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Increased density of honeybee colonies affects foraging bumblebees*

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Abstract – The increasing numbers of endangered wild bee species highlights the need for quantifying potential adverse effects of foraging honeybees. We analysed the response of bumblebees at genus and species level to experimentally increased honeybee density. The study was carried out on a *Phacelia tanacetifolia* field and adjacent patches of wild plants located in an agricultural landscape. Addition of one or ten *A. m. ligustica* colonies substantially increased total honeybee density not only on *Phacelia* but also on neighbouring patches of wild plants. The response of bumblebees (*Bombus* spp.) differed among species. Only minor spatial changes in the abundance of the short-tongued *B. terrestris*-group were observed on *Phacelia*. At wild plant patches, the *B. lapidarius*-group and the longer tongued bumblebee species (*B. muscorum*, *B. sylvarum*, *B. pascuorum*) responded with a shift between plant species. Limitations of competition avoidance in flower-impooverished landscapes are discussed.

Apis mellifera / *Bombus* / competition avoidance / foraging / exploitative competition

1. INTRODUCTION

Interspecific competition is assumed to be a major factor in structuring foraging communities on flowers (Schaffer et al., 1979; Pleasants, 1981; Zimmermann and Pleasants, 1982; Schoener, 1987; Westrich, 1989; Corbet et al., 1995). However, the mechanisms underlying these interactions are difficult to test in the field. Many studies on resource overlap and possible competition with native wild bees have been carried out in regions where honeybees had been introduced (Buchmann, 1996; Buchmann and Nabhan, 1996; Sudgen et al., 1996; Butz Huryn, 1997). Though honeybees are native to Europe, extraordinarily

high local densities may adversely impact species richness and abundance of wild bees (Westrich, 1989; Evertz, 1995; Corbet et al., 1995; Steffan-Dewenter and Tschamtko, 2000; Steffan-Dewenter and Kuhn, 2003).

The response to competition by honeybees is likely to be different for different species of wild bees (Strickler, 1979; Eickwort and Ginsberg, 1980). It has been suggested that oligolectic species are more sensitive to competition than polylectic and social species (Westrich, 1989; Evertz, 1995). In contrast, Schaffer et al. (1979) and Thorp (1996) assumed that high honeybee densities most detrimentally affect social generalists with a foraging behaviour similar to that of honeybees. The latter argument would apply to species such as *Bombus terrestris*, which is able to fly several kilometres and exploit bonanzas of one flower species on arable fields or mass resources in

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grassland (Hedtke, 1996; Osborne et al., 1999; Walther-Hellwig and Frankl, 2000; Goulson and Stout, 2001; Kreyer et al., 2004). Other *Bombus* species prefer to forage close to their nesting site (Witte and Seger, 1999; Walther-Hellwig and Frankl, 2000) and visit a variety of food plants during a single flight (Kratochwill and Kohl, 1988). Some mechanisms for avoiding intra-genus competition have been described for coexisting bumblebee species (abundant vs. rare, shorter-tongued vs. longer-tongued; Inouye, 1978; Hanski, 1982; Thomson et al., 1987; Prys-Jones and Corbet, 1991; Inoue and Kato, 1992; Goulson, 2003). Thus, evidence suggests that increased honeybee density differently affects various bumblebee species (Pleasants, 1981; Corbet et al., 1995). To obtain a deeper insight into the underlying mechanisms, investigations must be carried out that explicitly take into account species-specific differences in proboscis length and in foraging strategies.

In the study reported here we addressed three main questions. First we asked if an experimental increase in the density of honeybee colonies would lead to higher honeybee densities on resources or whether forager communities were already in some sort of density equilibrium (Schaffer et al., 1983). If increased honeybee densities could be achieved by increasing the number of colonies, we assumed we would observe a “temporal avoidance strategy” (i.e. bumblebees forage earlier in the morning or later in the evening, Corbet et al., 1993, 1995; Williams and Christian, 1991). We further assumed that spatial displacement from the mass resource *Phacelia tanacetifolia* due to exploitative competition should mainly affect short-tongued and abundant species of the *B. terrestris*-group that have a foraging strategy similar to that of honeybees. Short-tongued honeybees may have an advantage over long-tongued bumblebees when nectar depletion exceeds nectar secretion (Corbet et al., 1995). Second, we tested whether honeybees exploited small patches of wild flowers when a mass resource like *Phacelia tanacetifolia* is available since honeybees are assumed to concentrate on the most profitable resources (Seeley, 1995; Beekmann and Ratnieks, 2000). Finally, we asked how the different bumble-

bee groups respond to increased competition on patches of wild flowers.

2. METHODS

2.1. Experimental design

The experiment was carried out in July and August 2001 in the basin landscape ‘Amoenburger Becken’ (Hesse, Germany). The study area is exposed to intensive agricultural farming. The soil type is loess. One *Phacelia tanacetifolia* (Hydrophyllaceae) field (1.1 ha; length: 245 m, width: 45 m) located in the centre of the basin at an altitude of 215 m a.s.l. was selected. Surrounding the *Phacelia* field on three sides were field patches with neighbouring grain fields, and on the other side was grassland which included a small patch of abandoned grassland along a drainage ditch.

Honeybee density was altered by placing colonies derived from *Apis mellifera ligustica* (*A. m. ligustica*) on the field path of the small side of the *Phacelia* field that was opposite to the abandoned land and the drainage ditch. At least two yellow tergites of this honey bee contrast to the black tergites and the grey hairs characterizing the local honeybees (derived mostly from *Apis mellifera carnica*). The color markings allowed for easy differentiation between introduced and local bees. The following treatments were established: no *A. m. ligustica* colony 12th, 20th and 22nd of July, 3rd of August), 1 *A. m. ligustica* colony (17th, 18th, 27th, 28th of July, 2nd August) and 10 *A. m. ligustica* colonies (24th, 25th, 26th, 31st of July). These treatments are abbreviated in the following text as Lc0, Lc1, and Lc10, respectively. Differences in treatment sequences could not be avoided because of the relatively short full-flowering period of *Phacelia* and because equal weather conditions had to be maintained for all treatments. *A. m. ligustica* colonies were transported to the field early in the morning and the bees were allowed to adjust their foraging activities for one full day before the start of counting. For the control treatment, *A. m. ligustica* colonies were moved to a location at a distance of about 18 kilometres.

The number of local honeybee colonies within a radius of 5 km surrounding the experimental field was recorded before the experiment commenced. During the course of the experiment, counts in the *Phacelia* field were performed on randomly selected plots along a transect line in three different

zones of distance from the hive location (zone A: 10–40 m; zone B: 110–140 m and zone C: 210–240 m).

