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ORIGINAL PAPER

How is activity distributed among and within tasks in *Temnothorax* ants?

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Abstract How social insect colonies behave results from the actions of their workers. Individual variation among workers in their response to various tasks is necessary for the division of labor within colonies. A worker may be active in only a subset of tasks (specialist), perform all tasks (elite), or exhibit no particular pattern of task activity (idiosyncratic). Here we examine how worker activity is distributed among and within tasks in ants of the genus *Temnothorax*. We found that workers exhibited elitism within a situation, i.e., in particular sets of tasks, such as those associated with emigrations, nest building, or foraging. However, there was weak specialization for working in a particular situation. A few workers exhibited elitism across all situations, i.e., high performance in all tasks in all situations. Within any particular task, the distribution of activity among workers was skewed, with few ants performing most of the work and most ants performing very little of the work. We further found that workers persisted in their task preference over days, with the same individuals performing most of the work day after day. Interestingly, colonies were robust to the removal of these highly active workers; they were replaced by other individuals that were previously less active. This replacement was not short-lived; when the removed individuals were returned to the colony, not all of them resumed their prior high activity levels, and not all the workers that replaced them reduced their activity. Thus, even though some workers specialize in tasks within a particular situation and are persistent in performing them, task allocation in a colony is plastic and colonies can withstand removal of highly active individuals.

Keywords Division of labor · Individual variation · Response threshold · Social organization · Task allocation · *Temnothorax*

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Introduction

The behavior of social insect colonies emerges from the actions of their workers. Colonies perform many tasks such as foraging, brood care, and nest maintenance, without a central control allocating workers to the various tasks (Bonabeau et al. 1997). To achieve an effective task allocation, workers must differ in their task preference profiles. Indeed, social insect workers exhibit differences in their task performance, caused by both internal and external factors

(Gordon 1996). For example, in the honeybee *Apis mellifera*, which task an individual performs depends heavily on physiological state and genetic background, which vary with individual age and patriline (reviewed in Robinson (1992)), but in the harvester ant *Pogonomyrmex barbatus*, environmental conditions and interactions among workers are predominant in determining which worker performs each task (reviewed in Gordon (2010)). To our knowledge, the activity of all workers within a colony has not been examined repeatedly in various situations to determine how task allocation results from this individual variation in task preference. Here we examine how worker activity is distributed within and across tasks and how interactions with other workers shape task allocation in *Temnothorax* ants.

Task performance is a continuous variable and hence neither dichotomous nor discrete. In a classical division of labor say in a factory (Smith 1776), efficiency was promoted by workers specializing in particular tasks at which they became especially proficient. Hence, task switching was minimized. However, in many ant species, individual workers switch tasks frequently, suggesting that labor is not discretely divided among workers and that performing a certain task does not preclude a worker from performing other tasks (Traniello 1978; Gordon 1989; Sendova-Franks and Franks 1995a; Robson and Traniello 2002; Gordon et al. 2005; Seid and Traniello 2006). In addition, within each task, individuals vary in their workload (Jaisson et al. 1988; Retana and Cerda 1991; Gordon et al. 2005; Dornhaus et al. 2008; Beverly et al. 2009) often with an uneven distribution of work among individuals: Few individuals perform most of the work, most individuals perform very little of it, and others are inactive (Dornhaus et al. 2009). So, calling one worker a forager does not mean it performs the same amount of work as another individual who is also considered to be a forager, nor does it imply that this worker cannot perform another task such as patrolling.

The idea of "task response thresholds" provides a conceptual framework that allows us to better understand the graded nature of task performance. In this framework, whether or not a worker performs a certain task and how often or for how long it performs depends on its response threshold to that particular task (Robinson 1987; Bonabeau et al. 1996). An individual will perform a certain task if cues from the environment exceed its task-specific response threshold and will continue performing the task until the associated cues no longer exceed its response threshold (Theraulaz et al. 1998; Beshers and Fewell 2001). Variation among individuals in their response threshold to a particular task and differences within an individual in its response thresholds to various tasks will result in a wide array of behavioral types within a colony, allowing for task allocation. Those individuals with the lowest response thresholds for a certain task at a given time will perform it, ensuring there is always a subset of workers performing any task.

However, the "response threshold" model does not necessarily predict that colonies are composed of workers that are specialized in each of the tasks a colony performs. The distribution of work among individuals depends on how threshold levels are distributed across workers and across tasks, both within and between situations. There are three alternative hypotheses for how thresholds may be distributed within a colony: (1) Elitism: Colonies consist of "elite" workers, who will perform all or many tasks (response thresholds for all tasks are low), and "lazy" workers, who will perform little of any task (high response thresholds for all tasks). Activity level, or response thresholds, will be positively correlated among tasks within workers (Fig. 1a, d) (Robson and Traniello 1999). (2) Specialization: Colonies are comprised of workers that are specialized for various tasks. A specialized worker will perform only one or few tasks (response threshold for a particular task is low but thresholds are high for all other tasks). Activity levels in various tasks will tend to be negatively correlated. (Fig. 1b, e) (Oster and Wilson 1978). (3) Idiosyncrasy: Individuals in a colony will behave idiosyncratically in respect to which tasks each worker performs (response thresholds to various tasks are independent from one another). Activity levels in one task will not predict those in another task (Fig. 1c, f) (Oster and Wilson 1978). To test these hypotheses, i.e., how workers distribute their activity among tasks, we examined the activity of individually marked workers in multiple tasks. We use activity level, i.e., how many times an individual performs a certain task, as a proxy for its response threshold, because response thresholds can often not be measured directly (but see Weidenmuller (2004)).

Furthermore, variation in response thresholds among workers that perform a certain task may lead to an uneven distribution of work within that task (Jaisson et al. 1988; Retana and Cerda 1991; Gordon et al. 2005; Dornhaus et al. 2008; Beverly et al. 2009; Dornhaus et al. 2009). A normal distribution of activity among workers within a particular task would be consistent with the hypothesis that all individuals perform at a similar activity level, with some variation around the mean. A skewed or exponential distribution of activity among workers within a task would be consistent with the hypothesis that most individuals perform a small part of the task and few workers perform most of it.

