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Conservation of leafhoppers in floodplain grasslands – trade-off between diversity and naturalness in a northern German national park

Judith Rothenbücher* and Matthias Schaefer
*Institute of Zoology, Ecology Group, Berliner Str. 28, 37073 Göttingen, Germany; *Author for correspondence; (e-mail: jrothen@gwdg.de; phone: +0049-551-395529; fax: +0049-551-395448)*

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Abstract

The impacts of mowing and of flooding on the leafhopper communities of a river flood plain were investigated. Samples were taken by a motor-driven suction apparatus. In 2001 leafhoppers were collected in a variety of sites differing in land use (fallows, mown sites) and in flood intensity (high, medium, low, none). In 2002 samples were only taken in fallows subject to different flooding regimes.

In fallows, more species (43) were collected than in mown sites (33). Flooding had an effect only in fallows. Here, the most species-rich (29) communities occurred in sites not subject to flooding, whereas fewest species (21) were found in sites subject to regularly occurring long lasting winter floods. Mown sites were dominated by pioneer species. In fallows, the communities differed in respect to flood intensity. In fallows that were subject to summer and winter floods pioneer species prevailed. In contrast, in fallows that were flooded a long time during winter but not in summer, communities of very specialised species were found which were not very species-rich.

For the conservation of the typical leafhopper communities of floodplain grassland, management by mowing should be at least reduced if not totally stopped and natural flooding dynamics should be restored.

Introduction

The conservation of biotic communities and species under preferably natural conditions to maintain ecological stability and biological diversity is one of the main aims of national parks (IUCN 1994; Bibelriether 1997). Insects are rarely at the centre of conservation schemes, although they comprise – on a global scale – more than 50% of all described living species (Wilson 1992) and play an important role in most terrestrial ecosystems (Plachter 1994; New 1999). Furthermore, many conservation strategies are based on, and their implementation addresses, warm-blooded vertebrates, harvestable or other economically selected taxa, and vascular plants (New 1999). It is widely assumed that preservation of invertebrates can be indirectly achieved through habitat conservation (Plachter 1994; New 1999).

In the present study planthoppers and leafhoppers (Hemiptera: Auchenorrhyncha; hereafter referred to simply as 'leafhoppers') were chosen as a model group to investigate the ways in which conservation strategies carried out in a northern German national park contribute to the preservation of insects. Leafhoppers occur in high numbers of species and individuals in wet grassland (Nickel and Achtziger 1999). Additionally, they can easily be sampled and information on the ecology of most species is available in the literature which can be included for further analyses.

Habitat conservation management in grassland often includes regular cutting in order to prevent succession and brushwood encroachment (Cattin et al. 2003), to maintain or achieve a high plant diversity (e.g. Decleer 1990; Vercin et al. 2002; Cattin et al. 2003) or to preserve suitable habitats for selected target species (e.g. Preiksa 1999; Helmecke et al. 2003). Numerous studies investigating the impact of mowing on arthropods have been carried out in different types of grassland habitats (see Gerstmeier and Lang 1996). However, conclusions about the effects of mowing on species richness and diversity are incongruent. Gerstmeier and Lang (1996) differentiated between meadows of different moisture conditions and proposed habitat-specific management strategies. Thus, the impact of mowing seems to depend on habitat conditions such as soil moisture or flooding impact. Within the large amount of studies on the impact of mowing on leafhoppers, those carried out in temporarily flooded habitats are scarce (e.g. Heller and Irmler 1997; Nickel and Hildebrandt 2003).

The disturbance regime due to flooding, which creates a diversity of successional stages across the riverine landscape, is a key factor for plants and animals living in natural river floodplains. Thus, the restoration of natural flooding conditions is another important focus of floodplain conservation. Ecological restoration of large rivers should be (more) process-oriented instead of species-focused (Schiemer et al. 1999). Nickel and Hildebrandt (2003) stated that the responses of leafhoppers to mowing and flooding may be essentially similar in that a few generalist species are selected and effects are difficult to disentangle in field experiments. Therefore, they called for further investigations of the effect of flooding on leafhoppers.

It was the aim of the present study to analyse the impact of mowing and natural flooding on the leafhopper community. On this basis, conclusions will be drawn about the limits and possibilities of conserving insect communities in restored floodplain grassland.

Methods

Study area

The study was carried out in the "Lower Oder Valley National Park" (Figure 1), which is the only floodplain national park in Germany. At present inundation of the floodplain is regulated. In the so called "dry polder", dykes prevent inundation throughout the whole year. In the "wet polders", inundation is regulated by floodgates, which are integrated into dykes along the river. The gates are opened between November

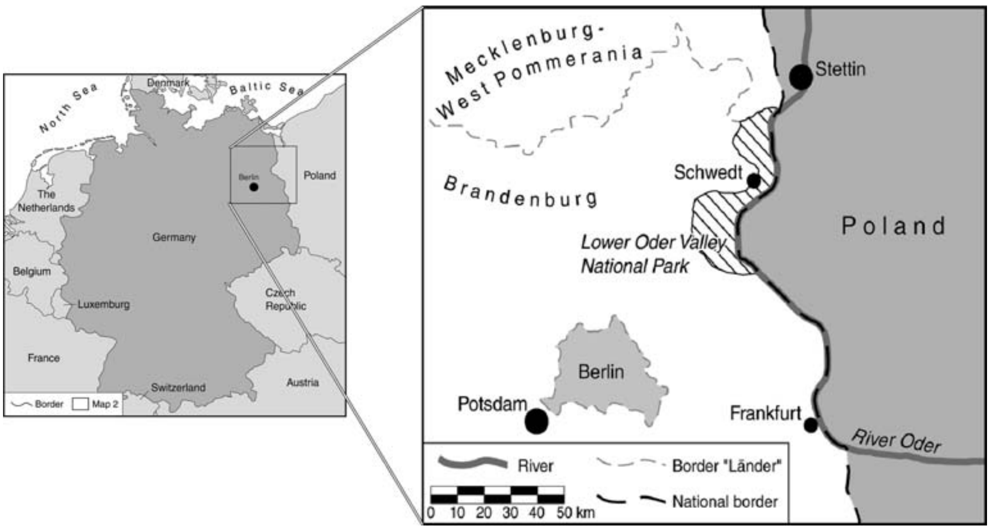

Figure 1. Location of the Lower Oder Valley National Park (Map design T. Rothenbücher).

and April each year, so the typical winter flood can inundate the floodplain. After closing the floodgates to prevent inundation during spring and summer, the water is pumped out of the polders to make land use possible. Currently, changes in land use as well as the management of the flooding regime are being attempted. Conservation management for selected target species such as the corncrake (*Crex crex*) is planned for 50% of the area, which includes regular cutting of the floodplain meadows (IUS 1998). The remaining area will be left for succession and a more natural flooding regime will be restored (IUS 1998). At present, about 10% of the national park area is declared as core zone. This area has been abandoned since 1995 and left for succession (Jehle and Pankoke 1999), however, flooding is still regulated. Currently, the study area consists of a mixture of sites differing in land use (i.e. sites mown twice a year, in late spring and late summer, and fallows) as well as in flood intensity.

