

The effect of repeated vibration signals on worker behavior in established and newly founded colonies of the honey bee, *Apis mellifera*

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Abstract Communication signals used in animal social interactions are frequently performed repetitively, but the function of this repetition is often not well understood. We examined the effects of signal repetition by investigating the behavior of worker honey bees that received differing numbers of vibration signals in established and newly founded colonies, which could use signal repetition differently to help adjust task allocations to the labor demands associated with the different stages of colony development. In both colony types, more than half of all monitored workers received more than one vibration signal, and approximately 12% received ≥ 5 signals during a given 20-min observation period. Vibrated recipients exhibited greater activity and task performance than same-age non-

vibrated controls at all levels of signal activity. However, vibrated workers showed similar levels of task performance, movement rates, cell inspection rates, and trophallactic exchanges regardless of the number of signals received. Thus, the repeated performance of vibration signals on individual bees did not cause cumulative increases in the activity of certain workers, but rather may have functioned to maintain relatively constant levels of activity and task performance among groups of recipients. The established and newly founded colonies did not differ in the extent to which individual workers received the different numbers of vibration signals or in the levels of activity stimulated by repeated signals. Previous work has suggested that compared to established colonies, newly founded colonies have a

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greater number of vibrators that perform signals on a greater proportion of the workers they contact. Taken in concert, these results suggest that vibration signal repetition may help to adjust task allocations to the different stages of colony development by helping to maintain similar levels of activity among a greater total number of recipients, rather than by eliciting cumulative effects that cause certain recipients to work harder than others.

Keywords Vibration signal · Modulatory communication · Signal repetition · Collaborative labor · Social organization

Introduction

A central objective in the study of animal social networks is to understand how communication signals are used to generate the patterns of information transfer that organize collective activities (Fewell 2003; O'Donnell and Bulova 2007a, b). An aspect of communication that may strongly affect information transfer is the repetition of signals. Signals used in social behavior are often performed repetitively, and this repetition may influence social interactions in a variety of ways, including maintaining a behavioral state among groups of individuals, causing cumulative excitatory or inhibitory effects on recipient activity, and increasing the accuracy of information transfer by reducing ambiguity arising from “noise” in signal production (Bradbury and Vehrencamp 1998; O'Donnell and Bulova 2007a, b; De Marco et al. 2008). Repetition effects may be particularly relevant for modulatory communication signals, which do not elicit specific responses in themselves, but rather alter the probability that recipients will respond to other signals and cues that influence behavioral decisions (Markl 1985; Anderson and McShea 2001). Modulatory signals can influence many activities, and their repeated performance may play an important role in adjusting group actions during collaborative social behavior (Hölldobler and Wilson 1990; O'Donnell 2003; Schneider and Lewis 2004; O'Donnell and Bulova 2007a). However, the function of signal repetition in modulatory communication has received little detailed study (O'Donnell and Bulova 2007a).

An example of a modulatory signal that is characterized by high levels of repetition is the vibration signal of the honey bee, *Apis mellifera*, which consists of a worker rapidly vibrating her body dorso-ventrally for 1–2 s, usually while grasping the body of a recipient with her legs. The signal causes a non-specific increase in activity that influences two main aspects of recipient behavior. First, it enhances information acquisition. Vibrated workers increase the rates at which they move through the nest, inspect comb contents, and engage in trophallaxis (liquid

food exchange), all of which potentially increase the acquisition of information about colony needs (Fewell and Winston 1996; Grüter et al. 2006; Cao et al. 2007). Second, the signal contributes to greater task performance. Vibrated recipients engage in a greater number of different tasks, spend more time in brood care, food processing, and nest maintenance, and have a greater likelihood of engaging in foraging (Schneider and Lewis 2004; Hyland et al. 2007). Thus, by operating in a non-specific modulatory manner, the vibration signal can influence many inter-dependent aspects of collaborative labor in honey bee colonies.

