Organization of work in the honeybee: a compromise between division of labour and behavioural flexibility

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Although the caste concept has been central to our understanding of the organization of work in social insect colonies, the concept has been the subject of considerable recent criticism. Theoretically, it has been suggested that temporal castes are too inflexible to allow a colony to rapidly reallocate labour in response to changing conditions. In addition, several authors have suggested that task switching is so prevalent that it precludes even the possibility of a rigidly controlled temporal caste system. This study addresses these two criticisms by presenting and testing a revision of the temporal caste concept that recognizes two categories of tasks: those that require a physiological specialization for their efficient performance, and those that all workers are equally able to perform. Only those tasks requiring a physiological specialization are relevant to the temporal caste concept. Two castes of honeybees were shown to vary in response to increased nectar influx, which requires a physiological specialization, but not to heat stress, which requires no specialization. This work suggests that the organization of work in social insect colonies reflects a compromise between selection for the benefits of division of labour and opposing selection for flexibility in task allocation.

Keywords: division of labour; task allocation; social insects; *Apis mellifera*; temporal polyethism

1. INTRODUCTION

The concept of caste, a group of workers specialized for a set of tasks, has been central to studies of the organization of work in social insect colonies (Oster & Wilson 1978; Bourke & Franks 1995; Beshers & Fewell 2001). Colonies are thought to contain two types of castes: physical, which are based on morphological differences, and temporal, which are based on temporary periods of specialization among monomorphic workers (Hölldobler & Wilson 1990). In the honeybee, temporal castes are thought to last from one to two weeks, and the sets of tasks performed by each caste are thought to be related to nest architecture (Seeley 1982).

Although the caste concept has clear value for explaining the existence of physical castes, the existence of temporal castes, or temporal polyethism, has been repeatedly questioned. Criticism has been both theoretical and empirical. Theoretically, it has been suggested that a system based on a deterministic relationship between age and role could not be sufficiently flexible to allow a colony rapidly to reallocate labour in response to environmental stress (Tofts & Franks 1992; Bourke & Franks 1995). Empirically, studies of task allocation have led some authors to suggest that task switching is so prevalent that it precludes the existence of an inflexible caste system (Calabi 1988; Gordon 1989).

This study proposes and tests a revision of the caste concept, which addresses these criticisms. This revision centres on recognizing that the concept of temporal caste applies only to certain tasks. Those tasks relevant to the caste concept, physiology-dependent tasks, are those for which a physiological specialization is required for the efficient performance of the task. Those tasks that are

organized independently of the colony's caste structure, physiology-independent tasks, are those that every individual in the colony is equally able to perform. A temporal caste is composed of individuals with a common physiological specialization. In the honeybee, this physiological specialization arises mainly from the activation and deactivation of glands that are necessary for the performance of particular tasks (Winston 1987; Seeley 1995). A more general definition of this physiological specialization would be a physiological state that results in workers being non-interchangeable on a time-scale that is significantly longer than the time-scale of task allocation. Thus, physiological specialization makes individuals within temporal castes temporarily non-interchangeable in a way analogous to how size makes members of physical castes permanently non-interchangeable. In honeybees, for instance, although it is known that workers can reactivate glands after they have atrophied, this reactivation requires several days, whereas the time-scale of task reallocation is, typically, only hours (Robinson 1992).

This revision of the temporal caste concept addresses the previously mentioned theoretical criticism by making temporal castes inherently flexible for two reasons: (i) workers spend only a small minority of their time performing physiology-dependent tasks; and (ii) most tasks are physiology-independent. Large amounts of task switching among physiology-independent tasks is critical to this idea; therefore, this model also has the potential to explain the large amounts of task switching observed in previous studies.

