitions that made some grasshoppers to move out. Or more likely, because sampling within the refuge after mowing (12 one meter square samples involving 2 people) disturbed the grasshoppers and scared some out the relatively small refuge area (16 m diameter).

Uncut grass areas are not only beneficial during the harvesting process, but after harvesting such long swards provide cooler areas that will be favored by some grasshopper species (Willott 1997). In addition to Orthoptera, many other grassland invertebrates will profit from uncut grass refuges. First, by directly reducing population mortality rates as shown for some beetles, spiders and butterflies caterpillars (Humbert et al. 2010; Thorbek and Bilde 2004), and second, as continuing shelter and food sources, such as nectar flowering plants for butterflies (Dover et al. 2010; Gerstmeier and Lang 1996). Sward architecture is also higher in uncut areas, a factor that was identified as primordial to promote invertebrate species richness (Woodcock et al. 2009). Ground nesting bird mortality due to mowing has long been known (e.g. Labisky 1957), and leaving unmown areas have also been proved to be beneficial for those birds (Broyer 2003).

Refuge at landscape scale

In eastern Switzerland, wet meadows classified as litter meadows are often found around lakes or along major streams. These meadows are mown once a year, but not before September first. Therefore grasshopper populations are not much affected by the direct impact of the harvesting process as most grasshoppers already reproduced at that time (Fig. 3). Population densities can reach 10 individuals / m^2 by middle of July on the whole meadow surface, such large population can potentially act as a source for nearby meadows. This is confirmed in Walter et al. (2004), where in that same region, the number of grasshopper species in ECA extensively managed meadows was found to be correlated with the proportion of species rich wet meadow nature reserves adjacent to the ECA meadows.

Management recommendations

Mechanized meadow harvesting processes have strong negative impacts on grasshoppers; mortality can be as high as 82% (Humbert et al. 2010). Therefore, when mowing, we recommend to leave uncut grass refuges and to leave these refuges untouched until the next harvest.

Only one harvesting model with 10% of the surface left uncut was investigated. Therefore we are not in the position to say if this is the optimal amount. However it is an amount accepted by the practitioners (Aargau 2009), and a 10% refuge permitted to gain a final grasshopper population approximately 60% higher than without refuge. Important is that the mowing process is performed in the direction of the refuge location to push the individuals in it, and that the location of the refuge should change from time to time to avoid vegetation succession (Grime 2001). Given the relatively low dispersal ability of the grasshopper we recommend a maximum of 30 m distance between two refuges. For invertebrates, the width of the refuge seems not to play an important role, but for birds, Grüebler et al. (2008) recommend to leave 20% uncut in form of strips of at least 10 m wide.

Where possible and adequate for the plant community, a late cut (after September 1st) is a safe measure regarding grasshopper populations. Similarly, for grasshoppers (Gardiner and

Hassall 2009) and for butterflies (Valtonen et al. 2006), also suggest a late cut and if earlier, then uncut refuges should be left.

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References

Aargau, 2009. Bewirtschaftungsverträge Naturnahe Landwirtschaft Richtlinien. Departement Finanzen und Ressourcen, Abtilung Landwirtschaft.

Badenhausser I, Amouroux P, Lerin J, Bretagnolle V, 2009. Acridid (Orthoptera: Acrididae) abundance in Western European Grasslands: sampling methodology and temporal fluctuations. J. Appl. Entomol. 133, 720-732.

Braschler B, Marini L, Thommen GH, Baur B, 2009. Effects of small-scale grassland fragmentation and frequent mowing on population density and species diversity of orthopterans: a long-term study. Ecol. Entomol. 34, 321-329.

Broyer J, 2003. Unmown refuge areas and their influence on the survival of grassland birds in the Saone valley (France). Biodiversity Conserv. 12, 1219-1237.

Crawley MJ, 2007. The R Book. John Wiley & Sons, Ltd, West Sussex, UK.

Dover JW, Rescia A, Fungarin˜o S, Fairburn J, Carey P, Lunt P, Dennis RLH, Dover CJ, 2010. Can hay harvesting detrimentally affect adult butterfly abundance? J. Insect Conserv. DOI 10.1007/s10841-010-9267-5.

