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ORIGINAL PAPER

Competition between honey bees and wild bees and the role of nesting resources in a nature reserve

Anika Hudewenz · Alexandra-Maria Klein

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Abstract The European honey bee exploits floral resources efficiently and may therefore compete with solitary wild bees. Hence, conservationists and bee keepers are debating about the consequences of beekeeping for the conservation of wild bees in nature reserves. We observed flower-visiting bees on flowers of *Calluna vulgaris* in sites differing in the distance to the next honey-bee hive and in sites with hives present and absent in the Lüneburger Heath, Germany. Additionally, we counted wild bee ground nests in sites that differ in their distance to the next hive and wild bee stem nests and stem-nesting bee species in sites with hives present and absent. We did not observe fewer honey bees or higher wild bee flower visits in sites with different distances to the next hive (up to 1,229 m). However, wild bees visited fewer flowers and honey bee visits increased in sites containing honey-bee hives and in sites containing honey-bee hives we found fewer stem-nesting bee species. The reproductive success, measured as number of nests, was not affected by distance to honey-bee hives or their presence but by availability and characteristics of nesting resources. Our results suggest that beekeeping in the Lüneburg Heath can affect the conservation of stem-nesting bee species richness but not the overall reproduction either of stem-nesting or of ground-nesting bees. Future experiments need control sites with larger distances than 500 m to hives. Until more information is available, conservation efforts should forgo to enhance honey bee stocking rates but enhance the availability of nesting resources.

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A. Hudewenz (✉) · A.-M. Klein
Institute of Ecology, Ecosystem Functions, Leuphana University of Lüneburg, Scharnhorststr. 1, 21335 Lüneburg, Germany
e-mail: hudewenz@leuphana.de

A.-M. Klein
Chair of Nature Conservation and Landscape Ecology, Institute of Earth and Environmental Sciences, University of Freiburg, Tennenbacherstraße 4, 79106 Freiburg, Germany

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Introduction

Wild and honey bees depend on pollen and nectar from flowers as food resource, in adult and larval stage. The flowers of most bee-pollinated plant species are visited by multiple bee species that deplete floral resources and provide pollination services (Vázquez and Aizen 2004). Of those, the European honey bee (*Apis mellifera* L.) is the most abundant bee species in Europe and probably worldwide because it was introduced to every continent of the world (Goulson 2003). It can be managed by humans and in Europe feral hives are assumed to be rare. The European honey bee is an eusocial bee species that is active during the entire growing season and visits a wide range of different plant species (Crane 1990). A managed hive consists of on average 40,000 individuals. Honey bees are flower constant (Wells and Wells 1983) and visit preferentially mass-flowering plant species (Steffan-Dewenter and Tscharntke 2000). Honey bee workers can communicate the location of resource rich flower patches (Von Frisch 1967). Taking the life history and behavior traits of honey bees together, they are highly efficient in depleting floral resources.

Wild bees are often specialized to a certain degree on certain plant species or plant communities (Minckley and Roulston 2006). This implies that their survival and occurrence is heavily dependent on the presence of these particular plant species. Most wild bee species are solitary. They build their own nests using natural materials like loamy or muddy soil, stems, leaves and resin. The majority of solitary bees are nesting in the soil (ground-nesting bees) but some species are using stems for nesting. A nest of a solitary wild bee comprises approximately 1–14 offspring. Due to the high efficiency of honey bees in depleting floral resources and their quantitative dominance, it is reasonable to hypothesize that solitary wild bees may be affected by competition with honeybees (Evertz 1995).

Honey bees are widely considered as native in Europe, meaning that native wild bees have cohabited with them for thousands of years. But because humans are frequently keeping bees for honey production and pollination services the abundance of honey bees became artificially high. Furthermore, due to the ongoing loss of habitat and adequate food resources, honey bees and wild bees need to coexist in the remaining habitat. Thereby, it is important to consider that bees are not only affected on a local scale but also on a regional scale, meaning that surrounding habitat affect bee communities depending on species-specific preferences (Jauker et al. 2009). Nature reserves are assumed to be suitable habitat for bees because of the lower disturbance compared to non-protected areas. In some regions this caused conflicting interests between nature conservationists and bee keepers: Nature conservationists are concerned about possible competition and prioritize the nature reserves as habitat for wild and unmanaged bees only and bee keepers require flower rich habitat which are not affected by the application of agro-chemicals to forage plants.