This physiological-caste hypothesis generates a number of predictions. First, increases in the demand for labour for physiology-independent tasks should be met by those individuals most efficiently able to meet the demand inde-

Table 1. Proposed castes of the honeybee with typical age range and physiological specialization(s) unique to each.

caste	typical age range (days)	caste-dependent task(s)	physiological specialization(s)	reference(s)
nurse	3–11	tending/feeding brood	hypopharyngeal glands secreting brood food	Fluri <i>et al.</i> (1982) Seeley (1995) Winston (1987)
food processor	11–20	processing nectar guarding	hypopharyngeal glands producing invertase venom gland fills poison sac mandibular glands producing alarm pheromone wax glands activated	Shearer & Boch (1965) Boch & Shearer (1966) Simpson <i>et al.</i> (1968)
forager	20+	foraging	40% decrease in body mass	Harrison (1986)

pendent of caste. Second, increases in the demand for labour for physiology-dependent tasks should be met primarily through activating reserve labour or task switching within the caste. Finally, behavioural repertoires, the task sets of previous temporal polyethism studies, should be a consequence of the performance of physiology-dependent tasks leading to biases in the performance of physiology-independent tasks located in the same region of the nest.

The honeybee, with its complex and intensely studied system of division of labour, is an ideal system for testing this model. Table 1 lists the castes of the honeybee with the physiological specialization(s) particular to each. Food processors, also called middle-age bees, and nurses form the two castes of workers within the nest. The distribution of the workers in these castes within the nest shows significant overlap (Seeley 1995), hence, the workers in these castes are exposed to many of the same stimuli for both physiology-dependent and independent tasks. Determining the relative response of these two castes to two environmental stresses, heat stress (physiology-independent) and increased nectar flow (physiology-dependent) will reveal the role of caste in task allocation. Simultaneously determining the location and task profile of different castes in the nest will elucidate whether caste behavioural repertoires are adaptive task sets or ephemeral consequences of a caste system organized around physiological specialization for a handful of tasks.

2. MATERIAL AND METHODS

Heat stress and behavioural repertoire experiments were conducted in Ithaca, NY at the Liddell Field Station, while nectar influx experiments were conducted at the Cranberry Lake Biological Station, NY. All experiments were performed from June to September 2001. Three colonies of honeybees were used, two in three-frame observation hives and one in a two-frame hive. The two- and three-frame colonies contained 2000–3000 and 4000–6000 workers, respectively. Each colony contained 300 individually marked workers, 150 nurses (aged 4–8 days) and 150 food processors (aged 14–18 days). Scan sampling and task identification methods followed those of Johnson (2002). Two scans of workers, once every 90 minutes, were performed in heat stress experiments both before and during the heat stress. Five scans of workers, once per hour, were performed in nectar influx experiments on both the low and high nectar influx days.

Methods for the thermoregulation experiment followed those of Johnson (2002), while methods for the controlling of the col-

ony's nectar influx followed those of Seeley *et al.* (1996) to control nectar influx and the methods of Johnson (2002) for data collection. Observations of bees trimming brood cells within the brood nest were collected using scans of individually marked workers in unstressed colonies.

3. RESULTS

Social regulation of the temperature of the brood-nest is a critical adaptation of the honeybee (Heinrich 1993). Deviations from the optimum temperature range of 33–36 °C can cause abnormalities in the development of the brood (Johnson 2002). In response to this challenge, the bees have evolved a complex group-level response (Seeley 1995). Bees respond to heat stress with two behaviours directed towards cooling the nest: fanning, which produces forced convective cooling, and tongue lashing, which generates evaporative cooling (Seeley 1995). These tasks are physiology independent and therefore, a similar response is expected from both castes to heat stress. Figure 1 shows the task distribution of nurses and food processors before and during heat stress. Because neither caste was performing thermoregulatory tasks prior to the heat stress, the response of each caste is simply the number of observations of thermoregulatory tasks during heat stress. The pre- and post-stress task distributions did not differ significantly between the two groups. Both groups, however, switched strongly to thermoregulatory tasks (36.4% versus 40.7%) under heat stress. Figure 2 shows the results of an additional trial of this experiment, which produced similar results. Again the pre-stress distribution did not differ between the castes ($\chi^2 = 7.79$, d.f. = 4, $p = 0.10$), nor did the post-stress task distribution ($\chi^2 = 7.76$, d.f. = 4, $p = 0.10$).

