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ORIGINAL PAPER

Within-nest temporal polyethism in the honey bee

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Abstract A well-regulated division of labor has been one of the core adaptations leading to the success of the social insects. Honeybee division of labor has been classically viewed as a sequence of age-related changes in task performance. Kolmes questioned this view arguing that his studies did not support the existence of any age-related within-nest specialization. To resolve this controversy, Kolmes and Seeley conducted a joint study with mixed results. They found support for a cell cleaning caste, but diverged on whether their results supported distinct nursing and middle age castes. In this paper, I follow up on their work to resolve the question of caste number in within-nest honey bees. To determine whether nurses (typically aged 4–12 days) and middle-aged bees (aged 12–20 days) have distinct task repertoires, I conducted focal animal observations on a large number of workers in both age groups working within the same nests at the same time. The results support their being two castes of within-nest bees. Young bees specialized on brood care tasks, while middle-aged bees specialized on nectar processing and nest maintenance. Middle-aged bees were observed caring for brood in less than 1% of the observations. Moreover, both castes exhibited movement patterns that correspond to the traditional view that nurses stay within the broodnest, while middle-aged bees move around a great deal in search of work throughout the nest. A review of studies conducted since the debate of Seeley and Kolmes supports the reliability of these results. This work has relevance for proximate models of temporal polyethism, as it is often assumed by such models that there is only one within-nest caste in the honeybee.

Keywords Temporal polyethism · Division of labor · Task allocation · Honey bees · Social insects

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Introduction

Division of labor in animal groups refers to adaptive biases in task performance. This phenomenon reaches its highest degree of sophistication in large insect societies (Wilson 1971; Michener 1974; Seeley 1995). Here, division of labor takes two forms: a reproductive division of labor between the queen and workers and another amongst the workers for the rest of the colony's tasks (reviewed in Oster and Wilson 1978; Hölldobler and Wilson 1990). Worker division of labor can be further divided into two forms: one based on variation in size, physical castes and the other on variation in age, temporal polyethism (Wilson 1976; Seeley 1982; Wilson and Hölldobler 1988; Page and Robinson 1991; Calderone 1991; Robinson 1992; Jeanne and Nordheim 1996; Huang and Robinson 1996; Calderone and Page 1996; O'Donnell 1998; Johnson 2003, 2005; Tripet and Nonacs 2004; Seid and Traniello 2006). The group level benefits of division of labor, increased productivity, and reliable task performance are thought to be integral to the great ecological success of the social insects (reviewed by Wilson 1987; Bourke and Franks 1995; Wilson and Holldobler 2005).

Honeybee division of labor has been classically viewed as a sequence of age-related changes in task performance (Ribbands 1953; Free 1965; Lindauer 1967; Winston 1987). Workers are thought to be semi-specialists that will

only perform tasks within a limited task repertoire (Seeley 1982). Seeley originally found support for four castes: cell cleaning (ages 1–3 days), nursing (ages 4–12 days), food processing and nest maintenance, called middle age bees, (13–20 days old), and foraging (over 21 days old). Although numerous studies support this view, one set of studies questioned it. Kolmes collected data which he claimed showed that there are no differences in task preference between workers of different ages working within the nest. He concluded that within-nest workers are generalists and that the honeybee only has two castes, the within-nest workers and the foragers (Kolmes 1985, 1986). Seeley, whose work supported the existence of four castes (reviewed in Seeley 1985, 1986), objected to this claim and a debate ensued. This ended with both authors agreeing to conduct a joint study to resolve the issue (Seeley and Kolmes 1991).

