Ethology

Intra-Patriline Variability in the Performance of the Vibration Signal and Waggle Dance in the Honey Bee, *Apis mellifera*

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Abstract

We examined intra-patriline behavioral plasticity in communication behavior by generating lifetime behavioral profiles for the performance of the vibration signal and waggle dance in workers which were the progeny of three unrelated queens, each inseminated with the semen of a single, different drone. We found pronounced variability within each patriline for the tendency to produce each signal, the ontogeny of signal performance, and the persistence with which individual workers performed the signals throughout their lifetimes. Within each patriline, the number of workers that performed each signal and the distribution of onset ages for each signal were significantly different. In each patriline, workers of all ages could perform vibration signals; vibration signal production began 3–5 d before waggle dancing; and some workers began performing waggle dances at ages typically associated with precocious foraging. Most workers vibrated and waggled only 1–2 d during their lifetimes, although each patriline contained some workers that performed the signal persistently for up to 8 or 9 d. We also found marked variability in signal performance among the three worker lineages examined. Because the vibration signal and waggle dance influence task performance, variability in signaling behavior within and between subfamilies may help to organize information flow and collective labor in honey bee colonies. Inter-patriline variability may influence the total number of workers from different partrilines that perform the signals, whereas intra-patriline variability may further fine-tune signal performance and the allocation of labor to a given set of circumstances. Although intra-patriline behavioral variability is assumed to be widespread in the social insects, our study is the first to document the extent of this variability for honey bee communication signals.

Introduction

Behavioral plasticity is a fundamental feature of the division of labor among workers in social insects. In the honey bee, *Apis mellifera*, at least three factors contribute to the expression of behavioral plasticity. First, worker behavior varies with age. Honey bees have an age-associated division of labor, in which workers perform a series of tasks in the nest when they are young (such as brood care, food processing and nest maintenance) and then switch to foraging for nectar and pollen outside of the nest at approx. 2–3 wk of age. This behavioral ontogeny is flexible and can be modified according to colony needs. Some younger workers can accelerate their behavioral development and become 'precocious foragers', whereas some older bees can reverse their development and revert to brood care (Robinson 1992; Huang & Robinson 1996). Such flexibility allows colonies to respond adaptively to sudden changes in colony population size and age demography (Robinson 1992).

Second, behavioral plasticity in honey bee colonies is influenced by paternal genotypic variation. Honey bee queens are polyandrous and mate with an average of 14 different males (Palmer & Oldroyd 2000; Tarpy et al. 2004), resulting in colonies that contain workers of multiple patrilines (subfamilies) that all share the same mother but have different fathers. Genetic differences among the fathers of each patriline contribute to differences in worker sensitivity to stimuli, which in turn influence both the tendency to perform particular tasks and the age at which they are initiated (Calderone & Page 1988; Fewell & Page 1993; Robinson & Huang 1998). This inter-patriline variability in response thresholds allows for smoother adjustments in labor allocations, a more resilient system of division of labor, and increased colony viability (Jones et al. 2004; Chapman et al. 2007; Matilla & Seeley 2007; Oldroyd & Fewell 2007; Oldroyd & Thompson 2007).

