

Long-range foraging by the honey-bee, *Apis mellifera* L.

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Summary

1. Waggle dances of honey-bees (*Apis mellifera* L.) were decoded to determine where and how far the bees foraged during the blooming of heather (*Calluna vulgaris* L.) in August 1996 using a hive located in Sheffield, UK, east of the heather moors. The median distance foraged was 6.1 km, and the mean 5.5 km. Only 10% of the bees foraged within 0.5 km of the hive whereas 50% went more than 6 km, 25% more than 7.5 km and 10% more than 9.5 km from the hive.

2. These results are in sharp contrast with previous studies in which foraging distances were much closer to the hive. In May 1997 the mean foraging distance was 1 km, showing that long-range dancing is not the rule in Sheffield.

3. The observed foraging distances described in this study may not be exceptional in a patchy environment where differences in patch size and patch quality are large. When travel distances to patches are large, distant patches can probably be utilized only by individuals that live in groups and recruit foragers to the patches found. Only then are the benefits of scouting for distant patches high enough to enable the exploitation of these patches.

Key-words: Central-place foraging, patch size and quality, social foraging, spatial heterogeneity, travel distance

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Introduction

One consequence of sociality is that individual workers primarily forage to aid group members. A second consequence is that foraging efficiency may increase, for example because individuals assist each other in finding foraging sites. This can be by following outbound foragers (so-called imitative foraging; see Wilson 1975) or by more sophisticated methods where returning foragers actively direct others to food sources. The best-known example of the latter is the honey-bee dance language.

Since the seminal work of von Frisch (1967), the foraging behaviour of honey-bee colonies can be studied by decoding the waggle dances of individual foragers. Waggle dances contain information on where the dancing bees foraged (von Frisch 1967) and make the honey-bee the only animal that directly tells the observer where it collected food. Because only foragers working better patches dance (Seeley 1995), not all patches on which the colony forages are represented by waggle dances.

By decoding waggle dances, Visscher & Seeley (1982) showed that honey-bees (*Apis mellifera*) regularly forage several kilometres from the nest. The most common distance was 600–800 m. The mean was 2.3 km and the circle enclosing 95% of the colony's foraging activity had a radius of 6 km. Similar results to those of Visscher & Seeley (1982) have been reported (see references in Seeley 1995, p. 50), but most other studies have shown shorter foraging distances. Much shorter distances

were found in a study by Waddington *et al.* (1994) where the foraging range was 745–1413 m and the mean distance 534–1138 m depending on the hive and location. The exact distance foraged seems to depend on the abundance of profitable forage and a foraging radius of only a few hundred metres was observed in agricultural areas (see references in Visscher & Seeley 1982). In the African Honey-bee *Apis mellifera scutellata*, mean foraging distances were 1200 m (Schneider 1989) and 420–620 m (Schneider & McNally 1993). In another study using African Honey-bees and African–European hybrids, Schneider & Hall (1997) found a mean foraging distance for the African colonies of 1073 m and 1387 m for the hybrid colonies. Von Frisch (1967; p. 65 and further) reported that the foraging range of honey-bees is up to 13.5 km. Because von Frisch was not able to train bees over a distance greater than 11–12 km, he concluded that this is the maximum foraging distance of honey-bees.

In this study we report long-range foraging by honey-bees (*A. mellifera*) to large patches of heather (*Calluna vulgaris*) and argue that this can be an important aspect of colony foraging under naturally occurring environmental conditions. Our data show that honey-bees forage on heather at distances much greater than previously found by Visscher & Seeley (1982). This is important because the foraging range described by Visscher & Seeley was itself considered exceptional in that foraging distances were greater than in previous studies.

