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# Division of labor in honeybees: form, function, and proximate mechanisms

**Brian R. Johnson**

**Abstract** Honeybees exhibit two patterns of organization of work. In the spring and summer, division of labor is used to maximize growth rate and resource accumulation, while during the winter, worker survivorship through the poor season is paramount, and bees become generalists. This work proposes new organismal and proximate level conceptual models for these phenomena. The first half of the paper presents a push–pull model for temporal polyethism. Members of the nursing caste are proposed to be pushed from their caste by the development of workers behind them in the temporal caste sequence, while middle-aged bees are pulled from their caste via interactions with the caste ahead of them. The model is, hence, an amalgamation of previous models, in particular, the social inhibition and foraging for work models. The second half of the paper presents a model for the proximate basis of temporal polyethism. Temporal castes exhibit specialized physiology and switch caste when it is adaptive at the colony level. The model proposes that caste-specific physiology is dependent on mutually reinforcing positive feedback mechanisms that lock a bee into a particular behavioral phase. Releasing mechanisms that relate colony level information are then hypothesized to disrupt particular components of the priming mechanisms to trigger endocrinological cascades that lead to the next temporal caste. Priming and releasing mechanisms for the nursing caste are mapped out that are consistent with current experimental results. Less information-rich, but plausible, mechanisms for the middle-aged and foraging castes are also presented.

**Keywords** Division of labor · *Apis mellifera* · Honeybees · Temporal polyethism · Social insects

## Introduction

Division of labor (DOL) in the honeybee is one of the most well explored phenomena in the study of animal behavior. Although studies go back to the 1800s, dedicated experimental work began in the 1930s and has continued to the present with numerous labs approaching the problem from every biological perspective (Rösch 1930; Lindauer 1952; Ribbands 1953; Free 1965; Seeley 1982, 1995; Calderone and Page 1988; Page and Robinson 1991; Page et al. 1992, 2000; Moritz et al. 2001; Page and Erber 2002; Robinson 2002; Grozinger and Robinson 2002; Grozinger et al. 2003; Johnson 2003, 2005, 2008a, b; Robinson et al. 2005; Elekonich and Roberts 2005; Slessor et al. 2005; Whitfield et al. 2003, 2006; Rüeppell et al. 2004; Amdam et al. 2003; Oldroyd and Thompson 2007; Schmickl and Crailsheim 2007, 2008; Beekman et al. 2007; Smith et al. 2008). Given the expansive nature of this work, it is necessary that any researcher take an integrative approach. To facilitate this, a synthesis of behavioral ecology, physiology, and neurobiology approaches to the subject is presented. The biological disciplines included in this study were chosen because they all share a focus on qualitative mechanisms, typically feedback processes, for regulating worker behavior. The important role played by genotypic variability, in contrast, is quantitative in nature, in that it causes variability within the context of general qualitative mechanisms (Calderone and Page 1988, 1991; Breed et al. 1990;

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Fewell and Bertram 1999; Kryger et al. 2000; Oldroyd and Thompson 2007). I therefore leave the role played by these effects to future work. The paper does not attempt to exhaustively review the many papers on honeybee DOL; instead, it conceptualizes the key results into two models: one at the behavioral level, the push–pull model, that explains the form and adaptive basis of DOL and another at the proximate level that explains how colony level needs are translated into individual-level patterns of physiological development.

## Honeybee division of labor

DOL refers to biases in the propensity of individuals to perform different tasks within a group (reviewed in Oster and Wilson 1978; Beshers and Fewell 2001; Smith et al. 2008). In those cases where DOL is so pervasive that workers ignore most tasks, the term, caste, is useful to refer to those individuals with the same task repertoire (Wilson 1976; Seeley 1982; Johnson 2003, 2005). There are two basic classes of DOL across the social insects: between queens and workers and amongst the workers for tasks unrelated to reproduction. We focus on DOL amongst the workers. In this case, there are two major forms: physical and temporal. Physical castes are morphologically special- ized for their task and are common in the ants and termites (reviewed in Wilson 1971; Hölldobler and Wilson 1990). Temporal polyethism refers to age correlated biases in task performance and is found throughout the social insects (reviewed in Oster and Wilson 1978; Robinson 1992; Beshers and Fewell 2001). As temporal polyethism is in part based on internal and physiological differences between workers, there is some overlap between these two classes of DOL, such that temporal castes could be considered temporary physical castes (Johnson 2003, 2005; Robinson 2009). The honeybee temporal caste system is depicted in Fig. 1 (based on Seeley 1982; Johnson 2003, 2005, 2008b). There are four castes and a winter bee generalist state. I first describe the task repertoire of each caste then explore the nature of transitions between them from the perspective that DOL is a colony level adaptation (Seeley 1989b; Linksvayer et al. 2009). The review will focus on DOL in the broadest sense. Hence, many fascinating aspects of within-caste task allocation, such as the dance language of the foraging caste, will only be touched upon.

## Cell cleaners

Newly emerged bees cannot fly or sting and are therefore developmentally immature (reviewed in Winston 1987;
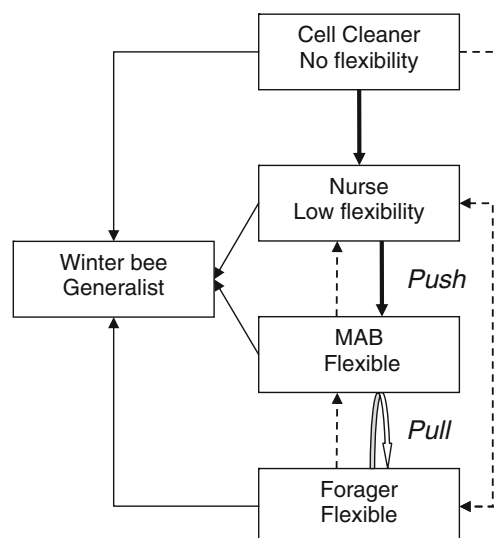


Fig. 1 *Apis mellifera* has two systems of social organization: temporal polyethism in the spring and summer and generalist workers in the winter. *Solid arrows* indicate natural caste transitions, while the *dashed arrows* show atypical caste transitions (experimentally induced or due to swarming).The push–pull model for temporal polyethism proposes that nurses are pushed from their caste by the emergence of newly emerged bees, while the middle-aged bees are pulled into the foraging caste via interactions with the foragers. Members of all castes are assumed to be able to switch to the winter state under the appropriate conditions

Calderone 1998). The first days of a bee's life are spent continuing development and acquiring these abilities. The task repertoire during this period consists of cell cleaning, with the rest of the time spent inactive or grooming (Seeley 1982). This group does not comprise a critical functional component of the colony, as members of other castes also clean cells. Hence, this caste may be the result of physiological constraints on honeybee development (Seeley 1982).

## Nurses

The nursing caste typically lasts for about 1 week, from ages 4–12 days (Ribbands 1953; Seeley 1982). Nurses feed a proteinaceous section to the young, as opposed to pollen, as is the case for other social bees (Michener 1974). This presumably increases the growth rate of the larva, which do not have to digest tough pollen cuticles. In addition to feeding the brood, nurses also transfer their proteinaceous secretion to the younger and older bees in the nest and are, hence, critical for their development and maintenance (Crailsheim 1991, 1992). Nurses also care for the queen by forming a retinue around her (reviewed in Winston 1987). Bees in the retinue regulate queen behavior via the rate at which they feed her and act as messenger bees by spreading the queen's pheromones about the nest (Velthuis 1972; Seeley 1979).