A third factor influencing behavioral plasticity is inter-individual variability among workers within a patriline. Workers sired by the same male share, on average, 75% of their genes. Nevertheless, variability occurs within a patriline because of recombination in the queen, developmental factors, and experiential differences among adult workers. Intra-patriline behavioral variability is assumed to be widespread in social insects (Frumhoff & Baker 1988; Page & Robinson 1991), but is usually considered to be less pronounced than that occurring between patrilines (Oldroyd & Fewell 2007). However, intra-patriline differences have not been studied much (Page & Robinson 1991), and this is particularly true for the performance of communication signals, such as the vibration signal and the waggle dance. The vibration signal causes a general increase in activity that enhances the performance of many tasks simultaneously depending upon recipient age (Schneider & Lewis 2004; Cao et al. 2007; Hyland et al. 2007), whereas the waggle dance is used to recruit foraging-age workers to food and nest sites (Seeley 1995; Visscher 2007). Together, the two signals influence many of the cooperative activities of honey bee colonies (Seeley 1995; Hyland et al. 2007). Intra-patriline variability in the performance of these signals, combined with other sources of behavioral plasticity, could contribute to finely tuned adjustments of tasks and play an important role in organizing information flow and colony labor allocations. Variability in vibration signal and waggle dance behavior is well documented. However, most studies have either concentrated on differences among subfamilies (Oldroyd et al. 1992, 1993; Kirchner & Arnold 2001; Arnold et al. 2002; Matilla et al. 2008), or examined colonies headed by naturally mated queens without distinguishing the degree to which variation arises from inter- vs. intra-patriline differences (Seeley 1994; Painter-Kurt & Schneider 1998).

We investigated intra-patriline variability in vibration signal and waggle dance behavior by generating lifetime behavioral profiles for workers from three unrelated lineages, each of which contained the progeny of a separate queen inseminated with semen from a single, different drone. Workers of the same lineage belonged to the same patriline, and intra-patriline genetic differences were solely due to recombination in the inseminated queen. In contrast, genetic differences among the lineages were due to different drones and queens, and were more reflective of differences among colonies rather than differences among patrilines arising from the same polyandrous queen. Although the focus of our study was on intra-patriline variability, we also compared among worker groups (henceforth referred to as inter-lineage differences) to more fully assess the plasticity in signaling behavior. Our specific objectives were to compare within and among lineages: (1) the proportions of workers performing each communication behavior; (2) the onset age for the performance of each signal; and (3) the number of days that a worker produced each signal during its lifetime.

Methods and Materials

Colony Set Up and Maintenance

Three unrelated queens were each instrumentally inseminated with the semen of a different unrelated drone, giving rise to three worker lineages, designated patrilines A, B and C. Each inseminated queen was maintained in a separate 45-l box hive on the campus of North Carolina State University. After 6–8 wk, when all workers in the box hives were the progeny of the inseminated queens, frames of capped brood were removed from each colony and transported to an incubator [32.5°C; 50% relative humidity (RH)] on the campus of the University of North Carolina at Charlotte, where the project was conducted. Each frame was kept inside a nylon-mesh cage labeled by patriline so that all emerged workers were of known paternity and there was no mixing of workers among combs.

We collected 1000 newly emerged workers from each of the three patrilines and marked them individually by gluing plastic tags with unique number–color combinations to the thorax (Opalinthplätchen, Chr. Graze, Endersbach, Germany). In addition to the individual identification provided by the tags, each tag also contained a paint mark that identified a worker as belonging to a particular patriline. Workers were marked within 12 h of emergence so that their exact age (in days) was known throughout the study. All 1000 workers collected from each patriline were tagged within a 2-d period.

Each group of tagged workers was added to a separate host colony headed by an unrelated, naturally mated queen, such that each patriline was fostered in a separate hive environment that contained a typical number of subfamilies. The host colonies were labeled A, B and C (colony A contained patriline A, etc.). We did not co-foster the patrilines within the same host colony, because this study was part of a larger investigation of honey bee communication behavior in which the three patrilines housed in separate colonies represented three experimental replicates.

The host colonies were initially maintained in four-frame hive boxes, to facilitate the acceptance of introduced tagged workers. Immediately after all tagged bees had been added to a host colony, the four frames of comb and all bees were transferred into a four-frame observation hive. Each observation colony contained approximately two frames of brood in all developmental stages, two frames of honey and nectar, and 5000–6000 workers, including the tagged individuals from one patriline. The three host colonies were set up simultaneously and experienced similar foraging conditions during the study period. Each colony was provided sucrose solution (50% by volume) ad libitum throughout the study to help equalize foraging success and food reserves among colonies. The study colonies were maintained in the observation hives for 5 wk, by the end of which time the vast majority of tagged workers had died.