Study sites and sampling procedure

Samples were taken by a motor driven suction apparatus four times between May and September 2001 and 2002, respectively. The samples were taken in study sites differing in land use and in flooding period and frequency (Table 1). Unfortunately, the study design became unbalanced due to changes in land use during the year 2001. All plots that are classified as "mown sites" were mown regularly twice a year during the years previous to the study and during sampling years. Precise data on winter flooding were not available because of non-accessibility of the area during the flooding period. The approximate number of days of inundation of the study sites during the winter flood preceding the 2001 and 2002 growing seasons were estimated. The altitude of each study site was compared with the water level of the river Oder at the nearest gauging station on a daily basis during the time the floodgates were open. Periods of summer flooding of the sites situated on the river bank were recorded in the field. For the analyses, flood intensity was classified as follows (Figure 2):

- High flood intensity: These plots are situated on the narrow river bank between the dyke and the river and are inundated not only by the winter floods (winter 2000/01: approximately 50 days; winter 2001/02: approximately 100 days), but also occasionally and unpredictably in summer after heavy rainfall (summer 2001: approximately 20 days; summer 2002: approximately 5 days). Therefore, they are the most heavily disturbed sites and their degree of naturalness is lowest.
- Medium flood intensity: These sites are situated in ditches in the wet polder and are subject to regular flooding for a long time during winter (winter 2000/01 & 2001/02: approximately 130 days). Flooding conditions in these sites are close to natural flooding conditions.

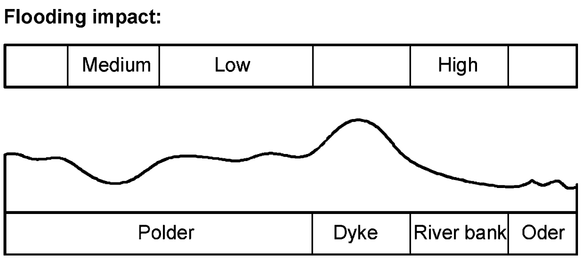

Figure 2. Schematic cross section of the floodplain showing the habitats studied (river bank, depressions in the polders, higher elevations in the polders) and the corresponding high, medium and low flooding impact.

Table 1. Study design. The number of study sites investigated is listed for each pair of influencing factors.

Year	Location	River bank	Wet polder		Dry polder
	Time of flood Flooding impact	Summer & winter High	Winter (long) Medium	Winter (short) Low	No flood None
2001	Mown grassland	1	5	2	2
	Fallows	2	2	5	1
2002	Fallows	3	3	3	3

• Low flood intensity: These sites are situated in more elevated locations in the wet polder and are subject to more unpredictable and short winter floods (winter 2000/01: approximately 80 days; winter 2001/02: approximately 100 days).
• No flooding: These plots are situated in the dry polder and are not flooded throughout the whole year.

Reed grass (*Phalaris arundinacea*) is the dominating plant species in the study area. For better comparability of the data, we tried to select study sites that were dominated by reed grass. As plant species are also affected by flooding, plant species composition differed between the study sites due to flooding impact (for details see Rothenbücher 2005). However, reed grass occurred in all but a few of our study sites.

On each study site (20×20 m) the suction apparatus (Stihl SH 85, diameter of the suction tube: 14 cm) was placed onto the ground ten times at random for approximately ten seconds to gather a mixed sample of each study site. Adult leafhoppers were determined to species level. Furthermore, a number of environmental variables were recorded and included in the analyses: number of plant species, vegetation structure, distance to the nearest stretch of water and distance to the nearest scrub or tree (for details see Rothenbücher 2005).

Habitat specialisation of species

Achtziger and Nickel (1997) divided Auchenorrhyncha occurring in Central European grasslands into four ecological groups based on the species' habitat preference, diet width, wing length and voltinism (Table 2). Later they introduced a specialisation factor leading from 0 for pioneer species to 3 for stenotopic species (Achtziger et al. 1999).

The average degree of specialisation of Auchenorrhyncha communities was calculated based on individuals, using the specialisation factor of each species:

$$DS_I = \frac{\sum_{i=1}^{S} SF_i \times n_i}{N}$$

where DS_I is the degree of specialisation based on individuals, S the total number of species, SF the specialisation factor of species i (0–3) and n_i is the number of individuals of species i.

Analysis

To test for significant differences among the mean number of species, mean diversity values (Shannon-Wiener-Index), mean degree of specialisation and mean number of pioneer, eurytopic, oligotopic and stenotopic individuals in mown sites and in fallows, we used analysis of variance (GLM, Scheffé test). If even after transformation the assumptions of the parametric test were not fulfilled, the effect of mowing was tested by Mann–Whitney U-Test. Statistical comparisons among the four flooding treatments (high, medium, low, none) were performed for mean number of species, mean diversity values, mean degree of specialisation and mean number of pioneer, eurytopic, oligotopic and stenotopic individuals using analysis of variance (ANOVA, Tukey test). Normality of data was tested using the Shapiro–Wilk Test (Shapiro and Wilk 1965); homogeneity of variances using the F_{max} Test (Köhler et al. 1996). If necessary, data were transformed to conform to assumptions of normality and homogeneity of variances.

The impact of the measured environmental variables on the species communities was assessed by Canonical Correspondence Analysis (CCA). To

Table 2. Definition of life strategies (Achtziger and Nickel 1997, Achtziger et al. 1999).

	Pioneer species	Eurytopic species	Oligotopic species	Stenotopic species
Habitat preference	Mainly in early successional stages	Eurytopic in various types of grasslands	Associated with specific abiotic conditions	Associated with specific abiotic conditions
Diet width	Polyphagous	Oligophagous on Poaceae	Oligophagous	Monophagous
Wing length	Macropterous	Macro- and brachypterous	Macro- and brachypterous	Brachypterous
Voltinism	At least bivoltine	Mostly bivoltine	Uni- or bivoltine	Uni- or bivoltine
Specialisation factor	0	1	2	3

assess whether the measured environmental variables were sufficient to predict the main variation in species composition, eigenvalues gained by CCA were compared to those calculated by Detrended Correspondence Analysis (DCA).

