Honeybee foraging in differentially structured landscapes

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Honeybees communicate the distance and location of resource patches by bee dances, but this spatial information has rarely been used to study their foraging ecology. We analysed, for the first time to the best of the authors' knowledge, foraging distances and dance activities of honeybees in relation to landscape structure, season and colony using a replicated experimental approach on a landscape scale. We compared three structurally simple landscapes characterized by a high proportion of arable land and large patches, with three complex landscapes with a high proportion of semi-natural perennial habitats and low mean patch size. Four observation hives were placed in the centre of the landscapes and switched at regular intervals between the six landscapes from the beginning of May to the end of July.

A total of 1137 bee dances were observed and decoded. Overall mean foraging distance was 1526.1 ± 37.2 m, the median 1181.5 m and range 62.1–10 037.1 m. Mean foraging distances of all bees and foraging distances of nectar-collecting bees did not significantly differ between simple and complex landscapes, but varied between month and colonies. Foraging distances of pollen-collecting bees were significantly larger in simple (1743 ± 95.6 m) than in complex landscapes (1543.4 ± 71 m) and highest in June when resources were scarce. Dancing activity, i.e. the number of observed bee dances per unit time, was significantly higher in complex than in simple landscapes, presumably because of larger spatial and temporal variability of resource patches in complex landscapes. The results facilitate an understanding of how human landscape modification may change the evolutionary significance of bee dances and ecological interactions, such as pollination and competition between honeybees and other bee species.

Keywords: foraging strategy; social insects; bee dance; gene flow; competition; landscape structure

1. INTRODUCTION

Honeybee foragers communicate the distance and direction of food resources to their nest-mates when they return to the colony (von Frisch 1965). The biology of this unique behaviour, called 'bee dance', has attracted much attention in behavioural biology since the pioneering work by Karl von Frisch (Dyer 2002). The dance language enables honeybee colonies to integrate information on the spatial distribution of food resources at a scale of several kilometres and to rapidly respond to temporal changes in resource quality (Seeley 1997). Remarkably few researchers have used the spatial information provided by bee dances as a tool to analyse the foraging ecology of honeybee colonies. Such studies could indicate which factors determine foraging distances, over which distances pollen might be dispersed by honeybees, and which environmental conditions may increase the advantages of social communication. Earlier studies focused on the foraging distances and temporal shifts of foraging patches in the same environment (Visscher & Seeley 1982; Beekman & Ratnieks 2000) or compared the forager distributions from matched colonies at one location (Waddington *et al.* 1994). Foraging distances have been shown to differ significantly between matched colonies (Waddington *et al.* 1994) and between seasons (Beekman & Ratnieks 2000). A second, less frequently

used parameter is dance activity in an individual colony. It has been shown that dance activity increases with the quality of a food patch and decreases with the distance from it (Seeley 1997). However, long unloading times owing to high rates of nectar intake also reduce dancing activity (Seeley 1992; Dyer 2002).

Bee dances have been never used, to the authors' knowledge, to systematically compare honeybee foraging in differentially structured landscapes and to match the estimated location of flower patches with the underlying land use. Landscape structure can be expected to affect the number, size, quality and distance of flower patches available for a honeybee colony. Complex landscapes with a high habitat diversity, a high proportion of semi-natural habitats and small mean patch area should provide a more continuous supply of nectar and pollen than structurally simple landscapes, which are characterized by a high proportion of agricultural crops and large mean patch size (Beekman & Ratnieks 2000; Steffan-Dewenter *et al.* 2002). Earlier studies showed that landscape structure has strong effects on species richness of solitary bees, abundance of flower-visiting honeybees at defined resource patches, and on plant–pollinator interactions (Steffan-Dewenter *et al.* 2001, 2002). Because honeybees store much less pollen than nectar, the pressure for pollen collection should be higher during temporal shortages of flowering plants. We studied foraging distances and dance activities of honeybee colonies in structurally simple and complex landscapes in central Europe to test the following predictions.