Gardiner T, Hassall M, 2009. Does microclimate affect grasshopper populations after cutting of hay in improved grassland? J. Insect Conserv. 13, 97-102.

Gerstmeier R, Lang C, 1996. Beitrag zu Auswirkungen der Mahd auf Arthropoden. Z. Ökologie u. Naturschutz 5, 1-14.

Grime JP, 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Second edition. John Wiley, Chichester, UK.

Grüebler MU, Schuler H, Muller M, Spaar R, Horch P, Naef-Daenzer B, 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. Biol. Conserv. 141, 3040-3049.

Guido M, Gianelle D, 2001. Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. Acta Oecol. 22, 175-185.

Humbert J-Y, Ghazoul J, Walter T, 2009. Meadow harvesting techniques and their impacts on field fauna. Agric. Ecosyst. Environ. 130, 1-8.

Humbert J-Y, Ghazoul J, Richner N, Walter T, 2010. Hay harvesting causes high grasshopper mortality. Agric. Ecosyst. Environ.

Humbert JY, Ghazoul J, Sauter GJ, Walter T, 2010. Impact of different meadow mowing techniques on field invertebrates. J. Appl. Entomol. In press. doi: 10.1111/j.1439-0418.2009.01503.x.

Labisky RF, 1957. Relation of hay harvesting to duck nesting under a refuge-permittee system. J. Wildl. Manage. 21, 194-200.

Marini L, Fontana P, Scotton M, Klimek S, 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. J. Appl. Ecol. 45, 361-370.

Marini L, Fontana P, Battisti A, Gaston KJ, 2009. Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach. Insect Conserv. Diver. 2, 213-220.

Narisu, Lockwood JA, Schell SP, 1999. A novel mark-recapture technique and its application to monitoring the direction and distance of local mowements of rangeland grasshoppers (Orthoptera: Acrididae) in the context of pest management. J. Appl. Ecol. 36, 604-617.

R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Thorbek P, Bilde T, 2004. Reduced numbers of generalist arthropod predators after crop management. J. Appl. Ecol. 41, 526-538.

Valtonen A, Saarinen K, Jantunen J, 2006. Effect of different mowing regimes on butterflies and diurnal moths on road verges. Anim. biodivers. conserv. 29, 133-148.

Van Wingerden WKRE, Musters JCM, Kleukers RMJC, Bongers W, van Biezen JB, 1991. The influence of cattle grazing on grasshopper abundance (Orthoptera: Acrididae). Proc. Exper. and Appl. Entomol., N.E.V. Amsterdam 2, 28-34.

Walter T, Hunziker M, Peter B, Ward P, 2004. Threatened grasshopper species profit from ecological compensation areas. Grass. Sci. Eur. 9, 234-236.

Willott SJ, 1997. Thermoregulation in four species of British grasshoppers (Orthoptera : Acrididae). Funct. Ecol. 11, 705-713.

Woodcock BA, Potts SG, Tscheulin T, Pilgrim E, Ramsey AJ, Harrison-Cripps J, Brown VK, Tallowin JR, 2009. Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. J. Appl. Ecol. 46, 920-929.

General discussion

This study is the first to demonstrate and quantify the very high impact of mechanical harvesting processes on field invertebrates, a factor that has been largely overlooked by management policies that aim to enhance the biodiversity of meadow fauna. This is important for many European agri-environmental programs for which effectiveness has been questioned, especially regarding their ability to improve invertebrate diversity (e.g. Herzog and Walter 2005; Kleijn et al. 2006; Knop et al. 2006; Roth et al. 2008; Taylor and Morecroft 2009).

Harvesting process and its impact on field invertebrates

Mowing as has long been known to affect ground nesting birds (e.g. Labisky 1957; Tyler et al. 1998). More limited information suggested that this is also the case for arthropods although the few studies on this subject were limited in both their scope and experimental design (reviewed in Chapter 1).

