

Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae)

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Abstract

Habitat fragmentation is generally considered to have detrimental effects on insect movement and associated pollen flow between plant populations. Against this background the role of forests as potential barriers for foraging bumblebees of the species *Bombus terrestris* agg. and *Bombus pascuorum* was studied in different experiments. *Bombus terrestris* agg. workers were found foraging at distances of up to 2.2 km from their nests. *B. terrestris* agg. as well as *B. pascuorum* individuals crossed 600 m of forestland between floral mass resources (*Phacelia tanacetifolia*, *Helianthus annuus*), although in general a high degree of site fidelity was observed. *B. pascuorum* workers accepted artificial floral resources within the forest, whereas the minor use of resources below forest canopy observed for *B. terrestris* agg. possibly indicates a preference for direct forage flights, probably leading above the forest canopy. Our results warn against experiments with genetically modified crop species with potential bumblebee pollination (e.g. *Brassica napus*), in which an isolating effect of forests is assumed.

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1. Introduction

During the past years the consequences of habitat fragmentation and loss have been a major concern of biological conservation (Settele et al., 1996; Yahner, 1996; Fahrig, 2001, 2002). Nevertheless, there is still poor knowledge about the actual impact of fragmentation at different levels of landscape scale and the underlying mechanisms. This can partly be attributed to the fact that the movement patterns of many organisms are quite unknown (Farina, 1998).

Owing to their habitat requirements such as the necessity of both nesting sites and foraging habitats, many bumblebee species are found to be threatened by loss or fragmentation of those habitats (von Hagen, 1994; Westrich, 1996; Kwak et al., 1998; Westrich et al., 1998). Also movement between different foraging

grounds is crucial to the role of bumblebees as pollen vectors. Accordingly, fragmentation of habitats will most likely affect wildflower populations (Steffan-Dewenter and Tscharnke, 1997; Kwak et al., 1998) as well as bumblebees themselves. The distances covered during foraging flights, as an indicator for spatial relationships between nesting sites and foraging habitats, are therefore of great interest (Westrich, 1996).

Although there are numerous studies of search and forage strategies of bumblebees, most have focused on small-scale movement patterns (for example Cheverton et al., 1985; Rasheed and Harder, 1997; Goverde et al., 2002). Only little is known about the large-scale movement patterns of bumblebees (Dramstad, 1996; Hedtke and Schricker, 1996; Osborne et al., 1999; Walther-Hellwig and Frankl, 2000a). On the contrary, it is widely assumed that bumblebees forage in close vicinity to their nests, mainly for reasons of energy economy (Bowers, 1985; Rotenberry, 1990). In addition to this, the impact of habitats which are usually not visited as foraging habitats and are therefore

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thought of as landscape barriers for pollinators, is quite unknown.

In this study, we analysed the foraging behaviour of the bumblebee species *Bombus terrestris* agg. and *Bombus pascuorum* at a landscape scale and in additional small scale experiments. In particular, we addressed the question of whether woodland acts as a potential barrier for foraging bumblebees (Bowers, 1985; Kwak et al., 1998).

2. Methods

2.1. Study area

The study area is situated in the southern part of the ‘Burgwald’, a mesozoic sandstone plateau in Hesse, Germany, close to the village Rauschenberg (Fig. 1). The area altogether covers about 6 km², from Rauschenberg in the East to Sindelsfeld in the south-west; its centre is situated at the coordinates 50°53' N, 8°53' E. The elevation of the study area is about 300 m. The landscape is characterized by a large proportion of woodland (about 50%) and agriculturally used land (see Fig. 1). Despite intensive agricultural use of grasslands and fields the area is abundantly structured by hedgerows, thickets and fallow land.

The forest surrounding the experimental sites is a beech forest with tree heights of about 25 m.

2.2. Bumblebee colonies and marking of workers

Bombus terrestris agg. here comprises the species *Bombus terrestris* str., *B. lucorum*, *B. cryptarum* and *B. magnus*, which are difficult to distinguish in the field (Obrecht and Scholl, 1984; Westrich, 1990; Mauss, 1994).

Bumblebees from altogether five colonies were marked as well as individuals found on the experimental

sites. One natural colony of *B. terrestris* s. str. and two of *B. pascuorum* were transferred into artificial nesting boxes and moved to the experimental sites. In addition to this, workers from two natural *B. terrestris* agg. colonies were marked.

For individual marking, coloured and numbered Opalith-plates were glued to the thorax of the bees (Kwak, 1987; Kearns and Inouye, 1993). Non-individual marking was done by applying fast-drying paint with a touch-up pen, where different colours marked different colonies and different marking days. The experiments were carried out from June to August 1998.