Their joint study used methods similar to those in their previous studies, with the exception that both authors conducted simultaneous observations. Two cohorts of bees were introduced into a single observation hive, and scan samples of their behavior over time were conducted. The results clearly supported the existence of a cell cleaning caste. Unfortunately, they ceased their observations too early to determine with complete clarity whether nurses and middle age bees are distinct castes. Seeley concluded they are, while Kolmes concluded they are not. The sticking point was whether a second shift in the behavior they observed was due to the bees switching to foraging or to middle age tasks. In this paper, I follow up on this study to resolve the question of whether there exists a middle age caste of bees distinct from both the nurses and foragers. This study is necessary, as a number of recent theoretical and proximate studies of honeybees have followed Kolmes' interpretation that only one within-nest temporal caste exists (Amdam and Omholt 2003; Amdam et al. 2004; Amdam and Page 2005; Page and Amdam 2007). If this were the case, then it simplifies our task of understanding the proximate basis of temporal polyethism because one need only explain nursing and foraging phases of behavior. If, however, workers are insensitive to brood-related tasks for much of the early part of their life, then it complicates the proximate basis of honeybee division of labor.

Previous temporal polyethism studies have recorded behavior using scan sampling (Seeley 1982; Kolmes 1985; Seeley and Kolmes 1991). This method is ideal for obtaining a first approximation of colony caste structure, but is not well suited for characterizing task repertoires in detail because so little data are taken per bee. For this reason, I chose to use focal animal observations in this study. This method exhaustively documents the behavior of workers over a given period of time. The study is simple in design. Nurses care for the brood, while middle-aged bees are thought to process food and maintain the nest. We know already that foragers do not work within the nest (Rösch 1930; Ribbands 1953; Lindauer 1967; Seeley 1995; Calderone and Johnson 2002; Weidenmuller and Tautz 2002). Thus, if the older within-nest bees, those aged 12–20 days, do not care for brood but work within the nest on other tasks, this will be strong evidence for a middle age caste. To test this prediction, I conducted focal animal observations on workers spanning the age ranges of both castes. The bees were working within the same colonies on the same days, so any differences in their behavior would be the result of differences in the bees and not to changes in task demand.

Materials and methods

Study site and colonies

The experiment was conducted at the Arizona State University Bee Lab in Mesa, Arizona during the months of October and November 2006. Three queen-right colonies of European honeybees (a mixture of *Apis mellifera carniola* and *Apis mellifera caucasia*) containing 5,000–6,000 bees were used. Colonies were housed in four frame observation hives connected, via tubes extending through the wall, to the outdoors where bees were able to forage naturally. A 50×100-cm^2 Plexiglas sheet (the dimensions of the colony surface) divided into 128 grid squares was placed over the face of the colony during all observations. This sheet was used to record the location of the bees. The two grid squares furthest apart within the list of all grid squares visited by a bee were used to determine the straight-line distance a bee traveled during the observation period.

The organization of brood and honey in each colony was standardized for each trial by replacing the frames in each colony a week before the beginning of the experiment. Two frames of open honeycomb (very few empty cells or capped honey cells) were placed into the two top positions of the hive, while a comb of open brood was placed into position three, and a comb of mixed open and closed brood was placed into position four (frame 1 being at the top of the nest, 4 the bottom). This setup allowed me to easily determine when bees had left the broodnest and also minimized the queen laying outside the broodnest. In each trail, I ensured that at least one of the bottom combs had sufficient pollen for a four-frame observation hive.

Focal bees

Frames of emerging brood were taken from unrelated source colonies in the afternoon and kept overnight in an incubator. The next morning, 200 newly emerged bees were individually marked with a tag on their thorax and a paint

mark on their abdomen before being introduced into observation hives. Bees were less than a day old when introduced. Different source colonies were used in each trial.

Two cohorts of bees were used in each trial of the experiment. The introduction of the cohorts was staggered in time so that one cohort would be aged 4 to 8 days while the other would be aged 14–18 days during the observation period. These are thought to be the typical age ranges for bees in the nursing and middle age castes. Each pair of cohorts was composed of bees obtained from combs of brood taken from the same source colony. Thus, variation in genes and environment were controlled for in the study. Each cohort was used in only one trial of the experiment.