## Middle-aged bees

Middle-aged bees (MAB) remain in their caste for a little over a week, from ages 12–21 days (Seeley 1982; Johnson 2008b). MAB have a task repertoire spread throughout the nest. Although their distribution overlaps that of the nurses, their behavior is quite distinct, as they show no interest in the brood (Johnson 2008b; Fig. 2). Instead, their task repertoire comprises some 15 tasks ranging from nest building and maintenance, to nectar receiving and processing, to guarding the nest entrance (Seeley 1982; Trumbo et al. 1997; Johnson 2003, 2008a, b). Studies suggest the MAB may be broken into two categories with continuous variability between them. Young MAB appear to spend more time on comb building and general colony maintenance, while older MAB may transition to nectar processing and other tasks, which put them nearer the entrance of the nest (Seeley 1995; Trumbo et al. 1997). MAB task allocation is via a coupled localization/diffusion process, which enables them to track changes in task demand over the entire nest without the need for communication amongst themselves about changing task demands (Johnson 2009).
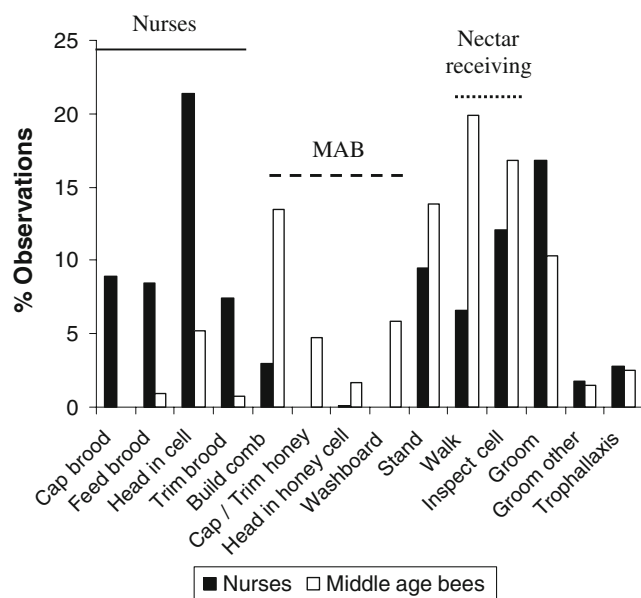


Fig. 2 Nurses and middle-aged bees (MAB) have overlapping work zones within the nest, which, along with strong individual-level variation in development rate, led to confusion over whether they were two separate castes. Johnson (2008a, b) showed, using focal animal observations, that nurses and MAB have distinct task repertoires. Nurses stay within the brood nest where they care for brood, while middle-aged bees ignore the brood and focus on all the many other tasks in the nest. That nectar receiving is a key task of MAB, but not nurses, and is apparent by noting the difference in walking between the two castes. Nectar receivers make long circuits from the dance floor to the honeycombs at the top of the nest, while nurses do not leave the brood zone

MAB activities must be tightly coupled to those of the foragers for the colony to collect the 20 kg of honey needed to survive the winter (Seeley 1985). This is because although the foragers collect nectar, they transfer it to MAB near the nest entrance for processing into honey and storage (reviewed in Seeley 1995). Hence, the number of MAB engaged in nectar receiving must be adjusted such that it matches the current foraging rate. The tremble dance, produced by foragers when they determine there are too few nectar receivers, serves to recruit more MAB to nectar receiving (Seeley 1992; Seeley and Tovey 1994). The MAB must also build new comb at a rate sufficient to ensure that enough space is available for incoming nectar (Pratt 1998).

## Foragers

Once the transition to foraging is made, bees no longer engage in within-nest tasks (reviewed in Winston 1987; Seeley 1995). Instead, they focus on foraging for the four resources colonies need: propolis, water, pollen, and nectar (reviewed in Robinson 1992; Seeley 1995; Calderone 1998). Of the four, pollen and nectar make up most of the foraging activity, except in periods of heat stress in which water collection can be as labor intensive (reviewed in Seeley 1995). Although biases in the propensity to forage for a specific substance have been found (reviewed in Calderone and Page 1991; Page and Robinson 1991; Beshers and Fewell 2001) and most bees specialize on either pollen or nectar on a given trip (Seeley 1985, 1995), over the course of their foraging career, most bees appear to be generalists (Seeley and Towne 1992). Needless to say, honeybee foraging via the dance language is quite involved and is the subject of much work (reviewed in Seeley 1995; De Vries and Biesmeijer 1998). How the foragers come to a consensus over the selection of a new home during the swarming process is also an active area of research (Seeley and Visscher 2004; Beekman et al. 2006; Visscher 2007).

## Natural caste transitions: the push–pull model

Bees living in healthy colonies in the spring and summer undergo three caste transitions: cell cleaner to nurse, nurse to MAB, and MAB to forager. The first transition appears to be a fixed developmental process, in that there is no evidence that it is variable under any conditions (reviewed in Beshers et al. 2001; Amdam and Omholt 2003). Hence, we will focus on the last two transitions from the vantage point of colony level needs. We will not discuss proximate mechanisms (which are left for the second half of the paper), but instead focus on ecological context, information demands, and adaptive bases.

## Nurse to MAB transition

Colony survival through the winter is low and dependent on colony size and honey stores (Seeley 1985; Winston 1987). As colonies begin either as swarms or small populations of over-wintered bees, growth rate is thus a central variable for colony fitness. Hence, there should be a premium on not neglecting the brood. Given this, it is likely that the ratio of larva to nurses is the primary variable controlling when a nurse leaves its caste. As long as this ratio is such that nurses are busy, they should stay with their task. In particular, we should expect transitions out of the nursing caste when nurses are replaced by newly emerged bees (Seeley 1985; Amdam and Omholt 2003). Figure 1 reflects this hypothesis by describing this transition as a pushing process, that is, newly emerged bees push older nurses out of the brood nest (Tofts and Franks 1992). Empirical circumstantial support for this hypothesis has long existed, as Milojevic (1940) and Haydak (1963) were able to produce nurses over several months old by continually removing pupal combs from the colony and replacing them with combs of open brood.

## MAB to forager transition

The MAB to forager transition is proposed to be considerably more complex than the nurse to MAB transition, as would be expected given the complex nature of cooperation between the MAB and foragers. There are three basic problems: one, maintaining a productive caste ratio between the two groups, two, ensuring the steady replacement of foragers as they die, and three, rapidly boosting the forager population during nectar flows. The first problem was touched on previously. MAB must be available to receive nectar at the maximum rate the foragers can bring it in, while building comb such that the colony does not run out of space (reviewed in Seeley 1995). Hence, not too many of them should switch to foraging no matter how much food is available in the field. The second problem is straightforward, as foraging honeybees have one of the highest metabolic rates known (Williams et al. 2008) and work themselves to death over a couple weeks (Visscher and Dukas 1997). Their continuous replacement is a necessity if the colony is to continue foraging at a steady rate. The third problem has not received as much attention from researchers of DOL (but see Huang and Robinson 1999), but from a behavioral ecology perspective, is a key problem. In many parts of the world, a colony loses weight for much of the summer and gains weight only during short highly profitable nectar flows (reviewed in Seeley 1985). During this time, there is a superabundance of food available, and the problem is to field as many foragers as

possible. Thus, when the environment is suitable, all the MAB not necessary for comb building and nectar receiving should be shuffled quickly to the foraging caste to maximize nectar collection. In contrast, when the environment is not suitable (during a dearth), the MAB should avoid becoming foragers, as the transition is associated with physiological changes that shorten a worker's life (reviewed in Amdam and Page 2005) and because it would be more profitable for them to wait until a nectar flow. Thus, we must explain several processes: ensuring sufficient comb builders and nectar receivers, governing the rate at which MAB become component to forage, and the sometimes sudden decision to begin foraging. I propose a two-part model based on a mixture of physiological and behavioral interactions.

