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Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae)*

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Abstract – A major determinant of bumblebees pollination efficiency is the distance of pollen dispersal, which depends on the foraging distance of workers. We employ a transect setting, controlling for both forage and nest location, to assess the foraging distance of *Bombus terrestris* workers and the influence of environmental factors on foraging frequency over distance. The mean foraging distance of *B. terrestris* workers was $267.2 \text{ m} \pm 180.3 \text{ m}$ (max. 800 m). Nearly 40% of the workers foraged within 100 m around the nest. *B. terrestris* workers have thus rather moderate foraging ranges if rewarding forage is available within vicinity of the nests. We found the spatial distribution and the quality of forage plots to be the major determinants for the bees foraging decision-making, explaining over 80% of the foraging frequency. This low foraging range has implications for using *B. terrestris* colonies as pollinators in agriculture.

Bumblebee / foraging / pollination / decision-making

1. INTRODUCTION

Pollen dispersal through animal pollinators is essential for plant reproduction. The efficiency of pollinators depends on various factors including the number of individuals that carry pollen from one flower to another, the number of pollen grains actually transferred on the flower, and the distance over which pollen is transferred. The latter is of particular importance with respect to rare and widely dispersed plants (e.g. Kwak et al., 1998) but also for the pollination service in agriculture.

Bumblebees (*Bombus* spp.) are regarded as most efficient pollinators, not only for the pollination of wild flowers but also for pollination services, used in both outdoor and greenhouse horticulture and orchards (e.g. Morandin et al., 2001a, b; Dasgan et al., 2004; Velthuis and van Doorn, 2006). They have been shown to be able to out-compete honeybees (*Apis mellifera*) in individual workers pollination

efficiency (Gauld et al., 1990; Westerkamp, 1991; Wilson and Thomson, 1991; Goulson, 2003). This is partly due to the more robust handling of flowers by bumblebees and their ability of buzz-pollination (e.g. in tomatoes) (Kevan et al., 1993; Morandin et al., 2001a,b; Goulson, 2003) but also due to fundamental differences in foraging strategies. Foraging *Apis* workers take advantage of their very sophisticated communication system, which allows efficient recruitment of large numbers of foragers to highly rewarding sites to exploit these in short time. The communication in bumblebees, however, is much less advanced and only the type of resource but not its position is communicated (Dornhaus and Chittka, 1999, 2001, 2004). Therefore, *Bombus* workers primarily forage based on individual experience and colonies have more scattered forage grounds (Westerkamp, 1991; Kearns and Thomson, 2001; Goulson, 2003).

In commercial use, the foraging range determines the optimal density of bumblebee colonies for facilitating pollination services. The foraging distance of workers has, therefore, been the research focus of many

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studies. Walther-Hellwig and Frankl (2000a) estimated a maximum foraging distance for *Bombus terrestris* of up to 1750 m in a mark and recapture study along a transect. They found the majority of the workers (75%) foraging in distances of less than 1500 m from the nest, and 43% of the foragers were found within a radius of 500 m. Other studies, also relying on transects but assigning *B. terrestris* workers genetically to common colonies, obtained much smaller maximum foraging distances of 758 m (Knight et al., 2005) or even less than 625 m (Darvill et al., 2004). Estimates based on a range of assumed colony densities and genetic colony assignment (Chapman et al., 2003) resulted in a maximum foraging distances ranging from 870–3900 m for *B. terrestris* workers. Obviously estimates of foraging ranges have one aspect in common: they are highly variable. They range from a few hundred meters to several kilometres, which is not particularly satisfactory given the high significance of bumblebees as commercial and natural pollinators. It is unclear to what extent the high variance among previous studies reflects differences among the studied colonies or resulted from different experimental approaches. Also, variable climate and weather conditions among studies are bound to generate additional variance for foraging distance. Finally, plant density is one of the most important factors for foraging distances. If forage is sparse, bees must fly much farther for rewarding food plants than in a setting with high plant density (Heinrich, 1976).

Here we study foraging flight distances of *B. terrestris* workers by choosing an experimental design that provided, for the first time, full control of the external factors by controlling both colony positions as well as location and quality of the forage in a linear transect setting. In addition to the flight distance, the role of these controlled external factors on flight distance could be determined.

