BUMBLEBEE NAVIGATION AND FORAGING BEHAVIOUR: A SHORT REVIEW

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Bumblebees are among the most important wild pollinators, helping crops and wild flowers to set seed and maintain their genetic variability. In recent decades, however, there has been a sharp decline in the number of bumblebees. In order to maintain and promote wild bumblebee populations, it is necessary to understand how bumblebees interact with their environment throughout their lifetime. This review focuses on how bumblebees navigate and forage in their local environment and provides an overview of the current research in this field. It also aims to show how such research can help shape landscape management practices to promote pollination services.

INTRODUCTION

More than one third of all human food is thought to depend on insect pollinators (McGregor, 1976). Of these pollinators, bumblebees are among the most important, providing pollination services to both crops and wild flowers (Corbet, 1987; Plowright and Laverty, 1987; Corbet *et al*., 1991). Wild bumblebee populations, however, are in decline (Williams, 1982; Rasmont ,1988; Kosior, 1995; Buchman and Nabhan, 1996; Westrich, 1996), which threatens to severely affect agricultural systems and crop yields worldwide. To begin reversing this trend, a better understanding of how bumblebees navigate and forage in their natural environment is needed.

This review details the behaviour of bumblebees as they begin their colonial life and how they move on to explore their environment. The present knowledge of bumblebee behaviours is presented and areas where further research is needed are highlighted. This review concludes with a short discussion on how understanding bumblebee behaviour is beneficial to their conservation.

COLONY FOUNDATION

A bumblebee colony begins with the queen. After emerging from hibernation in the spring, a bumblebee queen will search the landscape for a suitable nest location. As bumblebees cannot dig or create a cavity in which to house their nest, the queen searches for pre-exiting holes or areas of dense vegetation (Goulson, 2010). As a result, landscape features such as hedgerows, fence lines and forest edges have been found to have higher densities of bumblebee nests compared to features such as woods or grassland (Osborne *et al.* 2008a). Upon finding a suitable nest location, the queen will lay her first batch of eggs. This will give rise to the first workers who begin performing colony tasks both inside and outside the nest. As the worker caste is sterile and only has a life span of between 13-42 days (Rodd *et al*., 1980; Goulson, 2010), the queen continues to lay eggs throughout the colony's life. Depending on the species and the availability of suitable food sources, this workforce will reach between 30 to 400 workers (Free and Butler, 1959). Bumblebee colonies only have an annual lifecycle and, unlike honeybees, they do not store large quantities of honey or pollen in their nest (Heinrich, 1979). As such, the success of the colony is dependent on the availability of suitable food sources within foraging distance of the nest and environmental changes can prove fatal.

FIRST FLIGHT

A bumblebee worker will begin foraging outside the nest only a few days after transforming from its earlier larval stage (Brian, 1952). This is possibly due to the fact that the colony stores such limited amounts of food in the nest and workers must contribute to the colony's supplies as quickly as possible. Bumblebees have also evolved a range of adaptations that allow them to forage in many different environmental conditions. Workers of different species can usually fly in temperatures above 10°C (Heinrich, 1976), as well as under rain and high winds (Fox-Wilson, 1929; Corbet *et al*., 1993). Although ambient light levels are needed as bumblebees cannot fly in complete darkness, flights have been observed in the moonlight (Hulkkonen, 1928). As many other pollinators, such as honeybees, cannot forage under such a wide range of environmental conditions, bumblebees are an extremely effective wild pollinator (Goulson, 2010).

When leaving the nest to forage, most bumblebee workers will only carry enough honey to sustain them for a few minutes of flight. However, they will return with nectar and pollen loads, which can be up to 100% of their body weight (Heinrich, 1979). Workers leaving the nest for the very first time perform a series of looping flights ,which increase in area as they fly away. One of the suggested functions of this behaviour, termed 'orientation' or 'learning' flights, is to allow a bumblebee to memorise the landmarks and the landscape features that surround the nest (Baddeley *et al*., 2009; de Ibarra *et al*., 2009). When returning to the nest after a foraging flight, bumblebees have been observed to perform these very same flight patterns. This suggests that the bumblebees are effectively matching the 'views' of the landmarks and landscape features surrounding the nest that they acquired upon leaving it with the 'views' that they are experiencing when they return (Phillippides *et al*., 2013). Such a mechanism of matching their 'views' would allow them to accurately pinpoint the location of the nest and safely return home.