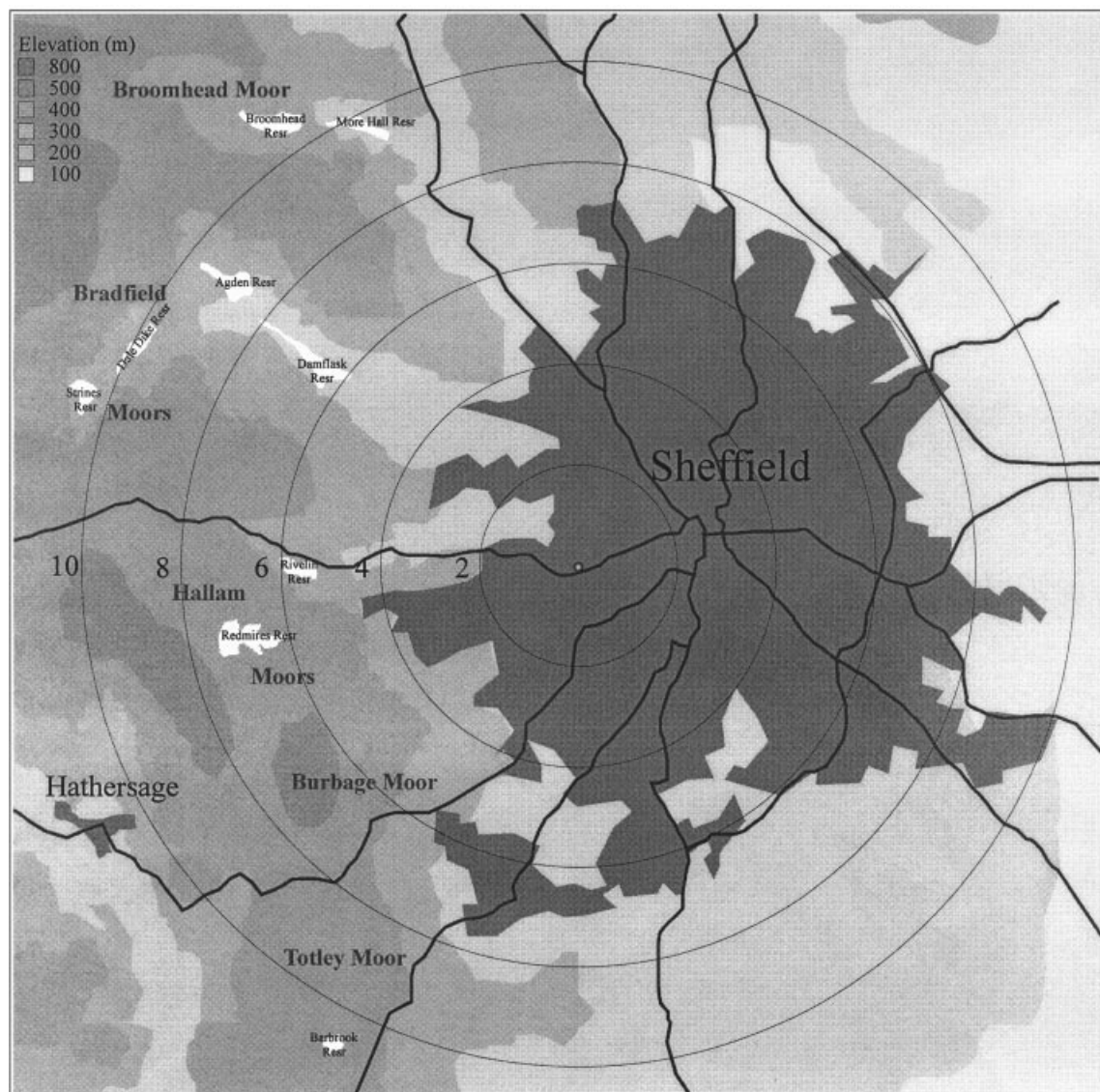


Fig. 1. Map showing the location of the heather moors relative to the location of the hive, which was located at the centre of the radial plot. The large patches of heather (elevation of 400 m or more) are marked on the map, but smaller patches occur throughout the region to the west of Sheffield.

