

Individual-level patterns of division of labor in honeybees highlight flexibility in colony-level developmental mechanisms

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Abstract Honeybee division of labor (DOL) has become a model system for exploring the genetic basis of complex traits and phenotypic plasticity. Although many highly informative behavioral studies have been conducted on this topic (both at the cohort and individual levels), most studies have focused on a few behavioral acts, such as the age of first foraging. Few studies have recorded large numbers of relatively complete individual-level patterns of DOL. Such fine-scale patterns would lay the foundation for rigorous molecular analyses of this phenomenon and allow us to differentiate between competing mechanistic models of DOL. Here, we record over 100 individual-level DOL patterns of bees living under natural conditions. We found that the transitions between castes (polyphenism states) are often gradual, with bees being in multiple castes at once. This is contrary to the traditional view that changes are abrupt. We also found that bees often skip castes, a key prediction of a recent model of DOL. We further confirm variation in the rate at which bees pass through castes and the age of first foraging. Taken together, these results greatly improve our understanding of this model system and allow for a strong revision of current models of honeybee DOL.

Keywords Honeybees · Social insects · Division of labor · Superorganism · Polyphenism

Introduction

The honeybee's complex system of division of labor (DOL) has long been a model system for many topics in biology (Page and Robinson 1991; Beshers and Fewell 2001; Johnson 2003; Robinson et al. 2008; Fischman et al. 2011). It is a particularly good model for understanding the genetic basis of complex traits and phenotypic plasticity (Ben-Shahar et al. 2002; Grozinger et al. 2003; Rueppell et al. 2004; Whitfield et al. 2006; Oldroyd and Thompson 2007; Smith et al. 2008; Johnson and Tsutsui 2011; Fussnecker et al. 2011). This is due to the sophistication of honeybee DOL (in terms of the number of alternative phenotypes) and because of the species amenability of study. Honeybees not only produce multiple phenotypes from the same genetic machinery but they produce these phenotypes in a flexible adaptive manner (Robinson 2002; Johnson 2010a). Essentially, as bees age, they pass through several developmental phases that specialize them for particular sets of tasks (Seeley 1982; Johnson 2008, 2010a). Although the transitions between phases are unidirectional under most conditions, under some circumstances, bees can accelerate or reverse their development to earlier phases (reviewed in Robinson 2002; Johnson 2010a). These circumstances, which can be controlled experimentally, have natural counterparts, making controlled laboratory studies relevant to our understanding of the adaptive basis of the bee's system of division of labor in nature. As conserved genetic pathways are thought to control common developmental and behavioral systems across wide evolutionary distances, this work has the potential to shed light on the mechanistic basis of polyphenism, and the intersection between development and behavior, across the arthropods (Stern 2000; Robinson et al. 2008; Carroll 2008; Bell and Robinson 2011).

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Honeybee DOL is characterized by four developmental phases, called temporal castes (Lindauer 1952; Seeley 1982; Wegener et al. 2009; Johnson 2008, 2010a). The first caste, called cell cleaners, is characterized by little else than cleaning cells and lasts for 3–4 days. The second phase is the nursing caste, during which bees primarily care for the brood. This typically lasts for days 4–12. The third caste, called the middle-aged bees (MABs), conducts nest maintenance and food processing tasks and typically lasts for about 9–10 days (ages 12–21 days). Finally, bees switch to the foraging caste after age 21 days and remain in this caste until they die. This synopsis of honeybee DOL requires several caveats. First, although descriptions of this system tend to focus on the behavioral component, it is important to recognize that different physiological specializations underlie each temporal caste (Winston 1987; Johnson 2003, 2005). Second, the preceding age ranges represent averages from many studies conducted in different parts of the world with different subspecies of *Apis mellifera*. It is known that these age ranges are responsive to environmental conditions and genotypic effects and can vary widely (reviewed in Winston 1987). Finally, and most importantly, this view of DOL is based on cohort-level studies, in which bees were identified by age only (bees were not individually marked). The present study resolves several issues stemming from this last caveat.