Until today, most studies about the competition between honey bees and wild bees focused on areas where honey bees were introduced by humans: Most of those found evidence for competitive interactions between native wild bees and managed honey bees observing altered flower visitation rates of wild bees (Schaffer et al. 1983), aggressive encounters between wild bees and honey bees (Pinkus-Rendon et al. 2005), reduced species richness of wild bees (Badano and Vergara 2011) and lower reproductive success of bumble bees (Thomson 2004) while some found no effect (e.g. Paini et al. 2005). Research conducted in Europe, where honey bees are considered as native (Steffan-Dewenter and Tscharntke 2000) or have been present for thousands of years, found contrasting results about the effect of honey bees on wild bees with studies showing no or weak effects (Steffan-Dewenter and Tscharntke 2000; Forup and Memmott 2005) to studies indicating stronger effects, e.g. on wild bee worker size (Goulson and Sparrow 2009) and abundance (Evertz 1995). Like some of the above mentioned studies, we argue that the effect of honey bees on wild bee reproductive success needs to be considered when studying competitive interactions for conservation purposes. Lowered visitation rates do not necessarily lead to lower reproductive success since especially generalist species can shift their niches temporally or spatially (Walther-Hellwig et al. 2006).

To add scientific evidence to the long-standing debate, we studied the impact of the presence and distance to honey-bee hives on the flower visitation (number of flower visits in a certain time unit) and overall reproductive success of wild bees in the Lüneburg Heath. For this we tested the following hypotheses:

1. Flower visitation of wild bees decreases in sites with honey bee-hives and with decreasing distance to honey-bee hives.
2. Wild bees produce fewer nests in sites with honey-bees hives and with decreasing distance to honey-bee hives.
3. The proximity and the quality of nesting resources affect the number of wild bee nests.

Methods

Study area and study design

Our study was conducted in the nature reserve Lüneburg Heath (53°N, 9°E) in northern Germany (Lower Saxony) (Fig. 1a). The Lüneburg Heath is a man-made habitat which covers around 9,500 ha with most of this area being coniferous forest as well as smaller oak and beech forests followed by heath areas covered by the common heather, *Calluna vulgaris* (L.). Bee keepers bring their hives in late July when heather plants start flowering and remove them after flowering ceased. Bee keeping has a long tradition in the Lüneburg Heath explaining the high number of honey-bee hives in the nature reserve. Before and after heather flowering only a few hives are present in the nature reserve.

We used two designs to study the flower visitation and reproduction of wild bees in relation to honey bee abundance: (1) The ground-nesting study (Fig. 1b) and (2) the stem-nesting study (Fig. 1c). To study competition with ground-nesting bees we selected ten heath sites (hereafter ground nest sites) in different distances to the nearest honey-bee hives with 110, 115, 190, 258, 260, 275, 281, 800, 800 and 1,229 m. All ground nest sites were at least 700 m apart of each other (Fig. 1a).

To study effects of honey bees on stem-nesting bees we selected nine heath sites (hereafter stem nest sites) of which five contained honey-bee hives whilst four were at least 500 m from the nearest hive (Fig. 1a). All stem nest sites