Results

Altogether, 3645 individuals belonging to 63 species of leafhopper were collected during the growing seasons of 2001 and 2002. *Javesella pellucida*, *Arthaldeus pascuellus*, *Erzaleus metrius*, *Anoscopus serratulae*, *A. flavostriatus* and *Errastunus ocellaris* were most abundant in the study area. *Javesella pellucida* clearly preferred mown sites, whereas *Erzaleus metrius* occurred predominantly in fallows subject to medium flood intensity. Twelve species are listed in the Red Data Book of Germany (Remane et al. 1998).

Impact of mowing

Altogether more species were caught in fallows than in mown sites (Table 3). Mean number of species and mean diversity values did not differ significantly.

The degree of specialisation was higher in fallows than in mown plots (Figure 3a). Stenotopic species were prevalent in fallows (GLM, $F = 7.36, p < 0.05$, transformation: $x^{-0.5}$), while in mown grassland most individuals were pioneer species (Figure 3b).

Table 3. Numbers of species and diversity on fallows and mown study sites. *U*-Test was carried out to test differences in mean numbers of species and mean diversity values. n.s. = not significant.

Treatment	Species		Diversity
	Total	Mean +/– SD	Mean +/– SD
Fallows	43	11.7 +/– 3.77	1.63 +/– 0.53
Mown sites	33	11.7 +/– 3.19	1.82 +/– 0.29
U-Test		n.s.	n.s.

Impact of flooding

Most species were caught in sites not subject to flooding; the sites that were least rich in species were those subject to medium flood intensity (Table 4). The highest average diversity values were found in fallows in the dry polder, the lowest diversity in sites subject to medium flood intensity.

The most specialised Auchenorrhyncha community was found in sites subject to medium flood intensity (Figure 4a). Pioneer species dominated in sites subject to high flooding influence (Figure 4b). Their number differed significantly from those collected in sites subject to medium flood intensity. Furthermore, most eurytopic leafhoppers were found in fallows located in the dry polder and fewest in sites subject to medium flood intensity.

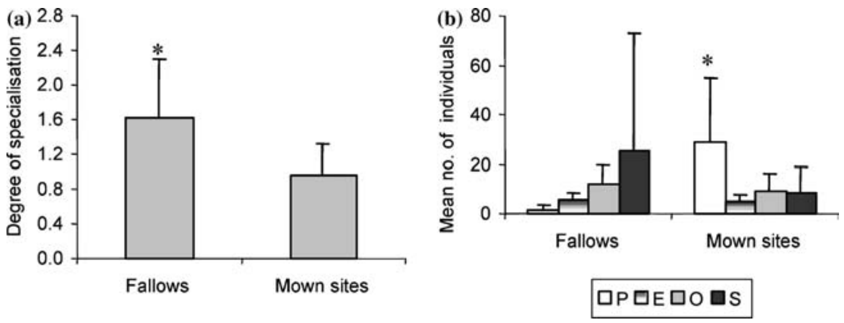

Figure 3. (a) Degree of specialisation of the leafhopper species based on numbers of individuals in fallows and mown sites (see methods). A Mann–Whitney *U*-Test was carried out: $z = 2.53$, $p < 0.01$. Significant differences are indicated by an asterisk. (b) Life strategy of leafhopper species. Pioneer (P), eurytopic (E), oligotopic (O) and stenotopic (S) individuals per 0.45 m^2 in fallows and mown sites. For each of the four categories, a Mann–Whitney *U*-Test was carried out separately. Significant differences are indicated by an asterisk. Pioneer individuals (*U*-test): $z = 3.77$, $p < 0.001$.

Table 4. Numbers of species and diversity in fallows differing in flooding impact. ANOVA and Tukey Test were carried out to test differences in mean numbers of species and mean diversity values. Different letters indicate significant differences between the treatments.

Flooding impact	Species			Diversity	
	Total	Mean +/− SD	Tukey grouping	Mean +/− SD	Tukey grouping
High	21	12.0 +/− 2.64	ab	1.60 +/− 0.22	b
Medium	19	9.7 +/− 2.08	b	1.56 +/− 0.43	b
Low	27	14.3 +/− 2.51	ab	2.14 +/− 0.08	ab
None	28	16.7 +/− 2.08	a	2.32 +/− 0.21	a
F		4.95		5.98	
p		0.03		0.02	

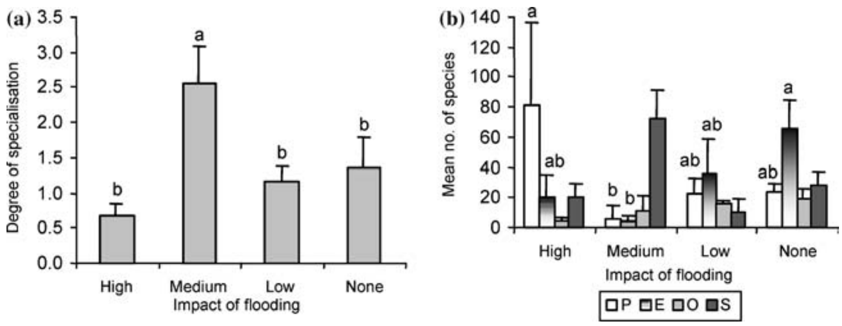

Figure 4. (a) Degree of specialisation based on numbers of individuals for sites differing in flooding influence (see methods). An ANOVA and Tukey Test were carried out: $F = 14.17$, $p < 0.001$. Bars marked with different letters are significantly different. (b) Life strategy of leafhopper species. Pioneer (P), eurytopic (E), oligotopic (O) and stenotopic(s) individuals per 0.6 m^2 on sites differing in flooding influence. For each of the four categories, an ANOVA and Tukey Test was carried out separately. Bars marked with different letters are significantly different. Pioneer individuals (ANOVA, transformation: $x^{-0.5}$): $F = 6.06$, $p < 0.05$; eurytopic individuals (ANOVA, transformation: $x^{-0.5}$): $F = 8.29$, $p < 0.01$; stenotopic individuals (ANOVA): $F = 3.88$, $p = 0.06$.

