



Worker propensity affects flexible task reversion in an ant

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Abstract

Social animals exhibit well-organized task allocation among group members. In ants, a large group of eusocial Hymenoptera, the division of labor among workers is maintained by behavioral flexibility, providing robustness against fluctuating environmental conditions. Under stable conditions, worker tasks shift from the inside (e.g., nurses) to the outside (e.g., foragers) of the nest as age increases along this gradient. If the colony's age structure is unbalanced, some workers compensate for vacant tasks, regardless of their age. However, such behavioral flexibility mechanisms are not clearly described in most ant species. In this study, using the ant *Diacamma* sp. from Japan, we focused on task reversion (i.e., foragers shifting to nursing roles, reverted nurses). By intermittent observation, we examined how the proportion of trials detected outside the nest of foragers, as foragers' behavioral propensity, impacts task reversion when caste composition is significantly altered. We revealed that foragers with low proportion were the most likely to become reverted nurses, suggesting that the worker propensity is strongly correlated to task reversion. Moreover, task allocation among workers emerged on day 2 after colony disturbance, suggesting that the division of labor can promptly reconstruct when the age structure of the colony is accidentally altered by external factors. It also illustrates the importance of behavioral propensity in maintaining social systems. We also discussed the mechanisms of flexible task allocation among the workers in terms of self-organized process.

Significance statement

In eusocial Hymenoptera (e.g., wasps, honeybees, and ants), the division of labor is maintained by workers' behavioral flexibility, which is itself driven by the needs of the colony. However, the detailed mechanisms underlying ant behavioral flexibility remain unclear. Focusing on task reversion in foragers shifting to nursing roles regardless of their age-dependent assigned task, we revealed that behavioral propensity strongly affects task reversion in the *Diacamma* sp. As ant colonies generally have an unbalanced age structure and inhabit unstable environments, behavioral flexibility is thought to be important to maintain the division of labor. Moreover, our study could be applied to examining molecular and physiological basis of task reversion in ant species.

Keywords Division of labor · Behavioral flexibility · Task reversion · Hymenoptera · Ants

Introduction

Division of labor driven by a self-organized process is a central feature at many levels of biological organization (Maynard Smith and Szathmáry 1995). Eusocial insects (e.g., ants and honeybees) construct highly diversified societies based on the reproductive division of labor between reproductive individuals (e.g., queens) and non-reproductive individuals (i.e., workers) (Wilson 1971; Bourke and Franks 1995). Among non-reproductive workers, individuals engage in different tasks, such as caring for broods, defending the nest, and foraging for food (Oster and Wilson 1978). In many social insect species, age polyethism has been observed to drive labor division among workers (Wilson 1971): younger workers perform tasks within the nest and are often called as

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nurses, while older workers take on tasks outside of the nest, such as foraging. When either the age structure or colony demands change, however, workers can switch from their age-dependent tasks into required tasks to maintain colony performance (Calabi and Traniello 1989; Gordon 1989; Robinson et al. 1992; Johnson 2003; Robinson et al. 2009).

Several models have been developed to explain mechanisms of the division of labor in social species (Beshers and Fewell 2001). The fixed response threshold model is a well-known self-organized mechanism for the division of labor (Bonabeau et al. 1996). The bulk of this model is as follows: workers have different thresholds to task-related stimuli, causing different responses to focal tasks among workers. For instance, when a focal worker performs a certain task, the task-related stimulus decreases; if no worker is assigned to the task, the stimulus increases and workers with a lower threshold perform the task. However, the fixed response threshold model cannot explain task change and subsequently task specialization (fixation) in the reorganized division of labor in fluctuating conditions. Therefore, recent theoretical and empirical studies have suggested that other mechanisms are required to explain flexible task allocation (Theraulaz et al. 1998; Robinson et al. 2009; Robinson et al. 2012; Crall et al. 2018; Ulrich et al. 2018). Therefore, the process of reconstructing division of labor is key to understand the mechanisms to generate the system.

