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Temporal Patterns of Division of Labor among Workers in the Primitively Eusocial Bumble Bee, *Bombus griseocollis* (Hymenoptera: Apidae)¹⁾

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With 5 figures

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Abstract

The primitively eusocial bee, *Bombus* (~~*Furciterrobombus*~~ ^{*Sepact*} *griseocollis*), possesses a complex temporal division of labor based on shifting patterns of principal tasks rather than on discrete age castes. Workers within a given age range perform ensembles of tasks which change quantitatively as the workers age. Functional classes of behavior, such as nursing or guarding, are not limited to a given age class of workers; all tasks are performed by workers of all ages. Colony ontogeny also influences worker behavioral ontogeny; significant differences in task performance exist among workers born in different phases of colony development. As the colony aged, young bees foraged with increasing probability. In the absence of foraging mortality, foragers shifted to nursing tasks, and were replaced by younger bees.

Introduction

The development of a caste structure is universal among social insects and is a principal theme in the evolution of social organization and behavior (DARWIN 1859; WILSON 1971; OSTER & WILSON 1978; TRANIELLO 1978). Ants and termites have developed a complex social system of reproductive and worker castes. The morphologically distinct reproductive caste consists of from one to several queens (termites have both a king and queen) who specialize in egg-laying. The remainder of the thousands of individuals produced in the colonies of most species are

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members of the mostly sterile worker caste, which may be further differentiated into morphological castes such as soldiers, majors, and minors, each of which specializes in one or a few tasks (reviewed in WILSON 1971). Superimposed on this integrated system of morphological castes is a further subdivision of worker labor based on age (see below). Caste specialization increases the potential ergonomic efficiency of a large colonial group (OSTER & WILSON 1978).

Eusocial bee societies are composed of only two distinct morphological castes, the queen, who is primarily the sole egg-layer in the colony, and the workers, who divide up the remainder of the colony tasks. In bees, workers are not divided into morphological castes. Rather, an effective division of labor exists as a result of the tendency of the workers to specialize on a set of tasks, forming distinct behavioral classes. In all highly eusocial bees that have been studied, workers undergo a sequential transition from one behavioral class to another as they age, a phenomenon known as age polyethism. The behavioral progression is from nurse to forager (reviewed in WILSON 1971, 1985; SEELEY 1985; WINSTON 1987).

The family Apidae includes bees that range from solitary Euglossini, through the primitively eusocial bumble bees (*Bombus*), to the highly eusocial honey bees (*Apis*) and stingless bees (Meliponini). Within the family, age polyethism has been demonstrated for *Apis mellifera* (reviewed in SEELEY 1985; WINSTON 1987) and a few species of stingless bees (reviewed in SOMMEIJER 1984). The closely related bumble bees are a pivotal group in which to study division of labor because they show traits of highly eusocial and primitively eusocial organization, and might therefore exhibit elements of age polyethism. Resembling highly eusocial bees, most *Bombus* species exhibit a significant size dimorphism between the queen and workers. The queen is commonly the principal egg layer in the colony and does not forage after worker emergence. Workers do all of the colony foraging, and usually do not mate, but may lay unfertilized eggs that develop into haploid males. Unlike the highly eusocial bees, bumble bee workers may exhibit significant size polymorphism. Also, their colonies are generally annual and die after the reproductive males and females emerge near the end of the colony cycle (see FREE & BUTLER 1959 for general review of *Bombus*).

Previous studies of division of labor in bumble bees revealed a fundamental division of labor among workers based on their size. Foragers are among the largest bees in the colony, while house bees, which remain on the nest, tend to be small (BRIAN 1952; FREE 1955; GARÓFALO 1978). Larger workers have a shorter lifespan (GOLDBLATT & FELL 1987) and concomitantly, so do foragers, compared to house bees (BRIAN 1952; GARÓFALO 1978). BRIAN (1952) also observed that age secondarily influences foraging. Among potential foragers larger individuals tend to begin foraging at a younger age. These investigations have been important in elucidating some trends in specialization of individuals. Colony-level trends in division of labor in bumble bees have not been studied sufficiently, however, to enable comparisons with highly eusocial ants and honey bees, or with other primitively social groups, such as the halictid bees and polistine wasps. Comparative analyses of colony organization are important because they elucidate the physiological mechanisms and environmental, genetic, and phylogenetic con-

straints that regulate caste and division of labor at diverse levels of sociality. With methods similar to those used in studies of ants (WILSON 1976; CALABI et al. 1983) and honey bees (SEELEY 1982; KOLMES 1985), featuring continuous observation of individuals throughout their lives, I reveal some new characteristics of colony-level division of labor in *Bombus griseocollis*.

