Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees

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Summary

1. Pollination is a vital ecosystem service, which is endangered by the ongoing declines of pollinators. These declines also affect bumblebees (Bombus spp.), which are important generalist pollinators in agricultural landscapes. Most studies focusing on the conservation of bumblebees have investigated the effects of local flower-rich habitats on bumblebee density and diversity. However, bumblebee densities do not necessarily correlate with the colonies' reproductive success (i.e. the presence or absence of males and/or queens).

2. We analysed the effects of landscape-wide availability of mass flowering oilseed rape Brassica napus on the growth and sexual reproduction of Bombus terrestris colonies. Thirty-two young colonies were established and monitored in different resource environments represented by 16 landscapes (circular study areas with 3000 m radius) with large or small amounts of oilseed rape. As an indicator of colony growth, we used weight gain, which was strongly correlated with the numbers of brood cells in the colonies.

3. The colonies gained significantly more weight in study areas with large amounts of oilseed rape particularly during early colony stages.

4. Despite early weight gain, the colonies in study areas with large amounts of oilseed rape did not reproduce more successfully. The frequencies of colonies that produced males and/or queens did not differ between the two resource environments.

5. Synthesis and applications. Early mass flowering oilseed rape has a beneficial effect on colony growth, which however, does not translate into a greater likelihood of colonies producing sexual offspring. This may be due to food plant scarcity later in the colony cycle. Conservation measures should enhance food plant availability in agricultural landscapes, particularly during the most critical phases of the colony cycle: the colony establishment in spring and the reproductive phase in mid- to late summer.

Key-words: agroecosystems, Bombus terrestris, bumblebee conservation, ecosystem services, forage plants, landscape-scale study, mass flowering crops, pollination, reproductive success

Introduction

Pollination is an important ecosystem service (Daily 1997), which is vital for the conservation of biodiversity, as pollinators ensure the reproduction of many wild plants (Allen-Wardell et al. 1998) and the production of entomophilous crops (Free 1993; Delaplane & Mayer 2000; Klein et al. 2007). The ongoing declines of pollinators is therefore a serious cause for concern (Biesmeijer et al. 2006).

Bumblebees (Bombus spp. Latr., Hymenoptera: Apidae) are important generalist pollinators for a wide range of wild plant species and crops in agricultural landscapes (Corbet, Williams & Osborne 1991; Free 1993; Williams 1996). They have longer colony cycles than solitary wild bees and the numerous workers can therefore provide pollination services throughout the entire growing season (Alford 1975; von Hagen 1994). Moreover, bumblebees can fly at lower temperatures and in more adverse weather conditions than solitary bees and honeybees (Heinrich 1979). Owing to habitat destruction and agricultural intensification, the diversity and abundance of bumblebees have declined considerably in North America and Europe over the last decades (Williams 1982, 1995; Cane & Tepedino 2001). These declines might have adverse effects for the pollination of wild plant populations and crops.
The urgency of conservation measures that effectively counteract the ongoing pollinator declines and help to sustain a vital pollination service in agro-ecosystems has been emphasized over the last years (Daily 1997; Kremen, Williams & Thorp 2002; Committee on the Status of Pollinators in North America 2007). Several studies have been conducted to identify the beneficial effects of flower-rich semi-natural habitats on bumblebee density and diversity (e.g. Russell & Corbet 1991; Banaszak 1992; Corbet 1995; Dramstad & Fry 1995; Ockinger & Smith 2007). Likewise, local-scale studies have been conducted to evaluate conservation schemes that helped to restore attractive foraging habitats for different bumblebee species (e.g. Pywell et al. 2005; Carvell et al. 2007).

Most studies on bumblebee conservation have focussed on the local attractiveness of additional foraging habitats in agricultural landscapes (but see Heard et al. 2007; Morandin et al. 2007). However, for the development of sustainable conservation schemes, the species-specific ecology of bumblebees (Sowig 1989; Walther-Hellwig & Frankl 2000; Westphal, Steffan-Dewenter & Tscharntke 2006a) and the spatial and temporal heterogeneity of nectar and pollen resources (Ranta & Vepsäläinen 1981) need to be considered. As bumblebees have large foraging ranges, they are able to exploit resources at a landscape scale (Chapman, Wang & Bourke 2003; Westphal et al. 2006a).

