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Experimental study of brood transport in red wood ants: from individual to group task performance

Экспериментальное изучение транспортировки расплода у рыжих лесных муравьёв: от индивидуального к групповому решению задачи

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Key words: Formicidae, social behavior, division of labor, colony organization, *Formica aquilonia.*

Ключевые слова: Formicidae, социальное поведение, разделение труда, организация семьи, *Formica aquilonia.*

Abstract. Preliminary results of the validation of original methods to study the division of labor in ant groups of different sizes during the brood transport to the shelter using the model species *Formica aquilonia* (Yarrow, 1955) are presented. Task performance depended on group size: when brood:worker ratio was about 4 or greater, the highest proportion (86 %) of successful tests was in groups of 10 and 30 individuals, 58 % in pairs of individuals, and 29 % in single workers. The following behavioral roles of inner-nest workers were identified: transporting the brood to the shelter (17 (14, 25) % of the group), brood care inside the shelter (47 (40; 70) %) and outside the shelter (20 (0; 39) %), and no contact with the brood (9 (3; 13) %). Brood transport was performed mainly (92–100 %) by a small number of highly active carriers (11 (7; 25) % of the group). Task efficiency (% brood transferred to the shelter) is assumed to be similar in group (59 (50; 78)) and pairwise (70 (45; 100)) tests. Pairwise tests may be used to analyze the effects of the behavioral role and experience of workers on their task performance. Social signals (jerking motor displays) may influence the decision to transport the brood. In the context of brood care tasks, the proposed methods were quite sensitive to variations in individual and group behavior of ants and effective for estimating the role of key individuals and communication in collective decision making.

Резюме. Представлены предварительные результаты апробации оригинальных методов изучения разделения труда в группах рабочих муравьёв разной численности при переносе расплода в укрытие на модельном виде *Formica aquilonia* (Yarrow, 1955). Выполнение задачи зависело от размера группы: при соотношении расплод : рабочие около 4 и выше доля успешных тестов была максимальна (86 %) у групп из 10 и 30 особей, 58 % у пары особей и 29 % у одиночных рабочих. Выделены следующие тактики поведения внутригнездовых рабочих особей: транспортировка расплода в укрытие (17 (14, 25) % группы), забота за расплодом внутри укрытия (47 (40; 70) %) и вне укрытия (20 (0; 39) %), отсутствие контактов с расплодом (9 (3; 13) %). Задача по транспортировке расплода в основном (92–100 %) выполнялась малым числом переносчиков с высокой активностью (11 (7; 25) % группы). Есть основания полагать, что эффективность выполнения задачи (% перенесенного в укрытие расплода) была сходной в групповом (59 (50; 78)) и парном (70 (45; 100)) тестах. Парные тесты могут применяться для анализа влияния поведенческой тактики и опыта рабочих на выполнение ими задачи. На принятие решения о транспортировке расплода могут оказывать влияние социальные сигналы (серии быстрых выпадов). В контексте задач по уходу за расплодом предлагаемые методы оказались достаточно чувствительными к различиям в индивидуальном и групповом поведении муравьев и эффективными для оценки роли ключевых особей и коммуникации в коллективном решении задачи.

Introduction

The social organization of ant colonies is based on a division of labor, including task specialization among groups of workers and task switching depending on the frequency of contacts with nestmates and other stimuli [Hölldobler, Wilson, 1990; Gordon, 2019]. Individual contributions to task performance vary widely at the colony level, with some workers performing a disproportionate amount of the task («elite workers» [Robson, Traniello, 1999]) and other individuals remaining inactive [Dornhaus et al., 2008]. Task performance may depend on the group composition, experience and personality traits of workers, and their mode of communication and recruitment [Ravary et al., 2007; Carere et al., 2018; Reznikova, 2021]. Most studies have focused on foraging tasks, where collective success depends on the information transfer from scouts to foragers [Reznikova, 2020]. The mechanisms involved in performing inner-nest tasks remain less understood.