Repetition in vibration signal performance occurs at two levels. First, the same signaler may vibrate many different workers. Vibration signals are produced primarily by successful foragers, who often roam through large areas of the nest while performing series of signals (up to 20 or more per minute) that can last from several minutes to over an hour (Schneider 1986; Painter-Kurt and Schneider 1998; Beismeyer 2003). As a signaler moves through the colony, she contacts and vibrates hundreds of individual workers, but her signals are preferentially directed toward less active bees of all ages (Lewis et al. 2002; Hyland et al. 2007). The performance of vibration signals on multiple different workers distributed throughout large areas of the nest can simultaneously influence a broad spectrum of colony activities that must be adjusted to changes in colony food intake and energy needs.

Second, an individual recipient may receive vibration signals repeatedly during a given period of time. The function of this repetition is unknown, but it could affect recipient behavior in at least two ways. First, it could cause cumulative increases in activity. Vibrated recipients show slight, significant increases in juvenile hormone titers, which may contribute to greater task performance by altering metabolic rates and response thresholds (Sullivan et al. 2003; Schneider et al. 2004). If the hormonal effects of individual signals are incremental, then repeatedly vibrating the same bee may cause cumulative effects that result in increased activity levels relative to other recipients. This, in turn, may help to fine tune colony labor allocations by eliciting increased work from certain bees. Alternatively, repeatedly receiving vibration signals could function to maintain a more or less constant behavioral state. If recipients vary in the degree and duration to which they respond to individual vibration signals, then some may require more signals than others to initiate and maintain a level of activity over a certain period of time. If so, then signal repetition could be used to generate more consistent levels of activity among groups of recipients.

Furthermore, the importance of repeated signaling on the same recipient may change with colony conditions. For example, newly founded honey bee colonies, which must quickly build combs and amass food reserves for winter

survival, have greater per capita vibration signaling activity that is more focused on inactive recipients compared to established colonies, which have fully constructed combs and large amount of stored food (Hyland et al. 2007). Differences in signaling activity and recipient selection may help to adjust worker activity to the labor and energy requirements associated with the different stages of colony development, and variation in the number of signals received by individual recipients may further calibrate task allocations to changing colony needs. Examining the influence of repeated vibration signals under different colony conditions could therefore increase our understanding of the role of signal repetition in organizing cooperative activity in honey bees, as well as the function of modulatory communication in insect societies.

The purpose of our study was to investigate the repeated performance of vibration signals on individual worker in established and newly founded colonies of honey bees. We had two main objectives. First, we assessed the extent to which workers received multiple vibration signals under the two colony conditions. Second, we examined the effects of repeated signaling on the behavior of workers from newly founded and established colonies with respect to (1) task performance and (2) rates of interaction with the nest and nest mates, which influence the acquisition of information about colony needs. Our goal was to determine if signal repetition was associated with cumulative increases in recipient activity or the maintenance of consistent behavioral states and if these responses changed with the stage of colony development. Given the labor needs associated with nest founding, we predicted that the effects of repeated vibration signals would be more strongly expressed in newly founded colonies.

Materials and methods

Colony setup and establishing populations of marked workers

Our study was part of a larger investigation that examined the influence of colony developmental state on honey bee communication behavior (Cao et al. 2007; Hyland et al. 2007). The methods used to set up colonies and establish populations of marked, known-age workers have been previously reported (Hyland et al. 2007) and are briefly summarized below.

Our general experimental plan was to establish pairs of four-frame observation colonies. One colony in each pair simulated the conditions of an established nest, with fully constructed combs filled with food and brood in all stages of development. The second colony in each pair simulated the nest conditions in a newly founded colony, in which all

combs must be built “from scratch”, while workers simultaneously initiate brood rearing and amass food reserves. These newly founded colonies were set up by transferring an artificially created swarm into an observation hive with four wooden frames, each of which was empty except for a 42×12 cm strip of wax foundation used to ensure that combs were built with the proper orientation in the hive (see Lewis and Schneider 2000 and Donahoe et al. 2003 for the methods of swarm creation). During each trial, both colonies were transferred into the observation hives simultaneously.

Within each colony, we established a population of individually recognizable, marked bees by gluing to the thorax of newly emerged workers plastic tags (Opalinthplättchen, Chr. Graze, Endersbach, Germany), each with a unique number/color/paint mark combination. Tagged individuals were added in cohorts of 100 bees each day until a total of 1,100–1,300 had been introduced into each colony. Workers for marking were emerged in an incubator (35°C; 50% RH) from combs taken from unrelated field colonies and tagged within 24 h of emergence. The glass walls of the observation hives were marked off in a grid of 4×4 cm squares to facilitate monitoring the behavior of tagged bees.