Most importantly, the holistic evaluation of conservation measures needs to be based on long-term fitness parameters, such as sexual reproduction. Most studies dealing with bumblebee conservation hitherto quantified only bumblebee density and diversity (e.g. Banaszak 1992; Heard et al. 2007), rather than quantifying effects of conservation measures on reproductive success. Very few studies have focussed on colony performance in relation to resource availability within the close surroundings of bumblebee nests (Bowers 1985, 1986; Goulson et al. 2002). Two studies on isolated meadows found a positive effect of enhanced food plant availability on colony performance (Bowers 1985, 1986), whereas a single study that was conducted at farm level in open agricultural landscapes and in suburban habitats did not find any effects of resource availability on colony performance (Goulson et al. 2002). Goulson et al. (2002) conclude that colony growth might be determined by resource availability at larger spatial scales that correspond to the large foraging ranges of bumblebees which extend beyond the area of single farms.

In addition to flower-rich semi-natural habitats, mass flowering crops, such as oilseed rape Brassica napus or Placelia tanacetifolia, have a positive effect on bumblebee abundance (Westphal, Steffan-Dewenter & Tscharntke 2003, 2006a) and colony size (Westphal, Steffan-Dewenter & Tscharntke 2006b; Herrmann et al. 2007). In common with studies focussing on semi-natural habitats, these studies did not quantify the effect of the availability of mass flowering crops on reproductive success. Although larger colonies usually reproduce more successfully (Müller & Schmid-Hempel 1992; Schmid-Hempel & Schmid-Hempel 1998), enhanced colony growth due to the availability of mass flowering crops during a short period of the colony cycle does not necessarily translate into production of higher numbers of young queens (gynes). However, the production of queens is of particular importance for colony fitness, as they determine the population size after hibernation and successful colony foundation in the following spring (Alford 1975; von Hagen 1994).

To analyse the beneficial effects of oilseed rape availability on colony performance (growth and reproductive success), we conducted a landscape-scale experiment with Bombus terrestris, which is a common bumblebee species throughout European agricultural landscapes (Williams 1982; von Hagen 1994). Due to its large foraging range, B. terrestris is able to exploit rewarding resources within a distance of at least 3000 m around the nest (Chapman et al. 2003; Westphal et al. 2006a). We established B. terrestris colonies in the centre of circular study areas (3000 m radius) with large (mean ± SE: 10·32% ± 0·57%) and small (mean ± SE: 5·17% ± 0·42%) amounts of oilseed rape, and monitored the colony growth and production of sexuals. The following hypotheses were tested:

1. Bombus terrestris colonies develop better in landscapes with large amounts of oilseed rape.
2. Larger colonies reproduce more successfully.
3. The beneficial effects of oilseed rape on colony growth translate into greater reproductive success (i.e. the presence or absence of males and/or queens) of the colonies.

Materials and methods

STUDY SITES

The study was conducted in the vicinity of the city of Göttingen in southern Lower Saxony, Germany. The rural study region (latitude 51°40′21.34″ N to 51°24′41.93″ N and longitude 9°43′30.36″ E to 10°14′32.30″ E) included a variety of land use types, which are characteristic for central European agricultural landscapes. The most dominant land use types were intensively managed annual crops, forest, and grassland. These were intermingled with settlements and extensively used semi-natural habitats, such as set-aside fields, calcareous grasslands, orchard meadows, hedgerows, grassy banks, and ditches.

