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Why do honey bees dance?

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Abstract The honey bee dance language, used to recruit nestmates to food sources, is regarded by many as one of the most intriguing communication systems in animals. What were the ecological circumstances that favoured its evolution? We examined this question by creating experimental phenotypes in which the location information of the dances was obscured. Surprisingly, in two temperate habitats, these colonies performed only insignificantly worse than colonies which were able to communicate normally. However, foraging efficiency was substantially impaired in an Asian tropical forest following this manipulation. This indicates that dance language communication about food source locations may be important in some habitats, but not in others. Combining published data and our own, we assessed the clustering of bee forage sites in a variety of habitats by evaluating the bees' dances. We found that the indicated sites are more clustered in tropical than in temperate habitats. This supports the hypothesis that in the context of foraging, the dance language is an adaptation to the particular habitats in which the honey bees evolved. We discuss our findings in relation to spatial aggregation patterns of floral food in temperate and tropical habitats.

Keywords *Apis mellifera* · Dance language · Evolution · Foraging · Orientation

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Introduction

Honey bees communicate the location of a rich food source using the waggle dance, moving on the comb in a repetitive figure-of-eight shaped pattern (Frisch 1967). The mechanisms by which bees encode distance and direction of a food source are well understood (Frisch 1967), and the long-standing controversy about whether recruits can actually use the information from the dances (Wenner 1967) is now resolved (e. g. Gould 1974; Polakoff 1998; Esch et al. 2001). But what were the ecological conditions under which the dance language evolved? What is its benefit to colony foraging efficiency under natural conditions? The experimental conditions under which the mechanisms of the bee dance language were explored were often inappropriate to probe its adaptive significance. Clearly, in artificial conditions with only a single ad libitum sucrose feeder placed somewhere in the flight range of a beehive, the benefits of communicating its location are obvious, especially if the feeder is located a large distance from the hive (Kirchner and Grasser 1998, Dornhaus 2002; Sherman and Visscher 2002). If, on the other hand, floral food is homogeneously distributed in space, there is no advantage in informing nestmates of the location of a profitable food source. Most natural distributions of flowers will be between these two extremes (Beekman and Ratnieks 2000; Osborne and Williams 2001; Steffan-Dewenter and Kuhn 2003). During foraging bouts in nature, bees often have to visit thousands of flowers widely scattered in space. Thus, understanding the adaptive significance of the dance requires us to measure the performance of bee colonies under *natural* conditions and compare it to performance under conditions where the information flow between dancers and recruits is impaired. We predict that the adaptive benefits of dance communication will depend on the spatial aggregation pattern of flowers around the colony, and therefore on the environment in which the bees forage.

In a recent paper, Sherman and Visscher (2002) have investigated benefits of location communication, using

natural food sources and not artificial feeders, and found such benefits in winter, but not in other seasons. However, their experiments were performed in a heavily disturbed suburban habitat, where the spatial aggregation pattern of nectar plants does not necessarily reflect the conditions relevant for natural honey bee foraging. To understand the selection pressures that led to the evolution of the honey bees' dance, colony foraging performance should ideally be quantified in undisturbed habitats, where human settlement and agriculture have not affected the distribution of floral food resources. Here we attempt to tackle this issue, by focussing on the comparison between temperate and tropical habitats. This is because *Apis mellifera*, the European hive bee in which the dance language was first described, occurred historically in temperate habitats west of the Iranian desert (Ruttner 1987). The colonization of sub-Saharan Africa originated from Europe via Arabia, and the honey bee spread in the new world tropics is man-induced (Ruttner 1987). However, *Apis mellifera* shares the dance with all other species of honey bees, most of which are limited in their distribution to tropical Asia (Ruttner 1988). The evolutionary origins of these dances are therefore thought to have occurred in an open-nesting tropical ancestor of extant honey bees (Dyer and Seeley 1989). These ancestral honey bees foraged under conditions wholly different from those of European *A. mellifera*. In tropical forests, floral food is mostly arboreal, and therefore highly clumped in space. Trees offer many thousands of flowers on very defined coordinates in space, and there are often large distances between trees flowering at the same time (Kress and Beach 1994). Conversely, Central and Southern Europe were probably not fully covered by forests after the last ice age as traditionally thought (Vera 1996). Instead, in temperate habitats, widely scattered herbs and shrubs form a significant component of a bee's diet (Heinrich 1979). We compared the success of colonies with and without location communication in temperate as well as tropical habitats. In addition, the spatial distribution of food sources in some examples of temperate and tropical habitats is explored here by evaluating the locations indicated in the dances of bees. We surmise that such dances provide a fairly accurate map of forage sites that are of sufficient interest for the bees.

