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Intra-Colonial Variability in the Dance Communication in HoneyBees (*Apis mellifera*)

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Abstract

Honeybees have evolved numerous mechanisms for increasing colony-level foraging efficiency, mainly the combined system of scout-recruit division of labour and recruitment communication. A successful forager performs waggle dances on the surface of the comb where it interacts with nectar receivers and dance followers. A forager uses tremble dance when it experiences difficulty finding a receiver bee to unload food upon return to the hive. A bee colony containing numerous subfamilies may increase its efficiency in dance communication if dances are realized by particular groups of specialized individuals or subfamilies rather than by undifferentiated workers. In this study, we determined the subfamily frequencies of waggle and tremble dancers in a colony headed by a naturally mated queen, where the 17 subfamilies can be identified by microsatellite genetic markers. Our results demonstrate that a genetic component is associated with the dance communication in honeybees. More than half of the waggle dances and the tremble dances were performed by workers from only four subfamilies in each case.

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Introduction

In most species of highly eusocial insects, workers exhibit age polyethism: they pass through distinct behavioural phases during their lives. Workers labour in the nest when they are young and forage outside when they are older (Robinson 1992).

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Genetic determinants of behavioural differences among workers within honey bee colonies have been demonstrated for several tasks, as for example, guarding the nest entrance, undertaking, foraging for nectar and for pollen (reviewed in Page and Robinson 1991). Robinson and Page (1989) have suggested that the subfamilies of a colony differ in task performance because they have different distributions of behavioural response thresholds for task-eliciting stimuli.

Genetic variance in foraging behaviour and dance communication is known to exist in honeybees (Oldroyd et al. 1992, 1993). Genetic variance in rates of pollen collection exists in colonies of selected bees (Mackensen and Nye 1969; Hellmich et al. 1985). In colonies of unselected bees, subfamilial variance has been demonstrated for various traits related to foraging, namely (i) in rates of pollen collection (Calderone et al. 1989; Robinson and Page 1989; Oldroyd et al. 1992), (ii) for preferred foraging distance (Oldroyd et al. 1993), (iii) in the average age at which bees first begin to forage (Calderone and Page 1988), (iv) among foragers (e.g. nectar and pollen foragers seem to belong to genetically different groups; Robinson and Page 1989; Dreller et al. 1995; Page et al. 1995) and (v) in the proportion of foragers which locate forage patches by independent scouting, as opposed to following recruitment dances (Dreller 1998).

At the individual level, the efficiency of a scout depends on its ability to find a rich food source, to communicate about its information to other workers, and to mobilize them to forage. Successful foragers perform waggle dances on the surface of the comb where they interact with nectar receivers and dance followers. The waggle dance is used for recruitment by communicating information about the distance, direction and quality of resources at distances greater than about 100 m from the hive (von Frisch 1967).

Genetical variance in dance communication related behavioural traits is well-documented on the level of subspecies with respect to their indication of distances to feeding sites (von Frisch 1967; Rinderer and Beaman 1995). Oldroyd et al. (1991) demonstrated subfamilial variance for propensity to undertake both waggle and round dances, and suggested a strong tendency for recruits to follow dances performed by a member of their own subfamily. However, in that study the results were confounded by the strong possibility of repeated observations on the same bee (Oldroyd and Rinderer 2001). Combined with genetic variance for foraging task or propensity to dance, repeated observations can lead to an artefactual appearance of positive subfamilial interactions during dance communication (Oldroyd et al. 1994; Oldroyd and Rinderer 2001). Recently, Kirchner and Arnold (2001) showed that neither in a colony consisting of only two subfamilies nor in a colony consisting of 17 subfamilies there was any evidence for subfamily discrimination among dancers and their followers.

A forager performs a ‘tremble’ dance when it returns to its hive laden with nectar, but experiences difficulty finding a receiver bee to unload her (Seeley 1992). The consequence of this dance is a dramatic increase of the number of bees engaged in nectar reception (Seeley 1992; Kirchner and Lindauer 1994; Seeley et al. 1996). The tremble dance constitutes a negative feedback system counterbalancing the positive feedback of recruitment by waggle dances (Kirchner 1993b;

Nieh 1993). It prevents the working force of the colony from flying out in search of a feeding site advertised by waggle dances when there are already so many foragers coming in that the food storers cannot unload them. One message of the tremble dance seems to be directed to the waggle dancers, telling them that further recruitment would not be profitable at the moment (Kirchner 1993a). There is presently no studies concerning the subfamilial variance for the tremble dance.