Experimental design

Three trials of the experiment were conducted each using a different colony. Each trial lasted 4 days. Focal animal observations were conducted for 4 to 6 h each day beginning at approximately 8 A.M. All identified workers were observed for 20 min or until lost. Each worker's behavioral state and location was continuously recorded by voice onto a digital voice recorder. I started each day by observing a nurse bee and then alternated throughout the day between observations of nurses and middle-aged bees.

Sampling procedure

Previous studies have found that within-nest bees are inactive approximately half of the time, depending on the influx of nectar and the amount of brood in the nest (Seeley and Kolmes 1991). Accordingly, much of the data collected on a random sample of bees are of them standing and grooming and are useless for determining task performance differences. For this reason, I employed two procedures for identifying bees to ensure that sufficient observations of active bees were obtained. Both procedures were identical, except that for the first procedure, I chose the first randomly identified active bee (not standing or grooming), while in the second, I observed the first randomly identified bee. The procedure was as follows. A random number generator was used to produce a list of random numbers. A random number between 1 and 128 was then used to identify a grid square in which to search for a marked bee. If no bee was present, another number was generated and the process replicated. Twenty-five bees in each caste were identified with procedure one, while the remaining bees were identified with procedure two.

Classification of worker behavior

Behaviors were identified as per Johnson (2002), which followed Seeley (1982). The only significant difference between the method I used for identifying tasks and that used by previous researchers is that in cases where a bee was walking and periodically (within 10 s) inspecting cells, I called the behavior "inspect cells" instead of dividing it into two periods of walking and inspecting a cell. I made this decision because workers often walk for long periods without inspecting cells, while instances in which a bee stops every few seconds to inspect cells most likely serve a greater purpose than just movement. Traditionally, researchers have classified such bees as patrollers and assumed they were collecting information (Lindauer 1967). Two tasks: "inspect cell" and "head in brood cell", also require some explanation. "Head in cell" refers to cases where a bee had at least her head, although usually her entire body, in a cell for at least 5 s. "Inspect cell" refers to the numerous cases in which a bee ducked her head into a cell for less than 5 s (typically less than 1 s).

Although some previous studies have attempted to identify the contents of all cells, I chose not to do this for the following reason. Cells containing first instar larvae and cells with eggs can be difficult to distinguish from empty cells or those with a small amount of nectar. This is particularly the case in crowded nests. In all cases where it was at all questionable what a cell contained, I called the relevant behavior either inspect cell or head in cell. As will be shown in the "Results" section, this decision did not affect our ability to interpret the results of the study.

Table 1 Behavior of the focal bees in each caste at the beginning of observations

Task	Nurses	Middle age
Build comb	0	4
Cap brood	11	0
Cap honey	0	2
Chew wood	0	1
Feed brood	19	0
Groom	1	3
Groom other	1	1
Head in cell	1	2
Head in honey cell	0	12
Inspect cell	10	9
Work propolis	0	1
Stand	5	8
Trim brood	5	0
Trim honey	0	3
Trophallaxis	1	1
Walk	1	6
Washboard	0	1
Work wax	1	2
Total	56	56

Statistics

The chi-square test and the Mann–Whitney test were used to test for differences between the behavior of young and middle-aged bees. The tests for differences in task repertoire (Table 2) required numerous comparisons. The Bonferroni procedure was thus employed with the result that a p value of 0.007 was required for significance within that context. The statistical package Minitab was used for all comparisons.

Results

In total, 112 bees were observed for a total of 2,238.3 min. Thirty-six bees were observed in colony 1, 41 in colony 2, and 35 in colony 3. Table 1 shows the task distributions of the bees in each age group when first identified. Most of the nurses were involved in brood care, while the middle-aged bees were involved in more varied tasks. Most of the middle-aged bees either had their head in a nectar cell (part of the nectar receiver task set) or were working wax in some manner. Although the entire colony surface was sampled, all of the nurse bees were initially identified in the brood-zone: 39 on comb 3 and 17 on comb 4. The middle-aged bees were mostly in the honey-zone: 29 on comb 1, 16 on comb 2; however, some were also found in the brood-zone: 4 on comb 3, and 7 on comb 4.