Methods

Influence of location communication on foraging success

We tested the effect of communicating location of food sources on foraging success by measuring foraging success of colonies in which direction communication was prevented, and of the same colonies under conditions where normal communication could take place. To prevent bees from exchanging information on food location via dances, we used a method similar to that employed by Sherman and Visscher (2002). In the dark hive, the angle of the dance relative to the direction of gravity on the vertical comb indicates the direction of food relative to the azimuth of the sun (Frisch 1967). Tilting the combs into a horizontal position

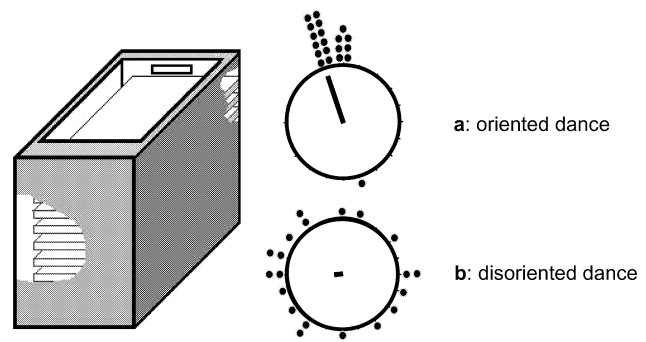


Fig. 1 Design of the experimental hives and orientation of the dances on the horizontal combs. Regular 10-frame hive-boxes were turned on their side and the frames fastened horizontally. The top was fitted with a glass window, such that the first comb was exposed to the sun if the window was uncovered. Forager bees could enter through a slit opening that led onto the first comb. If no light is allowed to pass through the window, dances become disoriented and waggle runs within each dance point in random directions. If the window is uncovered, bees are able to orient their dances, using the sun as a reference. The *right panels* show examples of single dances by a worker hive bee *Apis mellifera* with sight of the sun (*a*; length of mean vector $r=0.89$, $n=20$) and with directional cues removed (*b*; $r=0.17$, $n=20$). Each data point corresponds to the direction of a single waggle run (bins are 18°)

eliminates the possibility of using gravity as a reference. Bees then perform dances in chance directions so that dances lose their spatial information (Frisch 1967). Recruits can then only use cues outside the hive, such as scent marks, to find food sources (Kirchner and Grasser 1998). If bees are offered a direct view of the sun or a polarized skylight, oriented and functional dances are again performed even on a horizontal surface (Frisch 1967). We used specially constructed hives with horizontal combs (Fig. 1). The hives had a window above the comb on which dances were performed; by covering or uncovering the window we controlled whether bees were able to perform oriented dances. Experiments using artificial feeders showed the success of this technique in disrupting the flow of accurate information between scouts and recruits: when dances are disoriented, recruitment success is lower, especially when feeders are at remote locations from the hive (Dornhaus 2002). We compared the success of colonies with and without location communication in two temperate locations representative of the present distribution of European honey bees (*Apis mellifera*) and one tropical location representative of the habitats where the honey bees' dance evolved. These were: (1) a Mediterranean shrubland habitat in the Sierra Espadán Nature Reserve, Spain; (2) a Central European site near Würzburg, Germany, where agricultural land is mixed with natural meadows; and (3) a dry deciduous forest in the Bandipur Biosphere Reserve, India. At the sites (1) and (3) there was no intensive agriculture or other human influence on vegetation, and thus flower distribution pattern, within several kilometers of the colonies.

