



# Factors influencing the selection of recipients by workers performing vibration signals in colonies of the honeybee, *Apis mellifera*

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(Received 22 January 2001; initial acceptance 25 May 2001;  
final acceptance 18 July 2001; MS. number: A8978)

The vibration signal of the honeybee functions as 'modulatory communication' because it elicits a general increase in activity that may help integrate the behaviour of workers that perform different, interrelated task sets. Workers that produce vibration signals contact numerous other bees, some of which receive the signal while others are 'bypassed' (antennated but not vibrated). Vibrating bees may therefore select among potential recipients. We monitored vibration signal behaviour in six observation colonies to investigate the possible selection of recipients by vibrating bees and the factors that might influence these choices. Vibrating bees roamed throughout the nest and bypassed more than half of all workers contacted. Vibration signals were not directed towards specific worker age groups. There were no differences in the mean age of vibrated versus bypassed workers or the proportion of recipients that were of preforaging versus foraging age. The likelihood of receiving vibration signals was influenced by recipient activity level. Significantly more workers were vibrated if they were inactive versus active when contacted by a signalling bee. Signal production was not consistently influenced by relatedness. Vibrating bees from only a single patriline in one of our study colonies were more likely to perform signals on supersisters than on half-sisters. In all other colonies no kin preferences were observed during signal performance. Thus, vibrating bees may choose among potential recipients and direct their signals towards inactive workers of all ages and levels of relatedness. This, in combination with their movement throughout the colony, could help to activate simultaneously multiple worker groups that perform interdependent tasks, but which may be spatially segregated in the nest.

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Cooperative activities in social animals are often regulated by communication signals, many of which can be broadcast throughout the social environment without the preselection of particular recipients (Beshers et al. 1999; Gordon 1999). Other signals, however, such as tactile signals and some affiliative and dominance displays, are focused on specific recipients that are selected from among multiple potential receivers (Reeve 1992; Janik 2000). This selection allows a more controlled flow of information. Signals sent to specific recipients may be particularly important in highly social insects, whose cooperative activities involve interrelated tasks that must be coordinated within and among different worker groups (Seeley 1995; Gordon 1999; Lewis & Schneider

2000). Signals that can be focused on recipients appropriate for given tasks may facilitate the integration of these colony-level actions. Furthermore, such signals represent natural 'choice tests' by senders that may provide insights into signal function and the mechanisms that organize insect social behaviour.

An example of a communication signal that may involve the selection of recipients is the vibration signal of the honeybee. During signal production, a worker typically grasps a nestmate and rapidly vibrates her own body dorso-ventrally for 1–2 s at  $\approx 16$  Hz (Seeley et al. 1998). She then breaks contact and moves across the comb to another bee. A vibrating worker usually produces a series of signals (up to 20/min) that lasts from several minutes to over an hour, during which time numerous nestmates are encountered (Schneider 1986; Lewis & Schneider 2000). Some of these workers receive the signal, while others are antennated but then are not vibrated. Signalling bees may therefore direct their vibration

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activity toward only a portion of the potential recipients contacted.

The vibration signal functions as 'modulatory communication' (Markl 1985), because it operates in a non-specific manner to shift the probability that recipients will engage in suites of behaviour, with specific responses dependant upon recipient identity and contextual cues (Schneider 1987; Nieh 1998; Lewis & Schneider 2000). Workers receiving the signal respond with a general increase in activity that enhances an array of tasks, including foraging, brood care, food processing, nest site scouting and colony movement during swarming (Schneider et al. 1986a, b, 1998; Schneider 1987; Lewis & Schneider 2000). The vast majority of vibration signals are performed by bees of foraging age, often in response to successful food collection (Schneider 1986; Painter-Kurt & Schneider 1998; Seeley et al. 1998). Thus, the signal may help to integrate activity within and among different tasks, several of which must be coordinated with foraging success (Beshers et al. 1999; Lewis & Schneider 2000). Directing the signal towards specific workers could enhance this behavioural integration. The extent to which vibrating bees select among potential recipients, and the factors that might influence these choices, have received little attention. However, at least three characteristics could affect whether a worker is selected to receive vibration signals.