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Table 1. Characteristics of structurally simple and complex landscape sectors in a radius of 2000 m around the observation hives.
Means ± 1 s.e.m., ranges and results of one-way ANOVA are given ($n = 6$ landscape circles).

parameter	simple landscapes		complex landscapes		*F* value	*p* value
	mean ± s.e.m.	range	mean ± s.e.m.	range		
crop area (%)	83.9 ± 2.23	81.0–88.3	44.0 ± 8.9	30.1–60.5	18.96	0.012
semi-natural habitats (%)	4.7 ± 0.38	4.1–5.4	19.4 ± 2.7	14.6–24.1	28.29	0.006
forest and hedgerows (%)	4.8 ± 1.6	1.7–7.2	28.0 ± 9.8	16.7–47.7	5.51	0.079
built-up area (%)	5.0 ± 0.6	3.84–6.1	7.7 ± 3.2	2.47–13.6	0.64	0.468
mean patch size (m^2)	49 289 ± 5306	40 331–58 698	28 423 ± 2586.5	23 282.4–31 492	12.49	0.024

(i) Foraging distances are larger in structurally simple than in complex landscapes.
(ii) Foraging distances of pollen foragers are more affected than those of nectar foragers.
(iii) Dance activities are lower in structurally simple than in complex landscapes.
(iv) Seasonal changes in flower abundance affect foraging distances.
(v) Individual colonies differ in their foraging distances.

2. MATERIAL AND METHODS

(a) *Study region and study sites*

The study was conducted in 2001 in southern Lower Saxony, Germany, around Göttingen. The study region is a typical central European landscape characterized by intensively managed agricultural areas and patchily distributed fragments of forest and semi-natural grassland habitats. We selected three structurally simple landscapes and three structurally complex landscapes as study sites (figure 1). The mean distance to the nearest neighbouring landscape centre was 9700 m (range 8760–10 720 m). The cover of different land use types, for example, forest, grassland, built-up area and arable land, was calculated from existing digital maps (ATKIS-DLM 25/1, 1991–1996; Landesvermessungsamt+Geobasisinformationen Niedersachsen, Hannover, Germany) for circles of 2 km radius. The two landscape types were significantly different in the proportion of arable land, the proportion of semi-natural habitats and mean patch area (table 1).

(b) *Observation hives*

We used four glass-sided observation hives, each with two frames per brood (comb area 3872 cm²) and five smaller frames (comb area 6930 cm²) separated by a queen excluder in a honey chamber. Similar-sized colonies of approximately 4000 individuals were built in the spring using artificial swarms and young, mated queens (*Apis mellifera carnica*) from a commercial queen breeder (Imkerei Mehler, 54552 Neichen, Germany). All queens had the same mother and were mated at the same queen-mating station. An empty comb replaced one of the two brood combs at regular intervals to prevent overcrowding and swarming in the observation hives. The passage between the two sides of the comb was restricted for returning foragers by a diagonal wooden block to see all recruitment dances on one side of the comb (Visscher & Seeley 1982). During observations of bee dances, when the lateral door of the observation hive was opened, a tent of white cloth was constructed to prevent light-dependent misdirection (Visscher & Seeley 1982).

(c) *Experimental design*

The four observation hives were placed in the centre of two structurally simple and two complex landscapes of the six selected landscape circles on 11 May 2001. After 7 days, two of these observation hives, one from a simple and one from a complex landscape, were moved to the two empty landscapes. The colony from a simple landscape was moved to a complex landscape and vice versa. This procedure was repeated every 7–14 days (depending on weather conditions) until the end of July. Thus, each colony was placed in each of the six landscapes during the study. This experimental design prevented possible differences in colony growth and amount of stored food between observation hives located in simple and complex landscapes, which might have influenced foraging activity (Seeley 1997). Furthermore, we were able to independently analyse landscape, season and colony effects by replicating observations of each colony in each landscape.

(d) *Observation and decoding of bee dances*

Honeybee dances were observed from 12 May until 31 July on all days with suitable weather conditions, i.e. nectar and pollen foraging took place. One observation period lasted 30–40 min for each colony and all colonies were observed at least once on each observation day. The sequence of observations was randomly changed each day. Dancing bees were randomly selected on the comb. Dancers carrying pollen were scored as pollen foragers and the rest were assumed to be nectar foragers. We used a digital stopwatch to time the duration of a series of dance circuits and an acrylic glass circle with 2° intervals to measure the angle of the waggle run relative to the vertical. All dances for which at least five consecutive circuits could be measured were decoded. On average, we observed 20.76 ± 0.5 circuits (median 16.0, range 5–176) for each bee individual. The time of day of each dance was used to calculate the sun azimuth with the software program 'sun.exe' provided by Axel Wittmann (University Observatory Göttingen, Germany). The direction indicated in each dance was calculated by adding this azimuth to the recorded dance angle. The mean duration of a single dance circuit was used to calculate the flight distance according to a third-order polynomial fit presented by von Frisch (1965) and previously used by Waddington *et al.* (1994) and Beekman & Ratnieks (2000). The location of foraging sites was plotted into a land use map of the study region using the GIS-software ARC/VIEW 3.1 (ESRI Geoinformatik, Hannover, Germany). We measured the Gauss–Krüger coordinates of each observation hive site in the six landscapes with GPS and calculated the location of food sources by adding the distance to the right and the height for each decoded bee dance.