When nest chambers containing brood are damaged, ants carry the brood to temporary shelters that protect them from adverse environmental conditions. The performance of this task by ants has been studied mainly at the colony level, but less frequently at the group or individual levels [Meudec, 1973; Szczuka et al., 2014]. Group performance in brood transport may depend on group size and the task specialization of workers [Lenoir, 1981; Szczuka et al., 2014]. Individuals in groups may

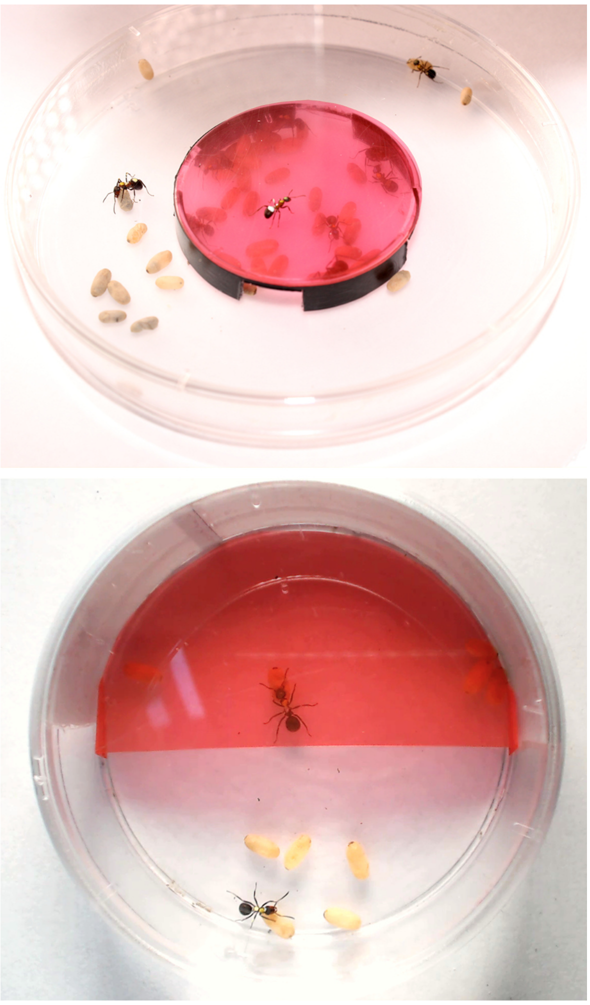


Fig. 1. Experimental setups for studying the organization of brood transport and care in group (10 workers, 40 pupae) and pairwise (2 workers, 10 pupae) tests.

Рис. 1. Экспериментальные установки для изучения организации транспортировки и ухода за расплодом в групповых (10 рабочих, 40 куколок) и парных (2 рабочих, 10 куколок) тестах.

differ in their behavioral tactics for interacting with the brood [Golovachev et al., 2022]. Nevertheless, task partitioning and the organization of brood retrieval in ants are still poorly understood.

In this study of brood transport in *Formica aquilonia*, the following research questions and methods to address them were raised: (1) Can the brood hiding task be observed in small groups of workers? (2) Do inner-nest workers differ in their behavioral roles in performing the task? (3) Do social signals influence the individual performance of this task?

Materials and methods

The *F. aquilonia* colony of 3000–4000 individuals with a queen and brood was collected from an anthill in a mixed forest in Novosibirsk Academgorodok (N54.83522, E83.10263). Ants were kept in artificial nests (20x15x2 cm) in plastic arenas (80x50x20 cm) with access to water and 20 % sugar solution. The preferred location of worker activity (nest or arena) was recorded. The inner-nest workers were individually marked with nitro dyes. Fully pigmented workers active inside the nest were selected.

A previous study on red wood ants showed successful brood transport in groups of at least 20 workers [Szczuka et al., 2014]. The low success rate in smaller groups could be related to the low brood:worker ratio (0.25–2.5) and the high acclimatization time of isolated groups (30 minutes) [Szczuka et al., 2014]. Therefore, we increased the brood:worker ratio to about 4 in group tests, 5 in pairwise tests, and 10 in individual tests. The acclimatization time of ants in the test arena before brood introduction was reduced to 5 minutes. Together with the shelter design (Fig. 1) and inner-nest worker selection methods, these new conditions allowed us to observe complete sequences of brood transport and care by groups of less than 20 workers and even by individual red wood ants.

