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Learning and Task Interference by Corpse-removal Specialists in Honey Bee Colonies

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Abstract

Undertakers are considered to be among the most specialized of pre-foraging honey bee (*Apis mellifera* L.) workers. In this study we examined a possible benefit and a cost of the corpse-removal specialty, the improvement in performance with experience, and interference by individuals attempting to perform the same task in the same location, respectively. Experienced bees removed corpses significantly faster than less experienced bees and also were less likely to drop corpses while exiting the hive (5.5% vs. 14.3% of attempts). Superior performance by experienced undertakers might occur as a consequence of learning, or by greater ability from the outset. Because active undertakers ($\geqslant$ 3 corpse removals) did not improve with experience over their own careers, learning was not demonstrated. An extreme specialist, Yellow 54, removed a total of 114 corpses (33.8% of experimentally introduced dead bees) from the hive over a 13-day period. This is the longest recorded tenure of undertaking to date and demonstrates how a few individuals can dominate this task in a honey bee colony. Yellow 54 removed corpses significantly faster than other active bees, but she demonstrated no obvious improvement in performance over her undertaking career. This suggests the possibility that active undertakers were more talented than less active undertakers, irrespective of learning. When two undertakers worked together to remove a corpse from the hive, they took longer to complete the task than did single individuals. When multiple undertakers flew together from the hive, they were less likely to clear a nearby obstruction than single undertakers and were more likely to drop the corpse within 1 m of the hive. Thus, mutual interference exacted a measurable cost as a result of the undertaking specialization while learning provided few benefits.

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Introduction

The evolution of division of labour is regarded as one of the principal reasons for the ecological success of social insects (WILSON 1987). Division of labour is thought to promote ergonomic efficiency in a number of ways, including the partitioning of complicated tasks (JEANNE 1986a), the employment of cooperative teams (FRANKS 1987), and learning by longer-term specialists (OSTER & WILSON 1978; SEELEY 1985). Specialization might promote learning by providing workers with more opportunities to perform a given task. In addition, specialization on a given task reduces the performance of other tasks which might interfere with effective learning. Improved task performance by specialists

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could reduce the need for non-specialists to switch to tasks that they perform less effectively. While learning has been demonstrated for foragers (HEINRICH 1979; MENZEL 1985; DUKAS & VISSCHER 1994), it is also expected for in-hive tasks (DOWNING 1992; FAHRBACH & ROBINSON 1996). Learning might be especially important for such hive activities as corpse removal and colony defence in which a small minority of workers participate. A convincing demonstration of learning would include both the superior performance of more experienced individuals and improvements by individuals as they become familiar with external stimuli associated with the task.

Costs of specialization have received less study than benefits. Possible costs include the failure to reallocate workers quickly to new tasks in response to changing demographic or environmental conditions (WILSON 1985; GORDON 1989a,b), the inefficient performance of specialists that are forced to perform duties outside their normal repertoire (WILSON 1984), the potential increase in inter-task travel time as specialists seek out a narrow range of stimuli to which to respond (WILSON 1976; SEELEY 1982), and the waiting time imposed by tasks requiring serial coordination (JEANNE 1986a). An additional cost of specialization, which has received only anecdotal attention, might occur when an individual interferes with a nestmate as they both respond to the same task-related stimulus.

Honey bees exhibit temporal polyethism by which adult workers pass through a number of developmental stages. Workers perform brood care in the nest interior when young, proceed to tasks associated with the nest periphery such as food storing, and end with foraging (reviews: SEELEY 1985; WINSTON 1987; ROBINSON 1992). Individuals, however, do not participate equally in all tasks. Only a minority of workers ever engage in rare tasks such as undertaking and guarding (SAKAGAMI 1953; VISSCHER 1983; MOORE et al. 1987; BREED et al. 1992), at least in part because of genetic differences among workers (ROBINSON & PAGE 1988, 1995).

The ancestral nesting pattern in *Apis* is thought to be the construction of a single exposed comb (MICHENER 1974). The use of enclosed cavities as protection for nests, which permitted geographic expansion into temperate regions, is thought to have necessitated the evolution of enhanced house-cleaning behaviours such as removal of debris and corpses of nestmates (VISSCHER 1988). These behaviours prevent the nest cavity from filling with debris and remove a potential source of disease. The latter function is suggested because corpses are removed 70 times as quickly as common debris of a similar size and shape (VISSCHER 1983).

