

Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape

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Abstract: In selected foraging habitats of an agricultural landscape flower visits of bumblebees and community structure of foraging bumblebees were studied, with special regard to the role of crops as super-abundant resources. Most crops represent temporal foraging habitats with high abundance of bumblebees but mainly with low diversity in the bumblebee forage community, in contrast to permanent foraging habitats such as, for example, a hedgerow. The high numbers of bumblebees in the monoculture of crop plantations consisted mainly of short-tongued bumblebee species. The role of foraging distances for the visitation rate of foraging habitats was studied by performing capture–recapture experiments with natural nests of *Bombus terrestris*, *Bombus lapidarius* and *Bombus muscorum*. Differences were found on the species as well as the individual level. The foraging distances of *B. muscorum* were more restricted to the neighbourhood of the nesting habitat than the foraging activity of *B. terrestris* and *B. lapidarius*. High percentages of *B. terrestris* workers were recaptured while foraging on super-abundant resources in distances up to 1750 m from the nest. Isolated patches of highly rewarding forage crops, in agricultural landscapes, are probably only accessed by bumblebee species with large mean foraging distances, such as the short-tongued *B. terrestris*. Species like the rare, long-tongued *B. muscorum* depend on a close connection between nesting and foraging habitat. A restricted foraging radius might be one important factor of bumblebee species loss and potential pollinator limitation in modern agricultural landscapes. Furthermore, long-distance flights of bumblebee pollinators have to be considered in the present discussion on gene flow from transgenic plant species on a landscape scale.

1 Introduction

The importance of bumblebees, and other wild bees, for pollination in agricultural areas has been increasingly emphasized within the last decade (CORBET et al., 1991; OSBORNE et al., 1991; WILLIAMS, 1995, 1996). Where honeybees are insufficient pollinators or are lacking due to mite epidemics then wild bees are the most important taxa that provide pollination services to numerous arable crops (FREE, 1993; O'TOOLE, 1993; WATANABE, 1994). Effective pollen dispersal by bumblebees and other wild bees is essential for maximum seed set in crops and in wild flowers (JENNERSTEN et al., 1992; STEFFAN-DEWENTER and TSCHARNTKE, 1997), as well as for maintaining genetic variability in small, isolated plant populations (KWAK et al., 1991; KWAK et al., 1996; YOUNG et al., 1996). Over the same time-period, an increase of endangered or locally and regionally extinct bumblebee species has been found in the agricultural landscapes of many countries (WILLIAMS, 1986; RASMONT, 1995; BANASZAK, 1996; AMIET, 1996; BUCHMANN and NABHAN, 1996; WESTRICH et al., 1998). In particular, the numbers of long-tongued bumblebee species, that are irreplaceable pollinators of flowers with long corollas, are declining (RASMONT et al., 1993).

For the survival of bumblebees in agricultural areas, and thus their availability as pollinators, there

are two necessary prerequisites: nesting habitat and foraging habitat (WESTRICH, 1996). Due to the general problem of finding the nests, only sparse and qualitative information is available about the spatial distribution of natural nest sites of the different species in a landscape (ALFORD, 1975; SVENSSON and LUNDBERG, 1977; FUSSELL and CORBET, 1992). As foraging habitats and food plants of bumblebees have been quantified for only a few agricultural areas (BANASZAK, 1983, 1996; FUSSELL and CORBET, 1991; CORBET, 1995), we chose several agricultural landscape areas to study in order to determine their suitability as temporary or permanent foraging habitats for different bumblebee species with special regard to the mass supply of crops.

Intensification in agriculture is usually accompanied by fragmentation and isolation of seminatural vegetation complexes (SETTELE et al., 1996) and the loss of small, uncultivated field boundaries that provide the majority of nesting places in an otherwise highly disturbed environment (BANASZAK, 1983; VON HAGEN, 1994). Therefore, information about the spatial relation between nesting and foraging habitat, which is expressed as the distances that workers or queens cover during forage flights, becomes of essential importance. In modern agricultural landscapes, bumblebees must often cross large areas of crops with little or no reward to reach isolated fields with crops

that offer nectar and/or pollen. Bumblebee colonies can only develop and finally reproduce successfully if food resources throughout the whole colony cycle are available within reachable distances. Although foraging behaviour of bumblebees and pollen dispersal has been investigated intensively on a small scale, such as single flowers or within and between patches of flowers (e.g. HEINRICH, 1976, 1979b,c; THOMSON et al., 1987; SOWIG, 1989; KWAK et al., 1991; GOULSON et al., 1998) only little information is available about the flight distances of foraging bumblebee species on a larger scale within the landscape (BOWERS, 1985; DRAMSTAD, 1996; SAVILLE et al., 1997).