First, vibrating bees could choose recipients based on their age. Honeybees have an age-based division of labour, in which older workers tend to perform foraging tasks, while younger bees usually perform in-hive activities such as brood care and food processing (Winston 1987; Seeley 1995). While age and task performance are generally correlated, there can be substantial individual variation, and age and task can become uncoupled if colony demography is sufficiently altered (Huang & Robinson 1996). Nevertheless, under most colony conditions age is a coarse-grained predictor of behaviour, especially for the division between foraging tasks and in-hive activities (Seeley 1995). Thus, if the vibration signal functions primarily to coordinate the tasks performed within certain age groups, on average there should be a difference between the age of workers that receive vibration signals and those that are contacted but not vibrated. In particular, vibrating bees could discriminate between foraging-age and preforaging-age recipients. While workers of all ages can be vibrated, age discrimination during signal performance has been previously suggested (Gahl 1975; Schneider 1985).

Second, vibration signals could be directed towards recipients based on their activity level. Because the signal elicits increased activity, a worker's degree of inactivity may affect whether it is vibrated. The influence of worker activity on receiving vibration signals has never been explored. However, several other social species produce tactile signals that are directed at inactive nestmates and elicit increased task performance (Reeve & Gamboa 1983, 1987; Velthuis & Gerling 1983; Reeve 1992).

Third, recipient choice could be influenced by relatedness. Honeybee queens mate with multiple drones,

resulting in numerous patriline (subfamilies) within a colony (Oldroyd et al. 1998). Workers sharing the same drone father are 'supersisters' ( $G=0.75$ ), while those sired by different drones are half-sisters ( $G=0.25$ ). Supersister preferences have been suggested for numerous worker interactions in honeybees (Getz et al. 1982; Frumhoff & Schneider 1987; Robinson et al. 1994). Bees performing vibration signals might therefore preferentially direct their signalling activity towards certain kin groups within the colony.

The goal of our study was to explore recipient choice by honeybee workers performing vibration signals. Our main objectives were to: (1) assess the extent to which vibrating workers selected among potential recipients and (2) explore how worker age, activity level and relatedness affected the likelihood of receiving vibration signals.

## METHODS

We monitored vibration signal behaviour during March–July 2000 using a total of six colonies maintained in four-frame observation hives. We established each colony by transferring four combs with 6000–8000 workers and a laying queen from field colonies maintained in 45-litre hive boxes (see Painter-Kurt & Schneider 1998 for details of colony set-up). We maintained three of the colonies (A, B and C) on the campus of the University of North Carolina at Charlotte. The remaining three (colonies R, 45 and 5) were maintained at the Carl Hayden Bee Research Center, Tucson, Arizona.

Our basic procedure was as follows. Throughout each day of observation we randomly selected bees performing vibration signals and monitored each until it stopped producing signals, left the hive or was lost from view. For every vibrating worker monitored, we recorded (1) the total time it was observed, using a digital stopwatch and (2) the total number of bees it contacted, defined as the number that were antennated at least briefly by the signaller during the period of observation. We categorized each contacted worker according to its age, activity level or relatedness to the vibrating bee (see below) and recorded whether each contacted worker received a vibration signal or was 'bypassed' (contacted but not vibrated). We also recorded each time a vibrating bee traversed one of the four combs in an observation colony, to estimate the degree of movement throughout the nest during signal production. We monitored each vibrating bee only once.