Materials and methods

A queenright colony of honey-bees of mixed European race, *Apis mellifera*, housed in a two-frame deep observation hive located in Sheffield (grid reference: SK 322 869), Yorkshire, UK, was studied in August 1996 (see Seeley 1995 for a description of the observation hive). The hive contained ≈ 4000 workers and one frame of brood. Dances of returning foragers were videotaped on 15 August (from 1045 to 1850), 16 August (from 0930 to 1750) and 19 August (from 0945 to 1345) 1996. During this period extensive patches of heather were in bloom on moors in the Peak District west of Sheffield (see Fig. 1). Because the data from August showed such long foraging distances, we obtained additional data in spring (1–3 May) 1997 to confirm that long-range dancing is not the rule in Sheffield. A second colony was used because the first one did not survive the winter.

All dances for which at least five consecutive circuits could be measured were decoded. For each dance, the time of day, angle of the waggle run, and the duration of five to 10 dance circuits were recorded. Because our bees were not individually marked, we cannot exclude the possibility that dances of the same foraging bee were recorded more than once on a given trip to the hive if the forager made more than one bout of dancing per trip. However, the pattern we describe is based upon a large data set and is therefore robust. For three circuits per dance the angle of the waggle run was recorded to the nearest 10° using a circle with 36 divisions drawn on a transparency. The Sun's azimuth at the time of each dance was computed using Sun97, an Excel Macro provided by W. F. Towne. Dance angles were transformed into patch directions relative to North by adding the Sun's azimuth at the time of dancing to the dance angle. To calculate the foraging distance, the duration to