To test whether the response thresholds of workers change according to their social environment, we conducted removal–return experiments. We tested the following hypotheses: (1) temporary replacement (unchanging internal thresholds): Removing highly active workers will lead to an increase in the activity of other workers that were less active earlier. The response threshold model suggests that removing individuals with a low threshold

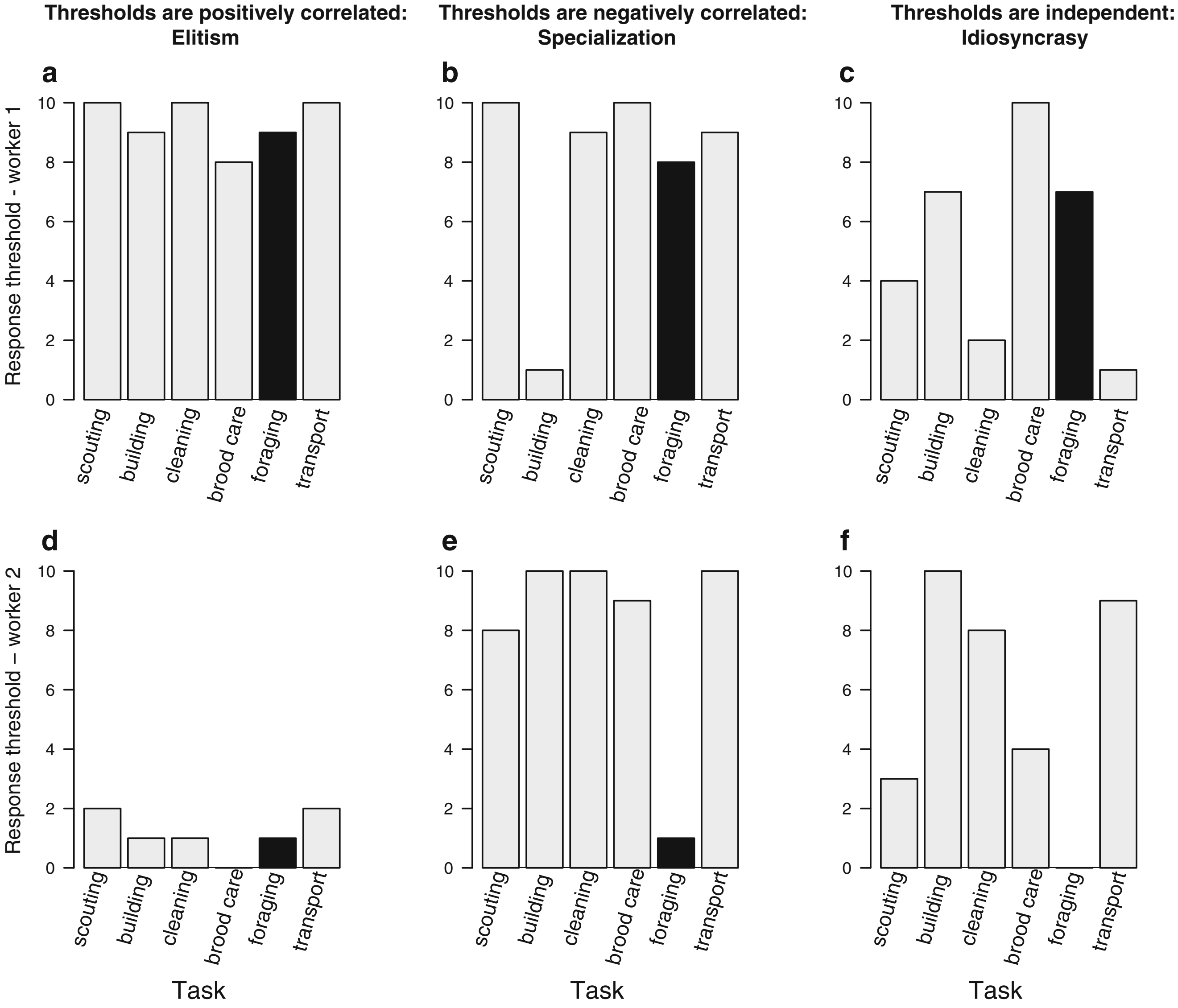

Fig. 1 Three hypotheses on how workers in a colony might differ in their task preferences (or response thresholds). Each *panel* depicts hypothetical response thresholds for six tasks. *Top row* (**a**–**c**): Worker 1 is not foraging—her response threshold for foraging (*black bars*) is always high. *Bottom row* (**d**–**f**): Worker 2 frequently forages because her response threshold for foraging (*black bars*) is low. **a**, **d** The elitism hypothesis in which thresholds in various tasks are positively correlated. **b**, **e** The specialization hypothesis in which thresholds in various tasks are negatively correlated. **c**, **f** The idiosyncrasy hypothesis in which thresholds in various tasks are independent of one another

will cause whichever individuals in the group that now have the lowest response threshold to become active (Theraulaz et al. 1998). If response thresholds are persistent, returning the previously highly active workers to the colony will revert the distribution of activity among workers to its prior structure and the returned workers will resume their earlier heightened activity levels. (2) Permanent replacement (changing internal thresholds): As in the previous hypothesis, removing highly active workers will lead to an increase in the activity of other workers that were less active earlier. However, response thresholds or task preferences of individuals may change over time or in response to social cues (Robinson and Huang 1998; Weidenmuller 2004), and upon return, the removed individuals will not resume their former role. (3) No replacement: The removed workers will not be replaced by others and the task will not be carried out by the colony until the removed individuals are returned.

Methods

We study the ants *Temnothorax albipennis* and *Temnothorax rugatulus* as model systems for task allocation and division of labor. These ants have small colonies (up to about 200–400 workers) and monomorphic workers. They usually have a single queen and are functionally monogynous and monandrous (Pearson et al. 1995;1997). *Temnothorax* ants live in pre-existing ephemeral cavities, such as cracks in rocks or hollow twigs or acorns and often emigrate to new nest sites (Franks et al. 2002).

Experiment 1: activity across and within tasks

Colony collection and housing

Eleven colonies of *T. albipennis* were collected in October 2004 in Dorset, southern England, and experiments were conducted between October 2004 and March 2005. All workers in the colonies were individually marked with paint dots, one on the head, one on the thorax, and two on the gaster (Sendova-Franks and Franks 1993). Each colony contained at least one queen (two colonies contained more: two and four queens, respectively) and brood of different stages. After marking, colonies contained a mean±SD=104±69 workers, and mean±SD=229±120 brood items. The number of brood items was determined as the number of brood transports during the emigration because small brood items are hard to distinguish on a photograph (this means that the number of eggs and small larvae was likely underestimated because these are often transported in clumps). The colonies were housed in nests made of a piece of cardboard from which a cavity had been cut, sandwiched between two glass slides. Internal dimensions of the cavity were 33×25×1 mm (width× depth×height), with a 3-mm-wide entrance. All ants could thus be observed through the transparent roof of the nest. For improved color discrimination, a light brown paper was placed underneath the nest. Nests were placed in large square Petri dishes (220×220 mm). Colonies were fed ad libitum with honey solution and dead *Drosophila* flies weekly.

How do workers distribute their activity among tasks?