### Determining the Influence of Age on the Selection of Recipients

We examined the effect of recipient age in colonies A, B and C. Each colony contained populations of known-age workers, established by adding throughout the study period groups of 300–500 newly emerged, marked bees. We collected workers for marking from brood combs maintained in an incubator (34 °C; 50% RH) and marked

them within 24 h of emergence. In each colony we created two marked populations. The first consisted of groups of 100 workers added every other day and labelled with individually recognizable tags (Opalithplättchen, Chr. Graze, Endersbach, Germany) glued to the thorax. The second consisted of cohorts of 200–400 bees added every 2–3 days that had been marked on the thorax or abdomen with a dot of Testors dope paint. All bees within an age cohort received the same colour and placement of mark, but each successive cohort was painted with a different colour or mark location. We selected vibrating bees from the tagged population, to ensure that each was monitored only once, although we occasionally monitored painted vibrators whose markings were individually recognizable. The paint-marked workers provided a large population of known-age bees that were potential recipients of vibration signals.

We recorded the age of each vibrating bee monitored and the age of every tagged or paint-marked worker that it vibrated or bypassed. Subsequently, we categorized each contacted worker as being of foraging age or preforaging age. Our marked bees typically began to perform waggle dances and engage in pollen collection when they were 15–16 days of age (see also Schneider et al. 1986a; Painter-Kurt & Schneider 1998). We therefore considered a worker to be of foraging age if she was at least 15 days old; workers less than 15 days of age were classified as preforaging-age bees.

We used two approaches to assess the influence of age on recipient choice. First, we compared the age of vibrated versus bypassed bees. Second, we compared the proportion of foraging-age versus preforaging-age bees that received vibration signals. The first approach allowed us to examine the influence of a worker's exact age on its likelihood of receiving signals. The second provided an estimate of the extent to which vibration activity was focused on certain age groups that potentially performed different task sets. There were considerable differences in the level of signalling activity among the individual vibrating bees monitored. To take this interindividual variability into account, we conducted our comparisons using a two-factor analysis of variance (ANOVA) with repeated measures on one factor (Glantz & Slinker 1990). This method blocked the data by individual vibrator (subject) and used colony as the between-subjects factor and 'contacted worker type' (vibrated versus bypassed) as the within-subject factor.

### Determining the Influence of Activity Level on the Selection of Recipients

We examined the association between a worker's activity level and its likelihood of receiving vibration signals in colonies A, B and C. For each vibrating bee followed, we classified every worker it contacted as active or inactive, and then recorded whether or not it was vibrated. Active bees included those that were walking, running, engaged in trophallaxis, grooming another bee, or performing the tasks of brood care, food processing,

comb manipulation, ventilating, attending the queen, or foraging (carrying pollen loads or performing or following waggle dances). A worker was considered to be engaged in brood care or food processing, if at the time it was contacted, it had at least its head inside a brood or food cell and was moving in the cell (Schneider 1987). Inactive workers included those that were standing stationary or sitting motionless inside a cell when contacted by a vibrating bee. We subsequently determined for each vibrating bee the proportion of active and inactive workers that received the signal and compared these proportions using a two-factor ANOVA with repeated measures on one factor.