Monitoring Patterns of Comb Use and Colony Development

Because communication behavior is influenced by colony conditions, we monitored patterns of colony growth throughout the study period. We used a grid of 4 × 4 cm squares drawn onto a glass sheet to estimate the amount of comb within each colony that contained brood, honey and pollen. Comb areas were measured four times during the study period, separated by at least 1 wk. On the same days that we estimated comb areas, we also weighed the colonies using a Kabota digital platform scale calibrated in 5-g increments (RACO, LLC, Cincinnati, OH). We subtracted from the colony weight the weight of the empty observation hive and wooden frames, resulting in an estimate for the combined weight of the wax combs, stored food, brood, and adult workers. The weighings were carried out at the end of the day after the foragers had returned to the nest.

Monitoring the Behavior of Tagged Bees

Every day during the 5-wk study period, each of the three observation colonies was scanned continuously from 08:00 to 17:00–18:00 hours by two randomly assigned observers. Throughout each day we recorded the identity and age of every tagged bee observed to perform vibration signals and waggle dances. If a tagged bee was observed to perform a communication signal multiple times on a given day, it was entered in the data files only once for that day. We also recorded the identity and age of each tagged bee that drifted from another host colony (identified by the patriline-specific paint marks applied to the tags). Each colony was monitored for a total of 330 h during the study period, which minimized the possibility that we missed tagged bees performing the focal behaviors.

Subsequently, we determined the total number and proportion of tagged bees within each patriline that were observed to have ever performed vibration signals, waggle dances, or both communication signals during the study period. Some workers in each of our patrilines began performing communication signals when 2–4 d old, and previous studies have revealed that approximately 90% of tagged bees introduced into observation hives survive to this age (Painter-Kurt & Schneider 1998). We therefore estimated the proportions of bees within each patriline that vibrated and waggled, by dividing the number observed by a value corresponding to 90% of the total tagged bees added, minus any drifters from that patriline. Additionally, for each tagged worker that performed the communication signals, we determined: (1) the earliest age at which it engaged in each behavior and (2) the number of days it performed each signal during its lifetime (defined as its persistence in signal performance). We also estimated the proportion of tagged bees from each patriline that drifted into a different observation hive during the study period, and the proportions, onset age, and number of days that the drifters vibrated and waggled in the foreign colony environments.

Statistical Methods

To examine patterns of colony comb use and growth throughout the study, we used a mixed-model two-way ANOVA without replication (SAS Institute 1997) to compare colony weight and comb areas of brood, honey, and pollen among the three host colonies. A separate analysis was conducted for each variable. In the analyses, the subject factor was 'colony' and the within-subject factor was 'time'.

Log-linear models were used to compare the number of bees that vibrated and waggle danced within and among the worker lineages. To examine the onset age and days of performance for each communication signal, we used repeated-measures ANOVA (SAS Institute 1997), in which individual worker was the subject, lineage the between-subject factor, and behavior (vibrate or waggle) the within-subject factor. If we found significant lineage × behavior interactions, we used Tukey's HSD tests (Sokal & Rohlf 1995) to conduct post hoc comparisons within and between lineages.

For a given behavior in honey bees, days of performance during a worker's lifetime can be influenced by onset age (Guzmán-Novoa et al. 1994). We therefore used Pearson's correlation analysis to examine the association between onset age and days of performance for vibrating and waggle dancing within each patriline.

To achieve normality, the data for onset age and days of performance were natural log-transformed prior to conducting the ANOVAS. Unless otherwise stated, the data for drifters were excluded from the analyses. The sequential Bonferroni adjustment (Rice 1989) was used to determine significance levels for the multiple comparisons made within and among lineages. Mean values are reported as ±1 SE.