Table 2. Foraging distances decoded from bee dances to three feeding stations in two landscapes. Mean distances ± s.e.m. and number of observations are given.

simple landscape			complex landscape		
feeder distance (m)	decoded distance (m)	number of dances	feeder distance (m)	decoded distance (m)	number of dances
263.7	264.3 ± 29.3	20	267.3	209.1 ± 25.4	12
501.9	559.3 ± 33.3	20	500.7	449.3 ± 27.7	20
1000	1053.2 ± 62.1	20	1008	1007.8 ± 53.6	18

Table 3. Effects of landscape type, month and colony on flight distances of foraging honeybees. Results of three-way ANOVA with first-order interactions are given ($n = 1137$).

factor	d.f.	F value	p value
main effects			
landscape	1	1.28	0.2570
month	2	4.89	0.0077
colony	3	12.93	0.0000
interactions			
landscape × month	2	5.51	0.0042
landscape × colony	3	0.78	0.5076
month × colony	6	0.83	0.5456

Table 5. Effects of landscape type, month and colony on flight distances of nectar-foraging honeybees. Results of three-way ANOVA with first-order interactions are given ($n = 688$).

factor	d.f.	F value	p value
main effects			
landscape	1	0.03	0.8653
month	2	2.88	0.0568
colony	3	7.61	0.0001
interactions			
landscape × month	2	2.66	0.0708
landscape × colony	3	0.19	0.9018
month × colony	6	1.74	0.1088

Table 4. Effects of landscape type, month and colony on flight distances of pollen-foraging honeybees. Results of three-way ANOVA with first-order interactions are given ($n = 376$).

factor	d.f.	F value	p value
main effects			
landscape	1	5.13	0.024
month	2	5.67	0.0037
colony	3	16.45	0.0000
interactions			
landscape × month	2	5.40	0.0049
landscape × colony	3	3.69	0.0122
month × colony	6	4.12	0.0005

Dance activity was quantified as the number of dancing bees observed per unit time. This measurement probably underestimates the real number of dancing bees if several bees dance simultaneously, but on average, bee dances were only observed during 34% of the total observation time. Thus, it seems to be an adequate relative index to compare dance activity between colonies, month and landscapes.

We tested the accuracy of our method by training bees of two observation hives, one in a simple and one in a complex landscape, to feeding stations at *ca.* 260, 500 and 1000 m in August 2001. Foragers were marked with different colours at the feeding stations and dances of returning marked bees were recorded and decoded in the same way as described above. The mean distances were close to the real distances and the error increased with increasing distance (table 2). The mean difference between real feeder distance and observed distance was $-37.06 ± 25.2$ m ($n = 60$) in the simple landscape and $34.61 ± 22.9$ m ($n = 50$) in the complex landscape (one-way ANOVA: $p = 0.0412$). Plotting the decoded foraging sites of marked bees in a map with the locations of the feeding stations confirmed the correctness of our

calculations and the plotted maps. The mean number of observed circuits per bee individual for this experiment was $22.6 ± 1.46$ (median 19, range 6–86).

(e) *Data analysis*

The statistical analyses of the data were performed using STATGRAPHICS PLUS for Windows 3.0 (Manugistics Inc., Rockville, MD, USA). For statistical analysis the foraging distance data were log-transformed to achieve normal distribution (Sokal & Rohlf 1995). We used multifactor ANOVA (Type III sums of squares) with foraging distance or dance activity as dependent factors and landscape type, observation month and colony as the three independent factors. We also checked for first-order interactions between the three independent factors. In the text we give the means ± 1 s.e.m. and medians of non-transformed data to improve the comparability with other studies.

