

Original article

Homing ability of the bumblebee *Bombus terrestris* (Hymenoptera: Apidae)

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Abstract – The ability of bumblebees to locate their nest site following artificial displacement was investigated. *Bombus terrestris* (Hymenoptera: Apidae) workers were marked with numbered tags and displaced up to 15 km from their nest. Bees returned from distances of up to 9.8 km, with the proportion of bees returning declining with distance of the release site from the nest. Bees were slow to return to their nests, often taking several days when even the most distant sites were all within 1 h direct flight time. These findings concur with those of earlier studies on various Hymenoptera, and they are consistent with previous suggestions that the most probable homing mechanism is a systematic search until familiar landmarks are encountered. Our results also suggest that the natural foraging range of *B. terrestris* may span several km.

Bombus terrestris / central place foraging / navigation / home range

1. INTRODUCTION

The ability of animals to return home when displaced to unfamiliar terrain has long fascinated biologists, perhaps because it is an ability beyond that of most humans. A variety of compass systems are found in diverse organisms, and include use of the sun, stars or geomagnetic fields (Walcott, 1996). Birds appear to be able to build up a

cognitive map of the landscape using visual and/or olfactory landmarks, and possibly also magnetic and auditory cues (Witschko and Witschko, 1999). Cognitive maps have also been inferred in mammals (Chmurzynski et al., 1998; Matthews and Best, 1997), decapods (Vannini and Cannicci, 1995) and bees (Gould, 1986, 1990). However, cognitive maps are hard to convincingly demonstrate (Benhamou, 1996), and the majority of

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workers contend that other explanations are more parsimonious for the data available for insects (Dyer, 1991; Menzel et al., 1996, 1998; Wehner and Menzel, 1990). Neither a compass nor a map is sufficient to navigate back when an organism is artificially transported to a novel location. If the organism is able to perceive information as to the direction of transport or is allowed to detect landmarks, then it could retrace its outward journey. However, pigeons are able to home even when anaesthetised and deprived of all outward journey information (Wallraff, 1980; Wallraff et al., 1980). This suggests that they possess some sort of coordinate system which enables them to determine their location relative to home, perhaps based on olfactory or magnetic stimuli (Able, 1994; Papi, 1986; Wallraff, 1990; Witschko and Witschko, 1988).

The Aculeate Hymenoptera also possess homing abilities, albeit over shorter distances than pigeons. The pioneering entomologist Jean-Henri Fabre demonstrated that the solitary sphecid wasp *Cerceris tuberculata* and the gregarious bee *Chalicodoma muraria* could return to their nests when transported several kilometres in dark boxes (Fabre, 1879, 1882). Similar experiments have since been performed on a range of solitary and social species (reviewed by Wehner, 1981; more recently Capaldi and Dyer, 1999; Chmurzynski et al., 1998; Schöne et al., 1993a, 1993b; Southwick and Buchmann, 1995; Ugolini, 1986; Ugolini et al., 1987). Most of these studies have examined homing from distances ranging from 100 m to 3–4 km, and all have found that at least a proportion of the released insects return. The greatest distance over which Hymenoptera have been found to home is 23 km in the Euglossine bee *Euplusia surinamensis* (Janzen, 1971).

We report on a study of homing in the bumblebee, *Bombus terrestris* (L.) (Hymenoptera: Apidae). We examine the relationship between displacement distance and the proportion of bees that return, and the time

taken to return. These data are then interpreted with regard to the most likely mechanisms that might be involved in homing in the Hymenoptera, and inferences are made about the likely foraging range of bumblebees.

2. METHODS

Five large nests of *B. terrestris* were purchased (Koppert Biological Systems, Berkel en Rodenrijs, The Netherlands) and placed in a suburban garden in Southampton, UK (01°24'W, 50°56'N, altitude 40 m), on the evening of 7 July 1999. On the following day, worker bees were captured throughout the day as they left the nest and marked by gluing honeybee queen-marking discs to the dorsal surface of the thorax. Different colours were used for bees from each of the five nests. Twenty bees per nest were marked. Nests were then left in position for nine days before experimentation began, to allow foragers to become familiar with the new location of the nest.