Maintaining sufficient comb builders and ensuring a steady rate of forager-ready bees can be solved by pacing the rate that MAB develop with respect to forager mortality. Here, I follow previous work and suggest that the social inhibition model (Huang and Robinson 1992, 1996, 1999; Beshers et al. 2001) governs this process. According to this model, the foragers produce an inhibitor, which suppresses the rate of development of within-nest bees (I assume its main function is to modulate MAB development and not that of nurses). Since forager mortality is a function of work effort (Schmidt-Hempel and Wolf 1988), as the foraging rate increases, so should the rate of MAB development because foragers will collectively produce less inhibitor as their population shrinks (Huang and Robinson 1992, 1996). Recently, Leoncini et al. (2004) identified this inhibitor as ethyl oleate present in the forager's crops and presumably transferred to MAB via trophallaxis.

In contrast to the social inhibition hypothesis, however, I propose that the inhibition process governs the rate at which MAB become competent to forage, but not the actual decision to change caste. This is because studies show that all the physiological machinery for foraging is in place prior to the transition to foraging (reviewed in Robinson 2002) and because the decision to forage appears to be too complex for a simple physiological process to govern. The size of the forager population varies throughout the year (Sekiguchi and Sakagami 1966), as do the demands of MAB. As discussed earlier, the task partitioning between MAB and foragers means that each caste is dependent on the other. Hence, we might expect the decision to switch to foraging to depend on the ratio of nectar receivers to foragers. In short, I propose that the oldest MAB are fully capable of foraging but do not for one of two reasons: one, they are needed as nectar receivers, or two, there is insufficient forage in the field to make it cost effective for them to switch. When either of these conditions changes, they transition to foraging.

The preceding argument proposes that the decision to forage is based on behavioral interactions. A short review

of the relevant behavior will therefore be useful. Nectar receivers make circuits between the dance floor where they unload foragers and the top of the nest where they store honey (Seeley 1989a). When there are many receivers relative to foragers, the time it takes foragers to find a receiver is short (reviewed in Seeley 1995). The converse, however, should also be true. Receivers should experience long wait times to find foragers when there are many receivers relative to foragers. It is also often the case where during periods of high nectar influx, all the foragers are busy, and there are few foragers following dances. During such times, one observes that most waggle dances are not being followed. Thus, MAB are searching for foragers needing unloading but only encountering dancing bees. Taken together, all the information necessary for a nectar receiver to determine the ratio of receivers to foragers, and the need for more foragers, is present on the dance floor and could be used to inform the decision to switch caste. Although this hypothesis will require explicit experimental support, there is circumstantial evidence to support it. Seeley (1995) observed during experiments in which he allowed uninhibited recruitment to a feeder that bees he had previously marked as nectar receivers began showing up at the feeder when foraging rates reached high levels. Further, the soldier class of bee is composed of forager-age bees that do not forage (Breed et al. 1990). Although their adaptive value has been proposed to be for defense, it is also likely they are waiting to be recruited to foraging (the two hypotheses are not mutually exclusive).

### Growth vs survival/division of labor vs generalists

As Fig. 1 indicates, there is another class of bee vital to honeybee organization, the winter bees. The winter state is characterized by great longevity and a generalist task repertoire (Winston 1987; Omholt 1988). Through the winter, all the bees participate in thermoregulation (reviewed in Southwick 1983). In mid to late winter, long before the foraging season starts, winter bees begin rearing brood, acting as nurses (reviewed in Seeley 1985; Winston 1987). Then, when conditions become favorable, they forage, some at an age of over 280 days (Sekiguchi and Sakagami 1966).

Honeybees, therefore, have two patterns of organization of work: DOL based on specialization in the spring and summer and what appear to be uniform generalists in the winter. These two patterns are not surprising from a behavioral ecology perspective. In the spring and summer, the goal is to grow as rapidly as possible, while also stockpiling the 20 kg of honey needed for over-wintering. To accomplish this, it is necessary to maximize work output at the colony level. DOL is a means of accomplishing this, as specialization leads to higher per capita work output than

is possible with generalists (Jeanne 1986, 1999). DOL, however, is costly, in terms of survivorship, as the foragers quickly work themselves to death. In the winter (or dry season in the topics), the goal shifts from growth and work output to survivorship (reviewed in Seeley 1985; Hepburn and Radloff 1998). In this context, each bee is valuable as brood rearing is difficult and costly. Hence, a generalist strategy in which a large investment is made to each bee's longevity and capacity to do any task should be preferable.

### A proximate model for temporal polyethism

A proximate model for temporal polyethism must explain two phenomena: the generation of caste-specific physiology and the adaptive mechanisms by which transitions between castes are controlled. Figure 3 illustrates a general hypothesis that accounts for these two phenomena. The mechanism for generating caste-specific physiology is proposed to depend on mutually reinforcing positive feedback mechanisms of behavioral and physiological processes that lock a bee into a particular behavioral phase. I will refer to these as caste priming mechanisms. Information-rich releasers (pheromones or other environment stimuli) are then hypothesized to disrupt specific components of the priming mechanisms to trigger endocrinological cascades that ultimately result in the activation of new priming mechanisms for generating the next caste-specific physiology. Given the honeybee caste system, we must explain the construction of four caste-specific physiologies and then explain what releasers trigger transitions between them. I will first focus on natural transitions before discussing the
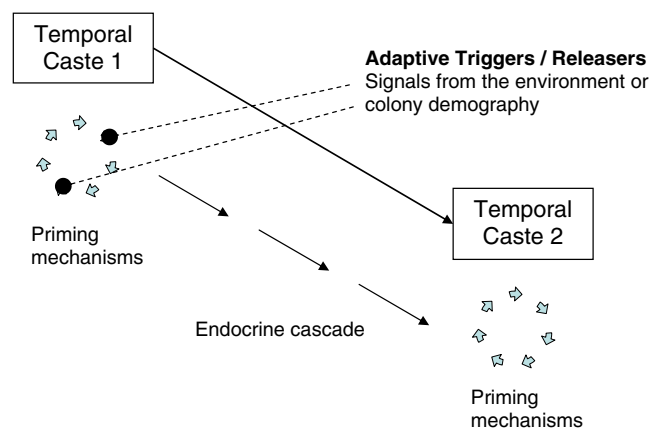
Fig. 3 General proximate model for temporal polyethism. Caste-specific anatomy and physiology is generated via a multifactorial mutually reinforcing priming mechanism. Transitions between castes are controlled by releasers that break the reinforcing mechanism and trigger an endocrinological cascade to the next caste. This simple model explains why so many different factors can all cause a change in caste because a break anywhere in the mutually reinforcing cascade will trigger a transition to the next caste

nature of the atypical transitions observed in colonies with experimentally altered demography.