We placed two *Apis mellifera* colonies with ten horizontal combs and approximately 5,000 workers in each of these locations. This is within the range of colony sizes observed in wild populations; it also ensures that bees are not limited by the space for honey storage. The colonies were switched between oriented and disoriented dancing every 2 days, by covering or uncovering the window over the dance floor. Overnight, hives were restored to their vertical position. Foraging success was assessed using daily weight changes of hives, which mostly reflect nectar intake (Seeley 1995). Experiments were performed in spring in the temperate habitats (24 March 15 April 2000 in Spain, 27 April to 25 May 2000 in Germany) and in the dry season in the tropical habitat (7 February to 9 March 2001). To test for effects of time of year, we repeated the same experiment with two three-comb hives monitored

over the entire foraging season from May to September in the central European location (9 May to 29 September 2000).

If no differences in foraging success were found between days on which bees were able to use the waggle dance to accurately communicate location and days on which they were not, this could potentially be due to the fact that bees compensate lower per-trip intake rates by making more trips per bee or dispatching more bees as foragers. To control for such effects of total number of foraging trips, we measured the number of bees leaving the colony per time interval (the colony's "activity") in two of the habitats (Spain and India). Activity was measured on 20 days at 1100, 1400 and 1700 hours for 5 min each for the colonies in the experiment run in Spain; in the experiment run in India, activity was measured on 12 days for 5 min every hour from 0600 to 1800 hours for both colonies.

Evaluation of honey bee dance maps

One explanation for differential effects of disorienting dances in different habitats is different spatial distribution of resources. It is therefore interesting to compare the resource distribution in different habitats. Since mapping the actual flower distribution in the foraging range of a honey bee colony (approx. 100 km²; Seeley 1995) is impossible, we used the information that the bees themselves provide on the locations where they forage, by analysing their waggle dances. In the Indian location, all dances occurring on the first frame of an undisturbed beehive were videotaped for 5 min every hour from 0600 to 1800 hours on 10 days during the experimental period. The direction of the waggle runs was measured for each dance and translated into the corresponding compass direction. The time per dance circuit was calculated by measuring the time needed to perform at least five waggle runs. The average number of dances recorded and analysed in this way was 31 per day. Time per dance circuit (T) was transformed into a distance from the colony (D) using the following formula (Waddington et al. 1994).

$$D = 89.695 - 345.256 * T + 228.224 * T^2 - 10.951 * T^3$$

This method has been used previously to create forage maps of honey bees in several habitats: temperate forest (Visscher and Seeley 1982); African tropical forest (Schneider 1989); a disturbed suburban habitat (Waddington et al. 1994) and a disturbed urban habitat mixed with more natural open moors (Beekman and Ratnieks 2000).

To see if the degree of clustering varied between different habitats, we calculated the patchiness coefficient *R* (Clark and Evans 1954) for our maps and those previously published. A value of 1 for *R* indicates random distribution, lower values indicate clumping, and higher values are a sign of hyperdispersion. *R* is calculated as the relation of observed mean nearest neighbor distances to expected nearest neighbor distances under conditions of random dispersion (for details on the calculation of *R* see Clark and Evans 1954). We calculated *R* for each published forage map that showed dances occurring on one day. All *R* are calculated for the area around the colony within the radius of the dance indicating the farthest location on the day for which the map was created. Likewise, for our own data, we calculated *R* for each day. We were then able to compare different habitats by their median patchiness, derived from the distributions of *R* for each habitat. Sample size for each habitat is thus the number of maps, i.e. the number of days, for which data were available.

