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Resource overlap and possible competition between honey bees and wild bees in central Europe

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Abstract Evidence for interspecific competition between honey bees and wild bees was studied on 15 calcareous grasslands with respect to: (1) foraging radius of honey bees, (2) overlap in resource use, and (3) possible honey bee effects on species richness and abundance of flower-visiting, ground-nesting and trap-nesting wild bees. The grasslands greatly differed in the number of honey bee colonies within a radius of 2 km and were surrounded by agricultural habitats. The number of flower-visiting honey bees on both potted mustard plants and small grassland patches declined with increasing distance from the nearest apiary and was almost zero at a distance of 1.5–2.0 km. Wild bees were observed visiting 57 plant species, whereas honey bees visited only 24 plant species. Percentage resource overlap between honey bees and wild bees was 45.5%, and Hurlbert's index of niche overlap was 3.1. In total, 1849 wild bees from 98 species were recorded on the calcareous grasslands. Neither species richness nor abundance of wild bees were negatively correlated with the density of honey bee colonies (within a radius of 2 km) or the density of flower-visiting honey bees per site. Abundance of flower-visiting wild bees was correlated only with the percentage cover of flowering plants. In 240 trap nests, 1292 bee nests with 6066 brood cells were found. Neither the number of bee species nor the number of brood cells per grassland was significantly correlated with the density of honey bees. Significant correlations were found only between the number of brood cells and the percentage cover of shrubs. The number of nest entrances of ground-nesting bees per square metre was not correlated with the density of honey bees but was negatively correlated with the cover of vegetation. Interspecific competition by honey bees for food resources was not shown to be a significant factor determining abundance and species richness of wild bees.

Key words Community structure · Foraging distance · Flower visitation · Conservation · Grasslands

Introduction

The importance of interspecific competition for the structure and diversity of communities has attracted much attention and controversy during recent decades (Connell 1983; Schoener 1983; Abrams et al. 1986; Trepl 1994). Interspecific competition for limited resources affects the reproductive success and survival of the species involved and may explain evolutionary specialization and niche differentiation. Although it is difficult to prove the evolutionary significance of interspecific competition observed in the field (Schoener 1986), both experiments in simplified and artificial habitats (e.g. Gause 1969), and mathematical models (e.g. Scudo and Volterra 1978; Chesson 1994) have shown its possible influence. Interspecific competition appears to be important in vertebrate communities (Schoener 1983) and less important in communities of herbivorous insects (Strong et al. 1984, but see Denno et al. 1995). In contrast, nectar and pollen feeders, especially bees (Hymenoptera: Apoidea), are often assumed to be strongly affected by interspecific competition for the high-quality food resources provided by flowering plants to attract pollinators (e.g. Eickwort and Ginsberg 1980; Schaffer et al. 1979, 1983; Plowright and Laverty 1984; Schoener 1986; Westrich 1989; Corbet et al. 1995; Sudgen et al. 1996). An increase in competitive effects may be expected after: (1) the introduction of new competitors, (2) changes in environmental conditions, and (3) increased abundance of a competitor.

Recently, nature conservationists concerned about the general decline in the numbers of wild bees have suggested the importance of competition by honey bees in Europe (e.g. Westrich 1989; Evertz 1995). In contrast to America, the honey bee, a native European species, has coexisted with other "wild" bee species for thousands of years. However, fundamental changes in landscape

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structure, and the domestication and concentration of colonies of honey bees by beekeepers, could potentially have disrupted the presumed ecological balance between native bee populations and honey bees.

Honey bees have been assumed to be superior competitors because of: (1) the high requirements for nectar and pollen of their large perennial colonies compared to solitary bees, and (2) the rapid exploitation of attractive patches of flowering plants by using a dance language to communicate direction and distance of food resources to other foragers (von Frisch 1965; Visscher and Seeley 1982). The susceptibility of wild bees to competition has been suggested to vary with their biology, i.e. whether they are social or solitary, oligolectic or polylectic species (Strickler 1979; Eickwort and Ginsberg 1980).

Despite these assumptions regarding competitively superior honey bees, unequivocal evidence does not exist in the literature that competition by honey bees significantly depresses the reproductive success or affects the survival of other bee species (Sudgen et al. 1996; Butz Huryn 1997). Some studies have shown an overlap in resource use and decreasing abundance of flower-visiting wild bees in the presence of honey bees foraging on the same plant species (e.g. Roubik 1983; Schaffer et al. 1983). But it remains unclear whether the observed shift in flower visitation patterns resulted in lower reproductive success and population size of the bee species involved (Sudgen et al. 1996; Butz Huryn 1997). Competitive effects have previously been studied almost exclusively only in areas where honey bees have been introduced (principally the Americas and Australasia), whereas only a few studies, producing contradictory results, have been done in Europe (Kribbe 1993; Pechhacker and Zeilinger 1994; Evertz 1995).