As a result of polyandry and sperm mixing, *Apis mellifera* colonies are assemblages of 6–20 subfamilies (Estoup et al. 1994). A subfamily consists of the offspring of the queen and one of her mates. Daughters of each drone are super-sisters having, on average, 75% of their genes in common by descent, whereas daughters of different fathers are half-sisters and have, on average, only 25% of their genes in common by descent (Page and Laidlaw 1988). Because of the genotypic variability in the same colony, which is because of the polyandry of the queen, the honeybee seems a good model to study the genetic basis of specialization of tasks in an animal society. However, until now, most of the studies concerning the task specialization in foraging activity have been conducted with colonies in which the number of subfamilies was experimentally reduced to 2 or 3 by artificial insemination of the queen. Such a colony does not reflect the natural situation, and results based on these colonies may be an artefact of the family structure compared with those in wild type colonies (Hogendoorn and Velthuis 1988; Calderone et al. 1989).

A ‘natural’ bee colony containing numerous subfamilies may increase its efficiency in dance communication if dances are realized by particular groups of specialized individuals or subfamilies rather than by undifferentiated workers. The aim of the present study was to determine whether subfamilial variations are found within the communication system, and particularly to unravel the subfamily composition of waggle dancers and tremble dancers. We therefore determined the subfamily frequencies of waggle and tremble dancers in a colony headed by a naturally mated queen, where the subfamilies can be identified by microsatellite genetic markers.

Methods

Biological Material

The experiments were conducted between May and Aug. 1997 using a honeybee colony (*A. m. carnica*) in which the 1-y-old queen has been naturally mated. The colony of about 6000 workers was housed in an observation hive in Konstanz, Germany. One side of the observation hive was open during the experiments in order to pick bees for genetical analysis directly from the combs. Nectar foragers were trained to artificial feeding sites at 500-m distance from the hive. They were individually marked at the feeder. The dance floor area of the observation hive was observed and videotaped.

Marked foragers which have been observed 10 times in a row to perform a waggle dance after returning from the feeding site were classified as waggle dancers. After their next return to the hive, one more dance was observed and the dancer and one or two of the dance followers were picked from the comb, frozen on dry ice and kept for a later determination of their subfamily membership. Dance followers were defined as bees attending a waggle dance persistently for several circuits. Marked foragers performing a tremble dance were observed for 5 min and then classified as tremble dancers and frozen for later analysis (the behaviour is known to be exhibited fairly persistently for up to 1 h, one single 5 min interval of observation was therefore regarded as sufficient to correctly classify the dancers as tremble dancers and as equivalent to the observation of 10 waggle dances lasting typically less than 2 min). A total of 146 foragers and 134 dance followers were collected. As most of the returning foragers performed waggle dances and only 10–20% performed tremble dances, we collected relatively more dancing workers among the total population of tremble dancers than among the total population of waggle dancers in order to make sure that the sample sizes would be sufficient for the analysis. A total of 87 waggle dancers and 59 tremble dancers were collected. Another sample of 172 workers (control bees) were taken randomly at night to represent the overall subfamily composition of the colony.

DNA Amplification and Genetic Analysis

DNA was extracted according to Garnery et al. (1990). The workers were assigned to their respective subfamily using four highly variable microsatellite loci (A29, A76, A107, B124) (Estoup et al. 1994). polymerase chain reactions (PCR) were carried out in a 10-μl reaction mixture using incorporation of ^{33}P-dATP
1 (Estoup et al. 1994). The loci were amplified using Uno Biometra thermocyclers through 30 cycles consisting of denaturation for 30 s at 94 °C, annealing for 30 s at 54–58 °C (depending on the locus), and elongation for 30 s at 72 °C. A sample of 2 μl of each reaction was run on 6% polyacrylamide sequence gels.

Statistical analysis

The data were cross-classified by subfamily ($n = 17$) and behavioural class (three behaviours, waggle dance, tremble dance and dance following, and control). The whole table was tested via a R × C Fisher's exact test (Monte-Carlo simulation in Pstat, loaded from http://www.wisc.edu/genetics/CATG/pstat/index.html – William Engels). The same test was then applied to the four classes taken pairwise in order to know (i) if the frequency distribution of each of the three behaviours was significantly different from that of the control, and (ii) if the frequency distribution of the waggle dancers was significantly different from that of the dance followers, and from that of the tremble dancers.