Results

Influence of location communication on foraging success

As in previous studies (Seeley 1995), there was high variation in daily weight changes (from -630 g to

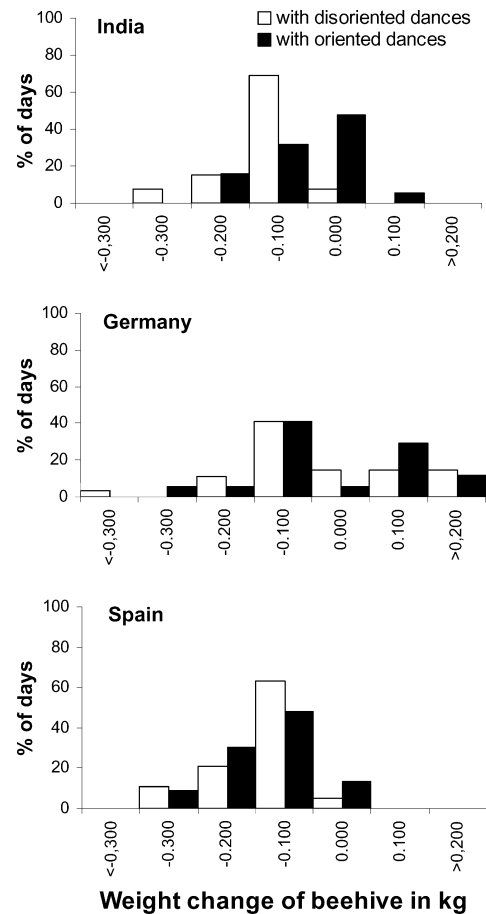


Fig. 2 Foraging success of honey bee colonies in different habitats with and without location communication, given as frequency distributions of daily weight changes. Only in the experiment performed in India were the two distributions significantly different. Values on the *x*-axis indicate lower limits of bins

+710 g). In temperate habitats, eliminating the ability to communicate direction resulted only in small and statistically not significant effects on colony foraging success: median daily weight changes of all colonies were 0 g (days with oriented dances) versus -40 g (days with disoriented dances) in the central European and -60 g (oriented) versus -75 g (disoriented) in the Mediterranean habitat (Kolmogorov-Smirnov-Test, central Europe: $Z=0.61$, $n=44$, $P=0.85$; Mediterranean: $Z=0.44$, $n=42$, $P=0.99$; Fig. 2). Neither was an effect of eliminating direction information found in the 3-comb hives monitored over the entire foraging season ($Z=0.68$, $n=187$, $P=0.74$). For the latter experiment, we also broke down the weight change data by spring (9 May to 20 June), early summer (21 June to 20 August) and late summer (21 August to 20 September), but did not find a significant difference in any season (spring: $Z=1.03$, $n=57$, $P=0.24$; early summer: $Z=0.41$, $n=83$, $P=0.97$; late summer: $Z=0.45$, $n=37$, $P=0.99$). Thus, foraging success in the experiments performed in temperate habitats was not significantly lower even if bees were not able to communicate information on the location of profitable

food sources via the waggle dance. This was not the case in the third habitat tested, the tropical dry forest in India. Foraging success there was increased with functioning communication: median weight change was +5 g on days with oriented dances compared to -65 g on days when dances were disoriented ($Z=1.45$, $n=45$, $P=0.02$; Fig. 2).

The flight activity of the colonies did not depend on the manipulation performed, which means that bees leave the colony in the same numbers when they have only followed disoriented dances. In the experiment in Spain the median number of bees leaving the colony in the 15 min measured was 161 on days with, and 119 on days without oriented dancing (Mann-Whitney U -Test: $U=171.5$, $n=38$, $P=0.79$). For the experiment in India, the median number of bees leaving the colony in the 60 min of measurement per day was also not significantly different between days with and without oriented dancing (medians were 759 and 699, $U=69$, $n=24$, $P=0.89$). In conclusion, colonies did not react to the manipulation by making more or fewer foraging trips, and foragers still left the colony in the same numbers when dances were disoriented.