The present study addressed two questions. First, the distribution and density of bumblebees in habitats with permanent and temporal flower availability was compared and second, the flight distance of individually marked bumblebees was analysed, using the three species *Bombus terrestris*, *Bombus lapidarius* and *Bombus muscorum*, and we tried to find correlations between flight distances and patterns of resource utilization in differently structured habitats.

2 Methods

2.1 Study area

The study area is situated in a basin landscape called 'Amöneburger Becken', Hessen, West Germany close to the village of Wittelsberg. The coordinates 50°46' N, 8°52' E bisect the study area of about 5.4 km², which ranges from 200 to 305 m in altitude. The Amöneburger Becken is covered by loess soil and used for intensive agricultural use. More than 70% of the study area was arable land and about 20% was covered by grassland. The main crops are cereals, *Beta vulgaris*, *Brassica napus*, *Pisum sativum*, and *Zea mays*. Numer-

ous drainage ditches but few trees and hedges are found in this open agricultural landscape. The southern part of the study area includes the heterogeneously structured outskirts of the village Wittelsberg, with fruit trees on meadows, pastures, hedges, dry meadows and an abandoned sand quarry.

2.2 Foraging habitats

Fifteen bee walk transects of 200 m × 2 m (BANASZAK, 1980; TERÄS, 1983) were established to count bumblebees at foraging habitats (table 1). They were chosen to represent characteristic landscape structures with semi-natural vegetation or arable crops. Because of the high bumblebee abundance in the *Phacelia tenuifolia* and the *Trifolium pratense* field, bee counts had to be restricted to squares of 2 m × 2 m. Bee walks were carried out between 0900 and 1900 h at temperatures above 12°C without rain or stormy wind from mid-May until September 1996. The bumblebee species, sex and the plant species visited were registered for any counted foraging bumblebee. The dominance structure of the foraging communities was calculated using the counts of four bee walks ranked by maximum abundance (June until August).

All flowering, insect-pollinated plant species were registered at every bee walk in the transects. The coverage of the different plant species flowering was estimated using the Braun-Blanquet scale (DIERSCHKE, 1994).

Bombus terrestris, *B. lucorum* and *B. cryptarum* could not be identified under field conditions and were treated as one species denoted as *B. terrestris*. Nomenclature of bumblebee species follows SCHWARZ et al. (1996), for plant species nomenclature we follow OBERDORFER (1983).

2.3 Capture-recapture experiments

For individual marking, apiarist's tags of different colours were glued to the thorax (PRYS-JONES and CORBET, 1987). The bumblebees were caught and fixed in a tube for mark-

Table 1. Foraging habitats listed according to the number of plant species (PS) used as food plants with mean number of bumblebee individuals (IN) per observation per 400 m², and mean number of bumblebee species per observation. Type of foraging habitat: Temporary (T), flower resources offered less than 3 weeks; Permanent (P), flower resources offered at least 8 weeks; M, mass supply of one plant species with a coverage > 35%

Foraging habitat	Type	Number of observations	PS food plants/ observation	Relative cover of food plants (%)	Mean IN/observation	Mean BS/observation
Dry meadow	P	15	17	31	5	3
Sand quarry	P	15	15	27	5	2
Ditch/meadow	P	15	12	26	13	5
Roadside	P	15	12	30	8	4
Path verge	P	10	12	19	6	2
Hedgerow	P	15	10	16	4	3
Hill track	P	14	9	24	3	2
Orchard pasture	P	15	8	24	10	3
Rape field margin	P	15	7	49	4	3
Mean P:	—	14.3	11.3	27	6.4	3.0
Wet meadow	T/M	5	4	41	16	2
<i>Sinapis arvensis</i> -field	T/M	8	4	37	14	3
<i>Trifolium repens</i> -field	T/M	5	4	100	25	3
<i>Phacelia tenuifolia</i> -field	T/M	49	1	100	1380*	2
<i>Trifolium pratense</i> -field	T/M	13	1	100	447*	4
<i>Helianthus annuus</i> -field	T/M	5	1	100	263	6
Mean T/M:	—	14.2	2.5	80	79.5	3.3
P (Mann-Whitney U)	—	—	< 0.001	< 0.005	< 0.001	0.77

*estimates from counts on 4 m²

ing honeybee queens. Six natural, underground nests of three species (one nest of *B. muscorum*, three nests of *B. lapidarius* and two nests of *B. terrestris*) located within a radius of 100 m were chosen and workers leaving the nest were marked individually from July to the end of August. Between 36 and 286 bumblebees per species were individually marked, depending on the size of the nests (fig.).