Impact of environmental variables

The Canonical Correspondence Analysis (CCA) based on the data collected in 2001 revealed three different groups of study sites: (i) fallows subject to medium flood intensity, (ii) fallows differing in flooding influence and (iii) all mown study sites (Figure 5a). The first axis largely correlates with the environmental variable ‘‘height of vegetation’’ and to a lesser extend with ‘‘flooding’’, whereas the second axis correlates with the factor ‘‘mowing’’. Comparing the eigenvalues of the axes gained by CCA to those of a Detrended Correspondence Analysis (DCA) reveals that the chosen environmental variables predict the main variation in species sufficiently well (Table 5).

In the CCA diagram based on data collected in fallows in 2002, four different groups of study sites could be distinguished: (i) one study site that was subject to medium flood intensity , (ii) two study sites subject to medium flood intensity, (iii) two fallows not subject to flooding and (iv) all other study sites (Figure 5b). Interestingly, the species assemblage of one site, which was located in the dry polder, was more similar to those of sites subject to low flood intensity than to the communities of the other plots not subject to flooding. The first axis of the diagram strongly correlates with the variable ‘‘height of vegetation’’, the second axis with the factor ‘‘flooding’’. Comparing the eigenvalues of the axes gained by CCA to those of a DCA reveals that the chosen environmental variables predict the main variation in species sufficiently well (Table 5).

Discussion

Mowing and flooding are both catastrophic events for arthropods. Mowing abruptly and drastically

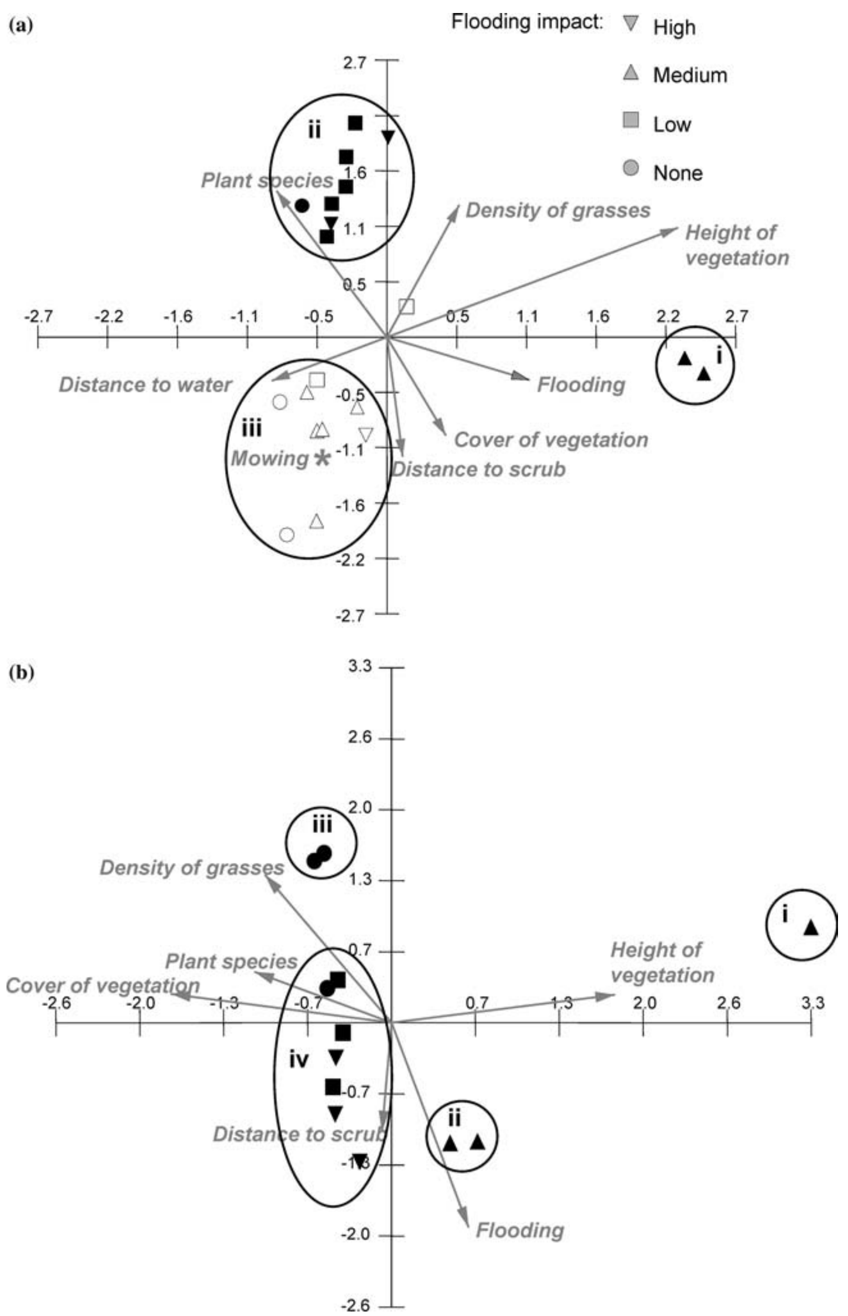

Figure 5. (a) CCA ordination diagram based on leafhopper species abundance and selected environmental variables sampled in fallows and mown sites subject to different flooding regimes (2001). All environmental variables except "mowing" are plotted as arrows; the nominal variable "mowing" is represented by its centroid. Open markers represent mown plots, solid markers fallows. (b) CCA ordination diagram based on leafhopper species abundance and selected environmental variables in fallows subject to different flooding regimes (2002). All environmental variables are plotted as arrows.

reduces the size and complexity of the vegetation layer leading to dramatic changes of microclimatic conditions in the meadow. During submersion terrestrial arthropods face low oxygen concentrations in the water, passive drift with high water and danger of cell destruction due to swelling

Table 5. Comparison of the eigenvalues and of the variance in the species data explained by the first two axes of the DCA and the CCA.

Year	Analysis	Axis 1	Axis 2	Variance explained
2001	DCA	0.747	0.390	43.54%
	CCA	0.661	0.413	39.06%
2002	DCA	0.925	0.295	37.23%
	CCA	0.847	0.514	41.56%

(Hildebrandt 1997). Furthermore, in the river floodplains of Central Europe, flooding duration and frequency vary from year to year. Both, mowing and flooding have short-term and long-term effects on the species communities. Short-term effects are directly related to the events of "cutting" or "flooding"; long-term effects are based on changes in the habitat which are the results of regular mowing and/or flooding events. The following discussion focuses on long-term effects of both factors.

