Foraging trip duration of bumblebees in relation to landscape-wide resource availability

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Abstract. 1. The study tested the hypotheses that bumblebees have shorter foraging trips in environments that provide abundant resources than in environments that provide sparse resources, and that shorter foraging trips translate into greater colony growth.

2. Six even-aged Bombus terrestris colonies were established in contrasting resource environments. Three colonies had access to abundant resources (Phacelia tanacetifolia fields with high flower densities), and three colonies were placed in an environment with sparse resources (scattered semi-natural habitats with food plants at lower densities).

3. A total of 870 foraging trips of 220 marked B. terrestris foragers were observed using automated camcorder recordings.

4. The duration of foraging trips was shorter in environments with abundant resources (66 ± 4.6 min) than in environments with sparse resources (82 ± 3.7 min). Within 34 days colonies that had access to abundant resources gained significantly more weight (129 ± 40 g) than colonies foraging on sparse resources (19 ± 7 g).

5. Thus, the spatial distribution and quality of resources at landscape level affected the duration of foraging trips and the colony growth. It was concluded that future conservation schemes need to improve the spatial and temporal availability of resources in agricultural landscapes to counteract the ongoing decline of bumblebees.

Key words. Agroecosystems, Bombus terrestris, colony growth, conservation, landscape structure, large-scale resource availability, Phacelia tanacetifolia, pollination.

Introduction

Survival, growth, and reproduction of animals strongly depend on their ability to allocate food resources successfully. Optimal foraging theory predicts that foragers tend to maximise the long-term net rate of energetic gain [(gain – costs)/time; reviewed in Krebs & Davies, 1993; but see Schmid-Hempel, 1987]. Thus, foragers have to consider time and energy budgets while collecting food (e.g. Heinrich, 1975; Pyke, 1980).

For most animals food resources are patchily distributed in space and time (Hansson et al., 1995). To optimise the foraging success in a variable resource environment, animals should search and exploit systematically the most rewarding resources (Dreisig, 1995). Consequently, they should relate the choice of a foraging patch to the spatial distribution of resources (e.g. to minimise travel time), as well as to resource quality (e.g. flower density or nectar volume) (Pyke, 1980; Cresswell et al., 2000; Hill et al., 2001). The spatial and temporal distribution of resources is particularly important for central-place foragers, like bumblebees and other social insects, since numerous foragers of a colony concentrate in a restricted area around the nest (Hamilton & Watt, 1970; Dukas & Edelstein-Keshet, 1998).

Bumblebees (Bombus spp. Ltr., Hymenoptera, Apidae) are vital pollinators in European agroecosystems (Corbet et al., 1991; Williams, 1996), where they rely on semi-natural habitats as important food resources (Banaszak, 1992) and nesting sites (Fussell & Corbet, 1992; Kells & Goulson, 2003). Semi-natural habitats provide diverse, but often scattered food plants, which are continuously flowering throughout the colony cycle from early spring to late summer (von Hagen, 1994; Corbet, 1995; Meek et al., 2002). Bumblebees also benefit from highly rewarding mass-flowering crops, like Phacelia tanacetifolia Bentham (Hydrophyllaceae) (Williams & Christian, 1991), which achieve higher flower densities than the food plants in semi-natural habitats, but bloom only over short periods of time (Westphal et al., 2003). Intensification of farming practices altered agricultural landscapes considerably (Matson et al., 1997; Tilman et al., 2001). Diminishing amounts of
Decision support systems for agriculture in Europe, and the socio-economic implications of climate change in the Mediterranean region.

Introduction

The rapid increase in the use of agricultural biotechnology has led to a growing concern about the environmental and socio-economic impacts of genetically modified organisms (GMOs). This concern has been fueled by the perception that GM crops may pose risks to human health and the environment. The debate over GMOs has become a major issue in public policy, with concerns ranging from the safety of GM crops to the economic implications of their use.

In this paper, we present an overview of the current state of the debate over GMOs and the decision-making processes that are used to evaluate their potential impacts. We also discuss some of the key issues that need to be addressed in order to make more informed decisions about the appropriate use of GMOs in agriculture.

