Stephen T. Trumbo · Zhi-Yong Huang · Gene E. Robinson

Division of labor between undertaker specialists and other middle-aged workers in honey bee colonies

Abstract A primary determinant of colony organization in temporally polyethic insect societies is inter-individual variation in behavior that is independent of worker age. We examined behavioral repertoires, behavioral correlates of adult development, and spatial distributions within the hive to explore the mechanisms that produce behavioral variation among middle-age honey bees (*Apis mellifera*). Individually labeled undertakers, guards, food storers, and wax workers exhibited a broad range of task-related behavior, but bees tagged as undertakers were more likely to subsequently remove a corpse from the hive and handle a corpse compared to other middle-aged bees. The activity level of undertakers was similar to other task groups, suggesting that undertaking specialists were neither hyper-active "elites" nor quiescent "reserves" that become active only when a dead bee stimulus is present. Undertakers also were more likely to remove debris and to remain in the lower region of the hive or near the entrance, even when not engaged in corpse removal; both preferences may promote colony efficiency by reducing inter-task travel times. Guards and undertakers were less likely to perform behavior normally associated with young bees compared to food storers and wax workers. Undertakers and guards also initiated foraging at earlier ages than the other task groups. These results suggest that undertakers and guards may be slightly developmentally advanced compared to food storers and wax workers. There also was evidence for lifetime differences in behavioral preferences which could not be explained by differences in adult development. Bees tagged as undertakers were more likely to subsequently remove a dead bee during their entire pre-foraging career compared to other task groups or members of their general age cohort. Differences in both the rate of adult development and individual behavioral preferences, both of which may be subject to genetic and environmental influences, are important determinants of inter-individual variation among honey bees of middle age.

Key words *Apis mellifera* · Division of labor · Honey bees · Social insects · Ergonomics · Hygienic behaviour

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Introduction

In most species of advanced social insects, workers show "temporal polyethism", performing different sets of tasks at different ages. Young individuals typically work close to the center of the nest, middle-age individuals work in the nest periphery, and older individuals work outside the nest, mainly foraging (Wilson 1971; Michener 1974; Seeley 1985; Winston 1987; Moritz and Southwick 1992). Not all workers in temporal polyethic societies, however, exhibit identical patterns of behavioral development (Jeanne 1988; Lenoir 1987; Robinson and Page 1988). Inter-individual variation among workers of the same age is thus another form of division of labor in insect colonies. The mechanisms and importance of this component of division of labor are less well understood than for temporal polyethism.

Inter-individual behavioral variability is well known in the honey bee, *Apis mellifera*. Differences in rates of behavioral development are apparent; some show precocious behavioral development, while others develop more slowly (reviewed by Robinson 1992; see also Calderone and Page 1991; Giray and Robinson 1994). There also is inter-individual variation in the degree of task specialization at a particular age or stage of behavioral development. For example, food storage, wax

working, guarding the nest entrance, and removing dead bees from the nest are among the tasks performed by middle-aged honey bees, approximately 2–3 weeks of age. However, while food storage and wax working are common tasks, guarding and undertaking are performed by only a small percentage of a colony's workers (Lindauer 1953; Sakagami 1953; Visscher 1983; Moore et al. 1987; Breed et al. 1990).

Highly specialized workers exert profound influences on colonial organization in diverse social insect species, and specialization has been hypothesized to lead to greater ergonomic efficiency (Oster and Wilson 1978; Möglich and Hölldobler 1974; Seeley 1985; Jeanne 1986). Efficiencies resulting from specialization have been well demonstrated for foraging (e.g., Heinrich 1979; Dukas and Visscher 1994) but not for hive workers (but see Downing 1992). Efficiencies might result from: (1) spatial preferences whereby specialists focus their activity in those parts of the hive where they are likely to encounter task-related stimuli; (2) performance of related tasks which require similar sensory and motor abilities; or (3) learning, in which performance improves with repetition. Rare tasks may be performed by highly active "elite" workers that perform all behaviors with greater frequency, by "idiosyncratic" workers with normal activity levels that partially or completely neglect more common tasks, or by "reserves" that are largely inactive in the absence of stimuli associated with rare tasks and come into action only when critical cues are present (Oster and Wilson 1978; Plowright and Plowright 1988). Descriptions of behavioral repertoire, activity level, and spatial preferences are necessary to both distinguish among these possibilities and to suggest how specialization might lead to efficiencies of labor.

We obtained such descriptions for middle-age honey bees, an attractive group to study because a variety of tasks, including undertaking, are performed by workers of the same age at different locations on the nest periphery (Seeley 1982). Undertaking is one component of hygienic behavior in honey bee colonies and is thought to decrease the likelihood of the spread of disease (Visscher 1988). We also used descriptive analyses to gain new insights into the mechanisms that underlie inter-individual variation in behavior in insect colonies. Previous studies of undertakers have suggested the possibility of both long-term and short-term differences in task preferences. In a study demonstrating a genotypic component to undertaking and guarding, Robinson and Page (1988) suggested that there may be genotypic differences in behavioral response thresholds for stimuli eliciting a particular task. The implication of this suggestion is that inter-individual variation in behavior can be caused by stable, perhaps permanent, differences in task preferences due to differences in worker genotype (environmental influences on long-term task preferences are also possible, but have not been demonstrated). Another possibility is that differences in behavioral development rates give rise to short-term differences in task preference. Huang et al. (1994) reported that un-

dertakers and guards have higher blood levels of juvenile hormone than similarly aged bees performing other tasks of middle age. High levels of juvenile hormone are associated with advanced behavioral development in honey bees in other contexts (Robinson et al. 1989). These results suggest that undertaking also can be explained, in part, by short-term differences in task preference associated with a more advanced state of behavioral development (again, due to either genotypic or environmental factors). To study the role played by both short-term and long-term differences in task preference, we followed the behavior of individually identified bees from the first observation of a middle-age task (undertaking, guarding, food storing, wax working), until they began to forage.

We consider four hypotheses for how short-term and long-term behavioral preferences can affect inter-individual variation among middle-aged bees (Table 1):

1. Hypothesis 1: behavioral differences among middle-aged bees are caused by differences in rates of adult behavioral development only. According to this hypothesis lifetime differences in task participation will disappear as workers eventually pass through each stage of development. This could be considered a finer-grained temporal polyethism than is recognized at present.

2. Hypothesis 2: behavioral differences among middle-aged bees are caused by long-term behavioral preferences only. According to this hypothesis, middle-aged bees follow one of several possible career paths, and some tasks are bypassed altogether.

3. Hypothesis 3: behavioral differences among middle-aged bees are caused both by differences in rates of adult development and long-term behavioral preferences.