Methods

Observations were made on 7 colonies of *Bombus griseocollis* raised in the laboratory from spring queens collected in the vicinity of Lawrence, Kansas, between late April and mid May, 1982. Colonies were confined to control for nutrition and forager mortality. The 7 colonies used were chosen from a pool of 60 laboratory nests because they produced their first brood of workers within the same 24-h period, 13–14 June. Using colonies that were at identical stages of development allowed for pooled analyses (see below).

All colonies were reared (methods of PLOWRIGHT & JAY 1966) in wooden boxes and fed 50 % honey water and fresh pollen collected by *Apis mellifera* workers. Each queen and her entire brood clump was transferred with some nesting material (upholsterer's cotton) to a 33.5 × 23.0 × 24.5 cm clear plexiglas observation box a day or two before the workers of the first brood emerged. Thus the queen had time to adapt to her new nest prior to worker emergence and the workers were not disturbed by nest transfer. Nest activities were observed in these boxes, starting when the first workers emerged. Foraging behavior was recorded when bees left the nest box through a 1 m long glass tunnel connected to a feeder box that contained dispensing units for the honey-water mixture. A small (approx. 0.5 g) pollen lump, formed from a homogeneous source of fresh pollen collected from honey bee hives, was placed directly into the nest box. Foragers were confined to the laboratory to control for differential mortality and severe resource shortages in the dry summer conditions of Lawrence. Of course, confinement eliminated foraging-related mortality. But my objective in this study was to observe division of labor in a controlled environment, in which all replicate colonies were exposed to identical food, temperature, humidity, and light. Within a uniform environment, I could determine the significance, if any, of inter-colony behavioral variability.

All colonies were maintained in the same room under identical temperature and light regimes. Each remained in darkness under an opaque cover (simulating a natural field nest) except during observation periods. Incandescent lighting was used because pilot observations showed no differences in behavior under infrared and incandescent light. Room temperature was held at approximately 20 °C throughout the study.

Following emergence, each callow worker (0–36 h old) was labeled on the thoracic dorsum with a numbered, plastic disc (Opalithplättchen). Bees were fed honey and pollen twice a day to encourage foraging and larval feeding activities, and observations started one half h after providing food. As colonies grew it became necessary to feed them a third time, after the afternoon observation session was completed.

Data-gathering Procedures

37,000 observations of queen and worker acts were recorded during 320 h of observation (40 h per colony). 304 workers were observed from mid-June to late Sep. over the entire 85-day period of colony life. All colonies were observed in random order, twice daily, morning and afternoon, for 15 min. When colonies became too large to record enough acts for each bee within the time period (see below), each colony was observed for 1/2 h once a day, alternating between morning and afternoon observations. All observations were made between 08.00 and 18.00 h. The colonies attained sizes of 25 to 66 workers (CAMERON 1985 a, Appendix I).

A scan sampling method was used. Bees were located in the colonies by age, oldest first. When the first marked bee (oldest) was found, its activity was recorded.

Observations proceeded until the activities of all marked bees were noted. The activity of each bee was recorded at least once during each 15-min session. For young colonies each worker was observed 10–15 times; later, as the colonies grew, each worker was observed 4–8 times during a period.

Classification of Worker Tasks

The following list describes the tasks recorded during observations. Nonsocial activities (e.g., self-grooming) and rare activities (those that represented < 1 % of total acts) have been excluded. The parentheses following each task enclose the two-letter abbreviation used in tables and figures when referring to that task.

1. *Anchoring* (AN): Constructing a wax network fastening the undersurface of a nest to the substrate. Workers secrete the wax from abdominal glands and use their mandibles to smooth and extend the connective structures.

2. *Drinking honey* (DH), *eating pollen* (EP), and *feeding larvae* (FL): To distinguish between self-feeding and food transfer to a larval cell, a bee was followed for several s. If it regurgitated into a larval cell the task, *feeding larvae*, was recorded. If it did not regurgitate, the activity was considered self-feeding (DH or EP).

3. *Incubation* (IB) behavior is exhibited as a bee wraps herself around a cocoon, maximizing the ventral abdominal surface area in contact with the cocoon by elongating and flattening her abdomen. A clearly observable abdominal pumping continues throughout incubation, resulting in heat generation for maintaining the temperature of a pupa inside its cocoon (for additional details, see CAMERON 1985 b).

4. *Inspecting* (IN) workers walk over the brood comb and antennate brood, food receptacles, and the waxy structures of the nest.

5. *Pulling cotton* (PC): Worker bumble bees commonly construct an insulative canopy around their brood clump. In my laboratory colonies, upholsterer's cotton was used as insulation, which workers teased with their forelegs and mandibles to make fluffy and pull up around the brood.