2.3. Foraging of *B. terrestris* agg. and *B. pascuorum* in relation to their nesting sites

This mark-recapture experiment was done in order to obtain information about the foraging ranges of *B. terrestris* agg. and *B. pascuorum* in relation to their nesting sites.

In total, 568 workers of three *B. terrestris* agg. nests were marked, 178 of them individually and 390 non-individually. In total, 178 workers of the two *B. pascuorum* nests were marked, 128 individually and 50 non-individually.

The surrounding area was systematically searched for marked workers on flowering forage plants. Altogether, we spent 277 h searching, not including the searching time on the *Phacelia* fields A and B.

2.4. Establishment of artificial resources at three distances from two *Bombus pascuorum* nests

At the edge of a beech forest lined with shrubs two *B. pascuorum* nests were placed. In front of the nests were intensively used meadows as well as a field of barley.

Buckets with cut *Helianthus annuus* were installed on the grassland and inside the forest at distances of 10, 50 and 150 m from the nests (Fig. 2). At each distance, five

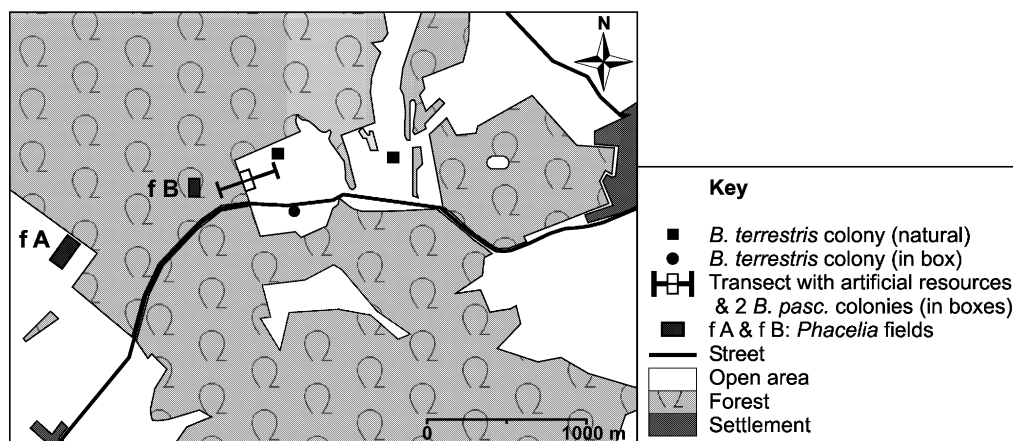


Fig. 1. Study area ‘Rauschenberg’.

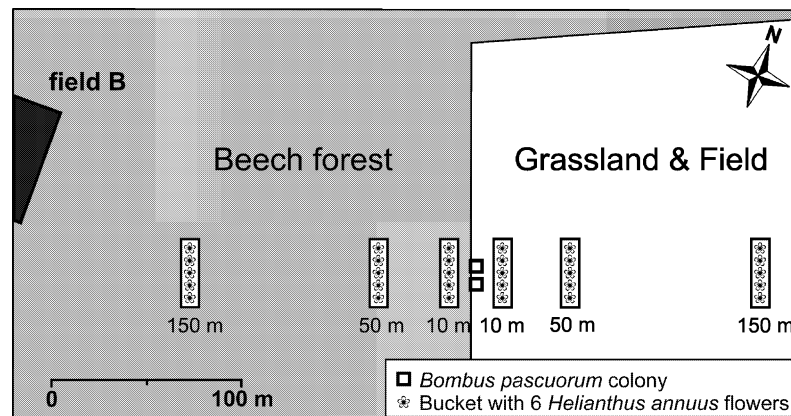


Fig. 2. Artificial resources at three distances to two *Bombus pascuorum* nests.

buckets were set up with a distance of 5 m between them. Every bucket was filled with six freshly cut *Helianthus annuus* flowers. On the 15th and 16th of August 1998 12–18 counts per day were performed along these artificial resources.

Foraging marked and unmarked *B. pascuorum* and *B. terrestris* agg. were recorded. During the counts, nearly all individuals from the two *B. pascuorum* colonies bore markings. Additionally, honeybees (*Apis mellifera*) were counted on these artificial resources.

The results were tested for significance with a Mann–Whitney *U*-Test.