In the experiment performed in Spain, there was no statistically significant correlation between flight activity and weight change (days of disoriented dancing: Spearman $r_{17}=-0.30$, $P=0.20$; days of oriented dancing: $r_{21}=-0.20$, $P=0.37$). In the experiment performed in India, where foraging success was influenced by the bees' ability to communicate, the colony's activity did significantly correlate with the change in hive weight when bees were able to communicate location (Spearman $r_{13}=0.74$; $P=0.004$), but not when bees were prevented from communicating location ($r_{11}=0.26$, $P=0.44$). This may indicate that, without accurate recruitment, many bees who left the hive were unsuccessful or not foraging at all, which would eliminate the tight correspondence of number of trips made and amount of nectar collected. Similarly, if nectar loads vary widely, as when they depend on the quality of the resources discovered by each individual, there will be no close connection between number of trips made and total nectar intake of the colony. However, if many foragers use the same food source as a consequence of precise recruitment, fewer unsuccessful trips, less variable nectar loads, and therefore a correlation between number of trips and foraging success, would be expected. The fact that we did not find such a correlation either in Spain or on days with disoriented dances in India supports the hypothesis that dances have a low impact on bees' foraging success in the temperate habitat.

Evaluation of honey bee dance maps

The analysis of the videotaped waggle dances in the experiment performed in India showed that bees were foraging up to 10 km from the colony, but most of the dances indicated sources much closer to the colony. The median distance indicated was 462 m. The average

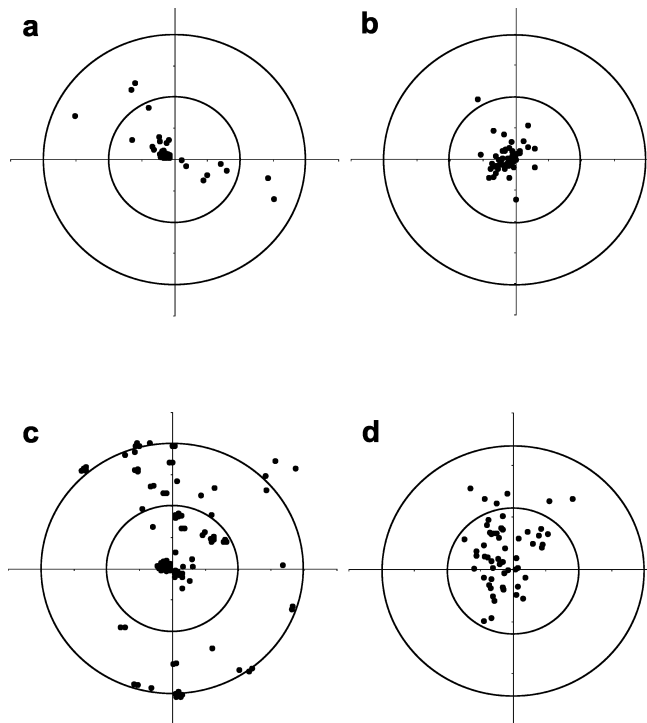


Fig. 3a–d Four examples of maps constructed from analysing waggle dances (**a, b** this study, dry forest habitat in India, $R=0.25$ and 0.56 , respectively; **c** Schneider 1989, mixed tropical forest in Africa, $R=0.52$; **d** Waddington et al. 1994, non-forested temperate habitat, $R=0.75$). These maps were specifically selected to visualize the pronounced clustering that can occur in tropical forest habitats (**a, b, c**), versus the more dispersed forage sites in non-forested temperate habitats (**d**). Each map represents foraging locations used by bees on one day (**a** and **b** are from the same colony on different days). The colony is in the centre of each map, circles are at 2 km intervals

patchiness coefficient R was 0.53 (SD 0.22 , $n=10$), indicating a high deviation from a random distribution (Fig. 3). To compare the patchiness of different habitats, we calculated the values for R for each day in each of the studies. Patchiness is significantly higher (indicated by lower values of R) in the tropical sites (Africa and India) compared to the temperate (all other) habitats (Mann-Whitney U -Test: $U=217$, $n=58$, $P=0.008$). Even within these groups, patchiness varies considerably (Fig. 4). The temperate forest habitat analyzed by Visscher and Seeley (1982) has a relatively high degree of patchiness compared to the other, non-forested temperate habitats. The degree of forest cover might therefore be an important value determining patchiness of honey bee food sources.