In the experiment with natural patches of wild plant species the almost monospecific patches consisted of species that differed in corolla type and length: three patches of *Polygonum persicaria* (Polygonaceae), two patches of *Epilobium angustifolium* (Onagraceae), two patches of *Centaurea jacea* (Asteraceae), and four patches of *Lotus uliginosus* (Fabaceae). *Polygonum* has small open flowers with the shortest corolla of all four species. *Epilobium* has a large shallow flower at which nectar also is easily reachable. The flowers of *Centaurea* form a small short tube and are grouped in an inflorescence. And finally, *Lotus* has flowers with standard, wings, and keel, and bee foragers need to push the petals apart to reach nectar and pollen. All four plant species are good quality food sources to honeybees, though estimates of foraging values slightly vary. According to Pritsch (1985), Maurizio (1994), and Zander (1997) the food value for honeybees can be ranked as follows: *Epilobium angustifolium* = *Centaurea jacea* > *Lotus uliginosus* > *Polygonum persicaria*. However, the value of *P. tanacetifolia* is generally considered to be superior to these native plants. It offers large amounts of nectar and pollen that is easily accessible to honeybees and bumblebees (Williams and Christian, 1991; Williams, 1997). We wanted to use naturally growing plants for our experiment rather than potted plants where sufficient and continuous humidity is very hard to maintain in summer. Therefore we had to accept that distance to the *A. m. ligustica* hives and the plant species were conflated. Mean patch size and distance to hive location were 10 m² and 200 m for *Lotus*, 630 m² and 220 m for *Epilobium*, 250 m² and 320 m for *Polygonum*, and 1000 m² and 600 m for *Centaurea*.

Densities of foraging honeybees and bumblebees were counted in a frame of 1 m². Counts were performed at temperatures above 15 °C in 3 to 5 series per day between 0900 h and 1800 h, and were stopped or interrupted when rain or stormy wind appeared. Moreover, three ‘dusk till dawn’ counts lasting from 0600 to 2100 h were performed on July the 22nd (no *A. m. ligustica* colony), July 24th (ten *A. m. ligustica* colonies), and August the 2nd (one *A. m. ligustica* colony), respectively. The number of samples was usually 10 per series on natural foraging patches and 45 per series on the *Phacelia* field. Mean daily flower covers of *P. tanacetifolia* and of wild flowers (% cover in steps of 10%) were as-

essed during one series of counts within the same 1 m² frame used for the bees.

2.2. Honeybee and Bumblebee species

The local grey-banded honeybees in the study area were derived predominantly from the subspecies *A. m. carnica*. Few yellowish bees of uncontrolled local breeding appeared in densities below 0.1 Ind m⁻² before *A. m. ligustica* colonies were introduced for the first time. Yellow honeybees therefore belonged with a very high probability to *A. m. ligustica* from the experimental hives. The very similar species *Bombus terrestris*, *Bombus lucorum* and *Bombus cryptarum* have been documented in this study area (Walther-Hellwig and Frankl, 2000). These three species were grouped as “*B. terrestris*-group”. All bumblebee foragers with a black body and red-orange hairs on the last three tergites were assorted to the “*B. lapidarius*-group”. A total of 20 control counts with determination to the species level revealed that approximately 98% of the individuals were *B. lapidarius* and approximately 2% were *B. soroeensis*. Bumblebee species of these two groups are rather common in the study area and have, on average, a shorter proboscis than *B. muscorum*, *B. pascuorum* and *B. sylvarum* (Hanski, 1982; Prys-Jones and Corbet, 1991; Corbet et al., 1995). *B. sylvarum* and *B. muscorum* are considered to be rare and endangered in the study area (Diekötter et al., 2001). For statistical analysis the three species with a longer proboscis were grouped as “Bb long-tongued”.

2.3. Statistical analysis

General regression models (GRM), an extension of general linear models (GLM), were used to test whether the introduced *A. m. ligustica* colonies significantly affected native honeybees and bumblebees with respect to their abundance and their relationship with the environment. To control against error accumulation due to replicate testing, multivariate models were performed; i.e., models simultaneously included the five groups of bees analysed as dependent variables: Yellow honeybees (Hb yellow), grey honeybees (Hb grey), *B. terrestris*-group, *B. lapidarius*-group and the total count of long-tongued *Bombus* species (Bb long-tongued). The *A. m. ligustica* treatments (Lc0, Lc1, Lc10; see above) were specified as categorical independent

variables. Environmental variables, such as flower cover, distance from the introduced *A. m. ligustica* colonies and time of the day were specified as continuous independent variables. The interactions of *A. m. ligustica* treatments with each of the environmental variables were also included in the models to test for changes in the correlation between bee groups and environmental variables under the influence of *A. m. ligustica* colonies. The control treatment (Lc0) was defined as the reference state in the regression models to allow for a direct comparison of regression coefficients under the *A. m. ligustica* treatments against those under the control treatment. Forward stepwise selection of parameters was applied to obtain models exclusively built from significant independent variables. Counts of bees were averaged across the observations made on replicate sub-plots within each hour, normalized to counts per 10 m², and then log-transformed $x_i = \ln(x+1)$. We checked against non-normality of residuals (Kolmogorov-Smirnov test) to ensure correctness of GRM results. The Statistica package (StatSoft Inc., Tulsa, USA), was used for all statistical analyses.

A significant main effect of the *A. m. ligustica* treatment indicated a general response of the respective bee group to the introduction of additional bees. Significant interactions between *A. m. ligustica* treatment and environmental variables reflected a shift of that bee group within the environmental space in response to *A. m. ligustica*. Depending on whether regression coefficients for Lc1 or Lc10 were significantly different from the reference model, we concluded that the effect occurred under high or low *A. m. ligustica* density, respectively.

3. RESULTS

3.1. Temporal activity of honeybees and bumblebees

The three ‘dusk till dawn counts’ revealed that the daily maximum for total honeybee density (Hbtotal) on the *Phacelia* field was at 1700 h during Lc0 (10.4 Ind_{Hbtotal} m⁻²) (Fig. 1). Lc1 shifted this peak to 1500 h (10.1 Ind_{Hbtotal} m⁻²) and Lc10 to 1300 h (11.3 Ind_{Hbtotal} m⁻²). No honeybees foraged before 0700 h and the mean density of bumblebee foragers at this time was only 0.02 Ind_{Hbtotal} m⁻². Temporal changes in foraging activity of total honeybee and total bumblebee foragers par-

alleled each other across all treatments, with maximum densities occurring between 1000 h and 1800 h, not only on *Phacelia* but also on the wild plant patches. Consequently, the analysis of the effects of additional honeybee colonies was confined to 0900 and 1800 h.