2.5. Site fidelity and movement between floral mass resources

We established two experimental sites which represented highly concentrated food supplies due to an abundant presence of flowering plants (Fig. 1). Field A had a size of 5000 m² (50 × 100 m) and was situated in the angle between two forest edges. The flowering resources on this site were sown *Phacelia tanacetifolia* and dispersed *Helianthus annuus* plants. Field B was 2100 m² in area (35 × 60 m) and situated isolated within the forest. On this site, exclusively *Phacelia tanacetifolia* was grown. Between these two mass resources there was a distance of 600 m covered by forest. The installed *B. pascuorum* nests of the previous experiment were another 225 m away from field B on the other side of the forest.

For this experiment, non-individual markings were applied. Different colours were used for the sites and each of the days. On field A altogether 584 *B. terrestris* agg. and 113 *B. pascuorum* workers were marked during 5 days; on field B, 779 *B. terrestris* agg. and 126 *B. pascuorum* workers were marked during 8 days.

Bee counts were performed on both sites in like manner; species, numbers and markings of observed bumblebees were recorded. On 17 days from the beginning to the end of August 1–10 15-min timed counts were

carried out in a defined, central area of the fields. In early August additional transect walks were carried out.

3. Results

3.1. Foraging of *B. terrestris* agg. and *B. pascuorum* in relation to their nesting sites

Thirty-two (5.6%) of the marked *B. terrestris* agg. workers from all three nests were recaptured including multiple recaptures. They were found up to 2.2 km away from their nests (Table 1). Marked *B. pascuorum* workers from both nests were recaptured altogether 100 times (56.2%) at distances of up to 800 m from the nests, multiple recaptures included.

The marked bees were mainly recaptured at the mass resources on the experimental fields A and B and south-west of these experimental sites near Sindersfeld, where the vegetation at road margins presented floral resources. Large numbers of *B. pascuorum* observations were also made on scattered natural resources close to their nests, mainly consisting of *Galeopsis tetrahit*. Probably due to the long corolla of this plant species only a few workers of the rather short-tongued *B. terrestris* agg. (Prys-Jones and Corbet, 1991) were found on these natural resources. The immediate surroundings of the *B. terrestris* agg. nests provided only sparse and scattered other resources in intensively managed grasslands and along linear landscape elements.

3.2. Establishment of artificial resources at three distances from two *B. pascuorum* nests

Altogether, 564 bumblebee observations were recorded during this experiment, 502 of which were *B. pascuorum* (205 marked, at least 31 different individuals; 297 unmarked) and 62 *B. terrestris* agg. (unmarked).

The recaptures of marked *B. pascuorum* belonging to the nests included in the experimental setup were distributed

Table 1

Distances between nests and floral resources covered by recaptured *Bombus terrestris* agg. and *B. pascuorum* workers (bold = observed at natural resource, no bold = observed on field A or B)

Distance [km]	0.1	0.2	0.3	0.4	0.5	0.6	0.8	1.0	1.5	1.6	1.7	2.2	Total
Recaptured workers of													
<i>Bombus terrestris</i> agg.	1	1	–	5	1	1	–	11	3	6	2	1	23 + 9
<i>Bombus pascuorum</i>	71	8 + 15	1	–	–	–	5	–	–	–	–	–	13 + 87

as follows at the different distances from the nests: 33% (68 observations, at least 15 different individuals) at distances of 10 m from the nests, 45% (92 observations, at least 23 individuals) at 50 m and 22% (45 observations, at least 13 individuals) at 150 m. The difference between the observations at 50 and 150 m is found to be significant ($P=0.011$).

Looking at the use of the different habitat types forest and grassland, neither marked nor unmarked *B. pascuorum* showed any significant difference in their observations. In contrast, these differences were found to be very significant ($P=0.008$) for *B. terrestris* agg., and highly significant for the additionally recorded 776 observations of honeybees, *Apis mellifera* ($P < 0.001$; Fig. 3).

Multiple recaptures of individually marked *B. pascuorum* workers show that individuals quite frequently moved between different distances (Table 2). Most individuals visited floral resources in the forest as well as in the grassland, but also preference for only one type of habitat was found. These results show that workers tend to use the same foraging grounds repeatedly. The patterns of site fidelities indicate that visitation of neighbouring exposures is more probable than of distant positions. In

a further experiment we were able to observe a small number of individually marked *B. pascuorum* workers on their flight trajectory between *Helianthus* exposures (unpublished data). These individuals showed a patch to patch movement and regularly visited several resources at different distances in a single foraging flight. However, our data were not sufficient for statistical analysis, so that these observations can only give hints for a potential trapline behaviour of *B. pascuorum*.