Although honeybee DOL has been the subject of many studies over the years, few studies have attempted to record complete individual-level patterns of DOL for a large number of bees (many studies have looked at associated traits such as age at first foraging with high sample sizes (Page et al. 1992, 2000; Pankiw et al. 1998; Schulz et al. 1998) and Lindauer's famous 1952 study looked at the lifetime behavior of a single bee). Because of this, we do not know whether the molecular machinery underlying DOL requires all bees to pass through a complete series of castes (with variation in the rate at which they do so), or whether bees can jump between castes that are typically not consecutive. Recently, the push–pull model of division of labor was proposed that stresses that caste changes are triggered by changes in the environment that necessitate a shift in colony-level caste ratios (Johnson 2010a). Further, it was proposed that primer pheromones (as a function of their presence or absence) facilitate the translation of environmental cues to changes in physiology and gene expression (Grozinger et al. 2003, 2007). This model should allow for great flexibility in how bees pass through the caste system, including caste skipping. A primarily internally driven developmental model for DOL, in contrast, could not easily account for caste skipping if it requires bees to pass through each stage. The primary emphasis of the present study is therefore to document whether patterns of DOL such as caste skipping are an important aspect of honeybee DOL. A second goal relates to the necessity of documenting fine-scale patterns of behavior in general. With next-generation approaches to the study of DOL (and

other behavioral processes) gaining traction, the sort of fine-scale patterns of behavior we collect here are now a necessity for guiding molecular research. Fine-scale quantitative data on how quickly bees can switch caste, for example, should help guide research on what sorts of molecular mechanisms are likely to be involved as different mechanisms operate at different temporal scales.

Materials and methods

Study site and colonies

This experiment was conducted at the Harry Laidlaw bee facility on the campus of the University of California, Davis during the months of June and July 2011. Two 4-frame observation hives were set up 3 weeks prior to the beginning of the experiment to allow the bees time to acclimate to their new hives and locations. Observation hives were kept within the facility, with bees allowed access to the outdoors via holes drilled into the walls. Both colonies had the same layout. The bottom two frames comprised the brood zone, while the top two frames comprised the honey zone. This was accomplished by limiting the queen to the bottom two frames of the hive with a queen excluder.

Focal bees were obtained from unrelated source colonies with naturally mated queens using standard methods (Seeley 1982; Johnson 2003, 2005). In short, emerging brood was collected from two source colonies and newly emerged bees were individually marked with plastic tags on the thorax and paint marks on the abdomen before being introduced to observation hives. Cohorts of 200 bees (each from a different host nest) were introduced to two observation hives. We observed a high level of drifting during the study probably due to the layout of the observation hives (they were both on the same wall facing the same direction). To control for this, we limited our analysis to those bees that were never observed to have drifted between colonies.

Little forage was available during the course of the present experiment, although both pollen and nectar were collected throughout. Both colonies appeared to lose weight overall (in terms of stored honey and pollen) during the course of the experiment. On a day by day basis, however, there were some days when colonies slightly gained weight and others when they lost. Quantitative measures of such losses and gains were not made, however. Hence, the important facts are qualitative in nature: both pollen and nectar were coming in, but overall the colonies lost some weight.

Experimental design

The experiment was designed to replicate past studies, in order to further help with the interpretation of such data while also

recording individual-level patterns of DOL. The basic idea was to introduce cohorts of individually marked bees and record their caste state, and other behavioral patterns, each day until they reached the final caste of foraging. We used a combination of scan sampling, which was used in previous studies (previous studies used paint marks only, however, not tags), along with observations of relevant regions of the nest. Observations began when bees were 3 days of age since it is known that their behavior is inflexible for the first few days of life (reviewed in Amdam and Omholt 2003; Johnson 2010a). Approximately 10 h of behavioral observations were conducted each day (5 h per colony) until greater than 95% of the bees in each colony transitioned to foraging.

Scan sampling

Two scan samples of each nest were conducted each day. Because of the large number of marked bees, each scan took approximately 1 h to complete. Scan sampling was conducted as per Johnson (2002, 2003). In short, the observer scanned the entire nest from left to right, starting at the top of the nest and working down. Every time a marked bee was encountered, its behavioral state was recorded along with its location (brood zone or honey zone). The diagnostics for task identification are reported in Seeley (1982) and Johnson (2002).