Results

Colony Demographics

The three host colonies did not differ in areas of brood comb ($F_{2,11} = 0.66$; $p = 0.549$), honey comb ($F_{2,11} = 1.32$; $p = 0.336$), pollen comb ($F_{2,11} = 1.24$; $p = 0.354$) or weight ($F_{2,11} = 4.00$; $p = 0.079$) during the study period (Table 1). Thus, even though the three groups of tagged bees were housed in different nests, they experienced similar colony environments, which facilitated inter-lineage comparisons.

Table 1: Mean ± SE areas of comb devoted to brood rearing, honey and pollen storage and weight for each of the host colonies during the 5-wk study period

	Colony A	Colony B	Colony C
Brood comb area	5540 ± 347.7	5148 ± 33.5	5092 ± 256.1
Honey comb area	744 ± 193.8	956 ± 37.2	668 ± 73.7
Pollen comb area	236 ± 79.3	404 ± 30.9	368 ± 76.7
Colony weight	5.03 ± 0.229	5.58 ± 0.026	4.87 ± 0.149

Comb areas are given in cm^2; colony weight is given in kg.

Proportions of Workers Performing Vibration Signals and Waggle Dances

On average, 44.9 ± 5.01% of the tagged bees performed vibration signals and 36.0 ± 8.12% performed waggle dances during the study period (Fig. 1). Within each patriline, there was a significant difference in the proportions of workers that performed the two communication signals (for each comparison: $\chi_1^2 > 5.54$; $p < 0.0186$). In patriline A, a greater proportion of workers waggled than vibrated, whereas the opposite trend was observed within patrilines B and C (Fig. 1). The proportion of workers that performed both communication signals was 17.1%, 29.1% and 11.2% in patrilines A, B and C, respectively, suggesting that there was only a moderate amount of overlap in the subgroups of workers that produced the two signals within each lineage. Thus, within each patriline, individual workers differed in their tendency to perform the two communication signals, although there was no consistent tendency to preferentially perform one signal.

There were also marked inter-lineage differences in the proportions of workers that performed the two signals. Patriline B had the greatest proportions

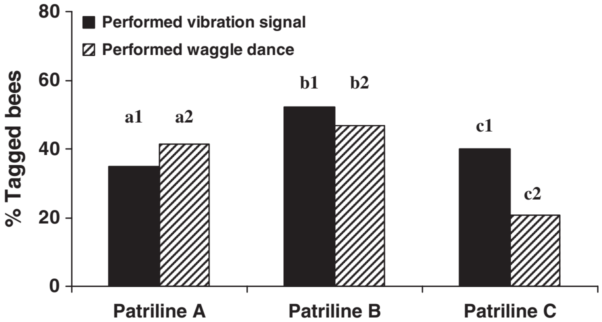

Fig. 1: The proportions of tagged workers within each patriline that performed vibration signals and waggle dances. Different numbers above the columns indicate significant intra-patriline differences; different letters indicate significant inter-lineage differences.

of workers that vibrated and waggled, patriline A the second greatest, and patriline C the least (for all comparisons: $\chi^2_2 > 54.5$; $p < 0.0001$; Fig. 1).

Onset Age for Performing Vibration Signals and Waggle Dances

When viewed over all three lineages, the mean ages at which workers began vibrating and waggling were 15.8 ± 0.21 and 19.3 ± 0.20 days, respectively (Table 2). The distributions of onset ages were highly significantly different for the two signals ($F_{1,1058} = 220.6$; $p < 0.0001$; Fig. 2). Furthermore, the degree to which the age distributions for the two signals differed varied markedly among lineages, resulting in a significant lineage × behavioral onset interaction ($F_{2,1041} = 11.8$; $p < 0.0001$; Fig. 2).

Within each patriline, workers began producing vibration signals 3–5 d before they began performing waggle dances (for each comparison: Tukey's test; $p < 0.0001$; Table 2; Fig. 2). The majority of vibrators began performing the vibration signal when ≥14 d old. However, within each patriline some workers began vibrating when only 2–4 d of age, and of the bees that produced the signal, 25.5 ± 10.9% did so when ≤10 d old. These trends were particularly pronounced in patriline B (Fig. 2). Workers that performed waggle dances typically began producing the signal when ≥15 days of age (Fig. 2). However, within each patriline, 1–8% of the bees began performing waggle dances when ≤10 d old.