Most undertakers have a brief tenure of specialization, but a few individuals spend as much as a quarter of their lives performing this task (SAKAGAMI 1953; VISSCHER 1988). Undertaking entails grasping a dead bee in the mandibles, pulling the corpse toward the hive exit, and flying from the hive to drop the corpse (VISSCHER 1983). Early observations of necrophoric behaviour described retinues of guards and 'mourners' attending undertakers; this 'assistance' sometimes includes multiple bees taking flight from the hive with the corpse (HOY 1788). Corpses normally are taken a minimum of 10 m and as much as 100 m from the hive before being dropped, provided the undertaker gains sufficient altitude upon exiting the hive (VISSCHER 1983, 1988).

In this study, we examined a potential benefit (learning) of the necrophoric specialization in honey bees, *Apis mellifera* L., by introducing dead bees into hives and comparing the performance of undertakers with varying corpse-removal experience and by tracking the performance of individuals as they gain experience. A potential cost (task interference) was assessed by comparing the performance of single individuals vs. 'teams'. Corpse removal provides a good model for examining the efficiencies of a hive specialization because of the longer tenure of a small group of specialists and the ability to quantify task performance.

Methods

Experiment 1 – Learning

Honey bee colonies were maintained according to standard techniques at the University of Illinois Bee Research Facility, Urbana, Illinois. Bees were typical of North American populations of *Apis mellifera* [a mix of predominantly European subspecies (PHILLIPS 1915; PELLET 1938)]. Three weeks before the initiation of experimental trials, colony 1 was established in an 8-frame observation hive by transferring a queen, brood frames, drones, and workers of mixed age from a field colony. To increase the likelihood of monitoring a small group of undertakers employed in their specialty for a number of days and to reduce the number of naturally occurring corpses, the size of the colony was kept relatively small (about 4500 as estimated by counting bees in a sample of quadrants). The experimental trials were conducted in the fall when the effects of colony age demography are expected to slow rates of behavioural development (HUANG & ROBINSON 1995, 1996). Workers that were not transferred to the observation hive were narcotized with CO_2 and immediately frozen for use as corpses. The observation hive was connected to the outside wall by a ramp (40 × 12 cm) covered by removable plexiglass sections. This permitted direct observation of undertakers pulling corpses toward the exit and provided access for experimental removal and reintroduction of bees.

To increase the likelihood of observing bees early in their corpse-removal career, the following procedure was employed. During a two-day pre-experimental period, more than 100 dead bees were placed into the hive. Workers that carried a dead bee at least 20 cm toward the hive exit were caught, tagged on the thorax with a numbered disk, and then reintroduced into the hive. Of 24 bees tagged as an undertaker during the pre-experimental period, only 3 continued their undertaking career during the experiment. Thus, it was possible to follow untagged bees (n = 61) that were observed to begin and complete their corpse-removal career during the experiment (previous work demonstrated that, in the absence of inclement weather, undertakers are unlikely to stop and then restart corpse removal after a two-day hiatus; TRUMBO et al. 1997).

Experimental learning trials were conducted during two sessions per day from 30 Sep. until 7 Oct., and again from 12 to 14 Oct. 1992 (undertakers were not active from 8 to 11 Oct. because of inclement weather). Each session consisted of the placement of up to 20 dead workers, one at a time, on the ramp at the point closest to the hive body. The performance of undertakers was measured as the time from the movement of a dead bee at least 5 cm from its original point of placement until the dead bee was carried across a line 20 cm away toward the hive exit. The requirement that a dead bee had to be moved at least 5 cm before recording began eliminated the inclusion of observations of bees licking, antennating, and briefly tugging on corpses (VISSCHER 1983). Undertakers that moved a corpse 5 cm from its placement point but were not successful in carrying the corpse 20 cm were scored as dropping the corpse. When an untagged undertaker successfully crossed the 20 cm line, its performance was first recorded and then it was caught, tagged, and reintroduced into the hive. Observation periods varied from 21 to 68 min depending on undertaking activity and the number of untagged undertakers that were handled. Because the hive was not monitored continually, these untagged bees may have acquired some corpse-removal experience before or between trials. For statistical comparisons, undertakers that removed at least three corpses in their lifetime (n = 19) were considered 'active'.