6. *Scraping wax* (SW): Workers recycle the wax envelope that covers cocoons by removing it with their mandibles in a scraping fashion.

7. *Working on a honey pot* (WH): Workers use their mandibles to reshape an empty cocoon into a food receptacle (honey pot or pollen pot); they periodically increase the volume of the pot by adding wax to the rim.

8. *Buzzing* (BZ): A conspicuous sound produced by some workers inside the colony in response to external disturbance of the nest. In this context it is considered as an alarm or colony-defense response.

9. *Foraging* (FO): Foragers can be recognized before leaving the nest or after returning to it by rapid movement and by probing many honey pots in succession. A returning forager, after probing consecutive honey pots, regurgitates the contents of her honey stomach into the pot that claimed her loyalty on previous visits. When a pot is full, she selects another that is empty or partially full.

10. *Perching* (PE): Perching bees stand at the nest entrance or on the periphery of the brood clump with their heads down and antennae raised above their heads. This posture is clearly distinguishable from the rarely observed resting posture in which bees stand on the substrate, usually in a corner, with their antennae hanging loosely in front of the face.

11. *Patrolling* (PA): Rapid walking over the brood clump or back and forth through the entrance tunnel, often for several min at a time. It is difficult to identify patrolling with the same clarity of the other tasks because it can also be a transition behavior. That is, *foragers* often patrol before making their first foraging trip and *perched* bees, if the nest is disturbed, will patrol for several min after other bees have returned to their tasks.

12. *Aggression* (AG) refers to worker-worker or worker-queen interactions, including grasping an appendage between the mandibles, butting at close range various areas of the body, and lunging toward the victim from a distance of several cm.

The above tasks were grouped into functional classes based on a cluster analysis using squared canonical correlation (ANDERBERG 1973; COOLEY & LOHNES 1971) applied to a contingency table (CAMERON 1985 a). Rare activities were included in this analysis, including *inactivity* (IA), *probing a honey pot* (PH), and *excavating* (EX) an empty cocoon.

Classification of Worker Cohorts and Age Classes

To investigate age polyethism, each individual was assigned to a cohort and to age classes based on the four natural phases of the pooled population growth curve of all colonies: initial, growth,

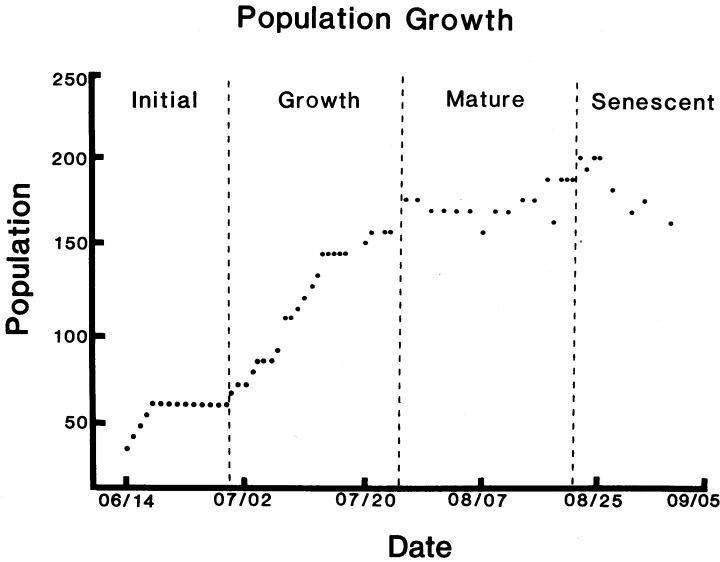


Fig. 1: Pooled population-growth curve of workers for 7 colonies. The dashed vertical lines distinguish the colony phases: Initial, Growth, Mature, Senescent

mature and senescent (Fig. 1). A cohort was composed of all of the workers that emerged during a colony phase, and was named after the phase in which it emerged. Cohorts were followed throughout the life of the colony as they aged and thus could be assigned to sequential age classes. For example, the Initial cohort passed through age classes 1, 2, 3, and 4, corresponding to the initial, growth, mature, and senescent phases (Fig. 1). Thus age class 1 of the Growth cohort corresponded in time to age class 2 of the Initial cohort, and so on.

Relative Probability of Task Performance

For each colony, relative probabilities of task performance (RPTP) (SEELEY 1982) were calculated for eleven of the above-defined tasks. Anchoring, pulling cotton, and inspecting were not included among the nursing tasks because they did not involve direct interaction with the brood. RPTP is defined as "the probability that a worker in a given age class will perform a particular task relative to the probability that a worker in some other designated age class will perform the same task" (SEELEY 1982, p. 289 for methods of calculation). The age class chosen for comparison was the one most likely to perform the task. Three of the four cohorts, Initial, Growth, and Mature, lived long enough to be examined for differences as they aged.