## Cell cleaner development

As mentioned previously, the cell cleaner stage appears to be inflexible. There is thus no priming mechanism for this caste, only a continuous process of development normally ending with the transition to the nursing caste. The only variable appears to be the availability of protein. If the colony has pollen stores, then a transition into the nursing caste occurs, if not, development is compromised (sufficient protein stores for brood food production are likely not present) and bees begin to forage earlier in life (Schulz et al. 1998; Toth et al. 2005).

## Nursing priming mechanisms and triggers

Based on existing data, a plausible priming feedback mechanism for the nursing caste has been mapped out (Fig. 4). Two mutually reinforcing processes facilitate a bee developing the physiological capacity to nurse and the propensity to stay within the caste. These processes are centered on two pheromones, queen mandibular gland pheromone (QMP) and brood pheromone (BP). When a worker feeds brood, she is exposed to both pheromones (which co-occur in the brood nest). BP stimulates the hypopharyngeal glands, which trigger pollen feeding, which maintains high vitellogenin (Vg) titers (and high nutritional stores in general), which in turn allows for the production of brood food, and perhaps the partial suppression of the normal age-based rise in juvenile hormone (JH)
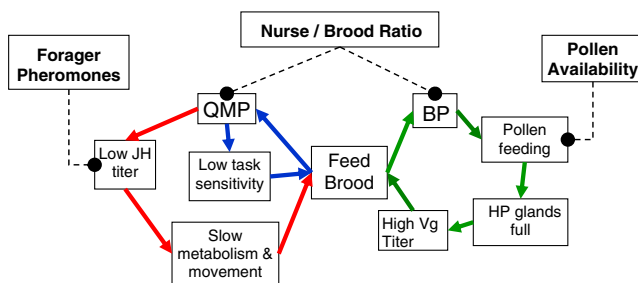


**Fig. 4** Model for the priming mechanisms of the nursing caste. The central behavior, brood feeding, exposes bees to queen mandibular gland pheromone (QMP) and brood pheromone (BP), two phero-mones with multiple priming effects. BP primes bees for the physiological demands of nursing, while QMP makes them unlikely to leave the brood zone and perhaps unresponsive to non-brood-care task stimuli. There are three key releasing mechanisms: pollen availability, forager pheromones, and most important, the nurse to brood ratio (all shown in *bold*). These releasers relate colony level information to the individual and trigger the adaptive transition to the middle-aged bees' caste

titer (Mohammedi et al. 1996; Le Conte et al. 2001; Pankiw et al. 1998, 2004; Pankiw and Page 2001; Pankiw 2004a; Guidugli et al. 2005; Nelson et al. 2007). QMP also suppresses JH production, leading to decreased metabolism and slow movement rates, which make a bee unlikely to leave the brood zone (Kaatz et al. 1992; Pankiw et al. 1998). QMP further depresses dopamine (Beggs et al. 2007), which along with other low neurochemical titers in the brain, many of which appear to increase in a purely endogenous aging process, may lead (via unknown neuro-logical mechanisms) to decreased task sensitivity (Taylor et al. 1992; Schulz and Robinson 1999; Pankiw et al. 1998; reviewed in Robinson 2002; Vergoz et al. 2007; Beggs and Mercer 2009). This decreased task sensitivity makes a nurse unlikely to work on tasks unrelated to brood care. The model proposes that a break anywhere in either of these cycles weakens the reinforcing process and facilitates a transition to the middle-aged caste. As mentioned previously, these breaks, or releasers, take the form of information-rich cues or signals that inform a bee when a change in caste is adaptive at the colony level. The most important of these for the nursing to MAB transition is the ratio of nurses to brood. When new workers eclose, the newly emerged bees are proposed to push the old nurses out of the brood zone and into the periphery of the nest. The nurses pushed out of the brood nest are then no longer exposed to either QMP or BP and the priming processes centered on these pheromones are turned off triggering the transition to the MAB caste.

The pushing process itself is proposed to be based on two effects, one physical and the other physiological and behavioral. A brood comb has approximately 6,000 cells (developing larva), but only space for about 2,000 adult bees (Winston 1987; Camazine 1991). This is because the developing bees are stacked vertically within the comb, while the adult bees stand horizontally on it. Thus, when bees emerge, there is physically not enough space on the comb for the nurses and newly emerged bees. Some of this pressure is relieved by the newly emerged bees spending a lot of time within cells, but as the cells get cleaned, this factor decreases. Hence, some of the bees must leave, and the question becomes who. As mentioned previously, the newly emerged bees are continuing development. To do this, they need pollen (located within the brood zone), and recent work suggests that they need heat as well for their flight muscles to develop (Huang, unpublished results). Further, authors have long noticed that newly emerged bees, which are often removed from the nest for marking, always return to the brood zone when returned to the nest (Robinson et al. 1994; Calderone 1998). Thus, in sum, when a comb of brood emerges, there is insufficient space for all the bees to remain in that location, and it is proposed that it is the nurse bees who tend to leave because the newly

emerged bees have physiological requirements for development that can only be satisfied within the brood zone.

## The MAB state as a long cascade

We now focus on the physiological basis of the MAB. Here, the general model is modified to account for the unique biology of the honeybee. Unlike for the nursing caste, which is proposed to be based on mutually reinforcing mechanisms that freeze a bee in place, it is proposed that the middle-aged caste is a long slow cascade of changing hormonal titers, the end result of which is the capacity to forage. This hypothesis explains why studies have had difficulty defining one clear MAB physiological state (Huang et al. 1994; Huang and Robinson 1995; Cash et al. 2005). It is proposed that the transition out of the nursing caste is dependent on three processes that may or may not interact. These are decreased exposure to BP, decreased exposure to QMP, and exposure to novel task stimuli (Fig. 5). Purely endogenous aging processes that affect various neurochemical titers also likely occur (reviewed in Amdam and Omholt 2003). Although the nature of the MAB defining cascade is poorly understood, as most studies of the proximate basis of DOL have ignored the MAB caste, the following preliminary hypothesis should be useful for guiding future research.

It is proposed that decreased exposure to BP, which stimulates the HP glands and is associated with pollen feeding (reviewed in Amdam and Omholt 2003; Le Conte and Hefetz 2008), causes a slow decrease in the titer of Vg. Simultaneous with this slow decline in Vg is a slight increase in JH, due to decreased exposure to QMP (Kaatz et

