
Comparing Foraging Behaviour of Small and Large Honey-Bee Colonies by Decoding Waggle Dances Made by Foragers

Author(s): M. Beekman, D. J. T. Sumpter, N. Seraphides and F. L. W. Ratnieks

Source: *Functional Ecology*, Dec., 2004, Vol. 18, No. 6 (Dec., 2004), pp. 829-835

Published by: British Ecological Society

Stable URL: <https://www.jstor.org/stable/3599110>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Functional Ecology*

JSTOR

Comparing foraging behaviour of small and large honey-bee colonies by decoding waggle dances made by foragers

M. BEEKMAN,^{†‡§} D. J. T. SUMPTER,[¶] N. SERAPHIDES^{††*} and
F. L. W. RATNIEKS[§]

[‡]School of Biological Sciences, University of Sydney, Sydney NSW 2006, Australia, [§]Laboratory of Apiculture and Social Insects, Department of Animal & Plant Sciences, Sheffield University, Sheffield S10 2TN, UK,

[¶]Centre for Mathematical Biology, Mathematical Institute, Oxford University, 24–29 St. Giles, Oxford, OX1 3LB, UK, and ^{††}Department of Agricultural and Environmental Science, University of Newcastle, Newcastle upon Tyne NE1 7RU, UK

Summary

1. We compared the foraging behaviour of two small (approximately 6000 bees) and two large (approximately 20 000 bees) honey-bee colonies over 6 days. We determined where the bees of each colony foraged, whether they collected nectar or pollen, the number of patches foraged at, the number of bees engaged in foraging, and the concentration of the nectar collected.

2. Even though the colonies were located in the same environment and had the same genetic background, foragers from different colonies used different forage patches.

3. Small and large colonies foraged at a similar distance in July when forage was abundant (mean foraging distance for small and large colonies was 0.67 and 0.62 km, respectively) whereas the large colonies foraged significantly further in August when forage was scarce (mean foraging distance for small and large colonies was 1.43 and 2.85 km, respectively).

4. Small colonies foraged at approximately the same number of patches as large colonies. The total number of foragers returning to the small colonies per minute was significantly lower than the number of foragers returning to the large colonies. This means that, relative to their size, small colonies foraged at more patches than large colonies.

5. The quality of the nectar collected by foragers of the small and large colonies did not differ. However, small colonies did collect more pollen than large colonies.

Key-words: *Apis mellifera*, colony size, foraging, honey-bee

Functional Ecology (2004) **18**, 829–835

Introduction

The food sources exploited by social insects are often ephemeral, widely scattered or both. One benefit of social life is that nestmates can direct each other to known food sources. Although the exact recruitment mechanisms differ among species, an insect colony's global foraging behaviour results from the decisions made by individual foragers and their interactions with colony members and the foraging environment (see for example Seeley, Camazine & Sneyd 1991; Biesmeijer & Ermers 1999). However, the nature of

interactions among colony members may set constraints on social foraging, so that small colonies do not always forage as efficiently as large colonies. For example, colonies of Pharaoh's Ants (*Monomorium pharaonis* L.) that are below a critical size cannot form a pheromone trail to a nearby food source, although larger colonies can (Beekman, Sumpter & Ratnieks 2001). Because pheromone trails are normally used to recruit nestmates to food sources, larger colonies should be more efficient in terms of the time taken for individual foragers to locate food.

The size of a honey-bee colony varies naturally during its life cycle. In temperate climates, the size of a colony can range from a few thousand bees just after winter or following nest-founding by a small swarm, to tens of thousands of individuals during early summer (Seeley & Morse 1976). It is therefore of interest to

[†]Author to whom correspondence should be addressed.
E-mail: mbeekman@bio.usyd.edu.au

^{*}Present address: Agricultural Research Institute, PO Box 22016, 1516 Nicosia, Cyprus.

know how colony size affects foraging behaviour of honey-bee colonies.

In this study we compared the foraging behaviour of two small and two large honey-bee colonies in the same urban environment by decoding their waggle dances (Frisch 1967) performed over a period of 6 days. In particular, we determined the proportion of pollen foragers, the mean distance of foraging sites, the sugar concentration of the nectar collected, and the number of patches foraged at by small and large colonies.