4. Hypothesis 4: there are no behavioral differences among middle-aged bees (null hypothesis).

We provide evidence that undertaking specialists are neither highly active elites nor an otherwise inactive reserve corps, but rather are truly idiosyncratic relative to other bees of the same age. Moreover, we find evidence to support hypothesis 3: behavioral differences among middle-aged bees are caused both by differences in rates of adult development and long-term behavioral preferences. We also suggest that if the undertaking specialization leads to greater colony efficiency, it is a consequence of strong spatial preferences within the hive and the performance of related behaviors requiring similar abilities.
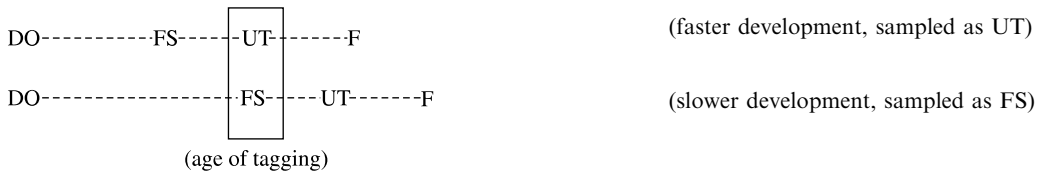
Materials and methods

To describe the organization of behavior among middle-aged honey bees and to explore the above hypotheses, we determined: (1) short- and long-term differences in task-related behavior; (2) differences in rates of behavioral development, by measuring both the likelihood of performing behaviors characteristic of young bees and the age of first foraging; (3) whether bees engaging in undertaking were more likely to perform the related task of debris removal; and (4) differences in spatial distribution within the hive.

Table 1 Four hypotheses to explain behavioral differentiation among middle-aged honey bees. Individuals of the same age that were sampled as undertakers and food storers are used as examples (*UT* undertaker, *FS* food storer, *DO* 1-day-old bee, *F* forager, *P* probability that a member of the subscripted task group will re-move a dead bee subsequent to tagging). The *box* indicates the age at which an individual was sampled and tagged, as well as the 3-day period of observations (*short-term*). *Long-term* refers to the period from tagging until foraging begins

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Hypothesis 1: Differences among middle-aged bees in the tendency to remove corpses are caused solely by differences in the rate of behavioral development.

Short term: $P_{UT} > P_{FS}$
Long term: $P_{UT} = P_{FS} = P_{DO}$

DO----------FS-----┌─UT─┬──────F   (faster development, sampled as UT)

DO----------------┤─FS─┼----UT------F   (slower development, sampled as FS)
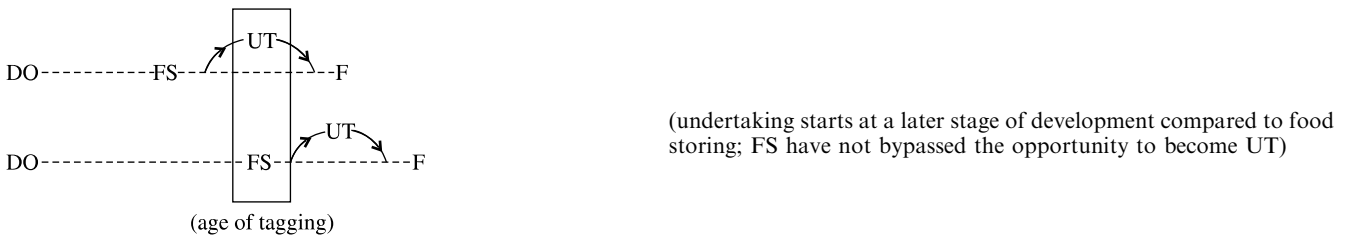
(age of tagging)

Hypothesis 2: Differences among middle-aged bees in the tendency to remove corpses are caused solely by long-term differences in behavioral preferences

Short and long term: $P_{UT} > P_{DO} > P_{FS}$

DO---------------┌─UT─┐-----------F   (UT and FS sampled on different career paths)
                       └─FS─┘

(age of tagging)

Hypothesis 3: Differences among middle-aged bees in the tendency to remove corpses are caused by differences in both the rate of development and long-term behavioral preferences.

Short term: $P_{UT} \gg P_{FS}$
Long term: $P_{UT} > P_{FS} = P_{DO}$

DO----------FS--┌─UT─┬--F

DO----------------┤─FS─┼─UT─┐--F   (undertaking starts at a later stage of development compared to food storing; FS have not bypassed the opportunity to become UT)

(age of tagging)

Hypothesis 4 (null): There are no differences in behavioral tendencies among middle-aged bees. short and long term: $P_{UT} = P_{FS} = P_{DO}$

Experiment 1: Location and behavioral analysis

Observation colonies

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; Pellett 1938)]. All colonies were derived from naturally mated queens.

Eleven colonies, unrelated to one another, were screened for undertaking activity during May 1993 by placing 50–75 dead bees into the rear of the hive body. In nine colonies, dead bees were removed from the hives within a few minutes. Two of these nine colonies, selected randomly, were then transferred from Langstroth hives to 8-frame observation hives (Robinson et al. 1994a). Each observation hive included a 40 × 12 cm horizontal ramp (covered by clear plexiglass) that connected the body of the hive to the outside. This arrangement permitted both undertaking and guarding to be observed readily.

The study was conducted at the time of year when colonies are normally expanding rapidly. Since it is very difficult to observe focal bees in overcrowded observation hives, only portions of the two original colonies were taken, as is usual in studies of this type. Bees of all age groups were taken from all regions of the hive. Observation hives were set up at least 4 weeks prior to the start of observations, ample time for a colony to achieve typical organization. Observation hives were set up with lower than normal population densities so that experimental trials could proceed without having to be interrupted to reduce colony size. Colony populations at the onset of experimental observations were estimated to be 9134 and 6947 for colonies 1 and 2, respectively. Populations were estimated at night by overlaying a 55-section grid over both sides of each of the eight frames, and counting all bees in five randomly selected grid sections. An absolute count was made of bees on the ramp. The hives were arranged so that frames containing uncapped brood were centrally located (sections 4–6; see Fig. 1). Frames containing food were placed in sections 3 and 8, and empty frames were located in sections 1, 2 and 7.

Focal bees

To obtain 1-day-old adult bees for experiments, frames of capped brood were removed from the Langstroth hive and placed in a 33 °C incubator. Over a 4-day period, approximately 1200 l-day-

Fig. 1 Labeling format and contents for the 8 frames (sections 1–8) and ramp (section 9) at the time observation hives were established

1 - empty	2 - empty	
3 - food	4 - brood	
5 - brood	6 - brood	
7 - empty	8 - food	9 (ramp)

Table 2 Behaviors[a] studied (*DVAV* dorso-ventral abdominal vibration)

Stand	DVAV another bee
Walk	Being DVAVed
Head in empty cell	DVAV substrate
Head in egg cell	Chew on hive
Head in larval cell	Fan
Head in honey cell	Festoon
Head in pollen cell	Dry nectar
Clean another bee	Mandibulate honey cell
Being cleaned	Guard
Lateral shake (cleaning dance)	Handle dead bee[b]
Groom self	Undertake[c]
Feed another bee	Remove debris
Being fed	Dance
Attend queen	Follow dance
Wax work	Walk with pollen
Smooth wood	

[a] Detailed descriptions of behaviors provided in Visscher (1983), Kolmes (1985), Seeley (1982) and Robinson (1987)
[b] Lick, antennate or pull on corpse without moving it 5 cm
[c] Moving the corpse at least 5 cm toward the hive exit (this criterion for undertaking differs from that used for assigning workers to task groups because a more rigid criterion for selecting focal bees was desired)

old adult workers from each colony were marked on the posterior dorsal surface of the abdomen with paint (Testor's PLA) and placed into the observation hive corresponding to their colony of origin. When the first paint-marked bees reached 9 days of age, marked food storers, wax workers, undertakers and guards were removed from the hive, chilled briefly, given a second contrasting paint mark on the abdomen, and individually tagged on the thorax with a numbered, colored plastic disk (Opalithplättchen, Chr. Graze KG, Endersbach, Germany).