3.3. Site fidelity and movements between floral mass resources

The vast majority of bumblebees of both species were recaptured on the same field where they had been marked. The numbers of recaptures on the field of the marking are considerable, in transect walks and timed counts altogether for *B. terrestris* agg. 144 marked workers on field A and 731 on field B, for *B. pascuorum* 24 on field A and 54 on field B. Recapture rates were higher for both species on field B, situated within the forest (Fig. 4). As non-individually marked recaptures are included, these rates will also include individuals which have been recaptured more than once.

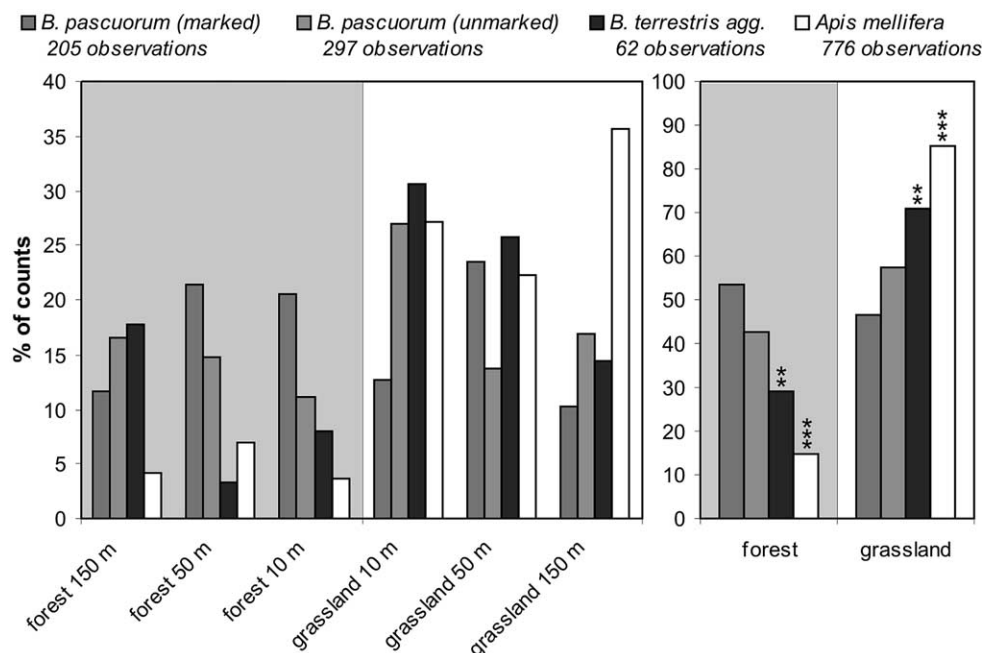


Fig. 3. Distribution of observations for each observed species on *Helianthus* exposures at different distances from the forest edge and habitats.

Table 2

Multiple recaptures of nine marked *Bombus pascuorum* individuals on *Helianthus* exposures at different distances from the forest edge and habitats

Ind.	No. of observations	Beech forest			Grassland			Visited habitats
		150 m	50 m	10 m	10 m	50 m	150 m	
I	25		●	●	●		●	b
II	11		●			●		b
III	8			●	●	●		b
IV	6			●			●	b
V	12		●	●				f
VI	6		●	●				f
VII	13				●	●	●	g
VIII	6				●	●		g
IX	3				●		●	g
No. of observations		0	16	34	13	8	19	

● = 1 observation; ● = 2–5 observations; ● = 6–9 observations; ● = > 10 observations. Visitation of b = both habitats; f = only forest; g = only grassland.

In the timed counts, *B. terrestris* agg. workers were found up to 19 days after marking on field B and 12 days after marking on field A and *B. pascuorum* workers were found up to 13 days on field B and 9 days on field A (Fig. 4). For both species on both sites, the number of recaptures was low at the beginning, reached higher values after a few days and then decreased until no marked workers were found anymore. In the timed counts no individual was caught on the first day after marking, though in transect walks some recaptures were documented on the first day after marking (unpublished data). Otherwise the same general pattern was found by both methods.

Individuals of both species were recaptured not only on the field of their marking, but also on the respective other field, showing that an interchange of workers between the two different sites did occur (Fig. 5). There were 27 *B. terrestris* agg. (3.5% of the marked individuals from field B, at least four individuals) found on field A which had been marked on field B. None of these individuals was recaptured on the marking day. Seventeen *B. terrestris* agg. (2.9% of the marked individuals from field A, at least five individuals) which had been marked on field A were found on field B. One individual was observed on field B in the afternoon after having been marked on field A the same morning. In total, eight workers of *B. pascuorum* (6.3% of the marked individuals from field B, at least five individuals) were found on field A which had been marked on field B. One *B. pascuorum* worker having been marked on field A (0.9% of the marked individuals from field A) was found on field B. There were no individuals of *B. pascuorum* found on one field having been marked the same day on the other field.