Materials and methods

THE HONEY-BEES

Four queenright honey-bee colonies of mixed European race but predominantly *Apis mellifera mellifera* were studied. These four colonies were established by combining bees and brood from two large colonies to make one very populous colony which was then divided into four. Two additional queens were used so that each of the four study colonies was queenright and had brood. Because the colonies were studied before eggs laid by the new queens had developed into adult workers (c. 21 days after egg-laying), the genetic composition of the four experimental colonies was the same throughout the experiment. This allowed us to investigate the effect of colony size while controlling for genetic variation among colonies.

The hives were located at the Laboratory of Apiculture and Social Insects, University of Sheffield, Yorkshire, UK. Two 'small' colonies (S1 and S2) had approximately 6000 bees and were each housed in modified 2-frame Langstroth observation hives (Seeley 1995). Each hive contained five frames. The lower two were arranged in a single layer behind glass, allowing observation of dancing. The entrance was located in the bottom of this lower part. The upper three frames were inside a wooden box, which was placed on top of the observation hive. The large colonies contained approximately 21 000 (L1) and 18 000 (L2) bees and differed from the small hives only in that the top box was larger and contained eight frames. For each colony the brood and the queen were in the top box. The range in colony size obtained in our experiment is within the natural range from small to moderately strong colonies (Seeley & Morse 1976). To estimate the number of bees per hive, at the end of the experiment the bees were anaesthetized using carbon dioxide and weighed. Subsamples were weighed and counted to estimate total populations.

RECORDING AND DECODING WAGGLE DANCES

Dances of returning foragers were videotaped simultaneously on 23, 24, 26, 29, 30 July and 2 August 1999, for 4 hours each day per colony using four video

cameras. Using a wooden baffle near the entrance (see Seeley 1995), most returning foragers were directed to one side of the hive which allowed almost all dances to be recorded with a single video camera per hive.

We decoded approximately 30 dances for each hour of videotape. We first decoded all dances for which at least five consecutive circuits could be measured without rewinding the videotape. If at the end of the tape we did not have 30 dances, we rewound the tape and decoded dances that had not yet been analysed (dances were identifiable by the time of dancing). For each dance, the time of day, angle of the waggle run, and the duration of five to ten dance circuits were recorded. In addition, we noted whether or not the dancer had pollen in her pollen baskets. Because our bees were not individually marked, dances of the same foraging bee were undoubtedly recorded more than once on a given trip to the hive if the forager made more than one bout of dancing per trip, or over several trips. However, because our aim was to determine the number of patches foraged at and because we decoded a large number of dances, this should cause minimal error in our interpretation of the data. Dances were decoded following Beekman & Ratnieks (2000).

NUMBER OF FORAGERS AND DANCE CHARACTERISTICS OF WAGGLE DANCERS

To collect returning foragers we temporarily closed the hive entrances and captured returning foragers. The bees were immobilized by chilling them for a few minutes. The abdomens of 20 bees not collecting pollen were gently squeezed so that the bee regurgitated a droplet of nectar. The sugar concentration was then measured with a refractometer. Sugar concentration was determined for all colonies on 29 and 30 July and 2 August.

To quantify the number of foragers, we counted the number of bees entering each hive for one minute, 20 times each day, between 09.30 and 13.00, on 29 and 30 July and 2 August. For a given rate of total nectar gain by the colony, bees adjust their dance threshold (a bee's decision whether or not to dance) depending on foraging conditions, such that the dance threshold is high (low) when foraging is abundant (sparse) (Seeley 1994). To determine whether the dance threshold differs between large and small colonies, we selected 37 bees that danced for the same patch in both a large (L1) and a small colony (S1) on 26 July 1999, and measured the total dance duration of each bee. The mean number of dancing bees was estimated by counting the number of bees dancing during 1 min every 5 min. This was done for all colonies on all days for all 4 h of observation.