Group tests. Experiments were performed in two variants: 10 workers with 40 pupae (brood:worker ratio = 4; n = 3) and 30 workers with 110 pupae (brood : worker ratio = 3.7; n = 4). Individuals were selected from inner-nest workers who participated in brood transport in experiments where pupae were offered near the nest entrance. A group of ants was placed in a round test arena (d = 9 cm for tests with 10 workers and d = 15 cm for tests with 30 workers) with a shaded shelter in the center (d = 5 cm, h = 1 cm, four entrances 0.5x1 cm) and pupae evenly distributed on the lighted part of the test arena (Fig. 1). The duration of the video recording did not exceed 60 minutes.

Individual and pairwise tests. To examine the role of the social environment on task performance, the most active workers in brood transport («active carriers») were tested individually (n = 7) and paired (n = 19) with inner-nest workers that did not participate in brood transport («inactive workers») in experiments with pupae offered near the nest entrance. For individual tests, active carriers were selected based on the high level of brood transport in previous group tests. For pairwise tests, other individuals from active carriers were selected based on (i) the high level of brood transport in previous group tests (n = 7) or (ii) experiments with pupae offered near the nest entrance without group test experience (n = 12). In both cases, active carriers were selected from individuals who transported more than three pupae to the shelter or nest chamber. Individual and pairwise tests were performed in round test arenas (d = 5 cm, h = 1 cm), half of which were illuminated and the other half were shaded shelters (h = 0.5 cm). On the illuminated part of the test arena, 10 pupae were evenly distributed, and 1 or 2 marked ants were placed (Fig. 1). The duration of the video recording was not more than 15 minutes for individual trials and not more than 30 minutes for pairwise trials.

In all tests, the shaded shelter had light-blocking side walls where the ants preferred to place brood. A red translucent coating (0.1 mm polyester film) on the top was used to record ant behavior inside the shelter (Fig. 1). After testing, the arenas were treated with ethanol to eliminate the influence of chemical cues.

A total of 33 observations (7 group tests, 19 pairwise tests, and 7 individual tests) with a total duration of 10 hours were performed.

Tests in which at least one worker transferred at least one pupa to the shelter were considered successful. The success rate was measured as the percentage of successful tests. Task efficiency in successful tests was measured as the proportion of pupae transferred to the shelter out of the total number of pupae. Statistical data processing was performed in SPSS 22.0 (Chicago, USA). Fisher exact test with Bonferroni correction was used to compare success rate between different tests. Due to the preliminary nature of the study, an a priori power analysis was performed on the success rate data using G*Power 3.1.9.7 [Faul et al., 2007] to estimate the required sample size to reach 80 % power (alpha = 0.025, beta = 0.20). Fisher exact test was used to compare frequency of behavior in response to social display between different tests. Mann-Whitney test was used to compare task efficiency, number of brood transported, and number of social displays between different tests. Wilcoxon signed ranks test was used to compare number of brood transported by different ants in a pairwise test. Spearman's correlation was used to assess relationships between behavioral variables. Medians [25 %; 75 %] are presented.

The present work is registered in ZooBank (www.zoobank.org) under LSID urn:lsid:zoobank.org:pub:FB0699C1-2BC5-43B3-AB44-5E81CFD08A1A

Results

Group tests. Due to the limited sample size of successful tests (n = 2 for groups of 10 individuals, n = 4 for groups of 30 individuals) and the approximately equal brood:worker ratios (4 and 3.7, respectively), further analysis of group tests was performed on the pooled sample (n = 6). In the group tests, red wood ants showed high success rates in hiding the brood; 6 out of 7 groups (86 %) transported pupae to the shelter.

One of four tactics prevailed in worker behavior: (1) brood transport from the lighted arena to the shelter, including brood clustering there (17 (14, 25) % of group size); (2) brood care under the shelter, including immobility near the brood, antennal touching, and clustering of the brood (47 (40; 70) %); (3) brood care outside the shelter (20 (0; 39) %); (4) walking or standing on the lighted arena without contact with the brood (9 (3; 13) %).

The majority of brood transport (92–100 % of pupae in the shelter) was performed by 1 to 6 workers (11 (7; 25) % of workers in the group). These highly active workers carried 9–33 pupae to the shelter (21 (11; 28)), which was several times higher than the number of pupae per ant (about 4.0).