Experiment 2 – Interference: Single vs. Multiple Undertakers

Eleven colonies of honey bees were screened for undertaking activity during early May 1993 by placing 50–75 dead bees into the rear of the hive body. In 9 colonies, dead bees were removed within a few min. Two of these 9 colonies were selected randomly for the experiments. Colonies were then transferred to 8-frame observation hives at least 3 wk prior to experimental trials. Hive density was estimated to be 6000–9000 bees. An inner ramp connected the hive body to an outside wall. An outer ramp (colony 2: 9 × 12 cm; colony 3: 7 × 12 cm) covered with plexiglass forced bees to walk a short distance before being able to fly. Beginning on 24 May, dead workers were introduced, one at a time, on the inner ramp. The time required for undertakers to carry a corpse the last 9 cm (colony 2) or 7 cm (colony 3) was recorded by observing the movement of undertakers beneath the plexiglass cover on the outer ramp. The number of undertakers pulling the corpse toward the hive exit was noted. The undertaker(s) then were followed visually as they flew from the hive, and their success in carrying the corpse over a 2.65 m high fence that surrounded the hives was recorded (hive exits were 1.02 m off the ground). If undertakers never reached the fence with the corpse, the distance from the hive exit to the drop point was measured. These colonies also were used to study other aspects of undertaking behaviour (TRUMBO et al. 1997).

Results

Experiment 1 – Learning

The times required for undertakers to move dead bees 20 cm toward the hive exit varied widely (5.6–207.0 s) in colony 1 and were not distributed normally. Log-transformed data and non-parametric tests therefore were employed to analyse the times for observed corpse-removal attempts 1, 2–3, 4–5, 6–8, 9–12, and 13–19. The association between removal time and number of removals was significant ($F_{5,230} = 2.81$, $p = 0.02$; regression of log-transformed data; Fig. 1a). It is clear from the median scores in Fig. 1(a) that most of the apparent improvement was between the first and later removals. A comparison of first

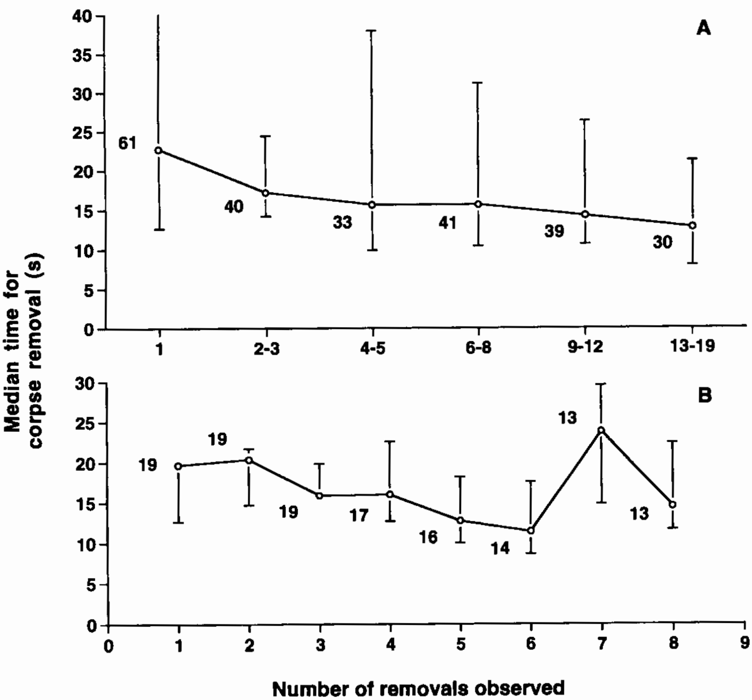

Fig. 1: Median times to remove corpses as a function of number of attempts observed for all undertakers (A), and for active undertakers (B) (at least three corpses removed during observations). The range delimits the middle 50% of corpse removal times. Sample sizes are shown adjacent to the median points (note that sample sizes do not decline uniformly along the abscissa in (A) because data from greater numbers of trials were combined for analysis)

with all other removals was highly significant ($p < 0.001$, Mann–Whitney U-test). The result is quite different, however, if data from only active undertakers (at least three corpse removals) are used in the analysis. In this case, no improvement with experience is indicated ($F_{4,178} = 1.84$, $p > 0.10$; Fig. 1b). In addition, times for later corpse removals are not significantly faster than removal times for first corpses ($p > 0.20$, Mann–Whitney U-test).

