COMMUNITY ECOLOGY 10(2): 182-188, 2009
1585-8553/$20.00 © Akadémiai Kiadó, Budapest
DOI: 10.1556/ComEc.10.2009.2.7

Factors affecting the structure of bee assemblages in extensively and intensively grazed grasslands in Hungary

M. Sárospataki[1], A. Báldi[2], P. Batáry[3,6], Z. Józan[4], S. Erdős[3,7] and T. Rédei[5]

[1] *Department of Zoology and Ecology, Szent István University, Gödöllő, Páter K. u. 1., H-2103, Hungary, Fax: +36-28-410-804, Phone: +36-28-522-085, e-mail: sarospataki.miklos@mkk.szie.hu*
[2] *Animal Ecology Research Group of the Hungarian Academy of Sciences and the Hungarian Natural History Museum, Budapest, Hungary*
[3] *Department of Zoology, Hungarian Natural History Museum, Budapest, Hungary*
[4] *Mernye, Hungary*
[5] *Institute of Ecology and Botany of the Hungarian Academy of Sciences, Vácrátót, Hungary*
[6] *Present address: Agroecology, Georg-August University, Göttingen, Germany*
[7] *Present address: PhD School of Environmental Sciences, Szent István University, Gödöllő, Hungary*

Keywords: Biodiversity, Body size, Grazing intensity, Honey bee dominance, Landscape structure, Nesting site, Species richness, Wild bees.

Abstract: Bees are the most important pollinators in Europe. We studied bee assemblages on 7 pairs of extensively and intensively grazed sites in three lowland grassland types in Hungary. No chemicals were applied on the grasslands. The bees were collected using sweep net surveys and 1 m wide transect surveys in 2003. We mapped land-use types (grasslands; arable fields; forests; built-up areas; marshy habitat and open water) based on aerial photographs within a 500 m radius of each study site. We captured 483 individuals of 124 *Apoidea* species in total. This shows very diverse and species rich bee assemblages in these semi-natural grassland areas. Both diversity and percentage of rare species were the highest on the Kiskunság alkali area. The dominance of honey bee (*Apis mellifera*) was very low at each site. Neither species richness nor abundances differed between extensively and intensively grazed sampling sites, among regions, and between edge and interior of sites. However, both species richness and abundance of bees correlated positively with species richness and cover of flowering plants, indicating the important role of food sources. From the landscape parameters wet areas were preferred by small species, while large species tended to avoid build-up areas.

Introduction

Pollination is an ecosystem service, provided primarily by bees which pollinate roughly two-third of the world's crop species, and thus essential in food production (McGregor 1976, Roubik 1995, Kearns et al. 1998, Biesmeijer et al. 2006, Klein et al. 2007). Unfortunately, bees and especially bumblebees are also declining in North America and Europe (Kearns et al. 1998, Sárospataki et al. 2005, Steffan-Dewenter et al. 2005), which reduces pollination service (Kremen et al. 2002), and many authors predict a worsening "pollination crisis" in a few years interval (Kearns et al. 1998, Steffan-Dewenter et al. 2005, Vamosi et al. 2006). Adverse effects of agricultural land conversion and intensified management practices are responsible for the decline (Kearns et al. 1998, Kremen et al. 2002, Morandin and Winston 2005, Tscharntke et al. 2005), including effects of fragmentation, creation of crop monocultures, intensive grazing and chemical use.

Intensification of agriculture is responsible not only for the decline of pollination service, but also for the general decline of biodiversity in Europe (de Heer at al. 2005). However, management intensity, and its consequences on farmland species are not homogeneous across Europe. Comprehensive data are available only for birds, which show that farmland bird populations in Central Europe are increasing – an opposite trend to that was observed in Northern-, Western- and Southern Europe (Donald et al. 2001, Cremene et al. 2005, Gregory et al. 2005). This may indicate less intensive agriculture than in Western Europe, thus may serve as example on how biodiversity in extensive farmland can sustain. Then, such examples can provide reasonable extensive systems that can be targeted by nature friendly agriculture in the intensive farmlands of Western Europe.

The ongoing reforms in agriculture in these post-socialist countries, and the recent introduction of the EU agri-environmental programs pose significant challenges in ecosystem services. How does the organization of bee assemblages change with agricultural management? We studied this question in extensively and intensively grazed grasslands in Hungary. On the other hand, it must take into consideration that with the new EU countries new biogeographical regions of Europe (e.g., the Pannonic region) joined the EU, and in these regions the grasslands have higher importance for biodiversity than in the former EU regions (Donald et al. 2002).

