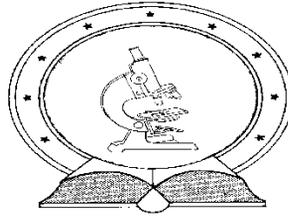


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**THE EFFECTS OF HABITAT RESTORATION AND
MANAGEMENT ON GRASSLAND MAMMALS AND WETLAND
BIRDS**

**ÉLŐHELYREKONSTRUKCIÓK ÉS TERMÉSZETVÉDELMI
KEZELÉSEK HATÁSAI GYEPEK KISEMLŐSEIRE ÉS VIZES
ÉLŐHELYEK MADARAIRA**

Egyetemi doktori (PhD) értekezés

MÉRŐ THOMAS OLIVER

Témavezető

Dr. Lengyel Szabolcs
tudományos tanácsadó

DEBRECENI EGYETEM

Természettudományi Doktori Tanács

Juhász Nagy Pál Doktori Iskola

Debrecen, 2015

A doktori értekezés betétlapja

Ezen értekezést a Debreceni Egyetem Természettudományi Doktori Tanács a **Juhász Nagy Pál Doktori Iskola Kvantitatív és Terresztris Ökológia doktori** programja keretében készítettem a Debreceni Egyetem természettudományi doktori (PhD) fokozatának elnyerése céljából.
Debrecen, 2015.

.....
a jelölt aláírása

Tanúsítom, hogy **Mérő Thomas Oliver** doktorjelölt **2009-2012** között a fent megnevezett Doktori Iskola **Kvantitatív és Terresztris Ökológia doktori** programjának keretében irányításommal végezte munkáját. Az értekezésben foglalt eredményekhez a jelölt önálló alkotó tevékenységével meghatározóan hozzájárult. Az értekezés elfogadását javasolom.
Debrecen, 2015.

.....
a témavezető aláírása

A doktori értekezés betétlapja

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MANAGEMENT ON GRASSLAND MAMMALS AND WETLAND
BIRDS**

Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a Környezettudomány tudományágban

Írta: **Mérő Thomas Oliver** okleveles Biológia tanár

Készült a Debreceni Egyetem **Juhász-Nagy Pál Doktori Iskolája**
(**Kvantitatív és Teresztis Ökológia Doktori program** programja)
keretében

Témavezető:

Dr. Lengyel Szabolcs

A doktori szigorlati bizottság:

elnök:

tagok:

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A doktori szigorlat időpontja:

Az értekezés bírálói:

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A bírálóbizottság:

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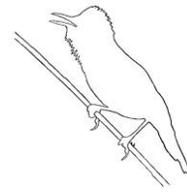
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Az értekezés védésének időpontja:

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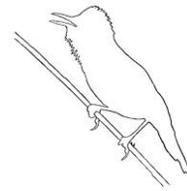
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General introduction

Human activities such as agricultural land use and urbanization have led to the loss, degradation, and fragmentation of natural habitats (Burgess and Sharpe 1981, Andren 1994). As a consequence, populations of many species have declined or disappeared, leading to decreased species richness and biotic homogenization, when only generalist species with high adaptive capability remain and specialist species decline or disappear. Habitat restoration can theoretically counter these processes (Young 2000, Lengyel et al. 2012), and the restoration of habitats and ecosystems has recently been incorporated into relevant policy instruments as explicit targets (e.g. Aichi Biodiversity Targets of the Convention of Biological Diversity: Targets 14 and 15, the European Union Biodiversity Strategy for 2020: Target 2). However, restoration is rarely implemented at spatial and temporal scales that are adequate to make a difference (Woodcock et al. 2010, Lengyel et al. 2014). The spatial and temporal scales used in habitat and ecosystem restoration are often small and short, respectively (Wagner et al. 2008). In addition, most conservation actions such as grassland restoration and management are primarily monitored based on plants and vegetation (e.g. Willems and Bik 1998, Barbaro et al. 2001), invertebrates less frequently (e.g. Déri et al. 2011, Rácz et al. 2013) and vertebrates very rarely (e.g. Moro and Gadal 2007). As a result, our knowledge on the design, implementation and impact of restoration remains limited in several aspects. In particular, we know little on how habitat restoration affects vertebrate animals such as birds and mammals.

Grassland restoration on abandoned cropland is one of the most frequently applied restoration techniques in conservation projects (Török et al. 2011, Lengyel et al. 2012). To evaluate the effects of restoration and management of habitats on higher trophic levels such as animals, the restoration should be implemented on a large spatial and long-term temporal scale because of the habitat requirements and the year-round life cycles of higher trophic groups. Furthermore, pure restoration often needs to be supplemented by management activities to reach and to maintain an adequately natural stage of the habitats. In the case of restored grasslands, this can be successfully done through extensive sheep or cattle grazing or mowing (Dudley 2008). The effects of restoration and habitat

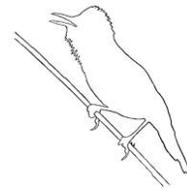


General introduction

management on small mammal assemblages were studied in restored agricultural, riparian, shrub or forest habitats (e.g. Moro and Gadal 2007, Stone 2007, Torre et al. 2007), while there is little information on the effects of large-scale grassland restoration and various management regimes (grazing, time dependent mowing) on vertebrate animals. For example, to the best of our knowledge, the effects of grassland restoration on small mammals has been evaluated in an MSc thesis in North America (Mulligan 2012).

Wetlands are one of the most threatened habitats on Earth; only in the last century, 50% of the wetland habitats disappeared (Silva et al. 2007). It is no surprise that wetland conservation and rehabilitation is one of the most important targets of the LIFE programme of the European Union (LIFE 2007). Between 1992 and 2006, the LIFE programme has cofunded 120 wetland-related projects to facilitate the conservation of wetland biodiversity (Silva et al. 2007). One of the commonest wetland habitats in Europe are reedbeds, which declined considerably in area and quality due to drainage occurring after river regulations and associated melioration systems (Newman 1995). Besides the declining area of reedbeds, the quality of the remaining reedbeds can also raise concern. This is because both the complete absence of water and the supply of constant amounts of water to reedbeds as well as the lack of proper management may speed up reedbed degradation by creating homogeneous vegetation cover, i.e. homogeneous reedbeds (Lougheed et al. 2008).

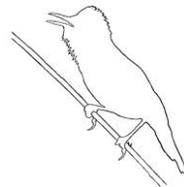
Homogenous reedbeds are occasionally managed to break up reed homogeneity and to maximize species richness and abundance of animals (e.g. Andrews and Ward 1991, Poulin et al. 2002, Korner 2013). Such management, however differs from the management of restored grasslands because the aim of reedbed management is to create a new patchy structure or a mosaic marshland which may be suitable for numerous of species. Appropriate management actions of varying intensity can result in several changes in the managed marsh habitat, which can lead to the creation and maintenance of heterogeneous patchy marshland (e.g. Korner 2013). However, most studies that discuss the effects of reed management on animal communities were spatially and temporally limited, and these often focused on one or a few groups, mostly on birds (Báldi and Moskát 1995, Poulin and Lefebvre 2002, Vadász et al. 2008, Valkama et al. 2008, Korner 2013).



General introduction

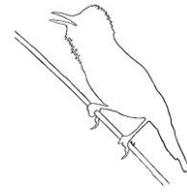
The management of habitats for biodiversity conservation is founded on two general principles in ecology: the species-area relationship (SAR, Connor and McCoy 2001) and the intermediate disturbance hypothesis (IDH, Connell 1978). The SAR predicts that the number of species increases with area (Pan 2013), and thus, management of larger areas should conserve more species. The IDH suggests that species diversity is maximized when ecological disturbance is at intermediate levels, i.e., neither too rare/mild nor too frequent/intense (Schwilk et al. 1997, McCabe and Gotelli 2000). Relying on these two principles, homogeneous reedbeds in the Egyek-Pusztakócs marshes of Hortobágy were managed in 2006-2009 by spatiotemporally variable grazing and burning (fire management) to maximize the diversity of marsh habitats for amphibians and birds. A review of the literature suggested that information on the combined effects of these two management actions on marshland species is lacking. The combination of these two management actions, which created a gradient from low-intensity to high-intensity disturbance, offered a good opportunity to fill this gap and to test predictions of the IDH.

The Great Reed Warbler (*Acrocephalus arundinaceus*) is an emblematic specialist bird species in reed habitats in the western Palaearctic of the northern Hemisphere (Cramp 1998). The breeding ecology of the Great Reed Warbler has been extensively studied in the past four decades (Beier 1981, Dyrz 1981, Petro et al 1998, Woithon and Schmieder 2004, Batáry and Báldi 2005, Trnka and Prokop 2010, Uzun et al. 2014). The majority of studies were conducted on large ponds and lakes, occasionally on canals (e.g. Dyrz 1981, Beier 1981, Bensch 1995, Fedorov 2000, Uzun et al. 2014), while smaller impoundments or successional marshes were less frequently studied (Mérő and Žuljević 2009). It is generally known that the breeding habits and success can be governed by numerous factors, such as weather variables, vegetation cover, predation pressure, and nest and brood parasitism by Cuckoos *Cuculus canorus* (e.g. Bensch 1993, Fischer 1994, Moskát and Honza 2000, Trnka and Grim 2013). However, the breeding success and factors determining it were not examined on small human-made ponds where reed was occasionally managed through burning at the end of the winter. Dyrz (1981) and Beier (1981) mentioned in their papers burnt patches, but did not report on differences in the breeding variables. Graveland



General introduction

(1998) reported on the effect of flooding on the breeding density of the Great Reed Warbler. Furthermore, he investigated the effects of reed variables on the breeding density and the characteristics of reed stems incorporated in the nests. This was also studied by Trnka et al. (2009), who compared the breeding parameters of nests found in mace *Typha* spp. and reed. In general, we have no information on whether and how post-winter burning influences the breeding parameters in extremely dry and extremely wet breeding seasons. Furthermore, there is a lack of studies on the relationship between breeding success and various properties of reedbeds such as reed density and reed quality.



Aim of the study

Aims of the study

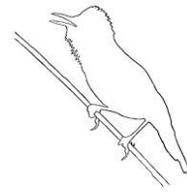
This Ph.D. dissertation contains four chapters published in scientific journals with impact factor. The four chapters present and discuss the effects of habitat restoration and habitat management, and vegetation structure on small mammal assemblages in grasslands (Chapter 1), on bird communities of alkali marshes (Chapter 2), and on the breeding success (Chapter 3) and breeding habits (Chapter 4) of a passerine bird species characteristic in reedbeds. Studies in Chapters 1 and 2 are based on a whole-community approach, whereas Chapters 3 and 4 present results from a species-based, autecological approach. The first part of the dissertation provides an Introduction general to all chapters (please see above). Detailed aims specific to each chapter are given next, followed by a joint Materials and Methods section for each of the four chapters. Finally, specific Introduction, Results and Discussion sections are given separately for the four chapters. I chose this structure so that the specific questions and the results and discussion to answer them can be viewed together to enable the reader to focus on the new results presented in this dissertation.

Chapter 1

The aim of this study was to evaluate the local and landscape-scale effects of habitat restoration and management on small mammal communities after a large-scale restoration of grasslands on former croplands. We sampled small mammals (voles, mice and shrews) in a space-for-time substitution design on natural grasslands (restoration target), restored grasslands (restoration process) and croplands (restoration start) and evaluated the effects of both local factors (management, elevation) and landscape-scale factors (proportion of different habitat types) on small mammal communities, with a special consideration to the restoration process.

Chapter 2

The aim of this study was to evaluate the impact of spatiotemporally variable management of reedbeds by grazing and burning on marshland bird communities and functional groups. First we tested the effects of management type or regime on the bird community and on the functional



Aim of the study

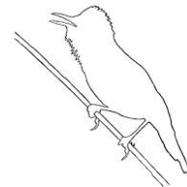
groups of birds. Second, we explored the possible difference in responses to management among functional groups including both passerines and non-passerines. Finally, we checked the potential interactions or synergies between the impacts of grazing and fire management.

Chapter 3

The first aim of this study was to explore the effect of reed burning, precipitation and changes in water level on breeding success and on clutch and brood survival in the Great Reed Warbler, a typical and emblematic species of reedbeds. The second aim of this study was to test whether breeding success varied with season in a comparison of nests started in the early and the late period of the breeding season.

Chapter 4

The general aim of this study was to examine the physical properties of reed habitats that affect the nest site selection of the Great Reed Warbler. The specific aims of this study were (1) to compare the physical properties (number, density and mean diameter) of nest-holding reed stems and those of reed stems in the surroundings; (2) to compare these physical properties among three reed habitats: mining ponds, small canals and large canals; and (3) to study how reed density affects breeding success.



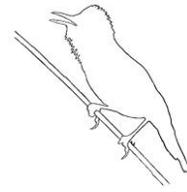
Material and methods

Material and methods

Study sites

The Egyek-Pusztakócs marsh-grassland complex (Chapter 1)

This study was carried out in the Egyek-Pusztakócs marsh and grassland complex (4073 ha, **Figure 1**) of Hortobágy National Park (eastern Hungary). The area, once a floodplain of river Tisza, is characterized by marshes in ancient riverbeds, alkali meadows around the marshes, and alkali and loess grasslands on higher (90-94 m a.s.l.) plateaus deposited by floods and wind. Due to the regulation of Tisza in the 1850s, the connection between the river and marshes ceased completely. The area was then gradually drained until the late 1960s, when several marshes dried out and the areal extent of croplands reached its maximum. The first phase of landscape rehabilitation involved the hydrological reconstruction of the marshes between 1976 and 1997, whereas the second step (2004-2008) restored grasslands on loess plateaus, lower-lying alkali steppes and meadows in ecological buffer zones around and corridors between the marshes. Grassland restoration was carried out on a total of 760 ha of former cropland using soil preparation by ploughing, sowing of two low-diversity seed mixtures, and annual mowing or grazing as post-restoration management. To our knowledge, this is currently the largest active (non-spontaneous) grassland restoration programme in Europe. More details on the restoration programme and its early results on vegetation development can be found in Lengyel et al. (2012) and on changes in arthropod communities in Déri et al. (2011) and Rácz et al. (2013).

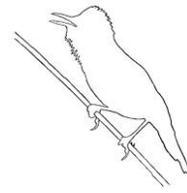


Material and methods



Figure 1. Satellite image of the study area in the Egyek-Pusztakócs marsh-grassland system. Dark green colors indicate marshes and dark and light brown colors usually indicate grasslands. Source: Institute of Geodesy, Cartography and Remote Sensing (2007).

The study site is characterized by a continental climate with large annual fluctuations in weather. The mean annual temperature is 9.5 °C and the mean total annual precipitation is 550 mm. We sampled small mammals in the spring (March-April) and autumn (September-October) of both 2011 and 2012 (four periods total). Spring in 2011 was characterized by high water and large flooded areas due to extremely high precipitation in 2010 (**Figure 2**, total 2010 precipitation in Hortobágy region: 950 mm, source: Hungarian Meteorological Service, <http://www.met.hu>). Summer in 2011 was dry (total precipitation: 350 mm) and water receded gradually from all grasslands. Winter in 2011/2012 again brought significant precipitation (**Figure 2**) and intense flooding at snowmelt. Summer 2012 had a long drought (total precipitation 270 mm), with near-average precipitation in only one (July) out of six months and with hardly any rain in August and September (**Figure 2**).



Material and methods

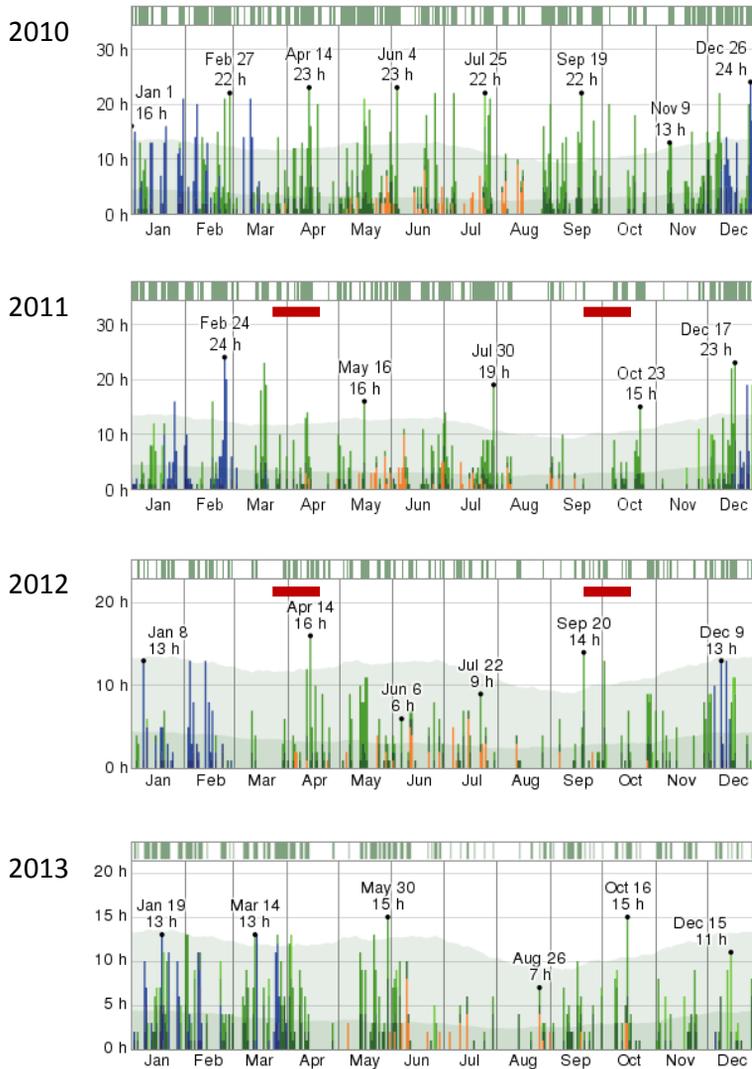
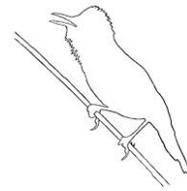


Figure 2. The number of hours per day with precipitation assembled from hourly present weather reports (days/months on the horizontal and hours of the day on the vertical axis) from the closest weather station with detailed measurement (Debrecen airport, c. 50 km E from the study site). Colour coding: green - rain; blue - snow, orange - thunderstorms, light blue shaded area - climate normal (average probability of precipitation per day). Bars at the top of the graphs indicate days with any precipitation (green) or no precipitation (white). Dark red horizontal bars in 2011 and 2012 indicate the sampling periods, data for 2010 and 2013 are shown for comparison only. Source: WeatherSpark (<http://www.weatherspark.com>).

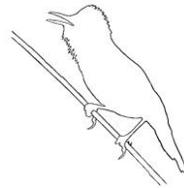


Material and methods

Fekete-rét marsh and management actions (Chapter 2)

The study area was the Egyek-Pusztakócs marsh and grassland complex, a spatially isolated unit (4000 ha) of Hortobágy National Park in eastern Hungary. The habitat complex was primarily formed by floods of river Tisza, and marshes are remnants of ancient flood ways. After the regulation of the river (1860s) and the construction of drainage canals in the early 20th century, water supply was cut off, the water table sank and the complex underwent several phases of drying. A landscape-scale rehabilitation programme, started in 1976, constructed canals and restored water supply from river Tisza to the marshes by 1997. After 1997, marshes have received constant amounts of water annually and were regularly exposed to winter reed-harvesting, which resulted in homogeneous reedbeds taking over the once diverse marshes by 2004 (**Figure 3**).

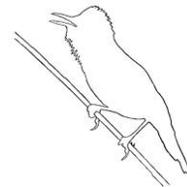
In order to open up reedbeds, control reed and increase the diversity of habitats by re-creating the former wetland mosaic, two management actions were designed in 2004: grazing/trampling by cattle and fire management (prescribed burning). These actions were implemented in Fekete-rét marsh N of the village of Tiszafüred-Kócsújfalu (N 47.55909°, E 20.93224°), the largest (600 ha) of the seven marshes of the Egyek-Pusztakócs system. These two management actions (detailed below) caused spectacular changes in the structure of marsh habitats in only six years (**Figure 3**).



Material and methods



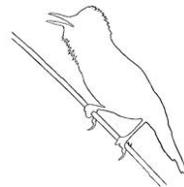
Figure 3. Aerial photographs of the southern half (c. 300 ha) of Fekete-rét marsh, taken before the start of management actions (2004, top) and taken in 2010 or after four years of grazing and two years with burning (2007, 2009) (bottom). Source: Google Earth.



Material and methods

Grazing – Grazing by Hungarian grey cattle was started in spring 2006. Trampling on rhizomes through controlled grazing has little effect on reed density but long-term grazing reduces the vigor of the reed plant considerably (Cross and Fleming 1989). Grey cattle are highly suitable for grazing in marshes as they will go after and consume reed even in deep water (up to 1.5 m) and have been used successfully to control reed in other national parks in Hungary (Kelemen 2002). The infrastructure for grazing (fold, wells, shepherds' accommodation etc.) was newly constructed in early 2006. Grazing was conducted every year between late April and late November by a stock of 180 grey cattle. Cattle were free to roam in the entire southern half of the marsh (c. 300 ha). However, grazing was concentrated in the SW part of the marsh (c. 200 ha) closest to the fold (**Figure 4**) and cattle also used meadows and grasslands (total c. 100 ha) surrounding the marsh.

Fire management – Burning took place in early September in both 2007 and 2009. Late summer is the most effective period to control reed by burning because most nutrients are in the inflorescence at this time (Engloner 2009, Ruiz and Velasco 2010) and burning in late summer effectively kills the nutrient-poor rhizomes (Cross and Fleming 1989). Fire management was designed and implemented in cooperation with professional fire crews. For fire control purposes, reed was cut in a 50-m-wide buffer zone around all wooden structures in the marsh (e.g. footpath, observation towers etc.) and in critical areas around the marsh to prevent the fire from spreading into grasslands. In 2007, the fire was started on the E side of the marsh and progressed westwards, whereas in 2009, the fire progressed from W to E with westerly winds. In 2007, reed burned for two days and the fire died on its own, whereas in 2009, it burned for three days and either died on its own or was put out by fire crews in critical areas. Both fires were of high intensity, with flames reaching up to 10-12 m, and both caused a near-total loss of old and green reed (**Figure 4**, **Figure 5**). The total area burned was 110 ha in 2007 and 130 ha in 2009. Although some areas were burned in only one year, there was also a substantial area that was burned in both years (**Figure 4**).