Task efficiency as a percentage of transported brood (Fig. 2) tended to increase with the percentages of brood carriers in the group ($r_s = 0.70$, $p = 0.13$), including highly active carriers ($r_s = 0.66$, $p = 0.15$) and nurses inside the shelter ($r_s = 0.73$, $p = 0.10$). Task efficiency significantly decreased with the percentage of nurses outside the shelter ($r_s = -0.88$, $p = 0.02$).

Individual and pairwise tests. Individual tests of highly active workers (n = 7) showed a lower success rate of brood transport at the tendency level compared to group tests (29 % and 86 %, respectively; p = 0.10, Fisher's exact test with Bonferroni correction), whereas the success rate in pairwise tests (11 out of 19 tests, 58 %) was similar to that in individual and group tests (p > 0.025, Fisher's exact test with Bonferroni correction). Power analysis indicated that sample sizes should be increased to n = 13 for group versus individual comparisons or n = 53–62 for pairwise versus group/individual comparisons to achieve a significant effect on the success rate.

In successful tests of pairs and groups of workers, task efficiency was found to be similar and made up about 60–70 % (Mann-Whitney test, p > 0.05; Fig. 2). In two successful individual tests, workers transported 10 % and 80 % of the brood. In successful pairwise tests, task efficiency tended to be higher when only the active carrier performed the task (n = 6) than in tests (n = 5) where both the active carrier and the inactive worker transported pupae into the shelter (90 (68; 100) and 40 (35; 75), respectively; Mann-Whitney test, p = 0.096). Overall, active carriers transported significantly more pupae into the shelter than inactive workers (6 (1; 10) vs. 0 (0; 3); Wilcoxon signed ranks test, p < 0.05). The method of selecting active carriers for pairwise tests did not affect the success rate (57 vs. 58 %; Fisher's exact

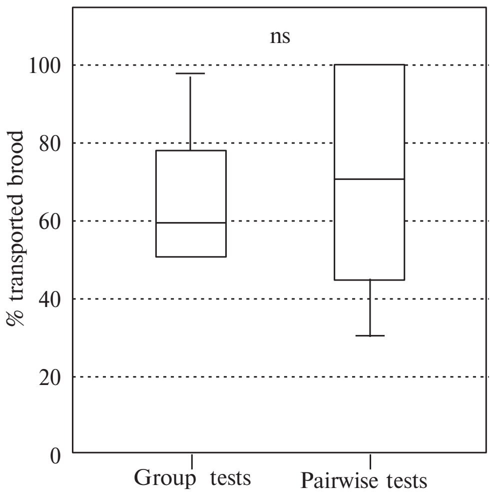
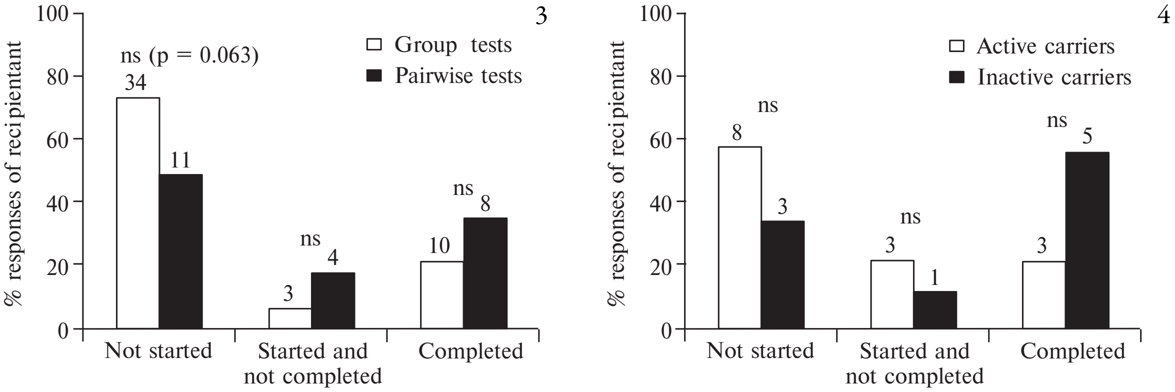


Fig. 2. Brood transport efficiency in successful group (n = 6) and pair (n = 11) tests. Proportion of brood transported to the shelter by *Formica aquilonia* Yarrow workers out of the total number of brood. Mann-Whitney test: ns — p > 0.05.