LANDSCAPE EFFECTS

It is not currently known if and how the topography of a landscape affects the flight of bumblebees and this is an area of ongoing research. Some clues can be gained, however, from the few studies that have investigated this relation. For example, bumblebee flight does not seem to be impeded by large landscape features such as woodland (Kreyer *et al*., 2004) and bumblebees are able to cross manmade structures such as roads (Bhattacharya *et al.* 2003). Bumblebees are also more likely to perform straight flights when flying along hedgerows compared to when they are flying in open fields, suggesting that they may follow linear landscape features (Cranmner *et al.*, 2012; Collet and Graham, 2015). An in depth understanding of the effects of landscape features on bumblebee flight will shed light on whether particular landscape features have significant effects on the floral resources that bumblebees use. This, in turn, will help us better understand the interaction between bumblebee flight and plant pollination in a particular landscape

FLIGHT RANGE CONSIDERATIONS

Although a basic idea of the flight ranges of a few bumblebee species are known, accurate measurements are difficult to ascertain given the current experimental techniques available. In most cases, indirect measures, such as mark-recapture techniques, are used to produce flight range estimates. At present, it is difficult to tease apart the different factors which may be influencing flight range (Goulson, 2010). For example, it is difficult to say whether the differences in the reported flight ranges in the literature are due to species differences; differences in the topography of the landscape and the floral resources available at the time of the experiment; or differences in the experimental techniques used. What does seem clear is that bumblebees can flexibly adapt their flight range depending on their local environmental conditions

FLOWER CHOICE

Bumblebee workers often begin foraging on their very first flight from the nest (de Ibarra *et al.*, 2009; Osborne *et al*., 2013). It is not known, however, what exactly attracts a bumblebee to begin foraging on a particular flower or flower patch. For example, it is not yet known if the first foraging location is largely due to a passive encounter between a bumblebee worker and a particular flower or whether it involves an active choice on the part of the bumblebee (Goulson, 2010). Although further research in the natural environment is needed, numerous laboratory studies have shed light on the factors that may play a significant role (reviewed in Orbán and Plowright,2014). Such factors include visual, olfactory and social cues as well as the quality of the food on offer.

With regards to visual cues, a complex interplay of flower colour, size, patterning and symmetry all have a significant effect on influencing a bumblebee's foraging choice. Olfactory cues also seem to play a role as bumblebees prefer the odours of flowers that are brought back into the nest by returning foragers (Dornhaus and Chittka, 1999). Recent research has also shed light on the role that social cues, in the form of other bees, may play in guiding bumblebees to forage on specific flowers. For example, naïve bumblebees that had never foraged before were more likely to land on flowers that were occupied by other bumblebees (Kawaguchi *et al*., 2006; Leadbeater and Chittka, 2009) or even honeybees (Dawson and Chittka, 2012). This suggests that workers are attuned to social cues when they have no previous knowledge of a particular flower type, taking advantage of the knowledge of the more experienced bees around them.

This effect is reversed, however, when bumblebees gain experience of their foraging environment. When they are familiar with a particular flower type, they tend to avoid occupied flowers of that type (Kawaguchi *et al*., 2006; Leadbeater and Chittka, 2009; Dawson and Chittka, 2012). To an experienced bumblebee, occupied flowers signal a recent depletion of that foraging source. Lastly, the quality and quantity of food on offer also seems to affect a bumblebee's foraging choice. In an experimental manipulation of nectar secretion rates, plants with higher rates attracted more bumblebees and had more of their individual flowers visited (Cartar, 2004). As such, it is clear that a complex interplay of factors guides the foraging behaviour of bumblebees.

CONSTANCY

Although more research is needed to establish the exact mechanisms governing the foraging behaviour of bumblebees, once a bumblebee has found a particular foraging source, it tends to return to the same type of flower and foraging site (Heinrich, 1976; Bowers, 1985; Waser, 1986; Dramstad,1996; Saville *et al*., 1997; Osborne *et al*., 1999). In doing so, they seem to bypass equally rewarding plant species. This phenomenon, termed 'flower constancy', suggests that bumblebees are capable of storing long term spatial memories (Burns and Thompson 2006). In addition, bumblebees have also been observed to 'trapline' between different flower patches: visiting particular plants in the same sequence over multiple foraging trips (Manning 1956; Thomson *et al*., 1982; Williams and Thomson, 1998). Rather than having a set and inflexible pattern, it is important to note that traplines seem to be constantly updated to match the changing foraging environment (Thomson and Chittka, 2001). Much like the questions that still surround what first attracts bumblebees to a particular flower or patch, here too further research is needed in order to determine the exact mechanisms that govern both flower constancy and trapline formation.