Further marking of outgoing bees was carried out on a daily basis from 16 July to 30 July (412 bees were marked in total). Commencing also on 16 July, batches of 10 marked bees were captured as they left their nests between 9.00 and 11.00 (British summer time). The first ten marked bees to exit were caught, regardless of which nest they were from. Bees were stored individually in opaque cardboard boxes, transported to release sites as quickly as possible by car, and all ten bees released at the same site in quick succession. Sites were randomly chosen with regard to both distance and direction, within a maximum distance of 15 km from the nests. If the site chosen was in the sea, a new site was selected. The actual release site was then the closest point to the selected site that could be reached by car (Fig. 1). Upon release, the behaviour of each bee was observed to determine the vanishing bearing. Bees were displaced only once, and

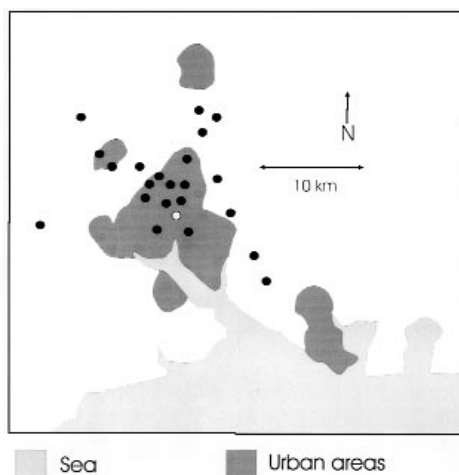


Figure 1. Release sites of each of the 22 batches of 10 bumblebees (●), in relation to the location of the nests (○), the southern coastline and major urban areas.

release sites were used only once. Bees were only displaced during warm, dry weather.

An alternative approach would have been to train bees to a feeder, and then displace them as they left for the nest. This would represent a more natural scenario in that the bee would be motivated to return directly to its nest. However, if bees had been trained to a feeder near their nest they would have gained little experience of natural foraging, and so their navigational abilities may have been artificially reduced.

Nests were monitored for returning bees for at least 2 h each morning and again during each afternoon. After nightfall, each evening the lids were removed from the nest boxes and any marked bees on the top of the nest were recorded. In total 22 batches of ten bees were marked and released between 16 July and 1 August. These commercial nest boxes incorporate a two-way entrance/exit and a one-way entrance valve. On 1 August, the two way entrance was closed so that returning bees could enter but no more bees could leave the nest. On 4 August

the nests were frozen and searched for marked individuals.

3. RESULTS

Of the 220 bees that were artificially displaced, in total 56 navigated home and were recaptured at the nest. There was a clear negative relationship between the proportion of bees returning and the distance of the release site (linear regression, $r^2 = 0.55$, $p < 0.001$) (Fig. 2). The furthest release distance from which a bee returned was 9.8 km. Of forty bees released at greater distances, none returned. The greatest proportion of bees recaptured (9/10) was at the closest release point (1.1 km). It must be noted that the proportion recaptured is a minimum estimate of the number that successfully returned to their nest. Some bees may have evaded observation on return, and subsequently died whilst foraging, since it was not possible to observe nests continually or to capture all individuals entering and leaving the nests.

Although an attempt was made to determine the direction of departure of released bees, this proved to be impossible. Released bees invariably began circling the release site. These circles increased in size and in altitude until the bees were lost from sight.

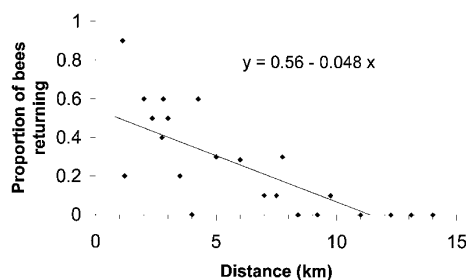


Figure 2. Homing ability of *Bombus terrestris* workers in relation with the distance from the release site to the nest. Each point is based on 10 bees.

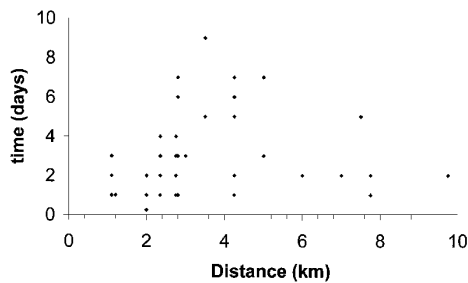


Figure 3. Return time from release to recapture at the nest site of *Bombus terrestris* workers following artificial displacement in relation with the distance from the release site to the nest ($n = 56$).

Interestingly, no relationship was apparent between the displacement distance and the time to recapture at the nest (linear regression, $r^2 = 0.015$, $p > 0.05$), although for shorter distances there is the suggestion of a weak relationship (Fig. 3). Times from release to recapture varied between 6 h (from 2 km) to 9 days (from 3.5 km). These represent maximum estimates of the return time.