Undertakers and guards were removed from the hive by lifting the plexiglass which covered the ramp and grasping bees with forceps. Food storers and wax workers were removed by opening one of three glass doors cut into the glass plates which made up the sides of the observation hive. Undertakers were selected based on the criterion of moving an introduced dead bee a minimum of 20 cm toward the hive entrance [many workers respond to olfactory cues from dead bees by stopping, antennating and licking the corpse, but only a small percentage will use their mandibles to grasp an appendage of the corpse and pull it toward the hive entrance (Visscher 1983)]. Guards were identified by their characteristic hunched posture (forelegs lifted) and making contacts with bees entering the hive (Moore et al. 1987); food storers by having their head in a honey cell in the nest periphery for a minimum of 30 s; and wax workers by manipulating wax in the nest periphery for a minimum of 30 s. Food storers, guards, and undertakers were tagged in colony 1, and food storers, wax workers, and undertakers in colony 2. In each colony, 26–34 bees were tagged in each task group. The age at which bees were first observed and tagged performing a designated task did not differ among task groups [colony 1: range, 9–22 days; mean ± SE = 17.1 ± 0.3 days (all task groups combined); colony 2: 9–22 days; 17.2 ± 0.3 days; Ps > 0.20, one-way ANOVAs for pairwise comparisons of task groups within colonies].

Observation techniques

Table 2 lists the behaviors observed. Location and behavioral sampling began on the first day paint-marked bees were selected, tagged and re-introduced into their hive (colony 1: 27 May 1993, colony 2: 1 June 1993). Two daily observations (duration varied with the number of tagged bees monitored) were made between 0900 and 1700 hours. Observations were made daily, regardless of foraging conditions, until 98% of tagged bees began to forage. Prior to each observation period, foraging activity was recorded as light (0–2 bees/min exiting the hive), moderate (3–20 bees/min) or active (> 20 bees/min). Each observation period consisted of three parts: a locational scan, a behavioral scan, and observations subsequent to the introduction of dead bees. Prior to the locational scan, any dead bees on the ramp were removed. The hive was then scanned slowly from top to bottom, on each side, followed by a thorough scan of the ramp and then the hive entrance (from outside). The frame (or ramp) location of all tagged bees was recorded.

Behavioral scans were conducted by starting at the top left corner of the hive and scanning across until a tagged bee was encountered. The first behavior (excluding standing or walking) was recorded. Standing and walking were recorded only if no other behavior was observed within 15 s. We biased observations toward task-related behaviors in this way, since it has been demonstrated that > 50% of unbiased observations are of workers standing or walking (Kolmes 1985). When a worker with a doubly-painted abdomen was observed with its head in a cell (obscuring the

numbered tag on the thorax), the cell was noted by marking the glass wall with a wax pencil. These were re-checked periodically until the tag number and cell contents could be recorded. Cell contents were checked using a narrow-beam light. After all eight frames had been scanned, the opposite side of the observation hive, the ramp, and the hive entrance were scanned, in that order.

At the completion of the behavioral scan, the following procedures were employed to increase the chance of observing undertaking and debris removal. Ten dead bees and several "chalk brood mummies" (larvae killed by the chalk brood fungus, *Ascophaera apis*; Gilliam and Vandenberg 1990), thawed to room temperature, were introduced on the ramp adjacent to the main portion of the hive body. To obtain corpses, bees from both colonies were shaken into plastic bags (at the time colonies were transferred from Langstroth to observation hives), narcotized with CO_2, and immediately frozen. All dead bees were re-introduced into their hive of origin. Chalk brood mummies were obtained from several hives, air-dried, and then frozen. Observations were made of any tagged bees removing corpses, handling corpses, or removing debris (chalk brood mummies or other debris not experimentally introduced into the hive). In addition, to obtain an estimate of the percentage of undertakers from the entire introduced cohort of 1-day-old bees (> 1200), untagged paint-marked-bees that removed a dead bee were caught, marked with a second, contrasting color of paint, and quickly re-introduced into the hive. No further observations of these undertakers were made.

Analyses

The following procedures were employed to analyze the short-term behavioral tendencies and locational preferences of each task group. The number and location of performances of each behavior by each task group in the 3 days following tagging was noted. For each task group the 4 most commonly performed behaviors (based on the number of behavioral acts or number of individuals, exclusive of standing and walking) were identified. For all task groups together there were a total of 7–8 common behaviors (out of a maximum number of 12) because task groups overlapped in the performance of some common behaviors. Differences among task groups in the frequency of performance of these subset of common behaviors were compared using *G*- tests. Long-term differences among task groups in the performance of undertaking were de-

termined by analyzing task-related behavior of tagged bees over their entire pre-foraging career.

Two analyses comparing differences in rates of behavioral development among the task groups were employed. First, we compared the percentage of individuals from each task group that performed behaviors characteristic of younger bees. These behaviors were: attending the queen, head in a cell with an egg, and head in a cell with a larva. Numerous studies have reported that all three of these behaviors are typically associated with younger bees (reviewed by Michener 1974; Seeley 1985; Winston 1987; Moritz and Southwick 1992). Second, we determined when bees made the transition from working in the hive to foraging, which is the most reliable indicator of behavioral development for honey bees (Seeley 1982; Robinson et al. 1989). The age of first foraging in colonies 1 and 2 was recorded as the first day on which dancing, walking with pollen or returning with nectar were observed.

Experiment 2: Determining age of first foraging in additional colonies

Two additional colonies (colonies 3 and 4) were used to further study differences in rates of behavioral development among middle-aged bees. Each colony initially had a population of $\sim$40,000 workers, and occupied two Langstroth hive bodies. Virtually all adult bees emerging over a 6-day period were marked to increase the likelihood of observing known age individuals performing rare tasks such as guarding and undertaking. This was accomplished by reducing the size of each colony by transferring $\sim$20,000 workers of all ages, three or four combs of young, unsealed brood, and the queen to a different one-story Langstroth hive and moving it to a location >7 km away from the original site. Then all (5–6) combs of older, sealed brood from each original colony were transferred to an incubator (33 °C). Workers that emerged from these combs over each subsequent 24-h period were marked on the dorsal surface of the thorax with a spot of paint (Testor's PLA) and reintroduced to their reduced, natal, colony. Approximately 6000 bees per colony were marked, at a rate of $\sim$1000 bees per day. Observations of guards and undertakers began when bees were 10 days old (corpses were introduced as described above). Guards and undertakers were collected, cooled on ice, tagged for individual identification (see above), and then returned to their hive, a process that took 20–40 min. A sample of food storers, age-matched with the undertakers and guards, was collected from the hive interior, and treated the same way. In each colony, the age of tagged bees in the three task groups did not differ (Ps > 0.20, one-way ANO-VAs).

To determine age at first foraging, observations of workers returning to the hive entrance were made each day for 1–2 h. Hive entrances were blocked with a mesh screen. Bees returning with pollen or with a distended abdomen were categorized as foragers.