Task repertoires

Table 2 shows the task repertoires of the two age groups of bees. The two tasks most relevant for determining whether middle-aged bees conduct nursing tasks are feeding and capping brood. Middle-aged bees were never observed capping brood and were observed feeding brood at a much lower rate than the nurse bees (Mann–Whitney test: W=2,382.5, N_1=56, N_2=56, P<0.0001). Further comparisons were made for tasks relevant for determining whether the two groups are distinct in task repertoire. Building comb, capping honey cells, trimming honey cells, and wash-boarding were pooled because they all involve working outside the brood-zone. Middle-aged bees performed these tasks at a higher rate than nurses (Mann–Whitney test: W=3,904.5, N_1=56, N_2=56, P<0.0001). Nurses, in fact, were not observed doing any work outside of the broodnest other

Table 2 Task repertoires of nurses and middle-aged bees determined using focal animal observations. Shown are the mean percentages of time spent by workers in each age group on each task and the percentage of bees in each age group observed performing each task at least once

Task	Nurse bees (N=56)			Middle-aged bees (N=56)			Significance
	Mean	SE	% Bees	Mean	SE	% Bees	
Attend queen	0.25	0.18	3.57	0	0	0	
Build comb	0	0	0	4.31	1.8	14.49	*** W=3,563.5, P=0.0001
Cap brood	8.92	2.08	41.1	0	0	0	W=2536.5, P=0.0001
Cap/trim honey	0	0	0	4.76	2.48	30.36	***
Chew wood	0	0	0	0.25	0.13	8.93	
Fan	0.49	0.33	7.14	0.13	0.13	1.79	
Feed brood	8.48	2.27	57.14	0.97	0.37	12.5	W=2382.5, P<0.0001
Follow dancer	0	0	0	0.07	0.07	1.79	
Get groomed	0	0	0	0.92	0.81	7.14	
Get shaken	0.43	0.27	5.36	0.48	0.27	8.93	
Groom	16.86	2.59	76.79	10.29	1.97	73.21	
Groom other	1.73	1.21	3.57	1.5	1.07	5.36	
Head in cell	21.37	3.38	73.21	5.2	1.7	58.92	W=2510.5, P=0.0001
Head in honey cell	0.13	0.13	1.79	1.7	0.6	28.57	
Head in pollen cell	0.18	0.18	1.79	0.09	0.07	3.57	
Inspect cell	12.08	1.6	85.71	16.85	2.33	80.36	W=3332.0, P=0.328
Work propolis	0	0	0	0.63	0.36	5.36	
Stand	9.51	3.37	32.14	13.86	3.33	60.71	
Trim brood	7.46	2.67	28.57	0.71	0.71	1.79	W=3580.0, P=0.0001
Trophallaxis	2.75	0.8	33.93	2.47	0.76	32.14	
Walk	6.57	1.11	69.64	19.87	2.67	80.36	W=3778.0, P=0.0003
Washboard	0	0	0	5.83	1.96	19.64	***
Work wax	3	1.06	23.21	9.2	2.47	46.43	

Data are pooled from all three trials. Tasks in bold text are critical for determining whether the two age groups form distinct temporal castes. Three categories (indicated by the symbol, ***) were pooled for statistical comparison.

than inspecting cells and inserting their heads into pollen cells. Finally, middle-aged bees were observed walking more than nurses (Mann–Whitney test: W=2,550.0, N_1=56, N_2=56, P=0.0003), a subject discussed further in the "Movement rates" section.