Besides the study of the effects of local farmland management, it is very important to survey the influence of landscape structure and composition (Tscharntke et al. 2005). The species with large home ranges are usually more influenced by large-scale landscape effects than species with small home ranges, and such differences may affect community structure and interactions (Tscharntke et al. 2002). The densities of the three pollinator guilds of bees (solitary wild bees, social bumblebees and honey bee) depend on landscape structure at different spatial scale, and local landscape destruction affects small bodied solitary wild bees more than social, large bodied bee species (Steffan-Dewenter et al. 2002).

In the present paper, we describe the bee assemblages of the three most widespread lowland grassland types in Hungary, and assess their relationship with grazing pressure, and other environmental factors, like landscape structure and composition, availability of nesting sites on the ground, and the flower composition of the vegetation.

Material and methods

Study area

Three different grassland types were included in Central- and Eastern Hungary. The first ("Heves") region is located at Heves Landscape Protection Area in Eastern Hungary, and is dominated by dry and wet alkali grasslands and marshes on solonetz soil. The second ("Alkali") and third ("Meadow") regions were in or near the Kiskunság National Park in Central Hungary. The Alkali region is covered by secondary Pannonic alkali steppe vegetation on solonchak soil. The Meadow region is more heterogeneous (mainly naturally), a mosaic of swamp meadows, calcareous purple moor grass meadows, salt steppes and Pannonic sand steppe grasslands, with scattered small forests form the landscape. For detailed area description, see Báldi et al. (2005).

In all regions, grasslands were the most abundant land-use type (over 60%). Most of the sampling sites were unfenced and none of them were fertilized or treated with pesticides. All sites have been grazed by cattle for at least 5 years from early spring until late autumn. The cattle density was about 0.5 cow per hectare on extensive, and >1 cow per hectare on intensive sites. The former stocking density corresponds to the regional agri-environmental prescription, the latter to the usual cattle densities of commercial farms in the area.

Seven pairs of (one extensively and one intensively grazed) grasslands were selected in all regions (altogether 21 pairs of sites). On the individual sampling sites, two 95 m long transects were marked (a total of 84 transects), one of them in the grassland edge (e.g., next to a channel or road) and the other one 50 m inside the grassland, parallel with the edge. The landscape structure and other environmental variables of each pair were as similar as possible – in this way we tried to control for all factors, except for the grazing intensity. The mean distance within pairs in all regions was 2.1 km, while between pairs it was 12.8 km.

Sampling method

Bees (*Hymenoptera: Apoidea*) were sampled along transects by two methods. First, we used sweep-netting standardized by number of sweeps in May, June and July in 2003. Sweep netting consisted of 3x20 sweeps with a heavy duty sweep net (38 cm internal diameter, 7215HS, BioQuip, Rancho Dominguez, CA, USA). Second, we used 1 m wide transect surveys (Banaszak 1980) to capture individually the large and fast species, which usually escape sweep netting. Each round lasted for 15 minutes per transect. Transect surveys were also repeated in May, June and July, 2003. Sampling was carried out between 10.00 a.m. and 4.00 p.m. on sunny days with no strong winds. Individuals were identified at the species level in the laboratory. The data from the two methods (sweep-netting and transect surveys), and from the three sampling occasions (May, June, July) were pooled. A more detailed description of the methods has been published by Batáry et al. 2007a.

Botanical and supposed background information was collected from ten 1 × 5 m quadrats along transects with 5 m distance between them. The percentage cover of each plant species, bare ground, cow faeces and plant litter was estimated. Mean grass height (cm) was also assessed.

To gain landscape parameters of each study site we mapped land-use types (grasslands; arable fields; forests; built-up areas; marshy habitat and open water) based on aerial photographs within a 500 m radius (for detailed description of landscape survey see Batáry et al. 2007a). The following variables were measured:

- mean area (with exception of built-up area and open water);
- patch density;
- percentage of area of land-use types.

Total length of five different types of boundaries was also measured:

- simple boundary – contact between different land-use types, 0 m wide;
- strip – boundaries with a strip of different vegetation, a trail, or a small ditch without water between fields, 0-2 m wide;
- natural boundary – boundaries involving additional structures, such as streams and hedgerows, >2 m wide;
- man-made boundary – e.g., channels, roads, paths, ditches, >2 m wide;
- combined boundary – the combination of the latter two (e.g., road with hedgerows), >2 m wide.