Discussion

Honey bees are unique among social insects in their ability to communicate food locations using the waggle dance. Why has this communication system not arisen in other social bees, for example bumble bees? Our study

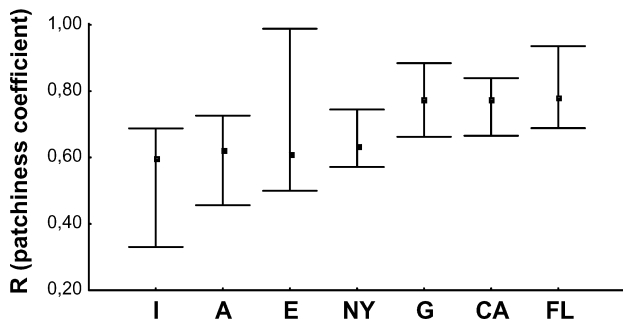


Fig. 4 In different habitats, the resources indicated by bees in their dances show different degrees of clustering. Temperate habitats tended to show more randomly distributed dances, reflected in values of R closer to 1. For each habitat the median of the values of R calculated for the days analysed is shown [habitats are *I* dry forest, India, this study, $n=10$ days; *A* mixed forest, Africa, $n=10$ (Schneider 1989); *E* temperate heather and disturbed habitat, England, $n=6$ (Beekman and Ratnieks 2000); *NY* temperate forest, New York, USA, $n=8$ (Visscher and Seeley 1982); *FL* disturbed habitat, Florida, USA, $n=10$; *CA* disturbed habitat, California, USA, $n=12$ (Waddington et al. 1994); *G* temperate disturbed habitat, Germany, $n=2$, own unpublished data]

provides experimental evidence that ecological factors, such as food source distribution, may determine the usefulness of communicating the locations of food sources. The waggle dance may be essential for efficient foraging in some conditions, but not in others. Of the three habitats in which we performed our experiment, foraging success was only improved by accurate dance communication in the Asian tropical forest, whereas we found no effect in either the undisturbed or the disturbed European habitat.

This coincides with the fact that we found food sources to be more clustered in the dance maps published from tropical habitats than those from temperate habitats. We therefore think that differences in spatial distribution of food sources are the most likely cause for the higher importance of dance communication for foraging success in our Indian experiment. It should be expected that foragers profit most from location information if there are few but rich resource patches that are widely spaced and profitable for only a short time. Such distributions might be more likely to occur in tropical habitats (Sherman and Visscher 2002). The results from our analysis of the distribution of sites indicated in bees' dances in tropical and temperate habitats support this hypothesis, but more extensive surveys and comparisons of more habitats at all times of the year are needed to draw conclusions about a general difference in resource distribution between temperate and tropical habitats. There are, however, reasons to suppose that such a difference could exist. In tropical forests, blooming trees are the main source of food for bees (Whitehead 1968). These often offer millions of flowers (Kress and Beach 1994) with large nectar amounts (Appanah 1990), but densities of trees in flower are often low (Janzen 1971; Frankie et al. 1974; Clark 1994), which creates an extremely patchy environment. In addition, food source locations might change frequently:

tropical trees often flower only for a few days (Primack 1985; Schneider 1989). In such a situation, communication about these few, ephemeral resources might be essential for efficient foraging. In temperate habitats on the other hand, the bees' diet contains a much higher portion of widely distributed herbs and shrubs (Heinrich 1979), since many trees are wind-pollinated (Whitehead 1968). Plant individuals often have only small numbers of flowers with usually minute nectar amounts (Heinrich 1976) and longer flowering times (Primack 1985). Both the spatial and the temporal distribution of food sources might thus differ between tropical and temperate habitats. These factors may make location communication less worthwhile in some temperate habitats, and occasionally even unnecessary. However, in those temperate habitats with continuous forest cover, communicating location may be as important as in tropical forest (Visscher and Seeley 1982).