ESTIMATING THE NUMBER OF PATCHES FORAGED AT BY EACH COLONY

To estimate the number of patches foraged at by each colony, we defined patches in terms of the points for

which the bees danced: each point for which a dance is given indicates a putative centre of a patch. A patch was then defined as the collection of all other points advertised by dances within radius r of this centre point. The patch radius, r , was set as the distance within which a bee dancing for the central point could send recruits following the dances. The patch radius is thus determined by the accuracy of the waggle dance communication. Towne & Gould (1988) determined the error in the dance communication by measuring how close a bee recruited to a feeder would arrive to that feeder. Towne and Gould thus established a relationship between distance from hive to feeder, which we will call d , and the average distance of a recruit from the feeder to arrival point, which we will call a . For d less than 100 they found that $a = 55$, so we define $a = 55$ for $d < 100$. For $d = 500$ they found that $a = 80$. Linearly interpolating between 100 and 500, we assume that $a = 55 + 0.0625 * (d - 100)$. For d greater than 500, dance communication error is determined by the lower bound for dance accuracy (i.e. approximately 4%, see Weidenmüller & Seeley 1999) and we assume that $a = 80 + 0.04 * d$. The mean distance from the feeder to the arrival point can be used to define the radius, r , of a forage patch, in terms of the accuracy of the dance. We define $r = 4a$, so as to ensure that the centres of patches, when laid out on the plane, are at least a distance from each other. Note that changing this factor changes the number of patches in an environment, but does not affect the estimate of the relative number of patches foraged at by small and large colonies.

We determined the number of patches for any set of dance points as follows: first we randomly listed the points for which dances had been performed. The first point in this list was considered the putative centre of a patch. Next, we removed all those points from the list that lay within the patch radius r . The procedure was then performed on the next point remaining in the list, making this the putative central point and removing all other points within r of this second point. This procedure was repeated until no points remained in the

list. The number of patches was then estimated to be the number of centre points found. To ensure that our estimate of the number of patches did not depend on the initial order of the list, we repeated the above procedure for 100 different random orderings, taking the minimum number of centre points found as our estimate of the number of patches foraged at.

Results

Figure 1 shows the patch locations danced for by the foragers of all colonies on all 6 days. Dancers carrying pollen are represented by triangles and those without by squares. Bees from different colonies differed in forage patch location (Fig. 1). For example, on 23 July all colonies foraged at the same patches located less than 1 km south-east and south-west of the hives, but each colony also had unique patches. Patches located 4–5 km south-west were only visited by colony S1 on July 23.

The median and mean foraging distances are presented in Table 1 as are the concentration of nectar collected, the number of foragers and the proportion of pollen collectors for all four colonies.

The two small colonies had similar numbers of dancing bees per minute, whereas colony L1 had, on average, 2.6 times as many dances as the small colonies (Table 2). This observation implies that the individual foragers in L1, S1 and S2 all had roughly the same dance threshold, i.e. propensity to dance on returning from a successful foraging trip. Furthermore, the total dance duration of bees foraging at the same patch in a small and large hive did not differ (mean over all 37 patches: 1 min 59 s for the large colony L1, and 1 min 40 s for S1) (t -test assuming independent samples, $t = 0.54$, $df = 72$, $P = 0.57$). Bees in the small colonies were therefore not more likely to dance than those in L1, because the number of waggle runs per dance (dance duration) decreases with dance threshold (Seeley 1995). In contrast, the dance threshold for colony L2 appears to be much higher than either L1 or

Table 1. Mean and median foraging distances in July and August, concentration of nectar collected, number of foragers, and the proportion of pollen foragers for all four colonies. Footnotes refer to statistical tests used

	S1	S2	L1	L2
Median foraging distance July (km)	0.35	0.53	0.50	0.48
Mean foraging distance July (km) ¹	0.67	0.68	0.62	0.62
Median foraging distance August (km)	0.23	0.38	2.81	2.75
Mean foraging distance August (km) ²	1.02	1.97	2.63	3.01
Nectar [%] (mean \pm SD) ³	32.3 \pm 2.9	31.8 \pm 3.4	33.1 \pm 3.4	31.7 \pm 1.0
No. foragers (mean \pm SD) ⁴	36 \pm 8	40 \pm 11	119 \pm 21	93 \pm 19
% pollen collectors (mean \pm SD) ⁵	33.2 \pm 10.7	39.7 \pm 20.7	25.2 \pm 10.0	23.2 \pm 14.3

¹One-way ANOVA, $F_{1,2468} = 3.591$, $P = 0.06$.