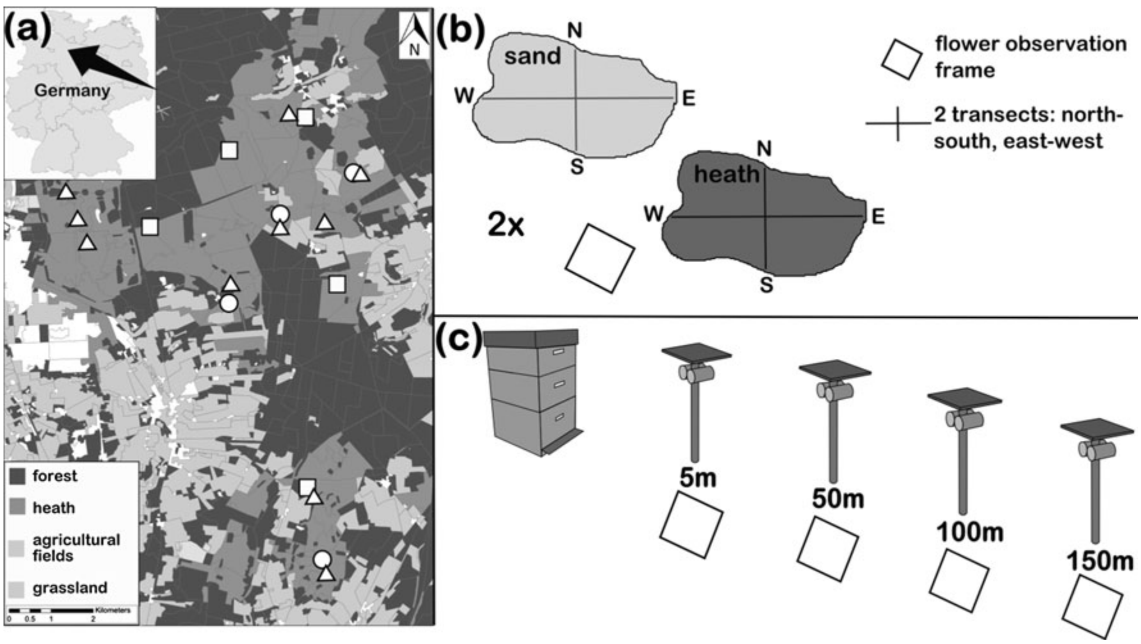

Fig. 1 **a** Map showing the different habitat types and the distribution of study sites in the study area of the Lüneburg Heath with *circles* showing stem nest sites without honey-bee hives, *squares* indicating stem nest sites containing honey-bee hives and *triangles* representing ground nest sites. **b** Study design for the ground nest sites with each site comprising two flower-visitor observations in 80 × 80 cm frames and two sand plots and two heather plots which were walked weekly along transects from north to south and from east to west during heath flowering while ground nests were counted. **c** Study design in stem nest sites with two trap nests attached to a wooden post and placed in different distance plots. Here, additional flower-visitor observations were carried out. These plots were either in different distances to honey-bee hives or from a random point

were at least 2 km apart. Stem nest sites with hives and without hives were distributed homogenously across the nature reserve. In each stem nest site, we established four distance plots. In the five stem nest sites containing honey-bee hives, plots were located at 5, 50, 100 and 150 m from the hive (Fig. 1c). In the four stem nest sites without honey-bee hives, the plots were chosen at the same distances but from a randomly selected point in the site.

Flower-visitor observations

In each ground nest site we observed the flower visitors in two plots (Fig. 1b) during heather blooming at 15th, 17th, 18th, 23th, 29th August 2012. These plots were all dominated by *C. vulgaris*. Flower-visitor observations were conducted inside a frame of 80 × 80 cm. The observation time was 10 min per day and plot, resulting in a total of 50 min per plot for all ground nest sites.

In each distance plot of all stem nest sites we observed flower visitors on *C. vulgaris* (Fig. 1c) at 17th, 23th, 24th, 26th August 2011 and 17th, 18th, 27th August 2012. Flower visitors inside a frame of 80 × 80 cm were observed for 5 min per day and plot, resulting in a total of 35 min per plot in all stem nest sites.

During observations we counted the number of flower-visiting bee species and the number of visits for each species. Additionally, we noted interactions between wild bees and honey bees during flower visitation that resulted in the displacement of a bee by another from the flower. Insects that could not be identified in the field were sampled using an insect net (Bioform online shop, item number A72a) and later identified in the laboratory. Flower-visitor observations were carried out in sunny weather with temperatures above 17 °C and wind velocity of less than 2.5 m s^{-1}.

Because of the importance of abundant flower resources for bees, the flower cover inside the observation frame of 80 × 80 cm and in the heath patch of each stem nest or ground nest site was estimated. The flower cover was measured as the percentage of flowers in relation to the observation frame or heath patch size.

Reproduction

Ground nests

In 2012 we counted the number of wild bee ground nests in four plots of each ground nest site (Fig. 1b). Two of these plots were always dominated by sandy and bare ground (hereafter "sand plots") while the other two plots also contained sandy, bare ground and were additionally dominated by *C. vulgaris* plants (hereafter "heather plots").

Each of the four plots contained two transects (5–20 m): one from north to south and one from east to west. Transects of heather plots had a length of 5 m. In nine of the ten sites the transect length in sand plots was as long as the patch of bare, sand ground. In the remaining site we selected a transect length of 5 m because the patch of bare, sand ground was approximately 20 times larger than in the other sites.

Each transect was walked weekly during the peak time of heather flowering in 2012 from 15th August to 5th September and once when heather flowering was ceasing on 21th September. During transect walks the number of ground nests of bees was counted up to 1 m to the right and left of the transects. On 3 days (every second week) we additionally measured soil humidity and ground temperature in 8 cm depth. In sand plots and in heather plots soil humidity and ground temperature were measured in three randomly selected places. Additionally, we estimated the percentage of vegetation cover in sand and heather plots, the flower cover as described above and counted the number of stones that were larger than 3 cm. Furthermore the slope of the ground was measured and the exposure to an ordinal direction was noted.