As we performed five different tests from the same experimental sample, we applied the corresponding full Bonferroni correction (Miller 1981) to the level of significance: the new α-level to which the probabilities extracted from the Fisher's exact tests are compared with $\alpha' = 0.0102$ in order to detect a significant difference with a confidence level of 5%.

Results

Genetic Structure of the Colony

Seventeen subfamilies were identified in the complete sample. The contributions of the fathers to the progeny of the queen were unequal ($\chi^2 = 41.8$, df $= 16$, $p < 0.05$). Table 1 shows that the subfamily probability distributions were, globally, different between the four classes of bees (Fisher's exact test: $p = 2 \times 10^{-6}$).

Intra-colonial variability in the waggle dance

The distribution of the subfamilies of the waggle dancers was significantly different from that of the control (Fisher's exact test, $p < 0.001$) (Table 1). This result suggests that a genetic component is associated with the waggle dance behaviour. For example, more than half of the waggle dancers (54%) belong to only four subfamilies (numbers 4, 5, 6, 10), whereas the proportion of these subfamilies in the colony was only 22.7%. One of them, subfamily number 5, appears particularly specialized, as its members performed 6.1 times more waggle dances than expected.

In contrast, six subfamilies (numbers 3, 13, 14, 15, 16, 17) were hardly involved in the waggle dances (11.5%), although they represented more than half (50.6%) of the controls. The remaining seven subfamilies (numbers 1, 2, 7, 8, 9,

Table 1. Number of waggle dancers, tremble dancers, dance followers and control bees of the respective subfamilies

Subfamily	Waggle dancers	Tremble dancers	Dance followers	Controls
1	5	10	14	9
2	3	4	4	7
3	1	6	6	7
4	9	8	15	12
5	9	3	7	3
6	17	3	19	13
7	5	8	8	4
8	4	2	3	5
9	7	1	8	7
10	12	4	11	11
11	3	0	2	7
12	3	3	9	7
13	3	0	6	23
14	0	2	5	14
15	4	1	6	17
16	2	2	6	14
17	0	2	5	12
Total	87	59	134	172

11, 12) were more or less in the same proportion among the waggle dancers (34.5%) as in the controls (26.7%).

Intra-Colonial Variability in the Tremble Dance

The distribution of the subfamilies of the tremble dancers was, significantly different from that of the controls (Fisher's exact test, $p < 0.001$) (Table 1). This result suggests again that a genetic component is associated with the tremble dance behaviour. For example, more than half of the tremble dancers (54.2%) belong to only four subfamilies (numbers 1, 3, 4, 7) whereas their proportion in the colony was only 18.6%. One of them, subfamily number 7 appeared particularly specialized, as it performed 5.9 times more tremble dance than expected.

In contrast, seven subfamilies (numbers 9, 11, 13, 14, 15, 16) were hardly involved in the tremble dances (13.6%), although they represented more than half (54.7%) of the controls. The remaining six subfamilies (numbers 2, 5, 6, 8, 10, 12) were more or less among the same proportion in the tremble dancers (32.2%) as in the controls (26.7%).