A total of 1,142 individually marked ants from the 11 colonies were observed in three situations that are important for the survival of colonies in this species: colony emigrations, wall building, and foraging. To ensure that all ants were available to perform in each of the three situations, so that we can detect elitism if it is present, only one situation was tested in each trial. Trials in each situation were conducted 1 week apart, and situations were always presented in the same order (colony emigrations then wall building and then foraging). We chose this time scale of weeks because it is likely to be insufficient for the transition of all ants into new tasks through temporal polytheism because it constitutes only a short portion of the lifespan of these ants (Sendova-Franks and Franks 1993; Blanchard et al. 2000; Robinson et al. 2009). A digital video camera with high color resolution (Panasonic NV-MX500 3CCD) was set up above the new nests in the emigration and building manipulations and the original nest during the foraging period. Individual activity in seven different tasks was recorded: scouting, brood transports, and adult transports during emigrations; collection of flies (protein) and collection of honey solution during foraging; and collection of 'stones' (sand grains) and movement of stones inside the nest during wall building. Seven hundred and thirty-four ants performed at least one of these seven tasks and the remainder of the ants, 408, either performed tasks that we did not record (e.g., brood care) or were inactive (Dornhaus et al. 2009). Activity was defined as the number of times an ant conducted a certain task (e.g., number of stone moves, number of brood transports). Definitions of these tasks and procedures to induce them are detailed below. After the videos were analyzed, all records (163 h; 5,739 task activities) were double-checked by a second person to ensure accurate recordings of ant identity across experiments.

Emigrations To induce an emigration of the colony, the top glass slide of the nest was removed, and both this glass slide and the rest of the nest were placed in a new, clean Petri dish. Any remaining workers were also moved from the old to the new Petri dish with a fine brush. At the same time, a new, identical nest was placed with its entrance 10 cm from the entrance of the old nest. The new nest was filmed until the last brood item had been carried there. The median duration from the start of the experiment to the last brood transport was 176 min. The videos were then analyzed to identify which ants entered the nest scouting for a new nest location (scouts) and which ants entered the nest carrying a brood item (brood transport) or another adult ant (adult transport).

Foraging Foraging behavior was observed following a 2-week period of starvation during which the ants only had access to water. A dish of 1:10 honey solution and small pile of freeze-killed *Drosophila* (approximately 15 flies) were placed in the foraging arena, both 10 cm from the nest entrance and from each other. Filming of the nest began 30 min before food was placed in the arena and ceased after 180 min. From the videos, we identified ants that entered the nest with fly parts as protein foragers. Ants that entered the nest but did not carry flies were observed for 10 min and if trophallaxis with nestmates occurred during this time, they were identified as honey foragers. Ants that returned from a trip outside but did not carry or regurgitate food were not counted in either of the foraging categories.

Wall building Building by workers was stimulated by initially causing the ants to emigrate to a new nest (as above).

The new nest lacked a cardboard wall in the front of the cavity, leaving a 33-mm gap rather than a 3-mm entrance. Colonies were provided with a pile (approximately 1–2 mm^3) of blue-dyed sand grains 10 cm from the nest entrance with which to construct a perimeter wall (Franks and Deneubourg 1997; Aleksiev et al. 2008). Filming started with the addition of the manipulated nest and removal of the glass cover of the original nest. Colonies were filmed for at least 360 min. Video analysis identified which ants collected sand grains (henceforth called stones) from the pile and brought them into the nest cavity and which workers moved the stones (i.e., picked up a stone inside the nest and moved it) (Franks and Deneubourg 1997).

Statistical analysis

Distribution of activity among tasks To examine whether there was a relationship among the ants' activity levels in the various tasks, both within and between situations, we used Spearman's correlation test. Significant positive correlation coefficients would support the elitism hypothesis, significant negative correlation coefficients would support the specialization hypothesis, and no relationship would support the idiosyncratic hypothesis. Because each task was used in six correlation tests, we used a Bonferroni correction for multiple testing to set significance level at p value=0.008. To visualize the graded nature of task allocation and to further examine whether certain task combinations are performed by particular individuals more commonly than others, we used hierarchical cluster analysis. For comparison purposes, we log-transformed and scaled activity data. We added 0.5 to all data before the log transform to include ants that were not active in a certain task, i.e., zeroes, in the clustering analysis. Scaling was carried out on the log-transformed data by subtracting the mean activity in a task and dividing by the standard deviation. We then used hierarchical cluster analysis with Euclidian distance and the "average" linkage method to cluster ants by their performance of the various tasks (Everitt and Hothorn 2011). Clustering grouped together ants with similar activity patterns. For example, all ants that were highly active in both honey foraging and brood transporters were placed together in one cluster. This clustering identified the various behavioral types in the colony and is a novel method for visualizing ants' work allocation both within and among tasks. Similar multivariate techniques have been used to investigate individual variation among stingless bee workers in temporal polytheism (Inoue et al. 1996).

Distribution of activity within a task We examined how activity within each task was distributed among those workers in the colony that participated in the task, i.e., excluding ants that did not perform the task. We calculated activity as the number of times a worker performed a task divided by the total number of times this task was performed in its colony. We then examined how these proportions were distributed among ants by using the Akaike information criterion (AIC) (Akaike 1974) as a likelihood ratio test (Clauset et al. 2009) to determine whether a Gaussian or an exponential distribution best fits the data. If a Gaussian (normal bell-shaped) distribution best fits the activity distribution, this indicates that task activity for each worker may stochastically vary around a mean and that response thresholds or task preference among active workers are similar. An exponential fit to the activity distribution indicates a right-skewed distribution, i.e., few highly active individuals perform a large proportion of the task and most individuals are less active and perform a small proportion of the task. This suggests that workers that participate in a task differ in their preference or response threshold for this task. The distribution of activity within tasks was similar for all colonies, so data analysis for the 11 colonies was pooled (see activity distribution within tasks for all colonies in Figure S1 in the supplementary material, and also Dornhaus (2008) and Dornhaus et al. (2009).

Experiment 2: removal and return of highly active workers

To examine whether highly active ants are replaceable and whether or not they resume their activity level when they are returned, we conducted emigration and removal–return experiments. We used two *T. rugatulus* colonies collected in the Santa Catalina Mountains in Arizona in 2008. When brought into the lab, all ants were individually marked and the colonies were housed as described in experiment 1. Six emigrations were induced, as described in experiment 1, to a new nest site 20 cm away from the old one. Each emigration was conducted on a different day with 2 weeks at most separating emigration trials. A total of 222 workers participated in at least one of the emigrations (139 in colony 1 and 83 in colony 2). Colonies were intact for the first three emigrations (numbered 1–3). We counted the number of transports, of both adults and brood, conducted by each individual during each emigration. We defined diligent workers as the 20 % of ants in each colony that conducted the most transports in the first three emigrations [summed number of transports for each ant in the first three emigrations (1–3)]. We use the term "diligent" to distinguish both from "performer" as used by Robson and Traniello (1999) to define workers that are both highly active and irreplaceable and also from the terms "efficiency" and "performance" that were used interchangeably by Dornhaus' (2008). Efficiency is different from diligence because efficiency measures the speed at which a task is performed. We refer to all of the other ants (i.e., the remaining 80 %) as "indolent" workers, which is the antonym of diligent. At the beginning of emigration 4, we removed the diligent workers as they left the nest. The removed ants were kept in a separate nest box with food and water during the rest of emigration 4 and during the following emigration, numbered 5. These ants were returned to the colony immediately before the last emigration, numbered 6. To compare transport activity between the first (1–3) and last (6) emigrations, we defined as "new diligent" the 20 % of ants that conducted the most transports in the last emigration (6).