Stem nests

We exposed two trap nests for stem-nesting bees at each of the four distance plots in all nine stem nest sites on 19th April 2011 and collected them on 25th October 2011 (Fig. 1c). A single trap nest consisted of a plastic tube with a diameter of 20 cm that was filled with approximately 160–200 reed stems of differing diameters (2–10 mm). On each of the four plots per site we attached two trap nests to one wooden post. Traps were covered by a roof to protect them against rain.

Traps nests were inspected every four to 6 weeks for reed stems containing completed stem nests. Reed stems with completed stem nests were removed and replaced by empty stems. In the lab, stem nests were opened and the number of brood cells of bees was counted. After trap nest collection in October, all reed stems were opened and inspected for bee stem nests. Nests were placed in test tubes closed with cotton wool and stored in climate chambers over winter with a temperature of 4 °C to simulate winter conditions. In February, stem nests in test tubes were placed in the laboratory at approximately 20 °C to initiate hatching. Subsequently the hatched adult bees were identified. For our analyses we included only those bee stem nests that were constructed in the time when honey-bee hives were present in the field from the beginning of August to the beginning of October.

Habitat and landscape variables

We calculated the percentage of different habitat types in a 500 and a 1,000 m radius around the stem nest plots and around the ground nest sites. The underlying map had a scale of 1:50,000 (provided by the State Office for Geoinformation and Land Development in Lower Saxony, Germany) and calculations were conducted using ArcMap 10 (ESRI 2011). The habitat types were heath, forest, grassland and agricultural fields. Furthermore, the distance from the stem nest plots to the closest woody habitat (group of trees with more than five individuals, forest edges or hedgerows) was measured and the tree cover per stem nest site was estimated as the amount of trees and bushes in relation to the site size because of the importance of woody habitat as nest building site for stem-nesting wild bees.

Statistical analyses

Data analyses were conducted using R 2.15.2 for Windows (R Development Core Team 2012). We analyzed the following response variables with generalized linear mixed models: (1) the number of wild bee flower visits per observation interval and plot in ground nest sites, (2) the number of wild bee flower visits per observation interval and stem nest plot, (3) the number of ground nests of wild bees per plot in ground nest sites, (4) the number of bee species of the two trap nests of each stem nest plot and (5) the number of bee stem nests of the two trap nests of each stem nest plot (glmer function in package "lme4" (Bates and Maechler 2010)). The response variables (1) number of wild bee flower visits in ground nest sites and (2) in stem nest sites were transformed to presence/absence data per plot and per observation (to avoid zero inflated count data) and analyzed using models with a binomial error distribution and the site as a random effect. The response variables (3) the number of ground nests, (4) number of stem-nesting bee species per trap nest pair and (5) the number of stem nests per trap nest pair were analyzed with generalized linear mixed models with a Poisson error distribution and site as a random effect. Explanatory variables containing percentage data were arcsine square root transformed.

The inclusion and order of explanatory variables were selected by using the Akaike information criterion (AIC). We compared models with one explanatory variable step by step, first with the null model, then with the model having the lowest AIC. The model with the lowest AIC was chosen as final model. Variables that were not included in the model because of a higher AIC are assumed not to be explanatory of the response variable. When explanatory variables were correlated (Table S.1 and S.2) separate models were established for these variables to avoid collinearity.

For the number of wild bee flower visits in stem nest sites and ground nest sites we compared as possible explanatory variables: number of flower visits by honey bees, number of honey-bee hives, presence or absence of honey-bee hives (only for data from stem nest sites), distance to honey-bee hives, flower cover inside the frame of 80 × 80 cm, flower cover of the site and vegetation density of the site. The same was calculated for the supplementary response variables number of flower visits conducted by oligoplastic wild bee species in (S1) ground nest sites and (S2) stem nest sites (Table S.3).

We tested the following explanatory variables for the number of ground nests: flower cover per plot, soil humidity, ground temperature, vegetation density, number of stones larger than 3 cm, exposition and slope of the ground, distance to agricultural field and the percentage of forest, heath, grassland, agricultural field and conservation area in 500 and in 1,000 m radius. Models were corrected because of overdispersion by adding an observational random effect to the model.