Determining how the two castes differ in the tasks "head in cell" and "inspect cell" is difficult using the task data alone. There was no difference in the rate at which bees in each caste inspected cells (Mann–Whitney test: W=3,332.0, N_1=56, N_2=56, P=0.33), while nurses were observed with their heads in cells more often than middle-aged bees (Mann–Whitney test: W=2,510.5, N_1=56, N_2=56, P=0.0001). Head in cell is the category I used whenever I could not determine with complete confidence the contents of a cell. Bees with their bodies completely in cells are cleaning them, unloading into them, feeding from them, or feeding brood within them. Fortunately, we can differentiate between these possibilities by looking at the locations within the nest where each caste performed the behavior. Figure 1a shows this comparison. Nurses more often had their heads in cells in the brood-zone (mostly on comb 4), while the middle-aged bees performed this task mainly in the honey-zone (chi-square test: χ^2=1,290.86, df=3, P<0.001). The middle-aged bees with their heads in cells were probably unloading nectar because most of their observations were on comb 1 which contained no pollen. The nurses with their heads in cells could have been feeding brood, eating pollen, or cleaning cells. Eating pollen is easy to rule out because pollen is clearly visible within cells. Figure 1b shows the distribution of brood feeding locations and head in cell locations, which differed significantly (chi-square test: χ^2=338.18, df=3, P<0.001). Based on this, it is reasonable to conclude that the majority of the nurses with their heads in cells were cleaning them. This would also be in accordance with previous temporal polytheism studies (Seeley 1982; Seeley and Kolmes 1991).

Inspecting cells is a task associated with many behaviors. Nurses inspect brood cells to determine which need feeding. Nectar receivers inspect cells when looking for a place to unload their nectar. Middle-aged bees are thought to inspect cells to determine if they contain pollen that

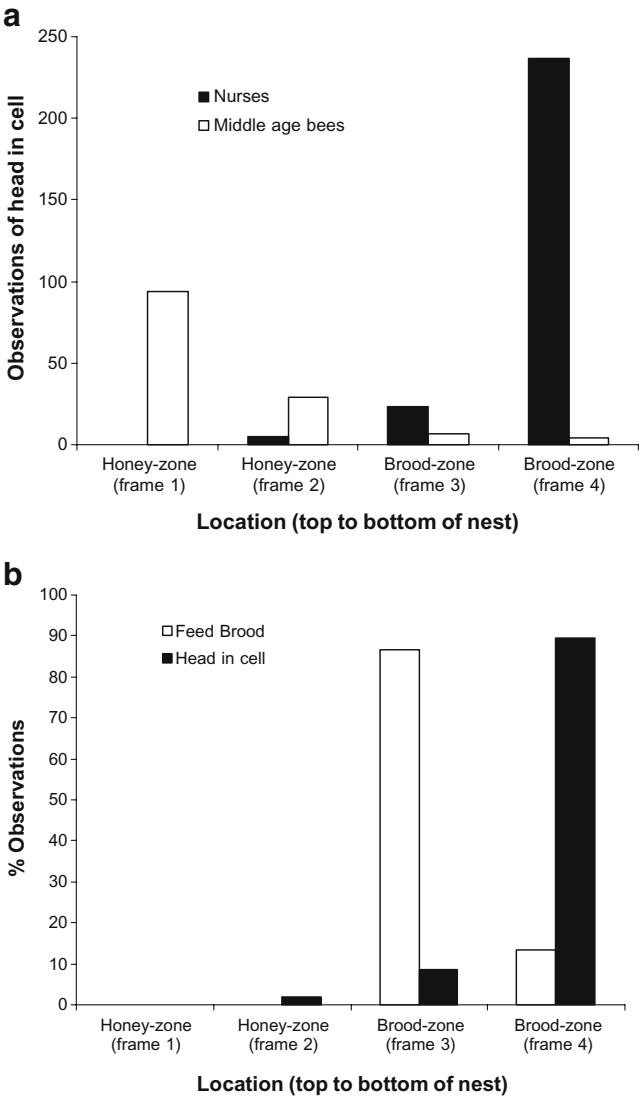

Fig. 1 **a** Distribution within the nest of head in cell events for nurses and middle-aged bees. Nurses performed this task within the brood-zone, locations 3–4, while middle-aged bees were more likely to perform the task within the honey zone, locations 1–2 (chi-square test: χ^2=1,290.86, df=3, P<0.001). **b** Distribution within the nest of head in cell and brood feeding events for nurse bees. There was a significant difference between the locations where head in cell events took place and brood feeding occurred (chi-square test: χ^2=338.18, df=3, P<0.001). This suggests that most of the nurses with their heads in cells were not feeding brood, but were more likely cleaning cells