Focal nest area observations

The purpose of the focal observations was to place as many bees as possible each day into one or more castes. Placing bees in the nursing, MAB, or foraging caste was based on observing bees conducting tasks that are central to only one caste. Previous studies identified such tasks as brood feeding, pollen feeding, and capping brood for nursing, building new comb, nectar processing in the honey zone, and guarding for MAB, and foraging for foragers (Johnson 2008). Pilot studies showed that the best method for rapidly identifying bees conducting such tasks is to continuously observe a region of the nest where a large amount of only a single of these tasks is being conducted. For nursing, for example, a large patch of older larva (which requires heavy feeding) is an area in which the majority of the bees are performing brood feeding. Hence, if one continuously observes such an area and records instances of brood feeding by marked bees, a long list is quickly produced. The periphery of the nest where honey is being stored (and no brood are present) and new comb is being build is such a place for identifying MABs, and the entrance of the nest where foragers come and go is such a location for foragers. Guards are also identified at the nest entrance by their characteristic stance and behavior (Moore et al. 1987).

The diagnostic tasks for the three castes represent behaviors that vary in how accurately they can be determined based on observations. Hence, we modified our procedure for each. For

nursing, because all nursing tasks are easy to identify, a single observation of any nursing behavior was sufficient for identifying a bee as a nurse. In practice, nearly all bees identified as nurses were observed multiple times feeding brood as this is a task that tends to occur in bouts. MABs are the most difficult to identify because their caste-specific tasks can sometimes be confused with other tasks, and are mainly identified by a combination of location and task (Johnson 2008). For example, processing and unloading nectar in the honey zone is a MAB task, which nurses do not do. However, nurses do occasionally drink from honey cells in the honey zone, and this task can be confused with unloading nectar. To prevent misidentifications of MABs, a bee was identified as a MAB if it was observed conducting any of the MAB diagnostic tasks more than twice in 1 day, or if they were observed conducting any of these tasks on two consecutive days (in which case they were labeled a MAB for both days). Guarding is an exception as it is easy to identify. Bees observed guarding a single time were labeled MABs for that day. With respect to identifying foragers, we also took measures to reduce the rate of misidentification. When observing the nest entrance, the identity of each bee exiting or returning was recorded, along with whether or not it had pollen. Bees that had pollen could be safely identified as foragers after one observation. Bees without pollen, however, had to be observed coming or going twice during a single day to be labeled a forager. Bees observed waggle or tremble dancing in the nest could also safely be identified as foragers. The dance floor area of the nest was easy to scan throughout the day as other observations were being made, and a tally of bees seen dancing was kept. Finally, to prevent confusing bees on orientation flights with foragers, observations of the nest entrance were only conducted in the morning before orientation flights and in the late afternoon (after orientation flights were observed to have ended).

Each day, four 15-min observations of the brood zone, the honey zone, and the nest entrance were conducted. The periods were spread throughout the day, and were dependent on weather conditions and when the bees conducted orientation flights (during which data were not taken).

Results

Age cohort patterns

Figure 1 shows the pooled results from the scan sampling component of this study (mathematical methods for generating these distributions are given in Seeley (1982). Data were pooled for display purposes only because each colony showed the same qualitative patterns (albeit with minor quantitative variation). Our scan sampling data set had far fewer observations of foraging than that collected by Seeley (due to the different sampling procedures employed), so we used the

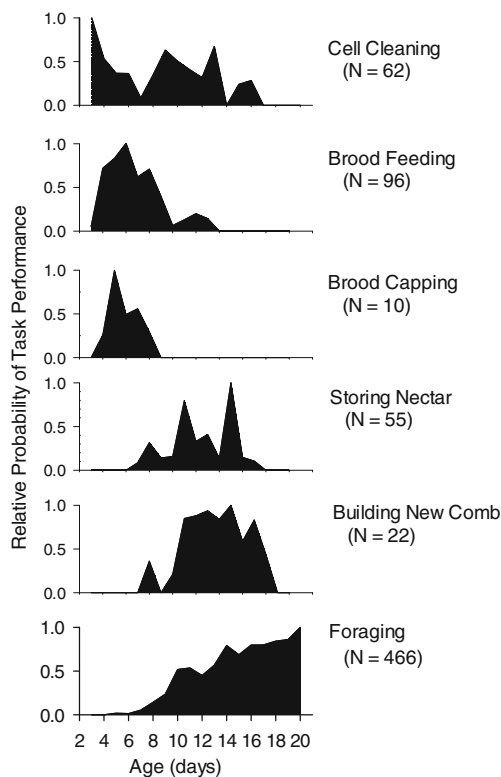


Fig. 1 Relative probabilities of task performance for tasks central to each caste. Data are pooled results from both colonies. The four age castes previously found by Seeley (1982) are easily recognizable. Brood feeding and capping brood, which encompass part of the nursing repertoire, occur earlier than nectar processing and comb building, which are part of the MAB task repertoire. Foraging has a mode at the end of the age distribution, indicating it comes last in the sequence

