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Thomas Seeley
Cornell University

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Author(s): Thomas D. Seeley
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Adaptive Significance of the Age Polyethism Schedule in Honeybee Colonies

Thomas D. Seeley

Department of Biology, Yale University, P.O. Box 6666, New Haven, Connecticut 06511, USA

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Summary. The adaptive origins of the honeybee's age polyethism schedule were studied by testing whether the schedule for labor inside the nest reflects a compromise between efficiency in locating tasks and efficiency in performing tasks. I checked two predictions of this hypothesis: (1) at each age a worker handles a set of tasks (rather than one task), and (2) the elements of each age's task-set co-occur spatially in the nest (rather than being spatially segregated). Most observations match these predictions, once workers reach the age of 2 days. The unpredicted specialization of 0 to 2-day-old workers on the single task of cell cleaning may reflect an unusual ease in locating work sites for this particular task. There are 5 female castes in honeybee colonies: the queen (reproductive caste), plus 4 age subcastes among the workers (cell cleaning caste, broodnest caste, food storage caste, and forager caste).

Introduction

In most species of social insects, the adult workers change roles as they grow older, usually progressing from nurse to forager. This phenomenon of behavioral change with age is called 'age polyethism'. In many species the behavioral changes are accompanied by regular shifts in the activity of exocrine glands. Past studies of age polyethism have focussed either on documenting these patterned shifts in behavior and physiology (reviewed by Free 1965; Wilson 1971; Michener 1974; Oster and Wilson 1978; Brian 1979), or, more recently, on analyzing the endocrine mechanism timing these shifts (Jaycox et al. 1974; Imboden and Lüscher 1975; Imboden et al. 1976; Lüscher 1976; Rutz et al. 1974, 1976; Fluri et al. 1977, 1982). Little work has been devoted to analyzing the evolutionary forces that have shaped the patterns of labor change.

One nearly universal property of age polyethism schedules – the progression from inside-nest to outside-nest labor – is evidently adaptive since it postpones the most hazardous labor, such as foraging, to late in a worker's life. Wilson (1976) found that the age polyethism schedule of the ant *Pheidole dentata* consists of a series of discrete task-sets such that tasks which are contemporaneous in the labor schedule are also spatially juxtaposed in the nest. Evidently, this ant's labor schedule is designed to minimize travel between tasks.

Honeybee workers display an extraordinarily elaborate division of labor by age. The present study examines the hypothesis that the honeybee's schedule for inside-nest labor reflects a compromise between selection for efficiency in *performing* tasks and selection for efficiency in *locating* tasks. Presumably a worker's task performance efficiency would be greatest if the worker performed just one task at each age. Such extreme task specialization, however, probably would impose low task location efficiency since workers would have to search relatively extensively for further work sites of their single current task. Therefore, one might expect that workers will not be extreme specialists, rather semispecialists, performing a set of tasks at each age. Such versatility is well documented (Lindauer 1952; Sakagami 1953; Seeley 1979). But what determines which tasks will be performed together at each age? Again, task location efficiency may be important. If the tasks performed concurrently also co-occur spatially in the nest, then the mean free path between tasks should be minimized, and this should help maximize efficiency in locating tasks. Prior studies support this idea qualitatively. They show that the workers' temporal changes in

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labor activities match a gradual spatial shift from the central broodnest, to the peripheral food storage areas, and finally to outside the nest (Gerstung 1921; Rösch 1925, 1927, 1930; Lindauer 1952; Sakagami 1953).

I predict that at each age a worker handles a set of tasks, and that what characterizes the elements of each age's task-set is spatial proximity in the nest. Testing these predictions involved three sequential stages: (1) determining the distributions of task performance probability vs age for tasks, thus identifying the task-set for each age of a worker, (2) plotting a map of work sites for each task, and (3) using the results of stages (1) and (2) to see if the task-set for each age maps onto a specific nest region, or, in contradiction to the hypothesis, onto spatially segregated sites about the nest.

Materials and Methods

Observation Colony. The observation hive, depicted schematically in Fig. 2, closely resembled the hive described by Seeley (1979). It differed from the prior hive only in its entrance location, and in its 150-quadrat sampling grid drawn on one of the hive's window-walls. All observations were made on the side covered by the grid. The hive was stocked with Italian bees (*Apis mellifera ligustica)* in mid-April, 1981. Thus the colony had plenty of time to become established in its new home before observations began in early August. The colony thrived throughout the summer. When the observations began, the colony contained about 21,000 bees (estimated by counting the bees in a sample of quadrats), which completely covered the hive's combs, and had stored about 7 kg of honey.