As an additional test of experience, pairwise comparisons were made during each session of the first less experienced (never observed to have removed a corpse) and experienced undertaker and the last less experienced and experienced undertaker (n = 36 pairs, Wilcoxon's matched pairs signed ranks test). This analysis eliminated variation in performance that may be caused by daily changes in general activity levels (the interval between a paired less experienced and experienced undertaker was never greater than 11 min). Experienced undertakers again were found to remove corpses significantly faster than first-observed undertakers ($p = 0.01$; Fig. 2).

Combining all trials, less experienced bees failed to complete a removal (movement of a corpse > 5 cm but < 20 cm) during 14.3% of attempts (n = 63) while experienced bees failed during only 5.5% of attempts (n = 128) ($p = 0.052$, Fisher's exact two-tailed test).

During learning trials, there was a single highly active undertaker (Yellow 54) responsible for the removal of 114 corpses (33.8% of the total corpses introduced into the hive). Yellow 54 was active for 8 consecutive days between 30 Sep. and 7 Oct. and again on 12 Oct. (a 13-day undertaker career; Yellow 54 was not observed to remove corpses during the 2-day pre-experimental tagging period). During her most active period (1–7 Oct.), Yellow 54 was responsible for nearly half of the corpse removals (109 of 235). Yellow 54 was significantly faster at removing corpses than other experienced bees (median time of 12.2 vs. 15.8 s, $p < 0.01$, Mann–Whitney U-test, first removals excluded from analysis). Yellow 54, however, did not show obvious improvement throughout her own career ($F_{8,100} = 0.65$, $p > 0.20$; Fig. 3).

In addition to Yellow 54, 12 other undertakers removed at least 8 corpses (9 of these

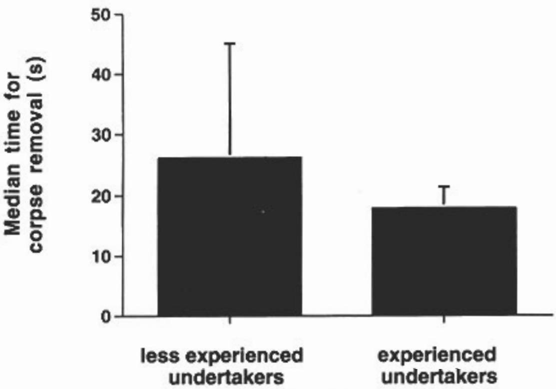

Fig. 2: Median time to remove corpses for 36 pairs of less experienced (untagged workers never previously observed to remove a corpse) and experienced undertakers. Pairwise comparisons of the first less experienced and first experienced undertaker, and the last less experienced and experienced undertaker, were made during each session. Range as in Fig. 1

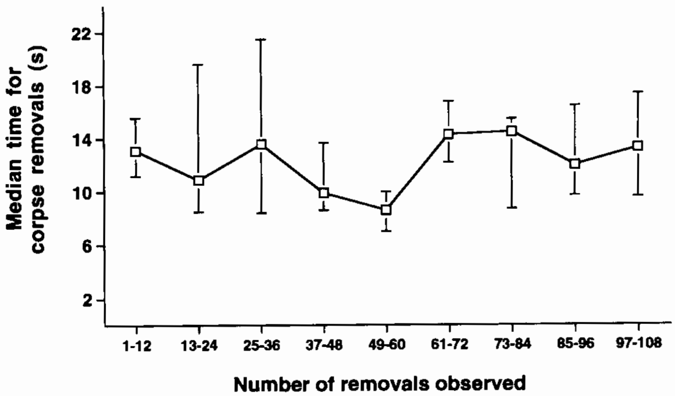

Fig. 3: Median times for bee Yellow 54 to remove the first through the ninth set of 12 observed corpses. Range as in Fig. 1

12 active undertakers were first observed to remove a corpse during the experimental trials, and not during the 2-day pre-experimental tagging period). To examine improvement in each of these individuals, the median score for the first half of all corpse removals was compared with the median score for the second half of corpse removals. Four workers performed better in the first half of removals, 7 were superior in the second half of removals, and there was a single tie (Wilcoxon matched pairs signed ranks test, $p > 0.20$). Performance of the three most active of these undertakers is shown in Fig. 4. It is possible that these analyses might obscure evidence of learning if learning occurs only in the first few corpse-removal attempts and if less experienced bees had undertaking experience prior to the experimental trials or in the intervals between trials. To minimize this bias, a separate analysis was conducted of all bees that were observed to remove more than one corpse, but which were not observed to remove corpses during the initial 2-day tagging period nor during the first 2 d of the experimental trials. Of 13 such identified bees, 6 removed corpses more quickly during removals 2–4 (determined as the median of these three cases) and 7 worked faster in the first attempt (Wilcoxon's matched pairs signed ranks test, $p > 0.20$). It should be noted that while a small number of undertakers was highly active, nearly two-thirds of tagged undertakers were never observed to remove a second dead bee (66%, $n = 61$); this finding is in agreement with three previous studies (SAKAGAMI 1953; VISSCHER 1983; TRUMBO et al. 1997), the last of which followed age-marked bees during their pre-foraging career.