The reversion from foragers to nurses is known as task reversion. It is an example of prominent plasticity, which provides us with an opportunity to investigate the proximate causes of flexible behavioral change. For example, when nurses are removed from a colony, some of the foragers switch their original roles to become nurses. The mechanisms of this task reversion have been studied extensively in honeybee (*Apis mellifera*) workers, where relatively young foragers have been shown to revert to nursing roles when nurses are removed in the colony. Furthermore, the juvenile hormone titers in reverted nurses became equivalent to those of young nurses (Robinson et al. 1992). Additionally, the DNA methylation level in the brains of reverted nurses changed to the same level as the original nurses (Herb et al. 2012). Task reversion is reported in several species of eusocial Hymenoptera (Calabi and Traniello 1989; Robinson et al. 1992; Tripet and Nonacs 2004; Bernadou et al. 2015; Kohlmeier et al. 2018), suggesting that it is an important trait to maintain the division of labor under fluctuating environmental conditions. Nevertheless, behavioral and physiological basis of task reversion remains largely unknown, aside from that observed in studies related to the honeybee.

According to previous studies using the honeybee, intrinsic variation of foragers related to their age is a remarkable feature to understand the mechanisms of task reversion (Robinson et al. 1992). While it is difficult to track the age of all workers in ant species, estimating the approximate age from the perspective of behavior would facilitate examining the relationship between physiological variation and task reversion. An

ant *Diacamma* sp. from Japan (Formicidae, Ponerinae), is the only species of the *Diacamma* genus in Japan, which is an ideal species to study task reversion. In this species, the division of labor among workers is based on age polyethism (Nakata 1995). Moreover, by detailed behavioral observation, Nakata (1995, 1996) revealed that brood caring behavior was mostly performed by young workers, although older workers never performed brood caring. Additionally, the time spent work outside the nest increases with age. These results suggest that time spent outside the nest is a good indicator of age of foragers as a behavioral propensity. Also, some ecological and biological background provides us to study behavioral flexibility in this species. Colonies reproduce by fission under natural conditions (Fukumoto et al. 1989) and the age structure of the colony dynamically changes (Nakata 1996), suggesting that the behavioral flexibility of workers is important for maintaining the division of labor.

This study aims to observe the behavior of before-manipulation control and manipulated (consist of a gamergate (functional queen, see Materials and Methods), broods, and foragers) colonies to describe the task reversion mechanism using *Diacamma* sp. We examine how the behavioral propensity of a forager affects this shifting role from forager to nurse in experimentally disturbed colonies.

Materials and methods

The *Diacamma* sp. from Japan (Formicidae, Ponerinae), is the only species of the *Diacamma* genus in Japan. It is a basal species in ant phylogeny (Moreau et al. 2006). A colony consists of a mated worker (gamergate, Peeters and Crewe 1984) as functional queen, and between 30 and 300 workers (Fukumoto et al. 1989; Kikuchi et al. 2008).

We collected five colonies with a gamergate of *Diacamma* sp. on Okinawa Island in April and October 2019. The colonies (A to E) consisted of 184, 170, 156, 165, and 149 workers, respectively. We transferred the colonies to rearing nests (110 × 80 × 33 mm) and maintained them in stable laboratory conditions (25 ± 1 °C; 14 L, 10D) until behavioral observations were started. Colonies were given mealworms and standard artificial diets (the ratio of protein:carbohydrates was 1:1) (Dussutour and Simpson 2008) and a sufficient amount of water.

Behavioral observations for the before-manipulation control colony

All workers in each colony were individually marked using enamel pens. Each experimental nest was connected to a large plastic box (40 × 60 × 20 mm), provided as a foraging arena. To prevent workers from escaping, the side of the box was coated using Fluon®.

We started observations 1 week after the colony transfer. In this species, worker tasks are allocated by age polyethism: young workers care for broods (eggs and larvae) as “nurses,” while older workers work predominantly outside the nest as “foragers” (Nakata 1995, 1996). By focusing on these distinctive behaviors, we carried out intermittent observations at brood area and outside the nest for 4 consecutive days (five observation trials each lasting for 10 min during 11:00–18:00 per day and the minimum interval between two observations was 50 min). We recorded all workers in front of eggs (hereafter, referred to as “brood position”) and outside the nest (hereafter, we called as “outside position”) (Fig. 1a). We divided workers into two categories (nurses and foragers) according to the following definitions: (1) workers not located at the outside position and detected at the brood position at least once during all trials (total 200 min) were classified as nurses; (2) workers who were never located at the brood position and located at the outside position at least once during all trials were categorized as foragers (Fig. 1b). Otherwise, we defined workers as undefined worker (Fig. 1b). In addition, we obtained the proportions of trials detected at the outside position to total trials each forager, as forager’s behavioral propensities.