Рис. 2. Результативность переноса расплода в успешных групповых (n = 6) и парных (n = 11) тестах. Доля транспортированного рабочими *Formica aquilonia* Yarrow в укрытие расплода от общего количества расплода. Критерий Манна-Уитни: ns — p > 0,05.



Figs 3–4. Brood transport performance by recipient ants to social signals (jerking motor displays). 3 — in group and pairwise tests; 4 — during stimulation by active carriers or inactive workers in pairwise tests. Numbers in the graph indicate sample sizes. Fisher's exact test: ns — p > 0.05.

Рис. 3–4. Выполнение переноса расплода муравьями в ответ на социальные сигналы (серии быстрых выпадов). 3 — в групповых и парных тестах; 4 — при стимуляции активными переносчиками или неактивными рабочими в парных тестах. Номерами на диаграмме указаны размеры выборок. Точный критерий Фишера: ns — p > 0,05.

test, $p > 0.05$), but it did affect individual task efficiency. Carriers with previous experience in group tests transferred more pupae to the shelter than carriers without such experience (10 (8; 10) and 3 (1; 6), respectively; Mann-Whitney test, $p < 0.05$).

Social signals. Workers interacted with each other through antennal touching, antennal contact, and food exchange. The ants demonstrated jerks and lunges with open mandibles toward the nestmate and placed their forelegs on the nestmate's body. This jerking motor display resulted in the recipient ant transporting one or more pupae to the shelter («task completed»), or picking up/transporting the pupae within the lighted arena («task performance started and not completed»), or touching/ignoring the pupae («task performance not started»).

The display was observed significantly more frequently in 6 successful group tests than in 11 successful pairwise tests (7 (5; 11) and 1 (0; 4), respectively; Mann-Whitney test, $p < 0.01$). The jerking motor display initiated complete or uncomplete performance of brood hiding by the recipient worker at the tendency level more often in pairwise tests than in group tests (52 vs. 28 %, respectively; Fisher's exact test, $p=0.063$; Fig. 3). In pairwise tests, whether the active carrier or inactive worker showed this display did not affect the frequency of the recipient ant's behavioral responses (Fisher's exact test, $p>0.05$; Fig. 4).

Discussion

A key task in maintaining ant colony structure is brood care, including feeding, grooming and maintaining nest conditions [Hölldobler, Wilson, 1990]. The original experimental setup allowed us to determine the threshold group size required for brood transfer to a suitable environment. We simulated the situation of nest chamber destruction with pupae exposure and observed the movement of pupae to a temporary shelter by *F. aquilonia* workers. Ants were shown to successfully relocate their brood in pairs of workers for the first time. Task partitioning among inner-nest workers was first demonstrated in red wood ants. The majority of individuals are inactive brood carers, while the minority of the group (11 %) are active brood carriers. Workers were able to recruit other individuals to carry brood in pairs and groups, although communication only slightly contributed in task completion. Overall, the proposed methods are suitable for evaluating the role of key individuals, experience, and communication in collective decision making during brood relocation.

Using a controlled number of workers with known behavioral characteristics, we generated the need to hide the brood in a safe place outside the nest. A shelter with dark walls and a red translucent cover proved to be a sufficient stimulus for ants to hide the brood from the first minutes of the experiment. This shelter design allowed us to distinguish individual ant markings and observe worker-brood and worker-worker interactions both in the test arena and inside the shelter (Fig. 1).

In our study of *F. aquilonia*, brood relocation was not only performed by the majority of groups (86 % success rate) consisting of 10 and 30 inner-nest workers, but also by 58 % of worker pairs, and even by rare (29 %) highly active individuals. When comparing the success rate between individual and group tests, power analysis revealed a more pronounced effect size. This may indicate that social influence plays an important role in brood transport task performance. The minimum group size of two individuals required for brood relocation was first demonstrated in ants.

Our data is consistent with the known effect of group size on ant collective behavior [Dornhaus et al., 2012]. Brood transport to a shelter was expressed in groups of at least 20 workers in red wood ants [Szczuka et al., 2014] and 5 workers in *Myrmica rubra* (Linnaeus, 1758) [Golovachev et al., 2022]. More successful performance of the brood carrying task may be associated with a higher brood:worker ratio. This ratio was 3.7–4.0 for groups of *F. aquilonia* workers, 5 for 2 workers, and 10 for 1 worker, whereas in the experiments of Szczuka et al. [2014] on *F. polyctena* Förster, 1850 this ratio was several times lower: 0.25–0.5 for 10–20 workers, 1 for 5 workers, and 5 for 1 worker. In *M. rubra* (Linnaeus, 1758), brood:worker ratio was 3.6, and groups of 5 workers transferred all the brood to the shelter in 55 % of trials [Golovachev et al., 2022]. Apparently, a high brood : worker ratio (about 4 or more) allows us to observe brood transport in ant groups of small size.