For the response variables, number of stem-nesting bee species and number of stem nests, we compared the following explanatory variables by AIC: flower cover per plot, tree cover per site, distance to woody habitat, distance to agricultural field and the percentage of forest, heath, grassland, agricultural field and conservation area in 500 and in 1,000 m radius. We also compared these explanatory variables for the most abundant stem-nesting wild bee species (Table S.3). Due to overdispersion we added an observational random effect to the models. Additionally, we calculated the Shannon Diversity Index and the Jackknife Estimator for Species Richness for the number of stem-nesting bee species for stem nest sites with honey-bee hives and without hives using the package "vegan" for R (Oksanen et al. 2007). Furthermore we conducted Mantel tests using the "ade4" package (Dray and Dufour 2007) to consider for spatial autocorrelation between ground-nest sites and stem-nest sites for each response variable. The Mantel tests did not give evidence for spatial autocorrelation.

Results

Flower-visitor observations

We observed 2,762 flower visits by honey bees and 40 flower visits by wild bees on heather flowers in ground nest sites. Our observations included only four wild bee species of which two are oligoplastic on common heather: the sand bee *Andrena fuscipes* Kirby and the plasterer bee *Colletes succinctus* L.. Additionally we observed *Epeolus cruciger* Panzer which is the cuckoo bee of *C. succinctus* and the cuckoo bee *Sphecodes reticulatus* Thomson.

With increasing flower cover inside the observation frame we observed higher numbers of wild bee flower visits in ground nest sites (Fig. 2a, Table 1). The number of wild bee flower-visits in ground nest sites was not affected by the distance to the nearest honey-bee hive. We found the same results for the number of flower visits only conducted by oligoplastic wild bees (Table S.3). Additionally, the number of wild bee flower visits did not decrease with increasing numbers of honey bee flower visits. We did not observe less honey bee flower visits with increasing distance to the nearest hive. Also the blossom cover did not explain the number of honey bee flower visits.

We observed a total of 2,125 flower visits on *C. vulgaris* by honey bees and 53 by wild bees in the stem nest sites. Heather flowers in these sites were visited by three ground-nesting bee species, the two oligoplastic bees, *A.fuscipes* and *C. succinctus* and *Andrena flavipes* Panzer.

The number of flower visits by honey bees in stem nest sites did not significantly increase or decrease with increasing distance to the hive. However, in sites without honey-bee hives we observed significantly fewer flower visits of honey bees (6 visits per plot and day SE 1) on *C. vulgaris* flowers ($t_{1,250} = -2.53$, $P = 0.01$) than on sites containing hives (10 visits per plot and day SE 1). With increasing flower cover inside the observation frame of 80 × 80 cm we observed higher numbers of honey bee visits ($t_{1,250} = 5.34$, $P < 0.001$).

We found fewer flower visits of wild bees in sites containing honey-bee hives (Fig. 2b, Table 1). The same is true for the number of flower visits only conducted by oligoplastic wild bees (Table S.1). The number of all wild bee flower visits in stem nest sites did not decrease with increasing flower visits of honey bees and in sites containing honey-bee hives the distance to the hives had no effect on the number of flower visits by wild bees.

During all flower-visitor observations we did not observe any interactions between honey bees and wild bees forcing wild bees to leave the flower.

Reproduction

Ground nests

We counted a total number of 398 wild bee ground nests during all 400 transect walks. The first model showed that in sites having high soil humidity we found significantly lower numbers of wild bee ground nests (Fig. 3a, Table 1) while a high flower cover led to increased numbers of wild bee ground nests (Table 1). We found higher numbers of wild bee nests when grounds had a high slope (Table 1). Additionally, with higher ground temperatures the number of wild bee ground nests increased (Fig. 3b, Table 1). The number of wild bee ground nests was neither affected by