focal observations for this task to give a clearer picture of the rate of transitioning to foraging. The temporal patterns match those found by Seeley (1982) and others. Four age ranges can be discerned reflecting the four age castes of bees. As per previous studies, all bees began as cell cleaners and ended as foragers (that every bee showed the same pattern precludes the need for statistics to demonstrate order of behavior for cell cleaners and foragers). For the nursing and MAB castes, the data also matched previous studies, but an analysis was conducted to demonstrate that nursing precedes MAB tasks. The nursing tasks of brood feeding and capping were conducted earlier than the MAB tasks of comb building and nectar processing (comparison of the mean age of performance for both sets of behaviors assuming observations of bees on different days are independent (General Linear Model, mean age nurse tasks, 6.61 ± 2.11 days; mean age MAB tasks, 12.95 ± 2.84 days; $F(1,180)=243.11$, $p < 0.0001$). There were no significant colony effects (General Linear Model, $F(1,180)=2.86$, $p=0.09$). Essentially, the data qualitatively match that of Seeley (1982), but have some quantitative differences. In short, the patterns are shifted to the left, indicating a faster process of moving through the castes in the present study.

Individual-level patterns

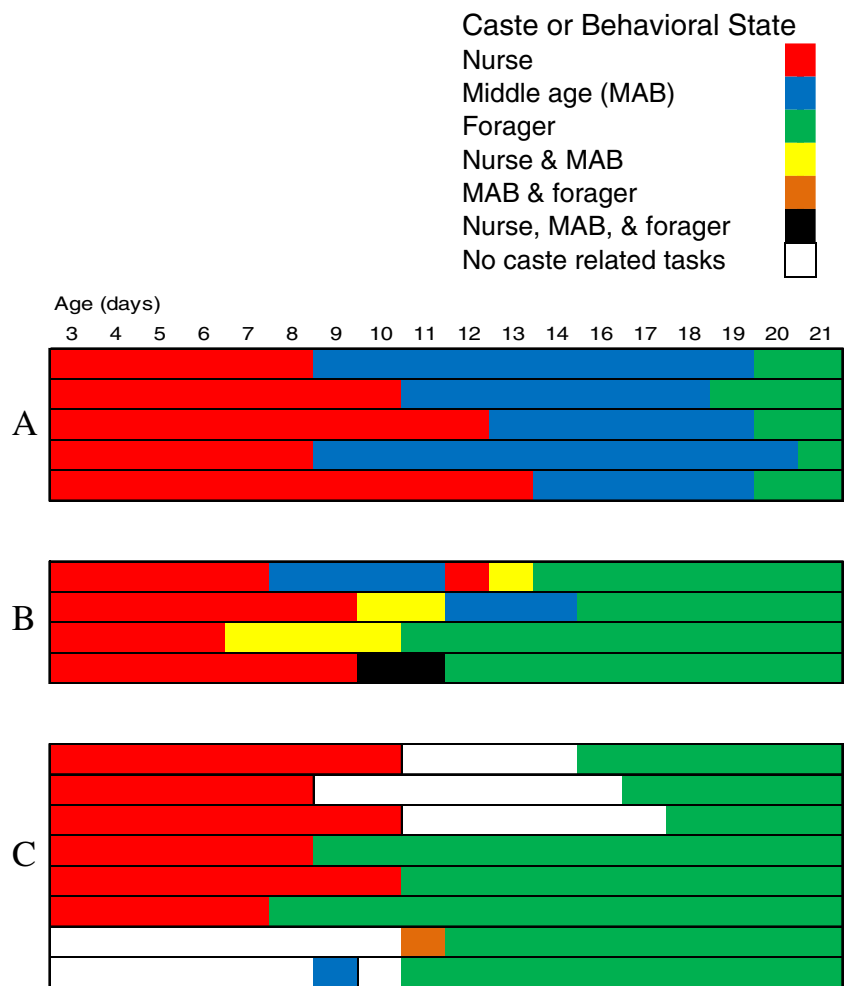
Figure 2 shows the variety of individual-level patterns we observed in this study. All the bees in the study spent the first couple of days in the cell cleaning caste. As this first caste is known to be a relatively fixed developmental process, we focus on the three more flexible castes. Part A shows the sort of “Typical” patterns that might be suggested by the cohort-level patterns. These bees passed through all three castes (nurse, MAB, and forager). They varied strongly, however, with respect to how long they spent in each caste.