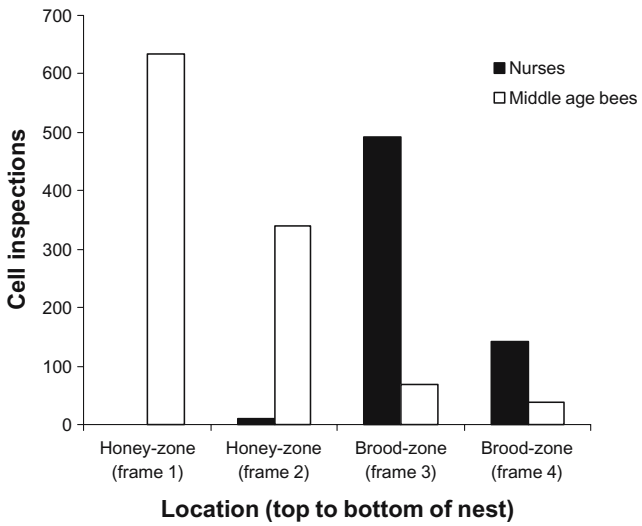

Fig. 2 Distribution within the nest of cell inspections for nurses and middle-aged bees. Nurse bees performed this task within the brood-zone, locations 3–4, while middle-aged bees were more likely to perform the task within the honey zone, locations 1–2 (chi-square test: χ^2=388.18, df=3, P<0.001)

needs packing and possibly just to monitor the colony state. As in the previous case, these tasks do not all occur in the same locations, so we can use this information to determine the most likely purpose of cell inspections. Figure 2 shows the distribution of cell inspections with respect to frame number (1 and 2 being the honey-zone and 3 and 4 the brood-zone). There is very little overlap between the distributions for the two castes. Nurses were more likely to inspect cells in the brood-zone, while middle-aged bees were more likely to inspect in the honey-zone (chi-square test: χ^2=388.18, *df*=3, *P*<0.001). This confirms that nurse bee cell inspections were associated with brood-zone tasks such as feeding brood and cleaning cells, while middle age cell inspections were for purposes other than brood care.

Movement rates

The classic view of temporal polyethism is that nurse bees work within the broodnest and middle-aged bees work everywhere else. Given this, it should be the case that middle-aged bees move farther than nurse bees as they look for work. Figure 3a shows the maximum straight-line distance traveled by nurses and middle-aged bees over the 20 min of observation. Middle-aged bees traveled farther than nurses (Mann–Whitney test: *W*=3970.0, N_1=56, N_2=56, *P*=0.0001). They were also more likely to leave the part of the nest (brood-zone or honey-zone) they were initially observed in (chi-square test: χ^2=11.72, *df*=1, *P*<0.001; Fig. 3b).