Notably, one bee that returned to its nest after being displaced by 4.3 km was observed on a subsequent occasion gathering nectar at the release site, which contained a large patch of nectar-rich flowers.

4. DISCUSSION

The results demonstrate that bumblebees possess impressive navigational abilities which enable them to return to their nests after being artificially transported in dark boxes to sites up to 9.8 km from their nest. This distance is approximately equal to that found in similar experiments on *A. mellifera* (Southwick and Buchmann, 1995). However, the results also demonstrate that they are very slow to do so, most taking several days to return. *B. terrestris* is capable of flying at speeds of up to $15.7 \text{ km}\cdot\text{h}^{-1}$ even when laden with a harmonic radar aerial

(Osborne et al., 1999), and so could theoretically return from even the most distant sites used in this study within 1 h. Of course it is likely that some marked bees returned unobserved and the time between release and recapture is a maximum estimate. Nonetheless sampling at the nests was intensive and it seems improbable that returned bees could evade recapture for long periods of time. Prolonged homing times have been found in other studies. For example of 374 *Anthophora abrupta* displaced up to 3.2 km from their nest, homing times varied from 20 min to 50 h (Rau, 1929).

So how do Hymenoptera locate their nests over many km? They may possess a coordinate system such as that used by pigeons, or they may have been able to obtain some sensory information during their outward journey, and use this to retrace their movements. Neither explanation seems likely, however, as both possibilities should enable the bee to return swiftly. Most recent authors have concluded that a third mechanism is most likely. Displaced insects are thought to use a systematic search for familiar landmarks, and then use these to locate their nest (reviewed by Wehner, 1981). Desert ants (*Cataglyphis* spp.) engage in systematic searches when displaced to unfamiliar terrain (Wehner, 1996). Honeybees are known to use visual landmarks to aid navigation between the nest and forage (Dyer, 1996; Kastberger, 1992; Wehner, 1981), and use a sun compass to relate the positions of landmarks and the nest (Wehner, 1994). Honeybee homing is also better when prominent horizon landmarks are present (Southwick and Buchmann, 1995). Searching for familiar landmarks could lead to protracted homing times, and explain why from more distant sites many bees fail to return. This hypothesis is also consistent with the circling behaviour of released bees. If this is the homing mechanism in use, then we might expect all bees released within their home range to successfully return to the nest, and to do so rapidly, while bees released beyond their

range should return slowly if at all. If all bees had a similar knowledge of the environment, this would lead to a stepped (non-linear) response between distance and both the proportion of bees returning and the speed with which they do so. With a larger data set, it may be possible to test for such relationships. However, individual bees are likely to vary in their ability to home according to their foraging experience (they typically live for only a few weeks) and also to the particular directions that they have previously explored, which will determine the number and distribution of familiar landmarks. Rau (1929) found that homing success in *A. abrupta* was strongly related to age, with older (and presumably more experienced) bees being much more likely to return to the nest. Such variability will obscure the relationship between displacement distance and success in homing.

It had long been thought that bumblebees forage close to their nests (Heinrich, 1976; Teräs, 1976), but recent calculations based on the energetics of foraging suggest that bumblebees could travel up to 8 km from their nest and return with a net profit (Cresswell et al., 1999). Using harmonic radar, Osborne et al. (1999) found that *B. terrestris* regularly flew further than was necessary to find patches of forage, and many flew beyond the 500 m range of the radar. It seems that bumblebee species vary greatly in their natural foraging range. Mark-recapture experiments and anecdotal observations suggest that species such as *B. pascuorum*, *B. sylvarum*, *B. ruderarius* and *B. muscorum* are “doorstep foragers”, mostly remaining within 500 m of their nests whilst *B. lapidarius* forages further afield (mostly < 1500 m), and *B. terrestris* regularly forage over > 2 km (Dramstad, 1996; Walther-Hellwig and Frankl, 2000; Witte et al., 1989). The outer limits of their foraging ranges are unknown. It seems improbable that a bee released 9.8 km from its nest could find familiar landmarks unless its home range were several km in radius. Since one marked bee which returned to its nest

from 4.3 km was subsequently seen foraging at the site where it was released, bumblebees are clearly capable of remembering the location of forage at such distances and successfully navigating too and from these patches. In our study, many bees successfully returned from considerable distances (> 5 km), so it seems likely that *B. terrestris* naturally forage over several km.