Material and methods

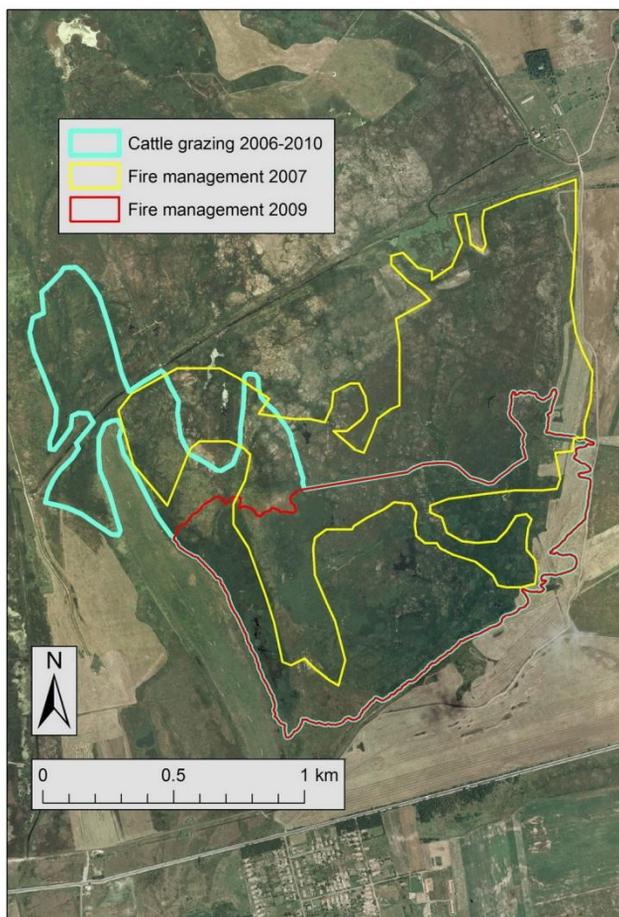
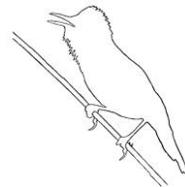


Figure 4. Aerial photograph of Fekete-rét marsh (in 2005), with location of management actions. Source of photograph: Institute of Geodesy, Cartography and Remote Sensing, Budapest, Hungary.



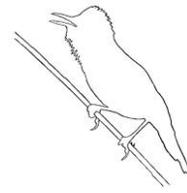
Material and methods



Figure 5. Aerial view of the southern part of Fekete-rét marsh in September 2007, with dark colours indicating burned areas. Source of photograph: Hortobágy National Park Directorate (Lajos Gál).

The Bager Pond (Chapter 3)

The study was conducted in Bager Pond (45°47'N, 19°05'E) in the suburban area of town Sombor, Vojvodina, North Serbia. Sombor is a typical lowland area (mean elevation 89 m a.s.l.) with a semi-dry continental climate, with mean annual precipitation of 590 mm (range: 400-900 mm). The mean annual temperature is 10.7°C. The warmest month is July, with a mean monthly temperature of 21.1°C and the coldest month is January, with a mean monthly temperature of 0.8°C (Tomić 1996). The complex of two ponds (total area 1.3 ha) was established in the 1960s in two pits in which clay had been dug for the local brickyard. Water level in the pond depends on both the precipitation in autumn, winter and early spring and the level of groundwater. Water level generally decreases throughout the summer and early autumn due to evaporation and the evapotranspiration of reed and other vegetation. In 2009, c. 85% and in 2010, c. 50% of the reed was burned at the end of winter while in 2008 and 2011 the reed was not managed. The pond is surrounded by meadows and corn fields (**Table 1**).



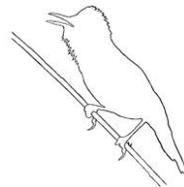
Material and methods

Table 1. Characteristics and dominant vegetation of Bager Pond. Data on precipitation were provided by the Water Management Company „Zapadna Bačka”, Sombor.

Year	Proportion of open water (%)	Mean water depth at breeding site (cm \pm SD)	Vegetation (%)		Precipitation in breeding season (mm)
			<i>Phragmites australis</i>	<i>Typha</i> sp.	
2008	10	59.4 \pm 29.24	85	5	104.0
2009	8	6.8 \pm 17.23	89	3	168.8
2010	7	108.2 \pm 37.20	92	1	457.5
2011	8	77.5 \pm 26.91	91	1	146.4

Reed habitats in the Sombor region (Chapter 4)

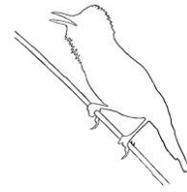
The study was performed in the region of the municipality of Sombor (1178 km²), which lies in the north-western part of the northern Serbian province of Vojvodina. Sampling was carried out at 11 locations in three different reed habitats (mining ponds, large canals and small canals), (**Table 2**). The mining ponds were formed by the excavation of clay or sand for the local brickyards. The water level in the mining ponds depends both on the precipitation in autumn, winter and early spring and on the level of the groundwater. In the summer and autumn, the water level decreases depending on the intensity of the evapotranspiration of the reed. The canal network in Vojvodina constitutes part of the Danube-Tisza-Danube hydro-system. The small canals are mainly melioration or irrigation canals used in agricultural water management (**Table 2**). Both the large and small canals contain a narrow (1 to 5 m) reed belt on their banks where Great Reed Warblers build their nests usually less than a metre above the water surface and usually within 5 m of the reed edge with open water. The water level in both canal habitats is regulated by the local Water Management Company “Zapadna Bačka”. While the water supply of the large canals mainly originates from the River Danube, the water level in the small canals depends mostly on the amount of precipitation.



Material and methods

Table 2. Central coordinates and extents of the study sites and the numbers of nests found.

Habitat	Location	UTM CR coordinate	Extent of area surveyed	Number of nests found
Mining ponds	Bager	57 22	1.3 ha	20
	Gakovo	58 14	1.4 ha	10
	Pista	47 88	0.7 ha	5
Large canals	Veliki bački kanal	56 18	4.0 km	17
	Plazović - Bački Monoštor	47 33	2.0 km	32
	Plazović - Bezdán	47 18	1.0 km	9
	Plazović - Kolut	48 02	1.0 km	11
Small canals	Eastern Mostonga	57 53	1.0 km	8
	Northern Mostonga	57 14	0.5 km	2
	Stara Mostonga	56 18	0.5 km	1
	Gradina lateral	66 27	1.0 km	9
Total				124



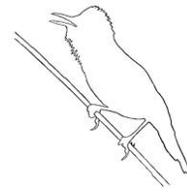
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Sampling design

Small mammal trapping (Chapter 1)

We sampled small mammals (mice, voles and shrews) at 12 sites in three habitat types (**Table 3**): two on croplands (wheat fields, starting point of restoration), eight on restored grasslands (process of restoration) and two on natural grasslands (restoration targets). Within restored grasslands, four levels of restoration age (three to six-year-old restorations) were replicated at two sites each ($n = 8$ sites). Sampling was conducted in the spring and autumn of 2011 and 2012 (four sampling periods total). Sampling sites were at least 800 m away from each other to minimize spatial non-independence. The sampled habitat patches ranged from 16 to 300 hectares in area (mean $66.6 \text{ ha} \pm \text{S.D. } 81.68$). None of the response variables (see below) showed significant correlations with patch area (Spearman rank correlations, n.s.), therefore, we did not control for patch area in statistical analyses. Sites were chosen to represent the management practices characteristic to the general area. Restored grasslands chosen were managed either by mowing early in the season (June, $n = 4$ sites), by mowing late in the season (August, $n = 2$) or by grazing by sheep (from April to November, $n = 2$) (Lengyel et al. 2012). The two natural grasslands sampled were not managed, whereas the two croplands were regularly ploughed. We also recorded elevation and vegetation height at each site. Although the differences in elevation were small (89-91 m a.s.l.), lower-lying areas were more often flooded and less suitable for small mammals than were higher plateaus. Elevation of the sites was determined from a detailed topographic map (accuracy: 0.5 m). We also measured the height of vegetation (accuracy 5 cm) 0.5 m from each trap in a random direction.

To characterize landscape configuration, we calculated the proportion of five habitat types (croplands, restored grasslands, natural grasslands, woodlands, and linear habitats such as roads and canals) at each sampling site. We used a habitat map prepared in 2010 of the entire Egyek-Pusztakócs system as part of other studies and used ESRI ArcMap GIS 10.0 to calculate the proportion of each habitat type in non-overlapping buffers of 400-m radius around each sampling site.



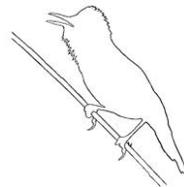
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We live-trapped small mammals using Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida, U.S.; **Figure 6**). Sherman traps have been repeatedly found to perform as well or, more frequently, better than other live traps in multi-species studies of small mammals (e.g. Morris 1968, Hayes et al. 1996, Anthony et al. 2005, Santos-Filho et al. 2006, Belant and Windels 2007, Kaufman and Kaufman 2007, Torre et al. 2010), and were found to cause less mortality than other live traps (Dizney et al. 2008). Because Sherman traps may be less effective at capturing small shrews than other live traps (Sibbald et al. 2006), I performed all analyses with or without data on shrews (i.e., mice and voles only). However, as the inclusion or exclusion of shrews led to qualitatively similar results, I present results based on the full dataset. Although Sherman traps are particularly effective in combination with other types of traps (e.g. pitfall traps, Longworth traps) to attain a full complement of small mammals found in a habitat (Sibbald et al. 2006), our study did not aim to find all species, rather, it aimed to characterise differences among habitat and management types by an adequately high, appropriately replicated constant sampling effort designed to achieve a reasonable compromise between the requirements of spatiotemporal replication and on-site effort intensity.

Table 3. General characteristics, local and landscape factors of sampling sites. Grassland: natural grasslands, restoration: restored grasslands, linear habitats: roads, canals.

Sampling site	Habitat type	Year restored	Area (ha)	Local factors	
				Elevation (m)	Management
Sóút É szántó	cropland	–	60	90.5	ploughing
Kilátó szántó	cropland	–	50	90.0	ploughing
27 ha-os gyep	restoration	2005	27	89.5	mowing early
Hagymás-hát	restoration	2005	26	91.0	sheep-grazing
Górés észak	restoration	2006	48	90.0	mowing early
Nyírházi halom	restoration	2006	28	91.0	mowing early
Csepregi szántó	restoration	2007	46	89.0	mowing late
K Csepregi	restoration	2007	21	90.0	mowing late
Csattag ÉK	restoration	2008	28	89.5	mowing early
Görbeszék-halom	restoration	2008	16	90.0	sheep-grazing
Csattag-hát	grassland	–	300	89.0	none
Fekete-rét DK	grassland	–	150	90.0	none

Landscape factors: Proportion of

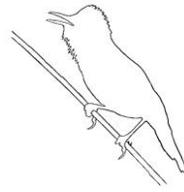


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	Cropland	Grassland	Restoration	Linear	Woodland
Sóút É szántó	0.99	0.00	0.00	0.00	0.00
Kilátó szántó	0.56	0.29	0.00	0.02	0.00
27 ha-os gyep	0.22	0.21	0.32	0.01	0.01
Hagymás-hát	0.00	0.08	0.36	0.00	0.00
Górés észak	0.00	0.03	0.86	0.02	0.04
Nyírházi halom	0.00	0.24	0.67	0.02	0.04
Csepregi szántó	0.00	0.06	0.60	0.00	0.00
K Csepregi	0.00	0.36	0.41	0.01	0.01
Csattag ÉK	0.00	0.00	0.59	0.00	0.00
Görbeszék-halom	0.06	0.47	0.35	0.00	0.02
Csattag-hát	0.00	0.77	0.00	0.00	0.00
Fekete-rét DK	0.00	0.99	0.00	0.01	0.00



Figure 6. Sherman live traps in field (left), baited with bacon and seed mixture (middle) and during installation (right).

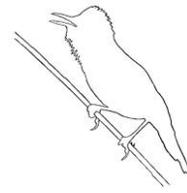


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Figure 7. Small mammal sampling sites in the Egyek-Pusztakócs marsh system.

At each of the 12 sampling sites (**Figure 7**), we installed 36 traps in a 6×6 grid covering 1 hectare (distance between traps: 20 m). We baited the traps with seed mixture (grains, sunflower) and bacon following the recommendations of the trap manufacturer and our previous experience. Traps were operated for five nights to ensure compatibility with the National Biodiversity Monitoring System of Hungary. Five nights appeared appropriate because captures peaked on day 2-4 and decreased by day 5 at each site. Total sampling effort amounted to 8640 trap-nights (36 traps×5 nights×12 sites×4 sampling periods). The traps were checked twice a day (7:00-9:00, 18:00-20:00 hours). Before each check, we counted potential avian predators in and 200 m around the sampling grids for 5 minutes from a distance. Small mammals captured in the traps were identified to species and weighed. We marked individuals by a permanent felt pen at the base of the tail to enable the detection of recaptures. Our previous experience showed that this marking could be detected for at least a week.



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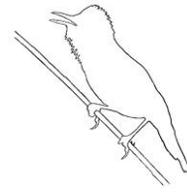
Bird surveys: experimental design and data collection (Chapter 2)

The experimental design consisted of an incomplete crossing of the grazing and burning management with six treatment levels (**Table 4**). Both cattle and fires were free to roam in the southern half of the marsh to mimic ancient disturbances as close as possible, which resulted in managed areas of irregular shapes. We digitized the areas actually grazed and burned in detailed ground surveys at the end of the vegetation period. We recorded point localities using a hand-held GPS receiver during walking along the visually identified borderline of regularly grazed/trampled and un-grazed marsh and burned and unburned reed. A spatial overlay of the obtained polygons allowed us to identify areas with six different combinations of management actions (treatment levels, **Table 4**). Because the 2009 fire involved only very small areas of non-grazed reed, two combinations of the treatments (non-grazed, new-burned; non-grazed, twice-burned) could not be replicated and were missing from a complete design.

Table 4. An overview of treatments in marsh habitat patches and the terminology used in this study.

Fire management		Grazing management	
Burned in	Grazed	Non-grazed	
2007	Grazed, old-burned	Non-grazed, old-burned	
2009	Grazed, newly-burned	–	
Both years	Grazed, twice-burned	–	
Never	Grazed, unburned (burning control)	Non-grazed, unburned	(overall control)

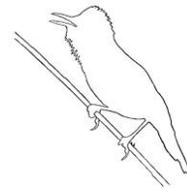
In each of the six treatment levels, we designated five 100-m-long transects as replicates (total $n = 30$). The exact transect locations (starting points) were selected randomly within similarly managed areas with the restriction that transects were at least 100 m apart from each other. The orientation of transects was selected randomly, except where the shape of the treated area restricted the orientation. Transects were found in the field by GPS coordinates. We walked transects once in April and once in May in 2010 to maximize the chances of recording both early-nesting and



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late-nesting species. Data from the two occasions were pooled per transect for analysis. We counted birds for 5 min each at 0, 25, 50, 75 and 100 m from the starting point of the transect and also counted birds when walking between the points (combination of point counts and the line transect method, Bibby et al. 2000, Gregory et al. 2004, Gibbons and Gregory 2006). We recorded all birds seen or heard but analysed only those that were within 25 m on both sides of transects. For reed-nesting passerines, we also mapped the territories based on the locations of singing males along the transect to avoid double-counting. Bird species were classified into functional groups based mainly on their feeding and nesting characteristics (Perrins and Cramp 1998).

We measured water depth to the nearest 5 cm at each of the five counting points. The measurements of water depth were averaged for each transect. We also quantified reed density and complexity at the three internal counting points (at 25, 50 and 75 m) to characterize the effect of management. The number of old (dry) and new (green) reed stems were counted in a circle (diameter 40 cm) positioned at a height of 1 m and 1 m in a randomly selected direction from each of the three internal counting points. We first estimated reed density by (i) the number of old stems (average of three points per transect), (ii) the number of new stems (average of three points per transect), (iii) the total number of stems (sum of old and new stems per transect), (iv) the mean number of stems (average of total number of stems at three points per transect), and (v) the proportion of old reed stems (per total number of stems in the transect) because old reed is important for the breeding of a number of reed-nesting passerines, especially for early-nesting species. Second, we estimated reed complexity by (i) the standard deviation (S.D.) of the mean number of all stems and (ii) the coefficient of variation (C.V.) in the number of all stems (standard deviation per mean of number of all stems) for each transect. We also recorded two variables that potentially reflect management, (i) the proportion of reed cover (1 for transects with a continuous cover of reed, 0.9 for transects with reed cover on 90 m etc.), and (ii) the proportion of the length of the transect where reed had been cut relative to the total length of the transect (e.g. 0.2 indicating that reed was cut on 20% of the 100-m length). Evidence of reed cutting was found in eight transects or 27% of $n = 30$ transects. We thus obtained five variables for reed density (mean number of old and new stems, total number of all stems, mean number of stems, proportion of old stems),



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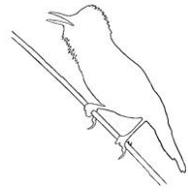
two variables for reed complexity (SD of the mean number of all stems and CV in the number of all stems), and two additional variables potentially reflecting management effects: reed cover, and proportion of transect length cut in each transect. We thus estimated nine variables for reedbed structure to allow for the possibility that responses of bird functional groups will differ by their preferences to different properties of reed.

The survey of Great Reed Warbler nests at Bager Pond (Chapter 3)

Fieldwork was conducted in four breeding seasons from 2008 to 2011, i.e. from May 25 to July 10 in 2008, from May 23 to July 30 in 2009, from May 20 to August 12 in 2010, and from May 17 to July 31 in 2011. The whole area of the pond was completely surveyed for Great Reed Warbler nests. The nests were checked regularly at six-day intervals in 2008 and five-day intervals in 2009, 2010 and 2011. During nest checks, the following data were collected: number of eggs, number of nestlings, number of lost eggs, number of lost nestlings and number of fledglings. Water depth was measured under each nest found. In cases when remains of eggs were found or nestlings disappeared, we concluded that the nest was predated. In all other cases, we recorded nest fate as 'perished'.

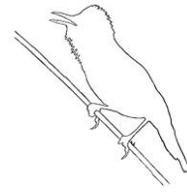
Nest survey and measurement of reed variables (Chapter 4)

Nests were surveyed at 11 locations throughout the entire breeding season in May, June and July in 2011. The physical variables of reed (number and diameter of reed stems) were measured at each nest and its surroundings. The diameters of both the supporting stems and the stems in the surroundings were measured with callipers at nest height; the number of supporting stems was recorded, and the number of stems in the surroundings was counted in a circle (diameter 0.5 m) and was extrapolated to an area of 1 m². The nest was in central position within the circle. Reed densities in the surroundings ranged from 50 to 380 stems/m², and nests were classified into three arithmetically equal-sized reed density categories: "sparse" (50-160 stems/m²), "intermediate" (160-270 stems/m²) and "dense" (270-380 stems/m²). Such an approach appeared reasonable as we wished to ensure similar numbers of nests in



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each of the three reed density categories. All nests found were regularly checked once every fifth or sixth day, when the number of eggs, the number of nestlings and the loss of eggs, the loss of nestlings or the loss of the whole nest were recorded.

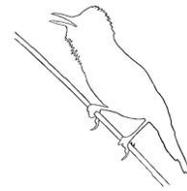


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Statistical analysis

Effects of grassland restoration and management on small mammal assemblages (Chapter 1)

Response variables were the number of species (species richness), and the number of individuals (abundance) of small mammals (rodents, i.e., mice and voles, and shrews). For both response variables, data from traps at one site ($n = 36$ traps) during one sampling period ($n = 5$ nights) were pooled to obtain one datapoint per site and per period (total $n = 48$). Exploratory analyses revealed a highly significant interactive effect of year and season on both species richness and abundance (richness, $F_{1,33} = 43.918$, $p < 0.0001$; abundance, $F_{1,33} = 36.242$, $p < 0.0001$) because richness and abundance increased substantially from spring to autumn in 2011 but not in 2012, while the effect of location was not significant ($p > 0.32$). To evaluate the effects of local and landscape-scale variables on the species richness and abundance of small mammals while also considering this temporal fluctuation, we constructed generalized linear mixed-effects models (GLMMs) with season (spring/autumn) nested within year as a random effect. GLMMs allow the incorporation of nested random effects even when variances are unequal and within-group errors are correlated, and are robust to unbalanced designs (Crawley, 2007). We fitted GLMMs using the ‘glmer’ function of R with Poisson error distribution and log link function, as recommended for count data (R Core Team, 2014). Local predictor variables were elevation (in m) and management (early mowing, late mowing, grazing on restored grasslands, no management on natural grasslands, ploughing on croplands) (**Figure 8**). Landscape-scale predictor variables were the proportion of five habitat types in 400-m buffers around the sampling sites. The five landscape-scale variables were not correlated (Pearson correlation, n.s.). To allow for testing whether predictor variables had similar or different effects in the four sampling periods, we also used sampling period as a fixed effect with four levels.



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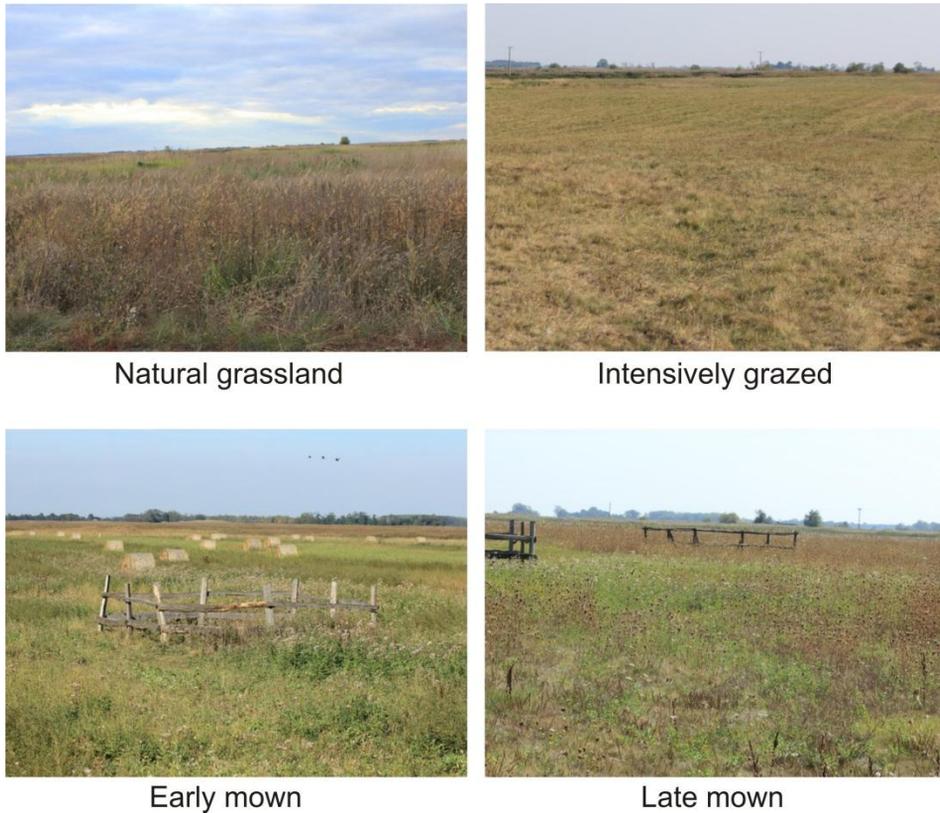
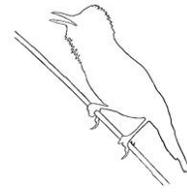


Figure 8. Sampling sites (unmanaged natural grassland and restored grasslands with three different management regimes) in the autumn in the Egyek-Pusztakócs marsh system, 2011-2012.

To test the effect of restoration age on small mammals, we repeated the GLMMs using data only from restored grasslands. In these models, both the local and landscape-scale predictors described above were included, and we also included the time since restoration (in years) to test whether and how small mammal communities change after restoration. In all GLMMs, we started with the full model including all main effects and their interactions with sampling period and removed non-significant terms in a backward stepwise algorithm (removal if $p \geq 0.1$) to obtain minimum adequate models. We then used the reduced model to estimate coefficients for predictors. For post-hoc comparison of management, a categorical variable, we specified contrasts to compare each management type to regularly ploughed croplands (restoration start) in the analysis of all sites, and to grazing in the analyses restricted to restored sites. In



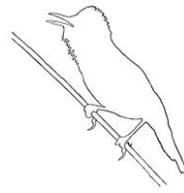
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additional statistical tests, data were log-transformed ($\log x + 1$) for parametric tests (one-way ANOVA), if necessary, to meet the assumptions of homogeneous variances and normally distributed residuals.