Experiment 3: Frequency and tenure of undertaking

In experiment 1 individuals were identified as undertakers (tagged and/or given a second contrasting paint mark) from among a large cohort (>1200). This experiment provided minimal estimates of participation and tenure of undertaking; many individuals were undoubtedly identified as undertakers during the middle to latter portion of their undertaking career, and some undertakers may have been missed altogether. A follow-up experiment (experiment 3), was therefore, conducted. A smaller cohort of introduced one day-old bees was followed more closely, thereby obtaining more accurate estimates of participation and tenure of undertaking. Ten days after the final behavioral observations were made in experiment 1, frames of capped brood were removed from observation hives and placed into the incubator. Each observation hive was reduced to four frames, again with bees of all ages, and with a population density of bees approximately the same as in experiment 1. This time, only 158 (colony 1) or 212 (colony 2) 1-day-old workers were paint-marked on the abdomen, individually tagged on the thorax, and introduced

into their hive of origin. Beginning 7 days later, brief observational scans of wax working and undertaking were made four times a day. Clumps of wax collected from the inside walls of the observation hive were added to the comb surface daily to induce wax working. Twice per day, 20 dead bees were placed on the ramp at the closest point to the main hive body and observations of undertaking were made as described earlier. Observations continued until 98% of tagged bees began to forage. Estimates were obtained of the percentage of this tagged cohort that worked wax or that became undertakers, and of the tenure of undertaking.

Experiment 4: Undertaking and debris removal

To further examine the possible association between undertaking and debris removal, a two-frame observation hive containing approximately 3000 bees was established from a different field colony in May 1992 (colony 5). Undertakers, guards, and food storers of unknown age were identified, tagged and re-introduced into the colony at two different times (June, $n = 28$ undertakers, $n = 20$ guards, $n = 27$ food storers; September, $n = 39$ undertakers, $n = 17$ guards, $n = 26$ food storers). During the 3 days following tagging, wood chips, small sections of straw, and chalk brood mummies were placed on the ramp twice a day and observations were made of removal of this as well as naturally occurring debris.
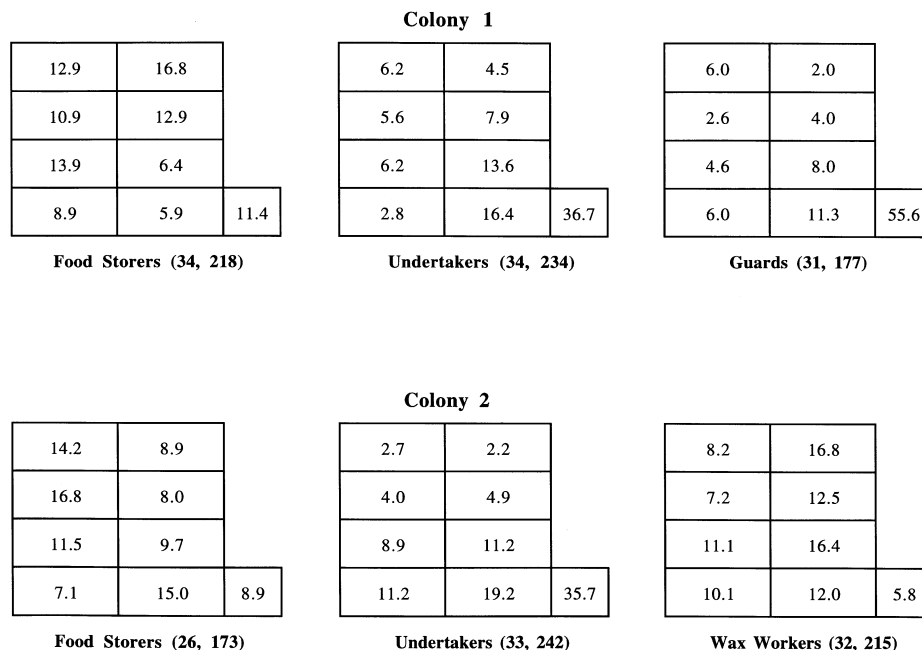
All statistical analyses employed SYSTAT (1992) unless specified otherwise.

Results

Spatial distribution of undertakers, guards, food storers, and wax workers

The percentage of observations occurring in each of the nine sections of the hive (eight frames and the ramp) is shown for each task group during the 3 days following tagging in experiment 1 (Fig. 2). Middle-aged bees were not strictly confined to a particular location within the hive. While undertakers (and guards) were located preferentially in the lower hive (bottom two frames and the ramp), only a small percentage of undertakers were observed exclusively in the lower hive (hive 1, 6 of 34; hive 2, 3 of 33). To eliminate bias based on unequal observations of individuals, locational information for each individual was weighted equally as follows: each tagged bee was scored as either more commonly observed in the "upper" (topmost six frames) or "lower" hive (lower two frames or ramp). Over half of the tagged undertakers in colony 1 were observed more frequently in the lower hive, which was significantly different from the distribution of food storers (Fig. 3). Undertakers and guards had a similar spatial distribution. In colony 2, over 90% of undertakers were observed more frequently in the lower hive, a pattern significantly different from food storers and wax workers (Fig. 3). It is clear that in the 3 days following their initial observation as undertakers, guards, food storers and wax workers, individuals from these groups were distributed differently within the hive. Moreover, this difference occurred in the absence of the primary stimulus for undertaking since dead bees were removed from the ramp prior to locational scans.

Fig. 2 Percentage of observations during location scans that occurred in each of the 9 sections of the hive for each task group during the 3 days following tagging. Observations from both sides of each frame were summed. Task groups had significantly different spatial distributions (colony 1, $G = 86.33$, $P < 0.001$, 16 df; colony 2, $G = 84.43$, $P < 0.001$, 16 df; 3×9 G-tests). The number of individuals observed and the total number of locational observations for each task group are shown in parentheses, respectively

Colony 1

12.9	16.8
10.9	12.9
13.9	6.4
8.9	5.9	11.4

Food Storers (34, 218)

6.2	4.5
5.6	7.9
6.2	13.6
2.8	16.4	36.7

Undertakers (34, 234)

6.0	2.0
2.6	4.0
4.6	8.0
6.0	11.3	55.6

Guards (31, 177)

Colony 2

14.2	8.9
16.8	8.0
11.5	9.7
7.1	15.0	8.9

Food Storers (26, 173)

2.7	2.2
4.0	4.9
8.9	11.2
11.2	19.2	35.7

Undertakers (33, 242)

8.2	16.8
7.2	12.5
11.1	16.4
10.1	12.0	5.8

Wax Workers (32, 215)

If a worker's location within the hive is correlated with a tendency to perform a task, then we might expect a change in location preference concurrent with a change in task preference. To examine this possibility, the location preferences of food storers and wax workers that removed a dead bee at a later point in their career were analyzed. A significantly greater proportion of individuals in these subgroups demonstrated a preference for the lower part of the hive during the 3 days following their first removal of a dead bee compared to other task group members during the 3 days immediately following tagging [colony 1, food storers: $P = 0.048$ ($n = 6$, 34); colony 2, food storers: $P = 0.021$ ($n = 8$, 26); wax workers: $P = 0.029$ ($n = 8$, 32); Fisher's exact tests]. In fact, the spatial distribution of

food storers and wax workers following removal of a corpse did not differ from the short-term distribution of bees originally tagged as undertakers (colonies 1 and 2, $Ps > 0.20$). These results, though based on small samples, suggest that food storers and wax workers changed their distribution within the hive coincident with the onset of undertaking.

Differences in behavioral repertoires of undertakers, guards, food storers, and wax workers

The percentage breakdown of each of the task-related behaviors during the short-term (3 days following tagging) is shown in Fig. 4 A and B. The number of tagged undertakers which were observed to remove at least one dead bee during this period was greater than for food storers ($P = 0.004$) and guards ($P = 0.001$) in colony 1, and food storers ($P = 0.007$) and wax workers ($P = 0.004$; Fisher's exact tests) in colony 2. In both colonies, undertakers were 6 times more likely to subsequently remove at least one dead bee than were individuals of other task groups; the null hypothesis (hypothesis 4) was clearly not supported.