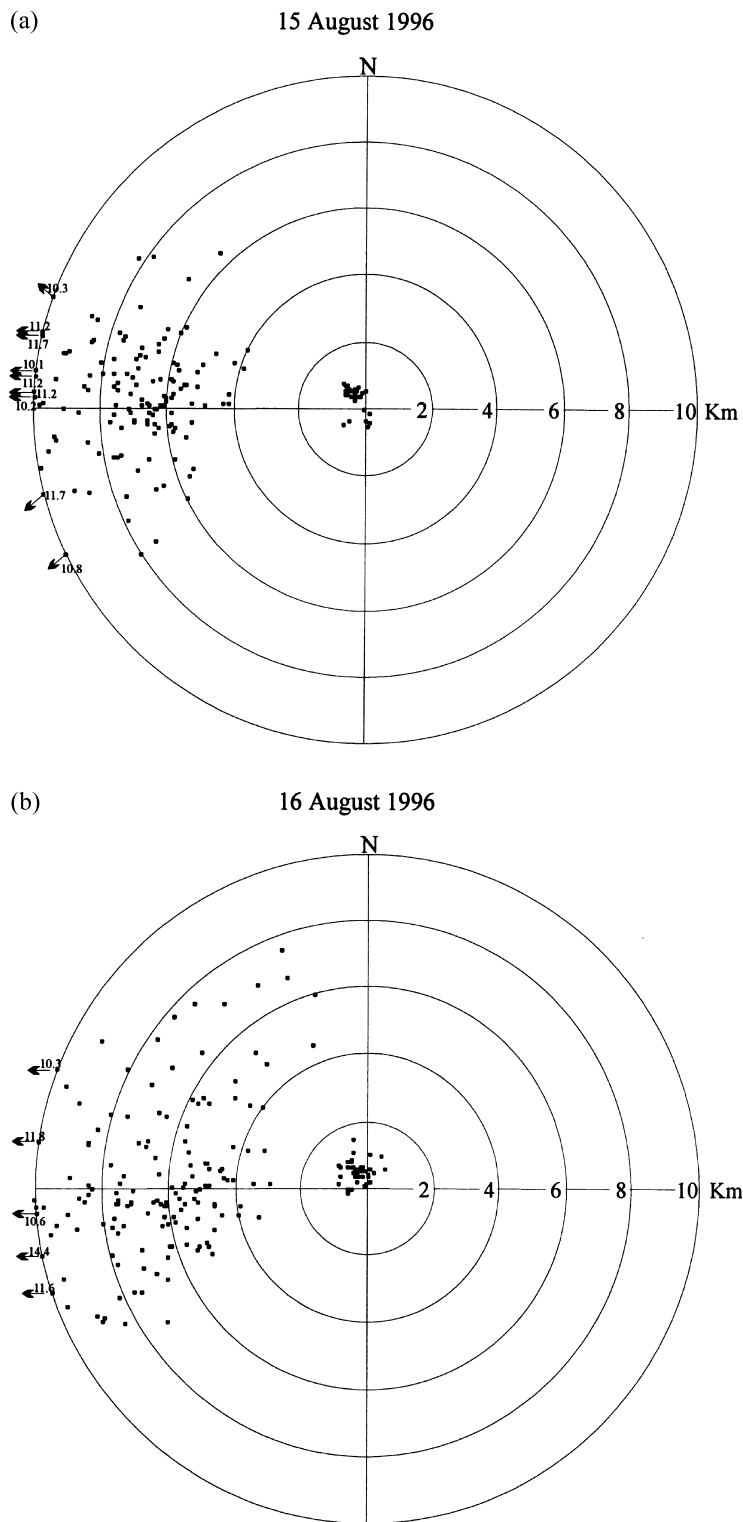


Fig. 2. Radial maps showing the foraging locations and distances for each day: (a) 15 August, (b) 16 August, (c) 19 August 1996, (d) 1 May, (e) 2 May and (f) 3 May 1997. Locations more than 10 km from the hive are indicated by an arrow on the outer circle. The distance in km is indicated beside the arrow.

distance curve of von Frisch was used (von Frisch 1967; Fig. 64). This graph was divided into two parts: 0–3.5 s and greater than 3.5 s. A polynomial fit ($R^2 = 0.992$) was used for dance durations of 0–3.5 s and a linear fit ($R^2 = 0.994$) for dance durations greater than 3.5 s.

Results

The dances of 444 bees were decoded for August 1996, and 456 for May 1997. Following Visscher & Seeley (1982) the foraging locations and distances for each day are presented as radial maps (Fig. 2) and histograms (Fig. 3).