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Résumé – La capacité de retour au nid de *Bombus terrestris*. On a étudié la capacité des bourdons à localiser l’endroit de leur nid après avoir été déplacés artificiellement. Cinq nids de *Bombus terrestris* (Hymenoptera : Apidae) ont été placés dans un jardin périurbain de Southampton, UK. Les ouvrières ont été marquées avec des étiquette numérotées et conservées individuellement dans des boîtes noires jusqu’aux sites de lâcher, qui ont été choisis chaque jour au hasard quant à la direction et la distance jusqu’à une distance maximale de 15 km des nids (Fig. 1). Sur chaque site des groupes de 10 ouvrières ont été lâchés. Au total 220 bourdons ont été déplacés entre le 16 juillet et le 1^{er} août 1999. Lors du lâcher les bourdons accomplissaient un vol en spirale centrifuge de plus en plus large jusqu’à ce qu’on les perde de vue. Les bourdons ont réussi à retourner à leur nid jusqu’à 9,8 km de distance. Le proportion des bourdons qui retournaient au nid a diminué significativement au fur et à mesure que la distance du lâcher au nid augmentait (Fig. 2). Les bourdons ont mis du temps à retourner à leur nid, souvent plusieurs jours même lorsque les sites de lâcher étaient tous à une heure de vol direct (Fig. 3). Ces résultats coïncident avec ceux d’études faites antérieurement sur divers Hyménoptères et sont en accord avec la supposition selon laquelle le

mécanisme de retour au nid le plus probable est une recherche systématique jusqu'à la rencontre de repères topographiques familiers. S'il en est ainsi, il est alors probable que les bourdons ont une aire naturelle de butinage de plusieurs km² autour de leur nid. De fait, on a observé un bourdon marqué, qui rentrait d'une distance de 4,3 km, reparti butiner les jours suivants sur le lieu de lâcher. Malgré de nombreuses études, on attend encore un test qui prouve définitivement l'hypothèse selon laquelle les Hyménoptères déplacés localisent leur nid par une recherche systématique de repères topographiques familiers et ceci reste un défi pour les futurs chercheurs dans ce domaine.

***Bombus terrestris* / orientation / retour au nid / aire de butinage / butinage à partir d'un point central**

Zusammenfassung – Heimfindevermögen der Hummel *Bombus terrestris*. Es wurde die Fähigkeit von Hummeln untersucht, nach künstlicher Versetzung zu ihrem Nistplatz zurück zu finden. In einem Vorstadtgarten von Southampton, UK wurden fünf Nester von *Bombus terrestris* (Hymenoptera: Apidae) aufgestellt. Die Arbeiterinnen wurden mit Nummernplättchen versehen und einzeln in dunklen Kästchen zu ihren Auflassungsorten gebracht. Richtung und Entfernung (bis 15 km vom Nest) der Auflassorte wurden jeden Tag nach einem Zufallsverfahren ausgesucht (Abb. 1). An jedem Ort wurden Gruppen von 10 Tieren aufgelassen. Zwischen dem 16. Juli und 1. August wurden insgesamt 220 Arbeiterinnen versetzt. Nach der Freisetzung flogen sie in immer weiter werdenden Spiralen um den Auflassort, bis sie außer Sicht gerieten. Die Arbeiterinnen fanden bis zu Entfernungen von 9,8 km zu ihrem Nest zurück. Hierbei nahm die Anzahl der Rückkehrerinnen mit zunehmender Entfernung signifikant ab (Abb. 2). Die Rückkehr zu den Nestern war langsam und nahm oft mehrere Tage in Anspruch, obwohl selbst die entferntesten

Auflassstellen alle innerhalb einer einzigen Flugstunde lagen (Abb. 3). Dieses Resultat entspricht früheren Untersuchungen an den verschiedensten Hymenopteren und steht mit der Vermutung in Einklang, nach der der wahrscheinlichste Mechanismus des Heimfindens eine systematische Suche ist, bis bekannte Landmarken gefunden werden. Hiernach wäre es wahrscheinlich, dass Hummeln natürlicherweise bis zu mehrere km Entfernung von ihrem Nest sammeln. Tatsächlich wurde beobachtet, dass ein markiertes Tier nach einer Rückkehr aus 4,3 km Entfernung an den folgenden Tagen zum Auflassort zurückkehrte, um dort zu sammeln. Trotz der vielfältigen Untersuchungen steht ein definitiver Beweis, dass versetzte Hummeln ihr Nest durch systematische Suche nach vertrauten Landmarken finden bisher noch aus und bleibt eine Herausforderung für zukünftige Untersuchungen.

***Bombus terrestris* / Sammeln von zentralem Ausgangsort / Orientierung / Heimatgebiet**

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