2. MATERIALS AND METHODS

2.1. *Bombus terrestris*

We used six commercially reared *B. terrestris* colonies, three colonies in each of two Styrofoam

outdoor boxes (80×30×22 cm) with about 100–130 workers per colony provided by the supplier (Katz Biotech AG). The workers were briefly treated with carbon dioxide gas to colour-mark them with paint pens (green, yellow, red, silver, white, blue, Edding XCXX®) according to their colony affiliation. The day after marking, all colonies were placed in the field in the shelter of a hedge along an agriculturally used field track (nest position: 51° 23.53' N, 11° 42.40' E; Fig. 1).

2.2. Transect

Bumblebee surveys were conducted at the end of the season from October 4 to October 14 2006, in the agricultural “desert” of the Querfurt plateau 30 km in the west of Halle/Saale, Germany. A 3100 m long straight field track, flanked by interspersed flower rich plots was used as a transect (Fig. 1). Satellite image analysis and explorations on foot ensured that the adjacent landscape (min 3 km from nest position) completely lacked any forage because the fields were ploughed and prepared for winter. The vegetation along both sides of the track consisted predominantly of Loesels rocket (*Sisymbrium loeselii*), several species of thistles (*Carduus crispus*, *Carduus nutans*, *Cirsium arvense*, *Cirsium acanthoides*, *Onopordum acanthicum*), corn poppy (*Papaver rhoeas*), mugwort (*Artemisia vulgaris*), dandelion (*Taraxacum officinalis*), yarrow (*Achillea millefolium*), camomile (*Anthemis arvensis*), and two species of bur (burdock (*Actium lappa*) and *Actium tomentosum*). The thistles were the only rewarding forage for the bumblebees during the experiments. Number of flowers and numbers of inflorescences within a 100 m interval along the track were used as determinants for patch quality.

2.3. Monitoring

Based on precursory observations the monitored transect length was restricted to 1600 m. This transect was in addition to the 100 m intervals divided into four monitoring sections. Daily flight entrance observations showed that foragers from all colonies left the nest exclusively in direction of the transect. Four observers monitored flight distances of marked foragers (three times a day, between 1000 and 1700 h) in a randomly assigned section by counting labelled foragers on flowers while slowly walking along the transect section (speed: 10 min per 100 m interval). Each section was covered twice

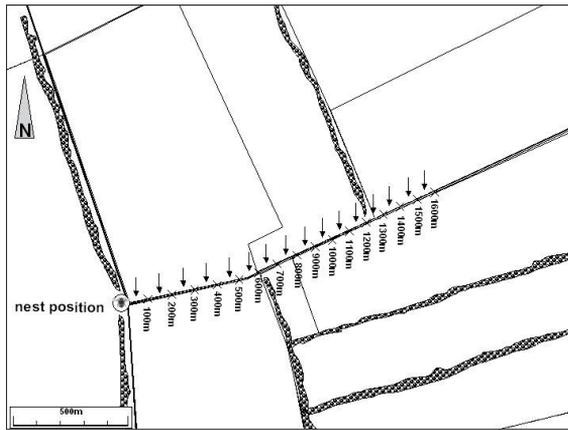


Figure 1. Study site in the Querfurt Plateau in Saxony-Anhalt Germany. Labelled *B. terrestris* workers from six commercial colonies were observed foraging on patches of thistle flowers along a 1.6 km transect with 100 m intervals (arrows). No food plants other than those along the transect were available within 3 km distance (white: harvested fields, dotted: woody boundary ridges).

per observation walk counting all individuals only once, which was possible due to low foraging frequencies (see results). Unmarked workers were neither recorded nor analysed because we had no information concerning the nest site of these workers. Monitoring was performed over a two-week period.

2.4. Data analysis

The forager counts per distance interval were pooled over all days and all colonies to obtain an overall distribution along the entire transect. The mean foraging distance was inferred from the mean distance between observation point and colony of all observed foragers. The mean maximum foraging distance was calculated as the mean of the maximum observed flight distance for a worker of each colony. The differences in the spatial distribution of workers of the different colonies were tested with a χ^2 -test. We adjusted for low observation numbers by pooling adjacent intervals resulting in four interval-groups of 200 m each (from 0–200 to 600–800).