Nectar foraging in the honeybee is a complex process requiring the coordinated efforts of nectar foragers and receivers. Foragers collect nectar and unload it to receivers (food processors) in the lower region of the nest near to the entrance. Food-processing bees then transport the nectar to the honey-storage area at the top of the nest. Previous work has shown that the process of unloading foragers and depositing the nectar in the honey-storage region of the nest is tightly linked (Seeley 1995). This is a physiology-dependent task (see the specializations outlined in table 1). Therefore, an increase in the demand for this task should be met solely by food-processing bees, despite the fact that the labour demand for the task is

Figure 1. Effect of heat stress on the task distribution of nursing (filled bars) and food-processing (open bars) bees, in trial 1. (a) Before heat stress, there was no difference between castes ($\chi^2 = 4.05$, d.f. = 4, $p = 0.4$). Nurses, $N = 71$, total number of observations, 91; food processors, $N = 53$, total number of observations, 80. (b) There was no difference in the overall task distributions between the two castes in response to heat stress, ($\chi^2 = 7.92$, d.f. = 4, $p = 0.09$). Nurses, $N = 73$, total number of observations, 93; food processors, $N = 45$, total number of observations, 56; troph., trophallaxis; therm., thermoregulation.

localized near the brood-nest. Specifically, since the actual unloading is of short duration, the effect of increased nectar flow on a task distribution obtained with scan sampling should be a large increase in walking. This increase in walking reflects the cycles carried out by food processors between the nectar-unloading area and the honey-storage regions of the nest.

Owing to the fact that both castes were performing the focal task at different levels before the treatment, the χ^2 -test was not appropriate here, as it was for the heat stress

Figure 2. Effect of heat stress on the task distribution of nursing (filled bars) and food-processing (open bars) bees, in trial 2. (a) Before heat stress there was no difference between castes ($\chi^2 = 7.79$, d.f. = 4, $p = 0.10$). Nurses, $N = 72$, total number of observations 102; food processors, $N = 58$, total number of observations 87. (b) There was no difference in the overall task distributions between the two castes in response to heat stress, ($\chi^2 = 7.76$, d.f. = 4, $p = 0.10$). Nurses, $N = 70$, total number of observations 85; food processors, $N = 48$, total number of observations 64; troph., trophallaxis; therm., thermoregulation.

experiment. The trials were therefore analysed together using logistic regression to test for a difference in the response of nurses and food processors to increased nectar influx (SAS Institute 1998). Response was calculated as the number of individuals within a caste that were observed walking during each scan. Specifically, I tested for an interaction between caste and environment that, if significant, would indicate that the two castes responded differently to the treatment.

Figures 3 and 4 show the effects of increased nectar flow on the task distributions of nursing and food-processing

Figure 3. Effect of increased nectar influx on the task distribution of nursing (black bars) and food-processing (open bars) bees. Trial 1. (a) Task distributions prior to the increase in nectar influx. Nurses, $N = 144$, total obs. 481; food processors, $N = 83$, total obs. 248. (b) Task distributions in response to increased nectar influx. Nurses, $N = 141$, total obs. 492; food processors, $N = 80$, total obs. 222.

bees. During the first trial of the experiment, the rate of nectar foragers entering the nest per minute increased from 1.1 to 5.9, a more than five-fold increase. During the second trial of the experiment, the rate of foragers entering the hive showed a greater increase relative to the first trial, with the number of foragers entering rising from 2.8 to 17.6 per minute. A significant interaction between caste and environment was found (odds ratio = 1.19, $Z = 3.16$, $p = 0.0016$), indicating that the two castes responded differently to the rise in nectar influx. Food-processing bees had both a larger decrease in standing and a larger increase in walking than the nurse bees. In addition, there was a significant interaction between

Figure 4. Effect of increased nectar influx on the task distribution of nursing (black bars) and food-processing (open bars) bees. Trial 2. (a) Task distributions prior to the increase in nectar influx. Nurses, $N = 63$, total obs. 241; food processors, $N = 96$, total obs. 327. (b) Task distributions in response to increased nectar influx. Nurses, $N = 63$, total obs. 248; food processors, $N = 85$, total obs. 277.

trial and time-period (odds ratio = 0.905, $Z = -1.97$, $p = 0.048$), which was to be expected, since the level of increase in nectar influx was considerably greater in the second trial of the experiment.