Statistical analysis

We first examined whether individuals behaved consistently across the first three emigrations to determine whether diligence is persistent. To test whether overall activity changed among emigrations 1, 2, and 3, we used a paired Wilcoxon rank sum test. To determine whether individual ants were persistent in their activity over days, we used Spearman's correlation test.

To examine whether diligent workers were replaceable, we compared the average number of transports among diligent workers and indolent workers during the three stages of the experiment: before removal, after removal, and after returning the diligent workers, using a Wilcoxon rank sum test to examine only those comparisons of interest. Because we conducted nine tests, we used a Bonferroni correction for multiple testing to set significance level at p value=0.006. To examine whether the distribution of work among individuals would be affected by the removal of the diligent workers, we compared the variance of the number of transports each ant performed among the three experimental stages. Results were similar for both colonies, so data from the two colonies were pooled (see Figure S2 and Table S2 in the supplementary material). Statistical analysis for both experiments 1 and 2 was conducted in R version 2.12.1 using non-parametric tests because the data were not normally distributed.

Results

Experiment 1: activity across and within tasks

Distribution of activity among tasks

We observed a significant positive relationship among the workers' activity levels in various tasks within a situation (Spearman rank correlation coefficients (ρ) and p values in Fig. 2 and in Table S1 in the supplementary material). Specifically, within emigrations, we found a significant positive correlation between the number of scouting trips, adult transports, and brood transports performed by each ant. Within foraging, the number of honey foraging trips performed by a worker significantly positively correlated with that individual's number of protein foraging trips. Within wall building, how often a worker moved a stone within the nest significantly positively correlated with the number of times it collected a stone from the pile (Fig. 2).

Correlations among activity levels in tasks across situations were either significantly negative or not significant. Of the 16 correlations among tasks across situations, we observed three significantly negative relationships and 13 non-significant relationships (Fig. 2; Table S1). Of the non-significant relationships, eight were in a negative direction. Overall, this suggests idiosyncrasy, i.e., activity in one task does not predict activity in another task. Most relationships were in a negative direction, suggesting there is weak specialization in particular situations, e.g., in either "emigration tasks" or in "foraging tasks." Ants that are more active in one situation tend to be less active in another situation.

Further examination of the ants' activity patterns using hierarchical cluster analysis revealed that certain task combinations are more common than others (Fig. 3). For example, performing all three emigration tasks was more common than performing only scouting together with brood transport. However, there is a large cluster of ants that performed only scouting and no transports, which explains the weaker correlation between scouting and the two transport tasks within emigrations (Fig. 2; Table S1). In addition, fewer foragers returned with protein than with honey, and of the protein foragers, approximately half also foraged for honey. However, ants that foraged for honey mostly specialized on this task and did not perform other tasks. Figure 3 allows us to explore activity distribution both across and within tasks. Interestingly, protein foragers that did not also forage for honey were the most active protein foragers (activity level indicated by color, Fig. 3). Moving stones was more prevalent than collecting stones and almost all stone collectors also moved stones. Those ants that both collected and moved stones (indicated as building specialists, Fig. 3) were the ones who conducted most of the stone collecting (compare their color with other stone collectors, Fig. 3). Ants that moved stones mostly specialized on this task, but these specialists were not the most active workers within the task (see also Franks and Deneubourg (1997)). Finally, the cluster analysis also revealed a few ants that were highly active in most tasks (denoted as "elites" in Fig. 3).

Distribution of activity within a task

Within each task, activity distribution among those individuals that performed the task was right skewed, indicating that few workers perform most of the task and most workers perform very little of it (Fig. 4). The activity distribution for

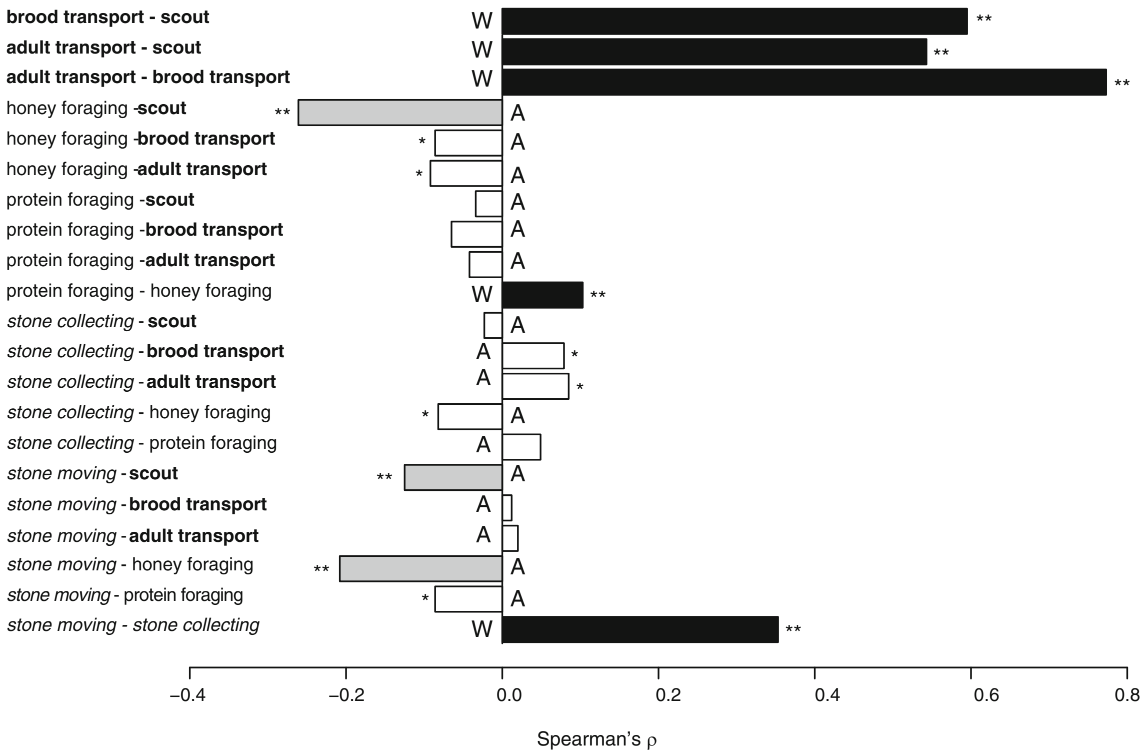

Fig. 2 Distribution of worker activity among tasks. *Bar* size is the Spearman's ρ coefficients of the relationship between worker activities in each task combination indicated on the *left*. Statistical significance (p value) of the correlations is indicated: *<0.05, **<0.008 (0.008 is the adjusted α using Bonferroni correction). Exact values can be found in Table S1 in the supplementary material. *Black bars* denote a positive relationship (p value <0.008), *gray bars* denote a negative relationship (p value <0.008), and *white* bars denote non-significant relationships. Tasks in the emigration situation (scout, brood transport, and adult transport) are indicated to the *left* in *bold*, tasks in the building situation (stone moving and collecting) are indicated in *italics*, and tasks in the foraging situation (protein and honey foraging) are indicated in *regular font*. *Letters* along the *y*-axis indicate whether the relationship is between tasks that are within (*W*) a situation or across (*A*) situations

all tasks showed a better fit with an exponential rather than a Gaussian distribution (see AIC values in Table 1).