### Determining the Influence of Relatedness on the Selection of Recipients

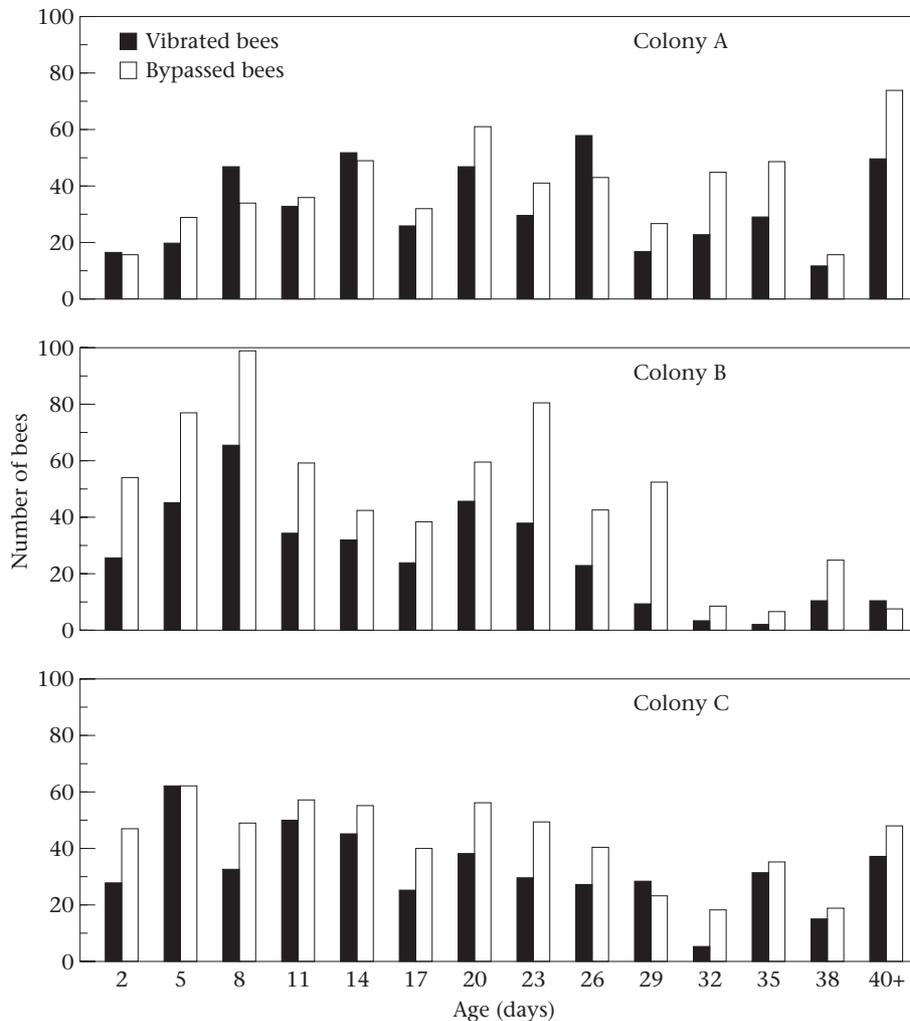
We examined the effect of relatedness in colonies R, 45 and 5. Each of these colonies contained two morphologically distinguishable patrines, established by instrumentally inseminating a Cordovan (*cd*) queen with the semen from one *cd* and one black drone. The *cd* is a recessive allele that produces a yellow cuticular coloration (Frumhoff 1991). Workers arising from the Cordovan × Cordovan cross possessed a 'light blond' cuticle, while those sired by the black drone had much darker coloration. Workers were classified as supersisters if they shared the same cuticular colour, but as half-sisters if they had different coloration. For every vibrator monitored, we recorded whether each bee contacted was a super- or half-sister, and whether it was vibrated or bypassed. In order to block by individual while also testing for the effect of both patriline (Cordovan or black) and relatedness (super- or half-sister), it was necessary to analyse each colony separately. We therefore used replicated goodness-of-fit tests (heterogeneity *G* test, Sokal & Rohlf 1995) to compare the number of super- and half-sisters that were vibrated versus bypassed by signallers of each patriline.

We used the sequential Bonferroni adjustment (Rice 1989) to determine significance levels for the multiple comparisons and interaction terms generated among the different colonies. All mean values are reported as  $\pm 1$  SE interval.

## RESULTS

We monitored a total of 265 vibrating bees ( $29.4 \pm 3.2$ /colony for each of the three recipient characteristics examined). Each was observed for  $13.0 \pm 3.8$  min, during which time it traversed  $2.4 \pm 0.6$  combs and contacted  $97.7 \pm 6.5$  workers. Of the contacted workers,  $46.4 \pm 1.9\%$  received vibration signals, while  $53.6 \pm 2.0\%$  did not. Thus, on average a vibrating worker produced signals while roaming over large areas of the nest and bypassed slightly more than half of all the potential recipients contacted.