There were pronounced inter-lineage differences in the onset age for vibrating and waggling (Table 2; Fig. 2). Workers began performing each of the two communication signals at the youngest age in patriline B, second youngest in patriline A and oldest in patriline C (for each comparison: Tukey's test; $p < 0.0001$).

Table 2: Mean ± SE age of first performance and the number of days of performance of the vibration signal and waggle dance in each of the three patrilines examined

	Patriline A	Patriline B	Patriline C
Age of first performance			
Vibration signal	16.6 ± 0.35^{1a}	12.1 ± 0.29^{1b}	20.1 ± 0.35^{1c}
Waggle dance	19.1 ± 0.32^{2a}	17.2 ± 0.27^{2b}	24.6 ± 0.36^{2c}
Days of performance			
Vibration signal	1.5 ± 0.05^{1a}	2.0 ± 0.06^{1b}	1.7 ± 0.06^{1c}
Waggle dance	1.5 ± 0.04^{1a}	2.1 ± 0.06^{1b}	1.4 ± 0.06^{2a}

Different superscript numbers within columns indicate significant intra-patriline differences.

Different superscript letters within rows indicate significant inter-lineage differences.

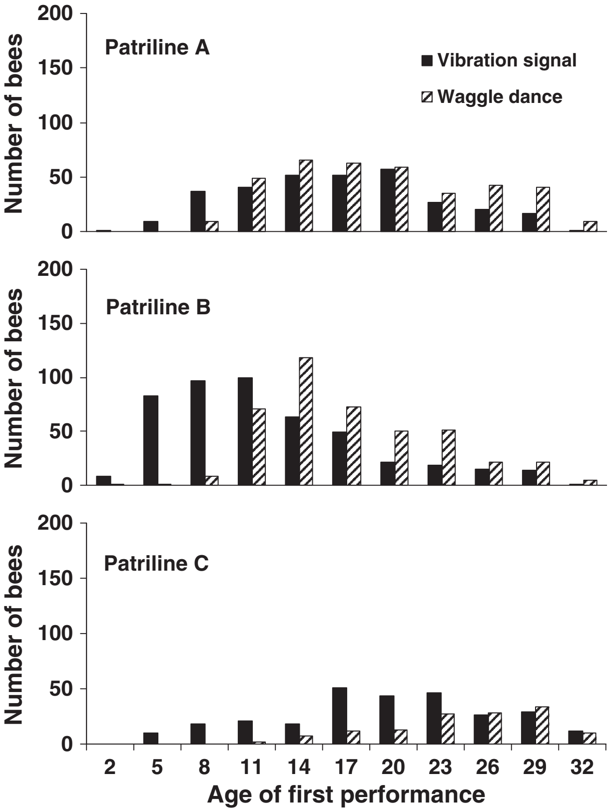

Fig. 2: Ages at which workers within each patriline were first observed to perform vibration signals and waggle dances. Values on the *y*-axis indicate the midpoints of 3-d age intervals (1–3 d, 4–6 d, etc.).

Number of Days of Performance of Vibration Signals and Waggle Dances

Most of the tagged workers exhibited low levels of persistence in performing the two communication signals (Fig. 3). On average, individual tagged bees performed vibration signals and waggle dances on only 1–2 d during the study period (Table 2). However, persistence in signal production was highly variable. Within each patriline, 1–4% of the workers produced the signals for five or more days, although these were not necessarily consecutive days of performance. The maximum number of days that workers in any patriline performed vibration signals or waggle dances was nine and eight, respectively (Fig. 3). In general, there was no difference in the number of days that workers performed waggle dances and vibration signals ($F_{1,1434} = 2.63$; $p = 0.105$), although this trend was expressed differently among the patrilines ($F_{2,1408} = 6.83$; $p < 0.0011$; Fig. 3).