Further comparisons of short-term behavioral repertoires were made by examining the performance of common behaviors (see Methods for details). There were significant differences among task groups in the frequency with which these behaviors were performed (colony 1: $G = 66.5$, $P < 0.001$, 12 df; colony 2: $G = 54.3$, $P < 0.001$, 12 df; 3×7 G- tests). These differences cannot be explained by unequal number of observations of individuals because the number of individuals which engaged in these behaviors also differed significantly among task groups (Table 3).
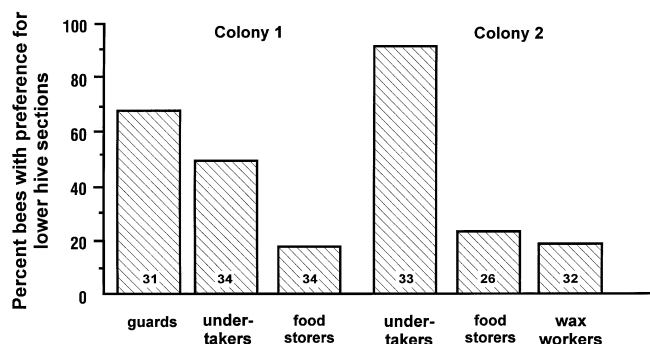

Fig. 3 Percentage of bees from each task group observed in the lower part of the hive (lower two frames and ramp) in more than half of the observations during the 3 days following tagging in colonies 1 and 2. Pairwise tests: colony 1, undertaker vs. food storer $P = 0.004$, undertaker vs. guard, $P > 0.20$; colony 2, undertaker vs. food storer, $P = 0.008$, undertaker vs. wax worker, $P < 0.001$; Fisher's exact tests, 1 df. Sample sizes shown at the base of the bars

Fig. 4 Percentage of observations of each task-related behavior during the 3 days following tagging for undertakers, guards, food storers and wax workers in **A** colony 1 and **B** colony 2. The *dashed lines* separate behaviors typically associated with young bees, middle-aged bees, old bees, and those that are largely age-independent, respectively, from top to bottom. The number of bees observed and the total number of observations of task-related behaviors for each task group are shown in *parentheses*, respectively
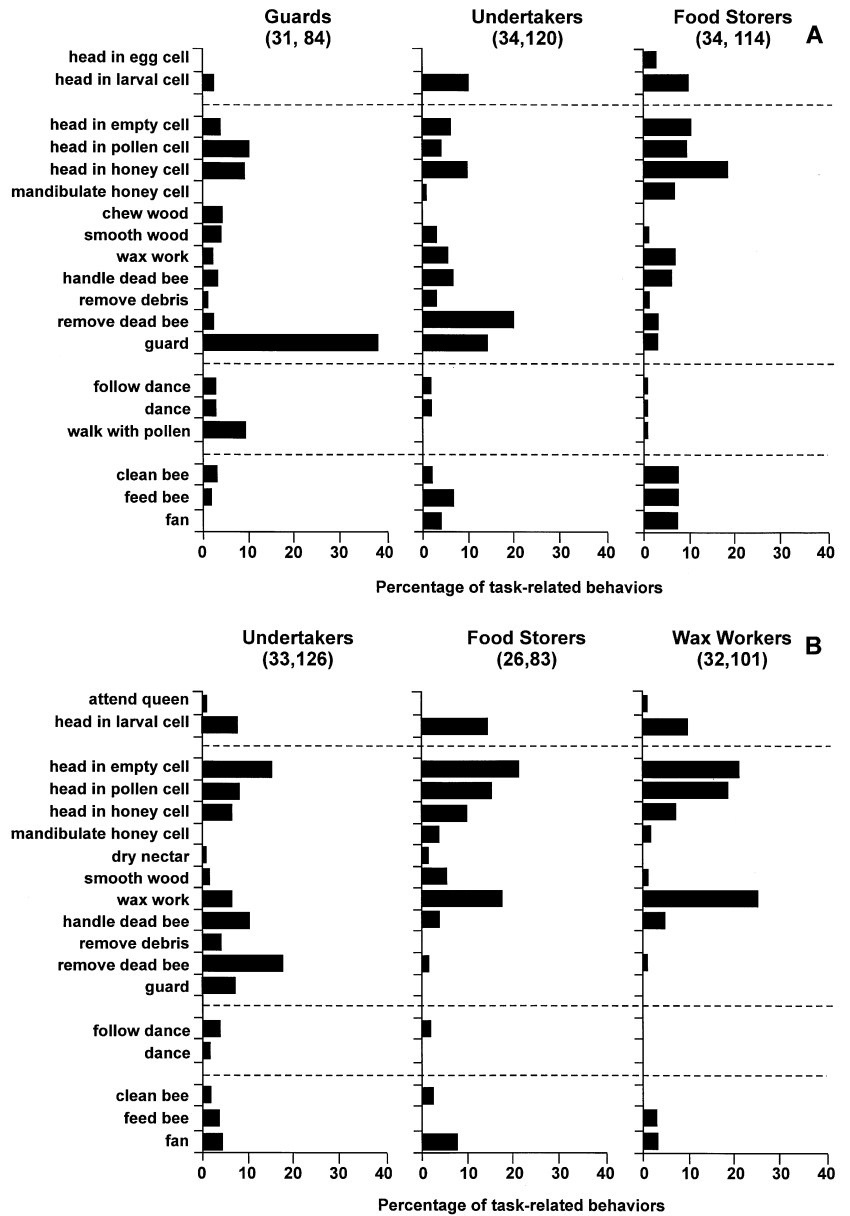
Table 3 Number of individuals of each task group that engaged in the most common behaviors[a] during the 3 days following tagging (*GD* guard, *UT* undertaker, *FS* food storer, *WW* wax worker)

Task group (n)	Behaviors – Colony 1						
	Guard	Remove dead bee	Being fed	Head in empty cell	Head in larval cell	Head in pollen cell	Head in honey cell
GD (31)	18	2	10	3	2	7	7
UT (34)	12	14	13	6	7	4	8
FS (34)	2	3	7	10	7	6	14
	$G = 46.7$, $P < 0.001$, 12 *df*, 3×7 *G*-test						

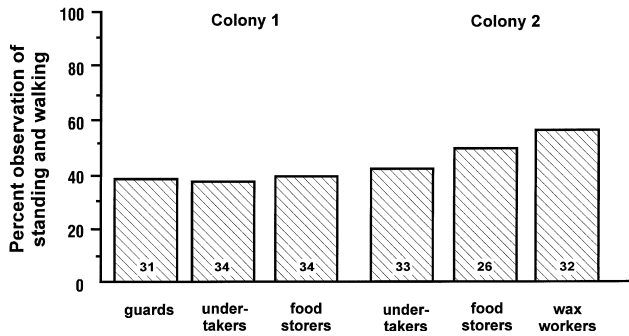| Task group (n)	Behaviors – Colony 2						
	Guard	Remove dead bee	Being fed	Head in empty cell	Head in larval cell	Head in pollen cell	Wax work	Handle dead bee
UT (33)	8	10	10	11	6	10	7	10
FS (26)	0	1	4	12	9	9	9	2
WW (32)	0	1	5	15	8	15	15	5
	$G = 36.6$, $P < 0.001$, 14 *df*, 3×8 *G*-test							