Table 1. Categories of sampled bee genera in Hungary according to tongue length, nesting site and body size (O'Tool and Raw 1991, Russel, Ikerd and Droege 2005).

Genus	tongue	ground nesting	body size
Andrena	short	yes	small
Anthidium	long	no	small
Anthophora	long	yes	small
Apis	long	no	large
Bombus	long	no	large
Camptopoeum	short	yes	small
Ceratina	long	no	small
Chelostoma	long	no	small
Coelioxys	long	no	small
Colletes	short	yes	small
Dasypoda	short	yes	small
Eucera	long	yes	small
Halictus	short	yes	small
Heriades	long	no	small
Hylaeus	short	no	small
Lasioglossum	short	yes	small
Megachile	long	no	small
Melitturga	short	yes	small
Nomada	long	yes	small
Nomioides	short	yes	small
Osmia	long	no	small
Pasites	long	yes	small
Pseudapis	short	yes	small
Rhophitoides	short	yes	small
Sphecodes	short	yes	small
Tetralonia	long	yes	small

Defining bee and plant traits

Rarity of bees was considered at the country level, and was determined by one of the authors (ZJ). Bees were classified with respect to the most important and frequently used traits (O'Tool and Raw 1991, Goulson 2003) as tongue length, nesting site and body size (Table 1). We used the genus level due to lack of some information, e.g., on the tongue length of species. The classification was based on O'Tool and Raw (1991) and Russel et al. (2005), and can be seen in Table 1. We should note that these categories refer to genus level, and some of the species may not fit (e.g., some *Anthophora* species have similar body size to *Apis mellifera*, still the genus is categorised as small, while *Apis* as large bodied genus). We used, however, the best category for the entire genus (Russel et al. 2005).

The depth of a flower is very important trait for the bees, because the nectar of a deep flower can be reached only by long tongued bees (O'Tool and Raw 1991). A flower was considered deep if its depth was at least 5 mm; there were, however a few exceptions, if the complexity of flower decreases the availability (e.g., *Trifolium* spp.).

Analysis

Linear mixed models using the Restricted Maximum Likelihood method were used with region, management and edge/interior position as fixed, and the pair of extensive and intensive sites as random factors. Type III sum-of-squares method was applied. Variables were log transformed to achieve normality.

We measured correlation between the following variables: 1) abundance of bees with different tongue length (long *versus* short) and cover of the insect pollinated plant species with different flower size (deep *versus* shallow); 2) abundance of ground nesting bees and bare soil or faeces cover (Table 1).

To analyse the landscape effects on the species richness and abundance of small bodied (mostly solitary) *versus* large bodied (social) bee species (Table 1), we made linear regression analyses with backward elimination of variables (a factor was removed if its F value had a significance level $p<0.1$). All landscape percentage data were *arcsin* transformed, other landscape metrics (patch density, mean area and boundary length) were square root transformed (Sokal and Rohlf 1981). Before performing a linear regression, we made a data reduction for landscape metrics because we had too many independent variables (21 landscape metrics). To reduce the number of independent variables, we made principal component analysis with VARIMAX rotation. For calculations the SPSS program was used (SPSS 1999).

Results

The sampled assemblages showed a high species richness (124 species, 483 individuals, including *Apis mellifera*), diversity and number of rare species (Table 2). The highest diversity and species richness were in the Alkali region, the number of rare species were the highest there as well.

The dominant species were *Andrena flavipes*, *Bombus hortorum*, *Halictus maculatus*, *Hylaeus variegatus* and *Pseudapis unidentata* (5.4, 5.4, 6.0, 5.4, 4.8%, respectively) at Alkali region, *A. flavipes*, *Anthophora bimaculata*, *A. mellifera* and *Bombus terrestris* (4.1, 5.8, 4.1, 27.3%, respectively) at Meadow region, and *A. flavipes*, *A. mellifera*, *B. terrestris*, and *Halictus seladonius* (8.2, 10.8, 6.2, 5.1%, re-

Table 2. Assemblage characteristics of bee assemblages on extensively and intensively grazed grasslands in three regions (Alkali, Meadow and Heves) of Hungary.