All experiments were carried out under blind conditions; data collection and data analysis were carried out by different people.

Behavioral observations for the manipulated colony

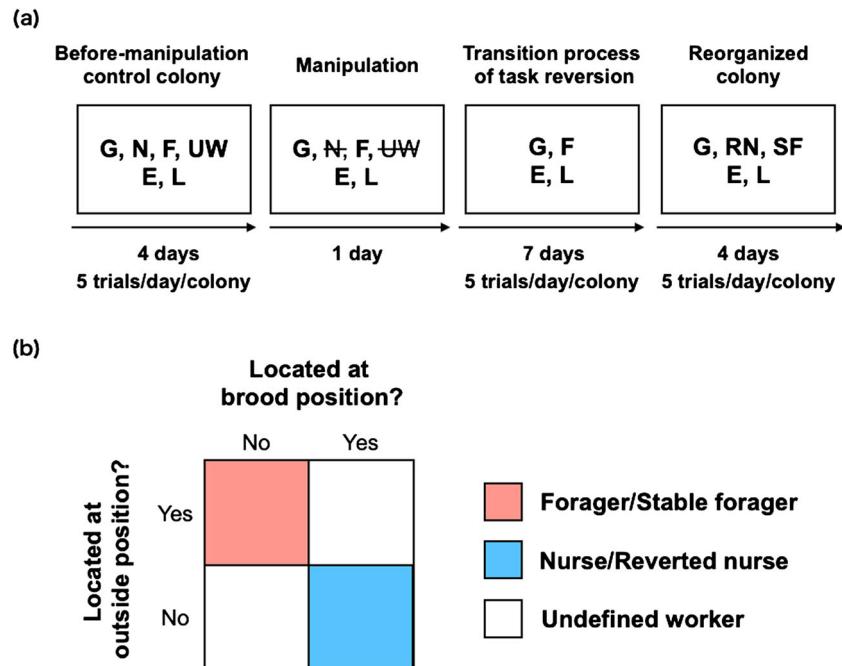
We left gamergates, foragers, some broods in the nests of colonies A to E (A 42 workers, 21 eggs, and four larvae; B 52 workers, 26 eggs, and five larvae; C 46 workers, 25 eggs, and five larvae; D 49 workers, 21 eggs, and four larvae; E 44

workers, 23 eggs, and 4 larvae), but removed the others (nurses, undefined workers, some eggs, and some larvae) from the colonies (Fig. 1a). The next day, we started our observations of worker behaviors for the next 7 days (the 1-day acclimatization period was set to allow the transition process of task reversion to occur; Fig. 1a). During this observation period, we carried out five observation trials per day per colony as the same schedule in the before-manipulation control colonies and recorded the workers at the brood position. Next, for each worker, we obtained the proportions of trials detected at the brood position to total trials at each observation day (Fig. 1a). On day 8 after the manipulation, we started observing worker behaviors using the same method as in the before-manipulation control colonies (Fig. 1a). We recorded the workers detected at the brood and the outside position, respectively. Then, we obtained the proportions of trials detected at each position to total trials for each worker, and we categorized the workers either as foragers or reverted nurses. Note that although we only observed two areas, the sum of these proportions is not 1 because the workers were sometimes located at the other area within the nest (data not shown). We hereafter used a term, the reorganized colony as replacement of the colony in this observation period. If workers were categorized as nurses in the reorganized colony, they were referred to as “reverted nurses” and workers categorized as foragers were referred to as “stable foragers” (Fig. 1b).