[a]Selection criteria for behaviors in text

Fig. 5 Percentage of observations of standing or walking for each task group during the 3 days following tagging. The number of individuals observed is shown at the *base of each bar*. Colony 1, $G = 0.14$, $P > 0.20$, colony 2, $G = 1.97$, $P > 0.20$; 3×2 G-tests, 2 df

Fig. 6 Percentage of bees that performed one of three behaviors typically associated with young bees (attend queen, head in egg cell, head in larval cell) during their pre-foraging career as a function of task group (G) and tagging date (D) (*open bars* bees tagged prior to 5 June 1993, *solid bars* bees tagged on or after 5 June 1993). Colony 1, $G_G = 10.12$, $P < 0.01$, 2 df, $G_D = 4.88$, $P < 0.05$, 1 df; colony 2, $G_G = 5.92$, $P = 0.06$, 2 df, $G_D = 5.46$, $P < 0.02$, 1 df. $G \times D$ interactions ns, $Ps > 0.20$ (3-way contingency tests, Sokal and Rohlf 1969). Sample sizes are shown at the base of the bars

Activity levels of undertakers, guards, food storers, and wax workers

If specialists like undertakers are elites (more active than other middle-age bees) or reserves (less active), we would expect to see differences in activity levels between undertakers and other task groups. There were no differences among task groups in the mean number of observed behavioral acts per individual in experiment 1 (colony 1, $F_{2,94} = 1.00$, $P > 0.20$; colony 2, $F_{2,88} = 2.27$, $P > 0.10$; one-way ANOVAs), nor in the mean number of task-related behavioral acts per individual (colony 1, $F_{2,94} = 1.50$, $P > 0.20$; colony 2, $F_{2,88} = 1.50$, $P > 0.20$) during the 3 days following tagging. In addition, the proportion of observations of standing or walking did not differ among task groups in either colony (Fig. 5). Since focal bees had both thorax and abdomen marks, bees from all task groups were observed with equal probability even if they were inside cells (Seeley and Kolmes 1989). Thus, the increased performance of a few behavioral categories (removing dead bees, handling dead bees, removing debris) by undertakers was not accompanied by increased activity. Inspection of Table 3 and Fig. 4 demonstrates that this was accomplished by the reduction, but rarely the total elimination, of most other behaviors.

Rates of behavioral development for undertakers, guards, food storers, and wax workers

Differences in undertaking activity of middle-aged bees in the absence of differences in rates of behavioral development would constitute support for hypothesis 2 (Table 1). In experiment 1, there were weak differences among task groups in the likelihood of performing behaviors characteristic of young bees (Fig. 6). In colony 2 there was a significant difference in the percentage of undertakers and food storers that were observed to engage in tasks associated with young bees ($P = 0.03$, Fisher's exact test). One explanation of why greater differences among task groups were not present was that
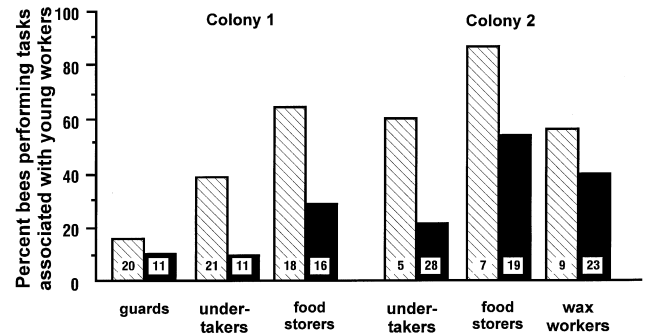
the probability of performing behaviors characteristic of young bees changed during the course of the experiment across all task groups. Of bees tagged prior to 5 June 46% exhibited one of these behaviors compared with 31% tagged on or after this date. This change appears to be related to changes in colony foraging activity. From the onset of behavioral observations through 4 June, only 24% of sampling periods had active foraging compared to 80% of sampling periods after this date. Cool, cloudy conditions and reduced foraging activity prior to 5 June were correlated with middle-aged bees performing more tasks normally associated with young workers. Increased presence of foragers in the hive may have exposed middle-aged bees to higher levels of an inhibitor of behavioral development, as suggested by the results of Huang and Robinson (1992, 1996). These factors may have obscured task group differences because individuals were tagged continuously during this entire period. When tagging date and task group were incorporated into one analysis, both factors were shown to affect the likelihood of performing behaviors characteristic of young bees (Fig. 6).

More robust evidence for differences among task groups in rates of adult development is provided by analysis of the age of first foraging in both experiments 1 (colonies 1 and 2) and 2 (colonies 3 and 4). Undertakers and guards started foraging at younger ages than the other middle-age task groups. Task group had a significant effect on age of first foraging in the three colonies (1, 3, and 4) in which both guards and undertakers were present (Fig. 7; two-way ANOVA, $F_{2,234\text{[task group]}} = 6.26$, $P = 0.002$, $F_{2,234 \text{[colony]}} = 6.37$, $P = 0.002$, $F_{4,234 \text{[task group} \times \text{colony]}} = 0.65$, $P > 0.20$). In colony 2 (no guards), undertakers initiated foraging significantly sooner than food storers and wax workers combined [$P < 0.01$, one-way ANOVA; no differences between food storers and wax workers ($P > 0.20$)]. These results suggest that undertakers and guards are
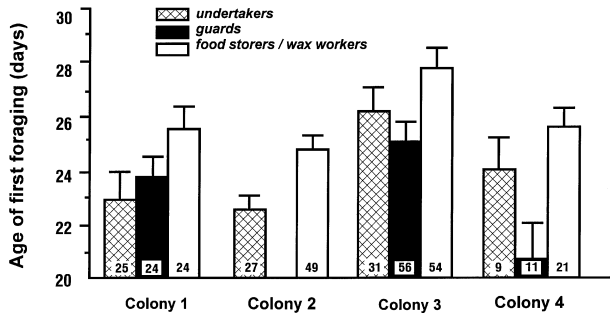
Fig. 7 Mean (±SE) age at which foraging began for undertakers, guards and food storers/wax workers. Sample sizes are shown at the *base of the bars*. Statistical analyses in text

somewhat developmentally advanced compared to food storers and wax workers. Thus, hypothesis 2 (differences among middle-aged bees are not due to differences in rates of development but are solely due to long-term behavioral preferences) was not supported.

Long-term behavioral tendencies of undertakers, guards, food storers, and wax workers

Are differences in rates of development the only cause of behavioral variation among middle-aged bees (hypothesis 1)? Or, are there also long-term differences in the tendency to engage in specialized behaviors such as undertaking that would indicate a role for stable differences in response thresholds (hypothesis 3)? If differences in rates of adult development were the sole explanation for behavioral differences among middle-aged bees then we would expect only short-term differences because food storers and wax workers would eventually pass through the developmental stage characteristic of undertaking. Thus, over their lifetime they would be just as likely to remove a dead bee as individuals originally tagged as undertakers (see Table 1). In experiment 1, long-term differences (as measured over the entire pre-foraging career) in the probability of undertaking were not as great as the sixfold short-term difference. During behavioral scans, however, tagged undertakers were still nearly 2.5 times more likely to remove a dead bee prior to foraging as compared to food storers and wax workers (Fig. 8). This does not support hypothesis 1, that behavioral differences among middle-age bees were due solely to differences in rates of development. These results and those described above thus support hypothesis 3, which predicts that short-term differences in behavior will be greater than long-term differences because short-term behavior is affected by developmental rates as well as by lifetime preferences.