²One-way ANOVA, $F_{1,413} = 39.82$, $P < 0.001$. Overall foraging distances (July and August combined): one-way ANOVA, $F_{1,2881} = 284.90$, $P < 0.001$.

³ T -test assuming independent samples after pooling all days, $t = 1.15$, $df = 3$, $P = 0.77$.

⁴One-way ANOVA on mean number of foragers per day, $F_{1,4} = 85.2$, $P = 0.001$.

⁵Wilcoxon paired test on differences of daily pollen foraging, $t = 0$, $P < 0.05$.

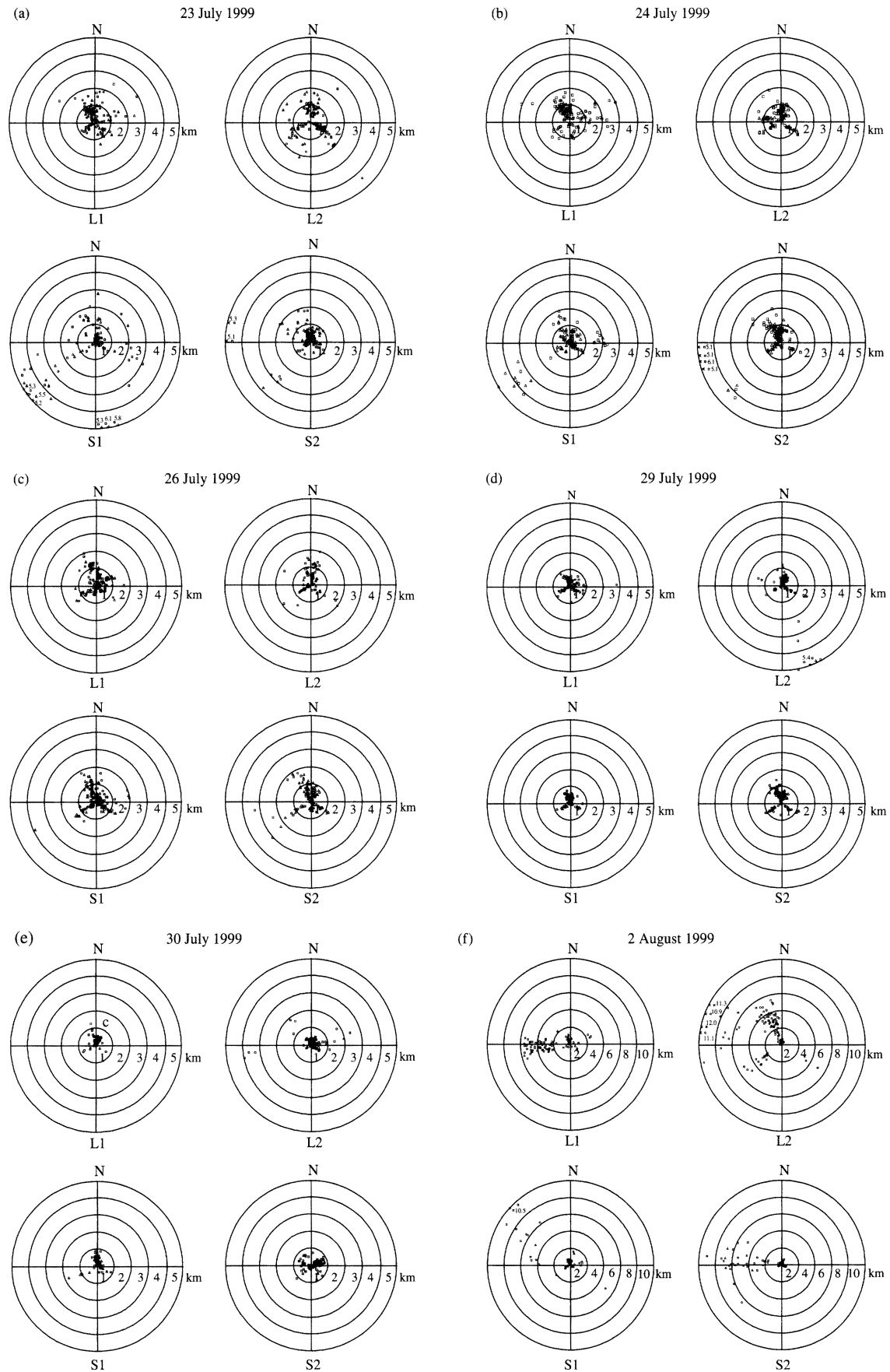


Fig. 1. Foraging locations indicated by dances for each colony and each day: (a) 23 July, (b) 24 July, (c) 26 July, (d) 29 July, (e) 30 July and (f) 2 August 1999. Triangles represent bees carrying pollen, squares represent bees without pollen. The scale for the 2 August plots is different because the bees foraged on distant heather moors. Locations outside the outer circle are indicated by an arrow with the distance in km. Total number of dances decoded for L1, L2, S1 and S2 are, respectively: 120, 124, 119, 120 (23 July); 124, 122, 120, 120 (24 July); 138, 76, 181, 131 (26 July); 120, 120, 120, 132 (29 July); 121, 120, 120, 122 (30 July) and 91, 120, 115, 89 (2 August).

Table 2. Number of dancing bees per minute for each colony (mean \pm standard deviation) and the estimated number of dancing bees in parentheses. The number of bees dancing was counted for 1 min with 5-min interval. The means of the 44 measurements per day (11 measurements per hour) are shown. The total number of dancing bees was estimated by comparing the colony where