We conducted four trials during the spring and summer of 2004 and 2005. Each trial included one established colony and one newly founded colony, and observations were conducted for 3 weeks in order to follow the first complete cycle of brood rearing in the newly founded colonies. All colonies initially contained 6,000–8,000 workers. During the course of the trials, the newly founded colonies built larger amounts of comb, devoted greater proportions of comb space to brood rearing, had greater per capita foraging activity, but declined in population size by half compared to the established colonies (Hyland et al. 2007). Similar patterns of growth and activity have been previously reported for newly founded and small honey bee colonies, suggesting that our manipulations simulated the labor and energy demands associated with the different stages of colony development (Eckert et al. 1994; Schneider and McNally 1994; Beekman et al. 2004).

Determining the number of vibration signals received by workers and the behavior of vibrated recipients

Throughout a trial, tagged bees that received a vibration signal were selected at random and monitored for 20 min each or until they were lost in the colony or flew from the hive. We recorded the following data for each recipient, using digital stopwatches when necessary: (1) the total number of vibration signals received during the monitoring period, including the initial signal that triggered observations, (2) number of grid squares crossed, (3) number of

cell inspections performed (defined as a bee having at least her head inside a cell for less than 5 s), (4) whether she was associated with foraging (flew from the hive or followed waggle or tremble dances), (5) the amount of time spent in trophallaxis (mouth-to-mouth exchange of liquid food), and (6) the amount of time spent in the tasks of grooming another bee, brood care, food processing, comb manipulation, ventilating (fanning), and attending the queen. A worker was considered to be engaged in brood care or food processing if she had at least her head inside a brood or food cell for ≥ 5 s and was moving in the cell (Lewis et al. 2002).

For each vibrated bee observed, we also monitored the behavior of a non-vibrated tagged bee as a control. Each control bee was selected to be of the same age, in the same initial location of the nest, and exhibiting the same initial level of activity as her vibrated counterpart. Each tagged control bee was selected within 1 h of monitoring the vibrated recipient and, whenever possible, was monitored by a separate observer simultaneously with her vibrated counterpart. If a control received a vibration signal during the observation period, observations were terminated and a new tagged control was selected. Each recipient and control was monitored only once.

To assess task performance, we determined for each recipient and control the number of different tasks performed and the proportion of time spent in all tasks combined. We also determined the number of recipients and controls that flew from the hive and followed recruitment dances to assess the influence of vibration signal activity on foraging-related tasks. To assess the rates at which vibrated recipients and non-vibrated controls acquired information about their colonies, we determined for each bee its movement rate (grid squares crossed per minute), cell inspection rate (inspections per minute), and the proportion of time engaged in trophallaxis. Movement through the colony and cell inspection activity may influence contact with stimuli from the combs, brood, and nest mates that affect task decisions, and trophallaxis is an important means of information transfer that influences brood rearing and foraging activity (Fewell and Winston 1996; Dreller and Tarpy 2000; Pankiw 2004; Grüter et al. 2006).

Statistical analyses

We categorized each recipient as receiving one, two, three, four, and greater than or equal to five vibration signals during a 20-min observation period (henceforth referred to as “times vibrated”). To ensure adequate numbers of recipients for the different levels of times vibrated, bees receiving five or more signals were combined in a single category. To examine the effects of the number of signals received on recipient behavior, we used factorial ANCOVA