Analyses of Age-based Division of Labor

The hypothesis of age-based division of labor was tested by an analysis of variance that accommodated a random effects in repeated-measures (split-plot) design (KUTNER 1974; Richard CUTLER and Lowell DETLOFF pers. comm.). A total of 11 tasks, 4 age classes, 3 cohorts, and 7 colonies were included in the analysis. Two complementary models were tested using the above technique: 1) one in which tasks were considered as a treatment factor, and 2) one in which tasks were considered as a response variable and each task was analyzed separately for effects. The error term used was colony \times cohort. Statistical programs were implemented in different procedures from the SAS User's Guide: Statistics (1982).

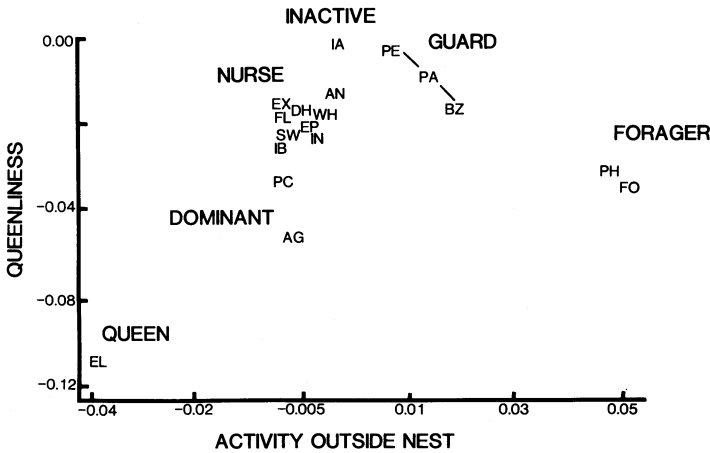


Fig. 2: Generalized plot of tasks plotted along the first two canonical variables. Numbers along axes are transformed eigenvectors. The tasks cluster into behavioral classes. Queen, Dominant, Nurse, Inactive, Guard, and Forager. Axes roughly correspond to queen-like behavior (queenliness), increasing from top to bottom, and activity outside the nest, increasing from left to right

Results

Description of Worker Tasks: The worker tasks described above were grouped into the behavioral classes of nurse, guard, forager, and dominant, based on the clusters of the canonical correlation (Fig. 2). The queen was isolated from the rest of the workers, primarily because she was the sole egg layer (EL). With respect to activity outside the nest, the foragers were most removed from the queen, who never left the nest once the first brood emerged. The aggressive bees under the dominant category were closest to the queen along both axes, while guards were least like the queen along the queenliness axis. Nurses were intermediate along both axes. Inactivity was rare, occurring only when a bee had recently emerged or was dying. Bumble bee workers and the queen worked continuously. Inactive bees were least like the queen along the queenliness axis, reflecting the high level of activity the queen maintains.

Behavioral Specialization of Callows

Tasks performed by callow workers (young bees from 1 to 36 h old) on days 1 and 2 following emergence were primarily those of nursing. For both days all but two of the tasks observed were nursing tasks (95 % on day 1, 80 % on day 2). Among nursing tasks, incubation comprised 45 % on day 1 and 38 % on day 2. No foraging or dominance behavior occurred, and guarding was at a low level (< 5 %).

Age Classes: Continuous versus Discrete

Results of the Relative Probability of Task Performance calculations are graphically displayed for each cohort in the histograms of Fig. 3. Workers performed various tasks with different probability as they aged. For example, the