We compared the small mammal species composition of restored and natural grasslands and croplands by non-metric multidimensional scaling (NMDS) using Sørensen similarity as implemented in the 'metaMDS' function of the R package 'vegan' (Oksanen et al. 2011). All statistical tests were implemented in R (version 3.1.1.).

Effects of management and reed properties on marshland birds (Chapter 2)

We used General Linear Models (GLM) to model the responses of the bird assemblage to the management treatment and various covariates describing reedbed structure. Response variables in GLMs were species richness, total abundance, Shannon-Wiener and Simpson diversity and evenness for all birds, and species richness and abundance for bird functional groups (e.g. **Figure 9**). Independent variables were management, nine variables of reedbed structure, and water depth. Because there was collinearity among the seven variables describing reed density and complexity (Pearson correlations, $r > 0.53$, $p < 0.01$), we only considered those three combinations of variables which were not correlated (number of old reed stems with S.D. of reed density; number of new reed stems with C.V. of reed density; and proportion of old reed stems with S.D. of reed density). The proportion of reed cover or proportion of reed cut were not related to the reed density or complexity variables, therefore, we entered these variables in all full models. Finally, there was no difference in water depth among the areas with different management actions (one-way ANOVA, $F_5 = 0.434$, $p = 0.821$). Furthermore, there was no significant correlation between water depth and either of the nine variables describing reedbed structure (Spearman correlations, $0.171 < r_s < 0.224$, $p > 0.230$).



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Great Bittern
Botaurus stellaris



Purple Heron
Ardea purpurea



Marsh Harrier
Circus aeruginosus



Blue Throat
Luscinia svecica



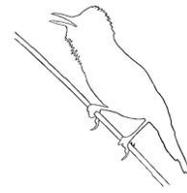
Great Reed Warbler
Acrocephalus arundinaceus



Moustached Warbler
Acrocephalus melanopogon

Figure 9. Common birds of the Fekete-rét marsh. Photographs by the author.

We first ran GLMs to select models that best described our data relative to the three combinations of reed density and complexity variables. We



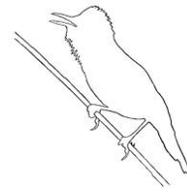
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used Akaike's Information Criterion to select the best of the three models for each response variable. In the second step, we ran the best-fitting full models and applied a backward stepwise algorithm to remove non-significant variables and interaction terms. The final reduced models were then fitted to estimate coefficients and to compare means.

The normality of variables was checked by the Shapiro-Wilk test and the homogeneity of variances was checked by Bartlett tests. One-way ANOVA was used if the assumptions of parametric tests were met, in other cases, we used Kruskal-Wallis tests to analyse the differences between the six treatments. We used the R environment (version 2.15.2) and SPSS 17.0 for statistical analyses.

Factors influencing breeding success in the Great Reed Warbler (Chapter 3)

Breeding success was estimated by the Mayfield method (Mayfield 1975), which uses data on egg-days and nestling-days to estimate egg and nestling survival. In this study, we defined "breeding success" as the probability that an egg produces a fledgling. Two Mayfield's statistics, i.e., the daily survival rate of eggs and that of nestlings, were compared by J-tests (Johnson 1979, Hensler and Nichols 1981) to test which period limits survival. Nest survival was estimated by the Kaplan-Meier survival test. We used one-way ANOVA to compare mean clutch size and number of fledglings among the years. In this study, breeding season is defined as the period between the finding of the first and last nest. The breeding season lasted 28 days in 2008, 40 in 2009, 64 in 2010 and 60 in 2011. The differences in survival between breeding seasons were tested with log-rank (Mantel-Cox) test. Mean clutch size, mean number of nestlings and hatchability of eggs (Mayfield 1975) were also calculated. The correlation between precipitation and breeding success was estimated for the entire breeding season by Spearman rank-correlations. The proportion of lost broods due to adverse weather or predation was tested with Chi-square tests. To study the effect of season, we grouped all nests in two categories based on whether they were first found in the first half of the breeding season (Early group, usually second half of May and the first half of June) or the second half of the breeding season (Late group, second half of June and the first half of July). We applied J-test to



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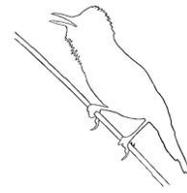
compare overall (2008-2012) and yearly egg and nestling daily survival rate between the Early and Late groups. Furthermore, J-tests were also used to compare daily survival of eggs and nestlings between the Early and Late groups considering years with burning (2009 and 2010) and unburned years (2008 and 2011). Finally, we recorded the condition of the reed around the nest either as fresh reed that had grown up after burning or as mixed, unburned reed that consisted of both old and new reed. We estimated the number of breeding pairs by the number of nests found in managed or in non-managed reed. This was possible because every individual was ringed with aluminium or colour rings (few females were only ringed with aluminium rings), and could be linked to a nest (either was re-captured at the nest or identified based on their colour ring code with binoculars or camera) (**Figure 10**). Polygyny was also recorded but in such cases we considered that each breeding female was one breeding pair. Statistical analyses were calculated in the R statistical environment (version 2.13.0, R Development Core Team 2011) or with the SPSS 17.0 statistical software. Maps were drawn in ArcGIS (version 9.3), and figures were formatted in CorelDraw X3 (version 13.0.0) software.



Figure 10. Great Reed Warbler nestlings and the parent defending the nest.

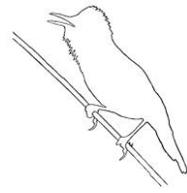
Effects of reed variables on nesting success (Chapter 4)

The basic descriptive statistics (means with standard deviation) of the reed variables were calculated for the supporting stems, for the old and new stems in the surroundings and for both together. We used the non-parametric Spearman correlation to check the relationship between both the number (density) and diameter of the supporting stems and those of the stems in the surroundings, separately for the old and new stems too. One-way ANOVA was used to explore the differences in density of the



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stems in the surroundings, the number of supporting stems per nest, and the diameters of the stems in the surroundings and the supporting stems (mean values) between the three reed habitats (**Table 2**). One-way ANOVA was followed by Tukey's HSD post hoc test to compare groups. Egg-days and nestling-days (Mayfield 1975) were calculated to estimate breeding success in the three reed stem density categories. The J-test (calculated in the program of Halupka 2009) was used to compare two Mayfield statistics, i.e. the daily survival rates of the eggs and the nestlings (Johnson 1979, Hensler and Nichols 1981). The "breeding success rate" was derived from the Mayfield method by Johnson (1979) and Hensler and Nichols (1981), where the number of egg-days, the number of eggs lost, the number of nestling-days and the number of nestlings lost were the basic data. The "hatching rate" is the ratio of the number of hatched nestlings and the number of eggs immediately before hatching. We used one-way ANOVA to check the differences in breeding success between the three reed density categories. The rates of survival of the clutches in the various reed density categories were examined with the log-rank test (corresponding to the Mantel-Cox test). Statistical analyses were carried out with the SPSS software package.



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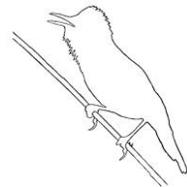
Local habitat management and landscape-scale restoration influence small-mammal communities in grasslands

Introduction

Habitat restorations are rarely implemented at spatial and temporal scales that are beyond the local scale (Lengyel et al. 2014). In most cases, the restoration is typically followed up by monitoring vegetation development, and studies of trophic groups other than plants are scarce (Mortimer et al. 1998, Woodcock et al. 2008, Brudvig 2011). This is surprising because many invertebrate and vertebrate animals are important for ecosystem functioning, and a full evaluation of restoration success needs to integrate higher trophic levels (animals) (Young 2000, Longcore 2003). Despite these calls, the number of studies of restoration effects on vertebrates is still low and most of them focus on birds in forests and shrubs (e.g. Brawn 1998, Germaine and Germaine 2002, Machmer 2002, Hoover 2008).

Small mammals (voles, mice and shrews) play important roles in ecosystems. Most voles and mice are herbivores or granivores and several species hoard plant seeds for storage. Small mammals may thus alter plant species composition (Howe, Brown 2000, Torre et al. 2007) and provide ecosystem services such as seed dispersal (Williams et al. 2001, Schnurr et al. 2004, Mohammadi 2010) and pollination (Vieira et al. 2009). Subterranean small mammals play a role in maintaining soil structure (Medin and Clary 1989). Finally, small mammals are important in grassland food webs, both as consumers or top-down regulators of vegetation and arthropods (e.g. most shrews are insectivores), and as a food resource for reptiles, birds and mammals (Casti n and Gons lbez 1999, Torre et al. 2007, Vieira et al. 2009, Mohammadi 2010).

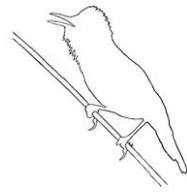
The proportion of grasslands has decreased considerably recently due to agriculture, and grasslands have become the focus of many conservation actions in Europe (Hedberg and Kotowski 2010, Kiehl et al. 2010) and North America (Gerla et al. 2012). The impact of grassland restoration on small mammals has been addressed in a handful of studies in North America. Stone (2007) found that restoration led to a short-term decline



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in the number of captures, total biomass and species richness of small mammals, followed by a partial recovery three to five years after restoration. A comparison of a successional gradient from prairie to forest (Moro and Gadal 2007) showed that time since restoration (abandonment) did not directly affect small mammals and that their abundance was highest in middle, rather than early or late, successional stages, where the structural diversity of vegetation was highest. Finally, in the most comprehensive study of grassland restoration and small mammals to date, Mulligan (2012) found that the colonization of restored fields occurred rapidly and was positively related to the connectivity of habitats, and that restored grasslands served as refuges during regional declines. Only the latter study involved a landscape context, which should be addressed and considered in practice (Brudvig 2011, Lengyel et al. 2014) because local studies may overlook larger-scale factors such as refuges and dispersal corridors that may influence restoration outcome.

This study had three aims. First, we used a chronosequence design (space-for-time substitution) to sample small mammals on natural grasslands (restoration target), restored grasslands (restoration process) and croplands (restoration start). Second, we then analysed the data to evaluate the effects of local factors (management, elevation) and landscape configuration (proportion of natural grasslands, restored grasslands, croplands, woodlands, and linear habitats such as roads and canals) on the species richness, abundance, and composition of small mammal communities. Finally, we further tested whether small mammal communities change with time since restoration, and also evaluated the links between the dynamics of small mammal communities and the spatial and temporal changes in habitats due to weather, restoration and management.



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Results

Number of captures

In total, we captured 421 individuals of 12 species (examples in **Figure 11**). We detected 20 individuals of three species in the spring and 359 individuals of 12 species in the autumn of 2011. In 2012, we caught 24 individuals of five species in the spring and 18 individuals of eight species in the autumn. Recapture rate was on average 9% ($n = 465$ captures total) and ranged between 0 and 30% per site ($n = 12$). Recaptured individuals were counted only once in all statistical analyses.



Bicolored Shrew
Crocidura leucodon



Common Vole
Microtus arvalis

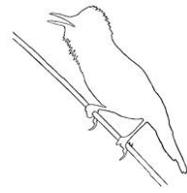


Strip Field Mouse
Apodemus agrarius



Wood Mouse
Apodemus sylvaticus

Figure 11. The most frequently captured small mammal species in the Egyek-Pusztakócs marsh system.



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The number of individuals captured per day was highest on day 4 (croplands and restored grasslands) or on day 3 (natural grasslands) and decreased by day 5 in each of the three habitat types and the proportion of captures peaked either on day 2 or day 4 in the four sampling periods (**Figure 12**). These results indicated that a sampling period of 5 days was adequate to survey small mammals.

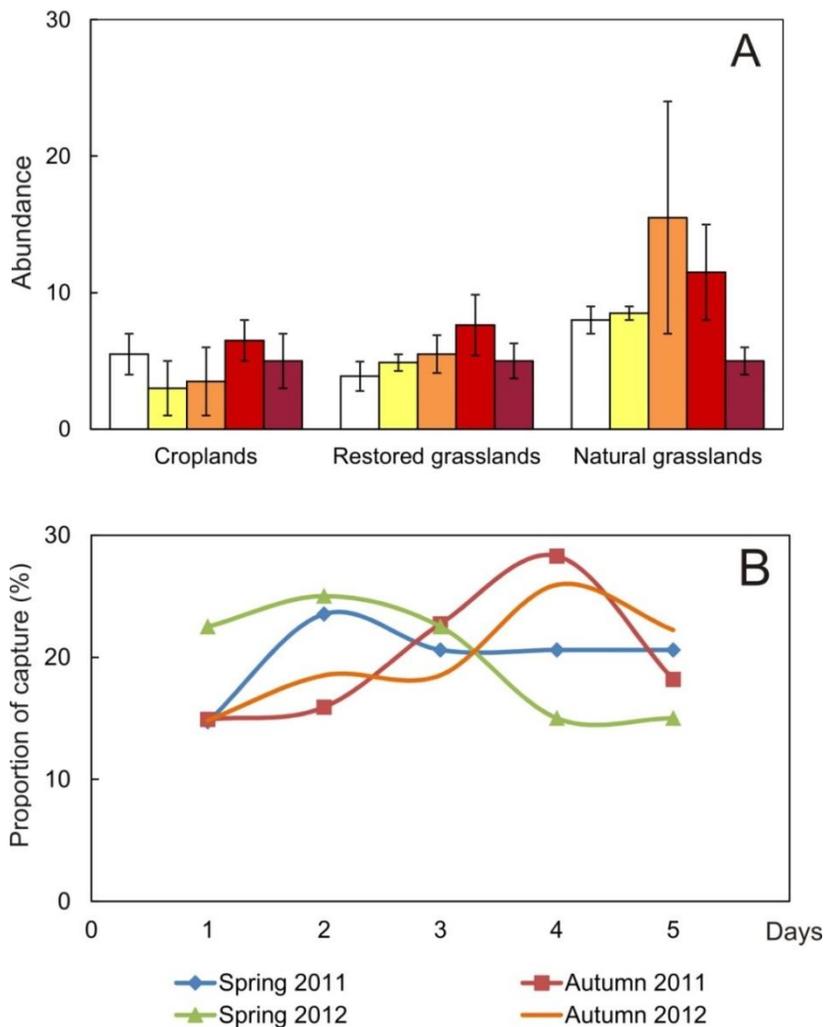
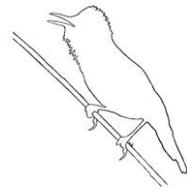


Figure 12. Mean \pm S.E. number of individuals captured on day 1 (white columns) through day 5 (violet column) in three habitat types based on $n = 421$ individuals, with



Effect of grassland restoration on small mammals

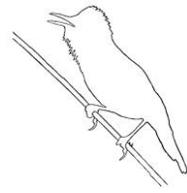
recaptures ($n = 44$) excluded (A), and proportion of all captures falling on day 1 through 5 in the four sampling periods (B).

Local and landscape-scale effects on species richness of small mammals

GLMMs showed that species richness was little influenced by the local and landscape factors studied. There was a weak interaction between sampling period and management (GLMM, $z = 2.178$, $p = 0.029$), likely because the number of species decreased less from autumn 2011 to spring 2012 in late-mown restorations than in other habitat types (**Figure 13A**). Furthermore, there were marginally non-significant effects of sampling period ($z = -1.907$, $p = 0.057$) and of the interaction between sampling period and elevation ($z = 1.915$, $p = 0.056$) on species richness. The latter was mostly because small mammals disappeared from autumn 2011 to spring 2012 in three of four sites under 90 m a.s.l. and only one individual was found in the fourth site. In areas at or above 90 m, at least one individual was caught in five of eight sites (total $n = 23$ individuals), suggesting higher chances for survival during the harsh late winter and spring flooding in early 2012. Neither the remaining local and landscape variables nor their interactions with sampling period influenced species richness significantly.

Local and landscape-scale factors influencing small mammal abundance

At the local scale, the abundance of small mammals was significantly influenced by management, elevation, and interactions between sampling period and management and between sampling period and elevation (**Table 5**). Significant coefficient estimates showed that early-mown restorations had more individuals, whereas late-mown and grazed restorations had fewer individuals than ploughed croplands (**Table 5**), particularly when abundance was generally high (autumn 2011, **Figure 13B**). The interaction between sampling period and management was because abundance decreased more from 2011 to 2012 in early-mown restorations than in late-mown restorations (**Figure 13B**). The interaction between sampling period and elevation was because the relationship between elevation and abundance was negative in autumn 2011 and slightly positive or constant in the three periods of lower abundance (**Figure 14**).



Effect of grassland restoration on small mammals

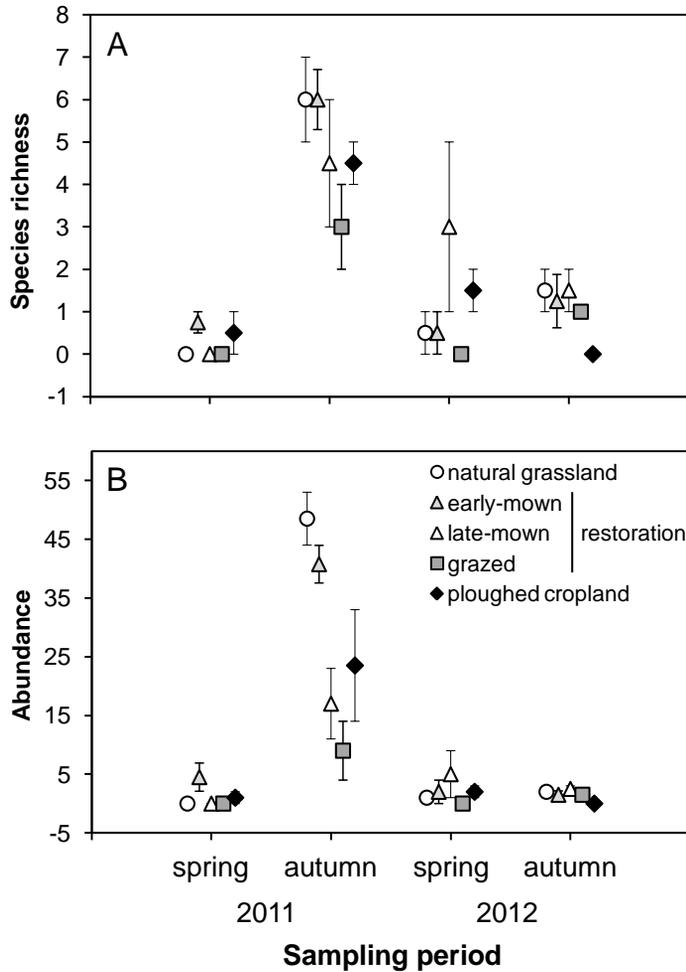
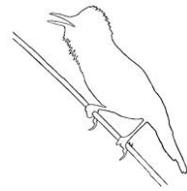


Figure 13. Mean \pm S.E. species richness (A) and abundance (B) in unmanaged natural grasslands, early-mown, late-mown and grazed grassland restorations and ploughed croplands in four sampling periods. Data points were jittered along the X axis for clarity.

In autumn 2011, when abundance was generally high, non-managed natural grasslands had taller vegetation (mean $5.8 \pm$ S.D. 2.98 cm, $n = 72$ traps) than either early-mown (3.6 ± 2.18 , $n = 144$), late-mown (3.5 ± 1.96 , $n = 72$) or grazed restored grasslands (3.2 ± 1.99 , $n = 72$) (one-way ANOVA on log-transformed data, $F_{3,356} = 12.060$, $p < 0.0001$; Tukey HSD-test, $p < 0.001$ for each of the three comparisons), and thus probably provided better chances to avoid predators than did restored grasslands.



Effect of grassland restoration on small mammals

This was supported by a negative correlation between average vegetation height and the number of predators in autumn 2011 (Pearson $r = -0.695$, $n = 10$ grasslands, $p = 0.026$). Predators most often recorded at the sites included Marsh Harrier *Circus aeruginosus*, Common Buzzard *Buteo buteo*, Kestrel *Falco tinnunculus* and Great Egret *Egretta alba*, and other potential predators observed in the vicinity were Red Fox *Vulpes vulpes*, Least Weasel *Mustela nivalis*, European polecat *M. putorius* and Steppe Polecat *M. eversmanii* (e.g. **Figure 15**).

At the landscape scale, the proportion of natural and restored grasslands influenced abundance positively, whereas the proportion of linear habitats had a negative effect on abundance (**Table 5**). None of the interaction terms between landscape variables and either sampling period or management influenced abundance significantly.

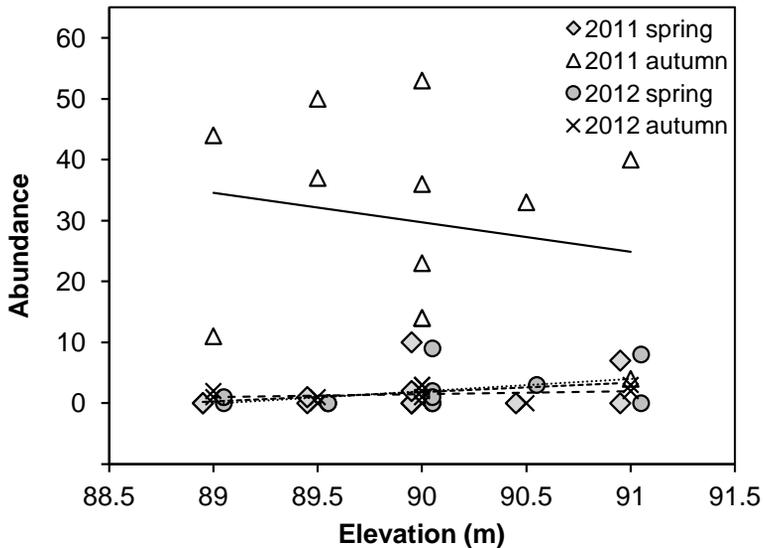
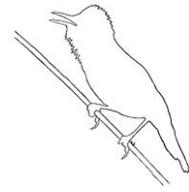


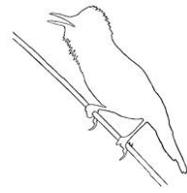
Figure 14. Relationships between abundance of small mammals and elevation. Spring datapoints were jittered along the X axis for clarity and lines are for visual guidance only (please see statistics in Table 5).



Effect of grassland restoration on small mammals

Table 5. Results of generalized linear mixed-effects models testing the effects of management, elevation and landscape variables on abundance of small mammals (random effect: season within year) in all sites and in restored grasslands only. Significant effects are highlighted in Bold.