(SAS Institute 1997) to compare the differences between recipients and controls within and between the established and newly founded colonies for (1) the number of tasks performed, (2) the proportion of time spent performing all tasks combined, (3) movement rate, (4) cell inspection rate, and (5) the proportion of time spent in trophallaxis. We compared the number of recipients and controls that flew from the nest and followed recruitment dances using $4 \times 2 \times 2 \times 5$ contingency tables (4 trials \times 2 colony types \times 2 bee types [recipient and control] \times 5 categories of times vibrated) analyzed by log-linear models. In the ANCOVA and log-linear models, the second-order interactions (colony type \times bee type \times times vibrated) allowed us to assess whether the influence of the number of signals received on the magnitude of recipient responses varied with colony developmental state. The third-order interactions (trial \times colony type \times bee type \times times vibrated) allowed us to assess whether the associations between number of signals received and the magnitude of recipient responses varied among trials. If significant interaction terms were present, we conducted post hoc paired comparisons using Tukey’s HSD tests (Sokal and Rohlf 1995). To achieve normality, proportional data were arcsine-transformed, and the movement rates and cell inspection rates for individual recipients and controls were square-root-transformed prior to analysis. The sequential Bonferroni adjustment (Rice 1989) was used to determine significance levels for all comparisons made between recipients and controls and between colony types. All statistical tests were two-tailed; mean values are reported as ± 1 SE.

Results

We monitored a total of 447 vibrated recipients during the course of the study (57.0 ± 3.1 recipients/newly founded colony; 54.9 ± 3.9 recipients/established colony) and an equal number of non-vibrated controls. On average, each bee was monitored for 17.9 ± 3.94 min.

Number of vibration signals received

The number of signals received by individual bees ranged from one to eight in the established colonies and one to 16 in the newly founded colonies. When viewed over all colonies, $56.5 \pm 2.1\%$ of the monitored bees received more than one vibration signal and $12.0 \pm 1.2\%$ received five or more signals during the observation periods (Fig. 1). The mean number of signals received was 2.5 ± 0.11 and 2.3 ± 0.12 for the established and newly founded colonies, respectively. The number of bees receiving the different number of signals was similar in the two colony types ($\chi^2_4 = 3.77$; $P = 0.430$; Fig. 1).

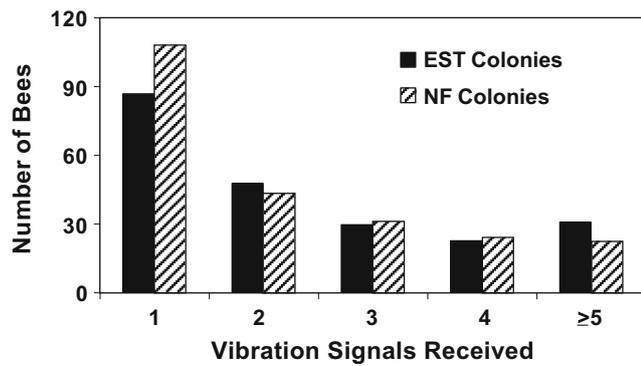


Fig. 1 The number of workers that received the different numbers of vibration signals during the 20-min observation periods in the established (*EST*) and newly founded (*NF*) colonies

Behavior of workers receiving different numbers of vibration signals

We found no trial effects for any of the activities examined for vibrated recipients (for each trial×colony type×bee type×times vibrated interaction: $F_{4,890}$ ranged from 0.76 to 2.76; P ranged from 0.057 to 0.483). Furthermore, in both colony types, vibrated recipients showed greater activity compared to non-vibrated controls for every behavior monitored (for each comparison: $F_{1,890}$ ranged from 10.3 to 62.4; P ranged from 0.003 to <0.0001; Tables 1 and 2). The only exceptions to this trend occurred for the proportion of time spent in trophallaxis by workers receiving one to two vibration signals in the established colonies (Table 1). The greater activity of recipients

compared to controls was observed for each of the different numbers of vibration signals received (for each bee type×times vibrated interaction: $F_{4,890}$ ranged from 0.27 to 2.11; P ranged from 0.15 to 0.90). Thus, regardless of the actual level of activity exhibited by bees receiving the different numbers of signals, vibrated recipients consistently showed greater activity than their same-age, non-vibrated controls. As a result, we focused our analyses on comparing the behavior of recipients of the different numbers of signals in the two colony types.