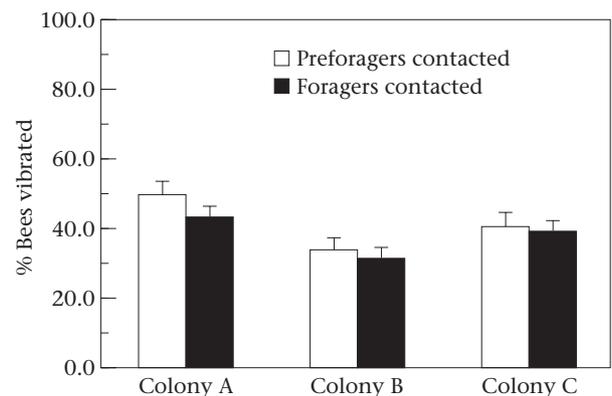
Age did not influence whether bees received vibration signals. As vibrating bees moved through the colony, they



**Figure 1.** Age distributions of vibrated and 'bypassed' workers in each of three colonies. Bypassed workers consisted of those that were antennated by a vibrating bee, but did not receive the signal. Values on the X axis represent the midpoints of 3-day age intervals (1–3 days, 4–6 days, etc.).

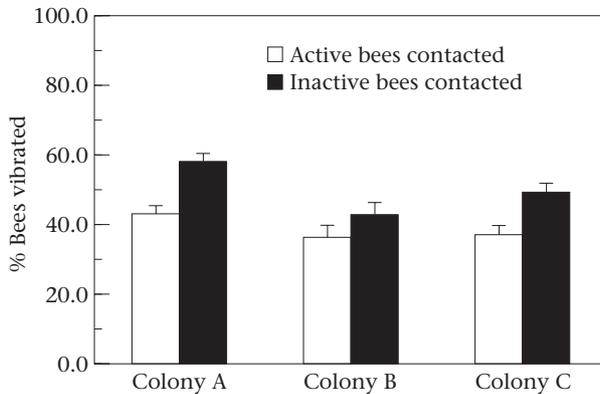
contacted and performed signals on workers of all ages (Fig. 1). The mean age of vibrated workers ( $19.6 \pm 0.65$  days) did not differ from the  $20.2 \pm 0.59$  days observed for bypassed bees (ANOVA:  $F_{1,86}=0.34$ , NS) and this tendency was the same in the three colonies (ANOVA:  $F_{1,2}=0.25$ , NS). Likewise, there was no difference in the proportion of preforaging-age and foraging-age bees that received vibration signals (ANOVA:  $F_{1,86}=2.11$ , NS; Fig. 2) and this tendency was consistent among colonies (ANOVA:  $F_{1,2}=0.36$ , NS). Bees performing vibration signals were  $26.5 \pm 1.08$  days old and 87% were of foraging age. Taken together, these observations suggest that signalling activity was not focused on particular age groups or directed preferentially towards recipients associated with only certain tasks or belonging to the same age category as the signaller.

The likelihood of a worker receiving vibration signals was influenced by its activity level. A significantly greater proportion of inactive versus active bees were vibrated (ANOVA:  $F_{1,93}=59.16$ ,  $P<0.0001$ ; Fig. 3) and