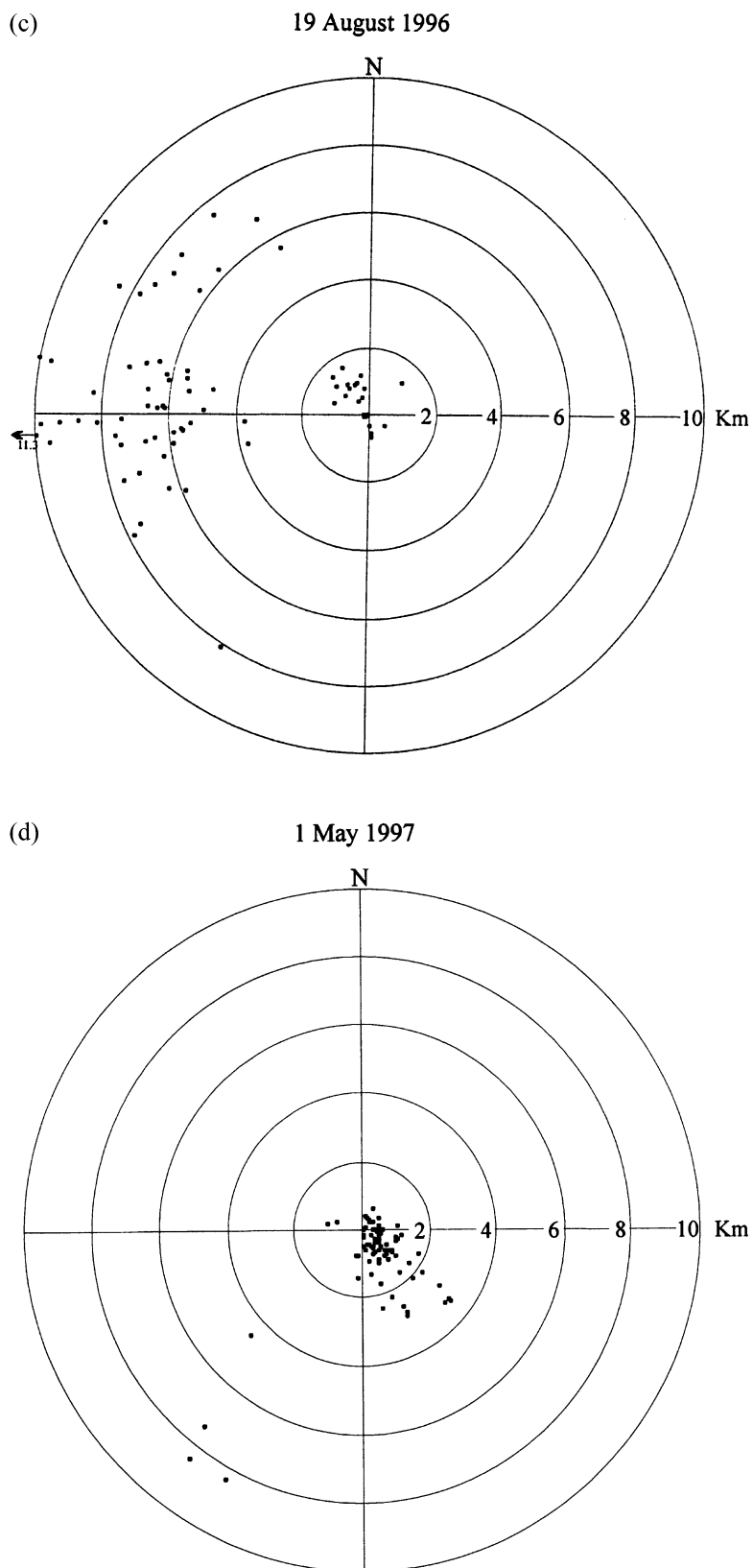


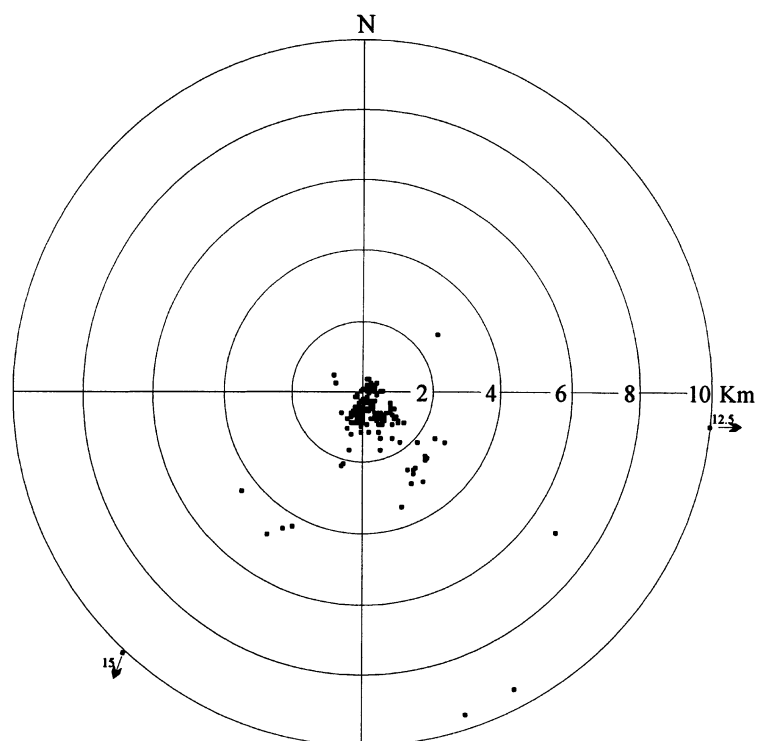
Fig. 2. Continued.