Response	Parameters	Estimate \pm S.E.	z value	Pr(> z)
Abundance (all sites)	(Intercept)	79.52 \pm 37.444	2.124	0.034
	Sampling period	-44.31 \pm 16.942	-2.616	0.009
	Management _{None}	-0.08 \pm 0.560	-0.140	0.888
	Management_{Early-mown}	1.99 \pm 0.417	4.762	< 0.0001
	Management_{Late-mown}	-2.20 \pm 0.514	-4.275	< 0.0001
	Management_{Grazed}	-1.80 \pm 0.677	-2.659	0.008
	Elevation	-0.89 \pm 0.417	-2.106	0.035
	Proportion of grassland	1.85 \pm 0.817	2.269	0.023
	Proportion of restoration	1.59 \pm 0.703	2.262	0.023
	Proportion of linear habitats	-35.78 \pm 11.824	-3.026	0.002
	Period \times Mgmt _{None}	0.07 \pm 0.204	0.344	0.731
	Period \times Mgmt_{Early-mown}	-0.64 \pm 0.186	-3.452	0.001
	Period \times Mgmt_{Late-mown}	0.88 \pm 0.208	4.238	< 0.0001
	Period \times Mgmt _{Grazed}	0.24 \pm 0.285	0.830	0.407
Period \times Elevation	0.49 \pm 0.188	2.609	0.009	
Abundance (restored sites)	Sampling period	-34.76 \pm 17.135	-2.028	0.043
	Management_{Early-mown}	2.11 \pm 0.395	5.343	< 0.0001
	Management_{Late-mown}	-0.97 \pm 0.460	-2.100	0.036
	Elevation	-0.36 \pm 0.430	-0.831	0.406
	Restoration age	-0.47 \pm 0.146	-3.204	0.001
	Proportion of cropland	3.56 \pm 1.670	2.132	0.033
	Proportion of linear habitat	29.24 \pm 14.529	2.012	0.044
	Period \times Mgmt_{Early-mown}	-0.68 \pm 0.173	-3.914	< 0.0001
	Period \times Mgmt_{Late-mown}	0.57 \pm 0.188	3.006	0.003
Period \times Elevation	0.39 \pm 0.190	2.027	0.043	



Effect of grassland restoration on small mammals



Kestrel
Falco tinnunculus



Least Weasel
Mustela nivalis

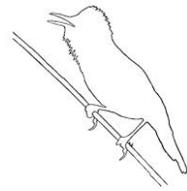
Figure 15. Frequently observed predators of small mammals in the Egyek-Pusztakócs marsh system. Photographs by the author.

Differences by restoration age

In the smaller sample of restored fields ($n = 8$), restoration age strongly influenced species richness (GLMM, $z = 29.020$, $p < 0.0001$) because sites restored in 2005 had fewer species ($1.3 \pm \text{SE } 0.74$) than sites restored in later years (2006: 2.3 ± 0.67 , 2007: 2.3 ± 0.80 , 2008: 1.9 ± 0.99). Restoration age also influenced the abundance of small mammals (**Table 5**), however, no consistent temporal trend could be observed (2005: 5.4 ± 4.54 , 2006: 13.3 ± 5.54 , 2007: 6.3 ± 2.82 , 2008: 8.4 ± 6.18).

Population variables

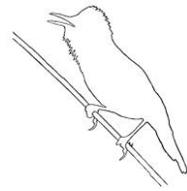
The proportion of females was significantly higher than expected based on unity in the autumn periods in both years (**Table 6**; 2011: 70%, $n = 277$, $\chi^2_1 = 42.892$, $p < 0.0001$; 2012: 82%, $n = 11$, $\chi^2_1 = 4.454$, $p = 0.035$), but not in the spring, when sexes were equally represented (2011: 50%, $n = 20$; 2012: 50%, $n = 24$). The proportion of gravid or lactating females was significantly higher in 2011 (30%, $n = 203$) than in 2012 (9.5%, $n = 21$) ($\chi^2_1 = 4.120$, $p = 0.042$). The proportion of juveniles caught in the autumn, however, was slightly higher in 2012 (39%, $n = 18$) than in 2011 (20%, $n = 345$) ($\chi^2_1 = 3.839$, $p = 0.050$). We found no juveniles in the spring of either year. There was no difference among habitat types, by management or by restoration age in adult sex ratio, proportion of gravid or lactating females, or proportion of juveniles (results not shown).



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Table 6. Number of individuals by species and age/sex in the four sampling periods.

Species	Year	Season	Male	Female (gravid/lactating)	Juveniles (male/female)
<i>Sorex araneus</i>	2011	spring autumn	3	4	
	2012	spring autumn	1	1	
<i>S. minutus</i>	2011	spring autumn	1	3 (1)	
	2012	spring autumn		2	
<i>Crocidura leucodon</i>	2011	spring autumn	12	1 (1) 47 (7)	1 (0/1)
	2012	spring autumn			1 (0/1)
<i>C. suaveolens</i>	2011	spring autumn	2	5 (2)	
	2012	spring autumn		1	
<i>Apodemus agrarius</i>	2011	spring autumn	15	16	3 (1/2)
	2012	spring autumn	3		
<i>A. flavicollis</i>	2011	spring autumn	1		
	2012	spring autumn		1	
<i>A. sylvaticus</i>	2011	spring autumn	7	6 (1)	5 (3/2)
	2012	spring autumn		1	
<i>A. uraliensis</i>	2011	spring autumn	2		
	2012	spring autumn		2 1	
<i>Mus spicilegus</i>	2011	spring autumn	2 6	6	
	2012	spring autumn	2	1	
<i>Micromys minutus</i>	2011	spring autumn		3	
	2012	spring autumn			
<i>Microtus arvalis</i>	2011	spring autumn	8 35	9 (3) 100 (47)	58 (12/46)
	2012	spring	7	8 (1)	



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		autumn		3 (1)	6 (2/4)
<i>M. subterraneus</i>	2011	spring			
		autumn		3	1 (1/0)
	2012	spring			
		autumn			
Total	2011	spring	10	10 (4)	0
		autumn	84	193 (58)	68 (17/51)
	2012	spring	12	12 (1)	0
		autumn	2	9 (1)	7 (2/5)

The body mass of adult Common Voles *Microtus arvalis* was significantly lower in 2012 than in 2011, both in spring and autumn (**Figure 16**). However, the body mass of Common Voles did not vary either with habitat type or management when year was also included in two-way ANOVAs (habitat type $F_{2,169} = 0.489$, $p = 0.614$; management $F_{1,167} = 0.644$, $p = 0.632$).

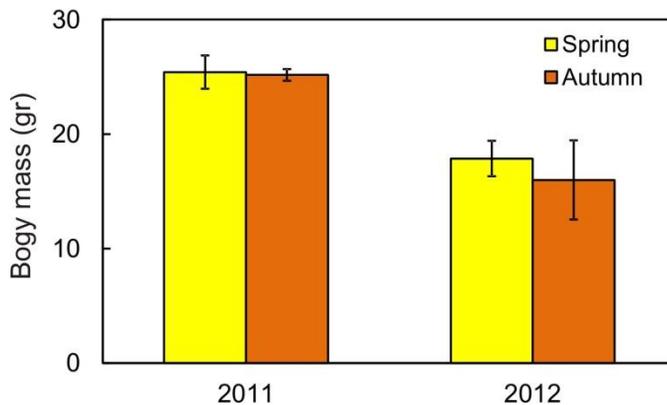
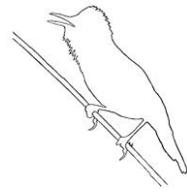


Figure 16. Mean \pm S.E. body mass (in grams) of Common Voles *Microtus arvalis* in croplands, and restored and natural grasslands of the Egyek-Pusztakócs marsh system in E-Hungary. Sample sizes from left to right are 17, 138, 15 and 3 individuals. Two-way ANOVA, Year $F_{1,169} = 16.694$, $p < 0.001$; Season $F_{1,169} = 0.265$, $p = 0.608$; interaction $F_{1,169} = 0.158$, $p = 0.691$).

Changes in species composition

Ordination based on NMDS showed that species composition varied greatly through the four sampling periods (**Figure 17**). There was no sign of a clear separation of species composition of the sites either by habitat type or management. The extent of the scatter of centroids confirmed that



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species composition was most diverse in autumn 2011, in the period of highest abundance, followed by 2012 autumn and the two spring periods (**Figure 17**).

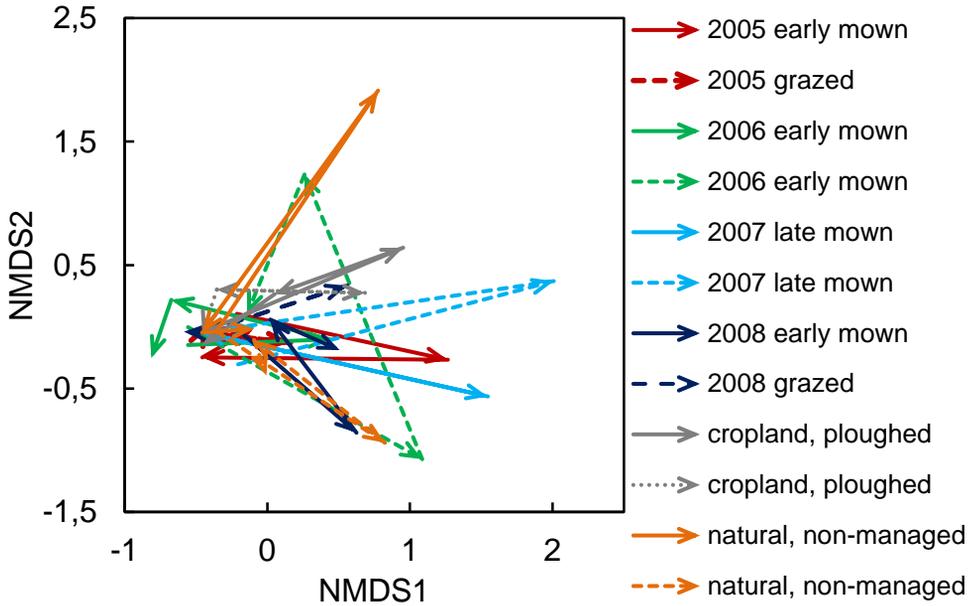
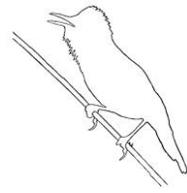


Figure 17. Changes in species composition of small mammals on restored grasslands (indicated by year of restoration and management), croplands and natural grasslands in four sampling periods from spring 2011 to autumn 2012. Symbols are omitted for clarity and arrows indicate temporal trends (trajectories). Ordination was conducted by non-metric multidimensional scaling using Sørensen similarity based on the presence/absence of species.



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Spatial distribution of small mammal species

The Common Vole was the most ubiquitous species (**Figure 18**). Although in the autumn this species was present almost everywhere (in 2011) or at most (67%) of the sites where small mammals were caught (in 2012, $n = 9$), in the spring of both years it was found only in the eastern part of the study area, which is thus a likely stronghold of the population. *Crocidura leucodon* was the second most common species in 2011, but disappeared from all but one (an eastern) site in 2012, where a single individual was captured. Other shrews, e.g. *C. suaveolens*, *Sorex araneus*, and *S. minutus*, were less common and were concentrated in the eastern part of the study area.

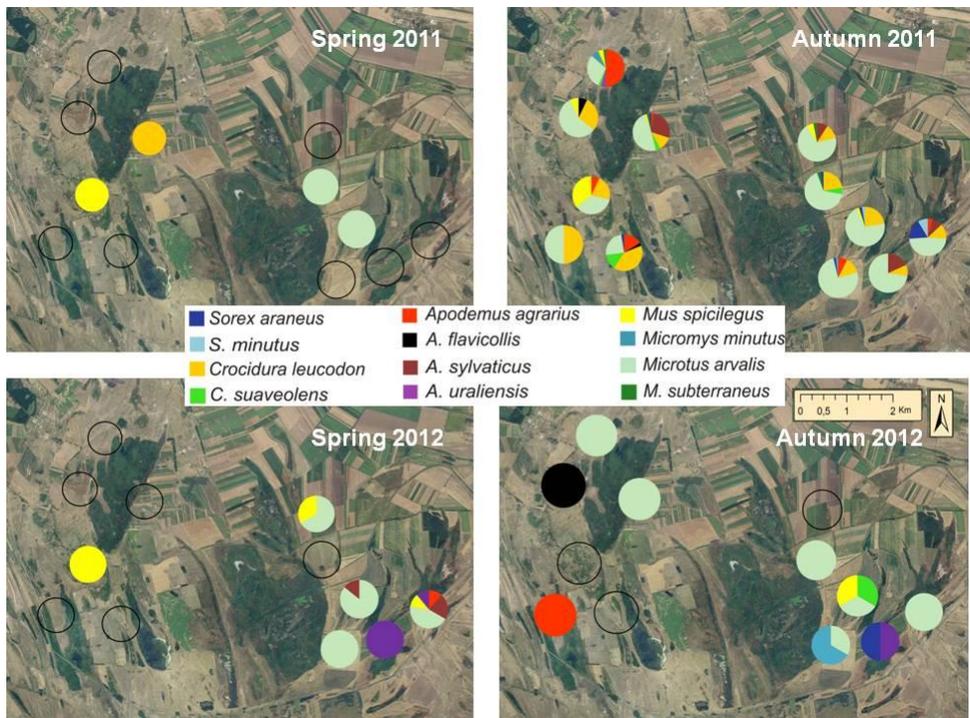
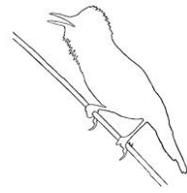


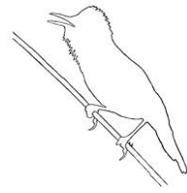
Figure 18. Spatial pattern of species occurrences in the four sampling periods.

Apodemus mice showed patchy distributions in the studied area. In both autumn periods, *Apodemus agrarius* was more common and *A. flavicollis* occurred only in the western part, while *A. sylvaticus* was present at three (in 2011) or two sites (in 2012) in the eastern part of the marsh system,



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although the latter was also caught at one western site in autumn 2011. *A. uraliensis* was captured at only one western site in autumn 2011 and two eastern sites in 2012. *Mus spicilegus* was caught at seven sites in 2011 and three in 2012, with two of the 2012 sites being the same as in 2011. One western site (a cropland) appeared particularly important as the species was detected here in both spring periods. *Microtus subterraneus* was recorded only in autumn 2011 at two northern sites each in the eastern and the western parts. Finally, *Micromys minutus* occurred only at one site and only in autumn 2011 ($n = 3$ individuals) (**Figure 18**).



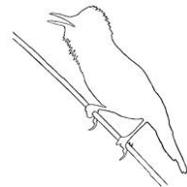
Effect of grassland restoration on small mammals

Discussion

At the local scale, management had the largest influence on small mammals. The management effect was mediated by vegetation height because sites with taller vegetation had more species and individuals than sites with lower vegetation. Elevation was also important because higher areas provided better chances for survival during unfavourable periods such as floods. At the landscape scale, small mammals were influenced positively by the proportion of natural and restored grasslands and negatively by the proportion of linear habitats. These results suggest that restored grasslands can be important landscape-level refuges, although when conditions are favourable, e.g. in autumn 2011, local management and not restoration or time since restoration *per se* appears to be most important in shaping small mammal communities in grasslands. Our study is the first to provide evidence of both local and landscape-scale factors influencing small mammal assemblages after grassland restoration. The patterns found support the view that the effects of population fluctuations and restoration are difficult to disentangle and that restorations play an unexpected but important role as refuges during regional declines of small mammals (Mulligan, 2012).

Several results showed that restoration provided habitats that were comparable or better than croplands for small mammals. Only three restorations and one cropland had small mammals after the spring 2011 bottleneck, and only restorations and natural grasslands had small mammals after the extreme summer drought of 2012. Moreover, the proportion of restored grasslands positively affected small mammal abundance after spring flood in 2011 and the summer drought of 2012. These results show that in only three to six years, restoration can lead to grasslands that serve as refuges for small mammals during unfavourable periods.

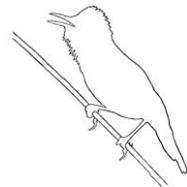
Our results also suggest that the effect of management was mediated by vegetation height. Vegetation cover was highest in unmanaged areas, and was low in mown or grazed sites in autumn 2011, and predators were more numerous in sites with lower vegetation. These patterns may explain the differences in small mammal abundance because vegetation provides safe microsites for the movement, hiding, feeding or food gathering activities of small mammals (Moro and Gadal 2007). The risks



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of predation on small mammals both by birds and mammals are probably higher when vegetation cover is low because small mammals can be more easily spotted and captured by predators at sites with poor vegetation cover (Sutherland and Dickman 1999). In extremely dry years such as 2012, areas with higher vegetation cover probably also provided more abundant food than areas which are mowed or grazed. A study in Switzerland found the highest density of small mammals in non-mown grasslands (Aschwanden et al. 2007), whereas an African study found that intensive grazing negatively affects the abundance and diversity of small mammals (Yarnell et al. 2007). Consequently, the differences in abundance in relation to management found here are likely to exist due to the mediating effect of vegetation cover.

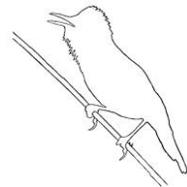
Our results showed that the large temporal, weather-driven fluctuations typical in small mammal communities (Merritt et al. 2001, Butet et al. 2006) may be modified by both local effects (elevation, management) and landscape-scale effects (proportion of restored/natural grasslands). Almost all species disappeared from lower-lying areas (< 90 m a.s.l.) during the winter, whereas populations of some species survived in higher areas. Higher areas may thus be particularly important refuges for several small mammal species during harsh winters and springs with extensive floods (Wijnhoven et al. 2005). During the winter, small mammal populations typically decrease to a minimum due to the combined effects of predation, cold weather, food shortage or competition for resources (Hansen et al. 1999, Aars and Ims 2002). The chances of successful survival during the winter are highest in refuge patches where vegetation cover is high enough and food supply is adequate (van Deventer and Nel 2006). Our observations followed these patterns because species richness and abundance increased with the proportion of restored or natural grasslands around the sites in each spring period, but they also provided further insight. For example, the connectivity of patches, as estimated by the proportion of linear habitats, negatively affected small mammal richness in spring 2012, likely due to the higher exposure of individuals to predators. These patterns suggest that homogeneous patches that are rich in natural and restored grasslands with no management or early mowing and that are poor in croplands, roads or canals thus can serve as refuges and can mitigate the fluctuations of small mammals.



Effect of grassland restoration on small mammals

The lack of a direct, local effect of restoration on small mammals is likely to be related to their broad food spectrum and life history traits (fast reproduction, good dispersal ability, quick colonization after local extinction etc.). The studied restoration led to the acceleration of secondary succession in vegetation development towards the target natural grasslands, with grassland-dominated vegetation forming as early as Year 2 after restoration (Lengyel et al. 2012). The species composition of arthropods (orthopterans, true bugs, spiders, carabid beetles) also changed considerably from Year 1 to Year 2 because species characteristic to target grasslands appeared in greater numbers in Year 2 and after (Déri et al. 2011). In only four years, the species richness of orthopterans (crickets and grasshoppers) has doubled and their abundance increased nearly ten-fold on restored grasslands compared to croplands (Rácz et al. 2013). The restoration of phytophagous insects, most of which specialize on certain plants, positively correlated with the restoration success of the vegetation in restored calcareous and mesotrophic grasslands (Woodcock et al. 2010), indicating that more specialized animal groups may more closely follow the vegetation restoration process. Our previous results with plant-feeding arthropod groups (Déri et al. 2011, Rácz et al. 2013, Lengyel et al. 2014) conformed to this explanation as their species richness, composition and abundance generally progressed gradually towards those of natural grasslands. In contrast, there was no such close post-restoration temporal tendencies in small mammal communities, because there was no clear temporal trends either in species richness, composition or abundance. This can be explained by the small mammals' generalist ecological characteristics and fast spatial and temporal population dynamics of local extinction and recolonization. The generally broad food spectrum and the life history characteristics of small mammals, in combination with their weather-driven population dynamics, make it likely that the restoration of small mammal communities does not correlate well with the restoration process of vegetation or other animal taxa.

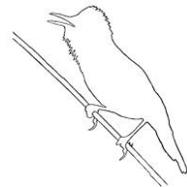
Population variables provided further insight into the annual changes in small mammals and weather as the underlying factor of these changes. In 2011, both the proportion of gravid or lactating females and the body mass of adult Common Voles were higher than in 2012. Spring and summer weather in 2011 was close to average but in 2012 these two seasons were extremely dry. The long drought in 2012 led to the drying



Effect of grassland restoration on small mammals

of grasses and forbs, and thus a shortage of green plant material, and, presumably, seeds, by early July. This food shortage may have resulted both in poorer body condition and the disruption of the reproductive cycle of voles, which can explain lower adult body mass and fewer gravid/lactating females in 2012 than in 2011. Food availability and quality are known to influence body growth rates, proportion of adults, reproductive activity and population density in a related species, the North American Prairie Vole *Microtus ochrogaster* (Desy and Batzli 1989, van Deventer and Nel 2006). A study conducted on the Iberian Peninsula reported that the body mass of the endemic *Microtus cabreræ* did not vary between seasons, but that it decreased from summer to winter, which was linked to food availability (Fernández-Salvador et al. 2005). In our study, the proportion of juveniles caught in the autumn, however, was slightly higher in 2012 than in 2011, which could be expected if adults of 2012, which weighed only 60% of the body mass of adults of 2011, also had lower survival.

The eastern part of the study site was a stronghold for the four shrew species, i.e. *Crocidura leucodon*, *C. suaveolens*, *Sorex araneus* and *S. minutus*, for two mouse species, i.e. *Apodemus sylvaticus* in 2011, *A. uraliensis* in 2012, and the commonest vole species (*M. arvalis*), whereas the western part appeared more important for only two mouse species (*Apodemus agrarius*, *A. flavicollis*). One reason for this difference may be that the landscape surrounding the eastern sites contained more grasslands (on average 70% vs. 57%, of which restored grasslands were 42% vs. 27%, respectively), slightly more woodlands (1.5% vs. 0.5%) and fewer wetlands (11% vs. 28%) than those of the western sites. Such landscape structure could provide more extensive or better feeding sites during summer droughts for both granivores/herbivores (mice and voles) and insectivores (shrews). The strong positive correlation between the proportion of grasslands and richness/abundance in autumn 2012 supports this explanation. Alternatively, it is also possible that habitats near the eastern sites provided better conditions for the overwinter survival of small mammals. This explanation is likely because, apart from one *M. spicilegus* individual, no small mammals were recorded in the spring of 2012 at any of the western sites (**Figure 18**), whereas 23 individuals of five species were detected at the eastern sites in the same period.

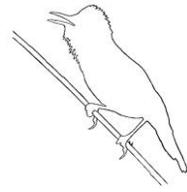


Effect of grassland restoration on small mammals

Our results throw light on important aspects of the temporal and spatial dynamics of small mammal assemblages, which influence ecosystem development after restoration. Our results show that the effects small mammals exert in grassland ecosystems (influencing plant species composition, seed dispersal, pollination, soil structure maintenance etc.) are not similarly present across seasons and years. The lesson these results teach about ecosystem services is that the natural (weather-determined) fluctuations in ecosystem service provider taxa, such as small mammals, need to be considered in biodiversity monitoring and incorporated in evaluations of ecosystem services. Our results suggest that at least some ecosystem services are temporally not stable, which needs to be reflected in the design and implementation of conservation actions for such services.

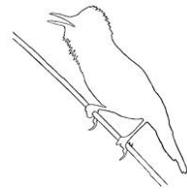
To our knowledge, this study is the first systematic study in Hungary that reports on species composition and abundance of small mammal assemblages inhabiting steppe-like grasslands. Other small mammal monitoring projects were conducted in shrubs, forests, marshes or tall weedy habitats. The only recent report on small mammals occurring in the study region comes from Dr. Zoltán Bihari, who surveyed small mammals in intensive, conventionally managed croplands (where pesticides and fertilizers are widely used) and extensive croplands, which were cultivated without the use of chemicals as part of the Egyek-Pusztakócs LIFE-Nature project. This survey (outlined in section 4 of the Monitoring Report of the LIFE-Nature project, http://life2004.hnp.hu/Pdf/EPuLIFE_MonitoringReport_EN.pdf) found 11 species of small mammals, of which the common vole *M. arvalis* and the steppe mouse *Mus spicilegus* were the most frequent. The maximum abundance of small mammals in extensive croplands was estimated at above 500 individuals per hectare, with the largest difference between extensive and intensive croplands in maize (corn) fields, mostly due to steppe mice. However, these data originate from various survey methods (hole counts, pellets mainly from Barn Owls, footprints and limited use of five live traps for short periods) in late summer of 2007 in agricultural habitats other than those surveyed in our study, which makes a direct comparison of the results with those of our study difficult.