al. 1992; Pankiw et al. 1998). JH is hypothesized to further depress Vg levels by inhibiting its synthesis (Fahrbach and Robinson 1996; Pinto et al. 2000). It is also likely that still unknown neural effects of decreased exposure to BP and QMP, along with the exposure to novel task stimuli, allow for the triggering of until now suppressed response thresholds for MAB tasks (Vergoz et al. 2007; Beggs and Mercer 2009). These effects together (high Vg, low JH, and low exposure to both BP and QMP) are proposed to lead to early MAB behavior, which is centered on comb building and nest maintenance. It is then proposed that JH continues to increase at a rate proportional to the amount of inhibitor received via trophallaxis from foragers until a threshold is reached at which point certain neurochemicals, such as octopamine, increase in titer (Harris and Woodring 1999; Wagener-Hulme et al. 1999; Schulz and Robinson 1999; Schulz et al. 2002a, b; Barron et al. 2002; Barron and Robinson 2005; Robinson 2002). An alternative is that high Vg titer inhibits JH production (Guidugli et al. 2005), so once Vg titer falls below a critical threshold, JH production surges triggering other neurochemical changes leading to the final stage of MAB behavior. The developmentally most mature MAB are hypothesized to be fully capable of foraging and to only require input from the releaser (recruitment via the dance language after failure to find work as a receiver) to rapidly make the change to foraging. The releaser would presumably lead to increased expression of the *for* gene, increase of octopamine in the antennal lobes, and other immediate precursors of foraging (Schulz et al. 2003; Ben-Shahar et al. 2002; Ben-Shahar 2005). Increased expression of the many other genes shown to change in expression with the transition to foraging would ultimately result as well (Whitfield et al. 2003, 2006; Alaux et al. 2009).
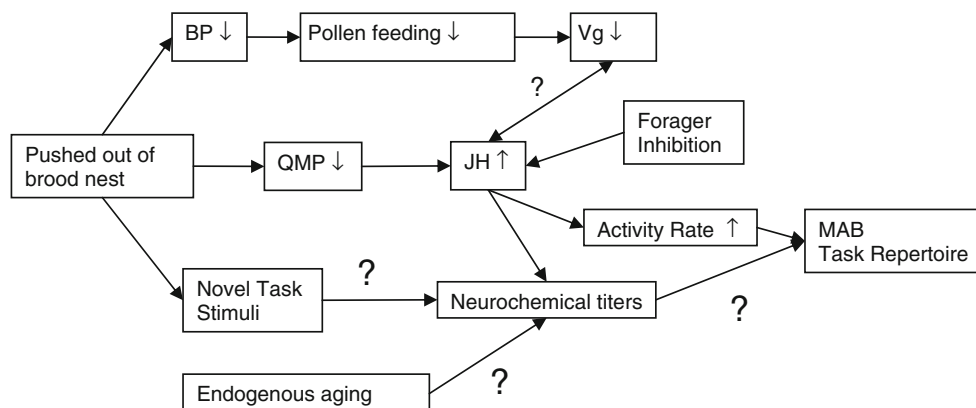


Fig. 5 The proximate basis of the middle-aged bees' (MAB) caste is hypothesized to be a long endocrinological cascade that controls the rate at which MAB acquire the capacity to forage. Too little research has focused on the MAB caste to allow for a mechanism as detailed as for nurses. However, there are four basic processes triggered by the following events: decreased exposure to brood pheromone, decreased exposure to queen mandibular gland pheromone, exposure to novel task stimuli, and an endogenous rise in neurochemical titers unrelated to the priming feedback mechanisms. *Question marks* stress portions of this process that are particularly poorly understood

## Forager priming mechanisms

We have been discussing a developmental process, most of which have a beginning and an end. Thus, we focused either on how workers are frozen in place developmentally (nurses) or the mechanism by which their rate of development is paced (MAB). In the case of the foragers, however, their physiological state is the end point. An elaborate priming mechanism may thus not be necessary for keeping them in place. A physiological mechanism for the maintenance of the forager state may therefore be as simple as the titer of some circulating peptide, such as JH, inhibiting the expression of genes associated with key factors associated with earlier castes (as proposed by Beshers et al. 2001; Amdam and Omholt 2003).

## Winter bee priming mechanisms and triggers

The winter bee state is much like the nursing caste, as it is characterized by low JH, active fat body, high Vg, and high immunocompetence (Fukuda and Sekiguchi 1966; Fluri et al. 1982; Huang and Robinson 1995; Amdam and Omholt 2003). It is, therefore, possible that the winter state is simply an extended period in the nursing caste. However, there are reasons why this is not likely the case. Winter bees do not transition out of their state when the amount of brood is low, or when the number of foragers is low, as do nurses. In fact, all of the bees in winter show the same physiological state, so the mechanisms that govern temporal polyethism are likely inactivated. A critical test of how similar nurses and winter bees actually are will be to measure the titers in winter bees of the neurochemicals known to show differential expression with respect to temporal polyethism. Nurses have low levels of dopamine and octopamine, for example, which presumably limits the scope of their behavior (Taylor et al. 1992; Wagener-Hulme et al. 1999; Beggs et al. 2007). If winter bees are generalists, however, and can do any task, then they should have higher levels of these neurochemicals (or at least greater ability to increase them quickly). Data from overage nurses in summer colonies suggests that this could be the case, as these bees have many important physiological differences with normal age nurses (reviewed in Wegener et al. 2009).

The transition to the winter stage obviously occurs with the arrival of the winter. Mattila and Otis (2007) recently showed that among the many cues that are correlated with the arrival of winter, the presence of pollen in the field seems to be the most important. In short, the decline in pollen supply, which is necessary for brood rearing (Keller et al. 2005), leads to a reduction in the amount of brood in the nest. Workers that emerge in colonies with little to no

brood transition to the winter bee state (Maurizio 1950; Omholt 1988). With respect to how the older bees know when to transition to the winter state, there is insufficient data for an elaborate hypothesis. Via some still unknown mechanism, the state of a broodless colony with inactive foragers triggers the bees to transition to the winter bee state. Of course, there are many variables associated with this condition that could be used as cues. How winter bees determine that it is time to begin brood rearing in the middle of winter is also poorly understood (Omholt 1987).

## Experimentally induced transitions

The model for the proximate basis of temporal polyethism proposes that a mutually reinforcing priming mechanism freezes a worker developmentally in place until an adaptive trigger is received from the environment or colony demography signaling that a change is necessary. Until now, I have focused on the adaptive triggers. However, the model can also explain many cases of experimentally induced transitions via the same mechanism. Instead of an adaptive trigger being received, however, the researcher artificially breaks the reinforcing mechanism in a place that would not happen naturally. Cases of experimentally induced acceleration of development (precocious foraging) can be explained in this way. Experimentally induced caste reversions, in contrast, are likely either of two things: adaptive strategies for reorganizing after a demographic disturbance or experimentally induced transitions to the winter bee (or some hybrid caste) stage.

Many studies have explored the transition to foraging by exposing young workers to substances involved in the transition to foraging. Treatment with JH or octopamine, for example, accelerates the rate at which workers become foragers (reviewed in Beshers et al. 2001; Robinson 2002). As Fig. 3 illustrates, according to the model, the maintenance of the nursing caste is based on reinforcing processes that continually expose a worker to two priming pheromones, BP and QMP. If treatment with JH or octopamine causes the nurse to leave the brood zone more often than normal (by increasing their activity rate (Fussnecker et al. 2006), for example), then it will break this priming mechanism. It is further likely that a break anywhere in the priming mechanism, such as an inability to synthesize a necessary physiological factor (Amdam et al. 2006; Toth et al. 2005; Toth and Robinson 2005), will break the priming mechanisms and trigger the endocrinological cascade to the next caste. I assume that nurses switch to the MAB caste and not directly to foraging in studies of precocious foraging because in such studies, the treatment is applied to the bees and then 7–10 days later, they begin to forage (reviewed in Robinson 2002; Elekonich and Roberts 2005).

A likely cause of the lag time between treatment and response is that the nurses transition to the MAB caste first then quickly transition from this caste to the foraging caste.