In this study we studied competition between honey bees and wild bees on fragments of semi-natural, calcareous grasslands in an agricultural landscape in Germany. Evidence for interspecific competition should be provided by: (1) resource overlap, (2) reduced flower visitation rates due to resource depletion, and (3) reduced rates of reproduction. These hypotheses were tested in this study. In addition, the foraging radius of honey bees and therefore the area of interaction between honey and wild bees, as well as habitat factors possibly limiting population size, were analysed.

Materials and methods

Study area and experimental sites

The study was carried out in the Leinebergland, near Göttingen, Germany, in 1994. The average temperature during the study period from April to August was 16.3°C (1.6% above the long-term mean), the rainfall was 325.8 mm (1.8% above the long-term mean), and the duration of sunshine was 1067.9 h (11.5% above the long-term mean; data from the meteorological station, Hannover). The study area is an intensively managed agricultural landscape with islands of semi-natural calcareous grasslands, mostly situated on the southern or western slope of hills. The grasslands developed by extensive grazing over a long period of time (at least decades). Today these habitats are characterized by a diverse vegetation with many endangered plants and species-rich bee communities. Many of them are nature reserves.

We determined the distribution of honey bee colonies in the study area and selected 15 grasslands ranging in proximity to honey bee colonies to establish a gradient from very low to very high honey bee densities. Five additional honey bee colonies were placed at each of four grasslands to increase the existing differences in hive densities. The number of honey bee colonies within a radius of 2 km around the studied grassland sites was between 3 and 65 colonies. At the eight grasslands with lower densities no colony was nearer than 500 m from the grasslands, whereas at each of the seven grasslands with higher densities, 5–20 colonies were placed directly on the grasslands. The mean area of the grasslands was 4.3 ha and was not correlated with honey bee densities (r^2=0.397, n=15, P=0.47).

Vegetation

To characterize the vegetation, all plant species in a 49-m^2 plot in the central area of each grassland were mapped in June and August. For each plot we estimated the percentage cover of vegetation, the mean height of vegetation, and the percentage cover of each plant species. Additionally, the percentage cover of shrubs overall on each grassland was estimated.

To estimate the resource availability of nectar and pollen, the species composition and percentage cover of flowering (melittophilous) plants were recorded at each grassland 5 times between April and August. For statistical analyses we used the arithmetic mean of the number and the cover of plant species flowering at each of the 5 observation times.

Foraging radius of honey bee colonies

The foraging radius of the honey bee colonies was estimated using two different methods. First, we established 40 small patches, each with four potted mustard plants (*Sinapis arvensis*, Brassicaceae), at increasing distances from honey bee colonies. Four patches were placed on each of four grasslands with an apiary, and four on each of four sites without an apiary. The remaining 32 patches were placed in the agricultural landscape around the grasslands and at different distances from the apiaries. At each patch we observed the number of flower-visiting honey bees for 15 min (19–28 June 1995).

Secondly, field observations were made on ten small calcareous grasslands at different distances from two apiaries in the Bratental, a nature reserve in the east of Göttingen (1994; unpublished data from Jens Rögener). Flower-visiting honey bees were recorded 10 times between April and August (i.e. two-weekly) on a permanent patch of 4×15 m for 30 min at each grassland. Additionally, species composition and percentage cover of flowering melittophilous plants on the patches were recorded. Measurements were made under suitable temperature and precipitation conditions between 0900 and 1700 hours at a randomly allocated time of day and distance to the nearest apiary.

Wild bee communities

In order to assess possible effects of competition by honey bees, three methods were used to measure the species richness and abundance of the wild bees in these communities: (1) transect sweeps measured the abundance of wild bees at flowers, (2) trap nests gave information on reproductive success, food resources and mortality, and (3) nest entrances of ground-nesting bees were counted to measure population density.

1. Observations were made along transects 5 times for 45 min at each of the 15 grasslands between April and August 1994. Along the transect all bee species and the flowering plant spe-

cies visited were recorded. If necessary, bees were collected with a sweep net (40 cm diameter) for identification. As an additional part of the transects, 100 sweeps through the vegetation at the height of the flower canopy and in the centre of each grassland were carried out to get small and inconspicuous species. Transects were made under suitable temperature and precipitation conditions between 0900 and 1700 hours. The time of day for observations at successive transects was randomized for each grassland.