On 4 August 1981, 100 newly-emerged, marked bees were added to the observation hive. Pilot experiments had shown that by adding only 100 marked bees, 93% of the quadrats would contain only 0 or 1 marked bees at any one time, a situation which simplified the sampling procedure described below. Newly-emerged bees were obtained by placing combs of sealed brood in an incubator. The bees were marked with powdered artist's pigment mixed in shellac (von Frisch 1967).

Several steps were taken to increase the probability of observing marked bees perform certain tasks. To encourage ventilation, I stoppered all ventilation holes in the observation hive, and sealed all seams between the hive's glass sides and wooden frame. Debris removal was encouraged by pouring 1 ml of dry hemlock needles in the top of the observation hive hourly during observations. Unfortunately, it was not feasible, given the sampling procedure described below, to leave part of the hive empty for comb building. Consequently, new comb construction was not observed.

Sampling Procedure. The 150-quadrat grid over one side of the observation hive enabled me to sample randomly among the marked bees, and also uniformly within the hive. I used the grid as follows. First, a Texas Instruments 59 calculator, equipped with an applied statistics module, was programmed to generate lists of random numbers uniformly distributed between 1 and 150, inclusive. Each number specified a particular quadrat. Then, guided by a list of random numbers, I inspected quadrats at random for marked bees. Upon encountering one, I determined what activity it was engaged in. Finally, the bee's location and activity were recorded with a code symbol on a glass sheet covering the observation side of the hive. This process of searching and recording was steadily repeated for 8 h per day, with all observations made between 08.00 a.m. and 18.00 p.m., thus when the colony was actively foraging.

Table 1. The tasks performed by honeybee workers

1. Cleaning cells	10. Removing debris
2. Feeding brood	11. Receiving nectar
3. Capping brood	12. Concentrating nectar
4. Trimming cappings	13. Storing nectar
5. Attending queen	14. Capping honey
6. Grooming nestmates	15. Packing pollen
7. Feeding nestmates	16. Guarding
8. Ventilating	17. Foraging
9. Shaping comb	

Approximately 850 quadrat inspections per day were made, yielding 268 ± 85 ($\bar{X} \pm SD$) marked bee encounters per day. A separate glass sheet recorded each day's observations. I observed the bees when they were 1, 3, 4, 6, 7, 9, 10 .. 24, 25, 27, 28 days old. On all days except the last, which was very rainy, good weather provided the marked bees with a full opportunity for foraging. Because the labor conditions were unusual on the last day, I did not use this day's observations in the data analysis. When calculating relative probabilities of task performance (see below), I pooled the observations from pairs of days, such as when the bees were 3 and 4, or 6 and 7 days old. Only the first (1-day-old bees) and effectively final (27-day-old bees) days of observation could not be pooled with another day's records.

Classification of Worker Bee Tasks. In Table 1 are listed all of the tasks recognized in this study. In creating a classification of bee tasks, I adopted Wilson's (1980) definition of a task: "a set of actions that flow from one to the next in such an integrated sequence that for the sequence to be halted by one worker and resumed by another worker would result in a substantial loss of time or efficiency." Note that the tasks listed in Table 1 do not represent the entire behavioral repertoire of worker bees. 'Non-task' behaviors include non-social activities such as self-grooming and self-feeding, and non-labor activities, such as walking about or resting.

Many of the tasks listed in Table 1 can be recognized at a glance when being performed by a bee, but several require close observation of the bee. Upon encountering a bee with its head in a cell, I distinguished between cell cleaning, brood feeding, pollen packing, and nectar storing using the techniques described by Sakagami (1953). I distinguished between bees receiving nectar from foragers and hungry bees simply being fed by nestmates by following the behaviour of donor bees after they had broken contact with their receiver bees. Foragers, even ones not bearing pollen, can be recognized by several traits. Usually they are distinctively active bees, pressing through other bees to find nectar-receiver bees, begin dancing, or dash back out the entrance for another foraging trip. Other times foragers are less excited, but they still repeatedly contact other bees to unload nectar, or they might follow dancers to find a new food source. These diagnostic traits of foragers also helped me distinguish foragers unloading food from non-foragers simply feeding nestmates. One difficulty, though, with foragers was that of identifying whether a bee seen scurrying out of the nest was a forager, or a non-forager starting an orientation flight. I classified all such bees as foragers. Because bees make orientation flights before beginning foraging, my records probably show bees beginning foraging at a slightly earlier age than is actually the case.