Part B shows more complex patterns. These bees were either in more than one caste at a time, or rarely appeared to revert back to a previous caste. Bees that were in more than one caste at a time were almost always in the process of switching castes. Hence, the transitions between castes are not always abrupt, but can be characterized by a period of time during which bees are conducting tasks in both castes. This was true of the nursing to MAB transition and the MAB to foraging transition. Overlap between the MAB and foraging transition was always between guarding behavior and foraging. One bee was observed to be in all three castes at once. In other words, this bee was seen feeding brood, processing nectar, and foraging on the same day.

Part C shows that bees may skip castes. The most common skipping was switching from nursing to foraging (foraging 1 day after their last observed period of brood feeding). Some bees, however, that appeared to skip the MAB caste (because they were never seen working on MAB tasks during the focal observations) did not switch immediately to foraging. We therefore used the scan sampling data to determine what tasks these bees were conducting. Figure 3 shows that these bees were working on general wax work or were highly inactive. Finally, a small number of bees were observed to never conduct nursing behavior. These bees were observed in the nest (primarily in an inactive state) for over a week before they began foraging (after spending a day or so as a guard at the nest entrance). A strong caveat is necessary when interpreting these last two classes of potential caste skippers, in that lack of observation is not evidence of lack of behavior given that the bees were not continuously observed. Hence, these bees could have performed nursing or MAB tasks when not under observation. In general, we view the first class of bees (those that switched from nursing one day to foraging the very next) as the best evidence of caste skipping.

Table 1 shows the overall results for these individual-level patterns. We only include those bees that were seen in at least two castes. Bees that were only seen to work in one caste either disappeared (got lost during orientation flights or drifted to other colonies) or were observed very few times overall. Hence, we focus on those bees that were observed continuously throughout their lives. Bees were split relatively evenly between those that passed through two castes and those that

Fig. 2 Individual-level patterns of division of labor in honeybees. Each row is a representation of the data we collected for a single bee. Bees were chosen that are representative of the variety of patterns found. **a** Many bees passed through all three castes, as is often assumed based on cohort-level studies. **b** Some bees exhibited complex patterns such as being in multiple castes at once. **c** Many bees switched from the nursing to the foraging caste from one day to the next, hence, skipping the MAB caste



passed through all three. Bees that skipped a caste transitioned earlier to foraging than did bees that passed through all three castes (General Linear Model, two castes, 11.62 ± 3.04 days; three castes, 13.07 ± 3.40 , $F(1,139) = 10.33$, $p = 0.002$).

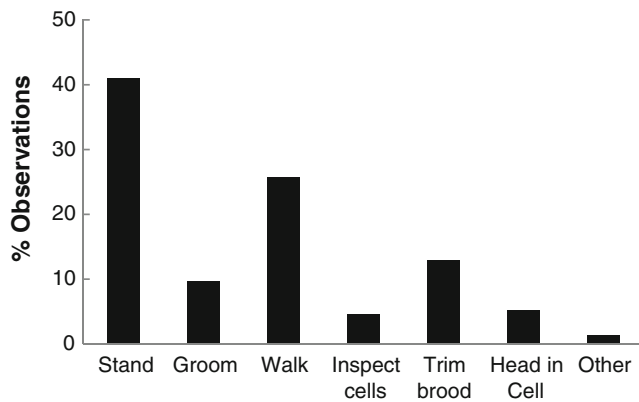


Fig. 3 Behavioral profiles of bees observed to skip the MAB caste, but which did not transition directly to foraging. Example profiles of such bees are shown in Fig. 2c. These bees were found to conduct general wax work and to have high levels of inactivity when not conducting caste-specific tasks

Although statistically significant, however, the magnitude of the difference was small. Colony effects were found to be significant (General Linear Model, $F(1,139) = 8.84$, $p = 0.003$), meaning there was a significant variation between colonies for how quickly bees in each category transitioned to foraging. Most of those bees that skipped a caste skipped the MAB caste (Table 1). In total, 16.9 and 24.6% were observed to be in more than one caste (as a result of a gradual transition between castes) in colonies 1 and 2, respectively. Few bees were observed to revert to previous castes in either colony.