The search for marked, foraging individuals covered a radius of 2000 m around the nest site. The searching time decreased with increasing distance from the nesting habitats from 180 h within 100 m radius to 30 h at 1500 to 2000 m radius.

For all three nests of *B. lapidarius* the mean recapture rate was 18%, in contrast to *B. terrestris*, which showed an average of only 10%. Of the *B. muscorum* nest 36% of marked workers could be found while foraging.

3 Results

3.1 Bumblebee species

In the monitored transects 5064 individuals (queens, workers, males) of 13 nonparasitic and five parasitic bumblebee species were recorded (table 2). All species could be observed regularly except the rare species *B. distinguendus* and *B. subterraneus* with only a few records of queens and males. Seasonal flight time of all regularly observed species overlapped from end of May until the end of August. Only *B. pratorum* was not found in the transects after 3 August.

3.2 Temporary and permanent foraging habitats

Based on the duration of the floral resource availability, two different types of foraging habitat can be distinguished: permanent and temporal foraging habitats

Table 2. Bumblebee species and numbers of registered individuals in the transects

<i>Bombus</i> spp.	<i>n</i>
Nonparasitic	
counted as grouped species:	2018
<i>Bombus lucorum</i> (L. 1761)	
<i>Bombus terrestris</i> (L. 1758)	
<i>Bombus cryptarum</i> (Fab. 1775)	
<i>Bombus lapidarius</i> (L. 1758)	1624
<i>Bombus pascuorum</i> (Scop. 1763)	774
<i>Bombus pratorum</i> (L. 1761)	155
<i>Bombus sylvarum</i> (L. 1761)	131
<i>Bombus muscorum</i> (L. 1758)	62
<i>Bombus hortorum</i> (L. 1761)	61
<i>Bombus ruderarius</i> (Müll. 1776)	56
<i>Bombus soroeensis</i> (Fab. 1776)	56
<i>Bombus distinguendus</i> (Morawitz 1869)	5
<i>Bombus subterraneus</i> (L. 1758)	3
Parasitic	
<i>Bombus rupestris</i> (Fab. 1793)	62
counted as grouped species:	57
<i>Bombus sylvestris</i> (Lep. 1832)	
<i>Bombus bohemicus</i> (Seidl 1838)	
<i>Bombus barbutellus</i> (Kirby 1802)	
<i>Bombus vestalis</i> (Geoff. 1785)	
Sum	3046

(table 1). High numbers of different food-plant species guaranteed sequential flowering in the permanent foraging habitats. In contrast, the crop-transects were either monocultures (*Phacelia tenuifolia*, *Trifolium pratense* or *Helianthus annuus* transects) or at least one forage plant species dominated with a cover of more than 35% in the vegetation (*Trifolium repens*, *Sinapis arvensis* transect, see table 1). Due to the short flowering periods of the crops and/or due to harvesting these abundant resources existed for only between 1 and 3 weeks and thus could only be used temporarily as foraging habitats. In the wet-meadow transect, a temporary mass supply was provided by abundant flowering of *Lathyrus pratensis* that was finished by mowing.

3.2.1 Number of food plant species, number of bumblebee species and bumblebee density

The comparison between permanent foraging habitats (P) and temporary/mass supply foraging habitats (T/M) revealed significant differences regarding the number of food plant species that were visited, the mean bumblebee densities per observation, and the relative cover of food plant species in the vegetation (table 1). In temporary foraging habitats one to four plant species formed up to 100% of the vegetation cover. In contrast, high numbers of different food plant species covered less than 50% of the vegetation in permanent foraging habitats.

The species richness of bumblebees did not differ between permanent and temporal foraging habitats (table 1).

3.2.2 Dominance structure of bumblebee foraging communities and distribution of bumblebee species

The foraging communities of T/M supply habitats were strongly dominated by either one or two species (79–99% of individuals counted per transect, see table 3). Only the *Trifolium pratense* field formed an exception in this respect. In four of the six T/M supply foraging habitats *Bombus terrestris* and *Bombus lapidarius* were the dominant species in the bumblebee forage community.