Impact of mowing and flooding on species numbers and diversity

Altogether more *species* were collected in fallows than in mown sites. However, no effect on the mean number of species was found. A lot of studies analysing the effect of mowing on leafhoppers have been carried out in a variety of grassland habitats and the results concerning the impact of mowing on species richness are very heterogeneous. On the one hand, more species were found in fallows than in mown meadows in temporarily flooded grassland (Nickel and Hildebrandt 2003) as well as in moist grassland (Klieber et al. 1995). On the other hand, Achtziger et al. (1999) found fewer species in fallows than in extensively used moist grassland. All these studies were carried out in areas differing in flooding impact, soil moisture and mowing intensity. Morris and Lakhani (1979) and Gerstmeier and Lang (1996) came to the conclusion that the response of Auchenorrhyncha is dependent on mowing frequency and, above all, on the cutting date. Mowing in July affected the leafhopper community more severely than in May (Morris and Lakhani 1979). Gerstmeier and Lang (1996) concluded, that in moist meadows cutting once a year or once in two years will lead to a maximum number of species. Additionally, species richness of Auchenorrhyncha is not only dependent on mowing intensity but also on soil moisture; Klieber et al. (1995) found an increase in species richness with decreasing mowing intensity and increasing soil moisture. These findings also suggest that flooding might affect species richness. Unfortunately, none of the studies took "flooding" into account as a separate factor, even though some were carried out in temporarily inundated grassland.

In the present study, a comparison of the species assemblages based on the results of the Canonical Correspondence Analysis showed that mowing had a stronger impact on the leafhopper community than flooding. The impact of flooding was mostly overridden by the impact of mowing and could only be identified in fallows. In the latter, the most species-rich community was found in sites not subject to any flooding impact, whereas the fewest species were collected in sites subject to medium flood intensity. Thus, in the study area, species numbers varied a lot in fallows due to flooding impact leading to a mean number of species which is comparable to that in mown meadows. However, it appears that in temporarily flooded grassland which is partially mown twice a year, more species occur in fallows than in mown sites.

As was the case for species numbers, no differences were found in mean α-diversity values between fallows and mown sites. However, in fallows, differences correlated with flooding. The patterns are basically consistent with those found for species numbers. Gerstmeier and Lang (1996) concluded that in moist meadows cutting once a year or once in two years will not only positively affect species richness but will also often lead to high values of diversity and evenness.

Ecological characteristics of the species

In the Lower Oder Valley more pioneer species, being mostly macropterous and polyphagous, were found in mown sites rather than in fallows, whereas in the latter a more specialised community occurred. Similar patterns were found by Andrzejewska (1979), Achtziger et al. (1999) and Nickel and Hildebrandt (2003). A prevalence of macropterous, bivoltine and polyphagous

Auchenorrhyncha was reported for ephemeral habitats (e.g. Novotný 1994, 1995).

The differences between the ecological characteristics of the species occurring in mown sites and those of fallows can be seen as a direct consequence of the disturbance caused by cutting. Additionally, these differences are based on changes in plant species composition, habitat complexity and microclimate in the aftermath of the cut. Nickel (2003) states that habitat disturbance favours macropterous, bi- and polyvoltine as well as polyphagous species. Novotný (1995) terms this combination of ecological characteristics "colonisation syndrome". A dominance of pioneer species, which were mostly bivoltine and polyphagous, was also found in fallows situated on the river bank where additional flooding events can occur in summer. These findings suggest that disturbance by flooding during summer has a similar effect on leafhopper communities as disturbance by mowing. However, the most specialised community was found in fallows subject to medium flood intensity. These sites were dominated by stenotopic (i.e. hygrophilous and monophagous) leafhoppers such as *Erzaleus metrius* and *Megamelus notula*.

Conclusions for the conservation of plant- and leafhoppers in floodplain grassland

As outlined in the introduction, the restoration of wet grassland often includes management by mowing and changes of the flooding regime. The present study revealed that in temporarily flooded grassland mown twice a year, fewer species occur than in fallows. Furthermore, mowing favoured pioneer species which are well adapted to disturbed habitats. Flooding in summer affected the leafhopper communities in a similar way. However, regular flooding for a long time during winter led to a community that was not very rich in species but consisted of many specialists.

These findings suggest that mowing should be stopped and a natural flooding regime should be restored if the aim is to preserve a specialised leafhopper community which is adapted to regular flooding events, i.e. a typical floodplain leafhopper community. The question of how to maintain open grassland habitats remains, i.e. how to prevent the growth of shrubs and trees. Achtziger *et al.* (1999) suggest a more extensive mowing regime. In moist grassland, mowing parts of the grassland in autumn resulted in an even more species-rich community than in fallows with a high proportion of specialists (Achtziger et al. 1999). But can we apply these findings to temporarily flooded habitats? Many of the specialist leafhoppers overwinter and tolerate winter submersion in the egg stage (Rothenbücher and Schaefer submitted). But currently we have no knowledge about mortality rates during the period of submersion. It is known for some ground beetles that, although a species is capable of surviving submersion, immigrating individuals are necessary to maintain a viable population (Fuellhaas 1997). This might also be the case for a number of leafhoppers. Mowing in autumn might further increase mortality rates in the egg stage and hence reduce the populations' chances of survival during winter submersion.

Grazing is another common form of management to maintain open grassland. The impact of grazing on leafhoppers was beyond the scope of the present study but has been investigated in a number of previous studies. As was the case in mown sites, Morris (1973) identified a number of species responding differentially to the impact of grazing. Nickel and Hildebrandt (2003) found that moderate grazing had less severe effects on species numbers and specialists than mowing twice a year.

Mowing and grazing are both common management measures in a variety of grassland habitats. However, in temporarily flooded grassland one might ask the question whether mowing or grazing is really necessary to keep shrubs and trees out. In the Polish parts of the Lower Oder Valley there are areas that belonged to the polder system until World War II. During the war, dykes were damaged and not rebuilt and the area has since been left to succession. The climax vegetation in the area mainly consists of alder and, to a lesser extent, willow forests, but at present large areas are still devoid of trees and dominated by grasses, sedges, reed and herbaceous species. This openness of the vegetation might be caused by the frequent flooding, especially the catastrophic summer flood in 1997 that had a severe impact on the plant communities (Jasnowska et al. 1999). These findings suggest that restoring natural flooding dynamics in floodplains might contribute equally well to the preservation of open grassland habitats.