Experiment 2 – Interference: Single vs. Multiple Undertakers

Twenty-one per cent of dead bees in colony 2 ($n = 51$) and 25% of dead bees in colony 3 ($n = 60$) were carried out of the hive by more than one undertaker. Most cases of multiple undertaking involved two individuals (102 of 111). The involvement of more than one undertaker was clearly inefficient as measured by two performance criteria. Single undertakers traversed the outer ramp significantly faster than multiple undertakers in both colonies 2 and 3 (colony 2, $p = 0.007$; colony 3, $p = 0.006$; Mann–Whitney U-tests; Fig. 5).

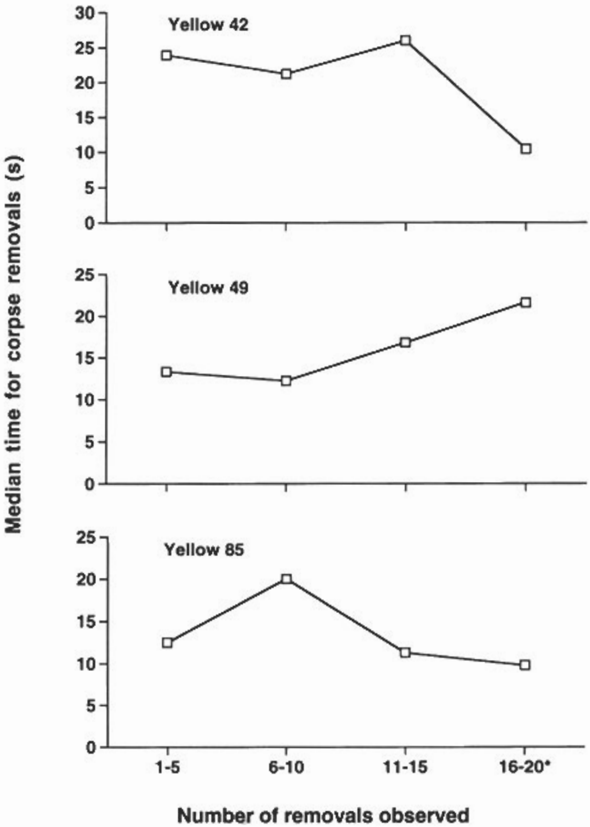

Fig. 4: Median time of corpse removals observed for the 2nd, 3rd and 4th most active undertakers. (*) Yellow 49 and Yellow 85 removed a total of 19 corpses

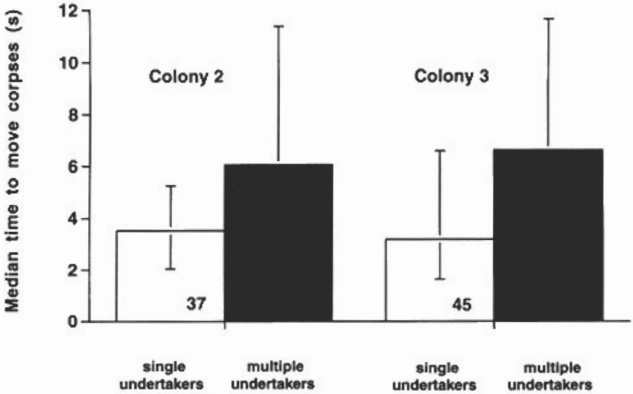

Fig. 5: Median time required by single and multiple undertakers to traverse the ramp for colonies 2 and 3. Range as in Fig. 1. Sample sizes are shown at the base of the bars

Although the times involved were quite brief, the mean time for multiple undertakers to traverse the ramp was more than 75% longer in colony 2 and more than 140% longer in colony 3. The number of undertakers handling the corpse also affected the probability that the corpse would be lifted over and beyond the fence surrounding the hives. Single undertakers were significantly more likely to clear the fence than multiple undertakers (colony 2: 37.8% vs. 0%, $p = 0.006$; colony 3: 62.2% vs. 21.4%, $p = 0.013$; Fisher's exact tests). Combining the data from both colonies reveals that over half the corpses were dropped within 1 m of the hive when carried by multiple undertakers; this was a rare occurrence for single undertakers (59% vs. 9%, 2×2 contingency test, $G = 28.73$, $p < 0.001$).