Discussion

General considerations

Superorganisms such as the honeybee are group-level adaptive units. What this means practically is that there are many levels at which one can explore their behavior. In the context of foraging, for example, there is a dance language composed of signals, such as the waggle and tremble dances, that underlies colony-level foraging decisions such as how many bees to

Table 1 Overall frequency of individual-level patterns of division of labor

	Colony 1		Colony 2	
	# Bees	%	# Bees	%
Pass through two castes	34	44.16	21	32.31
Pass through three castes	43	55.84	44	67.69
Skip nursing	3	3.90	2	3.08
Skip MAB	31	40.26	19	29.23
Dual castes	13	16.89	16	24.62
Caste reversion	2	2.60	7	10.77
Mean age at first foraging	12.43±3.31		14.21±3.88	
Total	77		65	

send out for pollen or nectar. This has been called social physiology as it is analogous to the physiological feedback loops that control group-level coordination of action in metazoan bodies (Johnson and Linksvayer 2010). Essentially, it is a colony-level regulatory process that allows for unity of purpose within a changing environment. In superorganisms, however, the workers are not clones, and there can also be a significant genotypic variation between workers that also affects traits such as foraging behavior. In general, fixed variation due to genotypic differences and social regulatory mechanisms are not mutually exclusive. They both affect behavior in qualitatively different ways. It can be difficult to determine, however, if a particular pattern is the result of a social regulatory process or genotypic variation. In the present case, both mechanisms are known to modulate the rate at which workers pass through the temporal polytheism system (reviewed in Page and Robinson 1991; Robinson 2002; Smith et al. 2008; Johnson 2010a). In short, it is likely that both mechanisms play some role. Here, we will focus on the role played by colony-level regulatory mechanisms controlling division of labor and leave the role of genotypic variation for future work.

A further confusing issue with respect to task choice in social insects are the concepts of division of labor and task allocation. In short, DOL is a type of task allocation, but not all types of task allocation are DOL (Ratnieks and Anderson 1999; Johnson 2010b). DOL refers to stable differences in worker task choice that in the case of very derived species such as the honeybee depend on developmentally controlled physiological mechanisms that change slowly as a worker ages (reviewed Robinson 2002; Johnson 2010a). DOL can also be based on morphological differences (Oster and Wilson 1978). Task allocation refers to the broader problem of how colonies allocate workers to tasks in a changing environment (Gordon 1996). Hence, task allocation can refer to division of labor, or to faster processes of labor allocation within a caste dependent on purely behavioral (neuronal) processes. Foragers, all of whom are in the same caste, for example, are allocated to different food locations and types based on task allocation mechanisms that have relatively little to do with the slower

developmental mechanisms controlling the size of the forager caste. This study is focused on individual variability in DOL; hence, we will not discuss recent work on individual variation in the context of faster moving task allocation processes (Arnold et al. 2002; Weidenmuller 2004; Chapman et al. 2007; Ravary et al. 2007; Duong and Schneider 2008; Jandt and Dornhaus 2009), even though such work could have some relevance in principle as it depends in part on genotypic variation, which also modulates, in a quantitative manner, DOL.

Cohort-level patterns of DOL

Figure 1 suggests that our results are consistent with previous research on honeybee DOL. The two major differences relate to the performance of cell cleaning and the rate at which bees passed through the castes. Seeley (1982) found that the peak for cell cleaning occurred at the beginning of a bee's life, and we found the same. However, cell cleaning fell off rapidly in his data set, while it fluctuated strongly in ours and remained high. The most likely answer for this is that the first caste (cell cleaners) is unlike the other castes in that no physiological specialization is required for it (reviewed in Johnson 2003, 2010a). The cell cleaning caste appears to be an extension of early development. In other words, it is a period in which flight musculature and other basic physiological systems are developing and during which a bee is not suited to complex tasks. Further, bees need to be in the brood zone, which is warmer than the rest of the nest, to facilitate this development (Stabentheiner et al. 2010). Essentially, cell cleaning might simply be a convenient task that bees perform until they finish basic development into an adult. The task of cell cleaning, however, is also conducted by other within-nest bees (nurses or MABs) as required. There were several time periods in the present study when large numbers of brood emerged creating a large demand for cell cleaning. This is reflected in the spikes of this activity across the age ranges. In other words, as cell cleaning is not physiologically determined, and not controlled by a division of labor mechanism, such as the push–pull

model, any within-nest bees (cleaners, nurses, or MAB) would participate in conducting the task. Perhaps in Seeley's colonies less brood emerged during the course of the study, and the older bees were not needed for this task?