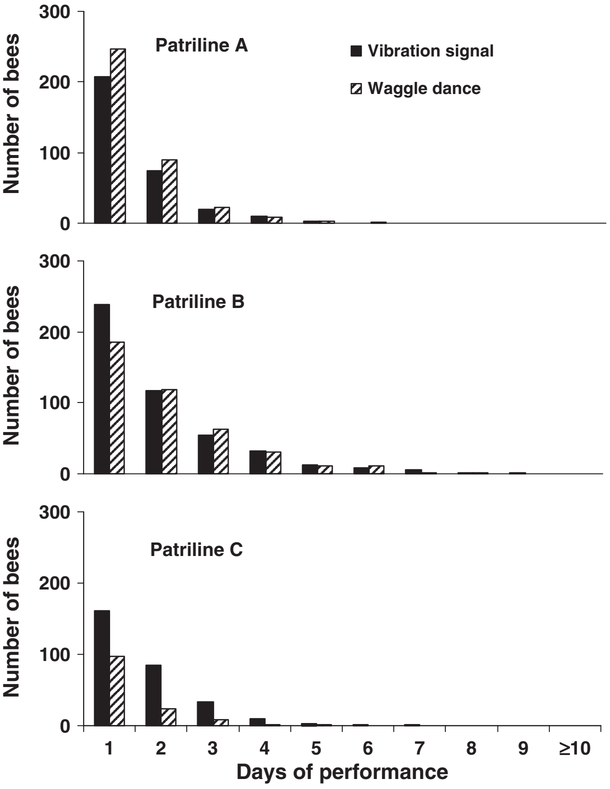

Fig. 3: The number of days that workers within each patriline were observed to perform vibration signals and waggle dances.

There was little intra-patriline variability in the number of days that workers vibrated and waggled. Within patrilines A and B, workers performed the two signals for a similar number of days (for both comparisons: Tukey's test; $p > 0.08$; Table 2; Fig. 3). In patriline C, workers performed vibration signals slightly, but significantly longer than they performed waggle dances ($p = 0.0011$) (Table 2).

In contrast, there was inter-lineage variability in the number of days that workers vibrated and waggled. These differences arose primarily because workers in patriline B tended to perform both signals on more days than workers in patrilines A and C (for all comparisons: Tukey's test; $p < 0.015$; Table 2; Fig. 3). However, the comparisons that reached statistical significance were associated with differences of only a fraction of a day, and never exceeded one complete day of performance (Table 2).

Association between Onset Age and Days of Performance

For both the vibration signal and waggle dance, onset age and days of performance were negatively correlated within each patriline (Table 3). Workers that began vibrating and waggle dancing at an earlier age performed the communication signals for a greater number of days during their lifetimes. These associations were highly significant, except for waggle dancing in patriline C (Table 3).

Table 3: Pearson correlation coefficients for the association between onset age and days of performance for vibration signals and waggle dancing within each patriline

	Patriline A	Patriline B	Patriline C
Vibration signal	−0.188*	−0.269*	−0.303*
Waggle dance	−0.329*	−0.265*	−0.120

*$p < 0.01$ with sequential Bonferroni adjustment.

Drifting behavior

The patrilines differed strongly in their tendency to drift from their host colony into one of the other observation hives used in the study. Only 21 (2.3%) of the tagged workers from patriline A and two (0.2%) from patriline B drifted into another colony. In contrast, 246 (27.3%) of the tagged workers from patriline C drifted during the study period. Of these drifters, 237 moved into the observation colony that housed patriline A (colony A) and 117 performed vibration signals or waggle dances while in this colony. Although we excluded drifters from our analyses, these bees provided an opportunity to examine the degree to which intra-patriline behavioral variability was influenced by colony environment.