The highest abundances of bumblebees were found in the temporary foraging habitats dominated by these two species (table 3).

In contrast, *B. pascuorum* reaches its highest dominance values in the foraging communities of the permanent habitats. In permanent habitats most foraging communities consists of two or three bumblebee species with a share of over 10% in addition to the dominating species. These foraging communities are more evenly structured than those of the temporary foraging habitats.

3.3 Foraging distances of *Bombus terrestris*, *Bombus lapidarius* and *Bombus muscorum*

Foraging distances varied among the individual workers of each bumblebee species in the dimension of hundreds of metres. However, the observed flight dis-

Table 3. Dominance structure in the bumblebee forage communities of permanent foraging habitats (*P*) and temporary/mass supply foraging habitats (*T/M*) as the percentage of each bumblebee species of total individuals counted (*B. y/b* = individuals of the species *Bombus sylvestris*, *Bombus bohemicus*, *Bombus barbutellus* and *Bombus vestalis* that could not be exactly determined during counting were grouped)

<i>Phacelia tenuifolia</i>	<i>Helianthus annuus</i> T/M	roadside T/M	rape field margin P	ditch/meadow P	<i>Trifolium repens</i> P	<i>Sinapis arvensis</i> T/M	path verge T/M	hedgerow P	P	wet meadow T/M	<i>Trifolium pratense</i> T/M	sand quarry P	hill track P	orchard pasture P	dry meadow P
<i>B. terrestris</i>	61	54	39	37	30	46	34	30	21	1	13	8	13	11	14
<i>B. lapidarius</i>	38	44	26	18	16	49	45	51	28	0	1	16	4	7	8
<i>B. pascuorum</i>	1	+	13	3	19	4	2	2	10	90	45	67	67	51	30
<i>B. sylvarum</i>	1	1	4	4	13	0	1	4	10	6	20	0	2	25	2
<i>B. ruderarius</i>	0	0	7	0	4	0	11	5	2	0	7	0	0	1	3
<i>B. pratorum</i>	0	+	3	0	1	0	0	4	0	0	0	0	0	1	2
<i>B. muscorum</i>	0	+	4	0	7	0	0	0	9	0	13	0	0	0	0
<i>B. soroeensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25
<i>B. hortorum</i>	0	+	1	1	4	0	4	0	7	3	1	1	6	1	0
<i>B. distinguendus</i>	0	+	0	0	+	0	2	2	0	0	0	0	0	0	0
<i>B. subterraneus</i>	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0
<i>B. rupestris</i>	0	0	3	24	2	0	0	2	5	0	+	3	4	1	2
<i>B. barbutellus</i>	0	0	0	0	+	0	0	0	0	0	0	0	0	0	2
<i>B. bohemicus</i>	0	0	0	1	+	0	0	0	2	0	0	0	0	0	2
<i>B. sylvestris</i>	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0
<i>B. vestalis</i>	0	0	0	3	0	0	0	0	2	0	0	0	0	0	6
<i>B. y/b</i>	0	+	1	8	2	1	0	2	3	0	0	4	4	0	5
Sum percentage	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
<i>n</i>	976	1051	109	65	204	72	96	57	56	78	238	70	52	140	60

Bold, Dominating species; *Italics*, species with a share > 10%; +, species with a share < 0.7%; P, permanent foraging habitats; T, temporary foraging habitats; M, one plant species' cover > 40%.

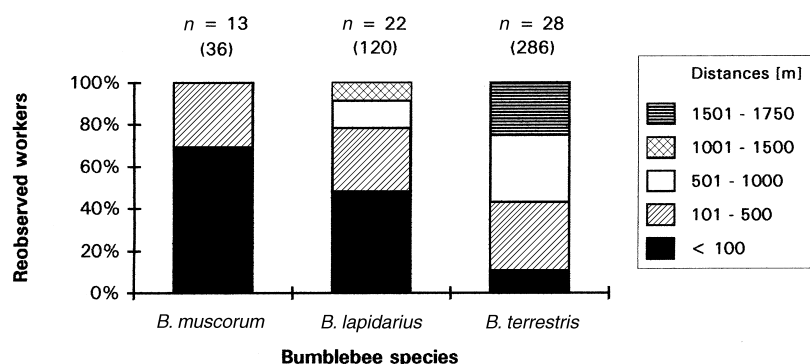


Figure. Proportions of recaptured workers at different distances from the nest, number of recaptured workers (n), and number of marked workers (in brackets) of the three species *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris*

tances also showed differences on species level (fig.). All re-observed workers of *B. muscorum* foraged on flowers within 500 m around their nest (fig.). Nevertheless, we found one *B. muscorum* worker entering the nest with pure *Phacelia tenuifolia* pollen in the corbiculum. As the nearest *Phacelia* field was about 650 m away, we suggest that single workers of this species also forage further afield.