Workers are thought to maximize the efficiency of task allocation by specializing in a set of tasks in one region of the nest (Wilson 1985; Seeley 1982). According to the model proposed, this task set should be a consequence of a caste's specialization for one or a handful of tasks that are localized in a particular region of the nest. No further specialization for additional tasks located in this region is expected, as there is probably a trade-off between degree

of specialization and flexibility in task allocation. Hence, the bias in performance of physiology-independent tasks found in previous studies should be due to the biases in the location of workers relating to the performance of physiology-dependent tasks.

Previous work on temporal castes in the honeybee has focused on determining the task sets of each caste from the perspective of the efficiency hypothesis outlined above. One task thought to be part of the behavioural repertoire of nurse bees, based on previous work, is the trimming of brood cells (Seeley 1982). Bees decrease the thickness of the wax layer over developing pupa, prior to the emergence of new workers. To determine if the age bias found in the performance of this task from previous studies was due to locational effects, as opposed to intrinsic factors, I recorded the task distributions of nurses and food processors and their spatial distributions in the nest during a period of high worker emergence. In colony 1, both castes had a similar spatial distribution in the nest, with nurses being observed for 63.1% of the time in the brood-nest and food processors for 52.1% of the time ($\chi^2 = 1.95$, d.f. = 1, $p = 0.16$). There was also no significant difference in the total percentage of observations of trimming of brood cells between the two castes (12.5% to 11.4%) ($\chi^2 = 0.05$, d.f. = 1, $p = 0.83$). In colony 2, however, there was a significant difference in the distribution of the two castes within the nest, with nurses being observed for 82.2% of the time in the brood-nest and food processors for 56.3% of the time ($\chi^2 = 14.95$, d.f. = 1, $p = 0.0001$). In accordance with this, there was also a difference in the total percentage of labour devoted to trimming of brood cells between the two castes, with nurses devoting 24.8% and food processors 12.8% of their time, respectively ($\chi^2 = 4.28$, d.f. = 1, $p = 0.039$). This pattern is consistent with the hypothesis that behavioural repertoires are a result of specialization for one or a few tasks within the repertoire. Age biases in the performance of the remaining tasks may be due to locational effects and not to intrinsic specialization for the performance of those tasks.

4. DISCUSSION

As expected if physiological specialization makes workers non-interchangeable on a time-scale longer than that of task allocation for certain tasks only, an increase in the demand for a physiology-dependent task was met by workers within the caste, while an increase in the demand for a physiology-independent task was met by workers independent of caste.

Previous studies of the organization of work in honeybees have found that workers spend a majority of their time either standing, walking around or patrolling for work (Seeley 1982; Kolmes 1985). The percentage of their remaining time spent on physiology-dependent versus physiology-independent tasks remains unclear, but is probably dependent on the amount of nectar influx into the colony. When the amount of nectar influx is high, middle-age bees are thought to spend most of their time nectar processing, in contrast to when it is low, when they spend more time on other tasks (Seeley *et al.* 1996). Wax working is the most common of these other tasks (Johnson 2002) and is physiology-independent because most wax workers do not have active wax glands (Pratt 1997). Nurse

bees are less active than middle-age bees and spend proportionally more of their time shaping and manipulating wax than nursing, their physiology-dependent task (Seeley 1995).

The work of Huang & Robinson (1999) has clearly demonstrated that temporal polyethism is, in part, a developmental process with an underlying physiological basis. This study completes this picture by relating the underlying physiology to the functional process by which tasks are allocated in undisturbed colonies on the time-scale that task allocation typically operates. This integration of information from multiple levels of biological organization is essential to understanding both the ontogeny and functioning of social insect colonies.

This study attempts to reconcile two opposing views on the organization of work in colonies of social insects: the older view that colonies have evolved to maximize labour efficiency by organizing work around a basic division of labour that centres on the specialization of workers into castes that partition all the colony's tasks, and the recent view that colonies have evolved workers that are highly flexible in task performance. This study suggests that division of labour in insect societies is dependent on an organizational structure that retains the benefits of division of labour while allowing for flexibility in task allocation.

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