Materials and Methods

Study region and study sites

The study was conducted in the rural countryside surrounding the city of Göttingen in southern Lower Saxony, Germany. The study region was located 23 km east–west and 15 km north–south of Göttingen and consisted of agricultural land-use types (arable fields and grasslands), forests, settlements, and various semi-natural habitats (orchard meadows, set-aside fields, calcareous grasslands, woods, hedgerows, grassy banks, and ditches).

Within the study region six circular landscape sectors with 3000 m radius were selected as study sites. A set-aside field was located in the centre of each study site as the experimental area, in which the experiment was carried out. Three landscape sectors represented environments with abundant resources, where flowers were available in high densities in Phacelia fields, and three landscape sectors represented environments with sparse resources, where food plants were available in semi-natural habitats. The radius of 3000 m for the landscape sectors was chosen to cover the potential foraging range of B. terrestris (Walther-Hellwig & Frankl, 2000; Darvill et al., 2004; Knight et al., 2005).

The current land use in the landscape sectors was mapped in summer 2002 using land register maps with a scale of 1:5000. The land-use maps were transferred into Geographical Information Systems (GIS, Topol 4.506, Gesellschaft für digitale Erdbewachung und Geoinformation mbH, Göttingen, Germany and ARC/View 3.1, ESRI Geoinformatik GmbH, Hanover, Germany) for landscape analysis. The percentage of semi-natural habitats, and the distance between the central fallow (i.e. the nest location) and the nearest P. tanacetifolia field were calculated to characterise the different resource environments. The landscape sectors differed significantly in the amounts of semi-natural habitats, and in the availability of mass-flowering Phacelia fields (Table 1). In the environments with abundant resources, mass-flowering Phacelia fields were available in the close surroundings of the central fallow (less than 600 m), whereas Phacelia fields were located only at large distances from the fallow (> 2700 m) in the environments with sparse resources. During the experiment other mass-flowering crops were not in bloom in any of the six landscape sectors.

Experimental design

Six even-aged B. terrestris colonies (approximately 30 workers and the founding queen) were purchased from STB Control (Aarberg, Germany). The cultured strain of B. terrestris originated from Germany. The colonies were not infected with pathogens or parasites. On 3 August 2002 one colony was placed inside the nesting chamber of large wooden observation boxes on each central fallow. The observation boxes stood on top of house bricks to prevent the intrusion of surface water. As B. terrestris usually nests below ground (Fussell & Corbet, 1992), the wooden boxes were equipped with a double roof covering for heat insulation to achieve a nest climate as close as possible to the natural conditions.

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The bumblebees could leave or enter the nesting chamber via a valve, which could be opened or closed manually. The exit hole of the observation box was located at one side of a closed porch to prevent the direct incidence of light. The bumblebees reached the exit hole through a Plexiglas tube (250 mm long, 20 mm diameter), which connected the nesting chamber with the porch. The nesting chamber and the porch were separated by the observation chamber for the mobile camcorder unit (see below).

During the experiment (from 3 August to 5 September 2002) the colonies were weighed every 10 – 12 days to monitor the colony growth. The maximum weight gain of each colony was calculated as the difference between the maximum weight of the colonies and the colony weight at the beginning of the experiment. The colonies were removed from the field prior to recording the foraging workers of the respective environments per landscape sector were due to accidental malfunction of the recording technique. In total 105 h were recorded in environments with abundant resources, and 122 h were recorded in environments with sparse resources.

Only foraging trips lasting between 10 and 210 min were considered for the statistical analysis, as short trips could be performed for orientation or defecation (Capaldi et al., 2000; Spaethe & Weidenmüller, 2002). An upper limit for the duration of foraging trips (210 min) was used, to minimise possible artefacts in the data, which might be due to missing or blurred pictures of foragers, i.e. the calculated trip duration would double if the camcorder recording missed out a return and a consecutive departure of a forager. In the literature, variable values found [e.g. 150 min (Goulson et al., 2002b), 139 min (Spaethe & Weidenmüller, 2002), 416 min (Osborne et al., 1999)]. As the majority of the recorded foraging flights was shorter than 210 min (96%), a trip lasting 210 min therefore represents an appropriate upper limit for the resource environments.