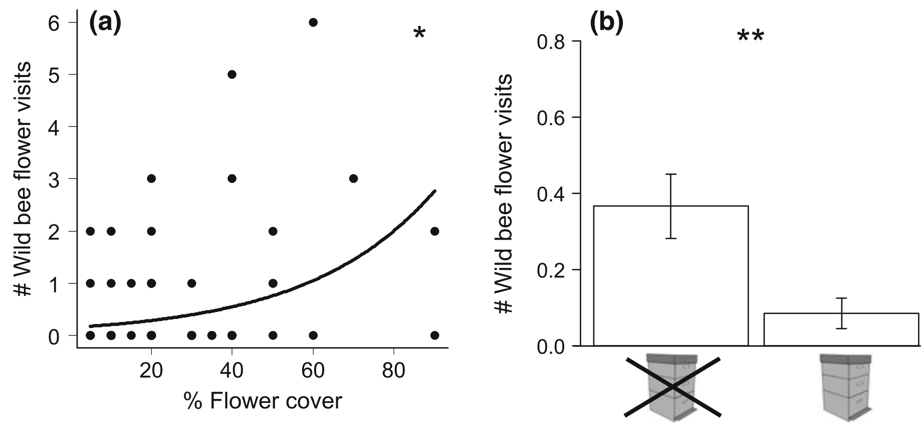

Fig. 2 **a** Total number of wild bee flower visits in ground nest sites with the flower cover per plot in percent and the prediction line of a Poisson GLM and **b** mean number with SE of wild bee flower visits of stem nest sites with honey-bee hives present or absent

Table 1 Effects of certain explanatory variables on each of the five tested response variables

Response variable	Explanatory variable		Estimate	Std. error	z value	*P* value
(1) # Wild bee flower visits (ground nest sites)	Flower cover		3.479	1.433	2.427	0.016
(2) # Wild bee flower visits (stem nest sites)	Honey bees absence		2.11	0.833	2.541	0.008
(3) # Wild bee ground nests	Model 1	Soil humidity	−0.994	0.183	−5.488	<0.001
		Flower cover	0.116	0.061	1.922	0.049
	Model 2	Slope	0.034	0.003	10.106	<0.001
	Model 3	Ground temperature	0.357	0.136	2.616	0.008
(4) # Stem-nesting bee species	Distance to woody habitat		−0.195	0.066	−2.936	0.003
	Honey bee hive presence		−1.188	0.471	−2.521	0.011
(5) # Wild bee stem nests	Distance to woody habitat		−0.298	0.088	−3.386	<0.001

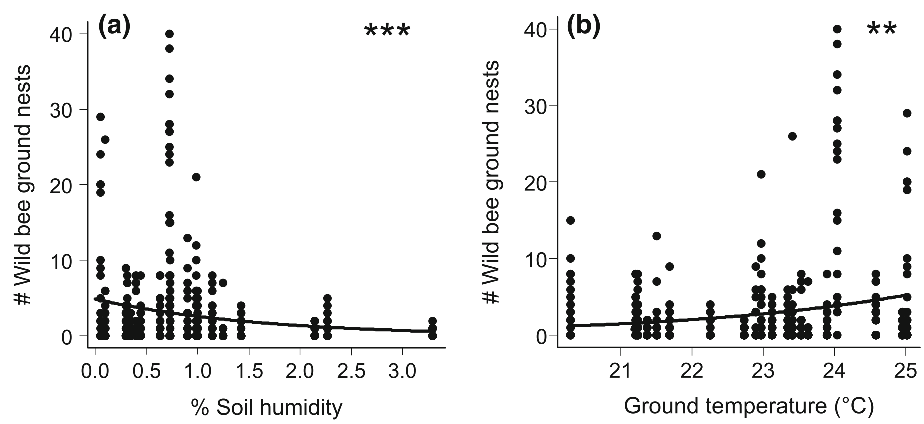

Fig. 3 The number of wild bee ground nests with **a** the soil humidity in 8 cm depth and **b** with the ground temperature in centigrade in 8 cm depth, both containing the prediction line of a Poisson GLM

the distance to the next honey-bee hive nor by the extent of certain habitat types in a 500 or 1,000 m radius.

Stem nests

We found a total of 110 bee nests containing 413 brood cells that were constructed during the time of heather flowering and when honey-bee hives were placed in the Lüneburg Heath. These nests were constructed by eight different bee species (Table S.4). The highest number of nests was found by *Heriades truncorum* (73 %), a stem-nesting wild bee that is specialized on flowers of plants belonging to the family *Asteraceae*. The number of stem-nesting bee species was correlated with their number of nests ($t_{1,34} = 3.07$, $P = 0.004$) and the number of bee brood cells ($t_{1,34} = 6.44$, $P = 0.002$).