The results of the present study help to understand the way in which natural flooding will affect leafhopper communities. Natural flooding dynamics of the lower river Oder, as an example of a typical lowland river of Central Europe, are characterised by regular and long lasting winter floods. Summer floods are more rare events and high water levels that are comparable to winter floods occur on average only once in ten years (Vössing 1998). At first sight, the study sites that were subject to high flood intensity (i.e. winter and summer floods) seem to be subject to a near-natural flooding regime. As outlined above, this flooding influence favours a leafhopper community which is similar to those found in mown meadows. But in contrast to the relatively wide floodplain of most lowland rivers, these study sites were situated on a very narrow stretch of river bank. Here, the water level rises and falls rapidly and the grassland as well as the leafhoppers are subject to widely varying water levels and strong currents. The inundated area of the floodplain was originally much wider. Consequently, one can presume that summer floods had a less severe impact on the leafhopper communities of these sites than they have on the communities of the current narrow river bank sites. The water flooded a larger area; thus inundation was slower and less severe or changes in the water level were only just detectable by a rise in the ground water level. Restoring natural flooding dynamics seems to favour areas which are comparable to some of our study sites subject to medium flood intensity. Here, long lasting floods occur regularly in winter, and during summer ground water levels remain relatively high. In these study sites we found a very specialised leafhopper community which, however, was only moderately diverse. Conversely, significantly more species were collected only in sites not subject to flooding at all. Thus, it seems that there is a trade-off between diversity and naturalness when the aim is to conserve leafhoppers in floodplain grassland. However, differences in the relief and in the distance from the river will, under natural flooding dynamics, lead to a number of habitat patches differing in flooding influence. Some might be comparable to those of our study sites subject to high, medium and low flood intensity. In our study, species similarity between these sites was 20–60%. Furthermore, in sites subject to medium flood intensity, a variety of patches can be found that are dominated by different plant species such as sedges (*Carex spp.*), sweet-grass (*Glyceria spp.*), reed grass (*Phalaris arundinacea*) and common reed (*Phragmites australis*). These differences might be due to different moisture conditions. For the present study, we selected only sites dominated by sedges and reed grass. In habitat patches dominated by other plant species one can expect to find a number of additional leafhopper species. Consequently, in a floodplain which is characterised by a lot of different habitat patches due to natural flooding dynamics one does not only find very specialised communities but also high β-diversity.

The results of the present study suggest that the typical leafhopper communities of floodplain grassland consist of a number of species specialised to floodplain vegetation which are mostly found in areas with regular and long lasting winter floods and of species that can cope with varying water levels throughout the year. For the conservation of these typical leafhopper communities, management by mowing should be at least reduced if not totally stopped and natural flooding dynamics should be restored. In many countries in Central Europe, recent plans to restore river valley habitats often include a change in flooding regime as well as habitat management by mowing or grazing. Future studies should focus on all three factors to find out whether the results of the present study can be generalised.

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Appendix

Appendix 1. Abundance of leafhoppers (individuals per m^2) collected in 2001 at sites differing in flooding influence and land use. Study sites: the first letter of the abbreviation indicates the impact of flooding: H = high, M = medium, L = low, N = none; the second letter refers to land use: F = fallow, M = mown; sites of the same variant are sequentially numbered. Ecological information on individual species (Nickel and Remane 2002) - WD = wing development: di = dimorphic, ma = monomorphic macropterous; DW = diet width: m1 = 1st degree monophagous, m2 = 2nd degree monophagous, o1 = 1st degree oligophagous, o2 = 2nd degree oligophagous, po = polyphagous; MP = moisture preference: hy = hygrophilous, eu = euryhygric, xe = xerophilous; LS = life strategy: P = pioneer species, E = eurytopic species, O = oligotopic species, S = stenotopic species.

Species	Study sites																			Ecology			
	HF1	HF2	HM1	MF1	MF2	MM1	MM2	MM3	MM4	MM5	LF1	LF2	LF3	LF4	LM1	LM2	NF1	NM1	NM2	WD	DW	MP	LS
Fulgoromorpha																							
Delphacidae																							
Anakelisia fasciata (Kirschbaum, 1868)	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m1	hy	S
Stenocranus major (Kirschbaum, 1868)	.	.	.	7	9	.	.	2	4	2	.	2	2	2	2	.	.	.	.	ma	m1?	hy	S
Megamelus notula (Germar, 1830)	.	.	.	.	15	2	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m2	hy	S
Euconomelus lepidus (Boheman, 1847)	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m2?	hy	S
Laodelphax striatella (Fallén, 1826)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	di	po?	eu	P
Paraliburnia adela (Flor, 1861)	.	.	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m1	hy	S
Mirabella albifrons (Fieber, 1879)	.	.	.	.	.	.	.	.	.	4	.	2	.	.	.	.	.	.	.	di	m2	eu	S
Muellerianella brevipennis (Boheman, 1847)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	di	m1	hy	S
Dicranotropis hamata (Boheman, 1847)	.	.	.	.	.	.	.	.	.	.	4	2	.	.	2	.	11	.	.	di	o1	eu	E
Xanthodelphax straminea (Stal, 1858)	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	di	m2	eu	S
Javesella pellucida (Fabricius, 1794)	4	4	26	2	.	33	28	15	65	70	2	2	.	.	20	15	13	20	76	di	po?	eu	P
Javesella dubia (Kirschbaum, 1868)	.	.	.	.	.	.	.	.	9	.	.	.	.	.	.	.	.	.	.	di	o1?	eu	E
Ribautodelphax albostriata (Fieber, 1866)	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	15	.	.	di	m1	eu	S
Cicadomorpha																							
Cercopidae																							
Neophilaenus lineatus (Linnaeus, 1758)	2	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	di	po	eu	O
Philaenus spumarius (Linnaeus, 1758)	.	2	.	.	.	.	.	.	.	.	.	.	.	7	.	.	7	.	.	di	po	eu	E
Cicadellidae																							
Megophthalmus scanicus (Fallén, 1806)	.	2	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	di	o1	eu	O
Anaceratagallia ribauti (Ossiannilsson, 1938)	.	2	.	.	.	.	.	.	.	2	.	.	.	.	.	.	20	15	4	di	o2?	eu	O
Aphrodes bicincta (Schrank, 1776)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	2	.	di	o1?	xe	O
Anoscopus flavostriatus (Donovan, 1799)	28	2	.	4	.	.	.	2	2	.	22	13	.	39	.	4	7	.	.	di	o1	hy	O
Anoscopus serratulae (Fabricius, 1745)	2	9	.	2	.	.	.	4	2	4	.	15	2	22	4	.	50	11	7	di	o1	eu	E
Cicadella viridis (Linnaeus, 1758)	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	2	.	.	ma	po	hy	O
Notus flavipennis (Zetterstedt, 1828)	.	.	2	2	4	2	.	.	.	2	.	.	.	.	.	.	.	.	.	ma	o1?	hy	O
Empoasca pteridis (Dahlbom, 1850)	.	.	2	.	.	.	.	9	4	.	.	.	.	.	.	2	.	2	.	ma	po	eu	P
Eupteryx atropunctata (Goeze, 1778)	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	ma	po	eu	O
Eupteryx cyclops Matsumura, 1906	.	.	.	9	9	.	.	.	.	.	.	.	.	.	2	.	.	.	.	ma	m1	hy	S
Eupteryx vittata (Linnaeus, 1758)	.	2	.	.	2	.	.	.	.	.	2	.	.	7	.	.	.	.	.	ma	o2	hy	O
Eupteryx notata Curtis, 1837	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	ma	o2	eu	O