3. RESULTS

(a) *Foraging distances*

A total of 1137 bee dances were observed and decoded. The distribution of all foraging locations in the six studied landscape areas and the underlying land use is shown in figure 1. The mean foraging distance was $1526.1 ± 37.2$ m, the median 1181.5 m and the range 62.1–10 037.1 m.

Mean foraging distances were $1569 ± 55.6$ m (median 1264.7 m, $n = 527$) in simple landscapes and $1488.9 ± 49.9$ m (median 1144.8 m, $n = 610$) in complex landscapes. Three-way ANOVA showed no significant differences between landscape types, whereas month and colonies significantly differed (table 3). Mean foraging distances were $1319 ± 53.2$ m (median 1076.3 m) in May, $1786.9 ± 96.6$ m (median 1329 m) in June and $1518.2 ± 51.3$ m (median 1184.4 m) in July. Mean foraging distances of the four observation colonies varied
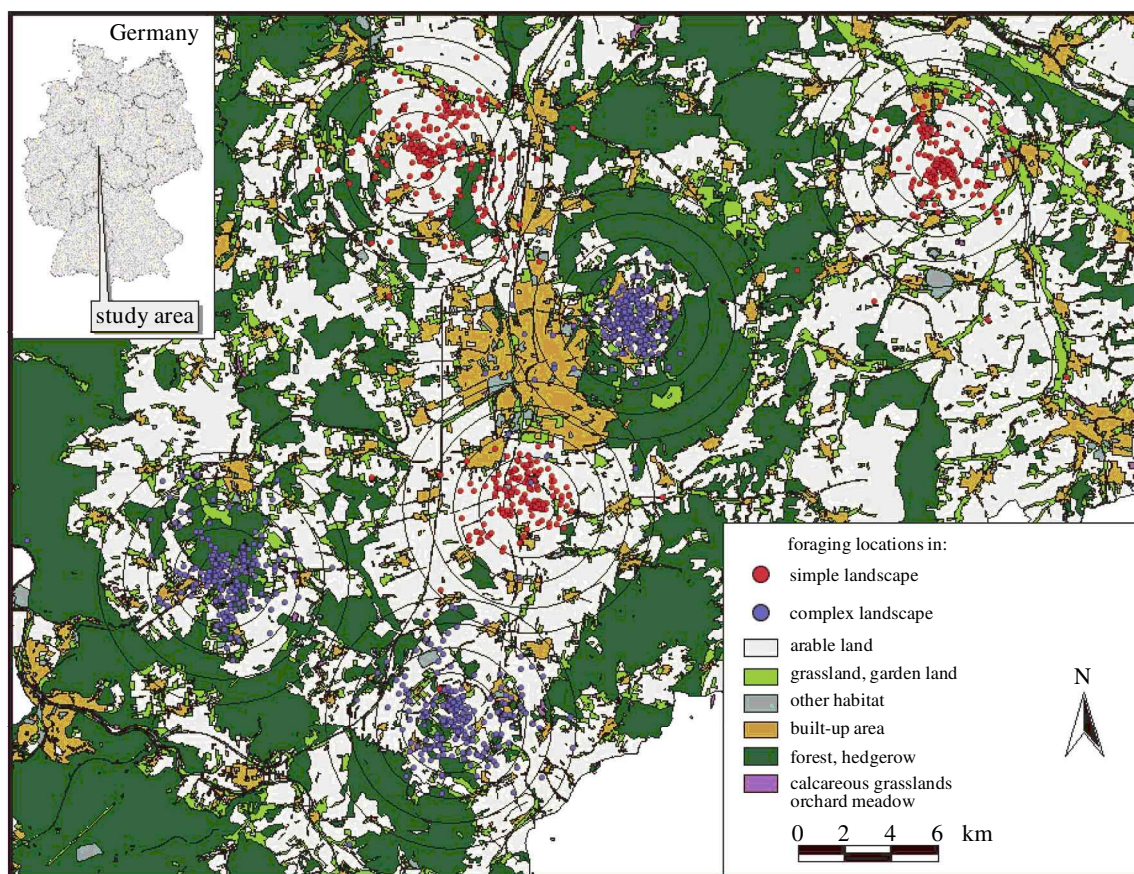
Figure 1. Map of the study area and the distribution of the main habitat types in southern Lower Saxony, Germany. The observation hives were located in the centre of the six study areas, each marked by a nested set of black circles at 1 km intervals. Each dot represents the foraging location of one honeybee inferred from recruitment dances. Foraging locations of honeybee colonies placed in simple landscapes are marked in red and in complex landscapes in blue.

between 1142 and 1885 m. The significant interaction between landscape type and month indicates landscape-dependent effects of season on foraging distances (table 3).