In August, the median distance foraged was 6.1 km, the mean 5.5 km and 95% of the bees foraged within a distance of 10 km. Only 10% of the bees foraged within 0.5 km of the hive whereas 50% went more

than 6 km, 25% more than 7.5 km and 10% more than 9.5 km. The colony foraged in two areas on all three days: one area close to the hive (less than 2 km) and one area much further away (5–10 km)

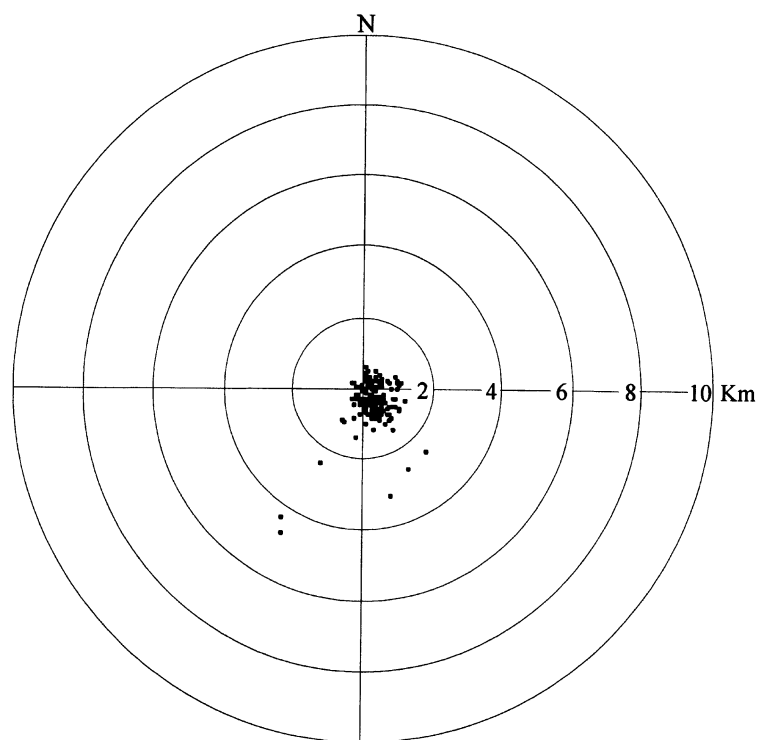
(e)

2 May 1997



(f)

3 May 1997

Fig. 2. *Continued.*

in the Peak District where extensive patches of heather were in full bloom on hilltops and moors. The mean patch distance in May was 1 km (see Figs 2d–f and 3).

Discussion

The foraging range for August is considerably greater than in previous studies. Visscher & Seeley