	Alkali			Meadow			Heves		
	Ext.	Int.	Total	Ext.	Int.	Total	Ext.	Int.	Total
Number of individuals	89	78	167	51	70	121	98	97	195
Number of species	50	42	70	38	28	56	31	45	60
Dominance of *Apis mellifera* (%)	1.12	5.13	2.99	5.88	2.86	4.13	16.33	5.15	10.77
Shannon diversity	3.69	3.50	3.92	3.53	2.42	3.34	3.07	3.56	3.63
Number of rare species	9	7	12	2	2	4	6	4	9

Table 3. Pearson correlation (in first lines) of bee species richness and abundance with plant species richness and cover in Hungarian grasslands. Two-tailed probabilities are given in the second lines; significant values at p<0.05 are in bold. N=84 for all cases.

		Bee			
		Species number (short tongue)	Abundance (short tongue)	Species number (long tongue)	Abundance (long tongue)
Plant	Species number (deep corolla)	0.138 0.211	0.079 0.473	0.281 **0.009**	0.316 **0.003**
	Cover % (deep)	0.245 **0.024**	0.209 0.057	0.291 **0.007**	0.348 **0.001**
	Species number (shallow)	0.204 0.062	0.168 0.127	0.104 0.345	0.149 0.176
	Cover % (shallow)	0.352 **0.001**	0.320 **0.003**	0.298 **0.006**	0.300 **0.006**

Table 4. Results of the linear regressions with backward elimination using the species richness and abundance of small versus large bee species as dependent variables and factors from the PCA as independent variables. The last row shows the variables that strongly correlated with factors from PCA (strong correlation means at least r=0.7). [a] + means positive, - negative correlation; Ar: arable field; BUA: built-up area; Fo: forest; Gr: grassland; Ma: marsh; Wa: water; Simple: boundary between different land uses or between fields of the same land use, 0 m wide; Strip: boundary with a strip of natural vegetation, 0-2 m wide; Manmade: boundary involving additional structures, like channels or roads, >2 m wide; Natural: boundaries involving additional structures, like streams and hedgerows, >2 m wide.

	Model		**Factor 1**		**Factor 2**		**Factor 3**		**Factor 4**		**Factor 5**		**Factor 6**	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Species richness														
Small species	6.298	**0.004**	2.550	**0.015**	-	-	-	-	2.469	**0.018**	-	-	-	-
Large species	2.963	0.093	-	-	-1.721	0.093	-	-	-	-	-	-	-	-
Abundance														
Small species	5.435	**0.008**	1.927	0.061	-	-	-	-	2.675	**0.011**	-	-	-	-
Large species	3.955	0.054	-	-	-1.989	0.054	-	-	-	-	-	-	-	-
PCA[a]			+Ma %; +Ma density; +Ma area; +Simple		+BUA %; +BUA density; +Manmade		+Fo %; +Fo area; +Strip		+Wa %; +Wa density		+Ar %; -Gr%; +Ar density		+Natural	

spectively) at Heves region. The dominance of *B. terrestris* at Meadow region was extremely high compared with the other regions. *A. mellifera* did not have high dominance values at any region (Table 2).

Neither the number of species nor of individuals differed between extensively and intensively grazed sites (t-test, t_{spec}=0.111; d.f.=82; p=0.912; t_{abu}=0.652; d.f.=82; p=0.516). Linear mixed models of species richness and abundance revealed no effect of management, region, edge/interior position and the interaction terms of these factors (all significances were p>0.1).

The most important local factor supposed to be the availability of flowers. Long tongued bees' (Table 1) species richness and abundance positively correlated with species richness and cover of deep flowers, but also with the cover of shallow ones (Table 3). The species richness of short tongued bees positively correlated with the cover of both deep and shallow flowers, although this was stronger with shallow flowers. Their abundance correlated only with shallow flower cover.

None of the correlations were significant at the p=0.1 level between bare soil or faeces cover and species number or abundance of bees nesting in the ground (Table 1).

Models of landscape structure for small species were significant, while for large species marginally significant (Table 4). Small species preferred marshy and wet areas, while large species seemed to avoid built-up areas (Table 4).