In view of these, the direct impacts of five alternatives but commonly used mowing techniques were investigated. The results demonstrate that mowing with a hand motor bar mower causes less caterpillar mortality than with rotary mower, though the difference is less marked with models of invertebrate made from bee wax (Chapter 2). Mowing with a tractor-powered bar mowers kill less adult grasshoppers than rotary mowers (10% vs. 20% mortalities, estimates from Chapter 3 and Oppermann et al. 2000). However, for caterpillars and invertebrate wax-models, impacts of tractor bar mowers are similar to rotary mowers, presumably because the main impact is due to the tractor wheels running over the cut grass (Humbert et al. 2010). Adding a conditioner to rotary mowers significantly increase invertebrate mortality two to three times compared to the same mowing technique without conditioner (Chapter 2 and 3).

The post-mowing harvesting stages have also substantial impacts on less mobile species (as represented by Orthoptera, Chapter 3). Indeed, raking coupled with baling impacts grasshopper populations to a similar degree as mowing followed by tedding. Consequently, any benefits gained in terms of reduced grasshopper mortality by using a tractor-powered bar mower over a rotary mower are mostly lost by the cumulative impact of the subsequent harvesting stages. This provides clear indication that the entire harvesting process needs to be consider for a complete assessment of harvesting impacts on field invertebrates.

Base on these developments, our mowing technique ranking in terms of impacts over the whole harvesting process on field invertebrates is, from least to most damaging: hand motor bar mowers < tractor-powered bar mowers and rotary mowers << rotary mowers with conditioner. This outcome empirically confirms earlier conclusions (see literature review Chapter 1). Note that hand motor and tractor-powered bar mowers were not differentiated in the review.

Small invertebrates seem less vulnerable to damage than larger ones (Chapter 2; Oppermann et al. 2000). Suggesting that predatory species may be more vulnerable than prey species, which generally have smaller body size. This can have profound agroecological implications as it may alters the equilibrium of the trophic cascades and consequently the top-down natural control of agricultural arthropod pests (Landis et al. 2000; Schmitz 2008).

Butterfly caterpillars are very vulnerable to the mechanized harvesting process, as direct caterpillar mortality due to mowing with a conditioner can reach 70% (Chapter 2), and tedding mortality about 30% (Humbert unpublished data). Courtney and Duggan (1983) reported that all their marked larvae of Orange Tip butterfly (*Anthocharis cardamines*) were lost when their experimental verge was mown on the 19 of June 1981. This may partially explain why, since the late 1940s, Lepidoptera and especially grassland specialists have undergone dramatic declines in Europe (Robinson and Sutherland 2002; Van Swaay et al. 2006). Many studies on butterflies have focused only on the adults; however, the presence of adults does not necessarily indicate suitability of the area for reproduction (Valtonen et al. 2006). If harvesting destroys the whole larval population, adults butterflies may still be seen in the meadow are they come from the surrounding habitats. Therefore, larval habitat requirements and impacts of agriculture practices on these resources clearly need to be considered in butterfly conservation action plans (see also Eichel and Fartmann 2008; Schwarzwälder et al. 1997)

Uncut grass refuge as mitigation measure

Providing uncut grass refuges is a simple and presumably the most efficient measure to mitigate the direct negative impact of the harvesting process (Chapter 4). As for Orthoptera, leaving a refuge equal to 10% of the meadow surface increases final grasshopper population by approximately 60%. Further analyses showed that higher a species is sensible to the harvesting process; higher is the gain from the refuge (Humbert et al. 2010). In the extreme case where a non-mobile species population is totally destroy by mowing; leaving 10% of the meadow uncut will save 10% of the population.

Uncut grass areas are not only beneficial as a safe zone, but after harvesting such long swards provide extra structures, cooler areas and food sources for many organisms; including grasshoppers (Willott 1997), but also for beetles, spiders and butterflies (e.g. Dover et al. 2010; Gerstmeier and Lang 1996; Thorbek and Bilde 2004; Woodcock et al. 2009).