Additional support for hypothesis 3 is provided by examining the long-term probability that wax workers and food storers would remove a dead bee. If differences among middle-aged bees were due to long-term behavioral preferences only, the probability that a food storer or wax worker would ever remove a dead bee in its ca-
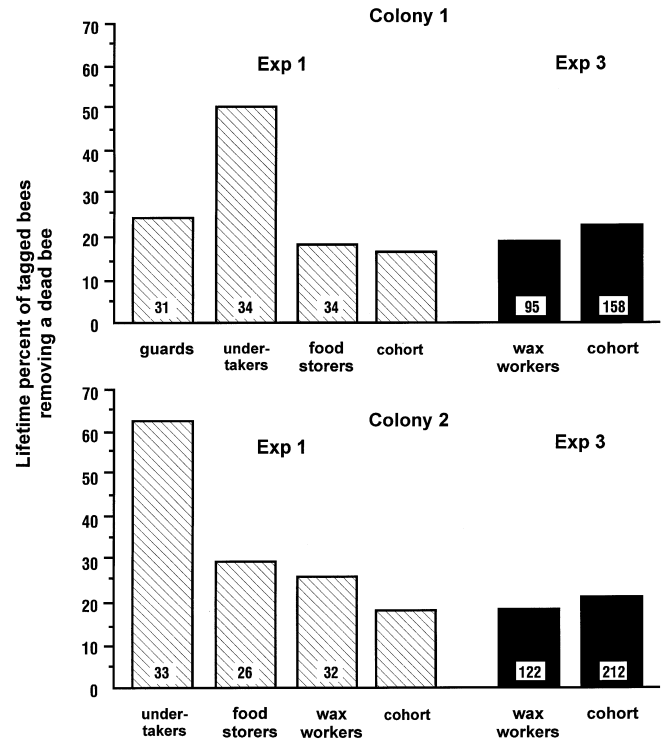

Fig. 8 Percentage of bees in each task group that removed a corpse over the long term (prior to foraging) in colonies 1 and 2. Colony 1, exp. 1: undertaker vs. guard, $P = 0.02$; undertaker vs. food storer, $P < 0.001$; undertaker vs. cohort, $P < 0.001$; colony 2, exp. 1: undertaker vs. food storer, $P < 0.02$; undertaker vs. wax worker, $P = 0.002$; undertaker vs. cohort, $P < 0.001$; Fisher's exact tests. The percentage of wax workers and of the cohort that removed a corpse during their lifetime in experiment 3 is shown for comparison. Sample sizes are shown at the *base of the bars*

reer would be lower than the lifetime probability of undertaking for 1-day-old bees, because middle-aged food storers and wax workers would have bypassed the undertaking career path (hypothesis 2). This was not found. In experiments 1 and 3, food storers and wax workers had the same probability of removing a dead bee prior to foraging as did 1-day-old bees (colonies 1 and 2, experiments 1 and 3, $Ps > 0.20$, pairwise comparisons, Fisher's exact tests, percentages shown in Fig. 8). Thus food storers and wax workers, like 1-day-old bees, had future opportunity to express undertaking, and had not yet demonstrated any behavioral bias toward or away from this specialty.

Ergonomic analysis of the undertaker specialization

If two task-related behaviors are performed in the same location and require similar skills, it should be more efficient for such behaviors to be performed by the same subset of individuals. This hypothesis was examined by studying both undertaking and debris removal, two behaviors which require dragging an object to the hive entrance and taking flight. Even with periodic additions of chalk brood mummies, debris removal was a rare

Table 4 Tenure of undertaking in experiment 3

Number of days observed undertaking	Colony 1 ($n = 158$)	Colony 2 ($n = 212$)
0	123	168
1	23	33
2	4	2
3	1	4
4	2	2
5+	5	3
Mean ($\pm$ SE) tenure of undertaking (excluding 0 s)	2.57 $\pm$ 0.53	1.73 $\pm$ 0.24

event, totaling only 0.8% of the combined behavioral acts of colonies 1 and 2. No individuals were observed to remove more than a single piece of debris from a hive in Experiment 1. Undertakers were more likely to remove debris than other groups of middle-age bees combined during the 3 days following tagging. This difference was significant only for colony 2 (colony 1: 8.8% of undertakers vs. 3.2% of food storers, $P > 0.20$, Fisher's exact tests; colony 2: 15.2% of undertakers vs. 0% of food storers and wax workers, $P < 0.005$).

The association between undertaking and debris removal also was examined in colonies 1 and 2 by following middle-age bees, originally tagged as guards, food storers and wax workers, over their remaining pre-foraging careers. Were those bees that eventually handled and/or removed dead bees the same individuals that removed debris? In colony 1 there were a total of 64 food storers and guards, 19 of which were observed handling or removing a dead bee between tagging and the onset of foraging. This subset of 19 bees was responsible for over half the debris removal by tagged food storers and guards (6 of 11, $P = 0.04$; Fisher's exact tests). The association was even stronger in colony 2. Of 46 tagged food storers and wax workers, 18 handled or removed a dead bee prior to foraging. These 18 bees were responsible for all but one act of debris removal by food storers and wax workers (10 of 11, $P < 0.001$).

Results supporting a short-term association between undertaking and debris removal also were obtained in experiment 4 (colony 5). In the 3 days following tagging, undertakers were the only bees to remove debris in both sets of observations (June: 4 of 28 undertakers vs. 0 of 47 non-undertakers, $P < 0.02$; September: 6 of 39 undertakers vs. 0 of 43 non-undertakers, $P < 0.01$; Fisher's exact tests).

Frequency and tenure of undertaking

In experiment 3 undertaking careers were followed from start to finish without the interruption caused by removal from the hive and tagging in experiment 1. This was accomplished by introducing a cohort of individually tagged one day-old bees (colony 1, $n = 158$,

colony 2, $n = 212$). The number of days each tagged bee participated in undertaking in experiment 3 is shown in Table 4. The majority of undertakers were observed to remove a dead bee on only one day of their lives. As a result, only 36% of the corpses removed in colony 1 and 28.3% of corpses removed from colony 2 were removed by a bee with known undertaking experience. A total of 22.8% and 20.8% of the bees in the tagged cohorts participated in undertaking in colonies 1 and 2, respectively. These estimates were comparable to, but slightly greater than, estimates in Experiment 1 (colony 1, 15.5%, colony 2, 16.9%) in which over 1200 1-day-old bees were introduced and observed for undertaking in each colony.

Discussion

Division of labor in insect colonies is based on polymorphism, temporal polyethism or differentiation among individuals of the same size and age class (Oster and Wilson 1978). The present study demonstrates that behavioral differentiation among middle-age honey bees is clearly present. Relative to other bees of the same age, undertakers exhibited short term differences (during the 3 days after being assigned to a task group) in behavioral repertoire and spatial distribution within the hive, and both short- and long-term differences (over the entire pre-foraging career) in the tendency to remove corpses. The robustness of these behavioral differences is suggested by the fact that we were able to distinguish the behavior of undertakers from other middle-aged bees after simply assigning individuals to task groups based upon a single, "task-group defining" observation.