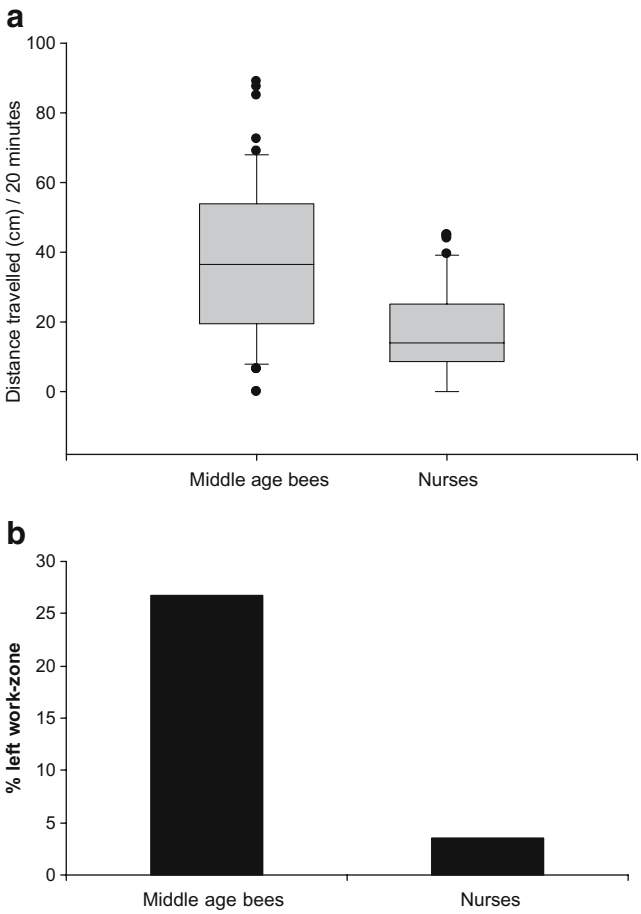

Fig. 3 **a** Maximum straight-line distance traveled over 20 min for nurses and middle-aged bees. Middle-aged bees traveled further than nurses (Mann–Whitney test: *W*=3,970.0, N_1=56, N_2=56, *P*=0.0001). **b** Percentage of workers in each caste that left the work zone (brood-zone or honey-zone) in which they were initially found. Middle-aged bees were more likely to change work zone (chi-square test: χ^2=11.72, *df*=1, *P*<0.001)

Discussion

The honeybee is a model system for studies of organization of work in the social insects. Division of labor within this species is being explored using genetic, developmental, and behavioral approaches (Seeley 1995; Huang and Robinson 1999; Toth and Robinson 2005; Whitfield et al. 2006; Page and Amdam 2007). Several theoretical models also seek to explain the phenomenon (Huang and Robinson 1999; Beshers et al. 2001; Amdam and Omholt 2003). An understanding of the basic pattern of division of labor is thus critical for a wide array of studies. This study resolves a long standing puzzle by showing that nurses and middle age bees are distinct temporal castes. Nurse bees have a small repertoire of tasks limited to the brood-zone. Middle-aged bees have a more varied task repertoire spread out over the entire colony. Middle-aged bees move long distances in search of work and in the course of working, while nurse bees move only short distances. A review of the relevant literature (to follow) strongly supports the reliability of this result, and a discussion of the present studies relevant to proximate studies of temporal polyethism shows its importance.

Several studies have observed both nurses and middle-aged bees in the course of addressing other questions (Seeley 1989; Pratt 1998, Crailsheim et al. 1996; Pfeiffer and Crailsheim 1999). None of the studies observed both castes at once, so a discussion alone would have been insufficient to address the question of caste number, but it is now worthwhile to tally the weight of evidence in favor of two castes of within-nest bees. Seeley (1989) observed 20 nectar receivers for a total of approximately 830 min. He recorded no cases of them performing any brood care tasks. He did, however, observe them performing typical middle age tasks such as shaping honey storage comb. Pratt (1998) observed a group of bees he initially identified building comb at the top of the nest for 500 min and only observed them involved in brood care 1.7% of the time. In addition, all of the temporal polyethism studies using scan sampling, except that of Kolmes which we now know used faulty methods, support the existence of a middle age caste

(reviewed in Winston 1987; Seeley 1995). Studies of nurse bees have always shown them to be specialized for their task and to rarely perform other work (Crailsheim et al. 1996; Pfeiffer and Crailsheim 1999). Taking these studies together, and including the absence of experimental evidence to the contrary, it is clear that nurses and middle age bees form two castes. These castes show almost no overlap in their primary task responsibilities of brood care and food processing. In every focal animal study to date, brood care has only represented approximately 1–2% of the observations of middle-aged bees. Given that most middle-aged bees do not care for brood at all, it is likely that those few middle-aged bees observed performing brood care are actually old nurses who have yet to make the transition to middle age tasks.