all dances were decoded with the dancing bees per minute for the other colonies. We used S1 on 26 July to calculate the total number of dances in July and S1 on 2 August to calculate the total number of dances on 2 August using: (known no. dances for S1 \times no. dances per min S1)/no. dancing bees per min focal colony

	S1	S2	L1	L2
23 July	6.2 \pm 1.1 (334)	5.9 \pm 0.4 (298)	14.4 \pm 2.3 (767)	7.4 \pm 0.9 (395)
24 July	9.0 \pm 1.4 (483)	5.6 \pm 0.6 (297)	16.8 \pm 1.7 (896)	8.5 \pm 2.0 (456)
26 July	2.8 \pm 0.6147*	5.2 \pm 2.1 (278)	11.5 \pm 3.6 (612)	0.9 \pm 0.873*
29 July	5.4 \pm 0.5 (287)	6.4 \pm 1.0 (341)	12.3 \pm 1.7 (656)	6.4 \pm 0.5 (342)
30 July	4.7 \pm 0.6 (251)	3.0 \pm 1.7 (157)	12.2 \pm 1.8 (649)	5.2 \pm 0.4 (276)
2 August	3.2 \pm 1.4115*	3.1 \pm 0.889*	11.7 \pm 4.0 (253)	6.1 \pm 1.5 (133)
Across all days	5.32 \pm 2.94	4.84 \pm 2.58	13.2 \pm 3.96	5.75 \pm 3.41

*Actual number of bees dancing on that day. (Note that the original data were more precise whereas the data in Table 2 are rounded numbers.)

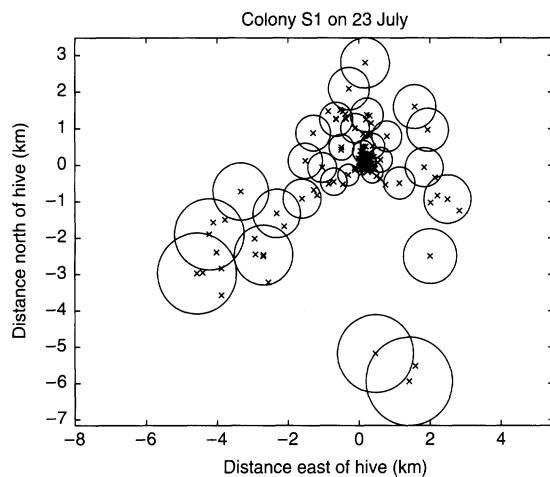


Fig. 2. A representative plot of the patches found by colony S1 on 23 July.

the small colonies. On one occasion, 26 July, the bees in colony L2 hardly danced at all. However, even when data from this day are discarded there are still only 1.2 times as many dances in L2 as in the small hives, despite there being 2.4 times more foragers returning per minute. With no other major differences between L1 and L2, this difference remains unexplained.