We observed 376 (35.3%) dances of pollen foragers and 688 (64.7%) dances of nectar foragers. Seventy-three bee dances could not be classified because pollen traps were active during the observations. The mean foraging distance of pollen foragers was 1636.3 ± 58.2 (median 1431.0) and of nectar foragers 1478.9 ± 49.2 (median 1098.3); both were significantly different from each other (one-way ANOVA: $F = 13.79$, $p = 0.0002$). The foraging distances of pollen collecting honeybees were significantly larger in structurally simple (1743.4 ± 96.6 m, median 1519.7 m) than in complex landscapes (1543.4 ± 70.97 m, median 1373.8 m) and also differed between month and colonies (table 4). Significant interactions between landscape and month indicate landscape-dependent seasonal changes of foraging distances for pollen (figure 2). Foraging distances of nectar-collecting bees were not significantly affected by landscape structure and month but differed between colonies (table 5 and figure 3).

(**b**) *Dance activity*

The number of observed dancing bee individuals per observation unit was used to calculate dance activity for a total of 151 observation units. On average, we observed 0.24 ± 0.008 dances per minute (range 0.03–0.44). Dance activity was significantly higher in complex landscapes

(0.27 ± 0.01) than in simple landscapes (0.22 ± 0.01) and increased from May to July, presumably due to increasing colony size (table 6 and figure 4). Dance activity did not vary significantly between the four observed colonies (table 6).

4. DISCUSSION

The main goal of our study was to compare the foraging distances and dance activity of honeybee colonies in differently structured landscapes. Additionally, we addressed seasonal and colony effects. We replicated observations of bee dances on a landscape scale. This is in contrast to earlier studies, which described the spatial distribution of resource patches for single or matched colonies in one environment. Our experimental design, with the regular rotation of observation hives, made it possible to independently test for landscape, season and colony effects. Foraging distances differed significantly between simple and complex landscapes for pollen- but not for nectar-collecting bees. Furthermore, landscape effects were subjected to seasonal changes and foraging distances varied between individual colonies. Dancing activity was significantly higher in complex than in simple landscapes, but did not depend on month or colony.

The overall mean foraging distance in our study was 1526 m. This is greater than the mean foraging distances of 534–1138 m for suburban environments (Waddington
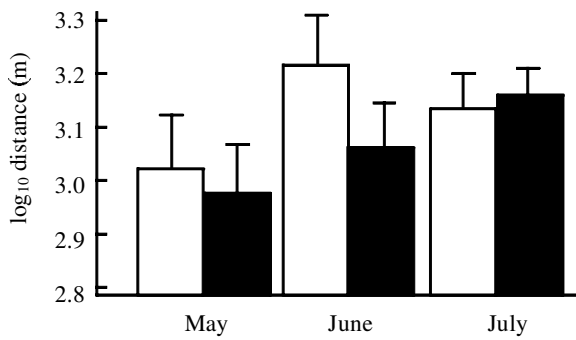
Figure 2. Effects of landscape type and season on foraging distances of pollen-collecting honeybees. Mean distances corrected for colony effects and 95% confidence intervals are shown. Statistical results of multifactor ANOVA—see table 4. Filled bars represent complex landscapes; open bars represent simple landscapes.
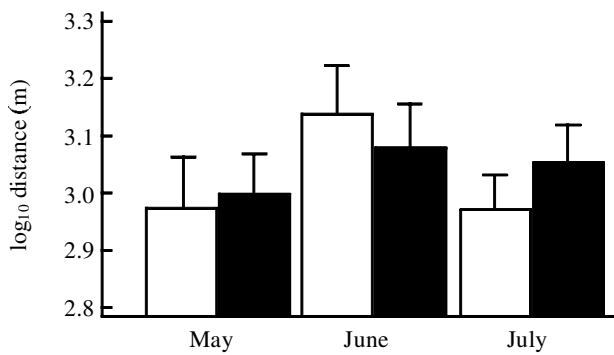

Figure 3. Effects of landscape type and season on foraging distances of nectar-collecting honeybees. Mean distances corrected for colony effects and 95% confidence intervals are shown. Statistical results of multifactor ANOVA—see table 5. Filled bars represent complex landscapes; open bars represent simple landscapes.