2. Trap nests can provide insights into the biology and ecology of above-ground-nesting bee species giving information on reproductive success, food resources and mortality due to natural enemies (Tscharntke et al. 1998). At each grassland with apiaries, four wooden posts each with four trap nests at heights of 80–100 cm above ground were installed at a distance of about 5 m, 50 m, 100 m, and 200 m, respectively, from the nearest apiary when honey bee colonies were placed on the grassland (*n*=7). On the remaining eight grasslands without apiaries four wooden posts each with four trap nests at heights of 80–100 cm above ground were installed at the same distances from each other. Trap nests were exposed between April and September 1994. Each trap nest consisted of 150–180 internodes of common reed (*Phragmites australis*), about 20 cm long with a range of internal diameters between 2 and 10 mm, placed inside plastic tubes of 10.5 cm diameter. In the laboratory, all reed internodes that contained bee nests (i.e. an internode with one or more brood cells) were opened and examined for species identification, number of cells, male:female ratio and parasitism rates.
3. To measure the density of ground-nesting bees at each grassland, ten patches (1×1 m) were selected at regular distances along the transect which was marked by the trap nests. At each patch, we counted the number of nest entrances of ground-nesting bees in soil, and estimated the percentage cover of vegetation between 12 May and 14 June 1994. Two grasslands were excluded because of unfavourable weather conditions. In total, 130 patches were counted.

Identification

The identification and nomenclature of plant species was based on Rothmaler et al. (1990). Most bee species were identified according to Schmiedeknecht (1930). Further literature, cited in Steffan-Dewenter (1998), was used for the genera *Lasioglossum*, *Halictus*, *Hylaeus*, *Megachile*, *Sphecodes*, *Coelioxys*, *Bombus* and *Psithyrus*. The nomenclature is based on Westrich (1989).

Statistical analysis

The statistical analyses of the data were performed using the software Statgraphics Plus for Windows 2.1 (Manugistics). If necessary, logarithmic or square-root-transformed variables were used to achieve normal distribution. Arcsine transformation (arcsin $\sqrt{p}$, where p is a proportion) was used for percentages (Sokal and Rohlf 1995). Stepwise multiple linear regression analyses were carried out to show the possible joint effects of independent variables. Simple regressions were checked for curvilinear relationships. ANOVAs were used to test for differences between two groups. Spearman rank correlations were used for the analysis of individual species that did not conform to a bivariate normal distribution (Sokal and Rohlf 1995). In figures showing significant correlations the regression line is shown. Arithmetic means±SD are given in the text. Overlap in resource use of honey bees and wild bees was calculated twice: First as percentage overlap (P). This is identical to the percentage similarity measure proposed by Renkonen (Krebs 1989). Secondly, we used Hurlbert's index of niche overlap (L), because it allows for the possibility that resources vary in abundance (Krebs 1989). Niche overlap can thus be expressed as

$$P_{jk} = \sum_{i=1}^{n} (\min p_{ij}, p_{ik}) 100 \text{ or} \qquad (1)$$

$$L_{jk} = \sum p_{ij} p_{ik} / a_i, \qquad (2)$$

where p_{ij}, p_{ik} = proportion resource i of the total resources utilized by the two species j and k, and a_i=proportional amount of resource i.

Results

Foraging radius and density of flower-visiting honey bees

In total, we observed 61 honey bees on the 40 experimental patches of flowering mustard plants. With increasing distance from the nearest apiary the mean number of flower-visiting honey bees significantly declined from 3.5 honey bees/15 min close to the apiary to <1 honey bees/15 min at an apiary distance of 1.5 km (Fig. 1A).

Similar results were obtained from observations of ten small calcareous grassland patches with natural vegetation. The number of flower-visiting honey bees per patch, which were observed between April and August, significantly decreased with increasing distance from the nearest apiary. At a distance of about 1.5 km, no honey bees were observed (Fig. 1B). In a multiple regression model, the percentage cover of flowering *Centaurea scabiosa* per patch, which was not correlated with distance from the nearest apiary, explained an additional 14% of the variance.

For the 15 study sites, abundance of flower-visiting honey bees on the calcareous grasslands increased with density of honey bee colonies within a 2 km radius around the grasslands (Fig. 1C).

Overlap in resource use

The resource overlap within the habitat, i.e. the percentage of plant species used by both honey bees and wild bees as pollen or nectar source, may have indicated the extent of possible competition. The observations of flower visits from the transect records were used here to estimate the resource overlap of honey bees and wild bees on the calcareous grasslands.