Discussion

The species number of bees recorded in this study cover about the 20% of the total species number of the Carpathian basin (Móczár 1960). This shows that the investigated grasslands maintain a significant bee species diversity of Hungary and of the whole Carpathian basin. The species richness and diversity of bees were high compared with those of Western European countries (Dauber et al. 2003, Hirsch and Wolters 2003, Kleijn et al. 2006), and the number of rare species was high as well. On the other hand, there are other Western European studies with similarly high species number (e.g., from Germany, Steffan-Dewenter and Tscharntke 2001). However, in this German study the individual number of the collected bees is much higher (2317 individuals of bees, not including *A. mellifera*). In our study, the number of species was very high (124 species) while the number of individuals was low (483, including *A. mellifera*) and this results in an extremely high diversity of bees. The grazing intensity in the present study even on the intensive sites was lower than that of extensive pastures in Western European countries (e.g., Kruess and Tscharntke 2002). Further, our sampling sites were pesticide and artificial fertiliser free on both management types, in contrast to Western European countries, where these agrochemicals are usually used even on fields with agri-environment schemes (Kleijn et al. 2006). Probably this relatively low intensification level results in the high diversity on the studied Hungarian grasslands. This result highlights the need for prescriptions allowing only chemical free grasslands in agri-environment programs to conserve species rich bee assemblages.

The relative density of apiaries and beehives (and accordingly the honey bee, *A. mellifera*) in Hungary is very high compared to other European countries (Jones 2004). However, we found a very low relative dominance of *A. mellifera* in our sampling sites, in contrast to similar studies in Switzerland and the Netherlands (Kohler et al. 2007). Steffan-Dewenter et al. (2002) found that the abundance of flower-visiting honey bees increased with decreasing proportion of semi-natural habitats at a large spatial scale. In this sense, the extremely low dominance of honey bee in our study sites probably indicates a high proportion of semi-natural habitats and the resilience of bee assemblages of these habitats against introduced species. Since native bee assemblages are at least so effective pollinators than the honey bee (Winfree et al. 2007), the conservation of natural bee assemblages via the conservation of chemical free grasslands, may support pollination service in the landscape.

There was no significant difference between bee assemblages of extensively and intensively grazed sites. It seems that the studied two intensification levels had not enough differences to shape bee assemblages. In similar studies of other animal groups, significant grazing intensity effect was shown only on specialist leaf-beetle species (Batáry et al. 2007b) and on grassland specialist birds (Batáry et al. 2007c) and a marginally significant effect on orthopterans (Batáry et al. 2007a). On the other hand, the grazing intensity had no effect on generalist leaf-beetles, generalist and specialist carabid beetles and weevils (Batáry et al. 2007b) and on birds in general (Báldi et al. 2005). These contradictory results probably show that our extensive and intensive study sites differ so little that only the specialist grassland species could indicate this small difference. In this sense the bees do not seem to be a good indicator of these relatively small grassland management differences. This is supported by results from Germany, where no management effects were found on bee assemblages among abandoned, mown and grazed orchards (Steffan-Dewenter and Leschke 2003). Presumably bees in general are influenced by complex environmental effects, because they usually need different habitats for nesting and feeding (Westrich 1996), and grazing or other treatments may have opposing effects on habitat quality in terms of feeding and nesting resources (Steffan-Dewenter and Leschke 2003).

Similar lack of effect in between-region and interior-edge comparisons suggests that some factors other than landscape management were responsible for the observed pattern. The most important candidate factor may be the availability of flowers (Kleijn and van Langevelde 2006). The positive correlation between long tongued bees with both deep and shallow flowers shows that long tongued bees can forage both deep and shallow flowers, and they tend to feed from a larger number of plant species (Harder 1985). However, Plowright and Plowright (1997) stated that long tongued bumblebees feed more slowly on shallow flowers than short tongued bees do. The lack of correlation between the abundance of short tongued bees and the cover of deep flowers shows that these species really cannot forage on flowers with deep corolla (Harder 1985).

Landscape structure had strong effect on small bees. This is in accordance with the study of Steffan-Dewenter et al. (2002) as they found that at small scales (up to 750 m) the landscape context has significant effect on small bodied, solitary bee species. In our study, the small species preferred landscape with marshy and wet areas, probably because they fly only short distances and need drinking water. The study year (2003) was extremely dry, forcing bees to drink frequently. Small bees fly only a few hundred meters (Gathmann and Tscharntke 2002), therefore their preferred habitats were near to wet areas. Large bees, with a flying distance in the order of kilometres (Walther-Hellwig and Frankl 2000) were able to move further apart from water, resulting in the lack of this effect in their habitat selection. Instead, large species avoided man-made structures, roads, farm buildings and villages.