Table 6. Effects of landscape type, month and colony on dance activity of honeybee colonies. Results of three-way ANOVA with first-order interactions are given ($n = 151$ observation units).

factor	d.f.	F value	p value
main effects			
landscape	1	9.90	0.002
month	2	3.97	0.0212
colony	3	1.74	0.163
interactions			
landscape × month	2	0.43	0.651
landscape × colony	3	2.57	0.057
month × colony	6	0.32	0.925

distances were generally low. In June these mass-flowering resources had ceased to bloom and only wild plant species in perennial habitats provided pollen and nectar sources. In simple landscapes in particular, which were dominated by annual crops, this should have led to a shortage of resources. In this month the largest overall mean foraging distances were observed and foraging distances of pollen-collecting bees were distinctly larger in simple than in complex landscapes. In July, resource abundance in simple landscapes again increased, for example, due to set-aside fields sown with *Phacelia tanacetifolia*, which provide a rich nectar and pollen source for honeybees (Steffan-Dewenter & Tscharntke 2001). This coincides with reduced overall foraging distances in July and a tendency for even larger mean foraging distances of nectar-collecting bees in complex landscapes.

In addition to the more pronounced effects of landscape structure on pollen foragers, overall mean foraging distances were greater for pollen than for nectar. This indicates that pollen was, at least temporarily, a limited resource which prompted honeybees to fly larger distances. As indicated by earlier studies, foragers perhaps remained inside the nest during times of poor forage to conserve their flight energy instead of flying greater distances (Visscher & Seeley 1982). Such a strategy may be more appropriate for nectar, which is stored in larger amounts in the combs than for pollen which is stored in smaller amounts and is vital for brood development. Thus, energetic constraints that limit nectar-collecting bees (Schmid-Hempel 1987; Cresswell *et al.* 2000) can be expected to be less relevant for pollen-collecting bees. Waddington *et al.* (1994) found no differences in distances between pollen- and nectar-foraging bees, presumably because the study was done in a suburban environment characterized by high densities of flowers.

A rather unexpected result of our study was that the four colonies significantly differed in mean foraging distances although we used closely related queens. Earlier studies already showed for matched but less closely related colonies that mean foraging distances in the same environment differ significantly (Waddington *et al.* 1994; Schneider & Hall 1997) and that foraging distances are genetically determined (Oldroyd *et al.* 1993). In our study, the most plausible explanation for the large differences of mean foraging distances between colonies also seems to be genetic variation, because variation due to other explanatory factors such as landscape structure or season

et al. 1994), and smaller than mean foraging distances of 2260 m for a temperate deciduous forest (Visscher & Seeley 1982), and of 5500 m for a patchy environment with isolated patches of blooming heather (Beekman & Ratnieks 2000). However, it is much larger than previously expected for agricultural areas (Free 1993). These general differences indicate that foraging distances are affected by landscape structure and dominant habitat types.

We compared simple landscapes dominated by large patches of annual, arable land with complex landscapes composed of small patches of diverse, annual and perennial habitat types. In contrast to expectations, overall mean foraging distances were not significantly different in simple and complex landscapes. However, pollen-collecting bees flew significantly further in simple landscapes than in complex ones. The landscape-dependent differences of honeybee foraging were most pronounced in June and less so in May and July. Other studies suggest that foraging distances increase when resources become scarce (Schneider & McNally 1993; Beekmann & Ratnieks 2000). In our study area, landscape type and season affected resource abundance. During May, rich resources were provided by oilseed rape, apple trees and other wild shrubs and herbs at all study sites. Accordingly, mean foraging
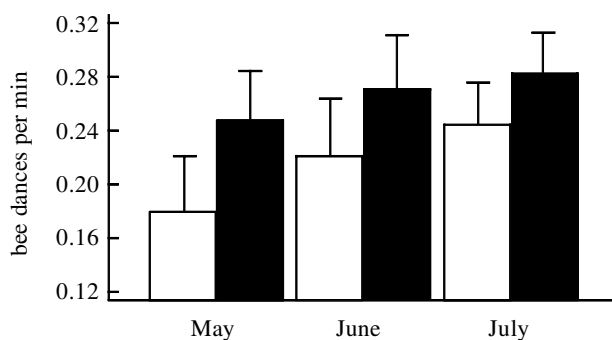
Figure 4. Effects of landscape type and season on the number of observed bee dances per minute. The mean number of bee dances per minute corrected for colony effects and 95% confidence intervals are shown. Statistical results of multifactor ANOVA—see table 6. Filled bars represent complex landscapes; open bars represent simple landscapes.