We found fewer number of wild bee species in sites containing honey-bee hives (Fig. 4a, Table 1). However, the Shannon Index per trap nest pair and plot did not differ between sites containing honey-bee hives and sites without hives. None of the eight bee species found in our trap nests built their nests only in sites without hives. The number of

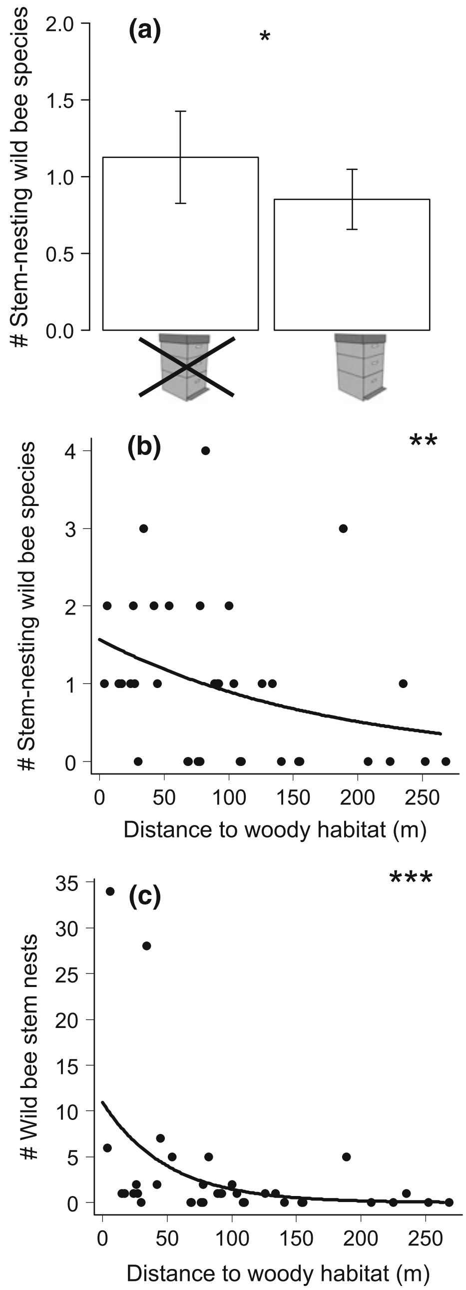

Fig. 4 The number of stem-nesting wild bee species per trap nest pair in **a** sites with honey-bee hives and without hives and **b** with the distance to woody habitat in meters and the prediction line of a Poisson GLM. **c** The number of wild bee stem nests per trap nest pair with the distance to woody habitat in meters and the prediction line of a Poisson GLM

stem-nesting bee species estimated with the Jackknife Estimator for Species Richness was 10.8 species in sites containing honey-bee hives and 5.9 species in sites without hives. This means that we found 64.8 % of the estimated stem-nesting bee species in sites with honey-bee hives and 84.8 % in sites without honey-bee hives. Additionally, the number of stem-nesting bee species increased with increasing proximity to woody habitat (Fig. 4b, Table 1).

The number of wild bee stem nest was best explained by a model including the distance to woody habitat. We found higher numbers of wild bee stem nests with decreasing distance to woody habitat (Fig. 4c, Table 1). We did not observe significantly different numbers of wild bee stem nests in sites containing honey-bee hives compared to sites without hives.

The number of stem nests built by *H. truncorum* increased with decreasing distance to woody habitat and with increasing percentages of heathland in a 500 m radius (Table S.3). Contrary, the number of *H. truncorum* nests decreased with increasing percentages of forest in a 500 m radius (Table S.3).

Discussion

Flower visitation

Our study shows that wild bees visit fewer numbers of *C. vulgaris* flowers in sites with honey-bee hives compared to sites without honey-bee hives. This may be caused by honey bees marking the flowers with a repellent scent (Giurfa and Núñez 1992). This acts as a sign for other honey bees, indicating that a flower was already visited and pollen and nectar were depleted (Giurfa and Núñez 1992). It was shown for some bumble bee species that they can detect the repellent scent left by heterospecifics and by honey bees, and reject flowers that were recently visited (Stout et al. 1998; Stout and Goulson 2001). However, it is not known if the observed wild bees can detect this repellent scent. Furthermore a high density of honey bees may deter wild bees and prevent them from visiting flowers. Yokoi and Fujisaki (2011) showed for two solitary wild bee species that they avoided to visit flowers on which dead honey bees were previously exposed as artificial visitors.

We did not observe less honey bee flower visits with increasing distances to the next hive. Beekmann and Ratnieks (2000) showed that honey bees forage in a mean distance of 5.5 km from the hive in heathlands. Nevertheless, and in contrast to our study, Evertz (1995) found increasing numbers of individuals of *C. succinctus* with an increasing distance to honey-bee hives of up to 1,230 m in a heathland in western Germany.