Statistical analysis

We analyzed the relationship between the ratio of trials detected at the outside position to all trials of foragers and task reversion using a GLMM with a binomial error distribution

Fig. 1 The experimental scheme and definition of behavioral caste used in this study. **a** Each experimental period is shown below the boxes. G, N, F, UW, E, L, RN, and SF indicate gamergate, nurse, forager, undefined worker, egg, larva, reverted nurse, and stable forager, respectively. **b** The relationship between the corresponding task of a worker during the experimental period and the behavioral caste. The red and blue regions correspond to forager/stable forager and nurse/reverted nurse, respectively



in R package lme4, using the *glmer* function (Bates et al. 2013). We binarized worker tasks as 1 and 0 for the reverted nurse and the stable forager in a reorganized colony, respectively. We set the task as a response variable, the ratio of observation trials detected at the outside position of foragers in the before-manipulation control colony as a fixed factor, and colony ID as a random effect. Second, the number of trials detected at the brood or that of the outside position of foragers in the reorganized colony were assigned as response variables. Then, the number of observation trials detected at the outside position in the before-manipulation control colony, colony ID, and the number of total trials were set as a fixed factor, a random effect, and an offset, respectively. Then, test of zero-inflation using the *testZeroInflation* function in package DHARMA (Hartig 2020) showed that both models had zero-inflations (the outside position vs the brood position, $P < 0.00001$; the outside position vs the outside position, $P = 0.0016$). Therefore, we constructed models using GLMMs with negative binomial error distribution using the *glmmTMB* function in R package glmmTMB (Brooks et al. 2017). Third, we analyzed the relationship between the ratio of observation trials detected at the brood position to total trials (five trials) of each observation day (1–7 days) during the transition process and the allocated tasks in the reorganized colony. We set the binarized tasks as a response variable, the ratio as a fixed variable, and colony ID as a random effect. The effect of fixed factors was compared with the null model, where the fixed effect was set to 1. Note that we verified that all constructed GLMM models had not overdispersion by *testDispersion* function in package DHARMA (data not shown). Finally, we pooled daily data for the nursing activity of all colonies and carried out a correlation analysis between that and the day of the transition process of task reversion. All statistical analyses were carried out using R 3.5.1.

Data availability

All data generated or analyzed during this study are included in this published article.

Results

The relationship between the behavioral propensity of foragers and task reversion

First, we observed that some foragers reverted to nursing in all colonies (A, 17/42 workers; B, 5/53 workers; C, 12/46 workers; D, 10/49 workers; E, 14/44 workers).

Second, to examine how the proportion of trials detected outside the nest (outside position) of foragers affects task reversion, we analyzed the relationship between the proportion of trials detected at the outside position in the before-manipulation

control colony and task allocation in the reorganized colony. The proportion of trials detected at the outside position in the before-manipulation control colony was negatively correlated with the probability of the task reversion (GLMM $\chi^2 = 11.811$, $P = 0.0006$, Fig. 2), meaning that foragers with low proportion of the outside position tended to shift from their original task back to nurse. Next, to gain a deeper understanding of how the behavioral propensity is related to behavioral patterns in the reorganized colony, we analyzed the relationship between the proportion of observation trials detected at the outside position in the before-manipulation control colony and the proportion of the outside position or brood position (worker located in front of broods) in the reorganized colony. Although the relationship between the proportion of the outside and that of the brood position in the manipulated colony is not completely independent, they would be good indicators to describe whether the behavioral propensity affected their task choice in detail (see also Materials and Methods). We found that the proportion of trials detected at the outside position was negatively associated with the proportion of the brood position in the reorganized colony ($\chi^2 = 178.94$, $P < 0.0001$, Fig. 3a). In stark contrast with the proportion of trials detected at the brood position, we found that the proportion of the outside position in the reorganized colony increased with the proportion of the outside position in the before-manipulation control colony ($\chi^2 = 67.089$, $P < 0.0001$, Fig. 3b). These results strongly suggest that