3.2. Foraging communities on *Phacelia*

No local bee colonies were found within a radius of 1 km around the *Phacelia* field. A total of 10 colonies were located within a radius of 2 km, 62 colonies within 3 km, 128 colonies within 4 km, and 202 colonies within 5 km. Local grey honeybees dominated the foraging community of the *Phacelia* field at Lc0, and individuals of the *B. terrestris*-group dominated the bumblebee community (Tab. I). About one percent of all foragers occurring in the *Phacelia* field were long-tongued bumblebee species.

Averaging over all distance zones showed that Hbtotal was not significantly increased under Lc1, since additional yellow honeybees displaced grey honeybees. However, it significantly increased under Lc10 (GRM: $P < 0.001$). The introduction of 10 colonies increased the average honeybee density on the entire *Phacelia* field from 5.7 individuals per m² to 7.4 individuals per m². The highest increase of honeybees was reached within the first 40 m with Lc10 where density almost doubled from 6.2 honeybees per m² to 11.2 honeybees per m². Total bumblebee (*Bombus* spp.) densities increased in the experimental treatments without a significant shift in the proportion of honeybees and bumblebees.

3.3. Effects of bee treatment on *Phacelia* on species group level

The multivariate statistical analysis of the density distribution of honeybees and bumblebees again showed that the main factor ‘‘Day Time’’ had no general effect on the foraging behaviour (Tab. II). The factor ‘‘Flower cover’’ had a general effect mainly on the distribution of grey honeybees. A general effect of ‘‘Distance’’ from the beginning of the *Phacelia* field

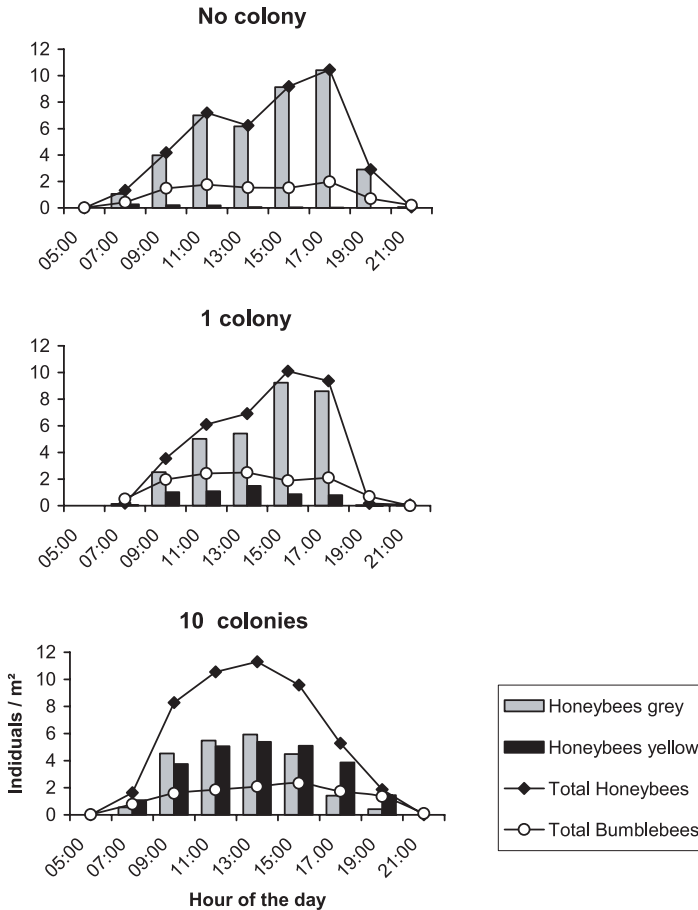


Figure 1. Mean forager density on the *Phacelia* field (dusk-till-dawn counts) without *A. m. ligustica* colonies (control), with 1 *A. m. ligustica* colony and with 10 *A. m. ligustica* colonies.

was shown for the yellow honeybees and for both the *B. lapidarius*-group and long-tongued bumblebees. While the density of the yellow honeybees decreased with the distance (GRM: $P < 0.001$), the density of the two bumblebee groups increased with distance (GRM: $P < 0.001$, Tab. II, Fig. 2).

A general strong effect of treatment with the additional *A. m. ligustica* colonies (Lc) was only found for grey honeybees (Tab. II). The density of grey honeybees shifted to farther distances from the honeybees at Lc10 compared to Lc0 (GRM: $P < 0.05$) and towards earlier foraging hours (GRM: $P < 0.001$).

The foragers of the *B. lapidarius*-group reacted to Lc10 with a slight increase in density at farther distances from the honeybees ($P < 0.01$; Tab. II, Fig. 2). The effect of the

A. m. ligustica treatment for the *B. terrestris*-group interacted with flower cover and distance (Tab. II) The density of *B. terrestris*-group foragers increased with farther distances and lower flower cover during Lc10 (GRM: $P < 0.001$, for both effects).

3.4. Foraging communities on wild plants

Grey honeybees of the control (Lc0) visited all wild flowers except *Lotus uliginosus*. The *B. terrestris*-group was also absent from *Lotus*, whereas long-tongued bumblebees formed over 40% of the foraging community on this species (Tab. I). Grey honeybees had the highest share of the foraging communities on *Polygonum persicaria* (about 74%). The

Table I. Mean density (Ind m⁻²) and share (%) of bumblebee (Bb) and honeybee (Hb) foragers on the *Phacelia*-field and on the four wild plant species (Treatment: Lc0 = without *A. m. ligustica* colonies, Lc1 = with one *A. m. ligustica* colony, Lc10 = with ten *A. m. ligustica* colonies).