4. Discussion

The number of recaptures of marked bumblebees during this study can be regarded as considerable, taking into account the mean lifespan of a bumblebee worker of about three weeks (Rodd et al., 1980), possible injuries imposed during the marking as well as the limited searching time spent at each place. The observed maximum foraging distances were high especially for *B. terrestris* agg. (up to 2.2 km), showing that these bumblebees do forage over large distances and indicating that there is a difference in the behaviour between species, as *B. pascuorum* were not found farther than 800 m from the nest. Similar results have been found

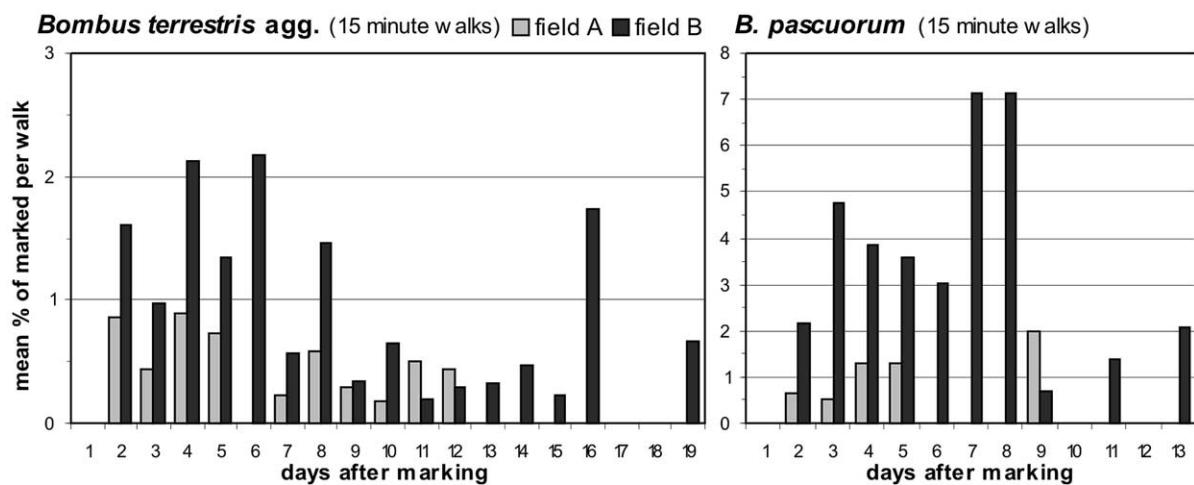


Fig. 4. Mean percentage of marked *B. terrestris* agg. and *B. pascuorum* recaptured per 15 minute walk on different days after marking at field A and field B.

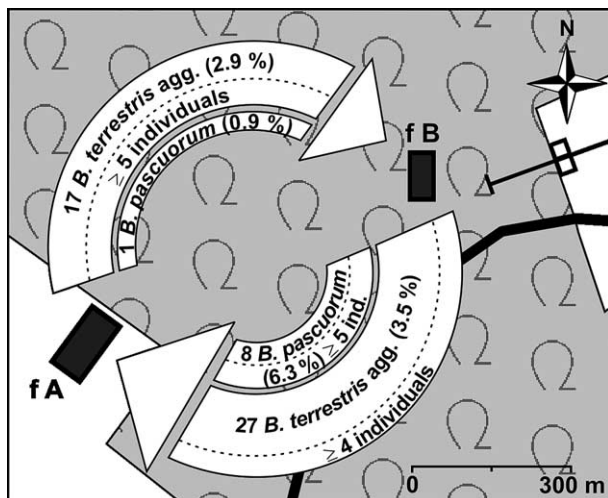


Fig. 5. Interchange of *Bombus terrestris* agg. and *B. pascuorum* workers between the floral resources of field A and field B: number of observations and minimum number of recaptured individuals; in total 1363 *B. terrestris* agg. and 239 *B. pascuorum* were marked.

before (Osborne et al., 1999; Cane, 2001; Walther-Hellwig and Frankl, 2000b), so the general assumption that bumblebees only forage close to their nest (Bowers, 1985) is to be questioned.