When the youngest bees are removed from a colony, about 20% of the foragers reacquire the ability to nurse (Page et al. 1992; Robinson 1992; Huang and Robinson 1996). It is clear that both the nurses and the foragers contain chemical signals that modulate the development of both groups and could be the basis of this ability (Huang and Robinson 1992, 1996; Pankiw 2004b; Leoncini et al. 2004). Further, the social inhibition model shows that the forager's inhibitor signal alone (Huang and Robinson 1999; Leoncini et al. 2004) could provide foragers with sufficient information to determine that reversion is necessary. However, it is still not clear whether the foragers use information from their own inhibitory signal, information from the nursing signal (still unidentified but demonstrated by Pankiw 2004b), or both. Modeling alone, which could show that any of the possibilities are plausible, will not address the issue. Experimental studies of colonies in which the young bees have been removed but the colony is supplemented with varying concentrations of their chemical extracts could resolve the question.

## Relationship to previous models

The model presented here owes large debts to several previous models. As Calderone (1998) pointed out previously, models such as the social inhibition model (Beshers et al. 2001) and the double repressor model (Amdam and Omholt 2003) are "innate developmental program" models (IDP). They posit that temporal polyethism is a flexible process proscribed by developmental programs that receive inputs from the environment. In contrast, the foraging for work (FFW) model proposes that temporal polyethism is the result of spatial environmental effects (Tofts and Franks 1992; Franks and Tofts 1994). The present model merges the IDP and FFW approaches.

While the IDP approach acknowledges that important input comes from the environment, most of the environmental effects considered relate to colony demography. Other environmental effects, such as the layout of tasks and fluctuations in their demand, are given little emphasis. Thus, while critics of the FFW hypothesis are correct that it neglects key developmental and physiological constraints (reviewed in Calderone and Page 1996; Calderone 1998), it is still likely that the type of spatial effects stressed by the FFW model and the physiological processes of the IDP approach interact to control the dynamics of DOL. The hypothesis proposed for the regulation of the nursing caste is a prime example, as the primer pheromones co-occur together in one region of the nest, and nurses have

neurophysiological characteristics that would seem to bias them against leaving this region. Future work will hopefully not only pay greater attention to such spatial effects but also to the rich body of behavioral work (reviewed in Seeley 1995) that can be the basis for hypotheses for caste transitions, such as the MAB to forager transition, that happen too quickly to be based on purely developmental processes.

## References

Alaux C, Le Conte Y, Adams HA, Rodriguez-Zas S, Grozinger CM, Sinha S, Robinson GE (2009) Regulation of brain gene expression in honey bees by brood pheromone. Genes Brain Behav 8:309–319

Amdam GV, Omholt SW (2003) The hive bee to forager transition in honeybee colonies: the double repressor hypothesis. J Theor Biol 223:451–464

Amdam GV, Page RP (2005) Intergenerational transfers may have decoupled physiological and chronological age in a eusocial insect. Ageing Res Rev 4:398–408

Amdam GV, Norberg K, Hagen A, Omholt SW (2003) Social exploitation of vitellogenin. Proc Natl Acad Sci USA 100:1799–1802

Amdam GV, Norberg K, Page RE, Erber J, Scheiner R (2006) Downregulation of vitellogenin gene activity increases the gustatory responsiveness of honey bee workers (*Apis mellifera*). Behav Brain Res 169:201–205

Barron AB, Robinson GE (2005) Selective modulation of task performance by octopamine in honey bee (*Apis mellifera*) division of labour. J Comp Physiol A 191:659–668

Barron AB, Schulz DJ, Robinson GE (2002) Octopamine modulates responsiveness to foraging-related stimuli in honey bees (*Apis mellifera*). J Comp Physiol A 188:603–610

Beekman M, Fathke RL, Seeley TD (2006) How does an informed minority of scouts guide a honeybee swarm as it flies to its new home? Anim Behav 71:161–171

Beekman M, Gilchrist AL, Duncan M, Sumpter DJT (2007) What makes a honeybee scout? Behav Ecol Sociobiol 61:985–995

Beggs KT, Mercer AR (2009) Dopamine receptor activation by honey bee queen pheromone. Curr Biol 19:1206–1209

Beggs KT, Glendining KA, Marechal NM, Vergoz V, Nakamura I, Slessor KN, Mercer AR (2007) Queen pheromone modulates brain dopamine function in worker honey bees. Proc Natl Acad Sci USA 104:2460–2464

Ben-Shahar Y (2005) The foraging gene, behavioral plasticity, and honeybee division of labor. J Comp Physiol A 191:987–994

Ben-Shahar Y, Robichon A, Sokolowski MB, Robinson GE (2002) Influence of gene action across different time scales on behavior. Science 296:741–744

Beshers SN, Fewell JF (2001) Models of division of labor in social insects. Annu Rev Entomol 46:413–440

Beshers SN, Huang ZY, Oono Y, Robinson GE (2001) Social inhibition and the regulation of temporal polyethism in honey bees. J Theor Biol 213:461–479

Breed MD, Robinson GE, Page RE (1990) Division of labor during honey bee colony defense. Behav Ecol Sociobiol 27:395–401

Calderone NW (1998) Proximate mechanisms of age polyethism in the honey bee, Apis mellifera L. Apidologie 29:127–158

Calderone NW, Page RE (1988) Genotypic variability in age polyethism and task specialization in the honey bee, Apis mellifera (Hymenoptera, Apidae). Behav Ecol Sociobiol 22:17–25

Calderone NW, Page RE (1991) Evolutionary genetics of division of labor in colonies of the honey bee (Apis mellifera). Am Nat 138:69–92

Calderone NW, Page RE (1996) Temporal polyethism and behavioural canalization in the honey bee, Apis mellifera. Anim Behav 51:631–643

Camazine S (1991) Self organizing pattern formation on the combs of honey bee colonies. Behav Ecol Sociobiol 28:61–76

Cash AC, Whitfield CW, Ismail N, Robinson GE (2005) Behavior and the limits of genomic plasticity: power and replicability in microarray analysis of honeybee brains. Genes Brain Behav 4:267–271

Crailsheim K (1991) Interadult feeding of jelly in honeybee (Apis mellifera L) colonies. J Comp Physiol B 161:55–60

Crailsheim K (1992) The flow of jelly within a honeybee colony. J Comp Physiol B 162:681–689

De Vries H, Biesmeijer JC (1998) Modelling collective foraging by means of individual behaviour rules in honey-bees. Behav Ecol Sociobiol 44:109–124

Elekonich MM, Roberts SP (2005) Physiological underpinnings of behavioral development in honey bees. Comp Biochem Physiol 141:362–371

Fahrbach SE, Robinson GE (1996) Juvenile hormone, behavioral maturation, and brain structure in the honey bee. Dev Neurosci 18:102–114

Fewell JH, Bertram SM (1999) Division of labor in a dynamic environment: response by honeybees (Apis mellifera) to graded changes in colony pollen stores. Behav Ecol Sociobiol 46:171–179

Fluri P, Luscher M, Wille H, Gerig L (1982) Changes in weight of the pharyngeal gland and titers of juvenile hormone, protein and vitellogenin in worker honey bees. J Insect Physiol 28:61–68

Franks NR, Tofts C (1994) Foraging for work: how tasks allocate workers. Anim Behav 48:470–472

Free JB (1965) The allocation of duties among worker honeybees. Symp Zool Soc Lond 14:39–59

Fukuda H, Sekiguchi F (1966) Seasonal change of the honeybee worker longevity in Sapporo, North Japan, with notes on some factors affecting life span. Jpn J Ecol 16:206–212