Experiment 2: removal and return of highly active workers

Persistence in activity level

Transport activity levels were persistent within individuals over days. The number of transports conducted by each ant was significantly positively correlated among the first, second, and third emigrations (Spearman rank correlation: emigrations 1 vs. 2: r_s=0.29, N=219, P<0.001; emigrations 2 vs. 3: r_s=0.28, N=219, P<0.001; emigrations 1 vs. 3: r_s=0.44, N=219, P<0.001). Furthermore, the number of transports did not differ among the first three emigrations (paired Wilcoxon signed-ranks test: emigrations 1 vs. 2: T=3,935, N=219, P=0.76; emigrations 2 vs. 3: T=3,752, N=219, P=0.24; emigrations 1 vs. 3: T=3,488, N=219, P=0.5).

Similarly, the number of transports conducted by each indolent worker was persistent across emigrations 4 and 5, when the diligent workers were absent (Spearman rank correlation: emigrations 4 vs. 5 for indolent workers: r_s=0.42, N=176, P<0.001; paired Wilcoxon signed-ranks test: emigrations 4 vs. 5 for indolent: T=2,646, N=176, P=0.95). This indicates that among the “indolent” workers, some were consistently more active than others. Moreover, once the diligent workers were returned, the activity level of the indolent workers remained the same as in the previous emigration when the diligent workers were absent (Spearman rank correlation: emigration 5 vs. 6 for indolent: r_s=0.4, N=176, P<0.001; paired Wilcoxon signed-ranks test: emigrations 5 vs. 6 for indolent: T=2,631, N=176, P=0.36).

Are diligent ants replaced by indolent workers when they are removed from the colony?

When diligent transporters were removed, indolent ants increased their activity of brood and adult transport (Fig. 5) supporting our first two hypotheses (temporary or permanent replacement) and rejecting the third (no replacement). By definition, diligent workers conducted more transports than indolent ants before removal, in the first three emigrations (diligent (1–3)>indolent (1–3), Wilcoxon signed-ranks test: T=7,267, N=219, P<0.0001). Previously indolent ants increased their transport activity when diligent workers were absent (indolent (1–3)<indolent (4–5), paired Wilcoxon signed-ranks test: T=

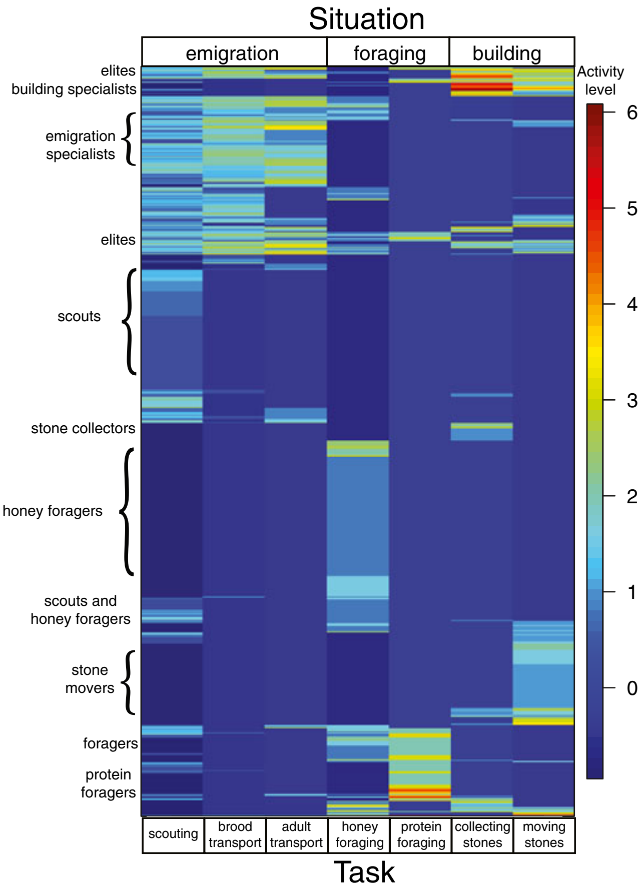

Fig. 3 Clustering of activity among and within tasks. Each *row* represents an ant and each *column* represents a task (noted below) in a certain situation (noted above). Ants are ordered based on a hierarchical clustering analysis (see illustration of this analysis in supplementary Figure S3); annotation to the *left* denotes possible labeling of these groups based on the task performance pattern of the ants in those *rows*. *Color* indicates level of activity (log-transformed and scaled). Workers who did not perform any of the tasks measured are not shown

3,523, $N=176$, $P<0.0001$) and retained high activity levels even after the removed ants were returned, supporting the permanent replacement hypothesis (indolent (4–5)=indolent (6), paired Wilcoxon signed-ranks test: $T=3{,}933$, $N=176$, $P=0.19$). Whether an indolent ant would increase its activity when the diligent transporters were absent could not be predicted from its activity level before the removal (Spearman rank correlation: average activity in emigrations 1–3 vs. average activity in emigrations 4–5 for indolent: $r_s=-0.06$, $N=176$, $P=0.44$). However, the activity level of indolent ants while the diligent ants were absent did not reach that of the original diligent transporters (diligent (1–3)>indolent (4–5) Wilcoxon signed-ranks test: $T=5{,}920$, $N=219$, $P<0.0001$).

Is replacement temporary or permanent?

Our findings support the "permanent replacement" hypothesis. When the diligent transporters were returned to the colony on emigration 6, they conducted fewer transports than before removal (diligent (1–3)>diligent (6), paired Wilcoxon signed-ranks test: $T=701$, $N=43$, $P=0.002$), and they did not differ in their activity levels from the indolent ants, i.e., those that were never removed from the colony (diligent (6)=indolent (6), Wilcoxon signed-ranks test: $T=3{,}765$, $N=219$, $P=0.95$; Fig. 5). The new diligent transporters (i.e., 20 % of ants that performed the most transports in emigration 6) conducted more transports than the diligent workers in the first three emigrations (new diligent (6)> diligent (1–3), Wilcoxon signed-ranks test: $T=418$, $N=87$, $P<0.0001$). These new diligent transporters also conducted more transports than the original, now returned diligent workers (new diligent (6)>diligent (6), Wilcoxon signed-ranks test: $T=210$, $N=87$, $P<0.0001$), or the indolent workers in this last emigration (new diligent (6)>indolent (6), Wilcoxon signed-ranks test: $T=761$, $N=220$, $P<0.0001$; Fig. 5).

The removal of diligent workers changed the distribution of work among individuals. When the previously diligent workers were absent, the work was distributed less evenly among the workers in the colony, i.e., there was greater variance in the number of transports an individual worker performed. While the diligent workers were absent, the variance of worker activity was the highest of the three experimental stages: before removal $\sigma^2=11.56$<after removal $\sigma^2=34.13$>after return $\sigma^2=27.79$ (Fig. 6).