The pairwise experimental design can be applied to analyze the effects of learning, specialization, and social environment on task performance by using different combinations of workers (young and old; naive and experienced; nurses and foragers, etc.). According to our preliminary data, workers' performance in brood relocation is influenced by their behavioral role and experience. In pairwise tests, the active carriers transferred more brood to the shelter than inactive workers (apparently brood carriers). Among active carriers, the number of brood transported was higher for those with previous successful experience in group tests. This confirms the important role of individual experience in the division of labour [Ravary et al., 2007].

The organization of brood relocation by a group of inner-nest workers of *F. aquilonia* was expressed as task partitioning with sequential performance of tasks by different numbers of workers: brood care outside (47 % of group), brood transport to the shelter (17 %), and brood care inside the shelter (20 %). The task efficiency of the ant group tended to increase with the number of workers transporting and caring for the brood inside the shelter and decreased with the number of workers caring for the brood outside. The task partitioning we observed in red wood ants is somewhat similar to the distribution of behavioral tactics in *M. rubra* groups, where about 20 % of workers care for brood outside, 22 % transport brood, 26 % care for brood inside the shelter, and 28 % switch between tasks [Golovachev et al., 2022].

It may be easier to manipulate worker composition in isolated groups than in entire ant colonies. This approach makes it possible to study the flexibility of task partitioning, the role of specialization and self-organization in brood relocation. For example, one would expect behavioral changes in less active individuals by excluding «elites», a subgroup of highly active individuals (11 % of the group in *F. aquilonia*) who perform the majority of the work (98 % in *F. aquilonia*) and whose presence is required to complete the task [Robson, Traniello, 1999]. The number of «elite» brood carriers varies from 4 % of workers in *Lasius niger* (Linnaeus, 1758) [Lenoir, 1981] and 8 % in *Camponotus fellah* (Dalla Torre, 1893) [Mersch et al., 2018] to 11 % in *Formica sanguinea* (Latreille, 1798) [Moglich, Holldobler, 1974] and 18–34 % of workers in *M. rubra* [Abraham, Pasteels, 1980]. The duration of such specialization can vary from 5 days to 3 months [Robson, Traniello, 1999]. Although the phenomenon of «elite» brood carriers has long been described, the resilience of the division of labor dependent on the activity of a small number of individuals remains poorly understood [Robson, Traniello, 1999; Dornhaus et al., 2008].

Recruitment may increase the efficiency of nestmate transport during nest migration in ants [Dornhaus et al., 2008; Stroeymeyt et al., 2011], but the advantages of communication during brood relocation are less apparent [Mersch et al., 2018]. In *C. fellah* (Dalla Torre, 1893) colonies, brood transport following changes in environmental conditions was performed by a small minority of workers who relied on private information and did not communicate or recruit other workers [Mersch et al., 2018]. In contrast, we first found that ant workers can recruit other nestmates to transfer brood to preferable conditions. The *F. aquilonia* workers used a jerking motor display in recruitment. This display in red wood ants is considered a non-specific signal that is displayed in a variety of situations. For example, similar alerting invitation signals given by returning foragers inside the nest may play a decisive role in food recruitment [Rosengren, Fortelius, 1987]. However, this communication had a limited effect when *F. aquilonia* workers relocated the brood (Figs 3–4). In only a third or fewer cases did workers receiving this display transfer the pupae to the shelter. This may be because most workers received information about the shelter during the pre-experimental adaptation period.

In summary, the proposed original methods for studying the organization of brood transport to the shelter were quite sensitive to variations in individual and group behavior of ants and effective for estimating the role of key individuals and communication in collective decision making. In perspective, these brood transport tests can be used to examine the proximate mechanisms of individual variation in inner-nest worker behavior and the ultimate consequences for the division of labor and adaptation of ant colonies to environmental disturbance.

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