Within this region, we selected 16 study areas (landscapes) that differed in the amount of oilseed rape fields. The circular study areas had a radius of 3000 m, which approximately represents the maximum foraging distance of B. terrestris (Westphal et al. 2006a). The experimental colonies were located on an old set-aside field in the centre of each study area. The current land use was mapped in all study areas using land register maps with a scale of 1:5000, which were transferred into Geographical Information Systems (GIS; Topol GmbH, Göttingen, Germany and ARC/View 3.1, ESRI Geoinformatik GmbH, Hannover, Germany). Based upon this digital land use database, we calculated the percentage of oilseed rape fields within each study area. The study areas were then grouped into landscapes providing large (mean ± SE: 10·32% ± 0·57%, minimum: 8·75%, maximum: 13·24%, N = 8) and small amounts of oilseed rape (mean ± SE: 5·17% ± 0·42%, minimum: 3·13%, maximum: 6·48%, N = 8; r-test: P < 0·0001). There was no difference in the percentage of semi-natural
habitats between the landscapes with large and small amounts of oilseed rape (t-test: $P = 0.749$, d.f. = 14). Oilseed rape usually flowers from late April until the end of May in our study region.

**B. TERRESTRIS COLONIES**

We purchased 32 *B. terrestris* colonies from STB Control, Aarbergen, Germany, which were kept in cardboard nest boxes with a transparent ventilated plastic top. According to the supplier, the cultured *B. terrestris* strain originated from Germany. The even-aged young colonies consisted of the founding queen and approximately 15 workers. Two *B. terrestris* colonies were placed on the set-aside field in the centre of each study area on 2 and 3 May 2002.

*B. terrestris* usually nests below ground, yet the species is very adaptable in its choice of nesting sites (Fussell & Corbet 1992b; von Hagen 1994). To achieve a nest climate as close as possible to natural conditions, we placed the cardboard nest boxes in special wooden boxes with a double roof covering for heat insulation. In addition, the wooden boxes were placed on top of four house bricks to prevent the intrusion of surface water. Bumblebees could leave or enter the nest boxes via a valve, which could be opened or closed manually.

At the beginning of the experiment, the cardboard nest boxes including the brood, all workers and the founding queen were weighed before opening the entrance. Subsequently, the cardboard nest boxes were weighed in the field during the daytime. Hence, the weight of the colonies during the course of the experiment might be slightly underestimated, as foraging workers were absent from the nests at the time of weighing. The net weight gain of the colonies was measured as weight of the colony in the fifth, eighth and 10th week of the experiment minus the initial weight of the nest. We define the weight gained by the 10th week of the experiment as ‘maximum weight gain’, since by the end of the 10th week the majority of the colonies (more than 90%) had maximized their weight and started to collapse.

At the end of the experiment, the colonies were collected from the field and placed in a freezer at −25 °C to kill and preserve them for subsequent dissection. For all 32 colonies, the total numbers of brood cells were recorded (mean ± SE: 257.9 ± 22.3, minimum: 72, maximum: 525), which correlated significantly with the maximum weight gain of the colonies ($R = 0.849$, $P < 0.0001$), and also with the weight gain of the colonies by week 8 ($R = 0.826$, $P < 0.0001$) and week 5 of the experiment ($R = 0.586$, $P < 0.0001$). These highly significant correlations indicate that the measured weight gain reflects the amount of brood and workers in the nests rather than the amount of stored nectar and pollen or nest mass (wax). For this reason, we use the weight gain of the colonies as an indicator of colony growth over the course of the experiment.

Unfortunately, it was not possible to distinguish the brood cells of workers, males, and queens unambiguously. Hence, the absolute numbers of sexuals that were produced by the individual colonies could not be estimated. Instead, reproductive success (i.e. the presence or absence of males and/or queens) was recorded during the inspections of the colonies and classified in three categories: (i) colonies that did not produce any sexuals; (ii) colonies that produced only males; and (iii) colonies that produced both young queens and males. Throughout the entire experiment, we checked the colonies for invading cuckoo bumblebees (*Bombus* (*Psithyrus*) spp.) and wax moths *Aphthonia sociella*, which are natural enemies of bumblebees that could seriously damage their nests (Alford 1975; von Hagen 1994). However, we did not find any parasitic bumblebee species or wax moth larvae in the nests.