Differences in the foraging strategies of the bumblebee species were also observed concerning the acceptance of resources at different distances from the forest margin. While *B. pascuorum* was recaptured both within the forest and on the grassland without significant difference, *B. terrestris* agg. as well as *Apis mellifera* showed a significant preference for the habitat with an open character. This indicates that for *B. pascuorum* forestland does not represent a barrier of unsuitable foraging habitat, at least as long as flowering resources are available there. So the habitat structure seems to be less important for *B. pascuorum* than the availability of flowering resources in close vicinity to the nest. Furthermore, *B. pascuorum* could be shown to forage preferentially on the offered resources in 10 and 50 m distances from the observed nests; the recaptures at 150 m were significantly fewer than at 50 m, thus indicating that resources closer to the nest are preferred if available. In this respect a direct comparison with *B. terrestris* agg. is not possible due to our experimental design (see location of nest sites in Fig. 1). However, during our searching time for marked individuals of both species on natural resources we regularly checked the surroundings of the *B. terrestris* agg. nests in a radius of about 200 m. Natural floral resources were only scarce and scattered around the nest sites. In spite of 84 h of searching time within 4 weeks we were able to find only one marked individual on a natural resource in a distance of about 100 m (Table 1). This and results of further studies (Osborne et al., 1999; Walther-Hellwig and Frankl, 2000b) support the assumption that workers of

B. terrestris agg. optimise their foraging success preferentially by the search for patches with high densities of awarding resources.

The different use of equal resource exposures in woodland and open grassland by *B. terrestris* agg. possibly reflects species-specific differences in the capability to detect floral resources. In contrast to floral mass resources (field B) and exposures on open grassland, new and scattered (artificial) resources below forest canopy were visited by *Bombus terrestris* agg. only in small numbers. The natural resources were sparse on the forest floor during the experimental period and small-scale patch to patch movement or trapline foraging (Thomson, 1996) was observed only for *Bombus pascuorum*. It is conceivable that the visual detection of floral resources is improved by the enlarged perspective of workers achieved during long distance foraging which seems to be typical of *B. terrestris* agg. This could also explain the high densities of *B. terrestris* agg. in the isolated *Phacelia tanacetifolia* field in the forest gap (field B) in contrast to low numbers on the *Helianthus annuus* exposures under forest canopy. The high efficiency in finding and exploiting rewarding floral resources might contribute to the conspicuous success of *Bombus terrestris* agg. in modern agricultural landscapes (Walther-Hellwig and Frankl, 2000a) and as an invasive species, which was shown for example in Tasmania (Hingston et al., 2002).

In comparison to other findings (Anderson, 1983; Thomson et al., 1987) and with respect to the average lifespan and mortality rates of bumblebee workers (Rodd et al., 1980), the observed recapture periods of up to 19 days for *B. terrestris* agg. and 13 days for *B. pascuorum* are considerable. The temporal course of recaptures even suggests that many workers were disturbed by the marking procedure, but nevertheless returned to their former foraging behaviour after 1–2 days. The high proportion of recaptures on the same site over such long periods of time emphasizes the high degree of site and resource fidelity of both observed species, as long as there was an ample supply of resources at these sites. This is in line with findings for other bumblebee species (Kwak et al., 1998; Bhattacharya et al., 2003).

Nevertheless, an interchange of workers of both species between the two different sites was observed, although they were separated by forest and a distance of 600 m. This shows that forestland cannot be considered an effective landscape barrier for foraging bumblebees. The temporal course of recaptures shows that the documented change of fields in general was not caused by the disturbance of workers during the marking procedure.

The strategies of passing the forest may differ between bumblebee species. *B. terrestris* agg. might rather fly above the forest canopy, as is suggested by a minor use of floral resources below the forest canopy as well as by

observations of bees leaving the resources in the direction of the forest in a steep angle. In contrast, the results of our experiments for *B. pascuorum* suggest that even single individuals seem to make foraging flights below the forest canopy as well as in grasslands in the form of traplines.

As our study has shown, bumblebees are not necessarily strongly restricted in their foraging range by landscape features thought of as potential barriers such as forests. For *B. terrestris* agg. and *B. pascuorum* forests do not seem to represent barriers. In other cases, the distribution patterns of foraging workers, for example of *B. muscorum* (Diekötter et al., 2001) suggest possible barrier effects of forests. In displacement experiments, Bhattacharya et al. (2003) found a non-significant tendency that forest prevented more bees from returning to their original foraging site than a road.

In drawing conclusions concerning the effect of these findings on pollen flow at a landscape scale and its impact, it is important to ask what type of food plant is concerned and whether interchange of pollen is an unwanted risk or a necessity. For transgenic crop plants, most likely grown at high densities in large patches and therefore representing attractive foraging grounds, our results make clear that one cannot rely on presumed isolating factors such as distance or landscape features. In contrast, this study has shown that an interchange of pollen is most likely to happen, and already small amounts of pollen are sufficient to transfer modified genes to other patches featuring the same crop or of closely related species (Cresswell, 1994; Rieger et al., 2002). Pollinator movement and resulting gene flow may however be diminished by distance and fragmentation, even more so between smaller populations of less rewarding forage plants or plant assemblages. Therefore, rare species in a landscape with only few flowering resources will be affected most (Kwak et al., 1998).