has already been removed in multifactor ANOVA. These findings strongly suggest that generalizations made from observations of single colonies should be considered carefully, and underline the advantage of our experimental approach to switch observation hives at regular intervals between the study sites.

A thought-provoking result in our study was that the dance activity of honeybee colonies was significantly higher in complex than in simple landscapes. Earlier studies have shown that bees are more likely to perform dances to nectar sources that are higher in concentration or closer to the colony (Dyer 2002). Accordingly, we would have expected similar dance activity in simple and complex landscapes in May when resources were abundant in all landscapes and foraging distances were similar. Another explanation for low dance activity could be a negative feedback loop due to reduced nectar uptake rates (Seeley 1992), but again this should result in a different pattern of dance activity with lowest activity in the months and landscapes with the highest resource abundance, i.e. in May and July and in complex landscapes in June. The consistently higher dance activity in complex compared with simple landscapes suggests a further influencing factor. We argue that variation in dance activity may also reflect differences in the spatial distribution, extent and temporal turnover of resource patches. In simple landscapes the allocation of foragers to the few highest quality resource patches may need a lower expenditure than in complex landscapes with many smaller and more patchily distributed resources. Thus dance activity seems to depend on landscape structure due to differences in the spatial distribution and temporal variability of resource patches and not only due to variation of the nectar income rate. Accordingly, landscape structure may change the evolutionary significance of the bee dance language.

Recent findings show that honeybees measure distances by optic image flow and not by energy consumption (Srinivasan *et al.* 2000) and that communicated distances may depend on the nature of the landscape through which the bee flies (Esch *et al.* 2001). This could result in a systematic error, i.e. bee dances in simple landscapes with low optic flow may communicate shorter than real distances, whereas the opposite would be the case in complex

landscapes. Thereby, the differences between simple and complex landscapes may have been an artefact. The results of our artificial feeder experiment do not support the above-mentioned predictions, because the calculated distances were larger than the real distances in simple and smaller in complex landscapes. However, these experiments were not replicated on a landscape scale and the influence of other local factors, for example wind velocity or flight altitude, cannot be excluded as in a related study (Esch *et al.* 2001).

Our results have some more general ecological implications for plant–pollinator interactions, gene flow and competition in a landscape context. Earlier studies have shown that pollinator diversity decreases significantly in simple agricultural landscapes (Steffan-Dewenter 2002; Steffan-Dewenter *et al.* 2002) and that pollination services may become disrupted (Steffan-Dewenter *et al.* 2001). The large foraging distances of honeybees, which even increased in simple landscapes during months with scarce resources, suggest that honeybees are able to maintain adequate pollination in such areas. However, this is only the case for plant species with flowers accessible to, and visited by, honeybees (Corbet 1996). Furthermore, greater foraging distances in simple than in complex landscapes could result in landscape-dependent differences of gene flow. This could take place either by actually moving pollen between fields or by in-hive pollen transfer from a larger area. Such effects could be of special importance for assessing gene escape from genetically modified (GM) crops such as oilseed rape to unmodified crops or wild relatives (Rieger *et al.* 2002).

In recent years, competition between honeybees and wild solitary bees has resulted in controversial discussion, but direct evidence for resource competition is still absent (Butz Huryn 1997; Steffan-Dewenter & Tscharntke 2000). However, the larger foraging distances for pollen suggest that pollen was a limited resource for honeybees in simple landscapes. In a related study, densities of flower-visiting honeybees on defined resource patches were higher in simple than in complex landscapes (Steffan-Dewenter *et al.* 2002). These results support the assumption that competitive interactions are altered by landscape structure and are more likely in structurally simple landscapes (Bronstein 1995).

In conclusion, this study significantly expands our knowledge of honeybee foraging in a landscape context. Future studies could attempt to relate these findings to pollination and gene flow of plant populations, disease transmission and possible competition with other bee species in differentially structured landscapes.

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