Task performance was not influenced by the number of vibration signals received. Bees that were vibrated the different number of times performed a similar number of tasks ($F_{4,437}=0.83$; $P=0.508$) and spent similar proportions of time performing tasks ($F_{4,437}=0.38$; $P=0.823$; Fig. 2). These results were the same in both the established and newly founded colonies (for number of tasks: $F_{4,437}=1.20$; $P=0.308$; for proportion of time in tasks: $F_{4,437}=0.59$; $P=0.668$). The number of signals received also did not influence the likelihood of flying from the hive ($\chi^2_4=5.63$; $P=0.228$; Fig. 3) or following recruitment dances ($\chi^2_4=3.27$; $P=0.513$; Fig. 3), and these patterns were exhibited similarly in both colony types (for each comparison: $\chi^2_4<2.20$; $P>0.705$).

The rates at which workers acquired information about their colonies also was not affected by the number of vibration signals received. Workers receiving the different numbers of signals did not differ in their movement rates ($F_{4,437}=1.08$; $P=0.368$; Fig. 4) or cell inspection rates ($F_{4,437}=0.53$; $P=0.716$; Fig. 4), and there were no colony type×times vibrated interactions (for movement rate:

Table 1 Activity levels of recipients (R) of the different number of vibration signals in the established colonies (EST) and their same-age, non-vibrated controls (C)

EST colonies		Vibration signals received				
		1	2	3	4	≥5
Number of tasks	R	1.95±0.12	2.17±0.18	2.23±0.22	2.17±0.25	2.16±0.18
	C	0.99±0.11	1.14±0.13	1.20±0.22	1.56±0.21	1.10±0.24
% Time in tasks	R	22.1±2.38	26.8±3.56	22.9±4.24	24.5±5.36	21.7±3.58
	C	9.4±1.69	11.4±2.38	9.5±2.12	14.8±4.03	8.6±2.79
% Flying from nest	R	8.0	16.7	6.7	8.7	3.2
	C	4.6	2.1	3.3	4.3	0
% Following dancer	R	14.9	12.5	10.0	4.3	9.7
	C	6.9	8.3	0	0	6.4
Movement rate	R	2.65±0.36	2.43±0.34	2.25±0.34	2.38±0.30	2.49±0.32
	C	1.36±0.12	1.20±0.14	1.53±0.31	1.91±0.41	1.49±0.24
Cell inspection rate	R	1.46±0.15	1.43±0.26	2.39±0.53	2.19±0.45	2.31±0.38
	C	0.74±0.08	0.99±0.17	1.32±0.27	1.76±0.45	1.10±0.19
% Time in trophallaxis	R	0.70±0.17	0.58±0.19	1.91±0.60	1.26±0.69	0.93±0.30
	C	0.81±0.22	0.96±0.48	1.03±0.41	0.68±0.24	0.35±0.14

Means are reported as ±1 SE

Table 2 Activity levels of recipients (R) of the different number of vibration signals in the newly founded colonies (NF) and their same-age, non-vibrated controls (C)

NF colonies		Vibration signals received				
		1	2	3	4	≥5
Number of tasks	R	2.00±0.12	1.63±0.18	1.94±0.21	2.00±0.23	2.31±0.27
	C	1.01±0.10	0.78±0.16	0.97±0.21	1.12±0.23	0.86±0.16
% Time in tasks	R	27.5±2.54	26.0±4.37	31.5±4.98	30.2±6.01	21.0±4.14
	C	10.9±1.62	6.0±1.63	9.1±2.49	16.5±3.95	6.6±2.05
% Flying from nest	R	8.3	11.6	3.2	8.3	4.5
	C	5.5	2.3	0	0	0
% Following dancer	R	15.7	11.6	12.9	16.7	4.5
	C	9.2	0	0	4.2	0
Movement rate	R	2.31±0.38	1.72±0.26	1.08±0.16	1.92±0.29	1.91±0.36
	C	0.94±0.21	0.68±0.19	0.61±0.12	1.02±0.21	0.83±0.16
Cell inspection rate	R	1.62±0.23	1.49±0.35	1.20±0.21	1.40±0.34	1.30±0.35
	C	0.65±0.11	0.25±0.09	0.56±0.17	1.09±0.34	0.98±0.26
% Time in trophallaxis	R	0.87±0.16	0.95±0.35	0.51±0.17	0.93±0.41	1.12±0.42
	C	0.56±0.14	0.59±0.29	0.32±0.15	0.69±0.34	0.38±0.21

Means are reported as ±1 SE

$F_{4,437}=0.27$; $P=0.90$; for inspection rate: $F_{4,437}=2.11$; $P=0.079$). Likewise, the number of signals received did not influence the proportion of time that workers spent in trophallaxis ($F_{4,437}=0.90$; $P=0.466$; Fig. 4), and this relationship was the same in the established and newly founded colonies ($F_{4,437}=1.75$; $P=0.138$).