Our results showed that Hungarian pastures have diverse and species rich bee assemblages. Even the intensively grazed grasslands showed this high diversity, and there is no significant difference between intensive and extensive sites. Therefore, both management intensities should be maintained. However, we should note that several important management options were not involved into this study, like abandonment or high intensification (e.g., fertilizer application) of grasslands. It seems that both of these changes result in decline of grassland biodiversity (Verhulst et al. 2004), but studies on bees, or even other insects are missing. Therefore, there is an urgent need to initiate studies to investigate the effects of the full range of farmland management on biodiversity.

Acknowledgements: We are grateful to G. L. Lövei and I. Steffan-Dewenter for useful comments on the manuscript, and to G. L. Lövei for linguistic revision. We thank the following persons for the botanical survey: A. Csecserits, Zs. Erős, L. Gálhidy, J. Honti, K. Kenderes, E. Kovács, I. László, B. Lhotsky, B. Mihók and R. Szabó. We thank the Kiskunság and Bükk National Park Directorates for permissions, staff for help, and landowners J. Csaplár, P. Oláh and F. Pongrácz for allowing us to work on their fields. The study was supported by the EU 5th FP 'EASY' (QLK5-CT-2002-01495), and the paper writing partly by the Faunagenezis project (NKFP 3B023-04). A.B. was a Bolyai research fellow of the Hungarian Academy of Sciences, P.B. was supported by the Alexander von Humboldt Foundation during the preparation of the paper.

References

Báldi, A., P. Batáry and S. Erdős. 2005. Effects of grazing intensity on bird assemblages and populations of Hungarian grasslands. *Agricult. Ecosyst. Environ.* 108:251-263.

Banaszak, J. 1980. Studies on methods of censusing the number of bees (Hymenoptera, Apoidea). *Polish Ecol. Studies* 6:355-366.

Batáry, P., K.M. Orci, A. Báldi, D. Kleijn, T. Kisbenedek and S. Erdős. 2007a. Effects of local and landscape scale and cattle grazing intensity on Orthoptera assemblages of the Hungarian Great Plain. *Basic Appl. Ecol.* 8:280-290.

Batáry, P., A. Báldi, G. Szél, A. Podlussány, I. Rozner and S. Erdős. 2007b. Responses of grassland specialist and generalist beetles to management and landscape complexity. *Diversity Distrib.* 13:196-202.

Batáry, P., A. Báldi and S. Erdős. 2007c. Grassland versus non-grassland bird abundance and diversity in managed grasslands: local, landscape and regional scale effects. *Biodivers. Conserv.* 16:871-881.

Biesmeijer, J. C., S.P.M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A.P. Schaffers, S.G. Potts, R. Kleukers, C.D. Thomas, J. Settele and W.E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351-354.

Cremene, C., G. Groza, L. Rakosy, A.A. Schileyko, A. Baur, A. Erhardt and B. Baur. 2005. Alterations of steppe-like grasslands in Eastern Europe: a threat to regional biodiversity hotspots. *Conserv. Biol.* 19:1606-1618.

Dauber, J., M. Hirsh, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agricult. Ecosys. Environ.* 98:321-329.

de Heer, M., V. Kapos and B.J.E. ten Brink. 2005. Biodiversity trends in Europe: development and testing of a species trend indicator for evaluating progress towards the 2010 target. *Philos. Trans. R. Soc. London [Biol.]* 360:297-308.

Donald, P.F., R.E. Green and M.F. Heath. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. London [Biol.]* 268:25-29.

Donald, P.F., G. Pisano, M.D. Rayment, and D.J. Pain. 2002. The Common Agricultural Policy, EU enlargements and the conservation of Europe's farmland birds. *Agricult. Ecosys. Environ.* 89:167-182.

Gathmann, A. and T. Tscharntke. 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71:757-764.

Gregory, R.D., A. van Strien, P. Vorisek, A.W.G. Meyling, D.G. Noble, R.P.B. Foppen and D.W. Gibbons. 2005. Developing indicators for European birds. *Philos. Trans. R. Soc. London [Biol.]* 360:269-288.

Goulson, D. 2003. *Bumblebees; Their Behaviour and Ecology*. Oxford University Press, Oxford.