Novelty of the study: Local and landscape factors weakly influenced species richness. At the local scale, the abundance of small mammals was



Effect of grassland restoration on small mammals

significantly influenced by management, elevation, and interactions between sampling period and management and between sampling period and elevation. The abundance of small mammals was highest non-managed natural grasslands and in early-mown restorations. Sites at higher elevation provided refuges during spring floods and summer droughts. At landscape scale, the proportion of grasslands positively influenced small mammal abundance, while linear habitats had a negative influence on abundance, especially during unfavourable periods. These results suggest that restorations provide landscape-scale benefits by increasing the area of grasslands that serve as refuges for small mammals in unfavourable periods.



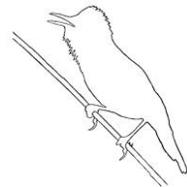
Chapter 2

Habitat management varying in space and time: the effects of grazing and fire management on marshland birds

Introduction

Habitat management for biodiversity conservation is usually guided by the species-area relationship (SAR) and the intermediate disturbance hypothesis (IDH). According to the SAR, the number of species generally increases with area (Connor and McCoy 2001, Pan 2013), thus, management of larger habitat patches should conserve more species. However, the relationship between the area and number of species is not linear; initially the increment of the species is fast, but becomes slower as area increases (Celada and Bogliani 1993, Báldi and Kisbenedek 2000, Paracuellos and Tellería 2004). According to the IDH, species diversity is maximized at intermediate levels of ecological disturbance (Schwilk et al. 1997, McCabe and Gotelli 2000). At low levels of disturbance, the diversity of species often decreases due to biotic homogenization (Lockwood and McKinney 2001). For example, in reed habitats, the characteristics and physiognomic structure of habitats becomes homogeneous in the absence of disturbance by mowing, cutting, flooding, or burning, at both the local and landscape scales (Lougheed et al. 2008). Under appropriate long-term management, the homogeneous structure of the reed habitat breaks up and a more heterogeneous structure is formed, which provides more suitable habitats for a wider spectrum of species through complexity in vegetation structure, and composition, density and biomass (Christensen 1997, Wiens 1997).

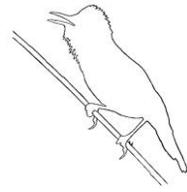
Freshwater wetlands are of outstanding importance for biodiversity and have become a priority in conservation (Schweiger et al. 2002, Bobbink et al. 2006). Wetlands have decreased considerably in size, number and quality in the last century in Europe (and in Hungary, Vásárhelyi 1995). Although wetlands have been subject to intensive research in conservation and restoration (Wheeler et al. 1995, Wagner et al. 2008), little is known about the appropriate spatiotemporal allocation and impact of reedbed management in wetlands (Ausden et al. 2005). The theory of adaptive ecosystem management has been present since the 1980s, but areas available for management are rarely large enough to accommodate



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and experiment with different management regimes (Groom et al. 2006). In temperate grasslands, spatiotemporally variable management by prescribed fire and by grazing resulted in highly heterogeneous habitats (Vinton et al. 1993, Hartnett et al. 1996, Fuhlendorf and Engle 2001). In most wetland studies, sampling areas are too small (under 1 ha) to evaluate the effects of disturbance or the undisturbed operation of natural ecological processes on higher taxonomic groups (Wagner et al. 2008). In addition, most studies followed up only one management action and focused on invertebrates (Ditlhogo et al. 1992, Ausden et al. 2005, Schmidt et al. 2005, Hardman et al. 2012). As a result, we generally know little on how spatiotemporally variable management affects vertebrates, their habitats and the ecological processes.

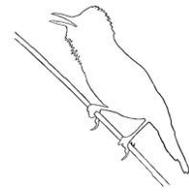
The management of reedbeds includes various actions such as periodical flooding (Graveland 1998, Poulin et al. 2002), mowing or cutting (harvesting, Poulin and Lefebvre 2002, Vadász et al. 2008), burning (Moga et al. 2010), grazing/trampling, excavating and herbicide application, or their combination (e.g. burning and cutting in Báldi and Moskát 1995). While effects such as grazing, change in water level, and burning may be considered threats under uncontrolled conditions, they can be important conservation measures as part of a management strategy aiming to apply these effects as controlled disturbances (Margoluis et al. 2009, Salafsky et al. 2009). A meta-analysis of 21 European studies on the effect of reed management by Valkama et al. (2008) found that management by harvesting, burning, mowing and grazing alters the structure of reedbeds, with reed, *Phragmites australis*, stems becoming shorter and denser in managed sites compared to non-managed ones. Plant species richness usually increases by management but invertebrate richness decreases after 1-2 years of management. In birds, the abundance of passerine species decreases on average by 60% after burning and reed harvesting (Valkama et al. 2008). Many reedbed-breeding passerines, mainly *Acrocephalus* warblers, actively avoid cut areas, while others show decreased abundance and diversity (Poulin and Lefebvre 2002, Vadász et al. 2008). Some reed songbirds, however, use managed areas, for example, the Aquatic Warbler, *Acrocephalus paludicola*, prefers cut reed stands (Tanneberger et al. 2009), while the Stonechat, *Saxicola torquatus*, and Marsh Warbler, *A. palustris*, prefer burned reed (Moga et al. 2010). We know much less on how reed management influences non-passerine birds. In addition, little is known on whether there are



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interactive or synergistic effects of two different management actions on birds (Valkama et al. 2008) to maximize their diversity and abundance in reedbeds.

The aim of this study was to evaluate the impact of spatiotemporally variable management by grazing and burning on marshland bird communities and functional groups. I addressed the following questions: (1) Do the responses of the bird community or functional groups to management differ by the type or regime of management? (2) Do the responses differ among bird functional groups including both passerines and non-passerines? (3) Is there interaction or synergy between the impacts of management by grazing and management by burning? To answer these questions, I applied a quasi-experimental approach in which experimental units (line transects combined with point counts) were replicated in similarly managed areas along a gradient of no management, one treatment (grazing), or two treatments (grazing and burning).



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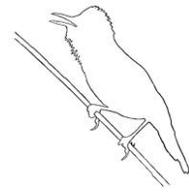
Results

Number of species and individuals observed

I recorded 1063 individuals of 45 bird species (**Table 7**; few species presented on **Figure 9**). The number of species breeding in the marsh or the surrounding area was 39 (n = 965 individuals), whereas migrants included 6 species (n = 98 individuals). Most birds were reed songbirds (49.5%), followed by gulls and terns (20.3%), wading birds (9.2%), ducks and geese (6.5%), farmland songbirds (5.8%) and rails, coots and grebes (4.8%). Three groups (storks and herons; cormorants; raptors) were represented by < 3% of the individuals and were not analysed by GLMs. The mean number of individuals per transect was $35.4 \pm$ (S.D.) 20.17.

Table 7. Functional groups, bird species and their abundance (total number of individuals) recorded in line transects in Fekete-rét marsh.

Functional group	English name	Scientific name	Abundance
Ducks and geese	Mallard	<i>Anas platyrhynchos</i>	16
	Garganey	<i>Anas querquedula</i>	18
	Greylag Goose	<i>Anser anser</i>	19
	Pochard	<i>Aythya ferina</i>	1
	Ferruginous Duck	<i>Aythya nyroca</i>	15
Cormorants	Great Cormorant	<i>Phalacrocorax carbo</i>	3
	Pygmy Cormorant	<i>Phalacrocorax pygmeus</i>	6
Storks and herons	Purple Heron	<i>Ardea purpurea</i>	5
	Bittern	<i>Botaurus stellaris</i>	4
	White Stork	<i>Ciconia ciconia</i>	2
	Great Egret	<i>Egretta alba</i>	3
	Little Egret	<i>Egretta garzetta</i>	5
	Little Bittern	<i>Ixobrychus minutus</i>	1
	Night Heron	<i>Nycticorax nycticorax</i>	1
Spoonbill	<i>Platalea leucorodia</i>	1	
Raptors	Marsh Harrier	<i>Circus aeruginosus</i>	1
	Kestrel	<i>Falco tinnunculus</i>	6
Rails, coots and grebes	Coot	<i>Fulica atra</i>	28
	Little Crake	<i>Porzana parva</i>	2
	Water rail	<i>Rallus aquaticus</i>	18
	Little Grebe	<i>Tachybaptus ruficollis</i>	3

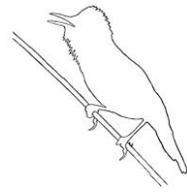


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Shorebirds	Common Snipe	<i>Gallinago gallinago</i>	5
	Black-winged Stilt	<i>Himantopus himantopus</i>	2
	Wood Sandpiper	<i>Tringa glareola</i>	78
	Redshank	<i>Tringa totanus</i>	3
	Lapwing	<i>Vanellus vanellus</i>	10
Gulls and terns	Black Tern	<i>Chlidonias niger</i>	208
	Black-headed Gull	<i>Larus ridibundus</i>	7
	Common Tern	<i>Sterna hirundo</i>	1
Reed songbirds	Great Reed Warbler	<i>Acrocephalus arundinaceus</i>	13
	Moustached Warbler	<i>Acrocephalus melanopogon</i>	13
	Sedge Warbler	<i>Acrocephalus schoenobaenus</i>	114
	Reed Warbler	<i>Acrocephalus scirpaceus</i>	63
	Reed Bunting	<i>Emberiza schoeniclus</i>	47
	Savi's Warbler	<i>Locustella luscinioides</i>	88
	Grasshopper Warbler	<i>Locustella naevia</i>	1
	Bluethroat	<i>Luscinia svecica</i>	71
	Yellow Wagtail	<i>Motacilla flava</i>	57
	Bearded Reedling	<i>Panurus biarmicus</i>	59
Farmland birds	Skylark	<i>Alauda arvensis</i>	35
	Barn Swallow	<i>Hirundo rustica</i>	25
	Corn Bunting	<i>Miliaria calandra</i>	1
	Whinchat	<i>Saxicola rubetra</i>	1
	Hooded Crow	<i>Corvus cornix</i>	1
Other	Common Cuckoo	<i>Cuculus canorus</i>	2
Total			1063

Effects on management on the bird community

The Shannon and Simpson diversity as well as the evenness of bird communities were significantly affected by management, whereas total species richness and abundance were not (**Table 8, Figure 20**). Shannon diversity and evenness were low in grazed patches burned twice and were uniformly high in all other treatments (**Figure 20C, E**), whereas Simpson diversity was highest in grazed patches burned twice and lower in all other treatments (**Figure 20D**). Species richness was not affected by any of the factors studied, although the effect of reed complexity was marginally non-significant (**Table 8**). Abundance appeared to be higher



Marshland management influences birds communities

in grazed patches with recent burning (burned in 2009 and burned twice), although large variation did not result in statistically significant differences among treatments (**Figure 20B**). Rather, bird abundance was negatively affected both by reed cover and water depth (**Table 8**), indicating more birds in transects with more open water and with shallower water.

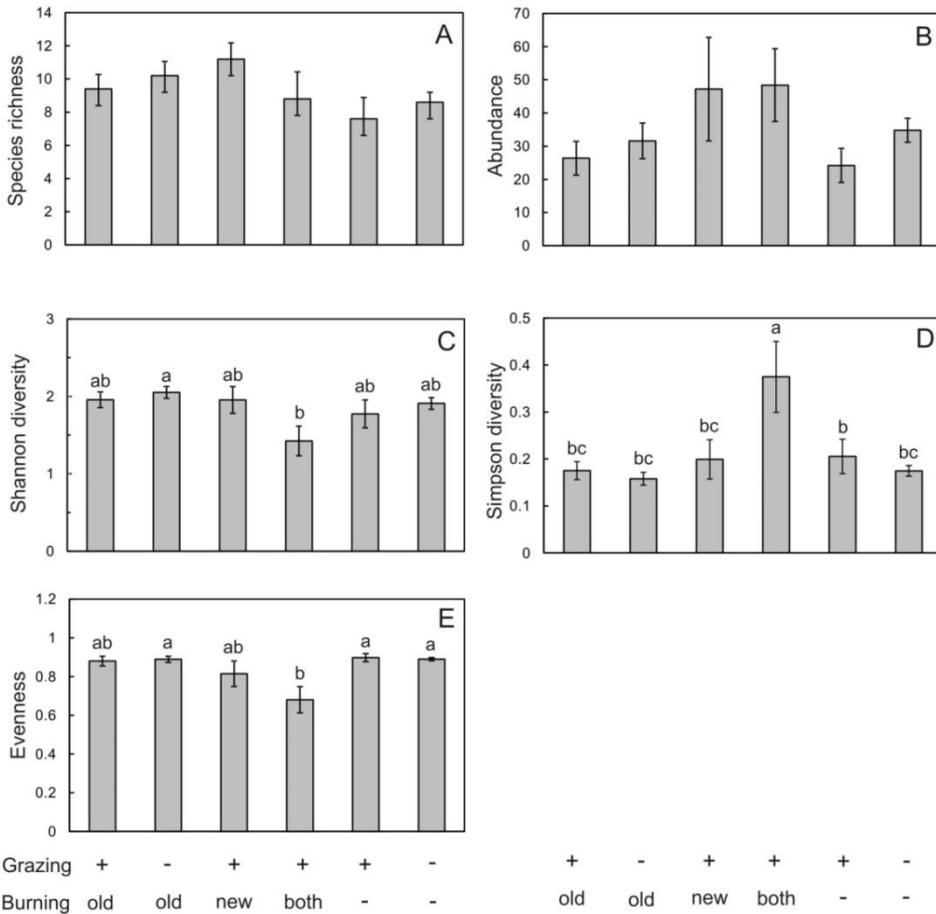
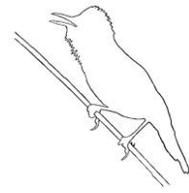


Figure 20. Mean \pm S.E. community parameters in management treatment levels. Groups not sharing lowercase letters are significantly different (Tukey's HSD test, $p < 0.05$).



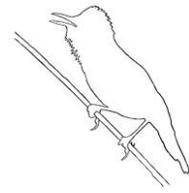
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Table 8. Results of general linear models testing the effects of management, reed properties and water depth on variables describing the marsh bird community. Models shown were obtained by a backward stepwise procedure in which non-significant ($p > 0.05$) effects were removed from full models specified after a model selection procedure. Significant effects are in Bold.

Response variable	Variables in reduced model	AIC	Coefficient \pm S.E.	F	p
Species richness	Reed complexity	53.70	1.87 ± 1.032	3.853	0.060
	Proportion of reed cut		-2.31 ± 1.430	2.608	0.118
Abundance	Reed cover	175.85	-52.19 ± 24.781	4.451	0.044
	Proportion of reed cut		-21.24 ± 10.849	3.225	0.084
	Water depth		-0.60 ± 0.291	4.336	0.047
Shannon diversity	Management	-69.95	-0.47 ± 0.184	3.324	0.023
	Reed complexity		0.19 ± 0.140	2.118	0.160
	Proportion of reed cut		-0.28 ± 0.223	2.398	0.136
	Water depth		0.01 ± 0.005	6.137	0.022
Simpson diversity	Management	-147.04	0.16 ± 0.051	5.317	0.002
	Water depth		-0.00 ± 0.001	8.138	0.009
Evenness	Management	-143.96	-0.16 ± 0.054	5.347	0.002
	Water depth		0.00 ± 0.001	7.500	0.011

Effects of management on bird groups

The response of birds to management varied greatly in different groups (**Figure 21, Table 9**). Ducks and geese had higher abundance in grazed newly-burned patches, followed by grazed twice-burned and grazed unburned patches (**Figure 21B**). There was no difference in species richness by treatment (**Figure 21A**). Wading birds as well as gulls and terns showed a similar pattern but both their species richness and abundance were significantly higher in newly-burned patches than in other treatments (**Figure 21C-F**). Reed songbirds showed a contrasting pattern in that both their species richness and abundance were lowest in

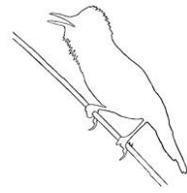


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newly-burned patches and were significantly higher in old-burned or unburned patches (**Figure 21G, H**). The species richness of farmland songbirds was higher in grazed patches with new burning than in non-grazed patches and was intermediate in other grazed patches regardless of whether patches were burned or not (**Figure 21I**), indicating the overall importance of grazing for farmland birds. Finally, the species richness of rails, coots and grebes was influenced positively by reed complexity (CV) and water depth and negatively by reed cover but not by management per se (**Table 9**).

Table 9. Results of general linear models testing the effects of management, reed properties and water depth on variables describing the marsh bird groups. Models shown were obtained by a backward stepwise procedure in which non-significant ($p > 0.05$) effects were removed from full models specified after a model selection procedure. Significant effects are highlighted in Bold.

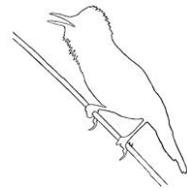
Response variable	Variables in reduced model	AIC	Coefficient \pm S.E.	F (df)	p
Ducks and geese SR	Density of new reed	-14.93	0.03 \pm 0.021	3.445 (1)	0.074
	Reed complexity		0.71 \pm 0.328	6.022 (1)	0.021
	Reed cut		-0.99 \pm 0.468	4.511 (1)	0.043
Ducks and geese AB	Management	68.12	5.80 \pm 1.802	3.782 (5)	0.011
Wading birds SR	Management	-30.81	0.00 \pm 0.000	13.067 (5)	< 0.0001
Wading birds AB	Management	103.23	10.16 \pm 3.232	4.246 (5)	0.007
	Reed cover		-15.34 \pm 7.422	3.838 (1)	0.062
Gulls and terns SR	Management	-48.99	0.96 \pm 0.263	6.137 (5)	0.001
	Reed SD		-0.02 \pm 0.019	1.186 (1)	0.288
	Reed cover		-0.70 \pm 0.311	4.261 (1)	0.051
	Reed cut		-0.01 \pm 0.006	4.893 (1)	0.038
Gulls and terns AB	Management	150.26	24.17 \pm 7.241	4.827 (5)	0.003
	Reed cover		-34.99 \pm 16.253	3.925 (1)	0.060
	Water depth		-0.42 \pm 0.187	4.951 (1)	0.036
Reed songbirds SR	Management	13.86	-5.08 \pm 0.876	21.796 (5)	< 0.00001
	Density of old reed		-2.68 \pm 1.359	3.787 (1)	0.065



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	Reed SD		0.10 ± 0.058	1.872 (1)	0.185
	Water depth		0.06 ± 0.019	9.024 (1)	0.007
Reed songbirds AB	Management	115.12	14.92 ± 4.322	19.179 (5)	< 0.00001
	Density of old reed		0.53 ± 0.156	13.084 (1)	0.001
	Reed cut		-6.97 ± 4.857	2.752 (1)	0.111
	Water depth		0.19 ± 0.104	3.623 (1)	0.071
Farmland songbirds SR	Management	-15.77	-0.99 ± 0.443	3.543 (5)	0.016
	Water depth		-0.04 ± 0.012	10.915 (1)	0.003
Farmland songbirds AB	Density of old reed	95.93	-0.14 ± 0.086	3.082 (1)	0.090
	Water depth		-0.15 ± 0.077	3.740 (1)	0.063
Rails, coot and grebes SR	Reed complexity	-24.66	0.62 ± 0.290	10.853 (5)	0.003
	Reed cover		-1.61 ± 0.921	4.373 (1)	0.046
	Reed cut		-0.66 ± 0.379	3.691 (1)	0.066
	Water depth		0.02 ± 0.010	4.500 (1)	0.043
Rails, coots and grebes AB	Reed cover	38.45	-7.18 ± 2.419	11.188 (1)	0.002
	Reed cut		-2.33 ± 1.098	5.264 (1)	0.030
	Water depth		0.06 ± 0.029	4.119 (1)	0.052

SR: species richness; AB: abundance



Marshland management influences birds communities

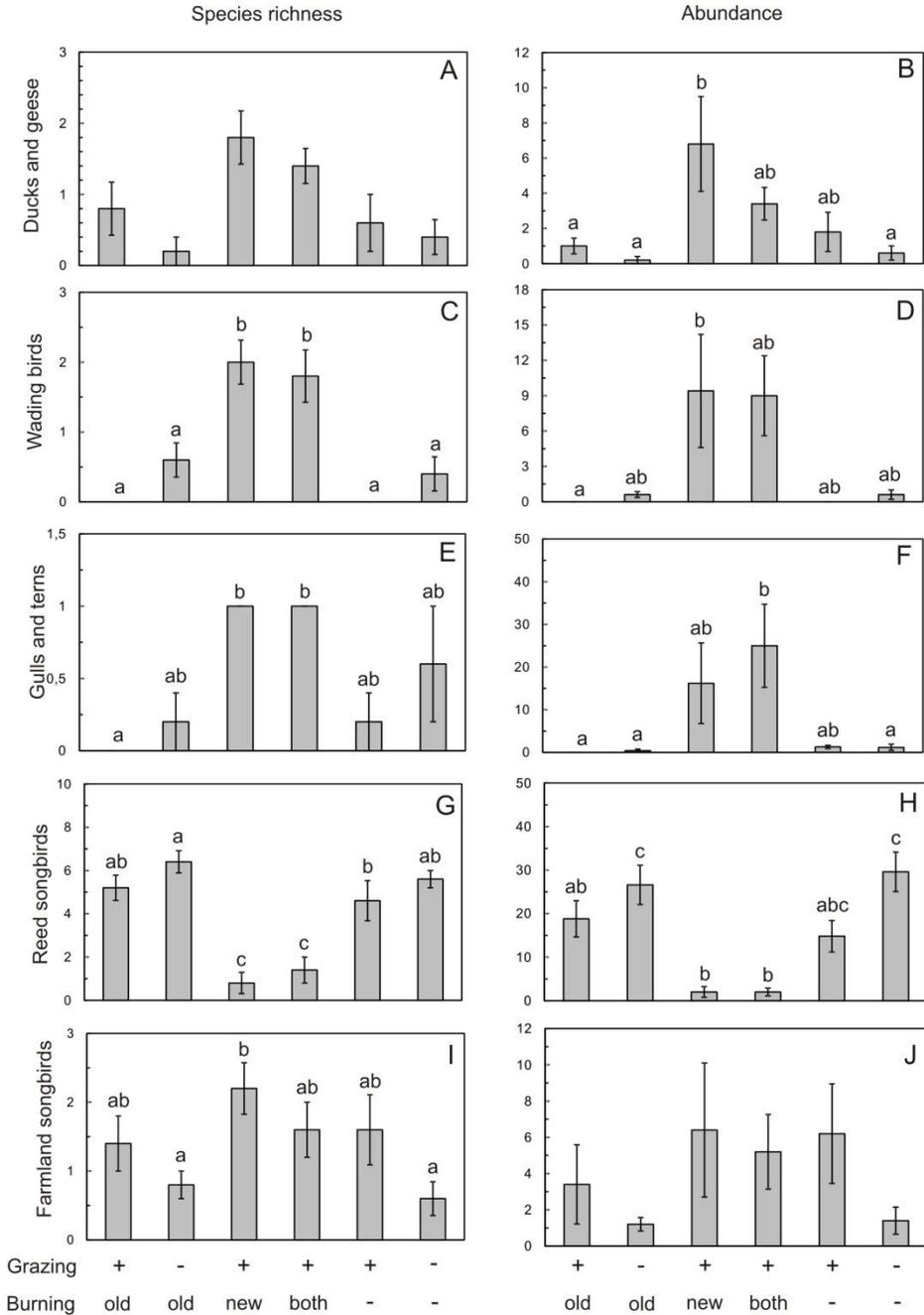
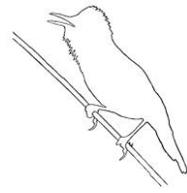


Figure 21. Mean \pm S.E. species richness and abundance of the five main functional groups in management treatment levels. Groups not sharing lowercase letter are significantly different (Tukey's HSD test, $p < 0.05$).