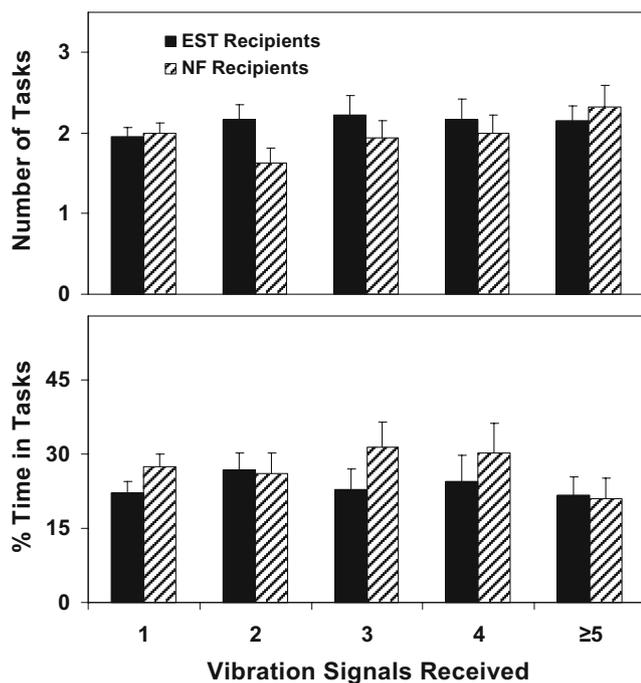


Fig. 2 Mean±SE number of tasks performed and proportion of time spent performing tasks by the workers that received the different numbers of vibration signals in the established (EST) and newly founded (NF) colonies

Discussion

Receiving repeated vibration signals was a common occurrence in both our established and newly founded honey bee colonies. More than half of the workers monitored received more than one vibration signal, and approximately one in eight were vibrated five to 16 times during a 20-min observation period. With the exception of

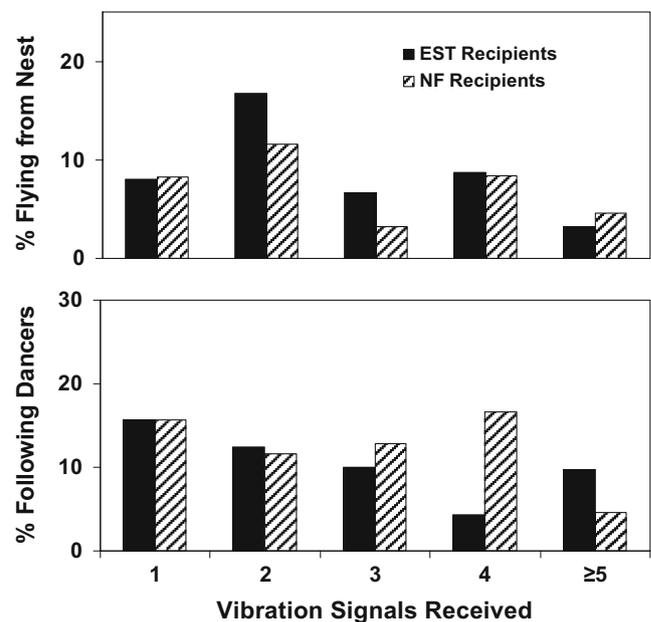


Fig. 3 The proportion of workers receiving the different numbers of vibration signals in the established (EST) and newly founded (NF) colonies that flew from the nest and followed recruitment dancers during the 20-min observation periods