	Treatment	Lc0		Lc1		Lc10	
		Ind m ⁻²	%	Ind m ⁻²	%	Ind m ⁻²	%
<i>Phacelia tanacetifolia</i>	Hb total	5.73	81	5.64	74	7.36	82
	Bb total	1.33	19	1.97	26	1.52	17
	Hb grey	5.61	79	4.69	62	3.67	41
	Hb yellow	0.12	2	0.95	13	3.69	41
	Bb short-tongued	1.26	18	1.86	24	1.52	17
	Bb long-tongued	0.07	1	0.11	1	0.05	1
	Flower cover [%]	47		40		50	
	Number of samples	1060		1335		1178	
<i>Polygonum persicaria</i>	Hb total	0.81	75	2.51	90	2.95	96
	Bp total	0.27	25	0.29	10	0.14	4
	Hb grey	0.80	74	0.61	22	0.35	11
	Hb yellow	0.01	1	1.90	68	2.60	84
	Bb short-tongued	0.23	25	0.25	9	0.11	4
	Bb long-tongued	0.00	0	0.02	1	0.01	0
	Flower cover [%]	37		42		50	
	Number of samples	91		175		110	
<i>Centaurea jacea</i>	Hb total	0.78	55	2.66	81	5.62	91
	Bp total	0.63	45	0.64	19	0.53	9
	Hb grey	0.77	54	1.40	42	1.60	26
	Hb yellow	0.02	1	1.26	38	4.02	65
	Bb short-tongued	0.51	36	0.53	16	0.49	8
	Bb long-tongued	0.12	9	0.11	3	0.05	1
	Flower cover [%]	15		13		15	
	Number of samples	195		150		105	
<i>Epilobium angustifolium</i>	Hb total	1.03	57	3.23	91	3.81	94
	Bp total	0.78	43	0.34	9	0.24	6
	Hb grey	0.90	50	0.63	18	0.56	14
	Hb yellow	0.13	7	2.60	73	3.25	80
	Bb short-tongued	0.48	26	0.18	5	0.18	4
	Bb long-tongued	0.18	10	0.08	2	0.03	1
	Flower cover [%]	13		16		20	
	Number of samples	94		263		145	
<i>Lotus uliginosus</i>	Hb total	0.00	0	0.00	0	0.00	0
	Bp total	0.29	100	0.43	100	0.51	100
	Bb short-tongued	0.16	57	0.12	28	0.17	33
	Bb long-tongued	0.12	43	0.31	72	0.35	67
	Flower cover [%]	18		15		13	
	No. of samples	44		88		44	

Table II. Results of the Multivariate Regression Model (GRM) for the five bee groups in the experiment on *Phacelia*. Factors were “Flower cover” per m², “Distance” from the location of the *A. m. ligustica* hives, “Day time” of bee counts, and treatment (Lc1, Lc10). Lamda = Wilk’s Lamda, SS = Sum of square error, R² = coefficient of determination, *P* = error probability, n.s. = not significant.

	Multivariate		Hb yellow		Hb grey		<i>B. terrestris</i> -group		<i>B. lapidarius</i> -group		Bb. long-tongued	
	Lamda	<i>P</i>	SS	<i>P</i>	SS	<i>P</i>	SS	<i>P</i>	SS	<i>P</i>	SS	<i>P</i>
Intercept	0.09	0.000	52.10	0.000	7.17	0.000	149.93	0.000	10.25	0.000	1.42	0.000
Flower Cover	0.17	0.000		n.s.	11.97	0.000		n.s.	0.44	0.000	0.42	0.000
Distance	0.30	0.000	4.57	0.000	0.08	0.048		n.s.	0.92	0.000	0.63	0.000
Day Time	1.00	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
Treatment (Lc)	0.65	0.000	3.96	0.000	0.54	0.000		n.s.	0.19	0.044		n.s.
Lc × Flower Cover	0.78	0.001	0.36	0.005		n.s.	0.76	0.000		n.s.		n.s.
Lc × Distance	0.54	0.000	0.73	0.000	0.13	0.049	0.66	0.000	0.22	0.024		n.s.
Lc × Day Time	0.65	0.000		n.s.	1.11	0.000		n.s.		n.s.		n.s.
Error			4.13		2.55		2.02		3.72		4.24	
Model R²			0.92		0.86		0.35		0.38		0.18	
Model p				0.000		0.000		0.000		0.000		0.000

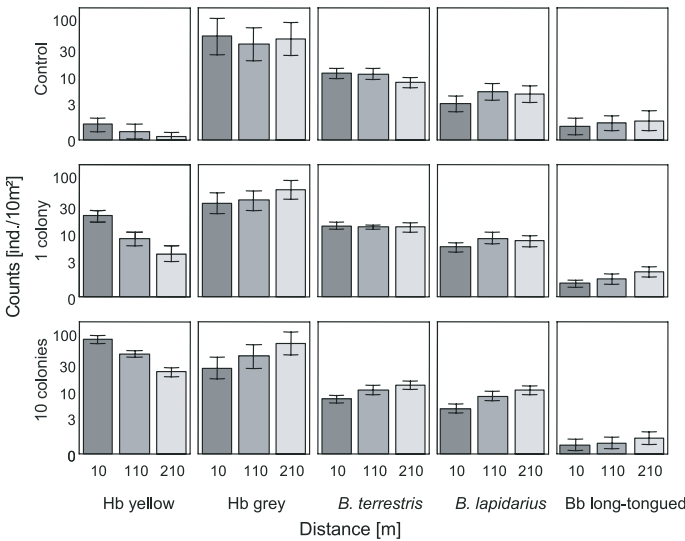


Figure 2. Responses of honeybee and bumblebee groups to introduced *A. m. ligustica* colonies on the *Phacelia* field in comparison to the control without *A. m. ligustica* colonies. Means and 95% confidence intervals of bee counts. Hb = Honeybees, Bb = Bumblebees, *B. lapidarius* = *B. lapidarius*-group, *B. terrestris* = *B. terrestris*-group.

B. terrestris-group dominated the bumblebee community on this plant. On *Centaurea jacea* and *Epilobium angustifolium*, grey honeybees contributed only about 50% to the foragers and the *B. lapidarius*-group was the most numerous bumblebee group.

The density of honeybees increased strongly under Lc1 on *Polygonum*, *Epilobium*, and *Centaurea*. But *Lotus* patches were still not visited by grey and yellow honeybees (Tab. I). No significant effects on the density

of total bumblebees (*Bombus* spp.) could be found under the treatment with *ligustica* colonies.