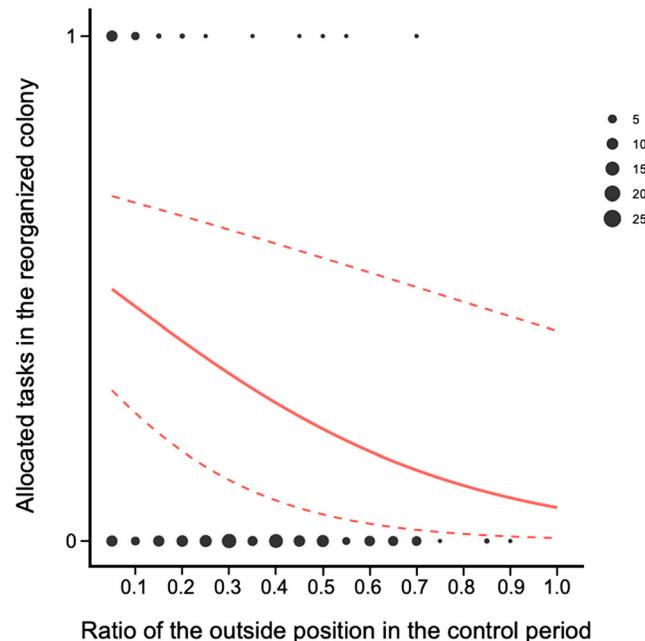


Fig. 2 The relationship between the proportion of trials detected at outside position and task reversion. The reverted nurse and the stable forager are coded as 1 and 0, respectively. The circle sizes indicate overlapping data points. The solid and dashed lines indicate estimated predictions and their corresponding 95% confidence intervals, respectively

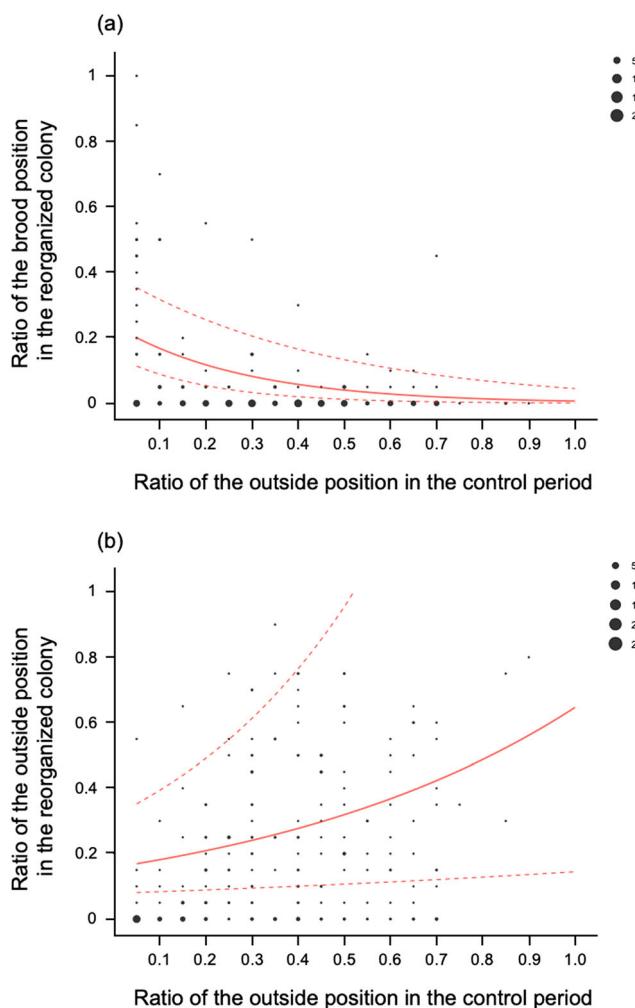


Fig. 3 The relationship between the proportion of trials detected at outside position in the before-manipulation control colony and the proportion of task-related positions in the reorganized colony. **a** The y-axis indicates the proportion of trials detected at outside position in the before-manipulation control and **b** reorganized colony, respectively. The circle sizes indicate overlapping data points. The solid lines and dashed lines indicate estimated predictions and their corresponding 95% confidence intervals, respectively

foragers' behavioral propensity affects their behavioral response in the reorganized colony.

The transition process of task reversion

To understand the behavioral change of foragers during the transition process, we analyzed the relationships between daily nursing activity and task allocation in the reorganized colony. We found that, on day 2 and 7 of the observation period, workers that spent little time brood caring tended to become stable foragers in the reorganized colony (GLMM day 2, $\chi^2 = 9.199, P = 0.0024$; day 3, $\chi^2 = 17.409, P < 0.001$; day 4, $\chi^2 = 8.767, P = 0.0031$; day 5, $\chi^2 = 15.83, P < 0.001$; day 6, $\chi^2 = 14.63, P = 0.0001$; day 7, $\chi^2 = 8.006, P = 0.0046$,

Fig. 4 and Fig. S1). However, such a significant relationship was not detected in the first observation day (day 1, $\chi^2 = 0.399, P = 0.527$, Fig. 4).

