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...
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 (Kriibe 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 4x15 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-