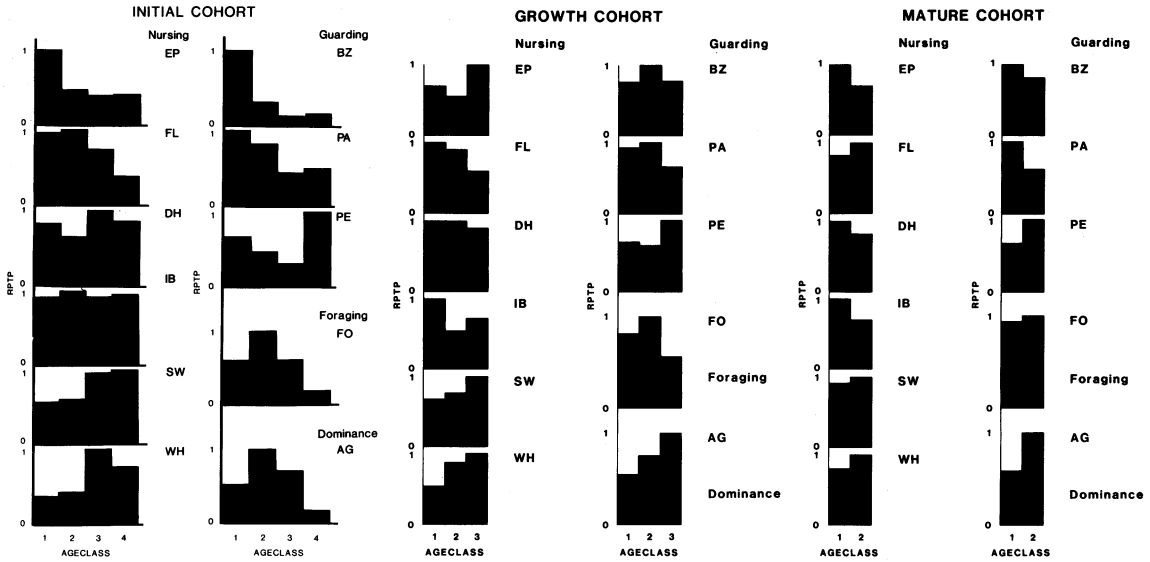


Fig. 3: Relative probability of task performance (RPTP), for 11 tasks, by workers of different age classes of the Initial, Growth, and Mature cohorts. Data are summed for duration of the study

Table 1: Task ensembles for callows and each of the four age classes of the *Initial* cohort. In the callow column, parentheses enclose % of the listed task; in the four age-class columns, parentheses enclose relative probability of task performance (RPTP) values. Only tasks with RPTP > 0.5 are included in the task ensemble for each age class

Callow	Age class			
	1	2	3	4
Nurse (95)	Nurse	Nurse	Nurse	Nurse
IB (45)	EP (1.0)	FL (1.0)	FL (0.70)	DH (0.90)
	FL (0.98)	DH (0.75)	DH (1.0)	IB (0.99)
	DH (0.85)	IB (1.0)	IB (0.98)	SW (1.0)
	IB (0.95)	SW (0.55)	SW (0.99)	WH (0.80)
	SW (0.50)		WH (1.0)	
	Guard	Guard	Guard	Guard
	BZ (1.0)	PA (0.80)	PA (0.48)	PE (1.0)
	PA (1.0)			
	PE (0.60)			
	Forager	Forager	Forager	
FO (0.55)	FO (1.0)	FO (0.53)		
	Dominance	Dominance		
	AG (1.0)	AG (0.65)		

Table 2: Results (p-values) of ANOVA in which the variable Task is treated as a response variable. Each task (see Methods for explan. of abbrev.) is analyzed separately for cohort, age class, and cohort \times age class (interaction) effects. Significant p-values in italics

Task	Cohort	Age class	Cohort \times age class
Nurse			
DH	<i>0.004</i>	0.177	<i>0.007</i>
EP	<i>0.050</i>	< <i>0.001</i>	< <i>0.001</i>
FL	<i>0.022</i>	< <i>0.001</i>	0.909
IB	<i>0.036</i>	0.078	0.114
SW	<i>0.046</i>	< <i>0.001</i>	0.856
WH	<i>0.004</i>	< <i>0.001</i>	<i>0.004</i>
Guard			
BZ	0.416	0.062	0.067
PA	< <i>0.001</i>	<i>0.002</i>	0.424
PE	<i>0.003</i>	<i>0.006</i>	<i>0.002</i>
Forager			
FO	< <i>0.001</i>	0.076	0.022
Dominance			
AG	0.056	0.337	0.922

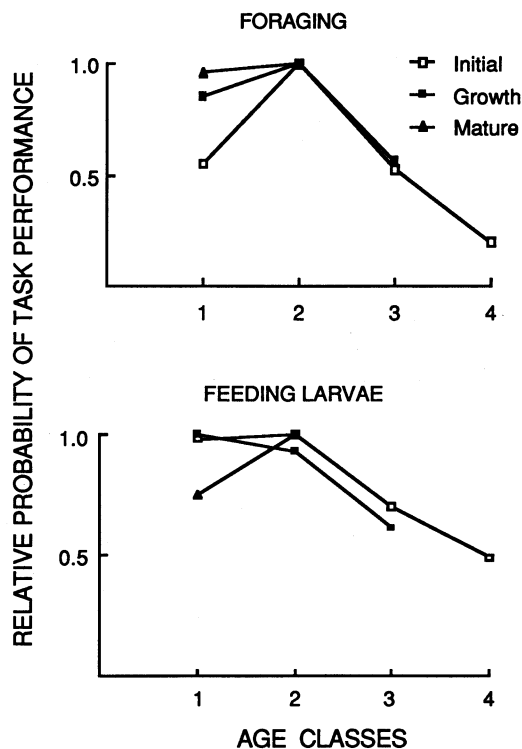
Initial cohort engaged in high levels of eating pollen, feeding larvae, foraging, buzzing, patrolling, and aggression when relatively young; scraping wax and working on honey pots at middle age; and scraping wax, perching, and incubating (a task performed at all ages with high probability) when old. However, all tasks were performed at all ages. Division of labor is discrete if there is an exclusive association between tasks and a given age, or is continuous under all other conditions of age/task association (WILSON 1976; CALABI et al. 1983). It is clear from these data that the division of labor in this species of bumble bee is continuous.