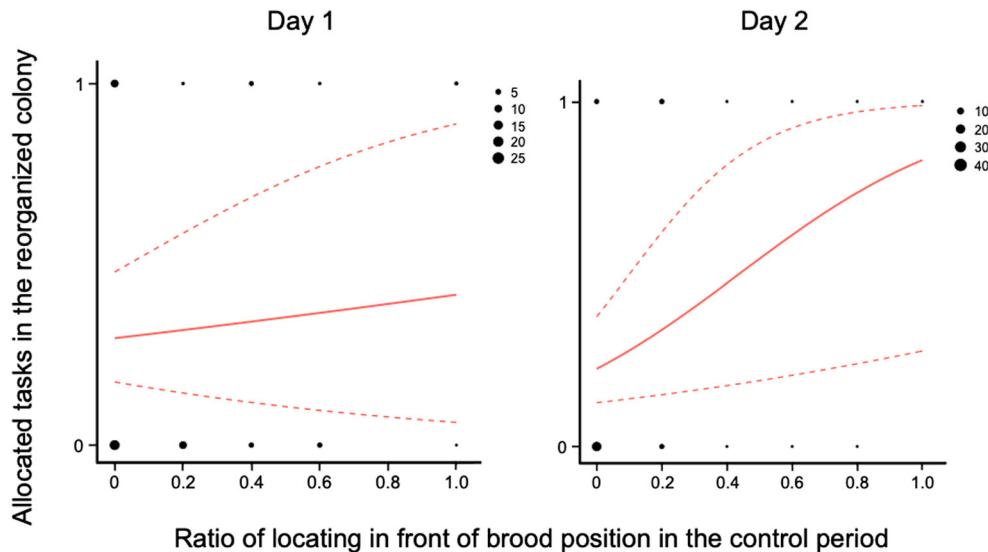
To examine the transition process (Fig. 5) in more detail, we also carried out the correlation analyses for the proportion of trials detected at the brood position on every two consecutive days. Although there was low correlation coefficient between day 1 and 2, other combinations had a relatively high correlation coefficient (Pearson's correlation test: day 1–day 2, $r = 0.298, P = 0.006$; day 2–day 3, $r = 0.591, P < 0.001$; day 3–day 4, $r = 0.675, P < 0.001$; day 4–day 5, $r = 0.591, P < 0.001$; day 5–day 6, $r = 0.633, P < 0.001$; day 6–day 7, $r = 0.653, P < 0.001$, Fig. 4). These results indicate that after day 2, the degree of nursing behavior was already fixed in each worker.

Discussion

Our results confirmed the task reversion from forager to nurse in *Diacamma* sp. after the age structure was altered and showed that task reversion was already complete 2 days after the manipulation of the colony (Fig. 3). This suggests that in this ant species, the division of labor was quickly reassigned after the colony disturbance. We can consider that the response observed in our results is a beneficial feature in terms of the colony life cycle of this species. In *Diacamma* sp., the age structure of the colony changes dynamically as the birth rate is not constant (Nakata 1996). Moreover, *Diacamma* colonies reproduce by fission; new colonies may hence consist of an unbalanced proportion of nurses and foragers in the initial stage of nest construction. A theoretical model suggests that the division of labor based on worker behavioral flexibility is favored when the age structure of the inside and outside workers is unbalanced (Wakano et al. 1998). Therefore, our results suggest that the rapid response of workers is important to reconstruct the division of labor in unstable environments.