Fussnecker BL, Smith BH, Mustard JA (2006) Octopamine and tyramine influence the behavioral profile of locomotor activity in the honey bee (Apis mellifera). J Insect Physiol 52:1083–1092

Grozinger CM, Robinson GE (2002) Microarray analysis of pheromone-mediated gene expression in the honey bee brain. Integr Comp Biol 42:1237

Grozinger CM, Sharabash NM, Whitfield CW, Robinson GE (2003) Pheromone-mediated gene expression in the honey bee brain. Proc Natl Acad Sci USA 100:14519–14525

Guidugli KR, Nascimento AM, Amdam GV, Barchuk AR, Omholt S, Simoes ZLP, Hartfelder K (2005) Vitellogenin regulates hormonal dynamics in the worker caste of a eusocial insect. FEBS Lett 579:4961–4965

Harris JW, Woodring J (1999) Effects of dietary precursors to biogenic amines on the behavioural response from groups of caged worker honey bees (Apis mellifera) to the alarm pheromone component isopentyl acetate. Physiol Entomol 24:285–291

Haydak MH (1963) Age of nurse bees and brood rearing. J Apic Res 2:101–103

Hepburn HR, Radloff SE (1998) Honeybees of Africa. Springer, Berlin

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge

Huang ZY, Robinson GE (1992) Honeybee colony integration: worker–worker interactions mediate hormonally regulated plasticity in division of labor. Proc Natl Acad Sci USA 89:11726–11729

Huang ZY, Robinson GE (1995) Seasonal changes in juvenile hormone titers and rates of biosynthesis in honey bees. J Comp Physiol B 165:18–28

Huang ZY, Robinson GE (1996) Regulation of honey bee division of labor by colony age demography. Behav Ecol Sociobiol 39:147–158

Huang ZY, Robinson GE (1999) Social control of division of labor in honey bee colonies. In: Detrain C, Deneubourg JL, Pasteels JM (eds) Information processing in social insects. Birkhauser Press, Basel

Huang ZY, Robinson GE, Borst DW (1994) Physiological correlates of division of labor among similarly aged honey bees. J Comp Physiol A 174:731–739

Jeanne RL (1986) The organization of work in Polybia occidentalis: costs and benefits of specialization in a social wasp. Behav Ecol Sociobiol 19:333–341

Jeanne RL (1999) Group size, productivity, and information flow in social wasps. In: Detrain C, Deneubourg JL, Pasteels JM (eds) Information processing in social insects. Birkhauser Press, Basel

Johnson BR (2003) Organization of work in the honeybee: a compromise between division of labour and behavioural flexibility. Proc R Soc Lond B 270:147–152

Johnson BR (2005) Limited flexibility in the temporal caste system of the honey bee. Behav Ecol Sociobiol 58:219–226

Johnson BR (2008a) Global information sampling in the honey bee. Naturwissenschaften 95:523–530

Johnson BR (2008b) Within-nest temporal polyethism in the honey bee. Behav Ecol Sociobiol 62:777–784

Johnson BR (2009) A self-organizing model for task allocation via frequent task quitting and random walks in the honey bee. Am Nat 174:537–547

Kaatz HH, Hildebrandt H, Engels W (1992) Primer effect of queen pheromone on juvenile hormone biosynthesis in adult worker honey bees. J Comp Physiol B 162:588–592

Keller I, Fluri P, Imdorf A (2005) Pollen nutrition and colony development in honey bees: part I. Bee World 86:3–10

Kryger P, Kryger U, Moritz RFA (2000) Genotypical variability for the tasks of water collecting and scenting in a honey bee colony. Ethology 106:769–779

Le Conte Y, Hefetz A (2008) Primer pheromones in social hymenoptera. Annu Rev Entomol 53:523–542

Le Conte Y, Mohammedi A, Robinson GE (2001) Primer effects of a brood pheromone on honeybee behavioural development. Proc R Soc Lond B 268:163–168

Leoncini I, Le Conte Y, Costagliola G, Plettner E, Toth AL, Wang MW, Huang Z, Becard JM, Crauser D, Slessor KN, Robinson GE (2004) Regulation of behavioral maturation by a primer pheromone produced by adult worker honey bees. Proc Natl Acad Sci USA 101:17559–17564

Lindauer M (1952) Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. Z Vergl Physiol 34:299–345

Linksvayer TA, Fondrk MK, Page RE (2009) Honeybee social regulatory networks are shaped by colony-level selection. Am Nat 173:E99–E107

Mattila HR, Otis GW (2007) Dwindling pollen resources trigger the transition to broodless populations of long lived honeybee each autumn. Ecol Entomol 32:496–505

Maurizio A (1950) The influence of pollen feeding and brood rearing on the length of life and physiological condition of the honeybee: preliminary report. Bee World 31:9–12

Michener CD (1974) The social behavior of the bees. Harvard University Press, Cambridge

Milojevic BD (1940) A new interpretation of the social life of the honeybee. Bee World 21:39–41

Mohammedi A, Crauser D, Paris A, LeConte Y (1996) Effect of a brood pheromone on honeybee hypopharyngeal glands. C R Acad Sci, Sér 3 Sci Vie 319:769–772

Moritz RFA, Crewe RM, Hepburn HR (2001) Attraction and repellence of workers by the honeybee queen (Apis mellifera L.). Ethology 107:465–477

Nelson CM, Ihle KE, Fondrk MK, Page RE, Amdam GV (2007) The gene vitellogenin has multiple coordinating effects on social organization. PLoS Biology 5:673–677

Oldroyd BP, Thompson GJ (2007) Behavioural genetics of the honey bee Apis mellifera. Adv Insect Physiol 33:1–49

Omholt SW (1987) Why honeybees rear brood in winter: a theoretical study of the water conditions in the winter cluster of the honeybee, Apis mellifera. J Theor Biol 128:329–337

Omholt SW (1988) Relationships between worker longevity and the intracolonial population dynamics of the honeybee. J Theor Biol 130:275–284

Oster GF, Wilson EO (1978) Caste and ecology in social insects. Princeton University Press, Princeton

Page RE, Erber J (2002) Levels of behavioral organization and the evolution of division of labor. Naturwissenschaften 89:91–106

Page RE, Robinson GE (1991) The genetics of division of labor in honey bee colonies. Adv Insect Physiol 23:117–169

Page RE, Robinson GE, Britton DS, Fondrk MK (1992) Genotypic variability for rates of behavioral development in worker honey-bees (Apis mellifera L). Behav Ecol 3:173–180

Page RE, Fondrk MK, Hunt GJ, Guzman-Novoa E, Humphries MA, Nguyen K, Greene AS (2000) Genetic dissection of honeybee (Apis mellifera L.) foraging behavior. J Heredity 91:474–479

Pankiw T (2004a) Brood pheromone regulates foraging activity of honey bees (Hymenoptera: Apidae). J Econ Entomol 97:748–751

Pankiw T (2004b) Worker honey bee pheromone regulation of foraging ontogeny. Naturwissenschaften 91:178–181

Pankiw T, Page RE (2001) Brood pheromone modulates honeybee (Apis mellifera L.) sucrose response thresholds. Behav Ecol Sociobiol 49:206–213

Pankiw T, Huang ZY, Winston ML, Robinson GE (1998) Queen mandibular gland pheromone influences worker honey bee (Apis mellifera L.) foraging ontogeny and juvenile hormone titers. J Insect Physiol 44:685–692