3.5. Effects of bee treatment on wild plants on species group level

The factor “Plant species” had the strongest general effect on all species groups, honeybees and bumblebees (Tab. III). Grey

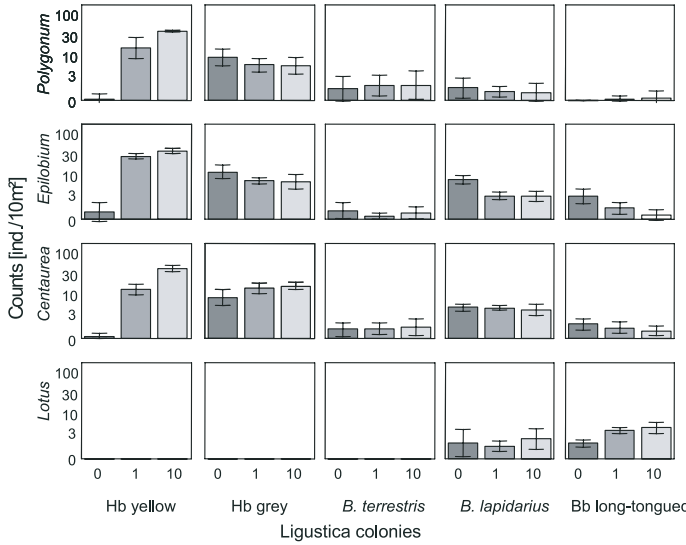


Figure 3. Responses of honeybee and bumblebee groups to introduced *A. m. ligustica* colonies on four wild plant species in comparison to the control without *A. m. ligustica* colonies. Means and 95% confidence intervals of bee counts. Hb = Honeybees, Bb = Bumblebees, *B. lapidarius* = *B. lapidarius*-group, *B. terrestris* = *B. terrestris*-group.

Table III. Results of the Multivariate Regression Model (GRM) for the five bee groups on the wild plants. Factors are the “Flower cover” per m², the “Day time” of bee counts, the wild “Plant species” *Polygonum*, *Epilobium*, *Centaurea* or *Lotus*, and treatment (Lc1, Lc10). Lamda = Wilk’s Lamda, SS = Sum of square error, R² = coefficient of determination, P = error probability, n.s. = not significant.

	Multivariate		Hb yellow		Hb grey		<i>B. terrestris</i> -group		<i>B. lapidarius</i> -group		Bb. longtongued	
	Lamda	P	SS	P	SS	P	SS	P	SS	P	SS	P
Intercept	0.33	0.000	1.74	0.000	60.63	0.000	0.82	0.000	22.69	0.000	9.82	0.000
Flower Cover	1.00	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
Day Time	0.79	0.001		n.s.		n.s.	0.43	0.000		n.s.		n.s.
Plant species (Ps)	0.28	0.000	1.08	0.000	21.01	0.000	1.85	0.000	1.29	0.000	3.42	0.000
Ps × Flower Cover	1.00	n.s.	0.59	0.000		n.s.		n.s.		n.s.		n.s.
Ps × Day Time	0.45	0.000		n.s.		n.s.	1.53	0.000	1.20	0.000		n.s.
Treatment (Lc)	0.69	0.000	0.29	0.001		n.s.		n.s.		n.s.		n.s.
Lc × Flower Cover	0.81	0.041	0.33	0.000		n.s.		n.s.	0.52	0.000		n.s.
Lc × Day Time	1.00	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
Lc × Plant species (Ps)	0.43	0.000	7.19	0.000	0.74	0.000		n.s.	0.51	0.011		n.s.
Lc × Ps × Flower cover	0.53	0.001		n.s.		n.s.		n.s.		n.s.		n.s.
Lc × Ps × Day Time	1.00	n.s.		n.s.		n.s.		n.s.	0.42	0.032	1.34	0.000
Error			1.79		2.90		2.88		2.80		2.96	
Model R²			0.97		0.89		0.55		0.71		0.66	
Model p				0.000		0.000		0.000		0.000		0.000

honeybees were slightly reduced at Lc1 and Lc10 on *Polygonum* and *Epilobium*, but were significantly increased on *Centaurea* (GRM: $P < 0.01$, Fig. 3). Bumblebee density was affected by the experimental treatment on certain wild plants, but the effects were

different for different species groups. Among the short-tongued species only the *B. lapidarius*-group directly reacted to the bee treatment (Lc × Plant species, Tab. III) The density of the *B. lapidarius*-group slightly increased on *Lotus* (GRM: $P < 0.01$), while it decreased

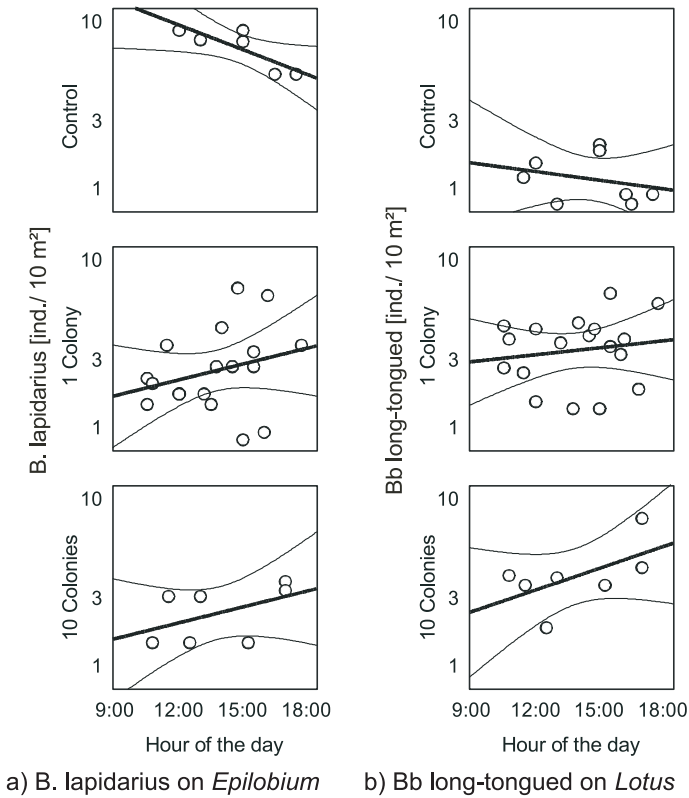


Figure 4. Response of the *B. lapidarius*-group (= *B. lapidarius*) on *Epilobium angustifolium* and the group of the long-tongued bumblebees (= *Bb* long-tongued) on *Lotus uliginosus* to introduced *A. m. ligustica* colonies in comparison to the control without *A. m. ligustica* colonies.

Linear regressions and 95% regression intervals of bee counts.

on *Polygonum* and *Epilobium* in combination with a shift in foraging time towards later hours and lower flower cover of *Epilobium* (GRM: $P < 0.01$ for both effects; Tab. III, Figs. 3, 4). Long-tongued bumblebee species were reduced on *Epilobium* and *Centaurea* and reacted to the honeybee treatment with a density increase on *Lotus* in combination with a shift towards later foraging hours (GRM: $P < 0.001$; Tab. III, Figs. 3, 4).