Results

Duration and number of foraging trips

Throughout 30 observations, a total of 870 foraging trips of 220 bumblebees was recorded. Fifty-four per cent of the bumblebees were merely observed on a single day. Twenty-nine per
cent of the marked bees were recorded on two different days, and 13% on 3 days. Only 4% of the marked bees were observed on 4–5 days during the observational period. On average the foragers spent 71.74 ± 1.98 min on their daily trips \((n=385)\). Fifty per cent of the recorded bumblebees performed more than one trip per day (on average 1.86 ± 0.06 trips per day, maximum eight trips per day, \(n=385)\).

**Effects of the resource environment on the duration of foraging trips and colony growth**

The foraging trips of *B. terrestris* workers lasted longer in landscape sectors with considerable amounts of semi-natural habitats, which provided sparse food resources \((t\text{-test: } t_3=2.728, P=0.053; \text{Fig. 1})\). The short duration of the foraging trips in the landscape sectors with *Phacelia* fields in the surroundings of the nests indicate that the foragers exploited this highly rewarding resource. Furthermore, significant differences between the maximum weight gains of the colonies in the differentially rewarding resource environments were found: colonies in environments with sparse resources gained less weight than colonies in environments with abundant resources \((t\text{-test: } t_3=4.168, P=0.014; \text{Fig. 2})\). Owing to shorter foraging trips to nearby *Phacelia* fields, the nests in the highly rewarding landscape sectors apparently increased their foraging rate, i.e. they collected greater amounts of nectar and pollen per unit time compared with the nests in landscape sectors, where no *Phacelia* fields were available, or located at large distance from the colonies.

**Discussion**

As mass-flowering *Phacelia* fields represent more rewarding resources than semi-natural habitats (Williams & Christian, 1991; Banaszak, 1992; Corbet, 1995; Williams, 1997), it was hypothesised that the foraging trips of *B. terrestris* workers would be shorter in agricultural landscapes, where flowering *Phacelia* fields were available, than in agricultural landscapes with scattered and less rewarding semi-natural habitats. Owing to shorter search and travel times foragers should be able to gather the same amount of rewards (i.e. nectar and pollen) much faster in landscapes where they can exploit highly rewarding resources systematically (Heinrich, 1976; Dreisig, 1995). As expected, the duration of foraging trips was shorter in environments with abundant resources than in environments with sparse resources. The short duration of the foraging trips was due to the availability of nearby mass-flowering *Phacelia* fields, which apparently were systematically exploited by the foragers. It should be noted that this experiment represents a temporal snapshot of contrasting resource environments. Before and after the flowering of *Phacelia* the colonies in the respective landscape sectors can only forage on few semi-natural habitats. Hence, they might suffer even stronger resource scarcity than the colonies in landscape sectors with larger amounts of semi-natural habitats.

To the authors’ knowledge, this study provides the first empirical evidence that the distribution of resources at landscape level affects the time bumblebees spend on their foraging trips. Consistent with the results presented here, other studies in single resource environments indicated that foragers performed shorter foraging trips, or increased their foraging rates when resources were abundant (Allen et al., 1978; Thomson et al., 1987; Goulson et al., 2002b). Likewise, a theoretical model predicts that, if resources in nest vicinity were meagre, foragers should elongate the duration of their foraging trips to exploit more distant, and more rewarding foraging sites (Cresswell et al., 2000).

Once a bumblebee has discovered a rewarding foraging site, it will memorise the location, and exploit the site as long as it will be rewarding (site and flower constancy) (Heinrich, 1976; Chittka et al., 1999; Osborne & Williams, 2001). Thus, on future foraging trips it will have to spend less time searching for a rewarding site (Heinrich, 1975). As semi-natural habitats provide more scattered and less abundant food plants than...
mass-flowering *Phacelia* fields, foragers in *Phacelia* fields might have considerably reduced travel time between flowers (Waddington & Heinrich, 1981). In addition, nectar and pollen in the open, shallow *Phacelia* flowers are easily accessible for the short-tongued *B. terrestris* workers (Williams & Christian, 1991), so that handling times would have also been brief (Laverty & Plowright, 1988). In contrast, the exploitation of different and not always easily accessible flowers in semi-natural habitats might cause longer handling times. Provided that the *B. terrestris* foragers collected on average similar loads, the foragers in the environments with abundant resources could collect more rewards per unit time than the ones in the environments with sparse resources, which presumably had longer search and travel times (Pyke, 1980). The strong influence of *Phacelia* might be due partly to *B. terrestris'* preference for large foraging patches with rewarding, and easy to handle flowers (Sowig, 1989; Walther-Hellwig & Frankl, 2000).