Discussion

How workers distribute their activity among tasks both within and between situations is a central question in the study of social insect behavior. A widespread assertion based on studies in which workers are polymorphic is that colonies are composed of "role clusters"—groups of workers that specialize in various tasks (Wilson 1980). Here we show that task allocation is more complex. In a species with little to no worker polymorphism, workers do not fall into discrete task groups. Instead, colonies may contain highly active generalist workers along with workers performing idiosyncratic combinations of tasks and some specialists. In our experiments, workers generally specialized in performing tasks within a certain situation as indicated by the lack of significant positive relationships between performances of tasks in different situations (Fig. 2), but not all ants were alike as some were greater task generalists than others (Fig. 3). In addition, few studies examine whether behavioral specialization is long-lasting or affected by social context. Here we showed that diligence in a certain task persisted over days but that it was dependent on social context: If previously diligent workers were absent, they

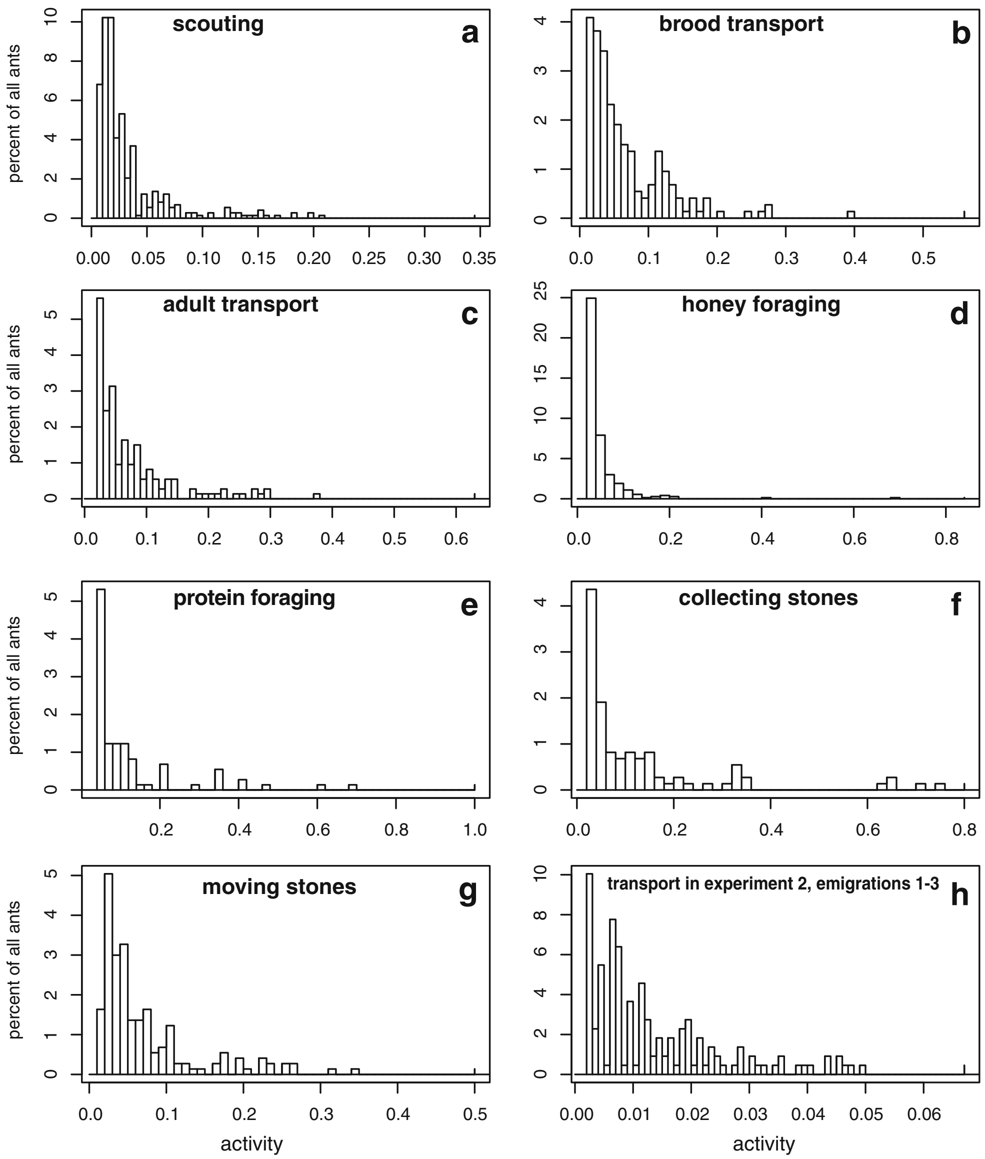

Fig. 4 Distribution of worker activity within tasks. Activity is the number of times a worker performed a particular task divided by the total number of times this task was performed in its colony (i.e., proportion of work within a colony). Percent is of all ants in all colonies that performed some proportion of a particular task (i.e., excluding ants that did not perform the task) for each of the seven tasks in experiment 1 (**a**–**g**) and for transports in the first three emigrations of experiment 2 (**h**). Fits to exponential and Gaussian distributions are given in Table 1

were permanently replaced. The “replacements,” i.e., individuals who became active in response to removal of diligent workers, stayed active in their new task, and removed workers did not necessarily resume their prior activity levels when returned to the colony. Therefore, it is possible that in response to changed social context (of either the removed or the remaining ants), workers change their response thresholds or task preferences, perhaps permanently. These

Table 1 AIC values for fitting a Gaussian (normal) or an exponential distribution to the activity distribution of the various tasks, a lower value indicates a better fit

Behavior	AIC Gaussian	AIC exponential	AIC (Gaussian)>AIC (exponential)
Scouting	−3,002.8	−4,700.5	Yes
Brood transport	−2,530.9	−4,700.5	Yes
Adult transport	−2,405.6	−4,700.5	Yes
Honey foraging	−2,369.1	−4,700.5	Yes
Protein foraging	−1,849.5	−4,686.2	Yes
Collecting stones	−1,766.5	−4,700.5	Yes
Moving stones	−2,489	−4,700.5	Yes
Transport in experiment 2	−1,330.26	−1,630.21	Yes