Regression analyses of foraging frequency on food plant distance and quality were performed with Statistica 6.0. The deviation of the observed foragers distribution from the expected distribution was tested with χ^2 -test also using Statistica 6.0.

3. RESULTS

In spite of the late season, weather conditions were most favourable, allowing for

unconstrained foraging with bright skies and daytime ambient temperatures ranging from 11 °C to 23 °C. In total 126 marked foragers were observed in the 10 days observation period. Unmarked bumblebees (including *B. terrestris*, *B. pascuorum*) were observed in very low numbers only (< 3 per day), and there was no competition for resources during the experiment. Bumblebee workers were almost exclusively (98.4%, $n = 126$) observed exploiting the thistle flowers along the transect and only these data are included in the analyses. Pollen loads of returning foragers were consistently pale yellow corresponding to the colour of the pollen of the thistle flowers available (Kirk, 1994), further indicating that workers exclusively foraged along the transect.

Because the overall flight activity was low the analysis was not obscured by counting the same animals multiply. Over the entire period we observed a mean of 1.39 ± 0.07 (SE) marked foragers per transect section ($n = 92$ section surveys). Bees marked with the same colour from the same colony only occurred in 24 cases (26%) with a mean of 2.5 ± 0.13 (SE) animals. The maximum number was four same colour animals and these could be unambiguously counted within the transect section. Hence, all animals were counted only once, eliminating any biases due to repetitive counts of the same animals.

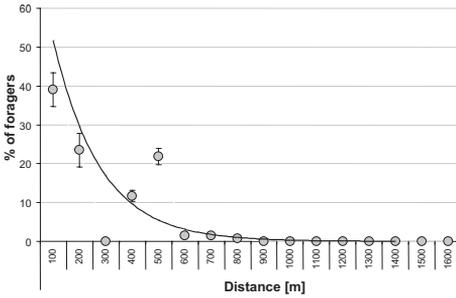


Figure 2. Non-linear regression of total foraging frequency (% (SD), $n = 126$) of labelled *B. terrestris* workers from six commercial colonies observed on thistle flowers along an exclusively food providing transect ($y = 90.42e^{-0.0056x}$, $R = 0.74$, $P < 0.01$). Each data point represents the mean (\pm s.e.) foraging frequency for each interval along the transect. Mean foraging distance was $267.2 \text{ m} \pm 180.3 \text{ m}$; mean maximum foraging distance $583.3 \text{ m} \pm 121.3 \text{ m}$ with a total maximum of 800 m.

The mean foraging distance for all observed marked workers was $267.2 \text{ m} \pm 180.3 \text{ m}$ with a maximum of 800 m. The mean maximum foraging distance per colony was $583.3 \text{ m} \pm 121.3 \text{ m}$. Most workers foraged on flower patches in the direct vicinity of their nest with about 40% of the workers ($n = 50$) observed within the first 100 m from the colony. 62.5% of all workers ($n = 80$) were observed within the first 200 m. Overall foraging frequency significantly declined over distance following an exponential regression ($y = 90.42e^{-0.0056x}$, $R^2 = 0.553$, $P = 0.009$; Fig. 2). However, the forager density showed both a distinct decrease at the 300 m interval and a marked increase at the 500 m interval ($\chi^2 = 57.82$, $df = 3$, $P < 0.001$) significantly deviating from the exponential regression. A one-tailed linear regression of patch quality (in terms of number of thistle inflorescences) on the residual foraging density explained 43.3% of the remaining variance ($y = 0.77x - 12.02$, $R^2 = 0.4324$, $P < 0.05$; Fig. 3). A multiple regression of both patch distance and patch quality on foraging frequency explained over 80% of the total variance ($R^2 = 0.804$, $F_{2,4} = 13.33$, $P < 0.05$).