Compared with the non-drifters of patriline C that remained in their host colony, the bees that drifted into colony A were less likely to perform vibration signals ($\chi_1^2 = 23.1$; $p < 0.0001$), but were as likely to perform waggle dances ($\chi_1^2 = 0.79$; $p = 0.375$; Table 4). The drifters and non-drifters from patriline

Table 4: The proportion of workers, mean ± SE onset age, and mean ± SE days of performance for the vibration signal and waggle dance by the non-drifters and drifters from patriline C

	Non-drifters	Drifters
% Bees performing		
Vibration signal	44.6^a	26.6^b
Waggle dance	20.1^a	22.8^a
Age of first performance		
Vibration signal	20.1 ± 0.39^a	19.7 ± 0.72^a
Waggle dance	24.3 ± 0.44^a	25.2 ± 0.62^a
Days of performance		
Vibration signal	1.7 ± 0.06^a	1.9 ± 0.18^a
Waggle dance	1.4 ± 0.07^a	1.3 ± 0.10^a

Different superscript letters within rows indicate significant differences between non-drifters and drifters.

C did not differ in the age of onset ($F_{1,242} = 0.10$; $p = 0.75$) or the number of days that each communication behavior was performed ($F_{1,325} = 0.86$; $p = 0.36$; Table 4). Thus, although colony environment may have altered the tendency of workers in patriline C to perform vibration signals, most of the observed variability in communication behavior was more strongly associated with intra-patriline factors.

Discussion

We observed pronounced variability in the tendency, onset age, and persistence with which genetically similar workers within patrilines performed the vibration signal and waggle dance. We also found substantial differences among the three lineages in the performance of the two communication signals. Our inter-lineage comparisons must be interpreted cautiously, because the three worker groups were unrelated and experienced different colony environments. However, the three host colonies did not differ in their growth and comb-use patterns, and comparisons of non-drifters and drifters from patriline C suggested that individual variation in communication behavior may have been influenced more strongly by within-patriline factors than differences in hive environment. Furthermore, the variability that we observed among unrelated lineages in different colonies was comparable with that reported for patrilines within the same colony (Painter-Kurt & Schneider 1998; Arnold et al. 2002). Notably, the variation that we observed for vibration signal and waggle dance behavior within each patriline was often similar to that occurring among the patrilines (Figs 2 and 3), and comparable to that reported for colonies containing numerous subfamilies arising from naturally mated queens (see Figs. 1-3 in Painter-Kurt & Schneider 1998).

Within each patriline, different proportions of workers performed vibration signals and waggle dances. Individual honey bees can perform both signals, and successful foragers will sometimes mix the signals during a bout of waggle dancing (Schneider 1986; Seeley et al. 1998). However, our results suggest that on average only about 10–30% of workers within a patriline perform both signals during their lifetimes, suggesting that the two forms of communication are produced by largely separate subsets of workers.

The mean proportions of workers that vibrated and waggled in our three patrilines (36–45%) were three to four times greater than the 11–12% previously reported for colonies containing multiple patrilines arising from naturally mated queens (Painter-Kurt & Schneider 1998). This raises the possibility that within colonies containing a typical number of subfamilies some patrilines are actively involved in vibration signal and waggle dance performance, while others may rarely or never engage in these activities, resulting in relatively low proportions when viewed over the colony as a whole. By chance, the three lineages we examined may have had an above-average tendency to perform the communication signals, or perhaps experienced conditions that triggered greater-than-average signaling activity. For example, the addition of 1000 newly emerged workers to each host colony within a 2-d period may have altered the age demography, potentially influencing the tendency to perform the signals.