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Management effects on reed

The proportion of old reed differed significantly among the six treatments (Kruskal-Wallis test, $\chi^2_5 = 18.683$, $p = 0.0022$), because newly and twice-burned areas combined with grazing had little old reed, whereas other treatments had at least 35% on average (**Figure 22**). Furthermore, the proportion of old reed was higher in non-managed than in grazed unburned patches, whereas there was no such difference by grazing between the two old-burned treatment levels (**Figure 22**). Finally, there was no difference among treatment levels in either mean reed density (one-way ANOVA, $F_5 = 1.77$, $p = 0.156$), reed complexity (SD: $F_5 = 1.02$, $p = 0.425$; CV: $F_5 = 1.30$, $p = 0.297$) or reed cover ($\chi^2_5 = 3.748$, $p = 0.586$).

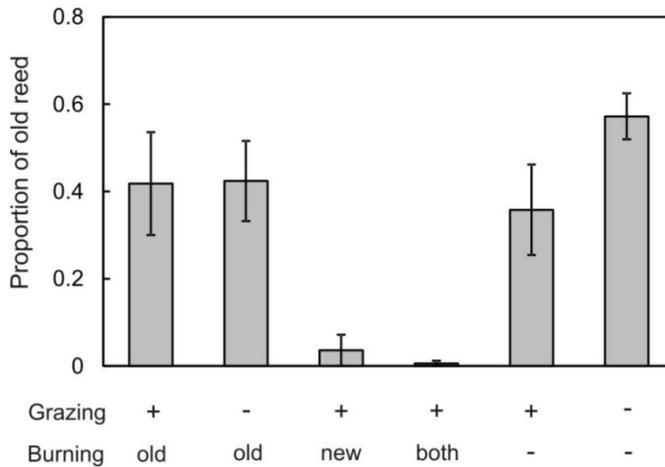
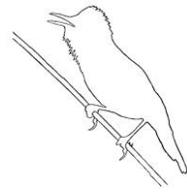


Figure 22. Mean \pm S.E. proportion of old reed in management treatment levels.



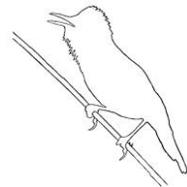
Discussion

General findings

We found that spatiotemporally variable management by grazing and burning led to a more heterogeneous landscape structure of marsh habitats, which increased bird diversity in three main ways. First, there were more species and individuals of non-passerines in recently burned patches than in unburned or old-burned patches. Second, there were more species and individuals of reed songbirds in unburned, old-burned or grazed patches than in newly-burned patches. Finally, there were more species of farmland birds in grazed patches, particularly in newly-burned ones, than in non-grazed patches. Our results thus indicate that spatiotemporally variable management may simultaneously benefit several functional groups of birds. Our findings also suggest that this benefit was mediated by management-caused changes in reed structure and increases in habitat diversity and was independent of the variation in water level, which further reinforces the importance of management by grazing and burning.

Effects of cattle grazing

Continuous grazing through four vegetation periods led to the establishment of trampled corridors and areas in the homogeneous reed, where old reed stems were partially destroyed and the growth of new reed was stunted. Grazing by cattle has been known to efficiently control reed (van Deursen and Drost 1990), although its effect depends on the type of livestock and grazing intensity (Vulink et al. 2000) and the duration of grazing (Korner 2013). In our study, grazing and trampling led to a mosaic-like patch structure of habitats (**Figure 3**), which was preferred by farmland birds and several reed songbirds. Although the number of wading birds and waterfowl also increased in a long-term grazing programme at Lake Neusiedler in eastern Austria (Korner 2013), we did not find such a tendency. In our study, wading birds and waterfowl preferred partially flooded areas with both grazing and burning, showing that grazing alone was not enough to create potential breeding, feeding or roosting habitats for these bird groups.

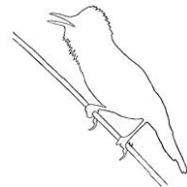


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For most reed songbirds, patches with a high proportion of old reed were preferable as their species richness and abundance was high relative to patches that were recently burned. The non-managed reed was characterized by high reed songbird diversity and evenness compared to managed stands, similarly to the findings in Valkama et al. (2008). For example, Báldi and Moskát (1995) compared species richness and abundance of reed passerines among cut, burned, non-managed reed and heterogeneous reed containing bulrush, meadows and trees. The abundance and species richness of reed passerines, a group which encompassed both reed and farmland songbirds in our study, was significantly higher in the control area than in managed or heterogeneous areas. Báldi and Moskát (1995) concluded that homogeneous reed stands were highly suitable for reed passerines, thus, they suggested limited or no management for reed passerines. Most other studies focusing on reed passerines also found higher diversity in homogeneous and unmanaged reed (Graveland 1999, Vadász et al. 2008). In several studies, the area-sensitive reed passerines positively preferred non-managed but heterogeneous reedbeds (Báldi and Kisbenedek 1998, Báldi 2004, Benassi et al. 2009). However, some authors reported that reed songbirds may differ in their preferences with regard to management (Poulin and Lefebvre 2002) or to water depth because some species nest exclusively in flooded non-managed reedbeds, while others have a wider tolerance regarding the absence of water (Neto 2006).

Effects of burning

The late-summer burning of reed resulted in shallow pools with low vegetation cover or open water surfaces in the next year (e.g. **Figure 3**), which was attractive to waterfowl and wading birds. This effect largely disappeared because reed grew back strong in these areas by year 3 after burning, resulting in no difference between old-burned and non-burned patches for the non-passerine groups. Our results thus suggest that burning is highly effective at controlling reed but that this effect is temporary at most. These results suggest that burning needs to be repeated every 2-3 years to reap its full benefits to non-passerine birds. In contrast, the species richness of passerines in (Moga et al. 2010) was higher in burned areas. However, in Moga et al. (2010) and other studies (e.g. Mérő et al. 2014) reed was burned in March of the year of the



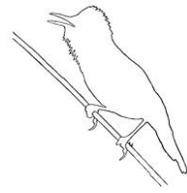
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survey. To our knowledge, our study is the first to report the next-year effects of late-summer burning of reedbeds.

We found that the proportion of old reed was significantly lower in the two recently burned and grazed patches than in the other four treatment levels. Experimental studies of spring burning and mowing of reed resulted in extensive damage to the shoots and differences in reed stem density and diameter; the reed compensate damages on young shoots due to spring burning by the growth of several thinner replacement shoots (van der Toorn and Mook 1982). Van Deursen and Drost (1990) found that reed stands might thus be in equilibrium with grazing pressure, but also reported that reed production can be reduced to 40% due to grazing compared to an ungrazed stand. In the spring the following year we still detected the effect of late-summer burning, furthermore, trampling by cattle in the burned areas throughout the autumn represented further damage to the reed plants which led to decreased reed productivity in spring. Our results thus suggest that the combination of burning and grazing leads to long-lasting damage to reed plants in areas burned in late summer, where non-passerines and farmland songbirds showed high richness and abundance the next spring.

Water depth

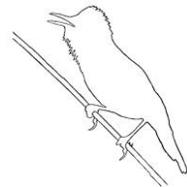
Besides management and reed properties, water depth also significantly influenced the bird community (in four of the five models) and some functional groups. There were positive relationships between water depth and Shannon diversity and evenness, and the species richness of reed songbirds, and rails, coots and grebes, and there were negative relationships between water depth and total abundance, Simpson diversity, the abundance of gulls and terns, and the species richness of farmland songbirds. These results are in line with expectations based on the general vegetation patterns largely determined by water depth and on the feeding and habitat use properties of the functional groups involved. For example, shallow water is more likely to host a diverse vegetation (bulrushes, *Schoenoplectus* spp., *Typha* spp., grasses e.g. *Alopecurus*, *Beckmannia*), which gradually gives way to more homogeneous reedbeds in waters of intermediate depth, whereas very deep water will usually be open water devoid of emergent vegetation but rich in floating or



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submerged vegetation (pondweed, e.g. *Potamogeton* spp., *Lemna* spp., *Ceratophyllum* spp. etc.). The positive relationship between water depth and the richness of reed songbirds and rails, coots and grebes can be explained that transects going through intermediate water depth likely provided better conditions for nesting and feeding for reed songbirds (mainly *Acrocephalus* spp., plus *Emberiza schoeniclus*, *Locustella luscinioides*, *Luscinia svecica*, *Motacilla flava*, *Panurus biarmicus*) and rails, coots and grebes (*Fulica atra*, *Porzana parva*, *Rallus aquaticus*, *Tachybaptus ruficollis*) than transects in shallower water. The somewhat surprising negative relationship between water depth and gull/tern abundance was because gulls and terns, which usually nest on floating vegetation in open water, often rested in cattle-trampled openings in shallow water or because shallower water probably provided better conditions for feeding. Finally, the negative relationship between water depth and species richness of farmland songbirds conformed to the expectations because habitats typically required by these species (*Alauda arvensis*, *Hirundo rustica*, *Miliaria calandra*, *Saxicola rubetra*, *Corvus cornix*) became rarer with increasing water depth.

Despite the influence of water depth on several response variables, in transects surveyed, there was no systematic variation in water depth among the different treatments, and there were no relationships between water depth and reed structure variables. Moreover, there was no interaction between management and water depth in any of the models. These findings indicated that the effects of management and water depth were independent from one another. These observations, however, also suggest that varying the water level as part of a long-term marsh management programme can be promising as an introduction of further disturbance to increase the diversity of marsh habitats and to benefit a variety of bird species. For example, many species such as ducks and geese, storks and herons, and coots and grebes require a minimum of water for nesting and feeding (Causarano and Battisti 2009, Nummi et al. 2013, Pöysä and Vaananen 2014). Beyond the pure presence of water, the changes in the water level can also affect the presence and abundance of these and several other groups of water birds (e.g. Causarano et al. 2009, Redolfi De Zan et al. 2010, Zacchei et al. 2011).

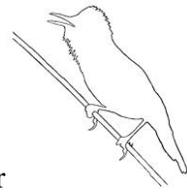


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Management and the intermediate disturbance hypothesis

The results of spatiotemporally variable, combined management by burning and grazing fit the expectations based on IDH in the study marsh. First, the IDH predicts that high disturbance will lead to lower diversity because fewer species will tolerate intense or too frequent disturbance. Our results support this prediction because total Shannon diversity and evenness were lowest whereas Simpson diversity was highest for the patches with highest disturbance (grazed and twice-burned). Because Shannon diversity is more affected by rare species while Simpson diversity is more affected by common species (Magurran 2004), this result suggests that patches with highest disturbance had disproportionately more of the common rather than the rare species. Second, the IDH predicts that low disturbance will be tolerated by a few species, leading to biotic homogenization. The finding that control (non-managed) patches had fewer species and individuals of all groups but reed songbirds appears to support this prediction because reed songbirds avoided combined, burned and grazed patches. However, because reed songbirds had many species, this pattern did not show for total diversity.

Novelty of the study: The diversity and evenness of bird communities were significantly affected by management, whereas total species richness and abundance were not. Shannon diversity and evenness were low in grazed twice-burned patches and uniformly high in all other treatments, whereas Simpson diversity was highest in grazed twice-burned patches and lower in all other treatments. Species richness was not significantly affected by any of the factors studied. More species and individuals of non-passerines were found in recently burned patches than in unburned or old-burned patches. Reed songbirds preferred unburned, old-burned or grazed patches to newly-burned patches. Farmland birds were most abundant in grazed patches. In summary, spatiotemporally variable management by grazing and burning led to a more heterogeneous landscape structure of marsh habitats by controlling old reed, which was reflected in an increase in bird diversity.



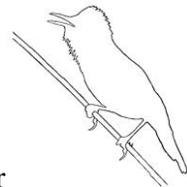
Chapter 3

Effect of reed burning and precipitation on the breeding success of Great Reed Warbler, *Acrocephalus arundinaceus*, on a mining pond

Introduction

Several studies examined how anthropogenic and environmental factors affect the presence of passerines in reedbeds (Báldi and Moskát 1995, Báldi 2001, Vadász et al. 2008, Moga et al. 2010). Báldi (2001) studied how inundation affected the local breeding passerines at Kis-Balaton wetland by comparing three periods (before, immediately after and years after inundation) and by quantifying the changes in community structure and composition, and the differences between areas and periods. Savi's Warbler, *Locustella luscinioides*, declined immediately after inundation, while Reed Bunting, *Emberiza schoeniclus*, and Sedge Warbler, *Acrocephalus schoenobaenus*, declined in the long term. In contrast, the Great Reed Warbler, *Acrocephalus arundinaceus*, was the only species with a continuous increasing trend. Vadász et al. (2008) reported that cutting of reed negatively influenced species richness and abundance of reed passerines on Lake Kolon in Central-Hungary. Savi's Warbler, Moustached Warbler, *Acrocephalus melanopogon*, Sedge Warbler and Reed Warbler, *Acrocephalus scirpaceus*, especially avoided cut areas, while the Great Reed Warbler did not (Vadász et al., 2008). Furthermore, Báldi and Moskát (1995) and Moga et al. (2010) recorded that Great Reed Warblers were similarly present in non-managed, burned and mowed reed stands. Although these studies show that Great Reed Warblers is largely tolerant to different management types and regimes, our knowledge about the effects of reed management and other environmental factors on the breeding success of this species is fragmentary.

Nests of small open-nesting birds are often difficult to detect in an early stage of the breeding season (Mayfield 1975). Due to the lack of information from the period before nests are found, estimates of mortality, survival and breeding success can be severely biased. Mayfield (1975) developed a method for estimating breeding success that reduces



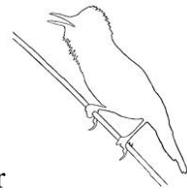
Factors governing breeding success of Great Reed Warbler

these potential sources of error. The proposed Mayfield estimator was further recognized as a maximum likelihood estimator (MLE). The asymptotic distribution of the MLE was calculated, which provides a measure of asymptotic variance (Hensler and Nichols 1981). Hereinafter MLE and variance can be used to test the significance of daily survival (Hensler and Nichols 1981). The Mayfield method can also be used well in studying the breeding biology of Great Reed Warbler. For example, Batáry and Báldi (2005) estimated breeding success of Great Reed Warbler by using the Mayfield method, while Petro et al. (1998) calculated the percent of failed and successful broods.

The breeding habits of Great Reed Warbler were already explored by several studies in the past 30 years (Beier 1981, Dyrzcz 1981, Woithon and Schmieder 2004, Batáry and Báldi 2005, Uzun et al. 2014). This species is a common breeder in middle latitudes of the western Palearctic, and it usually inhabits tall, dense and strong reed vegetation (Cramp 1998). Studies on the breeding biology of the Great Reed Warbler were mainly carried out on large ponds (Petro et al. 1998), fishponds (Prokešová and Kocian 2004), lakes (Fisher 1994, Woithon and Schmieder 2004, Batáry and Báldi 2005) or canals (Mérő and Žuljević 2009), but not on mining ponds. The first aim of this study was to explore the effect of reed burning, precipitation and water level changes on breeding success and clutch and brood survival of Great Reed Warbler on a mining pond. The second aim of this study was to present differences in breeding success between the early and the late periods of the breeding season.



Figure 23. Field work in early morning at Bager Pond and the oldest bird ringed as a breeding adult in 2008 and last recaptured in 2014 (minimum age: 7 years).



Factors governing breeding success of Great Reed Warbler

Results

General breeding success: egg and nestling survival

We found a total of 87 Great Reed Warbler nests in Bager Pond during 2008-2011 (**Figure 23**). The maximum number of females per one polygynous male was two. Mayfield breeding success for the four years averaged 0.43 and was very low in 2010 (0.48 in 2008; 0.67 in 2009; 0.17 in 2010; and 0.69 in 2011). The daily survival of eggs and nestlings did not differ (J-test, $z = 1.29$, $p = 0.198$). Although some nests were destroyed by predators (Little Bittern, *Ixobrychus minutus*; Grass Snake, *Natrix natrix*), most of the eggs and nestlings were lost due to cold, windy and rainy weather ($\chi^2 = 3.86$, $p = 0.0495$). Kaplan-Meier curves showed that nest survival was highest in 2011 (log-rank test, $\chi^2 = 30.23$, $p < 0.0001$; **Figure 24**) and lowest in 2010, which year differed significantly from the other three (log-rank tests; vs. 2008: $\chi^2 = 5.88$, $p = 0.0153$; vs. 2009: $\chi^2 = 10.78$, $p = 0.0048$; vs. 2011: $\chi^2 = 23.61$, $p < 0.0001$; **Figure 24**).

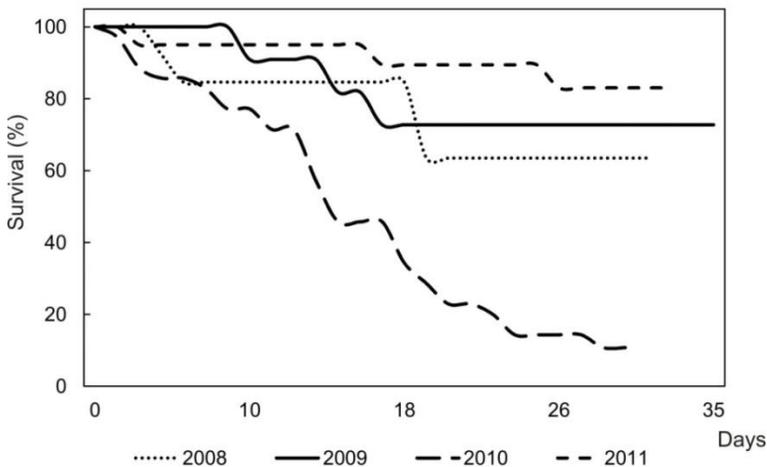
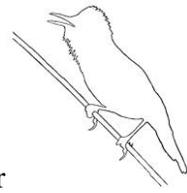


Figure 24. Kaplan-Meier survival curves of Great Reed Warbler nests in the breeding seasons 2008-2011.

The mean clutch size was 4.1 ± 0.17 (range = 1-7), while the mean number of fledglings was 2.0 ± 1.04 (range = 1-5). Mean clutch size did not vary among years (one-way ANOVA, $F_{3,70} = 0.387$, $p = 0.763$), whereas the mean number of fledglings differed among years because it



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was very low in 2010 ($F_{3,70} = 9.666$, $p < 0.0001$; **Figure 25**). The mean hatching rate of the four breeding seasons was 0.93, indicating that 7% eggs did not hatch (0.85 in 2008; 0.91 in 2009; 0.95 in 2010; 0.97 in 2011).

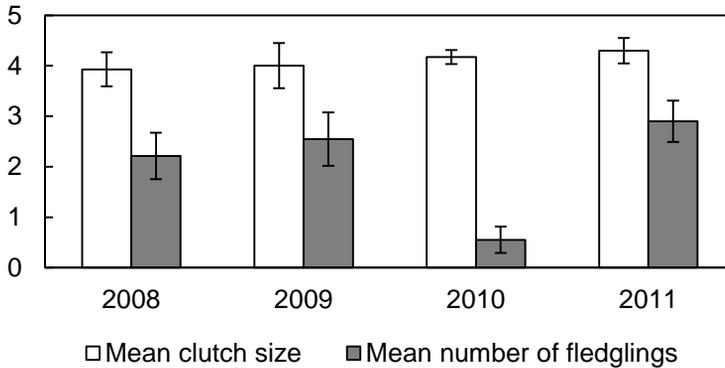
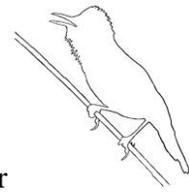


Figure 25. Mean (\pm SE error bars) clutch size and number of fledglings at Bager Pond between 2008-2011.

Breeding success in the Early and Late groups

Although most ($n = 55$) nests were found in the Early group ($\chi^2_3 = 14.78$, $p < 0.01$), breeding success was higher ($n = 32$, 60.4% on average) in the Late group than in the Early group (44.2% on average, data in **Table 10**), but this was statistically significant only in years with managed reed (2009, 2010; Mann-Whitney test, $p = 0.031$) and not in non-burned years (2008, 2011; **Table 10**). Both daily egg and nestling survival rates were significantly larger in the Late group than in the Early group in 2009 (extremely low water depth) and in 2010 (extremely high water depth, **Tables 10 and 11**). In years with average water depth and no management (2008, 2011), the daily survival of eggs and nestlings did not differ between the Early and Late groups (**Table 11**).

Daily egg survival was higher than daily nestling survival in the Late group in 2008 and 2010 and in the Early group in 2011 (**Table 10**). When data from all years were combined, the daily survival of eggs was lower in the Early than in the Late group (daily survival rate (DSR) Early group: 0.96; DSR Late group: 0.99; $z = 4.92$, $p < 0.0001$). In contrast, the



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daily survival of nestlings did not differ between the two periods (DSR Early group: 0.96; DSR Late group: 0.98, $z = 1.55$, $p = 0.121$).

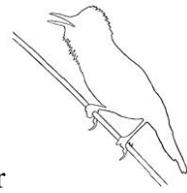
Table 10. Breeding success in the Early and Late periods at Bager Pond (2008-2011; z^* value is the result of J-tests comparing egg and nestling survival; level of significance: $*p < 0.05$, $**p < 0.01$).

Period	Year	Prec. amount (mm)	Value given for each group				Hatch rate	Breeding success (%)
			Daily survival rate		z^* value	p value		
			Egg	Nestling				
Early	2008	91	0.96	0.98	0.41	0.681	0.85	43.3
	2009	154	0.98	0.99	1.33	0.186	0.90	61.2
	2010	416	0.91	0.79	1.64	0.101	1.00	1.9
	2011	42	0.99	0.98	2.48	0.013*	0.98	70.4
Late	2008	104	0.99	0.95	2.82	0.005**	0.83	41.7
	2009	76	1.00	1.00	0.00	1.000	0.93	100.0
	2010	173	0.98	0.95	2.18	0.029*	0.94	39.4
	2011	125	0.98	0.98	0.29	0.765	0.95	60.6

There was a significant negative relationship between breeding success and the amount of precipitation (Spearman rho = -0.76, $p = 0.037$; **Figure 26**). The negative effect was mainly because of 2010, when total rainfall reached as high as 457.5 mm in the entire breeding season (**Table 1**). The rate of water level increase in the pond was so rapid in rainy periods that some nests with eggs or some others with chicks were submerged under water.

Table 11. Results of comparisons of egg and nestling survival between Early and Late groups (2008-2011; z^* value is the result of J-test; level of significance: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$).