Bumble bee task performance changed quantitatively with age, especially for the Initial cohort (Table 1). Each age class (including callows) engaged in a particular mix of probabilities of principal tasks, defined by high (generally > 0.50) RPTP's (Table 1). Age classes of the other cohorts displayed less variation with age (Fig. 3).

Quantitative Differences in Division of Labor between Age Classes

The descriptive treatment of the above data indicates that for a given cohort workers of an age class engage in a particular mix of tasks. Indeed, differences in the probability of engaging in a task depended on both age and cohort ($F = 4.93$, $p < 0.0001$, $r^2 = 0.1806$). Task \times age class ($p = 0.0175$) and task \times cohort ($p = 0.0071$) interaction effects, and cohort effects ($p = 0.0459$) were significant. Although there was no statistically significant age class effect ($p = 0.1199$), the trend was suggestive of an effect. Furthermore, of the 11 tasks analyzed (each task

Fig. 4: Age Classes: The relative probability of task performance for the tasks of foraging (FO) and feeding larvae (FL) by workers of different age classes (1—4) of the Initial (□), Growth (■), and Mature (▲) cohorts.



analyzed separately for effects), 9 of them had age or cohort effects, or both (Table 2). Aggression was influenced by cohort (although the effect was not statistically significant); only buzzing was unaffected by both age and cohort.

Discussion

These results demonstrate that *Bombus griseocollis*, a species that exhibits an intermediate degree of sociality, possesses a surprisingly sophisticated system of division of labor. This conclusion is based on a highly quantitative/statistical treatment of the data, analyzed at the age class and cohort level. In the present study, no conclusions are inferred about individual behavior.

Age Effects on Division of Labor

In *Bombus griseocollis* all tasks are performed to a greater or lesser extent by workers of all ages, throughout the life of the colony. An age class, though statistically distinguishable, is not behaviorally discrete. Functional classes of behavior, such as nursing or guarding, are not limited to a given age class of workers. Within each age class a set of principal tasks is performed (Table 1), as reflected by high probabilities of task performance. In the present study age classes span 2 or 3 week periods, each of which circumscribes a phase of colony

development (see Methods). Because most activities begin by the fourth or fifth day of a worker's life and may continue for several weeks (pers. obs.), it is unlikely that age-class divisions of shorter time periods would reveal classes of greater behavioral discreteness.

The particular proportions of tasks performed by an age class change from one colony phase to the next, as the bees age. For instance, foraging reached a maximum at about two weeks of age, then dropped to a relatively low level

