in V_1. There is no evidence for this, but the presence of another stator connection is a possibility if there is overlap in projection.

Finally, it is not clear why the ATPase motor has such a complicated stator moiety, with an overall U-shaped form that must avoid friction with the central rotating stalk, although it is likely to be related to its mechanical stability.

E. J. Boekema, J. F. L. van Breemen, A. Brisson, T. Ubbink-Kok, W. N. Konings, J. S. Lolkema

Groningen Biomolecular Sciences and Biotechnology Institute, University of Groningen, 9747 Groningen, The Netherlands

e-mail: boekema@chem.rug.nl

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Insect behaviour

Evolutionary origins of bee dances

Although bumble-bees are highly social insects, their foraging has been considered to be managed as an individual initiative[1–4], in which each bumble-bee visits flowers not only to collect food, but also to gather information about other potential food sources[5]. Here we show that bumble-bees instead use a primitive, but surprisingly efficient, recruitment system: by performing extended excitatory runs in the nest, a single successful forager can alert the entire foraging force of a bumble-bee colony. But in contrast to what happens in other social bees, such as honeybees, the recruits are not informed about the location of the food. Instead, the successful forager brings home the odour of the newly discovered food source, conveying to the recruits information about the species of flower. These findings about bumble-bee communication shed new light on the early evolutionary origins of the elaborate dance language of the honeybee.

To investigate whether bumble-bees (*Bombus terrestris*) can communicate information about the discovery of a food source, we connected a nest box with a bipartite flight arena. A single forager was allowed to collect sucrose solution from an artificial flower in one half of the arena, whereas all other bees had access only to the other half of the arena, which did not contain food. This procedure ensured that interactions between bees could take place only in the nest, not at the food source. The number of bees entering the empty flight arena to search for food was counted during 12 periods of 1 hour each, when foragers were rewarded.

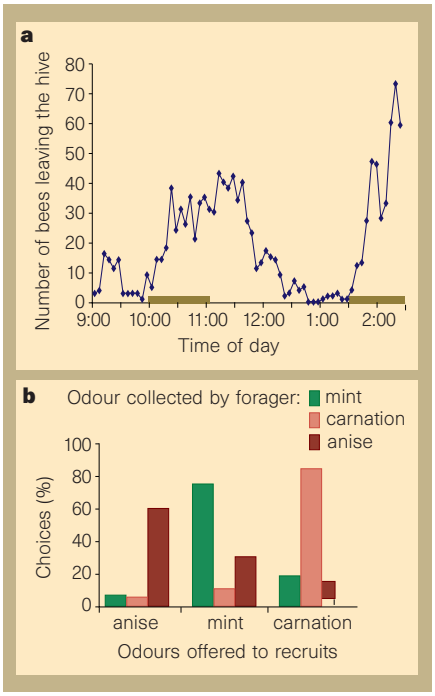

Figure 1 Recruitment in bumble-bees. **a,** The number of bees that leave the hive in a 5-minute period increases dramatically when one bee forages successfully (brown bars). **b,** Most bees choose the odour that is brought into the nest by a forager.

When compared with unrewarded control periods, the searching activity strongly increased when a single bee foraged ($P<0.01$, Wilcoxon test; Fig. 1a). Successful foragers in the nest, instead of just emptying their crop load and continuing to forage, would typically spend several minutes running across the nest, frequently bumping into nestmates and occasionally buzzing their wings.

Odour-preference tests indicated that bees leaving the hive strongly preferred the odour that was brought home by the forager ($n=90$, $P<0.001$, χ^2 test; Fig. 1b). Because floral scents are species specific, the odour helps recruits to find the food source used by the successful forager. To test whether positional information is also conveyed, we trained three foragers to collect sucrose from a feeder positioned 100 m west of the hive in an open field. Recruits had the choice between that feeder and two additional feeders placed 100 m north and south of the nest. New recruits distributed themselves randomly at these three feeders ($P=0.21$; χ^2 test). This failure of bumble-bees to recruit to specific points in space may explain why their communication has previously been overlooked. Bumble-bees therefore have a recruitment system that is specific for a flower species but independent of its location. This system for transmitting information resembles the round dance used by honeybees when food is found in the immediate vicinity of the hive[1,6].

But why have bumble-bees not evolved a communication system that includes information about where to forage? Such a system can be very costly. Honeybee recruits may take more than an hour to decide where to go, even if only two different locations are advertised[7]. They also take a long time to find a food source after receiving information about its location[8].

Bumble-bees live in small colonies, mainly in temperate habitats where floral food is less clumped than in the tropical habitats where the communication of honeybees and stingless bees evolved[1,5,6]. The advantage of communicating location might therefore not offset the cost. It may be sufficient to specify flower species to recruits, who can then rely on their own memory or searching ability to find flowers but still know when and for what to forage.

Understanding the communication of bumble-bees is central to reconstructing the evolutionary origins of the honeybees' waggle dance, which is one of the most complex systems in animal communication. Such a reconstruction requires us to compare the honeybees' behaviour with that of their extant relatives, the bumble-bees and stingless bees, which have excitatory motor patterns that serve to recruit nestmates to food sources[9]. This behaviour may be derived from a social facilitation of activity at the nest entrance, which is widespread among social insects[10]. Bumble-bees also share with stingless bees[9] and honeybees[1,6] the ability to learn the floral odours brought back by returning foragers. The bumble-bee recruitment system might therefore resemble that of the last common ancestor of the eusocial bees.

A. Dornhaus, L. Chittka

Lehrstuhl für Zoologie II, Biozentrum, Universität Würzburg, Am Hubland, 97074 Würzburg, Germany

e-mail: dornhaus@biozentrum.uni-wuerzburg.de

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