Appendix 1. (Continued).

Species	Study sites																			Ecology			
	HF1	HF2	HM1	MF1	MF2	MM1	MM2	MM3	MM4	MM5	LF1	LF2	LF3	LF4	LM1	LM2	NF1	NM1	NM2	WD	DW	MP	LS
Balclutha calamagrostis Ossiannilsson, 1961	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.	.	.	.	.	di	m2	eu	S
Balclutha rhenana W.Wagner, 1939	.	2	20	.	15	4	11	.	2	46	.	2	.	.	.	2	.	.	.	ma	m1	hy	S
Macrosteles laevis (Ribaut, 1927)	.	.	.	.	.	.	.	.	11	.	.	.	.	.	.	4	2	13	15	ma	po	eu	P
Macrosteles sexnotatus (Fallén, 1806)	.	.	4	.	.	13	13	13	.	.	.	.	.	.	.	.	2	26	122	ma	po	eu	P
Macrosteles viridigriseus (Edwards, 1922)	.	.	.	.	.	.	.	.	.	9	.	.	.	.	.	.	.	.	.	ma	o2?	hy	P
Deltocephalus pulicaris (Fallén, 1806)	.	.	2	.	.	26	2	30	9	9	.	.	.	.	35	4	4	7	.	di	o1	eu	E
Endria nebulosa (Ball, 1900)	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	di	m1?	hy	S
Paluda flaveola (Boheman, 1845)	.	.	.	.	.	.	.	.	.	.	.	.	4	11	.	.	.	.	.	di	o1?	hy	O
Elymana sulphurella (Zetterstedt, 1828)	.	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.	.	.	.	ma	o1	eu	E
Cicadula flori (J.Sahlberg, 1871)	.	.	.	.	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m2?	hy	S
Cicadula quadrinotata (Fabricius, 1794)	2	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	2	.	di	m2?	hy	O
Cicadula frontalis (Herrich-Schäffer, 1835)	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m2	hy	n.i.
Macustus grisescens (Zetterstedt, 1828)	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	di	o2	hy	O
Athysanus argentarius Metcalf, 1955	.	.	.	.	.	.	.	.	.	2	.	2	7	.	.	.	.	.	.	di	o1	eu	O
Euscelis incisus (Kirschbaum, 1858)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	di	o2	eu	E
Streptanus aemulans (Kirschbaum, 1868)	2	2	2	.	.	.	.	.	.	.	.	28	.	17	7	9	2	.	.	di	o1	eu	E
Streptanus sordidus (Zetterstedt, 1828)	.	2	.	.	.	39	4	33	26	24	2	.	.	.	2	2	2	.	.	di	o1?	hy	O
Metalimnus formosus (Boheman, 1845)	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m2	hy	S
Psammotettix kolosvarensis (Matsumura, 1908)	.	4	.	.	.	.	.	9	.	.	.	.	.	.	2	2	.	2	.	di	o1	eu	O
Psammotettix alienus (Dahlbom, 1850)	.	.	.	.	.	.	.	.	4	2	.	.	.	.	4	.	.	.	4	ma	o1	eu	P
Psammotettix confinis (Dahlbom, 1850)	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	ma	o1	eu	P
Errastunus ocellaris (Fallén, 1806)	4	22	2	2	2	.	.	4	7	17	30	65	54	39	9	33	13	7	.	di	o1	eu	E
Arthaldeus pascuellus (Fallén, 1826)	2	28	11	2	.	85	.	120	70	46	.	24	85	143	57	41	20	24	11	di	o1	eu	E
Cosmotettix costalis (Fallén, 1826)	.	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	di	m2?	hy	S
Mocuellus collinus (Boheman, 1850)	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	di	o1	xe	O
Erzaleus metrius (Flor, 1861)	4	.	4	241	170	4	.	2	9	17	.	.	.	.	4	33	9	.	.	di	m1	hy	S

Appendix 2. Abundance of leafhoppers (individuals per m^2) collected in 2002 at fallows differing in flooding influence. For abbreviations, see Appendix 1.