Altogether, 224 honey bees, 304 solitary wild bees and 671 bumble bees were observed to visit 57 flowering plant species; 37% of these plant species were visited by both honey bees and wild bees, whereas 58% were only visited by wild bees and 5% were only visited by honey bees. Plant species visited by both honey bees and wild bees were the more abundant and included about 64% of the total cover of flowering plants. Percentage resource overlap (P) between honey bees and wild bees was 45.5%, Hurlbert's index of niche overlap (L) was 3.1. Values >1 indicated that both groups used certain resources more intensively than others and that the preferences of the two groups tended to coincide (Krebs 1989).

Honey bees were observed to mainly visit *Hippocrepis comosa* (Fabaceae; 82 observed flower visits, i.e. *n*=82), *Origanum vulgare* (Lamiaceae; *n*=29), and

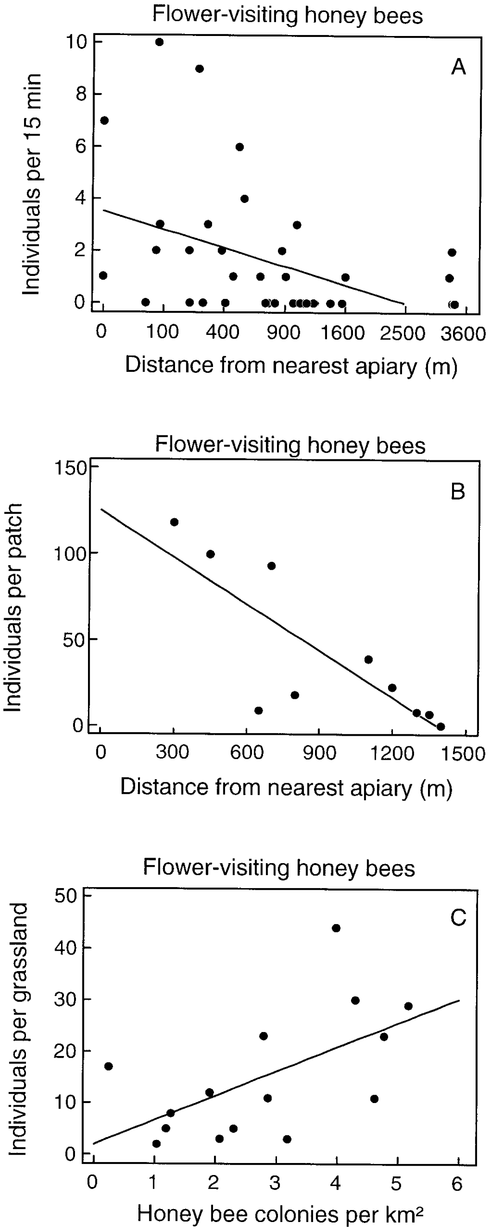

Fig. 1A–C The number of flower-visiting honey bees in relation to the distance from the nearest apiary or the density of honey bee colonies. **A** Relationship between the number of honey bees visiting an experimental mustard patch/15 min and the distance from the nearest apiary: $y=3.52-0.07\sqrt{x}$; $F=8.91$, $r=-0.436$, $n=40$, $P=0.005$. (Note: square-root scale for distance). **B** Relationship between the number of flower-visiting honey bees on small calcareous grassland patches with natural vegetation and the distance from the nearest apiary: $y=117.4-0.08x$; $F=15.78$, $r=-0.815$, $n=10$, $P=0.004$. The numbers of flower-visiting honey bees per patch were observed 10 times between April and August 1994. **(C)** Relationship between the number of flower-visiting honey bees on 15 calcareous grasslands and the density of honey bee colonies within a radius of 2 km: $y=1.97+4.71x$; $F=6.69$, $r=-0.456$, $n=15$, $P=0.023$