Harder, L.D. 1985. Morphology as a predictor of flower choice by bumble bees. *Ecology* 66:198-210.

Hirsch, M. and V. Wolters. 2003. Response of aculeate Hymenoptera to spatial features of an agricultural landscape. *J. Nat. Conservat.* 11:179-185.

Jones, R. 2004. European beekeeping in the 21st century: strengths, weaknesses, opportunities, threats. *Bee World* 85:77-80.

Kearns C.A., D.W. Inouye and N.M. Waser. 1998. Endangered mutualisms: The conservation of plant-pollinator interactions. *Ann. Rev. Ecol. Syst.* 29:83-112.

Kleijn, D. and F. van Langevelde. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic Appl. Ecol.* 7:201-214.

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

Klein, A-M., B.E. Vaissiere, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. Lond. [Biol.]* 274:303-313

Kohler, F., J. Verhulst, E. Knop, F. Herzog and D. Kleijn. 2007. Indirect effects of grassland extensification schemes on pollinators in two contrasting European countries. *Biol. Conserv.* 135:302-307.

Kremen, C., N.M. Williams and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Nat. Acad. Sci. U S A.* 99:16812-16816.

Kruess, A. and T. Tscharntke. 2002. Grazing intensity and the diversity of Orthoptera, butterflies and trap-nesting bees and wasps. *Conserv. Biol.* 16:1570–1580.

McGregor, S. E. 1976. *Insect Pollination of Cultivated Crop Plants.* U.S. Department of Agriculture–Agricultural Research Service, Washington, DC.

Móczár, M. 1960. *Fauna Hungariae: Colletidae - Melittidae.* Akadémiai Kiadó, Budapest (in Hungarian).

Morandin L.A. and M.L. Winston. 2005. Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecol. Appl.* 15:871-881.

O'Tool C. and A. Raw. 1991. *Bees of the World.* Blandford Publishing, London.

Plowright C.M.S. and R.C. Plowright. 1997. The advantage of short tongues in bumble bees (Bombus) - Analyses of species distributions according to flower corolla depth, and of working speeds on white clover. *Can. Entomol.* 129:51-59.

Roubik, D.W. 1995. *Pollination of Cultivated Plants in the Tropics.* Food Agric. Org. U.N., Rome.

Russell, K.N., H. Ikerd and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. *Biol. Cons.* 124:133-148.

Sárospataki, M., J. Novák and V. Molnár. 2005. Assessing the threatened status of bumble bee species (Hymenoptera: Apidae) in Hungary, Central Europe. *Biodivers. Conserv.* 14:2437-2446.

Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. (2nd ed.). Freeman, New York.

SPSS, 1999. *SPSS for Windows 10.0.* SPSS Inc., Chicago, USA.

Steffan-Dewenter, I. and T. Tscharntke. 2001. Succession of bee communities on fallows. *Ecography* 124:83-93.

Steffan-Dewenter, I. and K. Leschke. 2003. Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. *Biodivers. Conserv.* 12:1953-1968.

Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421-1432.

Steffan-Dewenter, I., S.G. Potts and L. Packer. 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.* 20:651-652.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess and C. Thies. 2002. Characteristics of insect populations on habitat fragments: A mini review. *Ecol. Res.* 17:229-239.

Tscharntke, T., A.M. Klein, A. Kruess,I. Steffan-Dewenter and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett. 8:857–874.*

Vamosi, J.C., T.M. Knight, J.A. Steets, S.J. Mazer, M. Burd and T-L. Ashman. 2006. Pollination decays in biodiversity hotspots. *PNAS* 103:956-961.

Verhulst, J., A. Báldi and D. Kleijn. 2004. Relationship between land-use intensity and species richness and abundance of birds in Hungary. *Agricult. Ecosys. Environ.* 104:465–473.

Walther-Hellwig K. and R. Frankl. 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *J. Appl. Entomol.* 124:299-306.

Westrich, P. 1996. Habitat requirements of central European bees and the problem of partial habitats. In: A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich and I.H. Williams (eds.), *The Conservation of Bees*. Academic Press, London. pp. 1-16.

Winfree, R., N. M. Williams, J. Dushoff and C. Kremen. 2007. Wild bees provide insurance against ongoing honey bee losses. *Ecol. Lett.* 10:1105-1113.

Received November 5, 2008
Revised May 20, 2009
Accepted September 4, 2009