**STANDARD ANALYSIS**

All statistical analyses were carried out with $r$ version 2.4.1 for Windows ($r$ Development Core Team 2006). The effect of the availability of mass flowering oilseed rape on the weight gain of *B. terrestris* colonies was analysed with general linear mixed effect models (*lme*, nlme package, Pinheiro & Bates 2000). To account for the variation in colony growth and to avoid pseudo-replication, we calculated the mean weight gains of the two colonies per study area separately for each of the three measurements taken in the fifth, eighth, and 10th week of the experiment. The mean weight gain for each measurement was log-transformed to achieve residual normal distribution. The fixed factors in the model were the availability of oilseed rape (factor with two levels: large and small amounts of oilseed rape in the study areas), the week in which the repeated weight measurements were conducted, and their interaction (oilseed rape availability × week). We accounted for additional variance due to temporal differences in colony growth and between study areas by fitting random slopes (week as repeated factor to avoid temporal pseudo-replication) and random intercepts (study area as blocking factor) in the model (Pinheiro & Bates 2000; Crawley 2002). Non-significant interactions were back-excluded from the model (Crawley 2002). For the final model, we used the identity variance function to account for potential effects due to heteroscedasticity between the two levels of oilseed rape availability (Pinheiro & Bates 2000). Model selection was based on the Akaike Information Criterion (AIC) and the likelihood ratio statistic (Pinheiro & Bates 2000).

The effects of the maximum weight gain on the reproductive success of the colonies were tested with analysis of variance (ANOVA) and Tukey’s post hoc test was used to test for differences between groups (Zar 1984). We used Pearson’s chi-squared test to analyse whether the frequencies of colonies that did not reproduce, that produced only males, and that produced both young queens and males were the same in the two different resource environments – high and low availability of oilseed rape flowers (Crawley 2002).

**Results**

**COLONY DEVELOPMENT**

The colonies located in the study areas with large amounts of oilseed rape gained significantly more weight than the colonies that were placed in study areas with only small amounts of oilseed rape (Fig. 1a). The mean weight gain of the colonies increased over the course of the experiment, with maximum weight gain by the 10th week (regression line in Fig. 1b).

The colonies developed equally in both high and low resource environments, as indicated by the non-significant interaction (lme: $F_{1,30} = 0.002$ $P > 0.9$), which was excluded from the final model (Fig. 1). However, details of the progression of colony development become more apparent when the mean weight gains were analysed separately for the fifth, eighth and 10th week of the experiment and the two resource environments (Fig. 1b). Colonies in study areas with large amounts of oilseed rape initially gained more weight than colonies in study areas with small amounts of oilseed rape. After the flowering of oilseed rape ceased and all the colonies had to rely on food plants in semi-natural habitats, the mean weights of the colonies in both resource environments converged.
As the weight gain of the colonies was slightly more variable in the study areas with small amounts of oilseed rape, we checked for possible effects of heteroscedasticity in the model. However, the inclusion of the identity variance function did not significantly improve the model ($P = 0.09$). For reasons of parsimony, we did not use the variance function in the final model (Fig. 1).

**REPRODUCTIVE SUCCESS**

The reproductive success (i.e. the presence or absence of males and/or queens) of the *B. terrestris* colonies was significantly influenced by their weight gain. The heavier and larger the colony, the greater was its chance of reproductive success.

The colonies that did not reproduce (22%) were on average smaller than the colonies that produced only males (60%) or the colonies that produced both males and young queens (18%; Fig. 2).

Despite the significantly increased weight gain of the *B. terrestris* colonies in the study areas with large amounts of oilseed rape, there was no difference in the reproductive success of the colonies that developed in the two different resource environments. The percentages of colonies that did not reproduce, that produced only males, or that produced both young queens and males were similar for both levels of resource availability ($\chi^2 = 4.01$, d.f. = 2, $P = 0.135$).