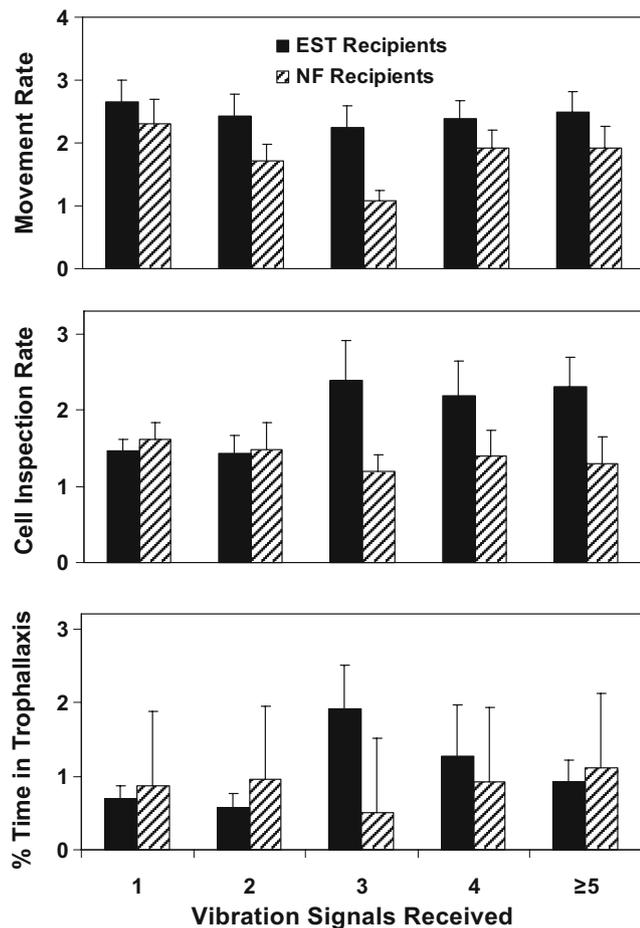


Fig. 4 Mean \pm SE movement rate, cell inspection rate, and proportion of time spent in trophallaxis by workers receiving the different numbers of vibration signals in the established (*EST*) and newly founded (*NF*) colonies

the proportion of time spent in trophallaxis by workers vibrated one to two times in the established colonies, recipients consistently displayed greater activity and task performance compared to non-vibrated controls. However, the activity levels of recipients were similar regardless of the number of signals received. Thus, we found no evidence that repeated vibration signals caused cumulative increases in recipient activity. These results must be interpreted cautiously because we do not know what recipients experienced prior to the vibration signal that triggered our observations. Furthermore, our methodology for assessing recipient behavior may not have been sufficiently fine-grained to detect differences among workers that were vibrated a different number of times. However, this seems unlikely given that we were able to detect differences between vibrated recipients and non-vibrated controls at all levels of signaling activity. Thus, although vibrated bees consistently showed increased activity compared to non-

vibrated controls, repeated signals on individual workers did not stimulate different levels of task performance among recipients, at least during our 20-min observation periods.

If repeated vibration signals do not produce cumulative effects, then why do so many workers receive multiple signals during a given period of observation? One possibility is that repeated signaling is a random event that serves no function. A single vibration signal may elevate worker activity to a level where further increases are unlikely, even if additional signals are received. The number of signals performed on an individual bee might then be an artifact of the distribution of vibrators in a colony. Workers in areas of the nest with numerous vibrators would have an increased chance of receiving additional signals, which then would have no further effects on their behavior. However, this scenario seems unlikely. The responses of vibrated workers are highly variable (Schneider 1987; Schneider and McNally 1991; Schneider et al. 2004; Cao et al. 2007), suggesting that for many recipients a single signal does not elevate activity to some upper limit that precludes further increases. Also, vibrators perform signals on only about half of the workers they contact as they move through the nest and tend to focus their signals on less active bees (Lewis et al. 2002; Hyland et al. 2007). Thus, it is unlikely that receiving vibration signals is a random occurrence, but rather recipients may be selected from an array of potential receivers.