From the pollinator's point of view, isolation of foraging or nesting habitats will also have different effects for different species or species groups. Further, modifications in foraging habitats and available food plants will affect them differently. Changes in agricultural land use have had strong effects on the diversity and distribution of wildflower communities in past decades involving a decline in plant–pollinator–interactions (Allen-Wardell et al., 1998). Most pollinator groups with specialized requirements for nesting sites and foraging plants as well as restricted foraging ranges are in decline in modern agricultural landscapes. Only a few pollinators, for example *Bombus terrestris* agg. or *Apis mellifera*, with large foraging ranges and effective capabilities to exploit resources available abundantly but only for short time periods, such as arable crops, will be less affected by changes in landscape patterns.

5. Conclusions

Habitat fragmentation is generally considered to have detrimental effects on pollen flow between plant populations. Against this background the role of forests as potential barriers for foraging bumblebees was studied. The influence of forests as extensive landscape structures on the movement of *Bombus terrestris* agg. and *Bombus pascuorum* was tested by different experimental approaches.

Marked *Bombus terrestris* agg. workers were foraging at distances of up to 2.2 km from their nests. Forest with a width of up to 600 m had no barrier effect on the use of floral mass resources (*Phacelia tanacetifolia*, *Helianthus annuus*) by this species group. We hypothesize that a minor use of experimental floral resources below forest canopy (*Helianthus annuus* exposures) hints to a predominance of direct forage flights above the tree layers.

Marked *Bombus pascuorum* workers also crossed forests with a width up to 600 m to reach floral mass resources. High visitation rates of experimental floral exposures (*Helianthus annuus*) on the forest floor indicate that the foraging behaviour of this species might be based on small-scale patch to patch movement (traplines) between resources which are found at short distances from the nest sites.

The results of our study highlight the need to address barrier effects of landscape structures at a species-specific scale. In our case, the foraging behaviour of the different bumblebee species potentially facilitates pollen flow between fragmented habitats. A quantification of actual pollen flow is not possible by our experimental approach. Neither are we able to assess the consequences for populations of endangered plant species in fragmented habitats. However, our results warn against experiments with genetically modified crop species with potential bumblebee pollination (e.g. *Brassica napus*), in which an isolating effect of forests is assumed.