Discussion

Although students of social insects agree that there are ergonomic advantages associated with having large numbers of workers and division of labour, there is some disagreement over whether individual specializations also make an important contribution to colony efficiency (SEELEY 1982; WILSON 1985; GORDON 1989a,b; VAN DER BLOM 1993). Task specialization might be expected to produce ergonomic benefits through learning, but clear demonstrations of such benefits for nest workers have been rare (but see DOWNING 1992). Because undertakers constitute a small subset of colony workers (1–2%) at any one time (VISSCHER 1983) and their tenure can be quite long (e.g. Yellow 54; also see SAKAGAMI 1953), they are a favourable group for which to measure learning. In this study, experienced undertakers worked faster and were less likely to drop dead bees compared with less experienced individuals. The clearest difference between experienced and less experienced undertakers was between the first and second corpse removals. If learning does occur, it perhaps requires but a few successful acts of securing a dead bee and finding the hive exit. Learning could not be demonstrated to occur progressively over a long series of trials. Because the vast majority of corpses in larger colonies are removed either by naive bees or by bees with considerable experience (VISSCHER 1983; TRUMBO et al. 1997), the benefits that could accrue from learning appear to be small.

It is possible that learning would have been more pronounced if the experience of bees before and between experimental trials could have been taken into account (this would be especially true if learning was focused during the first few trials). Although we cannot rule this out completely, analysis of the subset of bees that became active undertakers only after the experimental trials were well under way suggests that performance did not improve significantly over the first few observed learning trials.

An alternative hypothesis for superior performance of experienced bees is that the most active undertakers worked faster from the outset. If this occurs in the absence of learning, then experienced (more active) individuals should complete tasks more quickly than less active individuals, but active individuals should show no improvement over their careers. The lack of improvement by active undertakers, demonstrated most convincingly by Yellow 54 (114 corpses removed), makes it clear that a difference in talent is a possible explanation for the superior performance of active vs. less active bees. In an intriguing study, CHEN (1937) found that *Camponotus japonicus* workers that moved earth at a greater rate also were the ones that initiated this task more quickly and demonstrated less variation in effort. If behavioural tendencies are strongly biased toward tasks for which individuals are more competent, then specialization would result in clear efficiencies of labour. The possibility that differences in talent contribute to inter-individual variation in behaviour among social insects exhibiting polyethism warrants investigation.

Specializations are known to have potential costs as well as benefits. One recognized cost is that a lack of behavioural flexibility may prevent specialists from moving into tasks that urgently need to be performed (OSTER & WILSON 1978; GORDON 1989a,b). Limited moment-to-moment behavioural flexibility in undertakers appears to exact an additional cost because of mutual interference; too many workers can be committed to the same task at the same time. Multiple undertakers were slower than single undertakers in pulling corpses toward the exit and were more likely to fall immediately to the ground when attempting to fly with a corpse (presumably because of aerodynamic inefficiencies). Thus, undertakers are not effective coordinated teams, unlike army ants that carry large loads (FRANKS 1986), and teams of *Polybia* wasps that effectively partition nest-construction tasks (JEANNE 1986a,b).

In summary, we did not find that learning is an important component of the corpse-removal specialization, but did find support for the hypothesis that too many workers devoted to this task will create inefficiencies. The potential benefits from the learning of hive tasks may be limited owing to the notable flexibility and broad repertoire of pre-foraging bees (TRUMBO et al. 1997), the limited tenure of specialists except in rare workers (SAKAGAMI 1953; MOORE et al. 1987; TRUMBO et al. 1997), and less environmental variation to which to respond (compared with foragers). When accounting for the ergonomic effects of specialization, the benefits of learning must be offset by costs, which in this study consisted of interference with task performance by workers responding to the same stimulus. The hypothesis that consistent behavioural specializations among pre-foragers make a significant contribution to ergonomic efficiency through learning has yet to find widespread support.

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