The age at which workers began performing vibration signals was highly variable both within and among our three lineages. Within each patriline, workers performed vibration signals at an earlier age than waggle dances, and some started vibration activity when only 2–4 days old. Similar age distributions for vibration signal behavior have also been reported for workers arising from naturally mated queens (Painter-Kurt & Schneider 1998). Vibrators are often foragers (Schneider & Lewis 2004), although we do not know to what extent (if any) the signals of the young vibrators in our study colonies were associated with food collection. We also observed pronounced variability in the onset of waggle dance behavior, and within each patriline a small proportion of workers began waggling when ≤10 days old, ages typically associated with precocious foraging (Huang & Robinson 1992; Jassim et al. 2000). Subfamily differences have been reported for the behavioral ontogeny, of numerous honey bee tasks (Calderone & Page 1988; Whitfield et al. 2006; Chapman et al. 2007), the occurrence of precocious foraging (Jassim et al. 2000), and the tendency to perform waggle and tremble dances (Oldroyd et al. 1992, 1993; Arnold et al. 2002). However, to our knowledge, our study is the first to demonstrate substantial within-patriline plasticity in vibration signal and waggle dance behavior. Our results suggest that intra-patriline variability in the ontogeny of the two signals may be a significant source of behavioral plasticity in honey bee communication. Furthermore, we found negative correlations between the age of first performance and total days of performance for both vibrating and waggle dancing within each patriline. Thus, within-patriline variability in behavioral ontogeny may also contribute to plasticity in colony communication behavior by influencing the persistence with which individual workers perform the two signals.

The plasticity that we observed in vibration signal and waggle dance behavior is consistent with the response threshold model for the division of labor in social insects (Beshers & Fewell 2001; Oldroyd & Fewell 2007). In combination, inter- and intra-patriline variability for the two communication signals may play an important role in organizing and adjusting cooperative labor in honey bees. The vibration signal exerts a non-specific modulatory influence that enhances brood care, food processing, nest maintenance and foraging, and thus can influence a broad spectrum of colony activities simultaneously (Schneider & Lewis 2004; Cao et al. 2007). The waggle dance functions more specifically to regulate recruitment to food sites. The use of both communication signals varies with colony needs, which helps to adjust task allocations and foraging effort to changing conditions (Seeley 1995; Hyland et al. 2007). Furthermore, genetically diverse colonies have higher levels of waggle dance and vibration signal activity, greater numbers of signalers, and increased foraging activity than genetically uniform colonies (Matilla et al. 2008). When viewed in concert, these results suggest that inter-patriline differences in response thresholds for vibration signal and waggle dance performance may allow graded adjustments in the total number of workers producing the signals, whereas individual behavioral tendencies within patrilines may further fine-tune communication activity and labor allocations to a given set of circumstances. Inter-individual behavioral variability among genetically similar workers may have a major influence on collaborative interactions in many insect societies (Wiedenmüller 2004; Ravary et al. 2007). Our results suggest that inter-individual differences in communication behavior within patrilines potentially contribute to the organization of collective activities in honey bee colonies.

We cannot fully explain the sources of the individual variability observed within our patrilines. Individual variability in waggle dance performance is well documented and may arise through idiosyncratic differences in response thresholds and foraging experience (Seeley 1995). In contrast, the factors underlying individual variability in vibration signal behavior are unknown, in part because the genetic basis of signal production has not yet been explored and the signal may be associated with different stimuli in different worker age groups (Painter-Kurt & Schneider 1998). Individual variation in behavior is widespread in the animal kingdom, and forms the basis of behavioral syndromes, or animal ‘personalities’ (Gosling & John 1999; Sih et al. 2004; Groothuis & Carere 2005). Consistent individual differences in behavioral tendencies in many species may arise through individual-level selection acting on life-history tradeoffs between early vs. late reproduction (Wolf et al. 2007) or growth rate and mortality (Stamps 2007). However, in social insects, selection acting at the level of the colony is a primary force favoring the behavioral plasticity associated with division of labor and polyandry (Tarpy 2003; Wilson & Hölldobler 2005; Oldroyd & Fewell 2007). If the variability arising from intra-patriline differences in behavioral tendencies also promotes colony efficiency and resiliency, then it too may be favored by colony-level selection. Thus, group-level selection may be another possible route to the inter-individual behavioral plasticity that underlies ‘personalities’ in animals.

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