We did not observe stem-nesting wild bees visiting *C. vulgaris* flowers. This indicates that the stem-nesting wild bees in the Lüneburg Heath either are not notably foraging on *C. vulgaris* flowers because they are not attractive or that they use different plant species to avoid competition with honey bees. Generalist bee species are theoretically more able to avoid competition with honey bees than specialized bee species since they are able to shift to forage on different plant species (Walther-Hellwig et al. 2006). Most flower visits in our study were conducted by two ground-nesting wild bee species that are oligoplastic on common heather: *A. fuscipes* and *C. succinctus*. These wild bees visited fewer flowers in sites with honey-bee hives in direct proximity. Their narrow diet prevents them from switching to a different food plant. However, with the current honey bee density in the Lüneburg Heath they might be able to switch niches spatially by avoiding the direct proximity to honey-bee hives as they did in our stem nest sites.

Reproductive success

Our study shows that the number of ground nests of wild bees was not affected by honey bee abundance or distance to the next hive. The ground-nesting wild bees of the Lüneburg Heath were rather affected by the presence of dry and warm soils with higher slopes and high flower covers. Our results are supported by Potts and Wilmer (1997) showing preferences of ground-nesting bees for warm soils with higher slopes. This indicates that they are limited by the presence of adequate soils together with abundant flower resources. In summary, our results support the findings of Potts et al. (2005) that the existence of bare ground as nest site is the dominant factor shaping bee communities. This effect might be even stronger when food resources are abundant and do not limits the fitness or survival of bees like it seems to be in the Lüneburg Heath.

Our study lacks to take into account possible effects of honey bee abundance or presence on the species richness of bees in the ground nests. We assume that the counted wild bee ground nests were constructed by the two oligoplastic wild bee species *A. fuscipes* and *C. succinctus* because we frequently observed them entering the nests. As we did not identify the species for each ground nest, we cannot conclude if the reproduction of one specific species was negatively affected by the presence of honey bees.

We show that the number of stem-nesting bee species was affected by honey-bee hive presence without influencing Shannon diversity. Additionally, the Jackknife Estimator for Species Richness predicts that our sites with honey-bee hives are more species rich regarding stem-nesting wild bees than our sites without hives. All observed stem-nesting bee species built their stem nests either only in sites containing hives or in both, sites with and without hives. In sites containing honey-bee hives we found on average 0.28 bee species less per trap nest pair than in sites without honey-bee hives. The number of stem-nesting bee species but also the number of stem nests were additionally affected by the proximity to woody habitat. This is reasonable because stem-nesting wild bees use stems, dead wood and other plant and woody material for nest construction.

During heather flowering large monocultures of common heather flowers dominate the landscape. Between the *C. vulgaris* plants only a few different plant species flower in low numbers. Two of our stem-nesting wild bee species are specialized on different plant species than *C. vulgaris* and hence may not be affected from competition for floral resources with honey bees. One of these was *H. truncorum,* the species that built the highest number of nests and brood cells. However, we did not conduct flower observations on these scarce plant species why we do know if these plants were visited and exploited by honey bees.

In general, we found a low number of wild bee species that were active during heather bloom. It might be that the wild bee community was more species rich in former times when honey bees were less abundant and that wild bee species were already outcompeted.

We did not find an effect of higher percentages of particular habitat types on the overall reproductive success of ground-nesting or stem-nesting wild bees in the Lüneburg Heath, but for the single species *H. truncorum*. One reason may be that all sites were more or less homogenous regarding the landscape composition. Heath was the dominant habitat type followed by forest, arable land and grassland. Additionally, all sites were located in the nature reserve meaning a generally low human impact except for the increased honey bee stocking rates.

Conclusions

Overall, we conclude that current honey bee management in the Lüneburg Heath can affect the conservation of species richness but not reproductive success of stem-nesting wild bees. Even though we did not find an effect of honey bees on the overall reproductive success of ground-nesting bees, we cannot conclude that there is no effect because there may be species-specific effects. Hence, future research needs to account for (1) the species-specific reproductive success of ground-nesting bees and especially of the two oligoletic species and (2) different honey bee stocking rates before recommendations on honey bee management can be given. Additionally, future experiments should incorporate control sites that are more distant to the next hive than 500 m to investigate if our observed effects persist or strengthen. Honey bees have large foraging ranges of up to several kilometers (Beekman and Ratnieks 2000) and even on our control sites we observed many honey bees visiting the flowers. Until this information is available, conservation efforts should prioritize the enhancement of nesting resources and should not increase the stocking rates of honey bees in nature reserves.

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