The mean number of observed foraging workers per colony was 21.3 ± 6.6 . Irrespec-

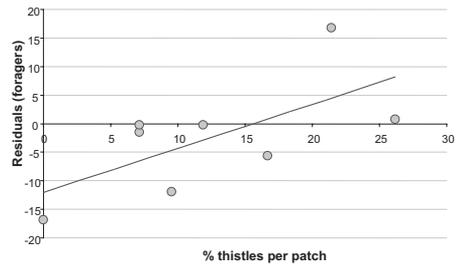


Figure 3. Linear correlation of residuals of *B. terrestris* workers foraging frequency representing the variance remaining unexplained by distance from the colony, and patch quality in terms of available thistle inflorescences [%] along the transect ($y = 0.77x - 12.02$, $R = 0.66$, $P < 0.05$ (one-tailed)). The patch quality accounts for over 43% of the remaining variance in foraging frequency (= 19.3% of total variance) underlining the importance of patch quality for the decision making in foraging bumblebees.

tive of the similar colony sizes (100–130 workers), there were significant intercolonial differences among the observed number of foragers ranging from three workers of the colony “red” (2.3%) to 40 workers of the colony “silver” (31.25%) ($\chi^2 = 50.76$, $df = 5$, $P < 0.001$).

4. DISCUSSION

Clearly, estimates of the mean and the maximum foraging distance are important parameters to assess the pollination effect of bumblebee colonies in both natural and agricultural conditions. In our study *B. terrestris* workers did not exceed foraging distances of 800 m, which is in line with several other studies that are based on transect data. Two recent studies employing a transect setting and microsatellite markers to assign sampled workers to their native colonies estimated maximum foraging distances for *B. terrestris* of 758 m (Knight et al., 2005) and less than 625 m (Darvill et al., 2004). Kwak et al. (1998) estimated even shorter pollination flight distances of *B. terrestris* workers between 75 m and 250 m based on pollen dispersal analysis. In contrast, several other studies suggest considerably larger foraging distances for this

species (e.g. Chapman et al., 2003; Westphal et al., 2006a). One reason might be the huge differences spatial distribution and attractivity of forage plants among the different studies. Differences in the abundance of bumblebees may not only affect monitoring efficiency but may also cause a competition situation (Stout and Goulson, 2001) that is assumed to lead to extended foraging distances (Dramstad, 1996).

Apart from studies that assess the foraging distance of workers in forage-rich areas (Osborne et al., 1999; Darvill et al., 2004; Knight et al., 2005; this study) experiments can also be designed to test for the maximum distance between a particular food source and the home colony. As an extreme example, Goulson and Stout (2001) showed that bumblebee workers return to their home nests after a 9.8 km displacement. However, calculations based on the foraging economics of workers suggest that flight distances may well exceed 10 km (Cresswell et al., 2000; Goulson, 2003). These large flight distances might occur under highly unsuitable foraging conditions or a lack of forage in the vicinity of the colony (Cresswell et al., 2000; Westphal et al., 2006b). Low forage abundance may therefore be a prime factor accounting for the large flight distances (Heinrich, 1976; Bowers, 1985). This is supported by Osborne et al. (2008) who found foraging distances of *B. terrestris* exceeding 1.5 km obtained by placing colonies at different distances to a highly attractive borage (*Borago officinalis*) field within a discontinuous foraging environment. The scattered forage patches interspersed with areas of forage scarcity may well have led to extended foraging distances and intracolony communication based on chemical cues (Dornhaus and Chittka, 1999, 2001, 2004) of borage pollen may have further enhanced the frequency of long distance foragers. Forage quality and availability can also explain the large flight distances found by Walther-Hellwig and Frankl (2000b) where a high percentage of *B. terrestris* workers were attracted by distant fields of *Phacelia tenuifolium* (a well-known and highly rewarding bee plant; e.g. Fussell and Corbet, 1992; Carreck and Williams, 1997) in an area with less attractive alternative forage. The excep-

tional attractivity of *Phacelia* forage may also explain the results presented by Dramstad et al. (2003), who stated a preferred foraging distance of bumblebees. The reported increase of foragers at a *Phacelia* plot after nest displacement might reflect the decreasing forage quality over time (authors mentioned wilting of the *Phacelia* flowers) and consequently the need to intensify foraging rather than a fixed preferred foraging distance. This becomes even more apparent since the availability of rewarding flowers may change over time and bees may have to exhibit very different foraging distances in different times of season (Heinrich, 1976; Bowers, 1985). For example Osborne et al. (1999), found a decrease of foraging distance in August ($201 \text{ m} \pm 18.7 \text{ m}$, range: 70–556 m) compared to that in June ($339 \text{ m} \pm 26.2 \text{ m}$, range: 96–631 m). Kwak et al. (1998) reported varying distances of bumblebee mediated pollen dispersal not only during the season (*May*: mean: $48.3 \text{ m} \pm 14.5 \text{ m}$ and $64.7 \text{ m} \pm 4.6 \text{ m}$, max: 100 m and 75 m; *June*: mean: $86.5 \text{ m} \pm 36.0 \text{ m}$, max: 230 m) but also between years.