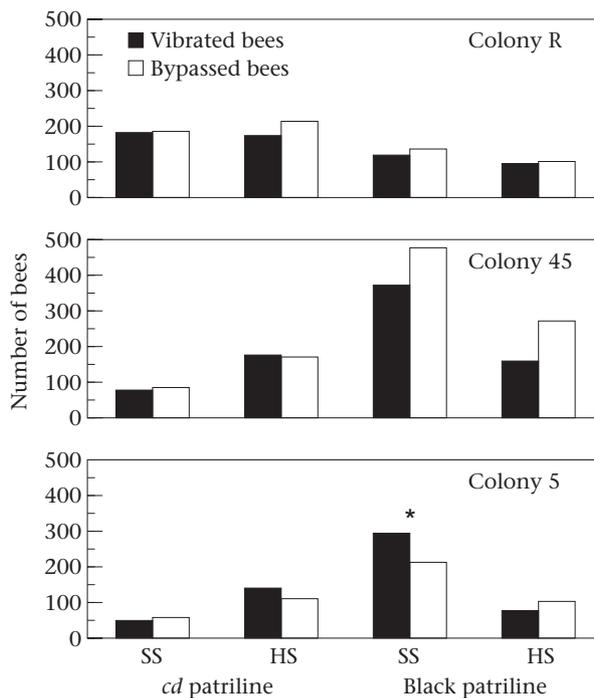


**Figure 2.** Mean + SE proportion of preforaging-age and foraging-age workers that received vibration signals in each of three colonies. Workers at least 15 days old were considered to be of foraging age; younger workers were of preforaging age.

this difference was similar among colonies (ANOVA:  $F_{1,2}=2.31$ , NS). On average,  $12.4 \pm 1.4\%$  more inactive than active workers were selected as recipients (Fig. 3).



**Figure 3.** Mean+SE proportion of active versus inactive workers that received vibration signals in each of three colonies.



**Figure 4.** Number of supersisters (SS) and half-sisters (HS) that were vibrated versus bypassed by signalling bees from the Cordovan (*cd*) and black patrilines in each of three colonies. A significant kin preference ( $*P < 0.05$ ) was observed for only the black patriline in colony 5.

Relatedness had little effect on whether workers received vibration signals. The black-patriline vibrators in colony 5 performed significantly more signals than expected on supersisters (replicated  $G$  test:  $G_{11} = 27.55$ ,  $P = 0.005$ ; Fig. 4). In contrast, the *cd* patriline in colony 5 and both patrilines in colonies R and 45 showed no kin preferences during signal performance (replicated  $G$  test: NS for all comparisons; Fig. 4). Furthermore, there were no significant heterogeneity values (replicated  $G$  test:  $G_H$  values NS for all comparisons), suggesting that there was little variability among vibrators in the extent to which kinship influenced signal performance. Thus, under most of the situations examined, relatedness did not influence recipient choice by vibrating bees.

## DISCUSSION

Our results suggest that vibrating bees roam over large areas of the nest and preferentially direct their signals toward inactive workers, but do not discriminate among potential recipients on the basis of age or relatedness. The ‘broadcasting’ of signals with respect to recipient age suggests that vibration signals may influence many different tasks. However, we did not monitor the responses of vibrated bees and thus we do not know whether our foraging- and preforaging-age recipients were in fact involved in food collection versus in-hive tasks. Workers within a colony can mature behaviourally at different rates (Robinson 1992; Huang & Robinson 1996) and some of the younger vibrated recipients may have been precocious foragers. Thus, the age range observed for recipients may not have reflected a broadcasting of signals, but rather a tendency to focus vibration activity on workers associated with only certain tasks. However, we observed large numbers of recipients in all colonies that were less than 10 days of age. It is unlikely that this many precocious foragers would have occurred in three separate colonies, especially since the earliest age at which we observed the onset of foraging by our marked bees was typically around 15 days. Therefore, signalling activity may well have been distributed broadly among different task groups.

We observed a significant kin preference by vibrating bees for only a single patriline in one of our study colonies. Slight, variable kin preferences have been suggested for many other honeybee activities (Visscher 1986; Frumhoff & Schneider 1987; Page & Robinson 1990; Oldroyd et al. 1991; Robinson et al. 1994; Tapy & Fletcher 1998). However, the impact, if any, of these preferences on the organization of colony activity is unclear. Kin preferences may be methodological artefacts arising from the use of a limited number of patrilines, rather than accurate indications of the importance of relatedness in colonies with a normal number of subfamilies (Carlin & Frumhoff 1990; Frumhoff 1991). Moreover, the use of the Cordovan marker may enhance the ability of bees to distinguish between super- and half-sisters (Frumhoff 1991). We used the Cordovan marker in colonies containing only two patrilines and found no consistent association between kinship and vibration signal activity. Thus, in colonies with a typical genetic structure, relatedness probably has little influence on vibration signal performance or its function in colony-level activities.