The age at first foraging, and the rate at which bees pass through the temporal caste system in general, is a variable that has been shown to vary strongly between studies (Page et al. 1992, 2000; Schulz et al. 1998; Pankiw et al. 1998; Rueppell et al. 2004; Toth et al. 2005; Elekonich and Roberts 2005; Wegener et al. 2009). In this study, bees passed relatively quickly through the caste system. While we do not know the reason for this, we hypothesized that it could have something to do with the caste skipping we observed. However, although bees that passed through all three castes transitioned later to foraging than those that skipped a caste, the age of first foraging for bees passing through all three castes was still low compared to other studies (≈ 20 days in Seeley's study to 13–15 days in this one, for example). It is likely that some aspect of the fact that the study was conducted during a time of little forage explains this pattern, but elucidation of the mechanism will have to await future studies. It could also have to do with the location of the studies (central California vs. upstate New York) or the genotype of the bees used (the bees in the present study were primarily of *A. mellifera carniolan* type rather than the *A. mellifera linguistica* used by Seeley). Genotypic variation between patrines could also have interacted with any or all of the above mechanisms to generate these patterns (Calderone and Page 1988, 1991; Page et al. 1992, 2000; reviewed in Beshers and Fewell 2001).

Individual-level patterns

The push–pull model of DOL proposes that bees switch caste according to the needs of the colony and that the layout of tasks, and the pheromones often associated with them, underlie this ability (Johnson 2010a). In short, the model proposes that primer pheromones, and other caste-related stimuli, occur in particular non-overlapping regions of the nest. Under normal circumstance, bees experience one set of these conditions at a time in a predictable manner as they age. In the brood zone, bees experience brood and queen pheromone, for example, whereas in the honey zone, they experience stimuli related to comb building or nectar processing. When the brood zone becomes too crowded and a nurse is pushed out of it, it therefore experiences a new set of task-related stimuli. Hence, bees transition through castes according to what looks like an internally driven mechanism, but in actuality it is a complex mixture of environmental cues and developmental programs (Tofts and Franks 1992; Franks and Tofts 1994; Huang and Robinson 1992, 1996). Such a mechanism can lead to a highly flexible process of development, including caste skipping and

being in multiple castes at once under certain adaptive and experimental conditions. This study was designed, in part, to verify this hypothesis.

We conducted this study during a period when bees can be predicted to show a high level of natural flexibility in caste transitions. Specifically, our colonies were usually bringing in enough nectar to maintain their current state, but not enough to grow. This is a common state for honeybees in the summer (Seeley 1985) as they tend to gain most of their weight in brief nectar flows, and either lose weight or break even through most of the summer. We chose the breakeven period because it is a period in which all four castes are necessary, but relatively less labor is necessary for one of the castes than is the case during rapid growth. In short, the MAB caste processes nectar into honey and builds comb, both of which are vital to a growing colony. However, when the colony is losing weight or merely breaking even with respect to how much nectar they take in and how much they consume, relatively less comb building and honey processing are necessary. Hence, MABs are still necessary to receive nectar from foragers (and to guard the nest and do several other tasks), but a smaller number of MABs are necessary than when the colony is growing. The contexts of either breaking even or losing weight are therefore ones in which we can predict to see normal transitions, along with a large amount of caste skipping, if skipping is possible. Our results supported this prediction. About half of the bees passed through all three castes, while the other half skipped the MAB caste and switched directly to foraging. This result shows previously unrecorded flexibility at the individual level that allows colonies to optimally allocate workers to castes with respect to changes in environmental conditions. With respect to the push–pull model (Johnson 2010a), it is likely that when bees leave the brood zone, and transition out of the nursing caste, if they fail to experience the relevant MAB task stimuli, then they skip over this caste to the foraging caste.

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