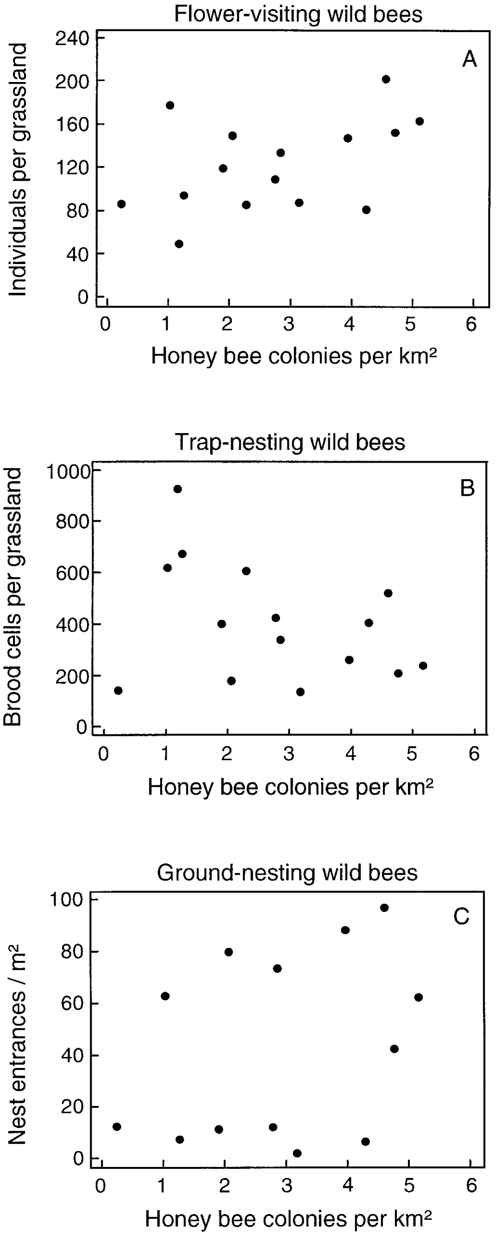

Fig. 2A–C Abundance of flower-visiting, trap-nesting and ground-nesting wild bees in relation to the density of honey bee colonies. **A** Plot of the number of flower-visiting wild bees on calcareous grasslands versus the density of honey bee colonies within a radius of 2 km (not significant; $r=0.454$, $n=15$, $P=0.089$). **B** Plot of the number of brood cells of trap-nesting wild bees on the calcareous grasslands versus the density of honey bee colonies within a radius of 2 km (not significant; $r=-0.355$, $n=15$, $P=0.193$). **C** Plot of the number of nest entrances versus the density of honey bee colonies within a radius of 2 km (not significant; $r=0.336$, $n=13$ grasslands, $P=0.262$). Arithmetic means of 10 plots/grassland were used

Centaurea jacea or *scabiosa* (Asteraceae; $n=22$). According to 1199 observations of flower visitation, the most important nectar and pollen sources for wild bees were *Hippocrepis comosa* ($n=168$), *Potentilla verna* (Rosaceae; $n=90$), *Lotus corniculatus* (Fabaceae; $n=79$), *Anthyllis vulneraria* (Fabaceae; $n=75$), *Centaurea scabiosa* ($n=63$), *Centaurea jacea* ($n=49$), *Cirsium acaule* (Asteraceae; $n=43$), *Prunella grandiflora* (Lamiaceae; $n=43$), *Leontodon hispidus* (Asteraceae; $n=29$), and *Scabiosa columbaria* (Dipsacaceae; $n=28$).

