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Bigger is better: honeybee colonies as distributed information-gathering systems

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In collectively foraging groups, communication about food resources can play an important role in the organization of the group's activity. For example, the honeybee dance communication system allows colonies to selectively allocate foragers among different floral resources according to their quality. Because larger groups can potentially collect more information than smaller groups, they might benefit more from communication because it allows them to integrate and use that information to coordinate forager activity. Larger groups might also benefit more from communication because it allows them to dominate high-value resources by recruiting large numbers of foragers. By manipulating both colony size and the ability to communicate location information in the dance, we show that larger colonies of honeybees benefit more from communication than do smaller colonies. In fact, colony size and dance communication worked together to improve foraging performance; the estimated net gain per foraging trip was highest in larger colonies with unimpaired communication. These colonies also had the earliest peaks in foraging activity, but not the highest ones. This suggests they may find and recruit to resources more quickly, but not more heavily. The benefits of communication we observed in larger colonies are thus likely a result of more effective information-gathering due to massive parallel search rather than increased competitive ability due to heavy recruitment.

In self-organized societies like social insect colonies, the flow of information among individuals shapes group organization. Some species have evolved elaborate communication mechanisms, allowing specific information collected by a few individuals to be shared with other colony members. One well-known example is the honeybee waggle dance, which is used to communicate the location of resources like food, water and nest sites (von Frisch 1967). Because successful foragers choose whether to dance and how long to dance based on resource quality (among other features), a forager choosing a random dance to follow is likely to be directed to a high-quality resource (Seeley & Visscher 1988). The dance communication system thus serves not only to recruit naïve foragers to specific locations, but also, at the colony level, to integrate that information, resulting in a dynamic allocation of foragers among resources that tracks changes in resource quality (Seeley 1986; Schmickl & Crailsheim 2004).

If the effective distribution of information within a group is key to group organization, we might expect communication to become more valuable with larger group size. First of all, in large groups, coordination may be more important because otherwise individuals interfere with each other's task performance (Pacala et al. 1996). For example, if there are many independently searching central-place foragers, they are likely to encounter the same nearby food sources, which will quickly be stripped of their reward. At the same time, effective coordination may become more difficult in large groups, because information must be distributed more widely (Naug 2009). However, as group size increases, more individuals mean that more information can be gathered and integrated, and the potential value of that information may be greater. In collective foraging, it has been suggested that larger groups may be able to find resources more quickly (Naug & Wenzel 2006) and/or recruit more group members to help collect them (Johnson & Hubbell 1987), both of which could provide an advantage in competition. Larger groups might also search their surroundings more effectively, identifying more potential resources, and then use communication to select the most profitable ones to concentrate on (Beekman et al. 2004).

Although there are many reasons to think that communication could be of particular benefit to large groups, there is surprisingly little evidence that this is so (Dornhaus et al. 2012). One theoretical study showed that large colony size and recruitment are complementary features of a collective foraging strategy that performs

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well when resources are rich and patchily distributed (Johnson & Hubbell 1987). In line with this general prediction, a comparative study across 98 ant species found that more complex communication systems seemed to be associated with larger mature colony size (Beckers et al. 1989). A similar relationship has been suggested among eusocial bees (Michener 1974). A particular contrast can be drawn between the 'cottage-industry' foraging strategy of bumblebees, and the 'big markets' foraging strategy of honeybees (Heinrich 2004). The bumblebees' strategy, which involves relatively few foragers, searching independently, may work particularly well for foraging on small, scattered resources in northern temperate regions. In contrast, the enormous colonies of honeybees, coupled with their unique dance communication system, may give them the opportunity to exploit rich, ephemeral resources in their ancestral habitat: tropical forests. Although it has been argued that dance communication may indeed be more valuable in tropical forests than in other environments (Dornhaus & Chittka 2004), there is no evidence so far that colony size plays a role. In fact, an agent-based model of honeybee foraging concluded just the opposite: that the benefits of communication are independent of colony size, regardless of environment (Dornhaus et al. 2006).

In this article, we empirically evaluate the benefits of dance communication for honeybee colonies of different sizes foraging on natural floral resources. We find that larger colonies benefit more from communicating location information than smaller colonies do. We then explore the evidence for several hypotheses about why this might be so. First, because larger colonies must forage over greater distances in order to feed the entire colony, communication about resource location might enable them to overcome that disadvantage (hypothesis H1). Second, larger colonies have more individual foragers searching in parallel, so they may be able to locate resources more quickly. Communicating about the location of those resources could allow them to take advantage of early discovery by mobilizing foragers to exploit the resource before others do (hypothesis H2). Third, larger colonies have more individuals available to be recruited, so they may be able to recruit more foragers to particularly rewarding resources, giving them an edge in the competition for high-quality, ephemeral resources (hypothesis H3).