**Discussion**

**BENEFICIAL EFFECTS OF MASS FLOWERING RESOURCES**

We have demonstrated that *B. terrestris* colonies benefit from the availability of mass flowering oilseed rape at a landscape-scale (i.e. within a radius of 3000 m around the colony). The availability of copious nectar and pollen resources in landscapes with large amounts of oilseed rape significantly increased mean weight gain of the colonies early in the colony cycle. This suggests that these colonies produced larger numbers of individuals (mean number of brood cells ± SE: 278 ± 34) than the lighter colonies in the study areas with only small amounts of oilseed rape (mean number of brood cells ±SE: 238 ± 36). Thus, earlier findings of high *B. terrestris* densities in landscapes with large amounts of oilseed rape (Westphal *et al.* 2003, 2006a) can be attributed to enhanced colony growth instead of higher numbers of established colonies in the landscape. Moreover, we can confirm the general pattern that bumblebee colonies grow until they begin production of young queens and males (Bloch 1999).
Our finding is further supported by a study using micro-satellites to determine the numbers and the sizes of Bombus pascuorum colonies in landscapes that represented a gradient of oilseed rape availability (Herrmann et al. 2007). B. pascuorum is another common bumblebee species in agricultural landscapes, although it differs in its spatial ecology and foraging strategy from B. terrestris. B. pascuorum has smaller foraging ranges (up to 1000 m) and exploits foraging habitats with more sparsely scattered food plants than B. terrestris (Sowig 1989; Walther-Hellwig & Frankl 2000; Westphal et al. 2006a). Nevertheless, the colonies of B. pascuorum also grew larger in landscapes that provided large amounts of mass flowering oilseed rape. Taken together, these studies confirm that bumblebee populations can substantially benefit from the availability of highly rewarding oilseed rape, irrespective of species-specific differences in spatial ecology and foraging behaviour.

**REPRODUCTIVE SUCCESS**

Bumblebees rely on an adequate and continuous supply of nectar and pollen from early spring to mid- or late summer for successful completion of the colony cycle and final production of sexuals (Alford 1975; von Hagen 1994). A continuous food supply cannot be provided by oilseed rape, since it flowers for a short period of time only (in our study region from the end of April until the end of May). During this period, bumblebee queens emerge from hibernation, found their colonies and rear the first generation of workers. Hence, the question arises whether the beneficial effects of oilseed rape on colony growth translates into greater reproductive success, and thereby increases the fitness of the colonies.

We found that the maximum weight gain of the B. terrestris colonies was positively related to their reproductive success (i.e. the presence or absence of males and/or queens). Only the heaviest and largest colonies produced both young queens and males, medium-weight colonies produced only males, and the smallest and lightest colonies did not reproduce. This finding is in agreement with other studies showing a positive relationship between colony size and reproductive success (Müller & Schmid-Hempel 1992; Schmid-Hempel & Schmid-Hempel 1998). Under natural conditions, the majority of bumblebee colonies produces males to ensure reproduction, and only a small number of colonies is able to produce both young queens and males (Pelletier & McNeil 2003; Ings, Ward & Chittika 2006). Pelletier & McNeil (2003) found that on average only 29% of the experimental colonies produced young queens under natural conditions, whereas on average, 83% of the colonies produced males. In the experiment conducted by Ings et al. (2006), 17% of the native colonies produced young queens and 100% of the native colonies produced males. Likewise, only 18% of our experimental colonies produced young queens (and males) while most of the colonies produced only males (60%).

Although it is known that early weight gain is an important factor determining the reproductive success of bumblebee colonies (Müller & Schmid-Hempel 1992; Imhoof & Schmid-Hempel 1999), we did not find higher frequencies of successfully reproducing colonies in the study areas with large amounts of oilseed rape. The frequency of colonies that did not reproduce, that produced only males, and that produced both young queens and males did not differ between the two resource environments. Bumblebees begin to produce sexuals only when the colonies have reached a critical size (Oster & Wilson 1978; Bloch 1999) and when sufficient resources are available to rear the larger larvae of males and, particularly, young queens (Bowers 1986; Beekman et al. 1998; Pelletier & McNeil 2003). Thus, the similar frequencies of successfully reproducing colonies in study areas with large and small amounts of oilseed rape can most probably be attributed to an insufficient supply of nectar and pollen at the point at which the colonies had reached their critical size for the production of young queens (i.e. after the flowering of oilseed rape ceased when the colonies had to rely on food plants in semi-natural habitats; Fig. 2).