There was no evidence that undertaking specialists were more or less active than other task groups. Conclusions based on our observations of activity levels should be taken with caution because our sampling procedure was designed to maximize observations of task-related behavior, rather than accurately measure activity levels. Nevertheless, undertakers did not appear to be "elite" workers (Plowright and Plowright 1988) that perform all task-related behaviors more frequently than nestmates, as occurs for example, among specialists of the ant *Tapinoma erraticum* (Meudec 1973). Likewise undertakers did not act like "reserves", individuals that maintain high thresholds for stimuli not associated with their specialty (Robinson 1992), as may occur in honey bee soldiers (Breed et al. 1990). Rather, the undertaking specialization was achieved by an increase in several behavioral categories (removing dead bees, handling dead bees, removing debris), along with reductions in the frequency, but not total elimination, of most other behaviors. The slight modification of the behavioral repertoire of undertakers, along with the brevity of the tenure of some undertakers, is not consistent with the notion of extreme behavioral specialization by subcastes (Oster and Wilson 1978).

Our results suggest that guards, like undertakers, differ from other middle-aged bees in two ways: guards have a locational preference for lower sections of the hive and they are developmentally advanced. Both undertakers and guards were less likely to engage in behavior typical of young bees than food storers and wax workers. Robinson et al. (1992) demonstrated that reversions among honey bee foragers were less common in developmentally advanced individuals, i.e., those with longer foraging careers. Undertakers and guards also initiated foraging at younger ages than food storers and wax workers. It is not possible from our experiments, however, to determine whether advanced behavioral development is a cause or a consequence of undertaking. Since undertakers and guards have higher levels of juvenile hormone than other middle-age bees (Huang et al. 1994), our findings provide additional indirect support that high juvenile hormone blood titer is related to faster behavioral development in adult honey bees (Robinson et al. 1989; Fahrbach and Robinson 1996).

Undertakers could be distinguished from guards based on performance of their behavioral specialty. These results are consistent with Breed et al. (1992) who found that workers removing dead and live bees were from different subpopulations. Differences between undertakers and food storers and wax workers were even more pronounced. Undertakers could be distinguished from these task groups based on both developmental rates as well as lifetime differences in behavioral tendencies. Together, these results suggest that the best explanation for behavioral differentiation among middle-aged bees involves differences in both rates of adult behavioral development and long term behavioral preferences (hypothesis 3). Theoretically, differences in rates of behavioral development and long term tendencies can be influenced by differences in worker genotype or experience. At present, there is evidence for only genetic effects (Frumhoff and Baker 1988; Robinson and Page 1988; Kolmes 1989; Stuart and Page 1991; Calderone and Page 1992; Giray and Robinson 1994; reviewed by Page and Robinson 1992).

Positive feedback models have been proposed as a mechanism promoting specialization in insect societies (Wilson 1971; Deneubourg et al. 1987; Traniello 1987; Plowright and Plowright 1988; Tofts and Franks 1992). Specialization thus could be achieved if an individual chose a task stochastically and then remained in that task as long as the required behavior was performed successfully and the appropriate stimuli were present. Our results suggest that positive feedback is unlikely to account for the undertaking specialty; removing corpses is performed sporadically, is interrupted by bouts of performing unrelated behaviors, and lengthy periods exist when the stimulus is not locally present.

This study also suggests that undertaking is perhaps a less rare specialization than previously recognized. We observed that 22.8% and 20.8% of a cohort removed at least one corpse in colony 1 and 2, respectively. This is higher than the only other published account, the estimate of Visscher (1988) of about 10%. To derive this estimate, Visscher used data from 3 of 15 undertakers observed by Sakagami (1953) that were observed removing corpses on more than one day. Our data suggest that a significant proportion of workers participating in undertaking participate for just 1 day. If we substitute our estimates of mean tenure of undertaking (colony 1: 2.57 days; colony 2: 1.73 days) into the equation used by Visscher, and use his values for all other parameters, we estimate that 19.3–28.6% of workers in Visscher's colonies engaged in undertaking at some point in their lives. This estimate is in general agreement with our results.

Variability in undertaker tenure raises the issue of how to define a specialist in an insect colony (Robinson et al. 1994b). Is any bee that removes even a single corpse an undertaker specialist, or are specialists only those that are more persistent? It is difficult to determine the appropriate time scale for specialization, and current definitions of worker specialization do not specify this parameter (see Oster and Wilson 1978; Calabi and Traniello 1989; Robinson et al. 1994a,b). Although we show that behavioral differentiation is evident even when "one-time" undertakers are included in analyses, perhaps more pronounced differences would emerge if analyses were limited to more persistent individuals. Behavioral studies of individuals that are grouped according to different tenures of undertaking might provide insight into how to define an undertaker specialist.

The ecological success of social insects is thought to be due, in part, to the ergonomic advantages associated with division of labor (Wilson 1985). If worker specialization is a key component of colony fitness (Oster and Wilson 1978), then it must be linked to improved colony performance. To date most demonstrations of colony ergonomic efficiency involve the ability to apply large numbers of individuals to a task, the ability to perform multiple tasks simultaneously, or the partitioning of larger tasks into several smaller ones that are performed repetitively (Jeanne 1986). Each of these advantages, however, can be accomplished by having large numbers of interchangeable non-specialists (Gordon 1989a,b). Direct links between long-term specialization and colony success are rare. On the other hand, behavioral flexibility has been linked convincingly to colony success (Schmid-Hempel 1991). Colonies respond adaptively to changes in age demography (Winston and Fergusson 1985; Huang and Robinson 1992, 1996), changes during the colony life cycle (Oster and Wilson 1978; Robinson et al. 1989), disturbances (Gordon 1989a,b), and changes in resource availability (Visscher and Seeley 1982). Whether task specialization also contributes to colony success is largely undetermined (Oldroyd et al. 1992). The critical tests will be to link task specialization with gains in efficiency.

In this study, two possible ways in which specialization can be correlated with colony efficiency were identified. Undertakers were more likely to be found in the area of the hive where corpse removal is most likely

to be performed, which should reduce inter-task travel time (Wilson 1976; Seeley 1982). Undertakers also were more likely to remove diseased brood, wood chips and straw than other middle-age bees. Performance of different tasks which require similar skills and which are carried out within the same area of the nest should be more efficient than performing random combinations of tasks (Wilson 1976). Removing debris is known to occur after brood rearing and prior to foraging (Rösch 1925; Seeley 1982), which is consistent with the present study. It is unlikely that undertakers removed debris because they could not distinguish between the two sets of stimuli; Visscher (1983) demonstrated that honey bees removed corpses over 70 times faster than debris of similar size, shape, and weight. More direct links between specialization and efficiency have been made for polymorphisms in ants (Wilson 1984) but such studies are rare for polyethic insect societies, especially for individuals working in the nest.

Another manner in which worker specialization can be linked to increased efficiency is through learning. Efficiency gains associated with learning are well documented for foragers (Heinrich 1979; Dukas and Visscher 1994) but sparse information is available for in-hive workers (but see Downing 1992). The brief tenure of most undertakers and guards (Breed et al. 1992) suggests that learning may not be an important component of these specializations (recent work has uncovered little evidence for improvement by undertakers; Trumbo and Robinson, in press). In the future, clearer links between specialization and colony performance will be required to demonstrate whether inter-individual behavioral variation is one key to "the heart of colonial organization" (Oster and Wilson 1978) or is simply a by-product of variation in genotype, experience and stochastic exposure to task-related stimuli.

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