The wide spectrum of reported foraging distances reveals foraging distance of bumblebee as a highly complex determinant that most likely reflects the high plasticity of the workers' foraging behaviour towards a variety of influences. Our data suggest that bumblebee foraging largely follows the prediction made by optimal foraging theory (e.g. Pyke, 1984), thus bees should preferably forage at the most rewarding source available at shortest distance from the colony (Heinrich, 1976; Pyke, 1984; Bowers, 1985; Goulson, 2003; Leadbeater and Chittka, 2005). Like for Pyke's (1978a) forager distribution data on *Bombus flavifrons*, the frequency of foraging bumblebees in our study showed a significant exponential decrease with increasing distance. More than half of the variance in foraging frequency could be explained by patch distance confirming the importance of resource spatial distribution on foraging behaviour. Nevertheless, we also found a significant deviation from this pattern with a local peak of foraging activity at 500 m (Fig. 2), which nicely underlines the importance of local forage quality for foraging decisions of workers.

The decision-making process in bumblebee workers is driven by economic principles leading to foragers high affinity towards rewarding resources (e.g. Heinrich, 1975; Harder, 1990; Waddington, 2001; Harder et al., 2001; Goulson, 2003). Consequently, precluding a negative correlation between forage quality and worker frequency an one-tailed linear correlation resulted in a significant positive contiguity of patch forage quality and bumblebees foraging behaviour ($P = 0.038$). Patch forage quality accordingly accounts for over 40% of the variance remaining unexplained by patch distance (= 19.3% of total variance) including the vast overrepresentation of foragers at 500 m.

These results show impressively how highly variable resources both in quantity and quality interfere with foraging patterns related to distance to the colony (e.g. Pyke, 1978a, b, 1984; Walther-Hellwig and Frankl, 2000a, b). In our case 80% of the distribution could be explained by these forage distance and quality indicating that foraging is largely determined by external (i.e. environmental) factors. This of course does not entirely exclude other influencing factors that might also play a role.

Dramstad (1996) argued that individual foraging distances might be extended to reduce the frequency of encountering already exploited flowers in close vicinity of the nest. Although forager density was very low in our study and over exploitation of nectar may have been unlikely this effect may have contributed to the 20% of the variance remaining unexplained in our study. Equally, the wide spectrum of other putative factors, such as flight economics (Heinrich, 1975; Wolf et al., 1999), ambient temperature (Kwon and Saeed, 2003), exploitation quantity (Schmid-Hempel et al., 1985; Spaethe and Weidenmüller, 2002), colony status (Heinrich, 1975; Catar and Dill, 1990; Catar, 1991) and predation risk (Lima, 1985; Dukas, 2001) may also have added to the residual 20% variance of foraging distances. Since we observed a significant variance for the number of observed foragers among colonies (ranging from 2.3% to 31.3% of total observations) we cannot exclude that also genetic factors have contribute to foraging distance. A high genetic plasticity is

a general phenomenon even among identically reared bumblebee colonies (Müller and Schmid-Hempel, 1992; Wolf et al., 1999; Beekman and van Stratum, 2000; Gerloff and Schmid-Hempel, 2005) including a considerable variance in workers learning performance, which is tightly related to foraging (Raine et al., 2006).

Our results confirm those studies in natural (Kwak et al., 1998) and agricultural (Morandin et al., 2001a, b) environments showing that short range pollen dispersal by foraging bumblebee workers is most efficient within the close vicinity of the colony (Morandin, 2001b).