Years	Egg		Nestling	
	z^* value	p value	z^* value	p value
2008	1.234	0.217	1.326	0.184
2009	3.196	0.001**	2.010	0.044*
2010	6.077	< 0.0001***	2.193	0.028*
2011	1.418	0.156	0.483	0.628



Factors governing breeding success of Great Reed Warbler

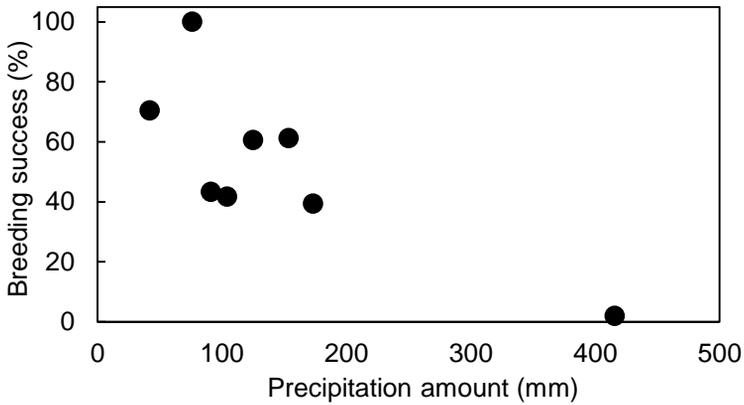


Figure 26. Correlation between the amount of precipitation in the breeding season and breeding success at Bager Pond, 2008-2011. Data points are Early and Late groups in four years.

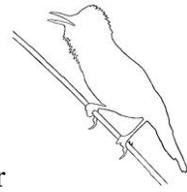
Effect of reed burning on breeding density and success

Great Reed Warbler rarely preferred fresh reed for breeding, because most pairs built their nests in mixed reed ($\chi^2_1 = 30.18$, $p < 0.0001$; **Figure 27**). In 2008 and 2011, reed was not burned, so all nests were in mixed reed. The proportion of nests in fresh reed was 27.3% and 12.8% in 2009 and 2010, respectively (**Figure 27**).

Mean (female) breeding density for the four years was 11.9 ± 2.97 pairs ha^{-1} . The number of nests and breeding density varied in the four years, and was lowest in 2009 (**Table 12**). The number of nests per hectare was higher than the number of pairs per hectare, especially in the extremely wet 2010, because the number of nests also included replacement clutches laid by pairs whose previous clutch failed for any reason.

Table 12. The number of breeding pairs (elliptoids on map, Figure 27) and number of nests (dots on map, Figure 27) for the four study years.

Year	Number of nests (ha^{-1})	Number of pairs (ha^{-1})
2008	13.1	10.8
2009	8.5	7.7
2010	30.0	12.3
2011	15.4	14.6



Factors governing breeding success of Great Reed Warbler

Breeding density correlated positively with water level in the pond in the spring ($\rho = 0.75$, $p = 0.037$). For instance, the breeding density differed greatly between 2009 and 2010 despite that fact that reed was burned in both years (**Figure 27**). The water depth differed largely between the two years (15.0 ± 26.55 cm in 2009 and 91.3 ± 37.77 cm in 2010). The spatial distribution of Great Reed Warbler nests showed aggregation in the first three years, while in 2011 a more even distribution of nests was recorded (**Figure 27**).

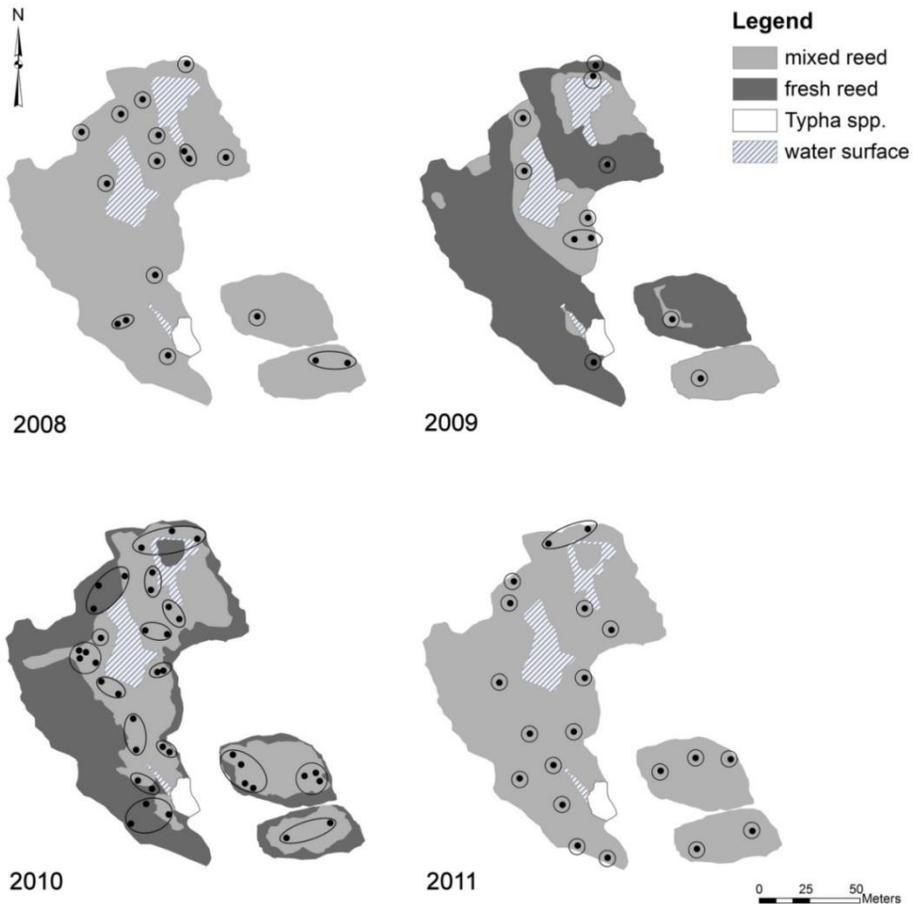
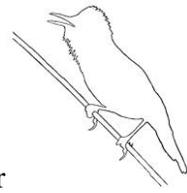


Figure 27. Spatial distribution of Great Reed Warbler nests and actual pairs on Bager Pond. Black dots represent Great Reed Warbler nests and ellipsoids indicate actual breeding pairs. Ellipsoids contain both successful and perished nests (dots) belonging to



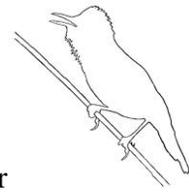
Factors governing breeding success of Great Reed Warbler

the same female. Elliptoids containing two (one original and one replacement clutch) or more dots show that one female laid one or more replacement clutches.



Figure 28. Reed burning in late winter and new reed in May mixed with old reed stands at Bager Pond in 2009.

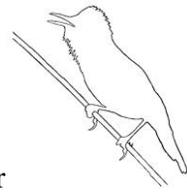
In years with burning (2009 and in 2010), breeding success was similar in fresh and mixed reed (fresh reed: 0.37, mixed reed: 0.32). Daily survival did not differ between eggs and nestlings in nests built in fresh reed (DSR for eggs: 0.96; DSR for nestlings: 0.97; $z = 0.73$, $p = 0.463$), whereas nestlings survived better than eggs in mixed reed (DSR for eggs: 0.94; DSR for nestlings: 0.97; $z = 2.64$, $p = 0.008$). In years with burning (2009 and 2010), combined egg and nestling daily survival rates were significantly higher in the Late group than in the Early group (DSR for eggs and nestlings in Early group: 0.94; DSR for eggs and nestlings in Late group: 0.97; $z = 4.06$, $p < 0.0001$). In contrast, in years with no burning (2008, 2011), there was no such difference between the groups (DSR for eggs and nestlings in Early group: 0.99; DSR for eggs and nestlings in Late group: 0.98; $z = 1.35$, $p = 0.178$).



Discussion

Total average breeding success for the four studied years (0.431) of Great Reed Warbler on mining pond Bager did not differ significantly from that reported by other studies. At Heřmanický fishpond (Czech Republic), average breeding success was 0.468 (Petro et al. 1998) and on large and small canals in northern Serbia, it was 0.420 (Mérő and Žuljević 2009). Hatching rate (0.927) was higher in our study than on Heřmanický fishpond (0.653, Petro et al. 1998), but was similar to that on a fishpond in Poland (0.887, Dyrzcz 1981) and to that on canals (0.940, Mérő and Žuljević 2009). According to Petro et al. (1998), eggs failed to hatch because some of them were not fertilized or because the embryos died. Petro et al. (1998) also reported that 7% of the eggs vanished and a similar proportion was predated or deserted. Our Kaplan-Meier survival curves showed that the survival of nests was better in the three drier years (2008, 2009 and 2011) than in the wet year (2010). Most nest failure occurred in our study due to bad weather conditions, mainly in 2010. The effect of weather may have been both direct (cooling and hypothermia of eggs/nestling) and indirect (more time spent away by parents to search for food and/or higher activity by predators, resulting in higher nest predation rates or higher rate of starvation by the chicks). We presume that Great Reed Warbler clutches and nestlings are probably more important sources of food to predators in adverse weather when food is hard to find, e.g. when cold temperatures and rainy weather prevail for several days. Great Reed Warbler nestlings are most sensitive to cold and wet weather, followed by low temperatures (Fischer 1994, Beier 1981), so if the female parent is away from the nest for a longer time, the body temperature of the chicks will fall and the probability of mortality is higher. In cold and wet weather, the parents also need more time to find food and to feed nestlings. Petro et al. (1998) identified three sources of nestling mortality: predation (4.3% of all nestlings), desertion (10.4%) and perished due to bad weather (20.0%).

Mean clutch size was generally higher in similar Central European studies than in this study on Bager Pond or in a previous study of ours on canals in Sombor (**Table 13**). The mean number of fledglings, however, was similar in this study to that found in most other studies, with the exception of studies by Hudec (1975), Dyrzcz (1981) and Mérő and Žuljević (2009) (**Table 13**).



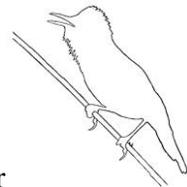
Factors governing breeding success of Great Reed Warbler

Table 13. Comparative overview of mean clutch sizes and number of fledglings of Great Reed Warbler in Central European studies.

Study area	Country	Clutch size	Number of young	Source
Moravian ponds	Czech Rep.	4.4	3.1	Hudec 1975
Milicz fishp.	Poland	4.8	2.2	Dyrcz 1981
Swiss lakes	Switzerland	4.6	3.1	Dyrcz 1981
Northern Bavaria	Germany	4.7	2.2	Beier 1981
Heřmanický fishp.	Czech Rep.	4.8	2.3	Petro et al. 1998
Velence Lake	Hungary	4.9	1.7	Batáry and Báldi 2005
Sombor (canals)	Serbia	3.9	1.0	Mérő and Žuljević 2009
Bager Pond	Serbia	4.1	2.0	this work

Studies in the Czech Republic showed that the first eggs were laid in the first (2%), second (24%) and third (57%) ten-day period of May and the first ten days (17%) of June (Petro et al. 1998). In our study, breeding began almost two weeks later than the first ten-day period of May. One exception was a four-egg nest in 2011 which was found on May 10. On the Milicz fishponds (Poland), the mean dates of laying of the first eggs were between May 19 and 25 in six years, and this was similar (May 21-24) on Swiss lakes as well (Dyrcz 1981). The latter results are similar to those of our study, where 69% of nests were found in the Early group. However, our study is special in that egg-laying also occurred in later periods of June and there were a few nests containing eggs even in July. None of the Central European studies mentioned above reported egg laying so late in the season.

In this study, the overall survival of eggs differed between Early and Late groups. However, eggs are better protected than nestlings from rainy and cold weather because the female does not leave the nest as often as in the chick-rearing period. We presume that not only the sensitivity of chicks to cold and rainy weather is responsible for mortality, but as we mentioned before adverse weather circumstances can result in chick starvation. If we consider the weather circumstances, years 2009 and 2010 were extremes; 2009 was very dry and 2010 had lots of precipitation. Water level is an important factor in the breeding of Great Reed Warbler (**Figure 25**), which can be clearly seen in these two years (**Figure 26**). If there is not enough reed area covered with water, Great Reed Warbler density decreases, because the quality of the breeding site is poor, e.g. breeding density in 2009 was only 7.7 pairs ha⁻¹. In the two

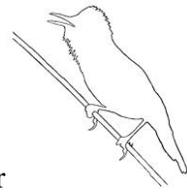


Factors governing breeding success of Great Reed Warbler

years (2008 and 2011) when the water depth varied between 60-80 cm at breeding site (Table 1), the number of breeding pairs was much higher (**Figures 25 and 26**).

The low breeding performance in 2010 meant that Bager Pond may have functioned as an ecological trap in that year. Despite the high breeding density, breeding success was very low due to high precipitation and rapid water level increase. Nevertheless, water rapidly submerged nests and Great Reed Warblers did not leave the reed habitat, they even raised occasionally a fourth brood. In an Oregon study of Spotted Towhees, *Pipilo maculatus*, adult birds preferred edges for breeding, where fledgling mortality was high due to predation by Domestic Cats, *Felis catus*, creating a severe ecological trap (Shipley et al. 2013). Several studies reported ecological traps established through anthropogenic habitat alteration or rapid environmental changes (Kokko and Sutherland 2001, Battin 2004, Lengyel 2006, Robertson 2012). In our study, Great Reed Warbler had low breeding success in 2010 which had no impact on breeding density and success in the next breeding season. However, there are cases where ecological traps lead to population sinks and eventually to deterministic local extinctions (Kokko and Sutherland 2001).

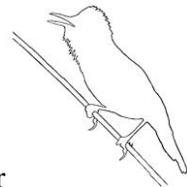
Mean breeding density was higher in this study than in previous studies. Although reed was burned in 2009 and 2010, the mean breeding density was still relatively high (c. 10.0 pairs ha⁻¹ combined). In 2008 and 2011, when reed was not burned, density was c. four pairs per ha higher (13.9 pairs ha⁻¹ combined). Nest densities varied between 0.5-0.8 nests ha⁻¹ at the Heřmanický fishpond between 1975 and 1979 (Petro et al. 1998) and between 1.5-3.1 pairs ha⁻¹ in Poland and between 0.4-2.3 pairs ha⁻¹ in Switzerland (Dyrcz 1981). It seems that breeding density shows fluctuations even in native, non-managed reedbeds, however, we presume that these densities also depend on reed quality (see Study 4). Furthermore, these studies were conducted on large reed habitats such as lakes and fishponds (Petro et al. 1998, Dyrcz 1981), where densities differ largely from canals (12.0 pairs ha⁻¹, Měrő and Žuljević 2009) and the reed habitat in this study. In our present study, the differences in breeding density are not only caused by reed burning but also by water level fluctuations. When reed is burned, male Great Reed Warblers arriving back from migration compete for reed patches that remain standing after the burning. New reed gets strong enough for breeding only



Factors governing breeding success of Great Reed Warbler

in mid-June. This difference in available breeding sites can explain why most nests were in mixed reed stands (**Figure 27**). In 2010, nest density was extremely high (30 nests ha⁻¹) because nests were destroyed by windy and rainy weather or were submerged because of rapid water level increase, and many nests were re-built close to the failed one. In contrast, there were no quality breeding sites in 2009 because only small reed patches remained after the burn at the start of the breeding season and water level was also low. Although we did not find differences in breeding success between fresh (burned areas) or mixed reed, other studies reported that mixed reed is denser and provide easier access to mammal predators (Dyrzcz 1981). Recorded Great Reed Warbler nest predators were the American Mink, *Mustella vison*, (Bensch 1993), Marsh Harrier, *Circus aeruginosus*, and Little Bittern (Dyrzcz 1981). Disease or loss of one or both parents also can lead to nest failure (Fischer 1994, Beier 1981). We found that new reed stems are not yet sturdy enough to hold the nests in the early part of the season, especially under rainy and windy conditions (pers. obs.). Our observations agree with previous ones in that Great Reed Warbler predominantly uses microhabitats where thick reed stems grow (Dyrzcz 1981, Graveland 1998). Dyrzcz (1981) also concluded that Great Reed Warblers mainly require mixed reed for breeding. Other studies also confirm the importance of mixed reed, e.g. the presence of reed passerines was lower in cut reed with much growth of new reed than in non-cut mixed reed stands (Báldi and Moskát 1995, Vadász et al. 2008). However, according to Moga et al. (2010) Great Reed Warbler preferred both burned and non-burned reed areas.

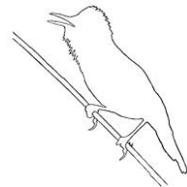
Probably the most interesting finding of this study is that clutches laid in the second half of the breeding season survived better. This is in contrast to the general observation that early clutches and young are more successful than later ones. Our observations suggest that this may be explained because the weather was more stable and dry in the Late than in the Early period. Alternatively, because this difference was found in years with reed burning (2009, 2010), it is also possible that the regrowth of the reed by the Late period resulted in strong and dense reed that could better hold the nests in adverse weather or could better hide the nest from predators than the freshly grown reed available for nesting in the Early period. Few studies report that earlier clutches in several species are larger and their breeding performance are better (Pied Flycatcher,



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Ficedula hypoleuca, Järvinen 1989; first brood of Barn Swallow, *Hirundo rustica*, Møller 2002) but some species show opposite trends e.g. Collared Flycatcher, *Ficedula albicollis*, (Sheldon et al. 2003), Great Tit, *Parus major*, and Blue Tit, *Parus caeruleus*, (Winkel and Hudde 1997). Studies done on the breeding biology of Lark Bunting, *Calamospiza melanocorys*, concluded that variability of climatic changes (e.g. daily or seasonal precipitation and temperature) affect breeding success during the breeding season (Skagen and Adams 2012). Even though this study provided several new insights, further, more detailed studies are necessary to fully disentangle the effects of weather, water level fluctuations, reed burning and season on the breeding density and success of Great Reed Warblers.

Novelty of the study: Nesting density was primarily influenced by water depth and was less affected by the burning management. In contrast, the nesting success of the Great Reed Warbler was higher in the late than in the early period of the breeding season in years when reed was burnt, while there was no such difference in years with no management. The main reason for the difference was that the daily survival rates of eggs were lower in the early period than in the late period, while the daily survival of nestlings did not differ between the two periods. Furthermore, we found that water level influences the survival of eggs and nestlings, because in years with extremely low or extremely high water depth, the eggs and nestlings survive better in the late period than in the early period.



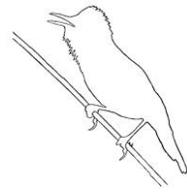
Chapter 4

Effect of reed quality on the breeding success of the Great Reed Warbler *Acrocephalus arundinaceus* (Passeriformes, Sylviidae)

Introduction

The Great Reed Warbler *Acrocephalus arundinaceus* Linnaeus, 1758 inhabits reed *Phragmites australis* habitats in middle latitudes of the western Palaearctic (Cramp 1998, **Figure 29**). This species uses strong, tall and dense reed for nesting in reedbeds in marshes, fishponds, mining ponds, canals or the banks of shallow, slow-flowing, lowland rivers (Leisler 1981, Nilsson and Persson 1986, van der Hut 1986, Cramp 1998, Graveland 1998, Prokešová and Kocian 2004, Batáry and Báldi 2005, Mérő et al. 2014). The sensitivity of reed-nesting species to habitat area, fragmentation and quality of the reedbeds are key factors that can affect the occurrence of reedbed-specialist bird species such as the Great Reed Warbler (Foppen and Graveland 1999, Benassi et al. 2009, Bosschieter et al. 2010, Benassi and Battisti 2011, Mortelliti et al. 2012). However, it is also known that the Great Reed Warbler selects its territory near or at the edge of the reedbed (Báldi 1999, Báldi and Kisbenedek 1999, Báldi and Kisbenedek 2000), and the nests are built within the first few metres of the reed edge, mainly adjacent to open water (Honza et al. 1993, Bensch 1993, Graveland 1998, Petro et al. 1998). Graveland (1998) earlier reported basic findings on the physical variables (e.g. the nest-supporting reed stem diameter and the reed stem density) in reedbeds hosting Great Reed Warbler nests, while Dyrz (1981) presented information on the proportions of old and new nest-supporting reed stems. Similarly to other reed passerine species, reed stem density is thus a relevant parameter in the breeding of the Great Reed Warbler. Reed stem density is substantially influenced by management, i.e. reed burning in the spring or reed cutting in the winter (Vadász et al. 2008, Báldi and Moskát 1995).

I report here on the physical characteristics such as the diameter and the number of nest-supporting reed stems (abbreviated as “supporting stems” hereafter) and compare these measures with the same measures of reed stems in the surroundings of the Great Reed Warbler nests. The aims of

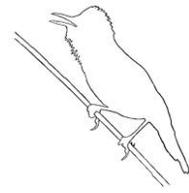


Reed influences nesting success of Great Reed Warbler

this study were (1) to characterize and compare the physical variables (diameter, number and density) of the supporting stems and the stems in the surroundings; (2) to test whether such relationships exist in different reed habitats by comparing three reed habitats: mining ponds, small canals and large canals; and (3) to study how reed density affects breeding success in the Great Reed Warbler.



Figure 29. The managed mining pond near Sombor and a recaptured Great Reed Warbler with Spanish alloy ring.



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Results

The number of supporting stems varied from 2 to 11 mm (mean $5.3 \pm$ S.D. 1.79), while their diameter varied between 2.5 and 14.0 mm (7.3 ± 1.71 mm). The old stems were 2.0 to 11.5 mm thick (5.9 ± 2.11 mm), and the new stems were 2.5 to 14.0 mm thick (7.4 ± 2.09 mm).

The mean density of the stems in the surroundings in this study was $219.0 \pm 62.15/\text{m}^2$ (old reed: $100.8 \pm 44.72/\text{m}^2$; new reed: $118.2 \pm 37.84/\text{m}^2$). The diameter of the stems in the surroundings varied from 2.0 to 14.0 mm (7.3 ± 1.55 mm), for the old stems from 2.0 to 14.0 mm (6.3 ± 2.38 mm), and for the new stems from 3.0 to 14.0 mm (7.9 ± 1.57 mm).

The density of the stems in the surroundings correlated positively with the number of supporting stems (Spearman $\rho = 0.405$, $n = 124$, $p < 0.0001$; **Table 14**). The diameter of the supporting stems showed a strong positive correlation with the diameter of the stems in the surroundings ($\rho = 0.769$, $n = 124$, $p < 0.0001$; **Figure 30**). There were also significant positive correlations between the diameters of the old and the new supporting stems and those of the old and the new stems in the surroundings (old reed, $\rho = 0.444$, $n = 124$, $p < 0.0001$; new reed, $\rho = 0.378$, $n = 124$, $p < 0.0001$).

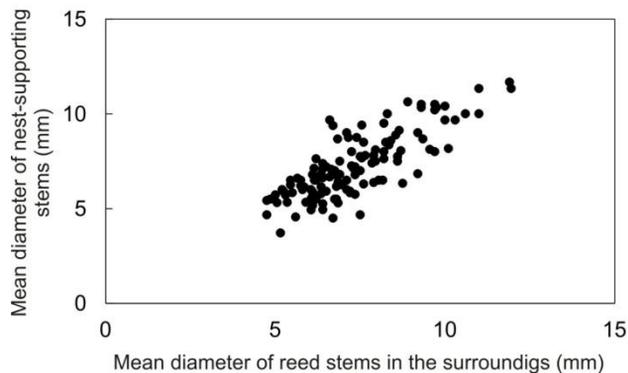
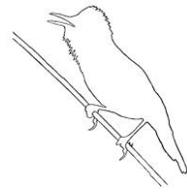


Figure 30. Relationship between the mean diameters of the supporting stems and the stems in the surroundings.