An alternate possibility, which is supported by our results, is that repeated vibration signals function to maintain relatively consistent levels of activity and task performance among different recipients. The differences in the behavioral and hormonal responses of vibrated workers suggest considerable variability in the degree and duration to which the activity of individual bees is affected by the signal (Schneider 1987; Schneider et al. 2004; Cao et al. 2007; Hyland et al. 2007). This, in turn, may reflect variability in response thresholds arising from genetic, developmental, and experiential differences among recipients. Because vibration signals are focused on less active bees, the number of signals a worker receives may depend upon its initial level of activity, the extent of its response to a given signal, and its ability to maintain a certain level of task performance. Some workers may require repeated vibration signals to initiate a level of task performance that other recipients can achieve with only one signal. Or, an individual bee may need to be vibrated repeatedly to maintain task performance if its response to each signal is low or decays rapidly, whereas other recipients may require fewer signals to maintain similar levels of activity. The differing numbers of signals received by individual bees may therefore function to maintain a relatively constant level of activity among groups of workers that vary in their behavioral tendencies and response thresholds, rather than

elicit cumulative effects that cause certain recipients to work harder than others.

The hypothesis that repeated vibration signals help to maintain a behavioral state is supported by the use of the signal to influence queen activity. Queens are vibrated only during reproductive swarming and queen replacement (Schneider and Lewis 2004). Laying queens are vibrated at variable, but more or less continuous rates throughout the 2–4 weeks preceding colony swarming. The signal elicits increased activity, which may help to establish and maintain a behavioral state that gradually prepares a queen to abandon the nest with the swarm (Fletcher 1975; Schneider 1991; Pierce et al. 2007). Virgin queens can be vibrated hundreds of times an hour throughout the rival elimination period, when they battle among themselves to the death to determine which will become the new laying queen of the colony. The extreme level of signal repetition during rival elimination may help to maintain a behavioral state that influences the timing and participants of queen battles and ultimately the outcome of the replacement process (Schneider et al. 2001; Schneider and DeGrandi-Hoffman 2003, 2008).

We found no evidence that colony developmental state affected the repeated performance of vibration signals on individual bees. Our established and newly founded colonies did not differ in the extent to which workers received multiple signals. Likewise, workers in both colony types showed similar increases in activity and task performance at all levels of signaling activity. Previous work has demonstrated that compared to established colonies, newly founded colonies have increased numbers of vibrators, which perform signals on a greater proportion of the workers they contact and focus their signaling activity more strongly on less active bees (Cao et al. 2007; Hyland et al. 2007). This, in turn, may result in higher per capita levels of signaling activity and potentially the activation of larger portions of the unoccupied workforce. Taken together, these results suggest that the repeated vibration signals may help to adjust worker behavior to the labor demands associated with colony development primarily by helping to maintain more uniform levels of information acquisition and task performance among a greater total number of workers, rather than causing a subset of recipients to labor at greater rates relative to others.

The repetition of modulatory signals to maintain behavioral states may be widespread in social animals. For example, “drumming” in ants, which is a modulatory signal produced by striking the substrate with the head or abdomen, is performed repetitively during nest cave-ins and predator attacks to maintain levels of activity for nest repair and defense (Fuchs 1976; Hölldobler and Wilson 1990). Biting interactions among *Polybia* wasps modulate

worker behavior, and the repeated biting of individuals may help to adjust and maintain colony foraging activity (O’Donnell 2003, 2006). The repetition of alarm calls in ground squirrels may modulate attentiveness and help to maintain vigilance during periods of predation risk (Owings et al. 1986; Loughry and McDonough 1988; Sloan and Hare 2008). Thus, using repeated signaling to maintain and coordinate activity levels among group members may be a common feature of modulatory communication in many social species. The importance of signal repetition may increase with increasing group size and the need to integrate the behavior of greater numbers of individuals for social activities (Anderson and McShea 2001; O’Donnell and Bulova 2007a). Many communication signals, such as alarm calls, mating displays, and some recruitment signals, are performed repetitively and broadcast throughout a social group. In contrast, tactile signals, such as the vibration signal of the honey bee, biting in wasps, and affiliative and dominance displays in many species, are directed toward specific recipients selected from among group members (Lewis et al. 2002; O’Donnell 2003). In large social insect colonies, such signals may be particularly important in directing information flow among workers, and repeated performance on certain individuals may help to maintain levels of information acquisition and task performance that fine tune labor adjustments to colony needs.

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