Figure 2 gives an example of how the above procedure yields the location of the patches. Table 3 provides an estimate of the number of forage patches for each colony, and for all the colonies combined on each day. The combined tally is computed by combining the dances for each day and repeating the patch estimate procedure. Figure 3 shows how the number of known patches increases as the number of dances decoded is increased for the four colonies on 24 July. Other days have patch increase plots of a similar shape. Notice that the number of patches increases more slowly as more dances are decoded. Fitting an exponentially saturating curve to the patch increase plots in Fig. 3 and extrapolating this curve up to the total number of dances performed (given in Table 2) shows no increase in the number of patches foraged at by any of the

Table 3. Estimated number of forage patches used by each of the four colonies on the 6 days. The combined tally is estimated by combining the dances for each day and repeating the patch estimate procedure used within colonies across all colonies. The number in brackets is the percentage of the total number of patches foraged at by that colony on that day

	S1	S2	L1	L2	Combined
23 July	31 (65)	19 (40)	19 (40)	16 (33)	48 (100)
24 July	18 (51)	15 (43)	20 (57)	12 (34)	35 (100)
26 July	16 (84)	17 (89)	18 (95)	15 (79)	19 (100)
29 July	6 (29)	9 (43)	11 (52)	13 (62)	21 (100)
30 July	8 (38)	9 (43)	12 (57)	8 (38)	21 (100)
2 August	15 (29)	17 (33)	20 (39)	26 (51)	51 (100)

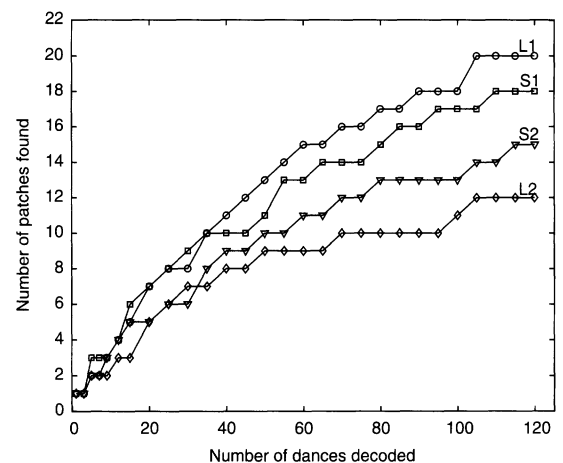


Fig. 3. Number of dances decoded vs the number of known forage patches for the four colonies on 24 July.

colonies on any of the days observed. This indicates that our estimate in Table 3 is a valid approximation of the total number of forage patches.

Colonies L1 and L2 had 3.5 and 3.0 times as many bees as colonies S1 and S2, and 3.1 and 2.4 times as many foragers returning per minute. Assuming forage trips take the same amount of time for both colonies

– which seems likely for 23–30 July as mean foraging distances were roughly equal for small and large colonies – the proportion of bees engaged in foraging in the large colonies was slightly smaller than in the small colonies. This may be due to increased demand for pollen in the small colonies: the small colonies foraged for more pollen than the large colonies on all days of observation. Small colonies tend to collect proportionally more pollen than large colonies because they rear proportionally more brood (Ratnieks 1986).

Over the six study days the large colonies foraged at a mean of 15.84 patches vs 15.00 for the two small colonies. Not only is the mean number of patches almost equal for small and large colonies, but small colonies also foraged at slightly more patches on 23 and 24 July, the same number on 26 July, and on slightly fewer patches on 29 and 30 July and 2 August. The difference between the large and small colonies is therefore not statistically significant (paired *t*-test on daily differences; $t = -0.410$, $df = 5$, $P = 0.69$). Despite the fact that between 2.4 and 3.1 times as many foragers returned to the hive per minute in large colonies, they foraged at only 1.05 times as many patches as the small colonies. Even if we exclude L2 from our analysis, because of its higher dance threshold, L1 foraged at only 1.11 times as many patches as S1 and S2 which is also not statistically significant (paired *t*-test on daily differences; $t = -1.059$, $df = 5$, $P = 0.34$).