There is a tight link between bumblebees foraging behaviour and the foraging environmental context. Distribution and quality of resources was the major determinant in bumblebee foraging explaining over 80% of the variance. Under favourable conditions with forage available in close vicinity of the nest, foraging distances will be short to moderate rarely exceeding 800 m. Consequently effective pollen dispersal will be constrained to a very limited range under these conditions. This also applies for *B. terrestris* colonies used for pollination in agriculture where forage is available in direct proximity of the nest and in high density. It further supports the strategy of using high bumblebee colony densities for pollination services in greenhouses and plantations (Morandin et al., 2001: mean: 11.6 ± 0.9 colonies/ha; van Ravestijn and van der Sande, 1991: 10-15 colonies/ha).

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La distance de butinage chez *Bombus terrestris* (Hymenoptera : Apidae).

Bombus / butinage / pollinisation / prise de décision

Zusammenfassung – Foragierdistanz bei *Bombus terrestris* L. (Hymenoptera: Apidae). Pollenverbreitung durch Tiere ist eine Schlüsselfunktion in Ökosystemen. Hummeln (*Bombus* sp.) gehören zu den effizientesten Bestäubern, sowohl von Wildpflanzen, als auch von Nutzpflanzen. Ein wesentliches Merkmal zur Bestimmung dieser Bestäubungseffizienz ist die Distanz, über die Pollen verbreitet werden können. Diese Entfernung hängt stark von der Flugdistanz von individuellen Sammlerinnen ab und dieser Parameter ist schon mehrfach untersucht worden, wobei eine große Vielfalt von Methoden genutzt wurde. So wurden Transekt-Beobachtungen, genetische Studien, Fang-Wiederfang-Experimente, Radar-Monitoring und theoretische Modelle angewendet, um die Flugdistanz abzuschätzen. Die Ergebnisse dieser Untersuchungen zeichnen sich hauptsächlich durch eine hohe Variabilität aus. Schätzungen reichen von wenigen hundert Metern bis zu mehreren Kilometern.

Wir nutzen hier ein Transekt-Experiment, bei dem wir sowohl die Entfernung der Blüten als Futterquellen als auch der Nestposition kontrollierten. Sechs *B. terrestris*-Kolonien mit farbmarkierten Arbeiterinnen wurden in einer ausgeräumten Agrarlandschaft an den Anfang eines als Transekt genutzten Feldweges positioniert. Die einzig vorhandenen Futterquellen wuchsen entlang dieses Feldweges (Abb. 1). Über zehn Tage wurden Sammlerinnen beobachtet und deren Entfernung zum Nest festgehalten. Unser experimenteller Aufbau erlaubte weiterhin die Abschätzung der Qualität der vorhandenen Futterquellen gemessen als Anzahl der blühenden Disteln (die einzig genutzte Futterquelle) pro 100 m-Intervall. Damit konnten auch Umwelteinflüsse auf das Flugverhalten einbezogen werden.

Die durchschnittliche Foragierdistanz von *B. terrestris* Arbeiterinnen betrug $267,2 \text{ m} \pm 180,3 \text{ m}$ (Maximum: 800 m). Fast 40 % der beobachteten Arbeiterinnen sammelten innerhalb von 100 m vom Nest. Über 60 % der Sammlerinnen entfernten sich nicht weiter als 200 m von der Kolonie. Insgesamt nahm die Foragierfrequenz exponentiell ab, je weiter sich eine Futterquelle von Nest entfernt befand (Abb. 2). Signifikante Abweichungen von dieser Verteilung bei 300 m und 500 m konnten auf die Qualität der Futterquellen (= Anzahl der Blütenstände) zurückgeführt werden. Blütenangebot konnte 40 % der Varianz erklären, die nicht von der Entfernung zum Nest abhängig war (Abb. 3). Im Einklang mit früheren Untersuchungen zeigten Sammlerinnen eher kurze Flugdistanzen, wenn die Qualität der vorhandenen Blüten gut und Blüten in direkter Nähe zum Nest vorhanden sind. Wir konnten zeigen, dass die räumliche Verteilung und Qualität der vorhandenen

Futterquellen Haupteinflussfaktoren für das Sammelflugverhalten von Hummeln sind und über 80 % der Foragierfrequenz erklären konnten. Die kurze Flugdistanz von Sammlerinnen sollte beim Einsatz von *B. terrestris* Kolonien für Bestäubungszwecke in der Landwirtschaft berücksichtigt werden.

Hummel / Sammeln / Bestäubung / Entscheidungsfindung**REFERENCES**

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