In contrast, only 43% of the recaptured *B. terrestris* workers ($n=11$) were found within a 500 m radius around the nest site (fig.). Almost 25% of recaptured *B. terrestris* ($n=7$) were foraging in habitats in distances between 1500 and 1750 m. Two different workers were repeatedly found at this maximum foraging distance of 1750 m.

For the three *B. lapidarius* nests, an average of about 78% of the recaptures ($n=18$) were made within 500 m around the nests and about 9% ($n=2$) were within the 1001–1500 m (fig.). The farthest re-observation of two *B. lapidarius* workers was at 1500 m. The foraging distances of the three species showed significant differences (Kruskal–Wallis test, $\chi^2=16.7$, d.f. = 2, $P < 0.001$).

3.4 Foraging habitats of recaptured workers

The farthest foraging habitats that were visited in the range 1001–1750 m by recaptured workers of *B. lapidarius* and *B. terrestris* were exclusively temporary foraging habitats in fields with *Phacelia tenuifolia* or *Helianthus annuus*. For medium distances (501–1000 m) almost all re-observations of *B. lapidarius* and *B. terrestris* were made at the crop *Phacelia tenuifolia*. At the low-density resources at roadsides, ditches or farm-tracks that bumblebees had to pass on their way to those distant crop fields, only one marked worker of *B. lapidarius* was observed.

Within a radius up to 500 m around the nests the recaptured bumblebees of all species were foraging in permanent foraging habitats (e.g. ditch/meadow transect, hedgerow transect, see table 1) on various food plant species that occurred in low density.

4 Discussion

4.1 Foraging habitats in agricultural landscapes

The reduction and fragmentation of foraging habitats in seminatural vegetation and the spatially concentrated offered resource abundance in field crops is specific about modern agricultural landscapes.

In our study we classified two different types of foraging habitats: (a) permanent foraging habitats with high numbers of visited food plant species with low relative cover flowering sequentially from May until September and (b) temporary foraging habitats where flowering lasted only a few weeks.

All surveyed field crops were temporary foraging habitats. In crops the temporary character is accompanied by the mass supply of only one forage plant species. Bumblebee abundance was extremely high in these temporary monocultures of *Phacelia tenuifolia*, *Helianthus annuus* and *Trifolium pratense*.

The analysis of the dominance structure in foraging communities revealed that the extremely high numbers of individuals on *Phacelia* and *Helianthus* consisted of 90% of *B. lapidarius* and *B. terrestris*. Thus, these two bumblebee species are obviously the main beneficiaries of the temporary mass supply of crops in the studied agricultural landscape.

Flower preferences of different bumblebee species based on tongue length differences certainly will influence the dominance structure within bumblebee forage communities (RANTA, 1983; TERÄS, 1985; PRYS-JONES and CORBET, 1987). In our opinion, however, too little attention has so far been given to the aspect of differences in foraging distances of bumblebee species.

4.2 Foraging distances of bumblebee species

Although bumblebees are in general a well-studied group of Hymenoptera, information on foraging distances of the different bumblebee species is rare and mostly based on single observations by chance. Some authors suggest that bumblebees generally forage

close to the nest (BRIAN, 1954; ALFORD, 1975; BOWERS, 1985; ROTENBERRY, 1990), as long foraging flights are both energy and time consuming (HEINRICH, 1976, 1979a). Others found that bumblebees avoid the close neighbourhood of the nest and forage at distances of more than 350 m and up to 600 m away from the nest (DRAMSTAD, 1996; SAVILLE et al., 1997). Few authors so far have suggested that bumblebee species differ in foraging radius (FREE and BUTLER, 1959; WITTE et al., 1989; HEDTKE, 1996).

In our study *B. muscorum*, *B. lapidarius* and *B. terrestris* shared a nest site with equal food availability. Nevertheless, the three species differed in the spatial use of foraging habitats in the surrounding landscape. The differences between *B. muscorum* and *B. terrestris* were most extreme.