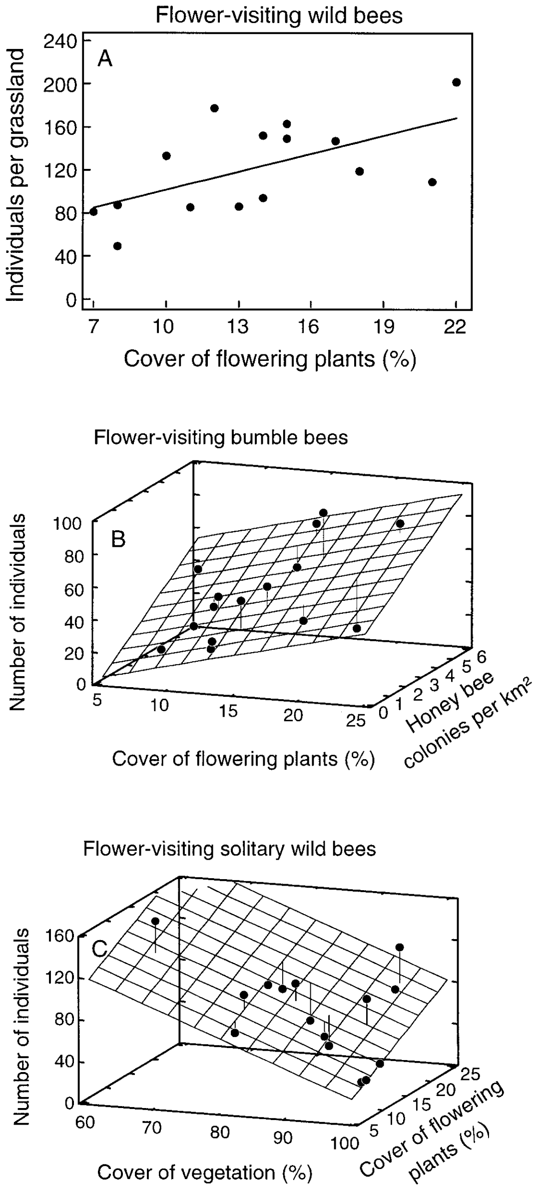

Fig. 3A–C Abundance of flower-visiting wild bees in relation to habitat parameters. **A** Relationship between the number of flower-visiting wild bees and the cover of flowering plants (%): y=46.12+5.56x; F=7.10, r=0.594, n=15, P=0.020. **B** Number of flower-visiting bumble bees in relation to the cover of flowering plants (x_1) and the density of honey bee colonies (x_2) within a radius of 2 km: y=–5.21+1.94x_1+8.45x_2; F=7.91, r=0.754, n=15, P=0.006. **C** Number of flower-visiting solitary, mainly ground-nesting bees in relation to the cover of vegetation (x_1) and the cover of flowering plants (x_2): y=245.5–2.37x_1+3.00x_2; F=9.90, r=0.789, n=15, P=0.003

Species richness and abundance of flower-visiting wild bees

In total we recorded 1849 individuals from 98 wild bee species during the transect observations on the calcareous grasslands. The most diverse and abundant genera were *Andrena* with 21 species (111 individuals), *Nomada* with 15 species (84 individuals), *Lasioglossum* with 13 species (537 individuals), *Sphecodes* with 8 species (80 individuals) and *Bombus* with 6 species (671 individuals). Altogether, 23 endangered species (Dorn and Bleyl 1993) and six rare species (Theunert 1994) were found. Eight oligolectic bee species with low abundance were observed.

With multiple regression analyses we tested for correlations between species richness or abundance of flower visiting wild bees with the density of honey bee colonies, the number of flower-visiting honey bees per grassland and four independent habitat parameters (percentage cover of flowering plants, species richness of flowering plants, percentage cover of vegetation, percentage cover of shrubs).

Neither the abundance of flower-visiting wild bees (Fig. 2A) nor the species richness of flower-visiting wild bees (r=0.194, n=15, P=0.488) were negatively correlated with the density of honey bee colonies or the number of flower-visiting honey bees (species richness: r=–0.08, n=15, P=0.77; abundance: r=–0.19, n=15, P=0.49). In stepwise multiple regression analyses, the abundance of flower-visiting wild bees correlated only with the percentage cover of flowering plants (Fig. 3A), whereas the species richness of bees could not be explained by the tested parameters. Further separation of the bees into social bumble bees and mainly solitary ground-nesting bees showed that, contrary to expectations, the abundance of flower-visiting bumble bees was positively correlated with both the density of honey bee colonies and the cover of flowering plants (Fig. 3B), explaining together 57% of the variance. The abundance of the other, mainly ground-nesting bee species (both with and without the inclusion of parasitic bee species of the genera *Nomada* and *Sphecodes* into the analyses), was negatively correlated with the cover of vegetation and positively correlated with the cover of flowering plants, explaining 62% (without parasitic species, 58%) of the variation (Fig. 3C).

Additionally, we tested the hypothesis that individual bee species were more sensitive to possible competition from honey bees than others. We included in our analyses each of 30 bee species occurring with more than five individuals on three or more sites during the transect observations. However, with one exception (*Sphecodes geoffrellus*, r_s=–0.55, P<0.05, six individuals observed) no significant correlations with the density of honey bee colonies or abundance of flower-visiting honey bees were found. Furthermore, 15 correlation coefficients were positive and 15 negative (with density of honey bee colonies) and 13 positive and 17 negative (with abundance of flower-visiting honey bees), respectively.

Effects on species richness and abundance of trap-nesting bees

A total of 1292 bee nests and 6066 brood cells were found in the 240 trap nests. Altogether we identified 18 bee species from seven genera, including four parasitic species . The most abundant species was *Osmia rufa* (55% of all nests). The other five *Osmia* species were less abundant (*O. leaiana,* 8%; *O. parietina,* 4%; *O. caerulescens,* 0.5%; *O. brevicornis* and *O. claviventris* <0.1%). The next most common genera were the leafcutter bees, *Megachile (*25% of all nests) with three species (*M. versicolor, M. alpicola* and *M. lapponica*), *Hylaeus* (14% of all nests) with three species (*H. confusus, H. communis* and *H. difformis*) and *Chelostoma* and *Heriades* each with one species (*C. fuliginosum* and *H. truncorum*, respectively, <5% of all nests).