Our finding that dance information has no bearing on foraging success in the two European habitats might therefore be explained by the distribution of food sources in these habitats. Food source distribution might explain our results in two ways: it either influences the importance of communication directly, by determining foraging efficiency with and without oriented dances, or in history, by causing differing selection pressures on bees living in different habitats. Dances of bees in habitats where communicating location information does not influence foraging success might have lost their precision, such that disrupting them is without effect. Indeed, there is evidence for relaxed selection on dance precision in temperate bees: there is higher scatter in the direction indication in dances of temperate honey bees than in dances of tropical species (Towne and Gould 1988) or even dances of the same bees communicating locations of nest sites instead of food sources (Weidenmüller and Seeley 1999), although this difference might also have adaptive explanations (Towne and Gould 1988; Weidenmüller and Seeley 1999). If the dance language has lost its importance for foraging in some habitats, stabilizing selection might nevertheless result from its function of communicating locations of nest sites (Weidenmüller and Seeley 1999).

Even though the precision of the dances of temperate honey bees may be lower than that of tropical bee species, tests using artificial feeders with defined co-ordinates in space still indicate that the dances are accurate enough to pinpoint a single food source in the foraging range of the colony, and that disorientation of dances has a strong effect under such conditions (Frisch 1967; Dornhaus 2002; Sherman and Visscher 2002). Therefore, our result that disorienting dances has no effect on colony foraging success cannot be explained by lack of precision in the bees' dances in the European bees as compared to those tested in India. *A. mellifera* was only established in India after the 1960s, using European strains (Chahal and Gatoria 1983). Therefore, these bees have not been exposed to tropical forest resource distributions long enough that a change in dance dialect seems probable.

Our study is the first to quantify the influence of accurate dance communication on foraging success in different habitats. To be able to generalize our results, and to show which habitat characteristics are important (latitude or forest cover, for example), measurements in more different habitat types have to be made, and over longer time spans. Also, it would clearly be desirable to measure effects of dancing in more colonies, since it has been shown that there can be variation in the precision of dances between colonies (Esch 1978). Since the number of colonies used in our experiment is small, and different colonies were used in the different habitats, we cannot fully exclude the possibility that colony-specific effects influenced our results.

Besides differences between habitats in spatial distribution of food sources, differences in the temporal distribution could explain why the effect of disrupting dance information was habitat-dependent. In our experiments, the colonies were deprived of accurate dance information for periods of 2 days. Two days might be too short to significantly affect foraging success in temperate habitats if profitable resources last for much longer periods of time, since experienced foragers can continue to visit sites already known to them. However, studies of changes in food patches visited by bees over time indicate that the turnover of the most profitable resources is usually much more rapid, with a high proportion of indicated sites changing from day to day (Seeley 1995), and it is also well known that nectar and pollen availability often changes in a matter of hours (Kleber 1935).

The results presented here are therefore consistent with the hypothesis that the honey bee dance language is an adaptation to the tropical conditions under which the genus *Apis* diversified, and may no longer be essential for efficient foraging in some temperate habitats. When food is less aggregated in space than in tropical forest, foraging by individual initiative, or communication only through floral scent and unspecific alerting signals (Lindauer and Kerr 1966; Dornhaus and Chittka 1999), may be as efficient as communication of location. In addition, competition by other bees, which may also differ between habitats, is likely to influence the temporal dynamics of resources (Steffan-Dewenter and Tschardt 2000), and thus the relative importance of the dance language. In order to understand the fitness advantage bestowed by a behavioral trait, we must measure this advantage in the economy of nature, not under artificial laboratory conditions. *Even if* the bee dance language strikes us as one of the most astonishing behavioral feats in animals, its complexity is by no means a warranty for its adaptiveness under any conditions. We need to understand the circumstances under which a given trait confers an advantage, if we are to identify the ecological conditions that might have favoured its evolution. Ideally, we should quantify the relative fitness benefits conferred by a given behavioral trait *relative to animals that lack this trait*. The problem is, there is often no natural variation in extant animals: for example, there are no known natural variants

or mutant bees that do not dance; thus we cannot measure natural selection in progress. But by using simple manipulations such as here, we might sometimes be able to construct behavioral phenotypes that allow more direct tests of adaptation.

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