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References

- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H.,

- Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P., Walker, S., 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* 12, 8–17.
- Anderson, D.J., 1983. Optimal foraging and the travelling salesman. *Theoretical Population Biology* 24, 145–159.
- Bhattacharya, M., Primack, R.B., Gerwein, J., 2003. Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biological Conservation* 109, 37–45.
- Bowers, M., 1985. Bumble bee colonization, extinction, and reproduction in subalpine meadows in northeastern Utah. *Ecology* 66, 914–927.
- Cane, J.H., 2001. Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* 5 (1), 3. Available: <http://www.consecol.org/vol5/iss1/art3>.
- Cheverton, J., Kacelnik, A., Krebs, J.R., 1985. Optimal foraging: constraints and currencies. *Fortschritte der Zoologie* 31, 109–126.
- Cresswell, J.E., 1994. A Method for quantifying the gene flow that results from a single bumblebee visit using transgenic oilseed rape, *Brassica napus* L. cv Westar. *Transgenic Research* 3, 134–137.
- Diekötter, T., Walther-Hellwig, K., Frankl, R., 2001. Verbreitung, lokale Häufigkeit und Gefährdung der Mooshummel (*Bombus muscorum*) und Waldhummel (*Bombus sylvarum*) im Amöneburger Becken. *Jahrbuch Naturschutz in Hessen* 6, 92–99.
- Dramstad, W.E., 1996. Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behavior* 9, 163–182.
- Fahrig, L., 2001. How much habitat is enough? *Biological Conservation* 100, 65–74.
- Fahrig, L., 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecological Applications* 12, 346–353.
- Farina, A., 1998. *Principles and Methods in Landscape Ecology*, first ed. Chapman & Hall, London.
- Goverde, M., Schweizer, K., Baur, B., Erhardt, A., 2002. Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. *Biological Conservation* 104, 293–299.
- Hedtke, C., Schrick, B., 1996. Heimfinden von *Apis mellifera* und 4 *Bombus*-Arten im Vergleich. *Apidologie* 27, 320–323.
- Hingston, A.B., Marsden-Smedley, J., Driscoll, D.A., Corbett, S., Fenton, J., Anderson, R., Plowman, C., Mowling, F., Jenkin, M., Matsui, K., Bonham, K.J., Ilowski, M., McQuillan, P.B., Yaxley, B., Reid, T., Storey, D., Poole, L., Mallick, S.A., Fitzgerald, N., Kirkpatrick, J.B., Febey, J., Harwood, A.G., Michaels, K.F., Russell, M.J., Black, P.J., Emmerson, L., Visoiu, M., Morgan, J., Breen, S., Gates, S., Bantich, M.N., Desmarchelier, J.M., 2002. Extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). *Austral Ecology* 27, 162–172.
- Kearns, C.A., Inouye, D.W., 1993. *Techniques for Pollination Biologists*. University Press, Colorado.
- Kwak, M.M., 1987. Marking a bumblebee without anaesthesia. *Bee World* 68, 180–181.
- Kwak, M.M., Velterop, O., van Andel, J., 1998. Pollen and gene flow in fragmented habitats. *Applied Vegetation Science* 1, 37–54.
- Mauss, V., 1994. *Bestimmungsschlüssel für die Hummeln der Bundesrepublik Deutschland*, fifth edn. Deutscher Jugendbund für Naturbeobachtung, Hamburg.
- Obrecht, E., Scholl, A., 1984. *Bombus lucorum* auct.—ein Artenkomplex—Enzymelektrophoretische Befunde (Hymenoptera, Apidae). *Verhandlungen der Deutschen Zoologischen Gesellschaft* 77, 266.
- Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36, 519–533.
- Prys-Jones, O.E., Corbet, S.A., 1991. *Bumblebees*. Naturalists' Handbooks 6. Richmond Publishing Co. Ltd, Slough.
- Rasheed, S.A., Harder, L.D., 1997. Economic motivation for plant species preferences of pollen-collecting bumble bees. *Ecological Entomology* 22, 209–219.
- Rieger, M.A., Lamond, M., Preston, C., Powles, S.B., Roush, R.T., 2002. Pollen-mediated movement of herbicide resistance between commercial canola fields. *Science* 296, 2386–2388.
- Rodd, F.H., Plowright, R.C., Owen, R.E., 1980. Mortality rates of adult bumble bee workers. *Canadian Journal of Zoology* 58, 1718–1721.
- Rotenberry, J.T., 1990. Variable floral phenology: Temporal resource heterogeneity and its implications for flower visitors. *Holarctic Ecology* 13, 1–10.
- Settele, J., Margules, C., Poschlod, P., Henle, K., 1996. *Species Survival in Fragmented Landscapes*, The GeoJournal Library. Kluwer, Dordrecht.
- Steffan-Dewenter, I., Tschamtkke, T., 1997. Bee diversity and seed set in fragmented habitats. *Acta Horticulturae* 437, 231–234.
- Thomson, J.D., 1996. Trapline foraging by bumblebees 1. Persistence of flight-path geometry. *Behavioral Ecology* 7, 158–164.
- Thomson, J.D., Peterson, S.C., Harder, L.D., 1987. Response of trapping bumble bees to competition experiments—shifts in feeding location and efficiency. *Oecologia* 71, 295–300.
- von Hagen, E., 1994. *Hummeln bestimmen, ansiedeln, vermehren, schützen*, fourth ed. Naturbuch Verlag, Augsburg.
- Walther-Hellwig, K., Frankl, R., 2000a. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology* 124, 299–306.
- Walther-Hellwig, K., Frankl, R., 2000b. Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). *Journal of Insect Behavior* 13, 239–246.
- Westrich, P., 1990. *Die Wildbienen Baden-Württembergs*, vols. 1 & 2. Ulmer, Stuttgart.
- Westrich, P., 1996. Habitat requirements of central European bees and the problems of partial habitats. In: Matheson, A., Buchmann, S.L., O'Toole, C., Westrich, P., Williams, I.H. (Eds.), *The Conservation of Bees*, Linnean Society symposium series 18. Academic Press, London, pp. 1–16.
- Westrich, P., Schwenninger, H.R., Dathe, H.H., Riemann, H., Saure, C., Voith, J., Weber, K., 1998. Rote Liste der Bienen (Hymenoptera: Apidae). In: *Rote Liste Gefährdeter Tiere Deutschlands*, ed. Bundesamt für Naturschutz, pp. 119–129, Schriftenreihe für Landschaftspflege und Naturschutz.
- Yahner, R.H., 1996. Habitat fragmentation and habitat loss. *Wildlife Society Bulletin* 24, 592.