Data Analysis. Distributions of relative probability of task performance were calculated for 13 of the 17 tasks listed in Table 1. The 4 tasks which were not used in the analysis (removing debris, concentrating nectar, capping honey, guarding) were observed only 4, 1, 5, and 0 times, respectively, out of 4823 encounters with marked bees. I never recorded guarding because it occurred at the entranceway's outer opening, thus outside the sampling grid. The tasks of concentrating nectar and capping honey are probably also underrepressented for colonies in general because there was little nectar forage available throughout the 28-day observation period.

The relative probability of task performance (RPTP) is defined as the probability that a worker in a given age group will perform a particular task relative to the probability that a worker in some other designated age group will perform the same task. The age group designated for comparison was arbitrarily selected to be the one most likely to perform the task. As a result, values of RPTP range from 0 to 1. Because the total number of behavioral acts (tasks plus non-tasks) recorded varied from day to day, calculating the RPTP for each age group-task combination involved two steps as follows:

$$p_{ij}=n_{ij}\Big/\sum_{i=1}^{k} n_{ij} \qquad (1)$$

$$r_{ij}=p_{ij}/p_{i_{\max}}, \text{ where} \qquad (2)$$

p_{ij} = probability of task i performance by a member of age group j

n_{ij} = number of performances of task i observed for members of age group j

k = total number of behavioral categories (both tasks and non-tasks)

r_{ij} = the relative probability of task i performance by a member of age group j

$p_{i_{\max}}$ = probability of task i performance by a member of the age group with the highest such probability.

Treating the data in this way automatically compensates for there being fewer bees still alive in the older age groups than in the younger ones. Using RPTP's also facilitates comparing distributions of task performance probability between frequently and rarely observed tasks, such as cell cleaning and brood capping, respectively.

Maps of Work Sites. To construct a map depicting each recorded work site for a given task, I photographed with color slide film the glass data sheet from each day of observations, then projected consecutive day's records against a sheet of paper and marked on it all instances of task performance for the task under consideration.

To quantitatively analyze the correlation between the location of each task's work sites in the nest and the timing of its performances in the life of a worker, I calculated the percentage of each task's work sites which were in either the broodnest or food storage region, and percentages of the total integral for each task's RPTP curve which lie within certain age intervals. Calculations of integrals for RPTP curves were made by summing the areas of the trapezoids defined by each task's RPTP curve and the relevant age boundaries. For the correlation analysis, I calculated Spearman's r_s, a distribution-free estimator, since neither variable was expected to be normally distributed.

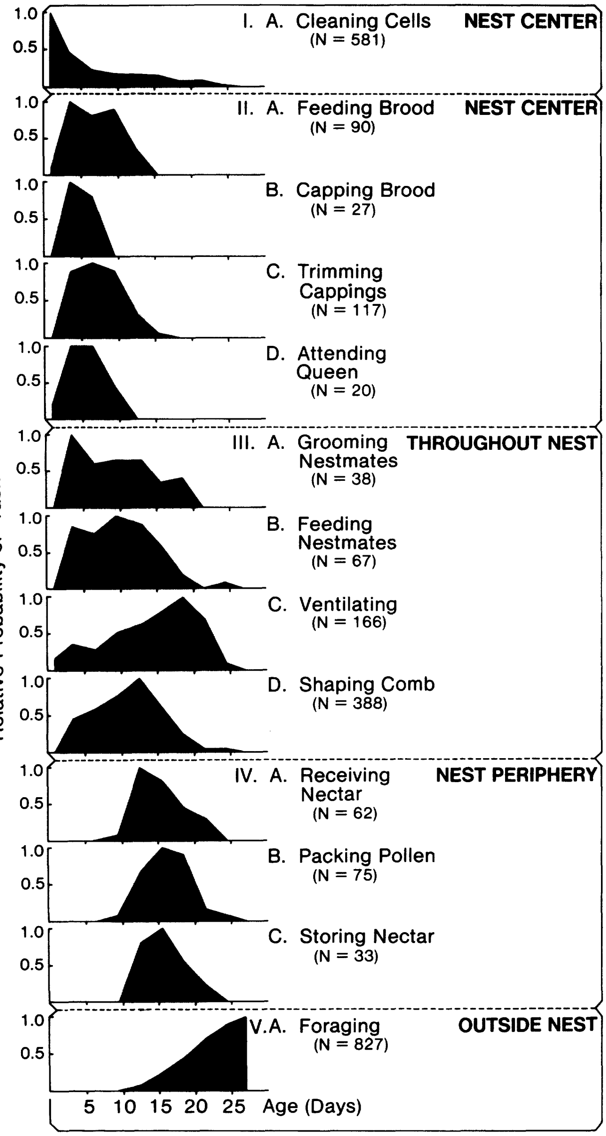

Fig. 1. The curves of relative probability of task performance, for 13 tasks, by workers of different ages. The curves are classified into five groups which are used in defining the age castes

Results

The Age Polyethism Schedule

The distributions of relative probability of task performance (RPTP) for the 13 most common tasks are shown in Fig. 1. One striking feature of this family of distributions is that nearly all the rapid changes in RPTP occur on or around the ages of 2, 11, and 20 days. This has two major consequences for the patterns of division of labor in honeybee colonies. First, as is shown in Fig. 1, the colony's tasks fall into 5 groups, with all the tasks in a group sharing a common age range over which their RPTP's are high (generally >0.30).