NAVIGATIONAL MECHANISMS

The exact mechanisms that bumblebees use to navigate to and from their nest and between different foraging sources are still largely unknown. However, many of the general mechanisms that underpin insect navigation are thought to apply to bumblebees as well. For example, it is thought that bumblebees, like honeybees, obtain their directional information primarily from the sun (Rossel and Wehner, 1984; Wehner *et al*., 1996). It is also thought that bumblebees keep track of the distance that they have travelled by monitoring their optic flow. Optic flow is the amount that an image appears to move across an animal's retinal view as it moves through space (Gibson 1950); and experimental evidence suggests that honeybees can judge the distance that they have travelled by monitoring the optic flow of the passing landscape (Srinivasan *et al.,* 1996; Esch and Burns, 1996; Esch *et al.,* 2001). Furthermore, honeybees are known to use local and global landmarks to aid their navigation (von Frisch, 1967; Cartwright and Collett, 1979; Cartwright and Collett, 1983; Chittka *et al*., 1995; Menzel *et al.,* 1998; Pahl *et al.,* 2011). Bees and other insects are also thought to keep a running total of the distance and direction that they have travelled from the nest using a process called 'path integration' (Mittelstaedt, 1983; Collett and Collett, 2000; Collett, Chittka and Collett, 2013). Working together, these mechanisms would allow an insect to navigate throughout its local environment and successfully return home.

SPATIAL COGNITION

In addition to using various navigational mechanisms to explore their local environment, bumblebees are also thought to memorise aspects of their environment as they fly through it. The exact mechanisms of spatial memory in bumblebees and other insects are currently unknown and the ways in which these memories might be organised in the insect brain is one of the most persistent debates within the field of animal navigation. This debate centres upon whether spatial memories are organised into a *single* representation of the world, known as a *cognitive map* (Tolman, 1948), or whether they are organised in a piecemeal fashion (Collett and Collett, 2002). For example, possessing a cognitive map would mean that bumblebees have an internal representation of their local landscape. This would allow them to compute their own position within this landscape and calculate novel routes to travel to specific locations, such as their nest. Alternatively, and more simply, bumblebees and other insects might be guided by similarities and disparities between their spatial memories and their current 'view' of the environment (Collett and Collett, 2002; Zeil, 2012; Collett *et al*., 2013). In this case, any disparities between a bumblebee's spatial memories and the 'view' that it is currently experiencing would signal to the bumblebee that it is not following the correct route to its destination. In addition, particular 'views' could also trigger memories of the direction that a bumblebee had previously flown in when travelling to a particular destination (Collett, 2009). If bumblebees, and other insects, possessed a cognitive map, this would suggest a level of complex mental processing that is not often associated with the insect brain. Without direct neurophysical evidence or further laboratory and field experiments, however, this debate will continue.

RETURNING TO THE NEST

Although bumblebees do not seem to directly communicate the location of profitable food sources to other workers in the nest, the rate of activity in the nest increases after a successful forager returns. After depositing their collected nectar and pollen, the returning forager will perform *excited runs*, bumping and climbing over other workers in the nest, releasing a pheromone, known as recruitment pheromone, as they do so (Dornhaus and Chittka, 2001). This recruitment pheromone has been found to encourage other workers in the nest to forage, but only when the nest is low on food reserves (Molet *et al*., 2008). It is hypothesized that one of the reasons that bumblebees have not evolved a direct means to communicate the location of food sources, unlike honeybees and their use of the waggle dance, is that few workers are actually present in the nest during the day. As such, the value of direct communication would be limited (Free 1955).

IMPLICATIONS FOR CONSERVATION

One of the primary factors that is thought to have led to the steep decline in the abundance of bumblebees in recent decades is the change in modern farming practices (Osborne and Corbet, 1994; Goulson *et al*., 2006). Among the effects of these practices is the loss of unimproved lowland and grassland (Fuller, 1987; Howard *et al*., 2003), which is a key nesting and foraging habitat of many bumblebee species. As bumblebees are central place foragers (Plowright and Laverty, 1984), always returning with gathered food to their nest, both their nest and foraging sites must be within their maximum flight range. The loss of key habitats has resulted in fragmented landscapes in which the distance between suitable nesting and foraging sites is ever increasing. Although it is doubtful that these trends can be fully reversed, the conservation and promotion of different bumblebee species can still be achieved. For example, although an increase in suitable habitat is needed in order to improve bumblebee species' densities, a *continuous* strip of habitat may not be needed. Rather, smaller patches of habitat within a more intense agricultural matrix may be sufficient as habitat connectivity has been shown to increase bumblebee species' densities (Goulson, 2010; Steffan-Dewenter, 2003). Field experiments investigating the flight range of different bumblebee species in particular environments may prove crucial in providing guidelines to create such interconnectivity.

CONCLUSION

The navigation and foraging behaviour of bumblebees is affected by both their unique life history as well as their local environment. As one of the most important wild pollinators of crops and wild flowers, understanding their movements is of particular relevance to landscape policy and management. Furthermore, insights into the mechanisms that bumblebees use to navigate and forage can also shed light on longstanding debates within the field of insect cognition. A detailed understanding of their behaviour will only be achieved through the use of complimentary field and laboratory investigations, using a range of different bumblebee species. It is only through such an understanding that we may be in a better position to protect both bumblebees as well as the fertility of our food supply

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