The density of the stems in the surroundings did not differ among the three habitat types (one-way ANOVA, $F_{3,5} = 0.927$, $p = 0.399$), while the



Reed influences nesting success of Great Reed Warbler

number of supporting stems varied significantly between the three habitats (**Table 14**; $F_{3,3} = 19.870$, $p < 0.0001$). The number of supporting stems was highest on mining ponds, while it was equally lower on large and small canals (Tukey's HSD tests, mining ponds vs. large canals, $q = 8.897$, $p < 0.0001$; mining ponds vs. small canals, $q = 4.871$, $p < 0.001$; **Table 14**). The diameters of the stems in the surroundings differed among the three habitat types ($F_{16,4} = 24.940$, $p < 0.0001$), with large canals having the thickest reed stems (**Table 14**; mining ponds vs. large canals, $q = 8.636$, $p < 0.0001$; large canals vs. small canals, $q = 7.200$, $p < 0.0001$). A similar tendency was found for the diameter of the supporting stems (**Table 14**; $F_{17,2} = 23.780$, $p < 0.0001$; mining ponds vs. large canals, $q = 9.109$, $p < 0.0001$; large canals vs. small canals, $q = 5.857$, $p < 0.0001$).

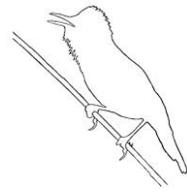
Table 14. Physical variables of the reed at the locations of Great Reed Warbler nests in the three habitats.

Physical variables of reed		Mining ponds	Large canals	Small canals
Stems in the surroundings	Mean density per m ²	225.4	211.2	202.6
	Mean diameter (mm)	6.4	8.1	6.4
Supporting stems	Mean number	6.7	4.7	5.2
	Mean diameter (mm)	6.1	8.1	6.5

Table 15. Physical variables of the reed at the locations of Great Reed Warbler nests, separately for the three reed density categories.

Physical variables of reed		Sparse reed	Intermediate reed	Dense reed
Stems in the surroundings	Mean density per m ²	137.3	206.1	297.9
	Mean diameter (mm)	7.7	7.4	6.9
Supporting stems	Mean number	4.3	5.3	6.3
	Mean diameter (mm)	7.9	7.3	6.7
Proportion of found nests (%)		20.4	50.8	28.8

The proportion of nests in the three reed density categories showed that Great Reed Warblers preferred the intermediate reed density (7.4 mm mean reed stem diameter) for nest-building because 51% of the nests were found in this category and only 20% and 29% in the sparse and dense categories, respectively ($\chi^2 = 18.659$, $df = 2$, $p < 0.0001$; **Table 14**).



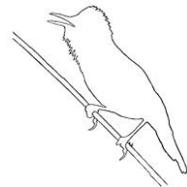
Reed influences nesting success of Great Reed Warbler

However, Great Reed Warblers laid larger clutches in intermediate and dense reed (**Table 16**; $F_3 = 4.56$, $p = 0.012$) and breeding success (both its rate and the mean number of fledglings) was highest in the dense reed ($F_3 = 3.17$, $p = 0.0454$; **Table 16**), closely followed by the intermediate category. Daily clutch and brood survival rates did not differ considerably in the three reed density categories (log-rank test, $\chi^2_2 = 1.943$, $p = 0.378$; **Table 16**). The daily survival rate of eggs was lower than the survival rate of nestlings only in sparse reed (**Table 16**).

Table 16. Breeding success of the Great Reed Warbler in the three reed density categories. Clutch size and the number of fledglings are given with standard deviation (SD).

Breeding parameters	Sparse reed	Intermediate reed	Dense reed
Mean clutch size	3.4 ± 1.57	4.3 ± 1.47	4.4 ± 1.23
Daily clutch survival rate	0.96	0.98	0.98
Hatching rate	0.934	0.921	0.942
Daily brood survival rate	0.98	0.99	0.99
Mean number of fledglings	1.9 ± 2.20	3.1 ± 2.08	3.4 ± 2.01
Breeding success rate	0.467	0.628	0.686
z value *	2.302	1.524	1.246
p value *	0.021	0.128	0.213

*: z values and levels of significance are from the comparison of daily clutch and brood survival rates by the J-test ($p < 0.05$)



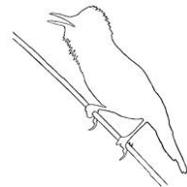
Reed influences nesting success of Great Reed Warbler

Discussion

In the present study, the diameter of the supporting stems averaged 7.3 mm (sparse reed: 7.9 mm; intermediate reed: 7.3 mm; dense reed: 6.7 mm), which is similar to the data reported by Graveland (1998): he found that the diameter of the supporting stems at the De Weerribben Lake was 6.2 mm, and at the Zwarte Meer was 8.0 mm. Accordingly, there are no major differences in reed stem diameter regarding the choice of supporting stems by the Great Reed Warbler between the study sites in The Netherlands and Serbia. The reed density recorded at the De Weerribben Lake (213 stems/m²) corresponds to the intermediate reed density in our study, while that at Zwarte Meer (335 stems/m²) falls in our dense reed category. As in our study, Graveland (1998) considered both old and new stems in estimating the reed density. Dyrz (1981, 1986) reported that the Great Reed Warbler lays clutches at sites where thick reed stems grow, but unfortunately he did not provide precise stem diameter data.

Our results suggest that the Great Reed Warbler does not preferentially select reed stems of specific physical properties for nest-building (at least from the aspect of the parameters considered in this study). This is supported by two findings: there was a significant positive correlation between the diameter of the supporting stems and that of the stems in the surroundings (**Figure 30**), and also a positive correlation between the number of supporting stems and reed density in the surroundings, indicating that Great Reed Warblers used a higher number of supporting stems for constructing a nest in dense reed than in sparse reed (**Table 15**).

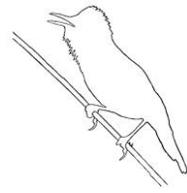
A reasonable explanation as to why the number of supporting stems was largest on the mining ponds (**Table 15**) is that there was little reed management at these habitats, whereas canals were often managed annually, rather through mowing than through burning. However, Great Reed Warbler nests were recorded in both non-managed and managed reed habitats. Dyrz (1981) and Mérő et al. (2014) likewise found Great Reed Warbler nests in both mixed reed (old and fresh stems) and fresh reed, but with a higher proportion of clutches in the mixed reed. Vadász et al. (2008) reported that the Great Reed Warbler favoured both, the interior regions of both cut and non-cut reedbeds. The Great Reed Warbler demonstrates a strong positive preference for the newly cut areas



Reed influences nesting success of Great Reed Warbler

because of the new formation at the edges (Vadász et al. 2008), since it is an “edge species” in reed stands (Báldi and Kisbenedek 1999, Báldi and Kisbenedek 2000, Báldi 2004). Similarly to our results, Vadász et al. (2008) found that a relatively low reed density was highly acceptable to the Great Reed Warbler. Our study revealed that the Great Reed Warbler built a higher number of nests in the intermediate reed density, whereas breeding success was highest in the dense reed. We presume that dense reed might protect the nests better from predators which attack the clutch from above, e.g. the Little Bittern *Ixobrychus minutus* (Mérő et al. 2013, Mérő et al. 2014), the Marsh Harrier *Circus aeruginosus* (Dyrzcz 1981), the Hooded Crow *Corvus cornix* and the Night Heron *Nycticorax nycticorax* (Mérő et al. 2013). The predators which attack the nests from below, e.g. the American Mink *Mustella vison* (Bensch 1993) and the Grass Snake *Natrix natrix* (Mérő et al. 2014), are probably equally potent dangers for the clutches in all three reed densities, because these predators tend to rely more on their senses of smell and hearing in finding the prey than on their vision. However, the loss of clutches can also be affected by rainy and cold weather circumstances (Beier 1981, Fischer 1994, Mérő et al. 2013, Mérő et al. 2014), when the reed density is likely to have little effect.

Novelty of the study: The Great Reed Warbler tends to select nest supporting reed stems that do not differ in physical properties from the available stems in the surroundings. The density of reed stems did not differ among mining ponds, large canals and small canals, while the number of nest supporting stems was higher on mining ponds than on canals. Large canals had the thickest stems both at the nest and in the surroundings. Most nests were initiated in reed of intermediate density, whereas larger clutches were laid and better nesting success was achieved in dense reed, even though the daily clutch and brood survival did not differ among the three reed density categories.



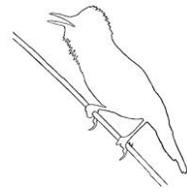
General conclusions and practical implications

General conclusions and practical implications

In conclusion of Study 1, habitat management was primarily important in shaping small mammal communities at the local scale and restoration had little effect locally. Management by mowing and grazing decreased vegetation height, which increased predation risks on small mammals. However, grassland restoration provided benefits to small mammals at the landscape scale by increasing the total area of grasslands, which provide better conditions for the persistence of small mammals during unfavourable periods.

The results from Study 1 have several implications for conservation practice. First, grassland restoration and management should re-create a mosaic of habitat types that combines restored and natural vegetation and no management in at least a portion of the landscape to maximize the chances of persistence for small mammals. The policy implications of our study are that both the local effects and landscape configuration should be considered in the design of restoration and management, and in the monitoring of biodiversity and ecosystem services. The restoration of small mammals as important providers of ecosystem services should also consider the inherent spatiotemporal dynamics of populations that operates at the landscape scale and that can be managed locally. Management in grasslands should vary similarly to that in our study, i.e. there should be refuge patches for small mammals by not managing the vegetation or by cutting the vegetation in late spring. In both cases, the elevation of the potential refuge patches should be considered, because low-lying areas get flooded in early spring, thus refuges should be planned at higher elevation.

In Study 2, I conclude that spatiotemporally variable combined management of reedbeds by grazing and burning positively affects the bird community. Grazing and trampling by cattle led to the opening up of homogeneous reedbeds, creating habitat patches preferred by farmland songbirds. Late-summer burning followed by autumn grazing was effective in controlling reed so that habitats suitable for several non-passerine groups (waterfowl, wading birds, gulls and terns) were established. Reed control led to the increase of open water surfaces with patchy reed, a habitat preferred by rails, coots and grebes. Finally, non-managed patches had high proportions of old reed, which provided

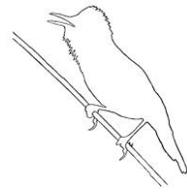


General conclusions and practical implications

habitat for reed songbirds. Many of these changes were mediated by the availability or proportion of old reed, which was the property of reed most affected by management. The spatiotemporally variable management thus led to an increased diversity of habitats and a more heterogeneous marsh landscape, which was reflected in the increased richness and abundance of bird functional groups.

Wetland managers are often faced with the choice of the hierarchical levels (populations/species or the entire community) they target with conservation actions. When the goal of conservation actions is to increase the density of area-sensitive and specialised bird species, e.g. Reed Warbler *Acrocephalus scirpaceus*, Little Bittern *Ixobrychus minutus*, then the population/species level is targeted. In contrast, when the goal is to increase the number of species, managers target the community level and use richness and diversity indices for follow-up. Reedbed management has to be prioritized based on the local conservation needs and managers need to consider the trade-off between increasing the size of homogeneous reed stands for reedbed specialist species on one hand and increasing the diversity of habitats by grazing, burning or water level management on the other. The exceptionally large spatial scales available for our experiment made it possible to provide an example for management to benefit the entire avian community without compromising the habitat requirements of specialists.

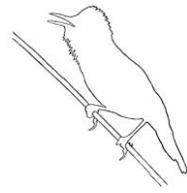
Study 2 provided several other practical implications. Grazing by cattle needs to be continuous and maintained over several years to keep the reedbed loose and heterogeneous. Late-summer burning can also efficiently control reed but burning in itself causes only a temporary effect that disappears in three years even in the presence of grazing, thus, it needs to be repeated every two or three years. Ideally, both actions should be carried out in the non-breeding period of birds or the inactive period of other animals of conservation importance. The late summer, after breeding ceases and before migration or wintering begins, offers a good time period. Trampling in burned areas in the autumn and early spring by cattle leads to the establishment of shallow banks with little or no vegetation, which is attractive for waterfowl, wading birds and gulls and terns. Generally we conclude that both management actions, grazing and burning, are needed to maintain a high diversity of habitats for marshland bird communities.



General conclusions and practical implications

The two species-based studies provided further insight into the processes found in Study 2. Although reed burning probably also affects the breeding density of the Great Reed Warbler by removing the old reed preferred by reed-nesting species for nesting, Study 3 concluded that water level is primarily responsible for the variable breeding density. Although reed burning did not affect breeding success of the Great Reed Warbler, nestling survival was generally higher than egg survival in mixed, non-managed reed. Despite the fact that there were two years with more precipitation in the late than in the early period of the nesting season, breeding success was higher in the late than in early period. This difference could also be explained that reed burning in the spring of these two years resulted in thick and dense reed only in the later part of the breeding season. Our results, which fill a gap in the knowledge of the breeding habits of the Great Reed Warbler, thus have high conservation relevance.

In conclusion of Study 4, I found that reed variables play an important role in the breeding parameters of the reed specialist Great Reed Warbler. The mean reed stem diameter and the reed density hardly differed from those at other study sites in Europe despite the great geographical distance. Our results also indicate that the Great Reed Warbler tends to select reed stems for nest-building that do not differ from those in the surroundings in density or diameter. However, this may also be due to the fine scale of the habitat selected in this study. I, therefore, suggest that further studies should be conducted on a broader scale (e.g. patch or landscape scale) in order to gain further insight. The diameters of both the stems in the surroundings and the supporting stems exhibited rather large fluctuations between the various reed habitats, which lead to the assumption that environmental factors such as the soil characteristics may affect the reed variables. Finally, Great Reed Warblers more frequently selected reedbeds of intermediate or high density for nesting, and they laid larger clutches and raised more young in these areas than in sparse reed. Further studies are necessary to clarify whether this is related to differences in individual quality (e.g. older more experienced birds selecting dense reed and young breeders forced to sparse reed) or to some other factors.

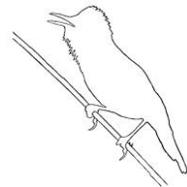


Általános összefoglalás és gyakorlati javaslatok

A jelen disszertáció négy fejezetben tárgyalja az élőhely-rekonstrukciók és kezelések hatásait gyepes kisemlős-közösségeire, és szikes mocsarak és nádasok madár-közösségeire, valamint az égetés, az időjárás és a nádasok tulajdonságainak hatását a nádspecialista nádírigó *Acrocephalus arundinaceus* fészkelésére és költési sikerére különböző nádas élőhelyeken.

Az 1. Vizsgálat eredményei szerint a lokális léptékben az élőhelyek kaszálásos és legeltetési kezelése volt a legfontosabb, míg a rekonstrukció hatása nem volt egyértelmű. A kisemlősök abundanciáját lokális, azaz élőhelyi szinten elsősorban a kezelés és a térszint, valamint ezen tényezők és a mintavételi időszak közötti interakciók határozták meg. A kaszálás és legeltetés a növényzetmagasság csökkentése révén növeli a predáció kockázatait a kisemlősökre. A legmagasabb őszi abundanciát a kezeletlen természetes gyepeseken és a korán (júniusban) kaszált gyepeseken találtam a később kaszált, juh-legelt és szántott területekhez képest. A magasabb térszinten fekvő területek refúgium szerepet játszottak a télvégi-tavaszi elöntések illetve a nyári aszályok során. Tájléptéken kimutattam, hogy a természetes és rekonstruált gyepesek aránya pozitív hatással volt a kisemlősök abundanciájára, míg a lineáris élőhelyek (utak, csatornák) negatívan befolyásolták azt. Eredményeim szerint a rekonstrukció a gyepes területének növelése révén kedvező hatással volt a kisemlősökre, mivel a gyepesek lehetővé tették a kedvezőtlen periódusok átvészélését a kisemlősök számára.

Az 1. Vizsgálat több eredménye is fontos gyakorlati védelmi jelentőséggel bír. A gyeprekonstrukciónak és a kezeléseknak különböző élőhelytípusokból álló mozaikos tájszerkezetet kell kialakítaniuk, mely a rekonstruált és természetes gyepes kombinációjából áll melyen legalább a táj egy részén a kezelés elhagyásával maximalizálhatóak a kisemlősök fennmaradási esélyei a kedvezőtlen periódusokban. A jelen kutatás tanulsága az is, hogy mind a lokális, mind pedig a tájléptékű tényezőket szükséges figyelembe venni a rekonstrukciók és a kezelések tervezésénél, illetve a biodiverzitás és ökoszisztéma-szolgáltatások monitorozásában. A kisemlősök fontos láncszemei az ökoszisztémáknak és számos ökoszisztéma-szolgáltatásban vesznek részt, ezért a rekonstrukciók és kezelések tervezésénél fontos figyelembe venni az állományaik belső tér-



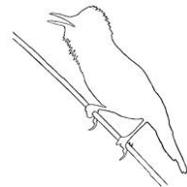
Általános összefoglalás és gyakorlati javaslatok

és időbeli dinamikáját, melyek tájléptéken működnek és lokális szinten kezelhetők.

A 2. Vizsgálat fő következtetése, hogy a térben és időben változatos égetéses és szarvasmarhával történő legeltetési kezelések hatékonyak voltak a homogén zárt nádasok felnyitásában, az élőhelyek sokféleségének növelésében és a madár-együttesek diverzitásának növelésében. A kezelés szignifikánsan hatott a mocsári madárközösségek egyenletességére és diverzitására. A Shannon diverzitás és az egyenletesség a kétszer égetett és legelt foltokban alacsony, míg a Simpson diverzitás magas volt a többi kezeléshez képest. A nem énekes madarak inkább az újonnan égetett, nyílt vízfelületekben gazdag foltokat preferálták, ugyanakkor a nádi énekesek a kezeletlen, régebben égetett és legelt foltokat preferálták, míg a mezőgazdasági területekhez kötődő madárfajok a legelt foltokban mutattak maximumot. A térben és időben változó kezelések elsődleges hatása az volt, hogy az égetéssel gyorsabban, míg a legeltetéssel lassabban, de tartósabban visszaszorult az öreg nád.

Ahhoz, hogy a nádasok heterogén szerkezete fennmaradjon, folyamatos és irányított, több éven át történő legeltetést szükséges alkalmaznunk. A késő nyári égetés ugyancsak képes erőteljesen féken tartani a nádat, de az égetés mellett fontos alkalmazni a legeltetést, mert az égetés hatása két-három éven belül eltűnik. Mindezek miatt az égetést két-három évente szükséges megismételni. Ideális esetben mindkét kezelést a madarak és más védett állatfajok inaktív, azaz nem reproduktív periódusában kell elvégezni. A késő nyári időszak kedvező időpontnak bizonyult, mivel ekkorra már lezajlik a költő madarak szaporodási időszaka, de még nem kezdődik el a vonulási és telelési periódus. Az égetés után a szarvasmarhák taposása kevés vegetációval borított lapos partokat és sekély vízfoltokat eredményeznek, melyek fontosak a lúdalkatúak, a gázlómadarak és a sirályfélék számára. Ennek következtében mindkét kezelési típus releváns annak érdekében, hogy a mocsári madarak számára sokféle élőhelyet biztosítson.

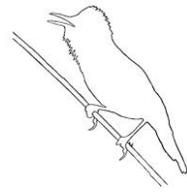
A 3. Vizsgálat eredményei szerint a költőpárok számára és denzitására elsősorban a vízszint-ingadozás hatott (magasabb vízszint több költőpárt eredményezett), míg a nádégetés kevésbé bizonyult fontosnak a nád gyors és erőteljes visszánövése miatt. A vizsgálat egyik legérdekesebb



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eredménye, hogy az égetéses években a nádirigó költési sikere magasabb volt a késői, mint a korai időszakban, míg a kezeletlen években nem volt ilyen különbség. A tojások napi túlélési rátája alacsonyabb volt a korai költési időszakban, mint a késői periódusban, míg a fiókák napi túlélési rátája nem különbözött a periódusok között. A vízszint hatással volt a tojások és fiókák túlélésére, mivel az extrém alacsony illetve extrém magas vízállású években a tojások és fiókák magasabb túlélési arányt mutattak a késői költési időszakban, mint a koraiban.

A 4. Vizsgálat eredményei szerint a nádirigó által fészeképítésre kiválasztott nádszálak denzitása és átmérője nem különbözött a környezet által kínált nádszálakétól függetlenül attól, hogy öreg vagy új nádszálakról van szó. A nádsűrűség azonban szignifikánsan befolyásolta a fészkek számát, a fészkek méretét és a költési sikert. A legtöbb fészek a közepesen sűrű nádban épült, míg a nagy fészkek és magasabb költési siker a sűrű nádasokra voltak jellemzőek. Ugyanakkor a napi túlélési ráták nem különböztek a különböző nádsűrűségi kategóriák között.



Acknowledgements

Acknowledgements

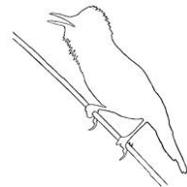
First of all I would like to thank my advisor, Dr. Szabolcs Lengyel for the possibility to participate in the doctoral training and a great project in restoration ecology. I am grateful to my advisor also for the useful comments, advices and his shared knowledge and experiences which helped my scientific work greatly during the doctoral training and the preparation of scientific manuscripts.

Furthermore, I thank my colleagues, the Department of Ecology and the Hortobágy National Park Directorate for supporting my scientific activities. I am particularly grateful to Renáta Bocz, László Polyák, Anna Farkas, Zsuzsa Nagy, Patrik Attila Mérő and Péter Balla for their help during the fieldwork. I acknowledge also Róbert Kis and his family for their kindness and advice during the fieldwork, and sharing their experiences related to the field characteristics.

I acknowledge my dear friend and colleague Antun Žuljević for sharing his experiences in basic ornithology, knowledge on birds, and in practical field techniques in bird surveys. Furthermore, his temper and objective advices were more than useful during my doctoral work.

Finally, I am grateful to my family, i.e. my father, mother and brother who supported my scientific work maximally and shared my aspirations.

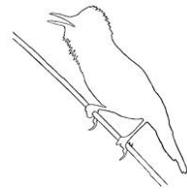
The restoration and management actions were co-financed by the EU LIFE-Nature program (LIFE04NAT/HU/000119, <http://life2004.hnp.hu>). These studies were funded by the Hungarian Scientific Research Fund (OTKA NNF 78887, NNF 85562, K 106133) and by the EU FP7 project SCALES (contract no. 226852).



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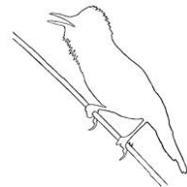
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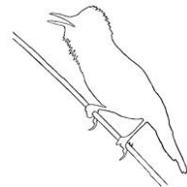
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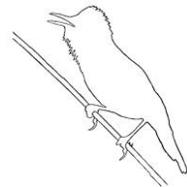
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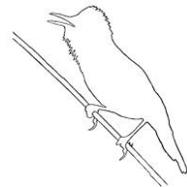
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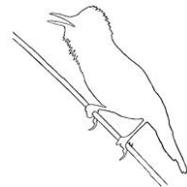
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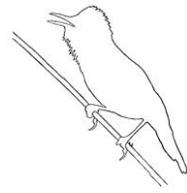
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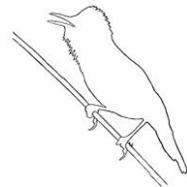
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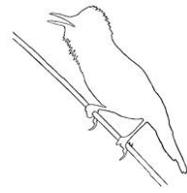
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