Discussion

Our results show clearly, and unexpectedly, that small colonies foraged at approximately the same number of patches as colonies with three times as many workers. Our results also show that each colony, irrespective of its size, foraged at only a subset of the available patches (Table 3). Therefore, the observation that both small and large colonies foraged at the same number of patches is not because all colonies discovered and exploited all available forage sites. Given that our small colonies had about three times less foragers than the larger colonies, it follows that the forager force of the small colonies was more thinly spread over patches.

How do our results compare with previous studies that used dance decoding to investigate honey-bee foraging? Waddington *et al.* (1994) found that in a habitat with abundant highly rewarding flowers, most foraging took place within 1 km of the colony and was not strongly focused on particular patches. Our results from 23–30 July are similar in that most bees foraged within 1 km of the hive. Each colony foraged at a mean of $51.0 \pm 19.2\%$ (mean \pm standard deviation) of the patches used by all colonies. Therefore, as in Waddington *et al.* (1994), colonies exploited different patches on the same day even though they foraged from the same location. The exception to this was 26 July when individual colonies foraged at 79% (L2) to 95% (L1) (Table 3) of the total patches used by all four colonies. On the other 5 days, the observed pattern of

foraging is consistent with the ability of honey-bee colonies to monitor a large area, exploiting a large number of sites, but focusing on only a limited number of patches, likely to be those of highest profitability (Visscher & Seeley 1982).

The observation that colonies foraged on different patches cannot be accounted for simply by the different nutritional needs of the colonies since there was no consistent difference in the proportions of nectar and pollen collected by equal-sized colonies. The most likely explanation for the observation that colonies forage on different patches, even when placed in the same environment, rests both on chance factors and the abundance of flower patches. It is relatively easy for an individual scout from a particular colony to find and recruit to a patch, and scouts from different colonies will discover these patches at random. Especially when the number of patches is large, as in our urban foraging environment, different colonies will discover a different subset of the available patches. When other foragers from the colony are recruited to and are actively exploiting a particular patch, they are more likely to persist with these than to switch to an unknown patch of equal quality. Hence, a forager visiting a rewarding patch will remain foraging on that patch for as long as the patch is rewarding and may dance for that patch if she judges the profitability sufficiently high (Seeley 1995). As a result, the overall foraging pattern of a honey-bee colony is not only the result of the available forage but is also determined by the way in which different patches are discovered by the colony's scouts.

Seeley (1987) studied the search abilities of honey-bee colonies by planting flower patches of buckwheat located at different distances in a forested environment that was poor in forage. His data showed that when the patches were nearby (1 km) 70% of the colonies discovered them, falling to 50% at 1.9–2.0 km and 0% at 3.2–3.6 km. These results are likely to be an underestimate of a colony's ability to discover forage sites as Seeley was unable to keep track of the origin of all foragers that visited his flower patches. However, his results suggest that a honey-bee colony will not discover all possible patches in its foraging environment unless they are close by.

Even though the above can explain why different colonies placed in the same environment do not necessarily forage at the same patches, it does not explain why our small colonies foraged at as many patches as the larger colonies, which had approximately three times as many foragers. What affects the number of patches foraged at by a honey-bee colony? The number of scouts a colony sends out is likely to affect the number of patches the colony initially discovers (assuming that patches are abundant). The discovery of a large number of profitable patches by these scouts will probably result in a diversity of patches being used by the colony if the scouts perform waggle dances upon return to their colony. This could lead to more patches foraged at when a colony has more scouts. However, a

large number of scouts could also reduce the number of patches foraged at as the colony would focus on the most profitable patches. Our study was not designed to elucidate the number of scouts and therefore it is unknown whether the number of scouts differed between our large and small colonies. We do know that our small colonies had fewer dances than the larger colonies but, again, it is not easy to see what effect the number of dancing bees will have on the patches foraged at by the colony. For example, if the chances of locating a dancing bee are lower when there are fewer dancing bees, then it may be that unemployed foragers scout, thereby discovering more forage sites.