Neither the number of brood cells per grassland (Fig. 2B) nor the number of species (r=–0.242, n=15, P=0.386) were significantly correlated with the density of honey bee colonies or increasing number of flower-visiting honey bees (brood cells, r=–0.37, n=15, P=0.175; species, r=0.045, n=15, P=0.872). Significant correlations were found only between the number of brood cells and the percentage cover of shrubs (y=97+12.5x; r=0.62, n=15, P=0.014), but not between the number of brood cells with other habitat characteristics (cover of flowering plants, species richness of flowering plants, cover of vegetation). Similarly, the number of brood cells of individual bee species did not significantly correlate with the density of honey bee colonies (two positive and seven negative correlation coefficients) or the abundance of flower-visiting honey bees (four positive and five negative non-significant correlation coefficients).

Additionally, we tested whether the male:female ratio (mean, 1.69±0.80, n=15) was affected by the density of honey bee colonies or one of the other habitat parameters, but no significant correlation was found. Furthermore, there was no correlation between the distance of the trap-nests (5–200 m) from the seven apiaries on the grasslands and the number of bee nests.

Effects on densities of ground-nesting bees

In stepwise multiple regression analyses using the parameters described, the number of nest entrances of ground-nesting bees per square metre was not correlated with the density of honey bee colonies (Fig. 2C) or the number of flower-visiting honey bees, but was negatively correlated with the percentage vegetation cover ($y=(13.1–0.13x)^2$, r=–0.43, n=130, P=0.001).

Discussion

In this study we examined (1) the foraging radius of honey bees to estimate the spatial scale of possible competitive effects, (2) the overlap in resource use by honey bees and wild bees, (3) the possible effects of increased honey bee densities on species richness, abundance and reproductive success of wild bees on calcareous grasslands, and (4) the significance of other habitat characteristics for bee communities.

Foraging radius and density of honey bees

Honey bee densities continuously declined with increasing distance from the nearest honey bee colony. On small grassland patches, flower-visiting honey bees were only observed at a distance of <1.5 km from the nearest apiary. Similarly, the density of honey bee colonies per square kilometre (within a radius of 2 km around the grasslands) was significantly correlated with the number of flower-visiting honey bees on the grasslands. This supports estimations of the effective foraging radius of honey bees in Europe of about 2–3 km (von Frisch 1965). Therefore, strong competitive effects should only be expected from colonies within this radius. However, such simple relationships between apiary distance and forager density were not found by Visscher and Seeley (1982), since foraging honey bees preferred the most profitable patches of flowers within a large foraging range. Accordingly, the depletion of nectar and pollen by honey bees should steadily decrease with increasing distance from a honey bee colony only if patches of similar resource values are compared.

Overlap in resource use

Honey bees exploited only about one third of all flowering melittophilous plant species which were visited by wild bees on the grasslands. Similarly de Pedro and de Camargo (1991), Roubik (1996) and Buchmann (1996) found that honey bees only foraged on 33%, 15–20% or 25% of all plant species within their study areas, respectively. In our study, percentage resource overlap was 45.5 and L was 3.1 between honey bees and wild bees, indicating that both groups intensively used identical resources and that the preferences of the two groups tended to coincide (Krebs 1989).

The fragmented calcareous grasslands in our study were only a small part (about 0.2%) of the total foraging area of the honey bees. Due to the preference for large, dense patches of flowering plants (e.g. Ginsberg 1983; Steffan-Dewenter and Tscharntke 1996), other habitats, especially mass-flowering crops or forests with honeydew-producing aphids may attract foraging honey bees much more than the relatively sparse but species-rich vegetation of these grasslands. Kribbe (1993) found that about 75% of the pollen collected by honey bee colonies placed on a calcareous grassland came from crops. Similarly, social wild bees, especially bumble bees, have much larger foraging distances (Heinrich 1979; Hedtke 1994) than solitary wild bees, i.e. assumed to be <500 m for most species, depending on body size (Westrich 1989; Wesserling and Tscharntke 1995). Thus, the vegetation within the fragmented grasslands was the most important pollen and nectar source for solitary wild bees, but was probably not as important for honey bees and bumble bees.

Abundance and species richness of bee communities

Despite the large overlap in resource use, we did not find a negative relationship between the densities of honey bee colonies and the species richness or abundance of flower-visiting bees or trap-nesting bees. Therefore, at least in this year, the experimental level of resource depletion by foraging honey bees did not significantly affect the abundance of foraging wild bees on the grasslands, but it may have changed the patterns of flowers visited (see Roubik 1978; Schaffer et al. 1979, 1983; Thorp 1996). The impact of a particular factor may not be equal on all species, and some may suffer more than others from resource-sharing with *Apis mellifera*. However, in our study we found no evidence for this.

Two contrasting hypotheses on how honey bees affect social or solitary wild bees have been proposed: first, social, polylectic wild bees should be most affected by competing honey bees due to similar foraging strategies (Schaffer et al. 1979, 1983; Roubik 1978, 1980). In contrast to this hypothesis, the abundance of flower-visiting bumble bees was even positively correlated with the density of honey bee colonies. This indicated similar flower preferences of both honey bees and bumble bees in our study area, but gave no evidence for competitive exclusion.