Species	HF1	HF2	HF3	MF1	MF2	MF3	LF1	LF2	LF3	NF1	NF2	NF3	Ecology WD	DW	MP	LS
Fulgoromorpha																
Delphacidae																
Anakelisia fasciata (Kirschbaum, 1868)	.	.	.	.	2	7	.	.	.	.	.	.	di	m1	hy	S
Stenocranus major (Kirschbaum, 1868)	7	2	15	8	2	.	.	3	5	.	.	.	ma	m1?	hy	S
Megamelus notula (Germar, 1830)	.	.	.	.	8	72	.	2	.	.	.	.	di	m2	hy	S
Eurysula lurida (Fieber, 1866)	.	.	.	.	.	.	.	.	3	.	.	.	di	m2	eu	S
Megadelphax sordidula (Stal, 1853)	.	.	.	.	.	.	.	.	.	.	8	.	di	m1?	eu	S
Laodelphax striatella (Fallén, 1826)	.	.	2	.	.	.	.	.	.	.	5	2	di	po?	eu	P
Paraliburnia adela (Flor, 1861)	.	2	2	.	2	.	.	.	.	.	.	.	di	m1	hy	S
Mirabella albifrons (Fieber, 1879)	.	2	.	.	.	.	.	.	20	.	.	.	di	m2	eu	S
Muellerianella brevipennis (Boheman, 1847)	.	.	.	.	.	.	.	.	.	.	30	39	di	m1	hy	S
Muellerianella fairmairei (Perris, 1857)	.	.	.	.	.	.	.	.	.	.	26	30	di	m2	hy	S
Acanthodelphax denticauda (Boheman, 1845)	.	.	.	.	.	.	.	.	.	.	.	2	di	m1	hy	S
Dicranotropis hamata (Boheman, 1847)	.	.	.	.	.	.	2	.	.	31	44	26	di	o1	eu	E
Javesella pellucida (Fabricius, 1794)	46	108	149	2	.	.	18	44	46	48	36	26	di	po?	eu	P
Javesella dubia (Kirschbaum, 1868)	.	.	10	.	.	.	13	3	.	3	43	.	di	o1?	eu	E
Ribautodelphax albostriata (Fieber, 1866)	.	.	.	.	.	.	.	.	.	.	3	.	di	m1	eu	S
Cicadomorpha																
Cercopidae																
Neophilaenus lineatus (Linnaeus, 1758)	.	.	.	.	.	.	.	3	8	.	8	.	di	po	eu	O
Philaenus spumarius (Linnaeus, 1758)	.	.	.	5	11	.	10	11	.	10	2	5	di	po	eu	E
Cicadellidae																
Megophthalmus scanicus (Fallén, 1806)	.	.	.	.	.	.	.	.	.	2	.	3	di	o1	eu	O
Anaceratagallia ribauti (Ossiannilsson, 1938)	.	.	.	.	.	.	2	.	.	.	.	.	di	o2?	eu	O
Anoscopus flavostriatus (Donovan, 1799)	5	5	2	3	2	2	18	20	7	10	11	20	di	o1	hy	O
Anoscopus serratulae (Fabricius, 1745)	2	.	.	.	.	.	3	3	.	31	.	5	di	o1	eu	E
Stroggylocephalus agrestis (Fallén, 1806)	.	.	.	.	5	3	.	.	.	.	.	.	di	m2?	hy	S
Evacanthus acuminatus (Fabricius, 1794)	.	.	.	.	.	.	.	2	.	.	.	.	di	po	eu	O
Evacanthus interruptus (Linnaeus, 1758)	.	.	.	.	.	.	.	.	.	2	2	.	di	po	hy	O
Cicadella viridis (Linnaeus, 1758)	.	.	.	.	.	.	.	.	.	2	.	.	ma	po	hy	O
Notus flavipennis (Zetterstedt, 1828)	.	.	.	.	.	11	.	.	.	.	.	.	ma	o1?	hy	O
Empoasca pteridis (Dahlbom, 1850)	.	.	.	.	18	.	.	3	.	.	.	.	ma	po	eu	P
Eupteryx atropunctata (Goeze, 1778)	.	.	.	.	36	.	.	2	.	2	.	.	ma	po	eu	O
Eupteryx cyclops Matsumura, 1906	2	.	.	21	5	.	3	3	.	.	.	.	ma	m1	hy	S
Eupteryx vittata (Linnaeus, 1758)	.	.	2	.	.	.	2	.	.	.	.	3	ma	o2	hy	O
Eupteryx notata Curtis, 1837	.	.	.	.	.	.	.	.	.	2	.	.	ma	o2	eu	O
Balclutha calamagrostis Ossiannilsson, 1961	.	.	3	.	.	.	.	.	3	.	.	.	di	m2	eu	S
Balclutha rhenana W.Wagner, 1939	.	7	21	2	.	.	.	.	.	.	.	.	ma	m1	hy	S
Macrosteles laevis (Ribaut, 1927)	.	3	3	.	.	.	.	.	.	.	.	.	ma	po	eu	P
Macrosteles sexnotatus (Fallén, 1806)	7	5	77	2	8	.	.	.	.	.	.	.	ma	po	eu	P
Deltocephalus pulicaris (Fallén, 1806)	.	.	.	.	.	.	.	.	.	2	.	.	di	o1	eu	E
Endria nebulosa (Ball, 1900)	.	.	.	.	.	.	.	2	3	.	.	.	di	m1?	hy	S
Paluda flaveola (Boheman, 1845)	.	2	.	.	.	.	.	3	.	.	2	.	di	o1?	hy	O
Rhopalopyx preyssleri (Herrich-Schäffer, 1838)	.	.	.	.	.	.	.	.	2	.	.	.	di	m1	xe	S
Elymana sulphurella (Zetterstedt, 1828)	.	.	.	.	.	.	2	.	.	.	5	7	ma	o1	eu	E
Cicadula flori (J.Sahlberg, 1871)	.	.	.	.	.	16	.	.	.	.	.	.	di	m2?	hy	S
Cicadula quadrinotata (Fabricius, 1794)	.	.	3	.	.	.	.	.	.	.	.	.	di	m2?	hy	O
Mocydia crocea (Herrich-Schäffer, 1837)	.	.	.	.	.	.	.	.	.	.	15	11	ma	o1	xe	O
Macustus grisescens (Zetterstedt, 1828)	.	.	.	.	.	.	.	.	10	.	.	.	di	o2	hy	O
Euscelis incisus (Kirschbaum, 1858)	.	.	.	.	.	.	.	.	.	5	.	.	di	o2	eu	E
Streptanus aemulans (Kirschbaum, 1868)	18	3	.	.	.	.	25	2	.	5	5	7	di	o1	eu	E
Streptanus sordidus (Zetterstedt, 1828)	.	.	.	.	.	.	.	.	.	.	2	.	di	o1?	hy	O
Metalimnus formosus (Boheman, 1845)	.	.	.	.	.	38	.	.	.	.	.	.	di	m2	hy	S

Appendix 2. (Continued).

Species													Ecology			
	HF1	HF2	HF3	MF1	MF2	MF3	LF1	LF2	LF3	NF1	NF2	NF3	WD	DW	MP	LS
Psammotettix kolosvarensis (Matsumura, 1908)	.	5	.	.	.	.	2	.	.	.	.	.	di	o1	eu	O
Errastunus ocellaris (Fallén, 1806)	13	16	.	3	.	.	30	10	8	.	5	8	di	o1	eu	E
Arthaldeus pascuellus (Fallén, 1826)	28	2	8	.	.	.	10	34	10	34	28	16	di	o1	eu	E
Cosmotettix costalis (Fallén, 1826)	.	.	.	.	.	21	.	.	.	.	.	.	di	m2?	hy	S
Erzaleus metrius (Flor, 1861)	.	.	41	107	38	.	.	.	.	.	.	.	di	m1	hy	S

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