Taken together, our results support the hypothesis that the vibration signal functions in a nonspecific, modulatory manner to coordinate the activity of workers that perform separate, but interrelated tasks (Beshers et al. 1999; Lewis & Schneider 2000). Vibration signals are often performed by successful foragers (Painter-Kurt & Schneider 1998; Nieh 1998; Seeley et al. 1998) and signalling activity increases after sustained periods of elevated foraging success (Schneider et al. 1986b). Foraging-age recipients respond to the signals with heightened locomotion that increases contact with the waggle dances and odour cues that recruit them to food sites (Schneider et al.

1986a; Nieh 1998). Younger recipients respond with increased time spent performing a variety of in-hive tasks, particularly brood care, food processing and comb manipulation (Schneider 1987; Schneider & McNally 1991). During periods of heightened food availability, each of these activities may need to be increased in a balanced manner. The movement patterns and recipient selection displayed by vibrating bees may therefore result in the simultaneous activation of numerous worker age groups that attend to different stimuli and which may be spatially segregated in the nest, but which perform tasks that must be adjusted to changes in resource abundance and foraging success (Seeley 1982, 1995; Lewis & Schneider 2000).

Selection among potential recipients may also occur when vibration signals are performed on virgin queens. Honeybee colonies rear multiple virgin queens during reproductive swarming and emergency queen replacement (Winston 1987; Taryp & Fletcher 1998). Emerged queens fight among themselves to the death, which results in a single survivor who becomes the new laying queen of the colony. Virgin queens can be vibrated hundreds of times an hour during the queen elimination period (Fletcher 1978; Schneider 1991). The signal may influence queen aggressive interactions and survival, and may give workers a degree of control over which queen inherits the nest (Schneider et al. 2001). There is tremendous variability in the vibration rates experienced by different queens within the same colony, suggesting that workers preferentially direct their signalling activity towards certain recipients (Schneider et al. 2001). While the factors influencing these choices are not understood, virgin queens may provide another avenue for exploring recipient selection by vibrating bees.

Directing information flow by choosing recipients may also occur for trophallaxis (liquid food exchange) and grooming. Both are tactile interactions that involve donor and recipient individuals, and represent mechanisms of information transfer in honeybees and other social insects (Winston 1987; Seeley 1995; Hölldobler & Wilson 1990). Nestmates can reject these interactions, and these decisions may be influenced by several worker characteristics (Korst & Velthuis 1982; Moritz & Hallman 1986; Frumhoff & Schneider 1987; van der Blom & Verkade 1991). Unlike the vibration signal, however, trophallaxis and grooming are not typically performed in sustained series by individual signallers that roam throughout the nest. The broadcast manner of dissemination may therefore be characteristic of signals like the vibration signal that function to modulate the parallel performance of related tasks by different worker groups (Lewis & Schneider 2000).

The selection of recipients by workers performing vibration signals potentially plays an important role in directing the flow of information in honeybee colonies. Interactions among social animals are often nonrandom (Reeve 1992; Catchpole & Slater 1995; Janik 2000), and selection of recipients by signallers may be a common feature of many social communication systems. For the highly social insects, understanding the factors that mediate these choices and how they affect the

organization of colony labour will allow us to develop a more complete picture of information flow during the cooperative activities that characterize these species.

### Acknowledgments

We thank D. Taryp and two anonymous referees for valuable comments on the manuscript. We give special thanks to D. Taryp for performing the instrumental inseminations. The work was supported in part by USDA grant 9 802 682 awarded to S. S. Schneider and G. DeGrandi-Hoffman.

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