Pankiw T, Roman R, Sagili RR, Zhu-Salzman K (2004) Pheromone-modulated behavioral suites influence colony growth in the honey bee (Apis mellifera). Naturwissenschaften 91:575–578

Pinto LZ, Bitondi MMG, Simoes ZLP (2000) Inhibition of vitellogenin synthesis in Apis mellifera workers by a juvenile hormone analogue, pyriproxyfen. J Insect Physiol 46:153–160

Pratt SC (1998) Condition-dependent timing of comb construction by honeybee colonies: how do workers know when to start building? Anim Behav 56:603–610

Ribbands R (1953) The behaviour and social life of honeybees. London Dover Publ Inc, New York

Robinson EJH (2009) Physiology as a caste-defining feature. Insect Soc 56:1–6

Robinson GE (1992) Regulation of division of labor in insect societies. Annu Rev Entomol 37:637–665

Robinson GE (2002) Genomics and integrative analyses of division of labor in honeybee colonies. Am Nat 160:S160–S172

Robinson GE, Page RE, Huang ZY (1994) Temporal polyethism in social insects is a developmental process. Anim Behav 48:467–469

Robinson GE, Grozinger CM, Whitfield CW (2005) Sociogenomics: social life in molecular terms. Nat Rev Genet 6:257–271

Rösch GA (1930) Untersuchungen ¨uber die Arbeitsteilung im Bienenstaat, II. Z Vergl Physiol 12:1–71

Rueppell O, Pankiw T, Nielsen DI, Fondrk MK, Beye M, Page RE (2004) The genetic architecture of the behavioral ontogeny of foraging in honeybee workers. Genetics 167:1767–1779

Schmickl T, Crailsheim K (2007) HoPoMo: a model of honeybee intracolonial population dynamics and resource management. Ecol Model 204:219–245

Schmickl T, Crailsheim K (2008) An individual-based model of task selection in honeybees. From animals to animats 10. Lect Notes Comput Sci 5040:383–392

Schmidt-Hempel P, Wolf T (1988) Foraging effort and life span of workers in a social insect. J Anim Ecol 57:509–521

Schulz DJ, Robinson GE (1999) Biogenic amines and division of labor in honey bee colonies: behaviorally related changes in the antennal lobes and age-related changes in the mushroom bodies. J Comp Physiol A 184:481–488

Schulz DJ, Huang ZY, Robinson GE (1998) Effects of colony food shortage on behavioral development in honey bees. Behav Ecol Sociobiol 42:295–303

Schulz DJ, Barron AB, Robinson GE (2002a) A role for octopamine in honey bee division of labor. Brain Behav Evol 60:350–359

Schulz DJ, Sullivan JP, Robinson GE (2002b) Juvenile hormone and octopamine in the regulation of division of labor in honey bee colonies. Horm Behav 42:222–231

Schulz DJ, Elekonich MM, Robinson GE (2003) Biogenic amines in the antennal lobes and the initiation and maintenance of foraging behavior in honey bees. J Neurobiol 54:406–416

Seeley TD (1979) Queen substance dispersal by messenger workers in honeybee colonies. Behav Ecol Sociobiol 5:391–415

Seeley TD (1982) Adaptive significance of the age polyethism schedule in honeybee colonies. Behav Ecol Sociobiol 11:287–293

Seeley TD (1985) Honeybee ecology. Princeton University Press, Princeton

Seeley TD (1989a) Social foraging in honey bees: how nectar foragers assess their colony nutritional status. Behav Ecol Sociobiol 24:181–199

Seeley TD (1989b) The honey bee colony as a superorganism. Am Sci 77:546–553

Seeley TD (1992) The tremble dance of the honey bee: message and meanings. Behav Ecol Sociobiol 31:375–383

Seeley TD (1995) The wisdom of the hive. Harvard University Press, Cambridge

Seeley TD, Tovey CA (1994) Why search time to find a food storer bee accurately indicates the relative rates of nectar collecting and nectar processing in honey bee colonies. Anim Behav 47:311–316

Seeley TD, Towne WF (1992) Tactics of dance choice in honey bees: do foragers compare dances. Behav Ecol Sociobiol 30:59–69

Seeley TD, Visscher PK (2004) Quorum sensing during nest-site selection by honeybee swarms. Behav Ecol Sociobiol 56:594–601

Sekiguchi K, Sakagami F (1966) Structure of the foraging population and related problems in the honeybee with considerations on the division of labor in bee colonies. Hokkaido Natl Agric Exp Sta Rep 69:1–65

Slessor KN, Winston ML, Le Conte Y (2005) Pheromone communication in the honeybee (Apis mellifera L.). J Chem Ecol 31:2731–2745

Smith CR, Toth AL, Suarez AV, Robinson GE (2008) Genetic and genomic analyses of the division of labour in insect societies. Nat Rev Genet 9:735–748

Southwick EE (1983) The honey bee cluster as a homeothermic superorganism. J Comp Physiol A 71:641–645

Taylor DJ, Robinson GE, Logan BJ, Laverty R, Mercer AR (1992) Changes in brain amine levels associated with the morphological and behavioral development of the worker honeybee. J Comp Physiol A 170:715–721

Tofts C, Franks NR (1992) Doing the right thing: ants, honeybees, and naked mole rats. Trends Ecol Evol 7:346–349

Toth AL, Robinson GE (2005) Worker nutrition and division of labour in honeybees. Anim Behav 69:427–435

Toth AL, Kantarovich S, Meisel AF, Robinson GE (2005) Nutritional status influences socially regulated foraging ontogeny in honey bees. J Exp Biol 208:4641–4649

Trumbo ST, Huang ZY, Robinson GE (1997) Division of labor between undertaker specialists and other middle-aged workers in honey bee colonies. Behav Ecol Sociobiol 41:151–163

Velthuis HH (1972) Observations on transmission of queen substance in honey bee colony by attendants of queen. Behaviour 41:105–129

Vergoz V, Schreurs HA, Mercer AR (2007) Queen pheromone blocks aversive learning in young worker bees. Science 317:384–386

Visscher PK (2007) Group decision making in nest-site selection among social insects. Annu Rev Entomol 52:255–275

Visscher PK, Dukas R (1997) Survivorship of foraging honey bees. Insectes Soc 44:1–5

Wagener-Hulme C, Kuehn JC, Schulz DJ, Robinson GE (1999) Biogenic amines and division of labor in honey bee colonies. J Comp Physiol A 184:471–479

Wegener J, Lorenz MW, Bienefeld K (2009) Physiological consequences of prolonged nursing in the honey bee. Insectes Soc 56:85–93

Whitfield CW, Cziko AM, Robinson GE (2003) Gene expression profiles in the brain predict behavior in individual honey bees. Science 302:296–299

Whitfield CW, Ben-Shahar Y, Brillet C, Leoncini I, Crauser D, LeConte Y, Rodriguez-Zas S, Robinson GE (2006) Genomic dissection of behavioral maturation in the honey bee. Proc Natl Acad Sci USA 103:16068–16075

Williams JB, Roberts SP, Elekonich MM (2008) Age and natural metabolically-intensive behavior affect oxidative stress and antioxidant mechanisms. Exp Gerontol 43:538–549

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge

Wilson EO (1976) Behavioral discretization and number of castes in an ant species. Behav Ecol Sociobiol 1:141–154

Winston ML (1987) The biology of the honey bee. Harvard University Press, Cambridge