Only one harvesting regime with 10% of the surface left uncut was investigated. Therefore we are not in the position to say if this is the optimal amount, although such a regime is acceptable by practitioners (DBVU and DFR of Canton Argovia 2009). It is important that the mowing process is performed in the direction of the refuge location as this encourages the movement of invertebrates towards the refuge. It is also important that the location of the refuge is periodically changed so to avoid vegetation succession (Grime 2001). Given the relatively low dispersal ability of grasshoppers, a maximum of 30 m distance between refuges is recommended. For invertebrates, the width of the refuge seems not to be important, although for birds 20% uncut strips of at least 10 m wide has been recommended (Grüebler et al. 2008). Nevertheless, the exact amount and where to place the refuges in the landscape will ultimately be a matter of compromise between the practice and conservation objectives, with this trade-off being a matter for further investigation. The long-term effectiveness of such refuges to promote biodiversity also remains to be tested.

Frequency, date and time of harvest

Given the strong negative impact of harvesting on the faunal abundance, reducing the number of harvests per year, and considering the date of harvesting are probably the major issue. In Europe, the number of cuts required to maintain the plant community is usually one or, at most, two cuts per year if the meadow is located on a productive site (Jantunen et al. 2007; Parr and Way 1988). In wet meadows, a late cut (after September 1st) is a safe measure regarding grasshopper populations (Chapter 4; Gardiner and Hassall 2009). However, the optimal date at which meadows should be cut vary according to the taxon (see Chapter 1 section 2) and habitats (Cattin et al. 2003; Morris 2000), thus appropriate date should be plan according to conservation objectives.

The time of mowing may also influence species vulnerabilities. We hypothesize that ectothermic species might be more affected if mowing occurs early in the day when temperatures are still low and invertebrates less mobile (see also Dover et al. 2010).

Stakeholders' interests

This thesis is the result of a work that has been requested and funded by 15 Swiss cantonal authorities responsible for nature protection and agriculture, demonstrating the high level of interest across Switzerland specifically, which we also expect to be reflected across Europe generally. The research results presented in this thesis, and the recommendation derived from it, have already been used to guide policy in Canton Argovia where farmers are no longer allowed to use conditioners in ECA meadows, and where a CHF 400.- subsidy per hectare per year is granted for leaving 5-10% of the meadow uncut (DBVU and DFR of Canton Argovia 2009). Another canton complimented the report and the study as „The study closes for us an important research gap. The results are applicable and the recommendations comprehensible. Now we will see how the results can be integrated in our ecological compensation program" (Original: Die Studie schliesst eine für uns im Vollzug tätige Fachstellen eine wichtige Wissenslücke. Die Ergebnisse sind praxistauglich aufbereitet und die Empfehlungen nachvollziehbar. Mal sehen, wie wir die Ergebnisse in unserer Abgeltungspraxis umsetzen).

Final management recommendations

As the enhancement of biodiversity is a primary objective in many extensive meadow systems, for which farmers often receive remuneration, the thesis allows some simple recommendations to be made by which the impact of mowing on field fauna might be minimized. In addition to meadows, these recommendations may also be applied to the maintenance of field margins, an increasing ecological element of concern in agricultural land (Marshall 2002), and the management of grassland nature reserves. The recommendations are presented in order of priority:

- **Number of cut per year:** Given the strong negative impact of harvesting, reducing the number of harvests per year should be limited to the minimum required to maintain the plant community (one or at most two).
- **No conditioner:** No conditioner should be used. At first sight this should not be problematic, as the vegetation in extensively used meadows is usually quite mature and dry at the time of harvest, and thus conditioners are useless. However, some farmers have only one mowing machine which has an integrated conditioner.
- **Refuge:** Leaving 10% of the area uncut when mowing with a maximum of 30 m distance between two refuges is recommended. The successful implementation of such a policy would be relatively easy to monitor. It is important that the mowing process is performed in the direction of the refuge location to direct the invertebrates to it, and that the location of the refuge change from time to time.
- **Fauna-friendly mowing techniques:** Using hand motor bar mower over tractor-powered bar and rotary mowers is recommended, though the practical limitations of this are recognized. The additional work that this would entail for the farmer will necessitate high incentive payments. Tractor-powered bar mowers are not recommended over rotary mowers as for Orthoptera there is no evidence of benefits over the entire harvesting process and for caterpillars and invertebrates wax-models impacts where similar to rotary mowers.
- **Cutting height:** The cutting height has a large influence on the degree of impact on field vertebrates such as amphibians and reptiles, although no such influence was found for field invertebrates. Nevertheless, from the context of biodiversity conservation the cutting height should be set ideally at 10 cm.