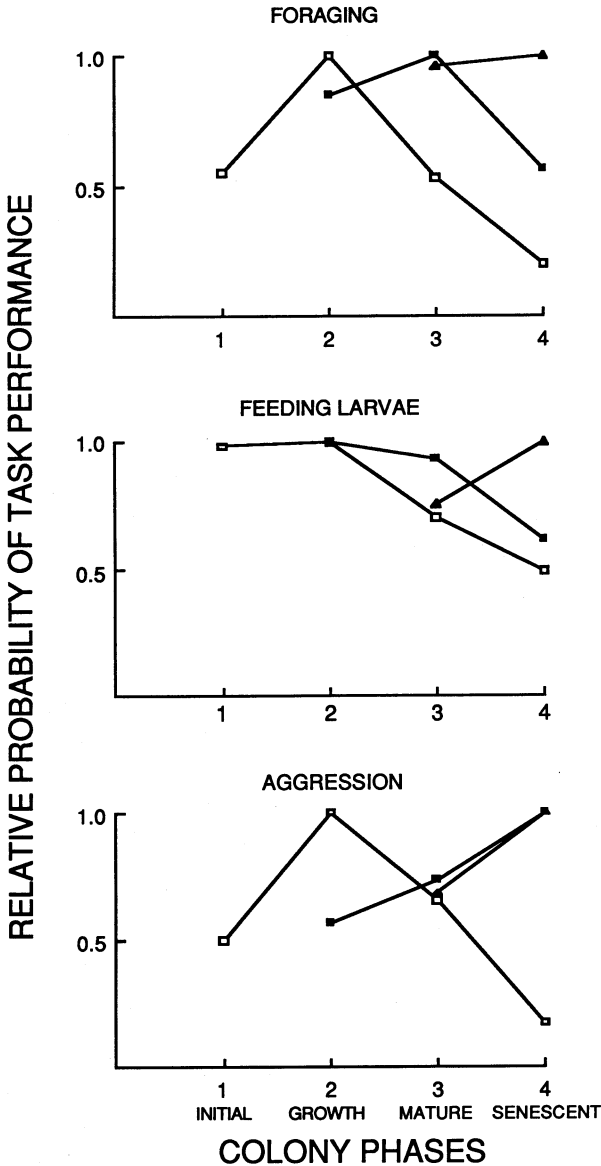


Fig. 5: Colony Phases: The relative probability of task performance for the tasks of foraging (FO), feeding larvae (FL), and aggression (AG) by workers of the initial (□), Growth (■), and Mature (▲) cohorts, living through their respective phases of the colony: Initial, Growth, Mature and Senescent

during the rest of the worker's life (Fig. 4). This trend held for each cohort. In short, with the exception of newly emerged bees, which engage primarily in incubation, most tasks are performed by bees of all ages. However, some tasks are performed with higher probability at one age than another.

Environmental Effects

That task probabilities vary with each colony phase suggests that environmental conditions modulate *Bombus* polyethism. The effects of changing environmental conditions on behavioral ontogeny are especially apparent for some nursing and foraging tasks.

Feeding larvae: Feeding larvae is, in part, an age-dependent activity (Table 2; Fig. 4) that appears to depend on colony demand (Fig. 5). Workers fed larvae with the highest probability during the late growth phase of the colony (phase 2) when the rate of egg production and larval brood was probably at its peak (MICHENER 1974; pers. obs.). Other studies of *Bombus* have demonstrated the influence of environmental effects on labor allocation. PENDREL & PLOWRIGHT (1981) found, in a laboratory study of *B. terrestris*, that workers compensated for a 50 % reduction in number by recruiting new workers to brood care and increasing the larval feeding rate. They also found that colony pollen consumption was positively correlated with larval biomass, presumably because nurse bees ate more pollen and regurgitated more food to larvae. The same has been shown in free-foraging colonies. FREE (1955) found that pollen was brought back to the nest in direct proportion to the number of larvae in the colony. Thus under different environmental conditions the same workers may perceive and respond to a given stimulus (e.g., larval biomass) with a high degree of flexibility.

Foraging: Foraging is another age-related behavior that appears to depend on colony demand. In the second and third phases of the colonies, when larval brood mass was at a maximum, foraging probabilities were correspondingly highest (Fig. 5). Fig. 5 also shows that the contribution to foraging by each cohort is not equal at any given time. For example, during the later stages of the colony (phase 3 and 4) workers of the Initial cohort (= old bees) contributed relatively little to foraging, while those of the Growth and Mature cohorts (= younger bees) contributed a maximum amount. My preliminary observations suggest that each successive cohort forages more intensively. The recent findings of GOLDBLATT & FELL (1987) for *B. fervidus* and *B. pennsylvanicus* support this apparent trend. In their comparative study of mortality rates of foragers and nurses, survivorship of workers that emerged in later cohorts was lower than that of workers from earlier cohorts. They argued that because the life-span of foragers was shorter than that of house-bees (also see RODD et al. 1980; GARÓFALO 1978), reduced survivorship of bees in the later cohorts was probably because more of them became foragers.

Even in my laboratory, in the absence of high forager mortality, foraging probabilities increased with each successive cohort as the colony aged. This suggests that foragers have a finite foraging career, independent of mortality factors. As they age, whether or not they die in the field (they usually do), they are replaced by young, vigorous (often larger) bees emerging in the colony. The

retired foragers still able to contribute to colony needs shift over to nursing tasks (in fact all foragers shift over to nursing tasks each night when foraging ceases). In *Bombus*, a shifting-balance system of forager replacement may be the ergonomic cornerstone of the colony, ensuring a per-bee maximal foraging-return rate throughout the season.