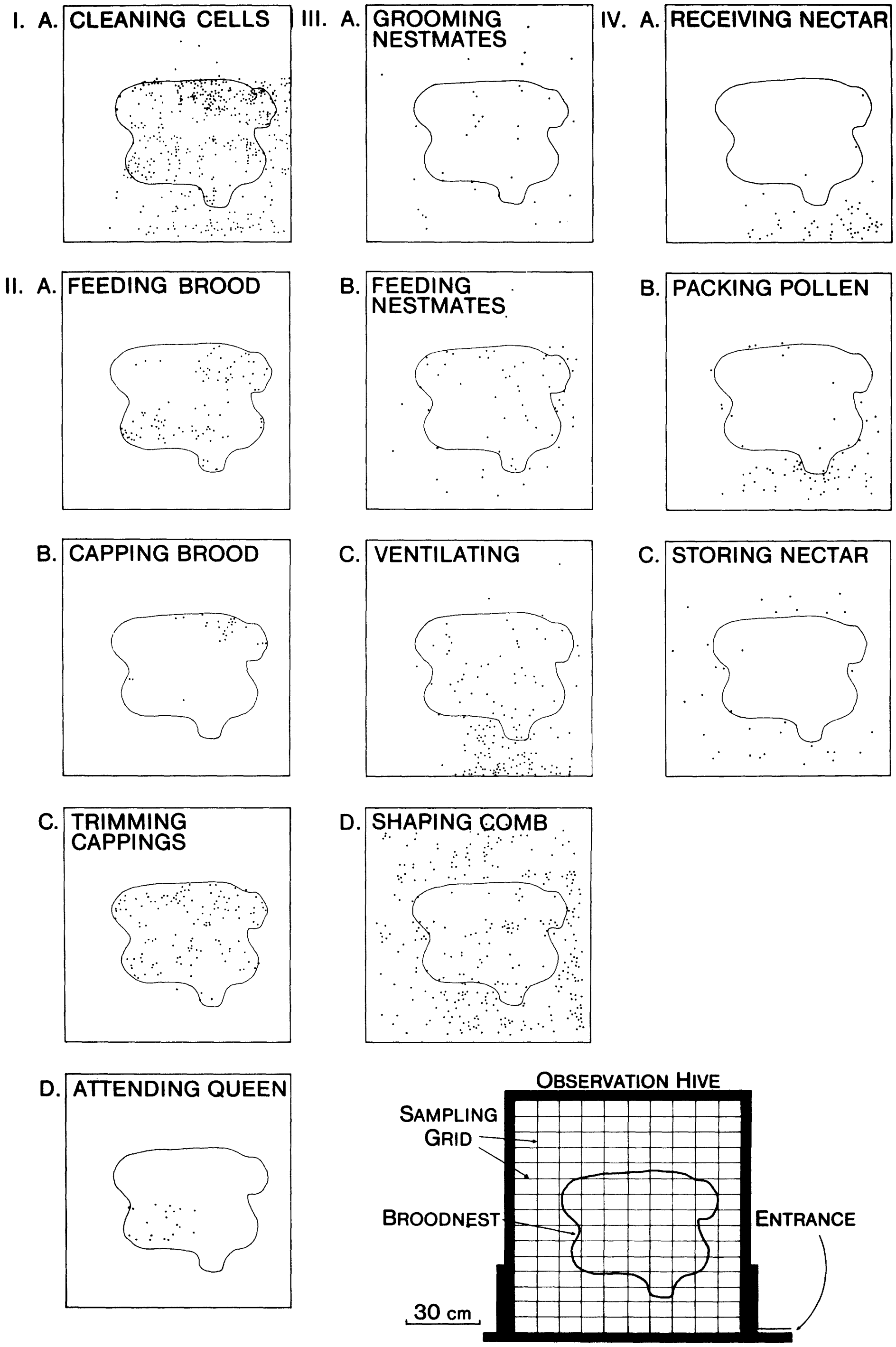

Fig. 2. Maps depicting the work sites for the 12 most common tasks performed inside the nest. *Lower right:* schematic diagram of the observation hive used in mapping the work sites of the various tasks

The age range of high RPTP for the group I task is about 0–5 days; for group II tasks, about 2–11 days; for group III tasks, about 2–20 days; for group IV tasks, about 11–20 days; and for the group V task, about 18+ days.