Our findings showed that workers that spent less time foraging were more likely to become reverted nurses (Fig. 2). Moreover, the proportion of trials detected outside the nest in the reorganized colony positively related to the proportion of the outside position in the before-manipulation control colony. In contrast, there was negative relationship between the proportion of trials located in front of broods in the reorganized colony and the proportion of trials detected outside the nest in the before-manipulation control colony (Fig. 3), suggesting that workers' behavioral propensity strongly impacts task reallocation. As the time spent at outside the nest increases with age in this species (Nakata 1995, 1996), the differences in behavioral propensity among workers are likely to be related to their individual age. In honeybees, relatively young foragers also tend to switch back to nurses (Robinson et al. 1992); therefore, the same may be true in this species. As eusociality evolved independently in

Fig. 4 The relationship between the proportion of trials detected at brood position during the transition process (day 1) and task reversion. The reverted nurse and the stable forager are coded as 1 and 0, respectively. The circle sizes indicate overlapping data points. The solid lines and dashed lines indicate estimated predictions and their corresponding 95% confidence intervals, respectively. Other days show the same trends as day 2 (Fig. S1 in Supporting Information)



ants and bees, it will be interesting to investigate of the propensity observed in this study is common across different social insect lineages. Moreover, several studies have suggested that some conserved genes in eusocial hymenopteran species are involved in the regulation of the division of labor (Amdam et al. 2004; Wurm et al. 2011; Corona et al. 2013; Oxley et al. 2014). Therefore, to understand the detailed mechanisms behind the division of labor, the relationship between task reversion and its molecular basis should be investigated. Further research on the relationship between worker propensity, age, and task reversion using various social insect species is required to provide the insight into this behavior.

This study showed that both stable foragers and reverted nurses cared the broods on the first observation day, but this task was predominantly done by reverted nurses in subsequent observation days (Figs. 3, 4). Different behavioral propensity between workers can be explained by differences in their response threshold to a specific stimulus derived from a focal task. In the fixed response threshold model, a variety of thresholds among workers can generate the division of labor

(Bonabeau et al. 1996). It appears that this model can be applied to the result of our first observation day: as brood care-related stimulus increases due to the relative absence of nurses, several foragers with relatively low threshold switched and performed this task. On subsequent days, however, the model does not fit. Instead, we hypothesized a mechanism for the task reversion process based on the reinforcement model for the response threshold (Theraulaz et al. 1998). After day 2, some workers, i.e., those with a relatively lower threshold, who responded to the increased stimuli showed a decreased threshold according to the experience with this task. After this, only foragers with a decreased threshold cared for the broods on the following day. Given that such experience-dependent task allocation is known to occur in clonal ant species (Ravary et al. 2007), it would be worth investigating experimentally whether task experience involves task reversion or not in *Diacamma* sp.

In general, the emergence of division of labor based on a self-organizing process involves social interactions and spatial fidelities among colony members, as well as signal-response dynamics (Beshers and Fewell 2001; Camazine et al. 2001; Gadau and Fewell 2009). Although our study revealed the importance of worker propensity for flexible behavioral change and the reorganization of division of labor, there are other factors, such as spatial fidelity (Crall et al. 2018), that contribute to the task allocation among workers which remain unknown. Also, although it is known that age polyethism is associated with expansion of behavioral repertoires of workers (Seid and Traniello 2006), the relationship between the changes of age-related repertoire and task reversion remains to be solved. Further behavioral and physiological research with novel approaches, such as interaction network (Shimoji et al. 2014), individual tracking (Fujioka et al. 2017), and gene expression (Shimoji et al. 2017) should provide a better understanding of the division of labor in insect societies.

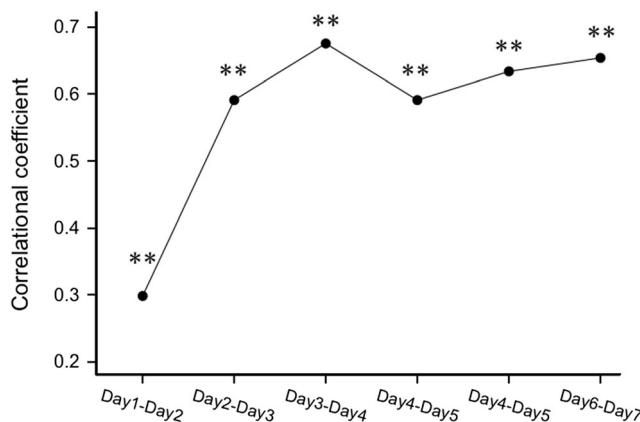


Fig. 5 Changes in correlation coefficient during the transition process. Asterisks indicate statistical significance ($P < 0.001$)

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