The result that relatively young bumble bees do most of the foraging is, to my knowledge, the first such finding for a social insect. This surprising new finding is contrary to our present knowledge of highly eusocial bees, in which generally the oldest bees forage and continue until death. The size variation among bumble bee workers may have favored selection on large workers for enhanced foraging capability. As the average size of workers increases over the season, younger bees tend to be larger than older bees. Because larger bumble bees forage more efficiently than smaller bees (BRIAN 1952; FREE 1955; FISHER 1987), it is probably of greater benefit to a colony to send out young (larger) bees to collect resources.

Aggression: Aggression among workers in *Bombus* is limited to dominance contests for egg-laying (VAN HONK et al. 1981; VAN DER BLOM 1986). As the colony grows too large for the aging queen her ability to inhibit worker ovarian development decreases, hence aggression is released among workers for the dominant egg laying position (RÖSELER & RÖSELER 1977; VAN HONK et al. 1980). In the present study essentially all aggression among workers occurred near the senescent phase of the colony by bees born late in the colony cycle (Fig. 5). In *B. griseocollis*, it is the young workers born late in the colony that respond aggressively as the queen loses control.

Evolution of Temporal Castes

Temporal caste systems are marked by reduction in number of tasks performed at each age (OSTER & WILSON 1978). Workers of the highly eusocial bees, honey bees and stingless bees, exhibit age-associated reduction and sequential performance of tasks during ontogeny. In general, workers perform approximately the same sequence of tasks from birth to death (reviewed in MICHENER 1974; SOMMEIJER 1984; SEELEY 1985; WINSTON 1987), though there is considerable flexibility in the system, which enables a colony to respond to a variable environment (RÖSCH 1930; RIBBANDS 1952; LINDAUER 1961; FREE 1965; SEKIGUCHI & SAKAGAMI 1966; WINSTON & NEILSON PUNNETT 1982; SOMMEIJER 1984; KOLMES 1985; WINSTON & FERGUSSON 1985).

In *Bombus*, callows exhibit strong reduction in number of tasks, but among the older workers only weak reduction has occurred. Callows specialize in incubation (see above) probably because they are physiologically constrained by wing softness, muscle development, and nervous-system maturation. Individual *Bombus* workers do not follow a rigid ontogenetic sequence of tasks; some individuals may never forage, while others may never guard (CAMERON, pers. obs.).

The biologically diverse species of stingless bees exhibit varying degrees of task reduction and flexibility. For example, *Melipona favosa* workers perform

some activities at all ages (e.g., waste-processing, SOMMEIJER 1984), resembling *Bombus* (see incubation behavior, Fig. 4). In general, stingless bee workers undergo an ontogenetic sequence of tasks, although the temporal organization of activity may be different from that of *Apis* (SOMMEIJER 1984).

In the highly eusocial ants and honey bees, age polyethism may have evolved as a compromise between task-performance efficiency and task-location efficiency (WILSON 1976; SEELEY 1982); thus workers perform ensembles of tasks that co-occur spatially in the nest. Spatial segregation in the relatively small nests of *Bombus* is probably not great enough for task-location efficiency to have favored the evolution of a strict age polyethism. Brood and storage cells of *Bombus* are spatially interspersed and contiguous. Perhaps among the large colonies of the Brazilian bumble bee, *B. atratus*, there is greater complexity of the nest structure and a tendency for spatial segregation of functions within the nest. In this species, one might also find a more discrete division of labor among workers.

Other effects on *Bombus* worker division of labor, such as glandular development, hormones, genotype, and the role of the queen (before and after emergence), require initial or continued investigation. Direct comparisons of *Bombus* with other social bees will enhance our understanding of the evolutionary significance of biological traits. For example, in *Apis mellifera* (L.), juvenile hormone (JH) is known to play a central role in regulating age-specific task performance among workers (JAYCOX 1976; SASAGAWA et al. 1986; ROBINSON 1987). In contrast, recent investigations of *Bombus* (CAMERON & ROBINSON in review) indicate that juvenile hormone does not play a regulatory role in the onset of tasks (foraging and nursing), at least not during the adult life of workers. Because *Bombus* workers lack the strict age polyethism exhibited in *Apis*, it is not surprising that juvenile hormone plays no role in regulating the onset of their foraging and nursing activities. Is *Apis* unique in its use of JH as a regulator of task performance? A study of the effects of JH on task performance in stingless bees would be informative.

B. griseocollis possesses a complex temporal division of labor based on shifting patterns of principal tasks rather than on discrete age castes. Because *Bombus* comprises species that exhibit different degrees of sociality, further investigation of the interspecific variation in social structure of different bumble bees would be valuable, particularly if placed in a phylogenetic context. It would help us to reconstruct the evolutionary pattern of caste development and division of labor among the social bees and improve our understanding of the interconnected roles of colony demography, nest architecture, and environmental factors in the evolution of social organization.

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