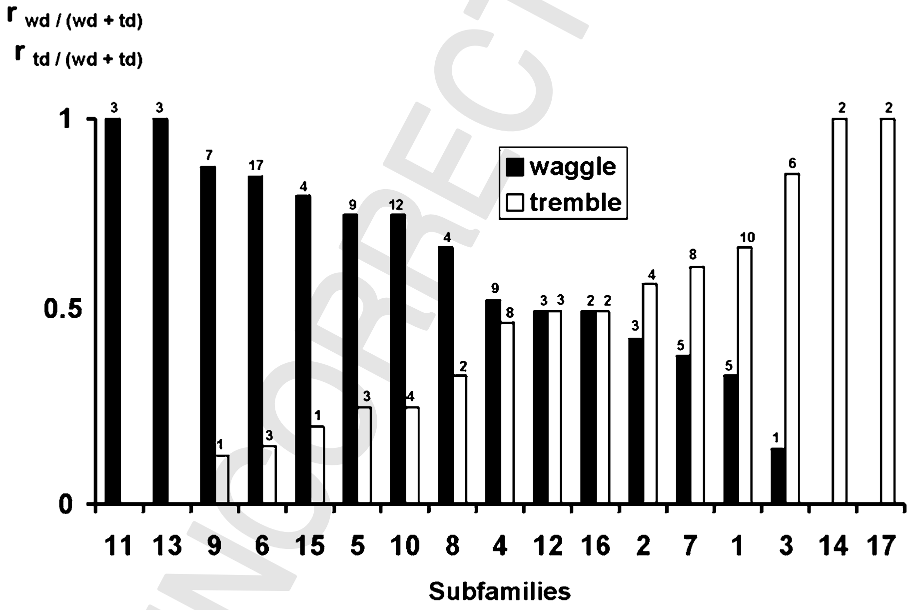

Fig. 1: Ratio distributions of relative frequencies of waggle dancers and tremble dancers. The ratio distributions of relative frequencies of waggle dancers and tremble dancers are $r_{wd/(wd+td)}$ (black bars), and $r_{td/(wd+td)}$ (white bars), respectively. The subfamilies have been ranked by decreasing values of the ratio of waggle dancers. The sample size is given over each bar

Figure 1 shows the ratio distributions of the waggle dancers' relative frequencies and the tremble dancers' relative frequencies on the total of the dancers (tremble and waggle together), i.e. respectively

$$r_{wd/(wd+td)}(s) = \frac{f_{wd}(s)}{f_{(wd+td)}(s)} \quad \text{and} \quad r_{td/(wd+td)}(s) = \frac{f_{td}(s)}{f_{(wd+td)}(s)}$$

where $f_{wd}(s)$, $f_{td}(s)$, $f_{(wd+td)}(s)$ are relative frequencies computed by dividing the number of bees in each subfamily (s) by the total number of bees in the corresponding class (respectively, wd, td or wd + td).

Subfamilies containing a large proportion of waggle dancers usually contain a small proportion of tremble dancers and vice versa. The distribution of the subfamilies of the waggle dancers and of the tremble dancers was significantly different ($p = 0.0022$).

Subfamily Frequencies in the Dance Followers

The difference between the distribution of the subfamilies of dance followers and the distribution of the controls is not significant when the Bonferroni correction is taken into account (Fisher's exact test, $p = 0.013$) (Table 1). Half of the dance followers (51%) belong to five subfamilies (numbers 1, 4, 6, 10, 12) whereas their proportion in the colony was only 30%.

There is no significant difference between the distribution of the waggle dancers and that of the dance followers (Fisher's exact test, $p = 0.2$).

Discussion

The microsatellites allowed us to collect behavioural data blindly and to later assign each worker precisely to its respective subfamily (Estoup et al. 1994). Using four hypervariable microsatellites, we have certainly detected all the subfamilies.

Genetic Structure of the Colony

Seventeen subfamilies were identified in the complete sample, which is close to previous results using microsatellites analysis (Estoup et al. 1994; Arnold et al. 1996). Unequal contributions of the fathers to the progeny of the queen were also in other studies (Moritz 1986; Estoup et al. 1994; Arnold et al. 1996).

Because of a good mixture of sperm in the queen spermatheca, the subfamily frequencies remain relatively constant over time for as long as the same queen is present (Laidlaw and Page 1984; Robinson and Page 1988, 1989; Estoup et al. 1994). Some sperm clumping occurs in young naturally mated queens, but the effects declines rapidly as queens mature (Kerr et al. 1980 cited by Oldroyd et al. 1992). As our queen was about 1-y old, there should have been no age-dependent differences among subfamilies in the course of the experiment. Therefore, our results should not be a consequence of possible age differences between control bees and dancing bees.

Genetic Factors Influence the Type of Dance

Our results demonstrate that a genetic component is associated with the dance communication in honeybees. Four subfamilies only performed half of the waggle dances (numbers 4, 5, 6, 10) and tremble dances (1, 3, 4, 7). Six subfamilies (11, 13, 14, 15, 16, 17) were so poorly represented in our three samples (waggle and tremble dancers and dance followers) that we can deduce that they are probably hardly involved in nectar foraging. Two subfamilies (numbers 5, 7) which were among the most numerous in the three samples were probably much involved in nectar foraging.