In addition to resource availability, colony growth of bumblebees can also be affected by other factors: predation and endo-parasitism (von Hagen 1994; Durrer & Schmid-Hempel 1995), intrinsic factors of the colony, such as the queen’s fecundity and queen–worker conflicts (Bloch 1999; Mehdiahabi, Reeve & Mueller 2003), possible competition with honeybees (Steffan-Dewenter & Tscharntke 2000), and microclimatic conditions (Unwin & Corbet 1991). These factors are independent of oilseed rape availability and thus presumably affected the colonies in both landscape types in a similar way.

**IMPLICATIONS FOR BUMBLEBEE CONSERVATION**

Our study highlights that bumblebee colonies can substantially benefit from mass flowering oilseed rape. Yet, the beneficial effects of landscape-wide resource availability early in the colony cycle cannot directly translate into greater reproductive success (i.e. the presence or absence of males and/or queens) if nectar and pollen resources are limited later in the colony cycle. Our results confirm the importance of continuous resource availability at a landscape scale for the successful production of sexuals – particularly queens (see also Pelletier & McNeil 2003). The provision of nectar and pollen is often insufficient in central European agricultural landscapes (see also Goulson et al. 2002). In contrast to honeybees (Seeley 1997), bumblebee colonies do not store great amounts of pollen and nectar; therefore, they are directly affected by resource shortages and can cope with a shortage only for a short period of time (Heinrich 1979; von Hagen 1994). Although the colonies in the study areas with large amounts of oilseed rape initially had more workers to collect nectar and pollen, this enlarged workforce could not compensate for the shortage of food plants, which often occurs in modern agricultural landscapes during the summer (Steffan-Dewenter & Kuhn 2003). Except for flowering crops, extensively managed semi-natural habitats represent the major foraging sites for bumblebees in agricultural landscapes (Fussell & Corbet 1991; Banaszak 1992; Corbet 1995). Yet, flower-rich semi-natural habitats have
become increasingly scarce due to agricultural intensification and habitat destruction or conversion (Hoekstra et al. 2005; Foley et al. 2005). Moreover, the abundance and diversity of flowering plant species have been reduced by modern agricultural practices, such as fertilizer and pesticide applications (Robinson & Sutherland 2002, and references therein). Not even flower-rich conservation measures had positive effects on the colony growth or reproductive success of *B. terrestris* colonies in UK farmland (Goulson et al. 2002). If a common and highly adaptable species with large foraging ranges, such as *B. terrestris* (Williams 1982; von Hagen 1994), currently suffers from resource limitation in agricultural landscapes, the fitness of rarer and more specialized bumblebee species with smaller foraging ranges will be affected much more.

Conclusions

We conclude that future conservation schemes should massively enhance landscape-wide nectar and pollen resource availability in agricultural landscapes to promote not only the abundance but also the fitness of bumblebee populations. Conservation measures should generally aim to provide a continuous supply of nectar and pollen throughout the colony cycle. In particular, more resources are needed during the most critical phases of the colony cycle: establishment and production of sexuals (Alford 1975; Baer & Schmid-Hempel 2003). Effective conservation measures could not only be the extensive establishment of various mass flowering crops that ideally flower throughout the season (e.g. oilseed rape, *Phacelia tanacetifolia*, and *Trifolium pratense*), but also the creation of additional flower-rich semi-natural habitats (Banaszak 1992; Walther-Hellwig & Frankl 2000; Pywell et al. 2005). Furthermore, the floristic composition of existing semi-natural habitats should be improved, for instance, by sowing seed mixtures that include the preferred nectar and pollen plants of a wide variety of bumblebee species (Fussell & Corbet 1992a; Corbet 1995; Carvell et al. 2006). Owing to the large foraging ranges of bumblebees, these conservation measures can only be effective when they are implemented at a landscape scale (Chapman et al. 2003; Westphal et al. 2006a; Heard et al. 2007). Future studies on bumblebee conservation should focus on long-term fitness parameters, as the production of sexuals, particularly young queens, is crucial for the survival of bumblebee populations.

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References

densities of a social bee (Bombus pascuorum) in agricultural landscapes. Molecular Ecology, 16, 1167–1178.

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