3.6. Summary of treatment effects on *Phacelia* compared to wild plants

Of all bumblebee groups on *Phacelia*, only the *B. terrestris*-group showed a significant response to the experimental treatment by spatial avoidance (foraging a farther distance from the *A. m. ligustica* hives) and by shifting to parts of the *Phacelia* field with a lower flower cover. Reduced density of the long-tongued bumblebees on *Phacelia* was not significant. A temporal shift in foraging time on *Phacelia* as

a response to the addition of *A. m. ligustica* colonies could not be established for bumblebees.

In contrast, the *B. terrestris*-group was not affected on the wild plants, but the *B. lapidarius*-group and especially the group *Bb* long-tongued showed a general response to the introduction of even one additional colony on wild plants combined with a shift towards later foraging hours. *Bb* long-tongued foragers were reduced on *Epilobium* and enhanced on *Lotus*.

When counts were analysed on the genus level *Bombus* spp. only, no significant effects could be found in both experiments.

4. DISCUSSION

4.1. Additional colonies increased honeybee densities

The first question of our study addressed whether an experimental increase in honeybee

density on an attractive floral resource like *Phacelia* was possible at all. In previous studies, the addition of honeybee colonies either displaced local honeybees without increasing total densities (Schaffer et al., 1983) or altered densities only to a level that made evaluating the effect of experimental treatment very difficult (Steffan-Dewenter and Tscharnke, 2000). In our study, total honeybee density slightly increased on the *Phacelia* field with the addition of one colony, mainly within the first 40 m around the hive location. Though the average honeybee density increased after the introduction of 10 colonies on the entire *Phacelia* field and almost doubled within the first 40 m, the increase was not proportional to the number of introduced honeybee foragers. This indicated that resources other than those in our observed experimental plots were also exploited by the additional *A. m. ligustica* foragers.

Nevertheless, we achieved higher honeybee densities not only on *Phacelia*, but also on all of the wild flower patches neighbouring the *Phacelia* field, except for *Lotus*. Honeybee densities were three times higher on these patches with the introduction of just one *ligustica* hive, even though patch size of the wild plants was small and resource values were lower than that of *Phacelia*. Thus, *A. m. ligustica* foragers used both superabundant mass resources and various other plant species occurring within short distances to the hive location. Small and scattered patches of resources in the vicinity of the hives might represent a generally underestimated steady source of food (Visscher and Seeley, 1982; Wenner and Meade, 1991). No interference competition caused by aggressive behaviour of grey or yellow honeybees could be observed on the flowers (reviewed in Butz Huryn, 1997). Effects of forager displacement were thus assumed to be caused by exploitative competition only.

4.2. Similar temporal foraging activity of bumblebees and honeybees

Grey honeybees responded to competition with bees from the introduced *A. m. ligustica* colonies on *Phacelia* by a significant shift towards earlier foraging. A similar response

could not be observed for bumblebees, neither in the dusk-till-dawn counts nor in the analysis of the main foraging time. This is in contrast to the study of Williams and Christian (1991) who suggested a diurnal niche differentiation for bumblebees on *Phacelia*. One explanation for our findings might be provided by the landscape context of our study area. The experimental site was located in the centre of a large basin landscape where cold air accumulated overnight. Honeybees arriving from warmer and sheltered hive locations at the basin edges might have been active as early as bumblebees nesting in the central basin. This contention is supported by the higher density of grey honeybees compared to yellow honeybees early in the morning, even though the *A. m. ligustica* colonies were located directly at the *Phacelia* field. Thus, landscape features probably prevented the bumblebee workers from profiting from their lower temperature thresholds (Corbet et al., 1993, 1995).

4.3. Bumblebee species react differently to increased competition

On the *Phacelia*-field as well as on patches of natural plant species no significant effects of increased honeybee densities could be found when the analysis was restricted to the genus level of *Bombus*. When the analysis focused on the groups of bumblebee species we observed different significant reactions, for some species clearly opposite to each other. This provided evidence that competition effects between honeybees and bumblebees cannot be generalized across studies for the genus *Bombus*, but may be generalized at least on species group level.

4.3.1. Foraging communities on *Phacelia*

In contrast to our initial expectation (cf. Pleasants, 1981; Corbet et al., 1995), competitive effects on the most abundant, short-tongued bumblebees (*B. terrestris*-group, *B. lapidarius*-group) were only weak. Foragers of the *B. terrestris*-group responded to the introduction of ten *A. m. ligustica*

colonies by foraging at a farther distance and in those parts of the *Phacelia* field that had a lower flower cover. The fact that foragers of the *B. terrestris*-group shifted their foraging towards the distant edge of the field might indicate that workers were able to detect areas with higher food rewards per flower (Pleasants and Zimmermann, 1979; Pleasants, 1981; Thomson, 1988), as the yellow honeybees concentrated their foraging on the first 140 m of the *Phacelia* field. Competition was thus avoided by spatial and not by temporal shifts.

Considering that an introduction of 20, 50 or even several hundreds of colonies is rather common when modern beekeepers move hives to a new place, the moderate spatial response of short-tongued bumblebees revealed for 10 additional hives might strongly increase under intensive beekeeping. As flight distances and homing ability of the short-tongued bumblebee species *B. terrestris* and *B. lapidarius* range around several kilometres (Hedtke, 1996; Osborne et al., 1999; Walther-Hellwig and Frankl, 2000; Goulson and Stout, 2001; Kreyer et al., 2004), foragers of these groups will probably avoid competition by searching for alternative resources on a larger spatial scale.

4.3.2. Foraging communities on wild plants

In contrast to the *Phacelia* experiment, the long tongued bumblebees, but not the *B. terrestris*-group, were especially affected by *A. m. ligustica* colonies on wild plants. Experimental treatment effectively reduced densities of this group on *Centaurea*, but increased it on *Lotus* patches. Thus, competition was avoided by shifting towards *Lotus* patches; i.e., the only resource that did not attract grey and yellow honeybees or *B. terrestris*-group foragers.

The nectar and pollen value of *Lotus uliginosus* for honeybees is comparatively high (Maurizio, 1994; Zander, 1997), but access (especially to nectar) is more difficult than on the three other wild flower species. The *Lotus* patches in our experiment probably were also less attractive to honeybees because they were comparatively small. Access to *Lotus* flowers is probably easier for the longer tongued and

heavier bumblebee species. Moreover, long-tongued bumblebee species will be more attracted by this plant if patches are located close to the nesting site and are part of a rewarding trap line (Thomson, 1996; Thomson et al., 1997). Such trap lines are formed by a sequence of various plant species providing supplemental food sources (Heinrich, 1979). The higher densities of long-tongued species on *Lotus* in the treatment with 10 *ligustica* colonies indicated that some workers subsequently shifted their foraging routes from strongly exploited resources to patches with reduced competition. There was a significant shift of long-tongued species to a later foraging time on *Lotus* during the treatments with 10 *A. m. ligustica* colonies. Workers probably probed *Epilobium* and then shifted to adjacent *Lotus* patches. Comba (1999) showed that experimental bagging of flowers on the usual trap line of single *B. pascuorum* workers only led to minor changes in the foraging route (see also Thomson et al., 1987). Though the exact proof for trap line foraging is difficult (Thomson et al., 1997), experiments with marked individuals suggest that *B. muscorum* and *B. sylvarum* also forage in repeated sequences on the food patches of our experiment (Walther-Hellwig, unpubl. data).