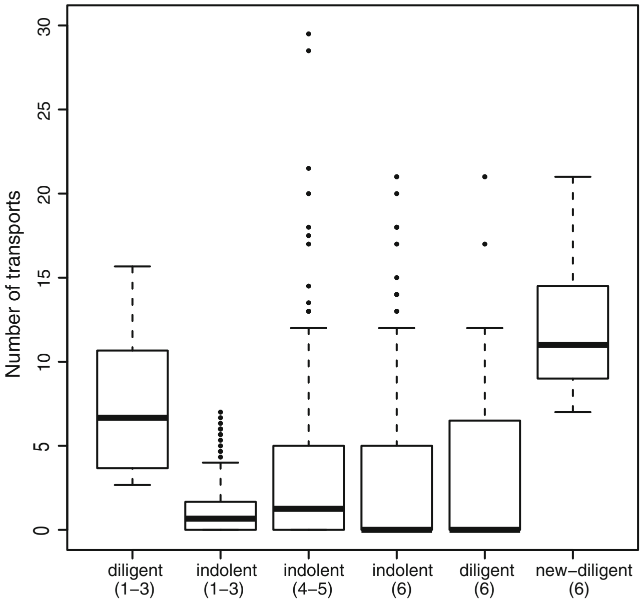

Fig. 5 Diligent workers are replaceable. Number of transports conducted by diligent, indolent, and new-diligent workers in the emigrations before removal (1–3), after removal (4–5), and after return (6) of diligent workers. *Boxes* indicate the lower and upper quartiles, *horizontal lines within boxes* indicate medians, *whiskers* extend to 1.5 interquartile range from the box, and *points* indicate outliers. See statistical significance of differences in the text

findings shed light on how colony behavior emerges from the interplay between internal response thresholds and external social and environmental stimuli (see Robinson et al. 2012).

Studies on other species of social insects have found both specialization in particular tasks (Wilson 1980; Sendova-Franks and Franks 1995a; Beshers and Traniello 1996; Ravary et al. 2007) and flexibility, i.e., workers performing more than one task (Traniello 1978; Gordon 1989; Jaisson et al. 1992; Rosengaus and Traniello 1993; Robson and Traniello 2002; Crosland et al. 2004; Gordon et al. 2005; Jandt et al. 2009). Our cluster analysis provides a novel view of how task performance is distributed among individuals and among tasks, providing specific information on which tasks may be grouped together and on the frequency of such groupings (Fig. 3), thus expanding upon prior work on task specialization of individually tagged ants (Sendova-Franks and Franks 1995a).We show that overall *Temnothorax* workers are specialized in certain situations: For example, the cluster analysis showed that only a few ants were active in more than one situation (emigration, nest building, or foraging). We also show that these ants do not simply differ in general activity level (which would create highly active "elite" workers and inactive "lazy" workers) because high activity in one situation does not predict high activity in another. Within a situation, we find that workers show consistently high or low activity across related tasks. This may be called "elitism within a situation." In addition, some small clusters of ants performed tasks in more than one situation frequently. Perhaps because of these individuals we did not find negative correlations among each pair of tasks in different situations across all ants, as complete specialization would have predicted.

The terms "specialization" and "elitism" have been used in various contexts and have various definitions in the literature. Specialization has been defined as high activity in a certain task when compared with nestmates (Visscher 1983; Julian and Cahan 1999), persistence of working in a certain task over time (Gordon 1984), or working primarily in a certain task when compared with the individual's activity in other tasks (Wilson 1980; Sendova-Franks and Franks 1995a; Beshers and Traniello 1996; Robson and Traniello 1999; Ravary et al. 2007). Here we use a combination of the first and last definitions: We consider specialization to take place when workers that are more active in one task compared to nestmates are

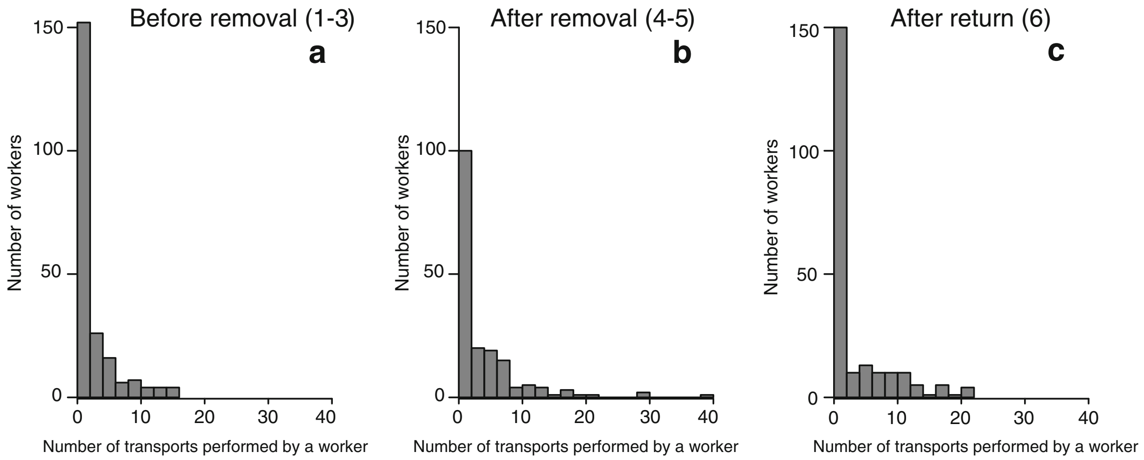

Fig. 6 Distribution of activity in experiment 2. Distribution of the number of transports conducted by each worker during the three experimental stages: **a** before the removal of diligent workers (1–3) (N=219), averaged among the three emigrations; **b** after the removal of diligent workers (4–5) (N=176), averaged among the two emigrations; and **c** after the return of diligent workers (6) (N=219)

less active in other tasks compared to nestmates. There is also little agreement about the term "elites." Some studies define elitism as high activity in one task (Kolmes and Sommeijer 1992; Hurd et al. 2003), and others define it as increased work in many tasks (Sendova-Franks and Franks 1995a; Trumbo et al. 1997; Robson and Traniello 1999; Gautrais et al. 2002; Robson and Traniello 2002; Hurd et al. 2007). We follow the latter definition by calling highly active generalist workers "elites." This term does not imply selfishness or preferential treatment of "elite" workers. Instead, these are workers that perform many or all tasks more frequently than nestmates. Note that it is impossible to determine if social insect workers are "specialists" or "elites," even with marked individuals, if activity in only a single task is quantified (e.g., Visscher 1983; Julian and Cahan 1999; Gardner et al. 2007).

Our study highlights that the definition of what constitutes a task can greatly affect how we view elitism, specialization, or idiosyncrasy. Our definition of a task was arguably too fine-grained, for example, ants may react to "colony emigration" as a single task that includes scouting, adult transport, and brood transport. Therefore, what we call "elitism within a situation" might be the performance of a single task and not three tasks. If this is the case, previous accounts of 20–40 tasks in ant colonies may be overestimates that do not reflect independent tasks. For example, Kolmes and Sommeijer (1992) did not find specialization in any of 32 behaviors in the stingless bee *Melipona favosa*, possibly because many of these behaviors were performed in one situation and could have been viewed as one task. O'Donnell and Foster (2001) found that various thermoregulatory behaviors are correlated with one another, further suggesting that multiple behaviors within one situation may in fact usefully be defined as one "task." In other studies, specialization was found when tasks were defined broadly, encompassing several behaviors all exhibited in a certain situation (Wilson 1980; Gordon 1984; Beshers and Traniello 1996; Ravary et al. 2007).