In conclusion, and in contrast to Pharaoh's ants, where colonies below a certain threshold size were unable to form a pheromone trail to a nearby food source, small honey-bee colonies do not seem to be constrained with respect to locating profitable forage sites, at least not in our study using colonies of 6000 workers. This is interesting because it is clear that there were fewer foragers advertising profitable forage sites in the small colonies than in the larger colonies (Table 2). Yet, our small colonies seemed to be able to locate an equal number of profitable patches as the larger colonies and brought in nectar of the same quality. Would the dance language communication system be constrained in even smaller honey-bee colonies than the ones we studied, for example with fewer than 1000 workers? Such colonies might well have insufficient foragers to scout out the local environment and to discover the best patches. However, under many conditions the availability of forage may be sufficiently high for colonies with zero communication of food sources to forage efficiently (Sherman & Visscher 2002; Dornhaus & Chittka 2004).

Acknowledgements

M.B. was supported by a postdoctoral fellowship from the research network 'Social Evolution' Universities of Århus, Firenze, Keele, Sheffield, Uppsala, Würzburg and the ETH Zürich, financed by the European Commission via the Training and Mobility of Researchers (TMR) programme and by the Australian Research Council. D.J.T.S. was funded by grants from the Engineering and Physical Sciences Research Council (EPSRC), the Defence Evaluation and Research Agency (DERA) and the Association for the Study of Animal Behaviour (ASAB). The authors also thank David Broomhead, Ben Oldroyd, Stephen Pratt and members of the Laboratory of Apiculture and Social Insects

(Sheffield) for useful discussions and comments. Ben Oldroyd is also thanked for his comments on previous versions of the manuscript.

References

- Beekman, M. & Ratnieks, F.L.W. (2000) Long range foraging by the honey-bee *Apis mellifera* L. *Functional Ecology* **14**, 490–496.
- Beekman, M., Sumpter, D.J.T. & Ratnieks, F.L.W. (2001) Phase transition between disorganised and organised foraging in Pharaoh's ants. *Proceedings of the National Academy of Science of the United States of America* **98**, 9703–9706.
- Biesmeijer, J.C. & Ermers, M.C.W. (1999) Social foraging in stingless bees: how colonies of *Melipona fasciata* choose among nectar sources. *Behavioral Ecology and Sociobiology* **46**, 129–140.
- Dornhaus, A. & Chittka, L. (2004) Why do honey bees dance? *Behavioral Ecology and Sociobiology* **55**, 395–401.
- Frisch, V.K. (1967) *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge, MA.
- Ratnieks, F.L.W. (1986) *Effect of colony population size on the efficiency of nectar collection and honey production in honey bee (Apis mellifera) colonies*. MSc thesis, Cornell University, Ithaca.
- Seeley, T.D. (1987) The effectiveness of information collection about food sources by honey bee colonies. *Animal Behaviour* **35**, 1572–1575.
- Seeley, T.D. (1994) Honey bee foragers as sensory units of their colonies. *Behavioral Ecology and Sociobiology* **34**, 51–62.
- Seeley, T.D. (1995) *The Wisdom of the Hive*. Harvard University Press, Cambridge, MA.
- Seeley, T.D. & Morse, R.A. (1976) The nest of the honey bee (*Apis mellifera* L.). *Insectes Sociaux* **23**, 495–512.
- Seeley, T.D., Camazine, S. & Sneyd, J. (1991) Collective decision-making in honey bees: how colonies choose among nectar sources. *Behavioral Ecology and Sociobiology* **28**, 277–290.
- Sherman, G. & Visscher, P.K. (2002) Honeybee colonies achieve fitness through dancing. *Nature* **419**, 920–922.
- Towne, W.F. & Gould, J.L. (1988) The spatial precision of the honeybee's dance communication. *Journal of Insect Behavior* **1**, 129–155.
- 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 and Sociobiology* **35**, 423–429.
- Weidenmüller, A. & Seeley, T.D. (1999) Imprecision in waggle dances of the honeybee (*Apis mellifera*) for nearby food sources: error or adaptation? *Behavioral Ecology and Sociobiology* **46**, 190–199.

Received 18 November 2003; revised 28 May 2004; accepted 8 June 2004