We assessed support for these three nonmutually exclusive hypotheses in two stages. In the first stage, we divided the hypotheses into two categories according to the predictions they make about the foraging performance of larger colonies compared to smaller ones, each with dance communication impaired and intact. If H1 is true, we predicted that larger colonies with impaired communication would perform worse than both smaller colonies and larger colonies with intact communication. If either H2 or H3 is true, we predicted that larger colonies with intact communication would perform better than both smaller colonies and larger colonies with impaired communication. In the second stage, we used patterns of foraging activity to distinguish between H2 and H3; in particular, we looked for peaks in activity that could be evidence of strong recruitment events. If H2 is true, we predicted that larger colonies with intact communication would have earlier peaks in foraging activity than any of the other three groups. If H3 is true, we predicted that larger colonies with intact communication would have higher peaks in foraging activity than any of the other three groups.

METHODS

Experiment

We measured the benefits of dance communication in honeybee colonies of different sizes by manipulating both colony size and communication and characterizing colony-level foraging success. The experiment was performed at the Santa Rita Experimental Range Headquarters in Arizona during the summer monsoon season (27 August–19 September 2011). This location and season was chosen because, in an earlier series of experiments across different environments, it was found to be the one where dance communication was of greatest benefit (Donaldson-Matasci & Dornhaus 2012). We assessed the diversity and abundance of floral resources twice during that period (2–4 and 16–18 September) using censored *t*-square sampling (Diggle 1983; Zimmerman 1991; Donaldson-Matasci & Dornhaus 2012).

The experiment was performed on eight colonies of domestic Italian honeybees, *Apis mellifera ligustica*. To control for genetic differences between colonies that could be linked to natural differences in colony size, we created four matched pairs of colonies. For each pair, we mixed stock from two original colonies to create one larger colony of about 6000 bees and one smaller colony of about 3000 bees. Although both these sizes would be considered small for managed honeybee colonies, 6000 workers is probably within the range observed for wild colonies in their natural habitat (Schneider 1990). All colonies were housed in 10-frame Langstroth hives, but the smaller colonies were given only five frames and were confined to one half of the box. Each larger colony received approximately twice as much stored honey, brood and empty honeycomb as the smaller colony in its pair. We estimated the number of bees in each colony by placing a 4×8 grid over each side of each frame and counting the number of squares covered by bees, and estimating the number of bees per square. We then took the average of two counts, one before and one after the experiment, as our estimate of the number of bees in each colony.

We used an established technique to manipulate the bees' ability to communicate the location of food resources (von Frisch 1967; Sherman & Visscher 2002; Dornhaus & Chittka 2004; Donaldson-Matasci & Dornhaus 2012). The waggle dance usually takes place on vertical honeycomb; the angle of the dance relative to straight up indicates the angle of the resource being advertised relative to the azimuth of the sun. When the hive is turned on its side so that honeycomb is horizontal, the usual reference point for the dance is removed. However, if a directional light source is available, it can be used as an alternative reference point for the dance (von Frisch 1967). This allows us to compare colonies that can communicate location information via the waggle dance (horizontal comb with a directional light source) with those that cannot (horizontal comb with a nondirectional light source). Each colony was housed in a modified hive box with frames held horizontally. Entering bees were constrained to walk across the top frame, so that the majority of dances would take place there (for example, Seeley & Towne 1992 found that 94% of dances take place within one frame-width of the hive entrance). The top frame was illuminated by a window, which was cut into the hive body. In the diffuse-light treatment, the window was covered with translucent white Plexiglas. In the oriented-light treatment, a cool fibre-optic light source was placed directly over the window. It has been shown previously that colonies in the diffuse-light treatment perform disoriented dances, while those in the oriented-light treatment perform directionally oriented dances that are as precise as those performed by colonies in the normal vertical position (Sherman & Visscher 2002). Furthermore, colonies in the diffuse-light treatment dance just as much, but recruit to artificial feeders less effectively than colonies in the oriented-light treatment (Sherman & Visscher 2002; Granovskiy et al. 2012).

The experiment consisted of eight 3-day treatment blocks, for a total of 24 days. During each treatment block, two pairs of colonies were given the diffuse-light treatment and two pairs were given the oriented-light treatment; in the following treatment block the treatments were switched. To measure foraging success,