Waggle dancers

There are at least two possible explanations for the existence of subfamilies specialized in waggle dances. First, these subfamilies could be specialized in the search of food sources (scouts). It has been shown that between 5 and 35% of a honeybee colony foragers locate foraging patches by scouting (Seeley 1983), and that scouts are specialists (Dreller 1998). Secondly, these subfamilies could be composed of foragers (scouts and recruits) which tend to communicate the location of the profitable food sources more frequently than do the other subfamilies. The subfamilies could have different thresholds for dancing, which regulate the motivation to perform a waggle dance after returning from a source (De Vries and
2 Biesmeijer 1998). The threshold for dancing is the level of nectar source profitability above which the returning bee is motivated to dance (Seeley 1995).

Dance followers

Successful foragers are surrounded by unemployed bees which show various responses to the waggle dance of the foragers (Seeley 1998). Seeley and Towne (1992) think that the different responses to the waggle dance signal reflect differences in the contextual information possessed by the various bees on the dance floor. In our experiment the repartition of the dance followers showed that three of the five subfamilies that were also those most involved in this behaviour (numbers 4, 6, 10) were the same three subfamilies that were also those most involved in the waggle dances.

Oldroyd et al. (1991) using colonies composed of only two subfamilies demonstrated a strong tendency for recruits to follow dances performed by a member of their own subfamily. Our results showing that the dance followers in a colony headed by a naturally mated queen belong to almost the same subfamilies as the waggle dancers do, however, not imply that each dance follower dances with a super-sister. On the contrary, we recently found no evidence for subfamily discrimination among dancers and their followers (Kirchner and Arnold 2001).

The appearance of positive subfamilial associations in two sub family colonies described by Oldroyd et al. (1991) seems to be an artefact caused by the variance for the tendency to perform and follow dances (Kirchner and Arnold 2001; Oldroyd and Rinderer 2001).

Tremble dancers

One explanation for the existence of subfamilies specialized in tremble dances is that their workers may be more sensitive than others to the duration of time that elapses until they find a nectar receiver to unload them (Seeley 1995). This search time is a reliable indicator of the current colony's nectar influx (Seeley and Tovey 1994; Seeley 1995).The existence of such specialized subfamilies means that the colony can cope fast with a rich nectar flow by mobilizing the nectar receivers and restraining the foragers (Seeley 1992; Kirchner and Lindauer 1994).

In *Apis mellifera*, genotypic variability among individuals with respect to performing specific tasks has been demonstrated using several approaches. Some studies have examined differences in behaviour among members of different subfamilies within a colony (Page and Robinson 1991). Some of these studies have been performed with artificial colonies containing a very small number of subfamilies, two or three (Robinson and Page 1988, 1989). However, results based on these colonies may be an artefact of the family structures compared with those in wild type colonies with queens that normally mate with up to 17 males (Calderone et al. 1989). Other studies were performed with natural colonies (Calderone et al. 1989; Dreller 1998). In those experiments, allelic variants of the enzyme malate dehydrogenase and random amplified polymorphic DNA fragments were used as phenotypic markers, but these techniques did not allow to determine conclusively the number of subfamilies present in the colonies, or the subfamily affiliation of individual bees. Recently, Kryger et al. (2000) have shown that the 16 subfamilies of a colony were represented in significantly different proportions in two subgroups of bees, water collecting bees and scenting bees.

The existence of a genetic component associated with waggle and tremble dancing fits well with the model of division of labour based on differences in behavioural response thresholds among members of different castes or subfamilies (Robinson 1992). Page and Mitchell (1998) and Page (1997) depicted the foraging behaviour of a colony as an informational network. Computer simulations have shown that if there is variation in response thresholds and a correlation between response thresholds and the stimulus environment, a strong division of labour will emerge as a self-organized property of the group. Foragers have different response thresholds, probably partially because of their different genotypes. An individual-oriented model which simulates the collective foraging behaviour of a colony of honeybees was constructed by De Vries and Biesmeijer (1998). This model simulates only a rather small range of collective foraging phenomena, but does not include genetic factors. Therefore, this model, like others (Bonabeau et al. 1996; Page and Mitchell 1998) could be extended with extra properties in the form of this genetic component associated with waggle and tremble dancing.

The presence of subfamilies showing various levels of specialization both for waggle and for tremble dances shows that subfamilies may vary not only in the probability of engaging in a rather rare activity, such as guarding and undertaking (Robinson and Page 1988), but, in addition, in the probability of engaging in a more common activity, such as dance communication.

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