A careful examination of temporal polyethism studies shows that the task repertoires of different castes are not always the same. In this study, for example, I never observed the nurses wash-boarding (smoothing wood) or the middle-aged bees trimming brood cells. I have observed both groups performing these tasks in previous studies, however (Johnson 2002, 2003). In an earlier study, I proposed a revision to Seeley's (1982) classic temporal polyethism model that explains these fluctuating task repertoires (Johnson 2003). I proposed that the concept of caste is only relevant for tasks requiring a physiological specialization that makes workers temporarily non-interchangeable for particular tasks. An example would be feeding brood, which requires that a bees' hypopharyngeal glands be actively producing brood food. The hypopharyngeal glands of middle-aged bees produce invertase, an enzyme used to ripen nectar into honey, and the glands of foragers are atrophied (reviewed in Winston 1987). Neither of these castes could easily switch to brood feeding. From this perspective, one would expect to see workers performing tasks for which a specialization is not required, but rarely ones for which they are not physiologically tuned. I collected data on nurses and middle-aged bees using experimental perturbations of task demand which strongly supported this view (Johnson 2003). Accordingly, the present study should be interpreted in terms of this model and not as evidence in support of earlier versions of temporal polyethism, which did not allow for much flexibility (Wilson 1976).

Proximate biologists have shown great interest in honeybee temporal polyethism. In particular, the recent studies of Amdam and Page (Amdam and Omholt 2003; Amdam et al. 2004; Amdam and Page 2005; Page and Amdam 2007) have attracted much attention. This work grows out of two hypotheses: a theoretical model of the transition from within-nest work to foraging by Amdam and Omholt (2003) and the reproductive ground plan hypothesis (Amdam et al. 2004) based on previous work by West-Eberhard (1996). The current study has much relevance for these hypotheses. First, the theoretical model of Amdam and Omholt explicitly assumes two castes, nurses and foragers. The reproductive ground plan hypothesis follows this work in assuming that all "hive bees" have the same physiological tuning. The present study, along with a previous study of mine, however, confirm the long suspected belief that the hive bees form distinct groups that differ both in behavior and physiology. Workers in the middle age temporal caste, which is a phase that lasts as long as nursing (about 8 days), are unresponsive to nursing tasks in spite of being in frequent contact with brood. Honeybee temporal polyethism, therefore, cannot be reduced to two castes that correspond to the life cycle phases of some solitary hymenoptera. The repertoire of middle-aged bees and the complex methods by which they coordinate their activities with the foragers have no antecedent in the behavior of solitary hymenoptera. This is not to say that models based on the existence of two castes cannot be revised to account for the existence of a third; it is simply the case that such a revision is necessary.

Finally, the term "hive bee" is in wide use by many researchers of temporal polyethism (Huang and Robinson 1999; Robinson 2002; Amdam and Omholt 2003; Amdam et al. 2004; Amdam and Page 2005; Toth and Robinson 2005; Whitfield et al. 2006; Page and Amdam 2007). In particular, proximate researchers have begun to discuss all of their work within this two behavioral group terminology. While it is the case that these studies have as their goal understanding the transition to foraging, which would, in theory, allow one to lump together the within-nest bees, in practice, it might be the case that *some* of the temporal patterns found in such studies relate more to the transition from nursing to middle age tasks than from working in the hive to foraging. Vitellogenin titer, for example, falls off sharply in the hemolymph of workers at the transition to middle age work as opposed to foraging (Rutz and Luscher 1974; Rutz et al. 1976). This makes sense if the pattern is related to the abandonment of nursing, as the middle-aged bees are no more responsive to the brood than are foragers (Table 2). Given that the middle age caste is so distinct from the nurses in terms of behavior and physiological tuning, it might be helpful to discontinue the use of the term, hive bee, altogether and discuss temporal polyethism with respect to all of the temporal castes.

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