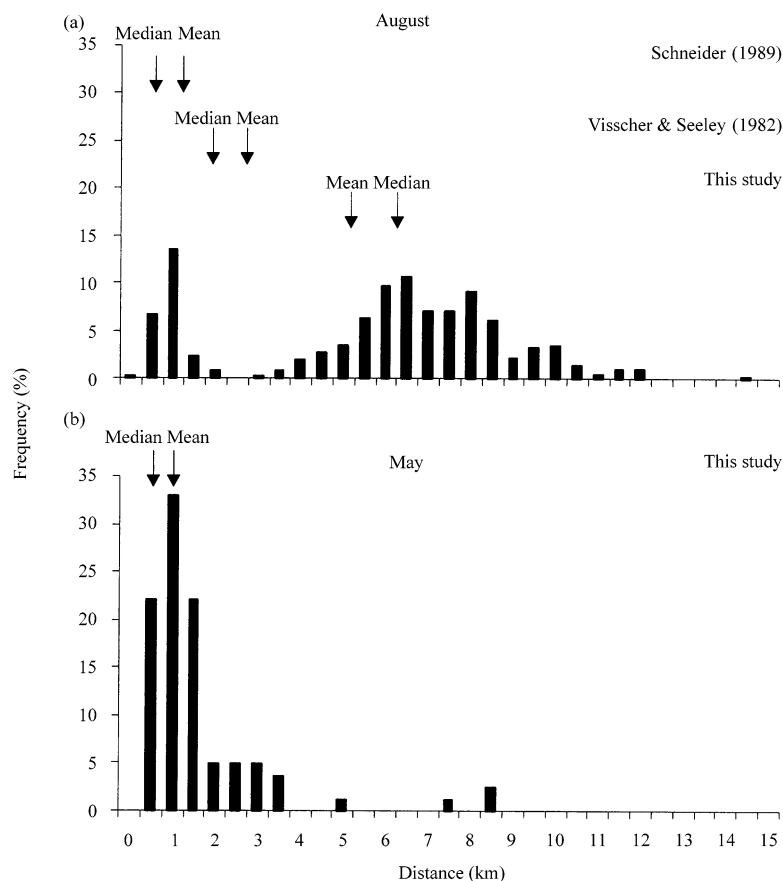


Fig. 3. Histogram plots of the foraging distances in August (all days pooled) and May (all days pooled). Also given are the average and median distances (50th percentile) for this study and two other studies in which the waggle dances of returning foragers were decoded.

(1982) observed a mean foraging distance of 2.3 km which is greater than foraging ranges observed in other studies where bees foraged over distances of a few hundred metres to just over 1 km. However, this is much lower than our August mean of 5.5 km. Because the bees foraged over much smaller distances in May (mean 1 km, median 0.68 km), the observed long-range foraging is due to the specific foraging conditions in August when immense patches of heather were in bloom. The heather patches can be more than 1 km across and mostly occur in an upland area of acidic rocks of several hundred square km. Heather (*Calluna vulgaris*) can produce large amounts of nectar. Crane (1976) classifies heather as one of the main nectar plants and states that 101–200 kg honey can be obtained by a colony foraging on 1 ha heather. For that reason beekeepers move hives onto heather moors. Because the bees also danced for areas closer to the hive within Sheffield where no heather is found, profitable patches were also available nearby. Bees will recruit both to nearby patches that yield nectar of low sugar concentration and to distant patches that yield nectar of a high sugar concentration (Seeley 1995). At the time that the August data were collected, hives in the same location as the

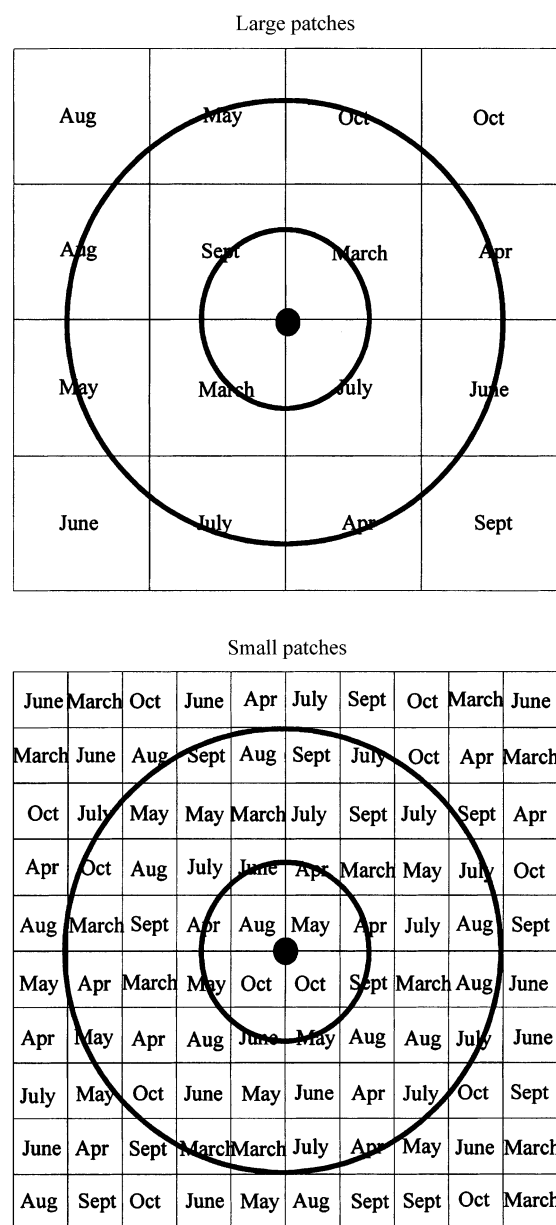


Fig. 4. Two environments: (a) with large patches and (b) with small patches. The patches differ in flowering season denoted by the name of the month. The two circles represent the foraging radius for two different species. A species that is able to forage over long distances (large circle) will be able to collect food in the best patches throughout the year even if patch size is large (i.e. some patches may be distant).

observation hive showed a strong tendency to rob (F. L. W. Ratnieks, personal observation) which is typical during periods of nectar shortage. The occurrence of robbing supports the idea that, overall, foraging conditions were poor, which makes far-away patches worthwhile.