Bumblebees responded differently to increased honeybee densities in our experiments, with the response of the abundant species (mainly short tongued) occasionally being opposite to that of less abundant species (longer tongued). Therefore our study supports the urgent need for increasing the level of taxonomic resolution for bumblebees in scientific studies beyond the genus level, even though some bumblebee species are hard to differentiate in the field. Results based on identification to the genus level will not help evaluate possible competition effects.

4.4. Competition is more detrimental to bumblebee species with a short foraging range

B. terrestris, *B. lapidarius* and honeybees are able to fly beyond their normal foraging area when resource depletion is strong.

Foraging ranges of the longer-tongued species *B. pascuorum*, *B. sylvarum* and *B. muscorum*, in contrast, seem to be more restricted to the immediate surrounding of nesting sites (Free and Butler, 1959; Witte and Seger, 1999; Walther-Hellwig and Frankl, 2000). Moreover, these species forage in trap lines (Comba, 1999) and on different plant species rather than concentrating on the most abundant flower species (Free, 1970; Kratochwill and Kohl, 1988; Kreyer et al., 2004).

Bumblebee species foraging close to their nesting site have a limited ability to shift to alternative food plants. It is not clear whether enforced foraging on alternative patches is equally rewarding if the additional costs for searching time and the possibly larger handling efforts are taken into account. Detrimental effects on the defence of bumblebee colonies against parasites and on brood development may result from a food shortage even of only one day (Sutcliffe and Plowright, 1990; Cartar and Dill, 1991).

One major problem in our approach was that strong exploitative competition may have already reduced the bumblebee species set on the *Phacelia* field before we managed to effectively increase honeybee densities. Local displacement effects may thus have taken place before our experiment started. The strength of this effect is difficult to estimate, but it might well be that some of the apparently weak responses observed on the mass resource could be much more important in the course of a complete colony cycle or after several years of increased competition. Stronger effects can probably also be expected when far more than 10 honeybee colonies are brought to an area, as it is quite usual to move up to hundred colonies of honeybees in migratory beekeeping.

The fact that longer tongued bumblebee species were displaced even from rather small patches of natural plant species neighbouring a mass resource supports the assumption of spatially restricted species being affected by competition in degraded "humanscapes" (Buchman, 1996). Mass flowering crops probably only enhance densities of abundant, spatially flexible bumblebee species (Westphal et al., 2003). Simplification of agricultural landscapes probably increases competition

among pollinators (Bronstein, 1995; Steffan-Dewenter and Kuhn, 2003), as pollen and nectar needs throughout the whole season must be taken into account. Our results suggest that the effects of local food deprivation and of high competition will be more detrimental to short-ranged, trap-lining bumblebee species than to spatially more flexible species.

5. CONCLUSIONS

Our aim was to study competition at the landscape scale. This is very difficult, because this level of spatial resolution does not allow for control of all of the multi-scaled factors influencing the abundance of foraging bees (Sudgen et al., 1996). However, investigations on measuring competition effects must be extended to the landscape scale and should be long-term studies rather than observing just a few weeks within the colony cycle. Observations should also be carried out at the species level to show that resource competition is indeed a real-world phenomenon (Thorp, 1996; Buchman, 1996; Roubik, 1983). Though factors such as quantity and quality of floral resources, nectar content, nectar composition, and corolla depth may control local competition among bee foragers (Corbet et al., 1995), communities at the landscape scale also depend on the spatial arrangement of floral resources (Kearns and Inouye, 1993; Steffan-Dewenter et al., 2002) and on the distances between nest and food plants (Westrich, 1996). High densities of honeybee colonies should not be a problem even for the long-tongued, short range bumblebees, as long as floral resources are diverse and highly dispersed, and mass resources on arable fields are accompanied by flower rich grasslands, path verges, or abandoned land. However, our study revealed that even the addition of one honeybee colony may lead to a strong increase in honeybee densities on smaller flower patches, even though a large *Phacelia* field was present. Many modern agricultural landscapes are poor in floral resources, at least in late summer. Under conditions of food shortage, detrimental effects of locally high honeybee densities on wild bee populations cannot be excluded.

In addition, flower impoverished modern landscapes cause problems to non-migratory beekeeping. Seasonal gaps in flower availability not only affect flower honey yields, but may also influence colony health (Lehnherr and Thomas, 2003). In principle, biodiversity conservation and beekeepers share the common aim of maximizing quantity and heterogeneity of floral resources in space and time. A promising common area of interest is an agreement on appropriate management practices that enhance the potential for permanent and diverse floral resources, at least in intensively managed agricultural landscapes.

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Résumé – Une densité accrue de colonies d’abeilles domestiques affecte le butinage des bourdons. Avec l’augmentation du nombre d’espèces d’abeilles sauvages en danger la question de la concurrence possible entre espèces due à une forte densité locale d’abeilles domestiques (*Apis mellifera*) est intéressante pour la protection de la nature et l’apiculture, et pas seulement en Europe. Dans les études effectuées jusqu’à présent les conséquences possibles d’une augmentation de la densité d’abeilles domestiques sur les bourdons ont surtout été considérées au niveau du genre *Bombus*, mais cela ne tient pas compte des exigences écologiques très variées des différentes espèces de bourdons. C’est pourquoi nous avons étudié les effets possibles de la concurrence au niveau des groupes d’espèces de bourdons dans un paysage agricole (bassin d’Amöneburg, Allemagne).

Les surfaces expérimentales comprenaient un champ d’1,1 ha de *Phacelia tanacetifolia* ainsi que des surfaces voisines plus petites ayant une végétation naturelle soit de *Polygonum persicaria*, *Epilobium angustifolium*, *Centaura jacea*, soit de *Lotus uliginosus*. Ont été installées dans le champ de phacélie soit aucune, soit 10 colonies d’*A. m. ligustica*.