One may predict that elitism can only be detected if there is no spatial and temporal conflict among tasks. If all tasks are tested simultaneously, ants working in one task might not be available to work in another (Tofts 1993). Even though we measured tasks within situations simultaneously, we still found a positive relationship among the ants' activity levels in the various tasks. The large number of ants performing only scouting, honey foraging, or stone moving (Fig. 3) could have resulted from greater availability of these tasks (e.g., building a wall might take longer than collecting the material for it), but this did not affect our ability to find elitism within situations. We separated the various situations in time so that activity in one situation did not reduce the opportunity to engage in another, enabling us to detect elitism across situations, had it existed. It is possible that we did not detect elitism because ants are active only on some days (e.g., Gordon et al. 2005) and carry out any task that is needed on the day they are active based on environmental stimuli or experience (Gordon 1989; Robson and Traniello 2002; Cao et al. 2007; Ravary et al. 2007; Le Conte and Hefetz 2008). However, when we repeated emigrations over multiple days in experiment 2, we found that both diligent and indolent workers were persistent in their performance of emigration work over days. Diligent individuals in general may retain or increase their activity level in a certain task because they become experienced (Langridge et al. 2008) or reduce their activity level over time due to wear (Schofield et al. 2011).

Various mechanisms, such as body size, genetic composition (Cassill and Tschinkel 1999; Julian and Fewell 2004), or task availability (Tofts 1993), have been implicated in determining the task repertoire of workers. *T. albipennis* workers are largely monomorphic and so size variation is an unlikely mechanism for specialization. In addition, their queens are only infrequently multiply mated (Pearson et al. 1995) and so genetic variation among workers is also small. Ants in some species may also change their task specialization over long time periods, e.g., due to temporal polytheism (Calderone 1995; Beshers and Traniello 1996; Gordon et al. 2005; Seid and Traniello 2006; Camargo et al. 2007). However, this has not been shown in *Temnothorax*, and the experiments conducted here were on a time scale of a few weeks which is unlikely sufficient for the transition of all ants into new tasks through aging because it constitutes only a short portion of the lifespan of these ants that may live up to several years (Sendova-Franks and Franks 1993; Blanchard et al. 2000; Robinson et al. 2009). We do know that in *Temnothorax*, a worker's spatial position is related to whether it performs brood care or other tasks (Sendova-Franks and Franks 1995b), prior experience affects who performs emigration transports (Langridge et al. 2008; Franklin et al. 2011), and foraging activity is related to the ant's physiology (Robinson et al. 2009; Robinson et al. 2012). The mechanisms underlying who performs building behaviors are yet unknown and warrant further investigation. It would be interesting to further investigate what causes variation among individuals in these underlying mechanisms governing task preference and whether the mechanisms underlying each task are independent or not of one another (see also Robinson et al. 2012).

Activity distribution within each task, among those individuals that performed the task, was right-skewed with few diligent ants carrying out most of the task and most ants performing little of it. Such individual variation in task performance has been described in other social insects (O'Donnell and Foster 2001; Hurd et al. 2003; Weidenmuller 2004; Pinter-Wollman et al. 2011) but not all (Kolmes and Sommeijer 1992). Experiment 2 shows that diligence is persistent over days but despite this persistence, individuals of *Temnothorax* ants are capable of increasing their activity levels when needed, e.g., when faced with extreme social pertubations. Colony emigration entails many risks such as losing workers while searching or moving into a new nest site. There is a tradeoff between the speed in which a colony chooses a new nest site and the accuracy of its choice (Franks et al. 2003), and it is possible that changes to worker composition may affect the nest choice process. When workers are removed, there are fewer ants to complete the various emigration tasks and so it would be interesting to further investigate how the numbers of workers and their activity pattern affect all aspects of emigration, including nest choice and emigration speed.

Colonies were robust to the removal of diligent workers, replacing them with previously indolent individuals. Thus, even though workers specialize in certain situations and are diligent and persistent in performing associated tasks, task allocation in a colony is plastic and colonies can withstand removal of specialized workers. On short time scales, of minutes and hours, removal of certain individuals often stops the activity of a colony (Robson and Traniello 2002; Donahoe et al. 2003; O'Donnell 2006; Schafer et al. 2006) but, on a time scale of days, removing highly active individuals results in their replacement by other workers (O'Donnell 1998; Breed et al. 2002; Gardner et al. 2007; Beverly et al. 2009). According to the concept of response thresholds, ants adjust their activity by comparing current environmental stimuli to their internal response threshold. If individuals with a low response threshold respond to a certain stimulus, they will reduce the need for workers in that task (because they are performing it), and individuals with high thresholds will not engage in that task (Robinson 1992; Bonabeau et al. 1996; Beshers 1999; Beshers and Fewell 2001). If workers with low response thresholds are removed, we would expect other individuals, with higher response thresholds, to begin performing the task as the environmental stimulus is allowed to rise to a higher level. This may be what happened in our removal experiment and has been shown in other species of social insects (e.g., *Polistes instabilis* foragers (O'Donnell 1998), honeybee, *A. mellifera*, undertakers (Breed et al. 2002), bumblebee, *Bombus huntii*, incubating workers (Gardner et al. 2007), and *P. barbatus* harvester ant foragers (Beverly et al. 2009)). The positive relationship we found between the activity of the indolent workers in emigrations 4 and 5 and the persistent activity of the diligent workers among emigrations 1, 2, and 3 suggests that there are internal thresholds that determine which individuals perform each task.

If internal thresholds are determined genetically or in early development, we would expect that upon return of the low-threshold, diligent workers to the colony, the individuals with high response thresholds would revert to their prior low activity levels and the returned individuals would resume high activity levels ("temporary replacement" hypothesis). This is not what we found. The removed diligent workers in our study did not resume their high activity level upon return to the colony, and the indolent workers that became active while the diligent workers were away did not reduce their activity after the original diligent workers returned. This supports the hypothesis that a changed social context (Jeanson et al. 2007) and individual experience (Moron et al. 2008) cause changes in task preferences or response thresholds of workers, thus supporting the "permanent replacement" hypothesis. It also implies that any current set of response thresholds found in the colony only explains task allocation in the short term and that there is an underlying mechanism that governs how these thresholds are set based on the workers' experiences.

Interestingly, the distribution of work among individuals was less equal when the previously diligent workers were absent (Fig. 6), and the new set of diligent workers performed more of the work than was carried out in the initial three emigrations by the original transporters. Although the removal of diligent workers increased the number of items to transport per worker, it is surprising that certain individuals performed more of the work, instead of more individuals performing the work more evenly. One explanation may be that transport workers increase their activity levels over successive emigrations (Langridge et al. 2008).

Colonies use plastic task allocation to respond to their environment. We show that despite apparent rigidity in the behavior of individual ants, in the form of specialized, diligent, persistent workers, task allocation is graded and the emergent behavior of the colony as a whole is robust to the loss of diligent individuals. Individual variation in response thresholds, both among and within tasks, results in a complex graded activity pattern of work allocation within a colony. When environmental perturbations affect colony composition or demography, workers adjust and tasks are re-allocated, allowing colonies to endure extreme ecological changes.

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