- **Cutting time:** To increase the probability of escaping mowing machines, mowing should not occur before 9:00 or 10:00 am according to site temperatures.
- **Cutting date:** Where possible and adequate for the plant community, a late summer cut is a safe measure regarding many invertebrate communities.

Effective management actions need to be based on an understanding of the long-term effects of the whole harvesting process in the context of local and wider dynamics of community interactions, immigration and metapopulations. The interaction among cut meadows and adjacent uncut refuges should be investigated to identify not only how management and planning of such refuges can be optimized to reduce mortality, but also to understand the extent to which meadows serve as sinks that could potentially undermine the viability of populations within the refuges themselves. From these perspectives, we remain far from a comprehensive understanding, but it has not been the intention of this thesis to provide it. Instead, we have sought to quantify the impacts of different but common harvesting processes to serve as a basis for further enquiry relevant to wider issues in agroecosystem ecology and biodiversity conservation.

References

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. Biol. Conserv. 113, 179-188.

Courtney SP, Duggan AE, 1983. The Population Biology of the Orange Tip Butterfly Anthocharis-Cardamines in Britain. Ecol. Entomol. 8, 271-281.

DBVU and DFR of Canton Argovia, 2009. Bewirtschaftungsverträge Naturnahe Landwirtschaft Richtlinien, Abteilung Landschaft und Gewässer und Abteilung Landwirtschaft, Aarau.

Dover JW, Rescia A, Fungarin˜o S, Fairburn J, Carey P, Lunt P, Dennis RLH, Dover CJ, 2010. Can hay harvesting detrimentally affect adult butterfly abundance? J. Insect Conserv. DOI 10.1007/s10841-010-9267-5.

Eichel S, Fartmann T, 2008. Management of calcareous grasslands for Nickerl's fritillary (Melitaea aurelia) has to consider habitat requirements of the immature stages, isolation, and patch area. J. Insect Conserv. 12, 677-688.

Gardiner T, Hassall M, 2009. Does microclimate affect grasshopper populations after cutting of hay in improved grassland? J. Insect Conserv. 13, 97-102.

Gerstmeier R, Lang C, 1996. Beitrag zu Auswirkungen der Mahd auf Arthropoden. Z. Ökologie u. Naturschutz 5, 1-14.

Grime JP, 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. Second edition. John Wiley, Chichester, UK.

Grüebler MU, Schuler H, Muller M, Spaar R, Horch P, Naef-Daenzer B, 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. Biol. Conserv. 141, 3040-3049.

Herzog F, Walter T, 2005. Evaluation des mesures écologiques, domaines biodiversité. Zurich. Les cahiers de la FAL 56. Agroscope Reckenholz-Tänikon Research Station ART, Zurich.

Humbert J-Y, Richner N, Sauter GJ, Ghazoul J, Walter T, 2010. Graslanderte-Prozesse und ihre Wirkung auf die Fauna. Zurich. ART Report. Agroscope Reckenholz-Tänikon Research Station ART, Zurich (*in press*).

Jantunen J, Saarinen K, Valtonen A, Saarnio S, 2007. Flowering and seed production success along roads with different mowing regimes. Appl. Veg. Sci. 10, 285-292.

Kleijn D, Baquero RA, Clough Y, Diaz M, De Esteban J, Fernandez F, Gabriel D, Herzog F, Holzschuh A, Johl R, Knop E, Kruess A, Marshall EJP, Steffan-Dewenter I, Tscharntke T, Verhulst J, West TM, Yela JL, 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243-254.

Knop E, Kleijn D, Herzog F, Schmid B, 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. J. Appl. Ecol. 43, 120-127.

Labisky RF, 1957. Relation of hay harvesting to duck nesting under a refuge-permittee system. J. Wildl. Manage. 21, 194-200.

Landis DA, Wratten SD, Gurr GM, 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomo. 45, 175-201.

Marshall EJP, 2002. Introducing field margin ecology in Europe. Agric. Ecosyst. Environ. 89, 1-4.

Morris MG, 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grassland. Biol. Conserv. 95, 129-142.