The observed foraging distances described in this study may not be exceptional for honey-bees in an environment where forage patches are large and vary in quality. Consider two landscapes, one with small patches and one with large patches (see Fig. 4). The quality of the

patches changes over time because different patch types have different vegetation with distinct flowering seasons. When the landscape consists of small patches, foragers can easily collect food in all types of patches without travelling long distances. In such a landscape colonies profit from the diversity in vegetation close to the nest. But if the patches are large, like the heather moors, colonies may be able to forage only in all patch types if workers have a long maximum foraging range.

Exploring patches that are far away from the nest is probably only possible for group-living individuals that share information on the location of patches among group members (Ruxton & Glasbey 1995; Seeley 1995). Honey-bees live in large groups – a large *A. mellifera* colony can contain up to 65 000 bees and they recruit foragers to patches found. The use of scout bees to explore the area around the hive for profitable patches and to transfer the information gained to bees inside the hive, avoids search costs paid by individual foragers such as bumble-bees (Schaffer *et al.* 1979). The transfer of information can make scouting over large distances profitable because, in principle, one scout finding a large patch 10 km away from the nest could directly and indirectly (via recruitment signals) recruit the entire foraging force of the colony.

The honey-bees studied here foraged in a patchy landscape where differences in patch size and quality were large. Although heather moors are highly profitable, travel distances were large because the hive was located at a distant several kilometres from the heather moors. Long travel distances will restrict the exploitation of a large but far away patch to species that live in large groups and make use of an efficient recruitment system. Long-distance scouting is costly because there is no guarantee that a patch will be found. Species without recruitment, such as bumble-bees, should not scout far from the nest because only the scout will benefit when a profitable patch is found. But a species such as the honey-bee, which transfers information among group members, can scout over long distances and exploit distant but profitable patches because it will gain a large benefit if a good but far away patch is found.

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References

- Crane, E. (1976) *Honey. A Comprehensive Survey*. Heinemann, London.
- Frisch, von K. (1967) *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge, MA.
- Ruxton, G.D. & Glasbey, C.A. (1995) Energetics of group foraging: analysis of a random-walk model. *IMA Journal of Mathematics Applied in Medicine and Biology* **12**, 71–81.
- Schaffer, W.M., Jensen, D.B., Hobbs, D.E., Gurevitch, J., Todd, J.R. & Schaffer, M.V. (1979) Competition, foraging energetics, and the cost of sociality in three species of bees. *Ecology* **60** (5), 976–987.
- Schneider, S.S. (1989) Spatial foraging patterns of the African honeybee, *Apis mellifera scutellata*. *Journal of Insect Behaviour* **2**, 505–521.
- Schneider, S.S. & Hall, H.G. (1997) Diet selection and foraging distances of African and European-African honey bee colonies in Costa Rica. *Insectes Sociaux* **44**, 171–187.
- Schneider, S.S. & McNally, L.C. (1993) Spatial foraging patterns and colony energy status in the African honey bee, *Apis mellifera scutellata*. *Journal of Insect Behaviour* **6**, 195–210.
- Seeley, T.D. (1995) *The Wisdom of the Hive*. Harvard University Press, London.
- Visscher, P.K. & Seeley, T.D. (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* **63**, 1790–1801.
- Waddington, K.D., Visscher, P.K., Herbert, T.J. & Raveret Richter, M. (1994) Comparisons of forager distributions from matched honey bee colonies in suburban environments. *Behavioral Ecology Sociobiology* **35**, 423–429.
- Wilson, E.O. (1975) *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, MA.

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