Secondly, solitary oligolectic bee species may be affected by competition with honey bees because they cannot escape competing honey bees due to their specialization on certain plant species and their limited foraging range (Westrich 1989; Evertz 1995). On the other hand, there is some evidence that oligolectic bee species are able to outcompete honey bees due to higher foraging efficiencies (Strickler 1979; Thorp 1996; Wcislo and Cane 1996). Because only a few oligolectic species were found in our study, we could not effectively test this hypothesis.

Our approach was to measure not only resource overlap but also population parameters to assess possible effects of competition on reproductive success. We expected that resource depletion by honey bees should result in at least locally decreased densities of susceptible wild bee species. However, honey bee densities neither correlated with the number of brood cells of trap-nesting bee species nor with the number of nest entrances of ground-nesting species. Therefore, we did not find any evidence that honey bees negatively affected the reproductive success of wild bees at the experimental densities employed. Only a few other studies have measured reproductive success in relation to honey bee densities. Roubik (1983) studied brood production and food storage of two native social bees after the experimental introduction of Africanized honey bees, but he did not find significant effects on native bee colonies. Sudgen and Pyke (1991) investigated population parameters of colonies of a native social bee species in Australia: One experimental site with honey bee colonies was compared with three control sites without honey bee colonies. In one of two seasons they found increased adult emigration but also increased brood-rearing success and a significantly lowered male:female ratio at the experimental site. Similarly, Schwarz MP, Gross CL and Kukuk PF (cited in Butz Huryn 1997) found higher survival rates and nest densities of the native bee *Exoneura* sp. in experimental sites with honey bee colonies than in control sites. This result contrasts with our hypothesis that resource limitation induced by competition should result in lower reproductive success and a higher male:female ratio because of the lower parental food investment necessary for the production of males (e.g. Frohlich and Tepedino 1986). In our study, male:female ratios did not vary significantly in relation to honey bee densities.

Two European studies on competition are of special interest, because results from America or Australia may be different due to the status of the honey bee as an introduced species. Evertz (1995) found that the reproductive success of *Megachile rotundata* was higher at one experimental site without honey bees compared to one site with honey bees. However, due to the only partial resource overlap, the small foraging radius (50 m) of *M. rotundata* in this latter study, and the lack of replication, these results are difficult to interpret. Pechhacker and Zeilinger (1994) studied the abundance of trap-nesting bees at different distances from one large apiary (about 60 colonies), but they did not find evidence of competitive effects.

The results of the present study provided some evidence that the abundance of trap-nesting as well as ground-nesting bees depends on the availability of nesting places. The abundance of trap-nesting bees increased with increasing cover of shrubs which could be correlated with the amount of dead wood and therefore availability of nesting places (Tscharntke et al. 1998). The abundance of ground-nesting bees was negatively correlated with the cover of vegetation because the digging of nests depends on open soil. Therefore, succession significantly affected the wild bee communities in contrasting directions. Above-ground nesting bees profited from the succession to bushes and trees, whereas below-ground nesting bees profited from halted succession and open soil, e.g. due to sheep grazing.

Conclusions

Although competition between honey bees and wild bees is often expected, we did not find any evidence for significant effects at the densities of bees and flowers we studied. Further, no other study has unambiguously shown negative effects of honey bees on the reproductive success of wild bees, although resource overlap and competitive exclusion from the most profitable flower patches have been demonstrated. The lack of competitive effects could be explained by: (1) differences in foraging radius, habitat preferences and food selection between honey bees and wild bees, (2) the greater relevance of intraspecific competition to honey bees compared to interspecific competition with other bees, and (3) the limitation of wild bee populations by other factors like availability of nesting sites or abundance of natural enemies, but not by food resources.

In the future, more studies are required to evaluate the relative importance of factors influencing the population dynamics of wild bees. Life-table analyses (see Varley et al. 1973) should include food quantities in habitats with and without honey bees, reproductive success, and the significance of nesting sites and parasitoids, in order to identify key factors of population dynamics.

With respect to conservation, we suggest a more moderate approach than the total ban on beekeeping which is sometimes demanded for nature conservation areas (e.g. Evertz 1995). The honey bee densities of our study that were near the European-wide average of 3.1 colonies/km^2 did not appear to affect wild bee populations. To be on the safe side, bee densities in conservation areas should not exceed this level. We conclude from our results that for the conservation of wild bees it is much more important to protect and manage their habitats.

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