Regarding the overall foraging success of a bumblebee (i.e. net rate of energetic gain), the bumblebee’s time and energy budget need to be considered (Pyke, 1980; Cresswell et al., 2000). The economic costs in terms of time that foragers spend flying between foraging sites and between flowers might constitute more than 80% of a foraging trip, whereas the energetic costs for long-distance flights are negligible: the nectar costs for a 24 min flight to a foraging site could be compensated by the exploitation of 24 additional flowers, which would only last 1 min (Heinrich, 1979). In contrast, a bumblebee, which is continuously foraging in the nest vicinity, would collect more than triple the amount of nectar during the same time than the ‘long-distance forager’ (provided that load size and floral rewards were similar). As the energetic costs of foraging are less constraining than the time an individual spends on foraging (Beutler, 1951; Heinrich, 1975), it can be assumed that the foragers exploiting the *Phacelia* fields had a substantially greater foraging success than the foragers, which had to rely on semi-natural habitats as food resources (Pyke, 1980).

The colonies in environments with abundant resources gained significantly more weight than the colonies in environments with sparse resources, indicating that the greater foraging success in landscape sectors with highly rewarding resources translated into improved colony growth, and therewith a better chance of successful reproduction (Bowers, 1985; Goulson et al., 2002a; Pelletier & McNeil, 2003). Thus, mass-flowering crops, such as *Phacelia*, can have a significant effect on the foraging success and colony growth of generalistic bumblebees. However, they merely represent additional resources, as they flower over short periods of time, do not offer suitable nesting sites (Fussell & Corbet, 1992; Kells & Goulson, 2003), and do not account for various food-plant preferences of more specialised bumblebee species (von Hagen, 1994; Walther-Hellwig & Frankl, 2000).

The individual foraging behaviour of bumblebees might be affected by the state and energy requirements of the colony (Cameron, 1989; Cartar & Dill, 1990; Cartar, 1992). Possible effects of the colony state on the duration of foraging trips were minimised by starting with equally sized and even-aged colonies in the present study. During the course of the experiment, the colonies developed differentially: the ones exploiting *Phacelia* fields produced larger amounts of brood than the ones in the less rewarding resource environments.

In conclusion, bumblebees apparently modify their foraging behaviour in relation to large-scale resource availability. If highly rewarding resources are available, *B. terrestris* foragers seem to exploit them (Dreisig, 1995). Although the less rewarding landscape sectors provided comparatively larger amounts of semi-natural habitats, which are considered as important foraging habitats (Banaszak, 1992; von Hagen, 1994; Corbet, 1995; Meek et al., 2002), *B. terrestris* benefited to a greater extent from the highly rewarding *Phacelia* fields. Owing to agricultural intensification, the diversity and abundance of food plants in semi-natural habitats has been substantially reduced (Fussell & Corbet, 1991; Goulson, 2003; Benton et al., 2003). Hence, the foragers found apparently only limited amounts of rewarding food plants in the landscape sectors with sparse resources. Consequently, their foraging success was adversely affected by longer search and travel times (Pyke, 1980; Cresswell et al., 2000).

Even in landscape sectors with comparatively large amounts of semi-natural habitats (i.e. in the sparse resource environments), the foraging success of *B. terrestris* was presumably limited by resource availability. Hence, the amount of semi-natural habitats and the floral resources within these habitats should be substantially enhanced in Central European agricultural landscapes (e.g. up to 25%; Banaszak, 1992). The presented results emphasise the need for future conservation schemes that consider the spatial and temporal availability, as well as the floristic composition of resource patches to sustain diverse and large bumblebee populations, and their vital pollination service in agroecosystems (Bronstein, 1995; Williams, 1996).

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References


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