Les densités de butineuses ont été comptées durant 4 à 5 j. L’introduction expérimentale des colonies d’*A. m. ligustica* a provoqué une nette augmentation de la densité totale d’abeilles domestiques non seulement sur le champ de phacélie, mais aussi sur les parcelles de végétation naturelle (Tab. I). Si l’on exploite les comptages sur phacélie uniquement pour le genre *Bombus*, il n’y a pas de corrélation significative. Si on les exploite au niveau des groupes d’espèces, on trouve pour le groupe *B. terrestris* des modifications spatiales faibles mais significatives sur la phacélie (Tab. II). Les butineuses du groupe *B. terrestris* se sont concentrées sur les parcelles ayant une faible densité florale et qui étaient plus éloignées des colonies d’*A. m. ligustica*.

Sur les parcelles de végétation naturelle, les densités d’abeilles domestiques ont été multipliées par trois sur toutes les plantes, y compris sur *Lotus* dès l’apport d’une colonie d’*A. m. ligustica* (Tab. I, Fig. 3). L’analyse des résultats au niveau de l’espèce montre des oppositions nettes entre les divers groupes de bourdons : le groupe *B. terrestris* n’a montré aucune réaction à l’augmentation de la densité des abeilles domestiques, alors que le groupe *B. lapidarius*, ainsi que les espèces à langue longue (*B. muscorum*, *B. sylvarum* et *B. pascuorum*) ont réagi en butinant plus intensément les parcelles de *Lotus* sans abeilles domestiques. Des modifications temporelles dans le comportement de butinage afin d’éviter la concurrence n’ont pu être observées dans un périmètre restreint que pour *B. lapidarius* sur *Epilobium* et pour les bourdons à langue longue sur *Lotus* (Fig. 4).

Pour les bourdons à langue longue qui ont un rayon d’action réduit, des effets négatifs de fortes densités locales d’abeilles domestiques ne sont pas à exclure même sur des ressources en masse, si une concentration sur les plantes alternatives des prairies, jachères ou zones de bordure voisines n’est pas possible. Puisqu’en cas de forte concurrence alimentaire non seulement les espèces d’abeilles sauvages mais aussi la santé des colonies d’abeilles domestiques en souffrent, l’effort pour maintenir des paysages fleuris mais avant tout riches et variés en plantes représente un but important et commun aux groupements d’apiculteurs et aux associations de protection de la nature.

Apis mellifera / *Bombus* / butinage / compétition alimentaire / évitement de la compétition

Zusammenfassung – Auswirkungen erhöhter Honigbienendichten auf Hummelsammlerinnen. Vor dem Hintergrund der zunehmenden Bestandsgefährdung von Wildbienen ist die Frage nach möglichen Konkurrenzeffekten durch lokal hohe Honigbienendichten nicht nur in Europa eine Frage von naturschutzfachlichem und imkerlichem

Interesse. In bisherigen Untersuchungen wurden mögliche Folgen erhöhter Honigbienendichten auf Hummeln vorwiegend auf dem Niveau der Gattung *Bombus* betrachtet. Dieser Ansatz wird aber den sehr verschiedenen ökologischen Ansprüchen der einzelnen Hummelarten nicht gerecht. Daher wurden in der vorliegenden Studie in einer Agrarlandschaft (Amöneburger Becken, Deutschland) mögliche Konkurrenzeffekte auch auf Artgruppen-niveau untersucht.

Als Versuchsflächen dienten ein 1.1 ha großes *Phacelia tanacetifolia*-Feld sowie benachbarte, kleinere Untersuchungsflächen natürlicher Pflanzenbestände mit entweder *Polygonum persicaria*, *Epilobium angustifolium*, *Centaurea jacea* oder *Lotus uliginosus*. Es wurde entweder kein, ein oder zehn Völker von *Apis mellifera ligustica* direkt an das *Phacelia*-Feld gestellt und an je vier oder fünf Probetagen die Blütenbesucherdichten gezählt.

Das experimentelle Einbringen von *A. m. ligustica* Völkern führte zu einer deutlichen Erhöhung der Gesamthonigbienendichte nicht nur auf dem *Phacelia*-Feld, sondern auch auf den benachbarten Probeständen der natürlichen Pflanzenarten (Tab. I). Wertet man die Zählungen auf *Phacelia* lediglich für die Gattung *Bombus* aus, so ergeben sich keine signifikanten Zusammenhänge. Wertet man die Funde nach Artengruppen aus, so ergeben sich für die *B. terrestris*-Gruppe schwache, aber signifikante räumliche Veränderungen auf *Phacelia* (Tab. II). Sammlerinnen der *B. terrestris*-Gruppe wichen auf Bereiche mit niedrigerer Blühdichte und größerer Entfernung von den *A. m. ligustica* Völkern aus (Abb. 2).

Auf den Probeständen mit natürlichem Pflanzenbestand verdreifachte sich die Honigbienendichte bereits bei einem *A. m. ligustica* Volk auf allen Pflanzenarten, bis auf *Lotus* (Tab. I, Abb. 3). Bei der Analyse der Ergebnisse auf Artniveau zeigen sich auch auf den natürlichen Nahrungspflanzen deutliche Gegensätze zwischen den verschiedenen Hummelartengruppen: Die *B. terrestris*-Gruppe zeigte keine Reaktionen auf die erhöhten Honigbienendichten, während die *B. lapidarius*-Gruppe sowie die langrüssligen Hummelarten *B. muscorum*, *B. sylvarum* und *B. pascuorum* mit einem verstärktem Sammeln auf honigbienenfreien *Lotus*-Flächen reagierten. Zeitliche Veränderungen im Sammelverhalten zur Konkurrenzvermeidung konnte in geringem Umfang nur für *B. lapidarius* auf *Epilobium* und für die langrüssligen Hummelarten auf *Lotus* beobachtet werden (Abb. 4).

Gerade für die langrüssligen Hummelarten mit räumlich stärker eingeschränktem Sammelradius sind negative Auswirkungen von lokal hohen Honigbienendichten selbst an Massenressourcen nicht auszuschließen, wenn ein Ausweichen auf pflanzenartenreiche Blütenangebote benachbarter Wiesen, Brachen oder Randstrukturen nicht möglich ist. Da unter starker Nahrungskonkurrenz nicht nur die Wildbienenarten leiden, sondern

auch die Gesundheit der Bienenvölker, ist das Bemühen um nicht nur blüten- sondern vor allem Pflanzenarten reiche, blühende Landschaften ein wichtiges gemeinsames Ziel von Imkereivereinigungen und Naturschutzinitiativen.

Apis mellifera / *Bombus* / Sammelverhalten / Konkurrenzvermeidung

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