Oppermann R, Handwerk J, Holsten M, Krismann A, 2000. Naturverträgliche Mähtechnik für das Feuchtgrünland, Voruntersuchung für das E & E - Vorhaben. Bonn. ILN Singen, Bonn.

Parr TW, Way JM, 1988. Management of Roadside Vegetation - the Long-Term Effects of Cutting. J. Appl. Ecol. 25, 1073-1087.

Robinson RA, Sutherland WJ, 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157-176.

Roth T, Amrhein V, Peter B, Weber D, 2008. A Swiss agri-environment scheme effectively enhances species richness for some taxa over time. Agric. Ecosyst. Environ. 125, 167-172.

Schmitz OJ, 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319, 952-954.

Schwarzwälder B, Lörtscher M, Erhardt A, Zettel J, 1997. Habitat utilization by the heath fritillary butterfly, *Mellicta athalia* ssp. *celadussa* (Rott.) (Lepidoptera: Nymphalidae) in montane grasslands of different management. Biol. Conserv. 82, 157-165.

Taylor ME, Morecroft MD, 2009. Effects of agri-environment schemes in a long-term ecological time series. Agric. Ecosyst. Environ. 130, 9-15.

Thorbek P, Bilde T, 2004. Reduced numbers of generalist arthropod predators after crop management. J. Appl. Ecol. 41, 526-538.

Tyler GA, Green RE, Casey C, 1998. Survival and behaviour of Corncrake *Crex crex* chicks during the mowing of agricultural grassland. Bird Stud. 45, 35-50.

Valtonen A, Saarinen K, Jantunen J, 2006. Effect of different mowing regimes on butterflies and diurnal moths on road verges. Anim. biodivers. conserv. 29, 133-148.

Van Swaay C, Warren M, Lois G, 2006. Biotope use and trends of European butterflies. J. Insect Conserv. 10, 189-209.

Willott SJ, 1997. Thermoregulation in four species of British grasshoppers (Orthoptera : Acrididae). Funct. Ecol. 11, 705-713.

Woodcock BA, Potts SG, Tscheulin T, Pilgrim E, Ramsey AJ, Harrison-Cripps J, Brown VK, Tallowin JR, 2009. Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. J. Appl. Ecol. 46, 920-929.

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Publications

Peer-reviewed

Humbert J-Y, Ghazoul J, Richner N, and Walter T, 2010. Meadow harvesting techniques and their impacts on field fauna. Agriculture, Ecosystems and Environment doi:10.1016/j.agee.2010.09.012.

Humbert J-Y, Ghazoul J, Sauter GJ, and Walter T, 2010. Impact of different meadow mowing techniques on field invertebrates. Journal of Applied Entomology 134: 592-599

Humbert J-Y, Mills LS, Horne JS, and Dennis B, 2009. A better way to estimate population trend. Oikos 118: 1940-1946.

Humbert J-Y, Ghazoul J, Sauter GJ, and Walter T, 2009. Mowing impacts on invertebrate models. Grassland Science in Europe 15: 61-63.

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

* Highly cover by the media.

Schwander T, Humbert J-Y, Brent CS, Helms Cahan S, Chapuis L, Renai E, and Keller L, 2008. Maternal effect on female caste determination in a social insect. Current Biology 18: 265-269.

Other publications

Humbert J-Y, Richner N, Sauter GJ, Ghazoul J, and Walter T, 2010. Graslandernte-Prozesse und ihre Wirkung auf die Fauna. Zurich. ART Report 724. Agroscope Reckenholz-Tänikon Research Station ART, Zurich.

Humbert J-Y, Richner N, Sauter GJ, Ghazoul J, and Walter T, 2010. Effets sur la faune des processus de récolte des prairies. ART Report 724. Agroscope Reckenholz-Tänikon Research Station ART, Zurich.

Humbert J-Y, and Walter T, 2009. Wirkung von Grasernte-Techniken auf die Fauna. KBNL Inside. 2/09.

Humbert J-Y, Beerli C, and Jacot K, 2006. Effets des ourlets semés sur les campagnols et les taupes. Revue suisse Agric. 38: 285-290.