It has been assumed on the basis of releasing experiments that workers of *B. terrestris* and *B. lapidarius* might forage as far as 3–4 km (HEDTKE, 1996). Even from the point of view of energy gain, HEINRICH (1979a) assumed that forage flights of 5 km could be effective, if the foraging habitats visited are more rewarding than others close by. Indeed, marked *B. terrestris* and *B. lapidarius* workers were found foraging on such abundant, but temporary resources such as *Phacelia tenuifolia* or *Helianthus annuus* fields in distances up to 1750 m. *Bombus terrestris* and *B. lapidarius* gained a higher proportion of their food from distant temporary foraging habitats. In contrast, the majority of observed workers of the *B. muscorum* colony visited a variety of food plants scattered alongside neighbouring farm-tracks, ditches, path verges and a small meadow. Thus, a high percentage of the *B. muscorum* colony relied on the permanent foraging habitats, of which one (a farm-track) was at the same time the nesting habitat.

Thus, we suggest that the observed differences in bumblebee abundance between the permanent and temporary/mass supply foraging habitats are essentially influenced by the different mean foraging distances of the species.

It is unlikely that the high numbers of *B. lapidarius* and *B. terrestris* workers in the *Phacelia tenuifolia* field all came from nests neighbouring the field. The dominance structure in such super-abundant resources probably reflects far more the bumblebee densities of long-distance foragers within a certain landscape unit. Bumblebee species with a smaller mean foraging radius will not be able to use such isolated resources. Other studies indicate that it is probably not only *B. muscorum* that has a smaller foraging range than *B. terrestris* and *B. lapidarius*, but also the medium- and long-tongued species *B. pascuorum*, *B. sylvarum* and *B. ruderarius* (WITTE et al., 1989; HEDTKE, 1996). Certainly species with a more restricted range do not avoid abundant field crops if they are within a reachable distance as, for example, the *Trifolium pratense* field in our study also shows. This transect was within a few hundred metres of wet grassland, set-aside grassland and a road embankment – all landscape elements that offered permanent food resources and nesting habitats.

According to our results *B. terrestris* and *B. lapidarius* are spatial generalists that are able to use temporary crop resources concentrated in a few, isolated spots within a landscape, whereas, a more restricted foraging radius forces *B. muscorum* (supposedly also *B. pascuorum*, *B. sylvarum* and *B. ruderarius*) to be a flexible generalist with regard to the food plants. Therefore an intensive use of all flower resources in the immediate surrounding of the nest (several hundred metres) becomes necessary.

The spatio-temporal heterogeneity of resources (RANTA and VEPSÄLÄINEN, 1981), thus, does not have equal effects on all bumblebee species. Those species with a large foraging radius will have advantages in using the changing resources on offer.

Set-asides, grasslands, ditches, field margins, grassy banks, roadsides, interfaces and hedgerows are more or less undisturbed nesting habitats (BANASZAK, 1983; WESTRICH, 1990; FREE, 1993; VON HAGEN, 1994) and provide food resources in low abundance but over a long period. Studies in agricultural landscapes of Poland revealed that the diversity in wild bee fauna in crop plantations were positively correlated with the plantations' contact to such 'refuge habitats' (BANASZAK and CIERZNIAK, 1994; BANASZAK, 1996). SCHWENNINGER (1992) registered higher numbers of bee species in agricultural areas with higher proportions and higher quality of small, seminatural landscape elements. The positive effect of such uncultivated, flower-rich, mostly linear landscape elements on faunal diversity and also on field crops has already been documented for other animal taxa in agro-ecosystems (e.g. RUPPERT, 1993; KRUESS and TSCHARNTKE, 1994; KRAUSE, 1997).

The differences in foraging distances of pollinators are a key factor for pollination service in agricultural landscapes, especially for plant species that rely on long-tongued bee pollinators. Furthermore, the present discussions on the gene flow of transgenic crops (MIKKELSEN et al., 1996; CHÈVRE et al., 1997), reveals our missing knowledge on foraging distances at the landscape scale. Evidence of pollinator limitation in endangered wild plants (BUCHMANN and NABHAN, 1996; FISCHER and MATTHIES, 1997) even indicates that such effects of landscape fragmentation on pollinators were generally underestimated in the past. In traditional central European land-use systems, pollinator limitation was prevented by a small-scale landscape mosaic of arable fields and permanent habitats. With respect to other ecological services, the conservation of such permanent habitats is certainly preferable to artificially grown and managed bee colonies for the solution of pollination problems in modern agricultural landscapes.

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