A second consequence of the more or less synchronous changes in RPTP is that the honeybee's age polyethism program contains 4 age castes, where an age caste is defined as a set of colony members, distinguished by age, that specialize on particular tasks for prolonged periods of time (Oster and Wilson 1978). The age ranges (approximate) and task-sets of the 4 castes are as follows: age caste 1, 0–2 days, the task of group I (cell cleaning); age caste 2, 2–11 days, groups I, II, and III tasks; age caste 3, 11–20 days, groups III and IV tasks; age caste 4, 20+ days, the task of group V (foraging).

Table 2. Comparison between the proportion of each task's work sites in either the broodnest or food storage region of the nest, and the proportion of each task's performances in either the 2–11 day or 11–20 day age interval. The symbol r_s denotes Spearman's rank correlation coefficient

Task		No. of observed work sites	% work sites in broodnest	% RPTP integral in 2–11 day interval	% work sites in food storage region	% RPTP integral in 11–20 day interval
I.	A. Cleaning cells	581	77	55	23	23
II.	A. Feeding brood	90	100	83	0	14
	B. Capping brood	27	100	96	0	0
	C. Trimming cappings	115	98	80	2	16
	D. Attending queen	20	95	92	5	2
III.	A. Grooming nestmates	38	39	60	61	37
	B. Feeding nestmates	67	58	42	42	38
	C. Ventilating	166	30	26	70	53
	D. Shaping comb	388	18	45	82	50
IV.	A. Receiving nectar	62	5	8	95	80
	B. Packing pollen	75	12	3	88	80
	C. Storing nectar	33	6	4	94	85
r_s			0.90		0.95	
Significance			$P \ll 0.0001$		$P \ll 0.0001$	

With the honeybee colony's labor organized into 4 discrete age castes, the question of whether the daily task-set for inside-nest workers maps onto a single nest region, or onto a patchwork of locations, simplifies to whether each of the first 3 caste's task-sets maps onto a single nest region.

Spatial Patterns of Task Performance

Maps showing the work sites for 12 of the 13 most common tasks are shown in Fig. 2. One task, foraging, is conducted outside the nest and so although foragers can be recognized in the nest, their work sites cannot be portrayed as for the other 12 tasks.

Does the task-set of each inside-nest caste map onto a single nest region? Yes. Age caste 1 performs a single task, cell cleaning, so there is no question of different tasks in different regions. As is shown in Fig. 2 and Table 2, age caste 2 individuals can perform all their tasks within the boundaries of the broodnest, although some of these tasks – such as grooming nestmates, ventilating, and shaping comb (group III tasks) – also occur outside the broodnest. Finally, members of age caste 3 can encounter all their tasks in the peripheral, food storage region of the nest (see Fig. 2 and Table 2). This close mapping between the age interval in which each task is performed and the spatial distribution of its work sites in the nest is quantified by the correlation analysis shown in Table 2. Note that one does not see a caste performing combinations of spatially segregated tasks such as capping brood and receiving nectar, or attending the queen and storing nectar. What one does see is combinations of tasks such as attending the queen, grooming nestmates, feeding brood, and ventilating, all of which occur in the broodnest; or shaping comb, storing nectar, feeding nestmates, and packing pollen, all of which occur on the nest's periphery.

Discussion

In general, the temporal and spatial labor patterns in a honeybee colony support the hypothesis that the honeybee's age polyethism schedule for inside-nest labor reflects a compromise between task performance and task location efficiencies. Once workers reach the age of 2 days, they perform sets of tasks, and the tasks of each age group co-occur spatially in the nest.

However, one striking feature of the age polyethism schedule – an initial caste specialized on the single task of cell cleaning – at first seems to contradict the hypothesis. The crux of the matter is why 1-day-old bees do not perform other tasks in the broodnest. Perhaps they do not feed brood because they must feed on pollen for a day or so before their brood food glands become active (Kratky 1931). But why don't these bees perform other broodnest tasks whose motor patterns resemble cell cleaning movements, such as grooming nestmates, shaping comb, and trimming cappings, or those requiring only the simplest movements, such as ventilating? I suggest that very young bees have been selected to specialize on cell cleaning because newly-emerged bees can easily locate a long series of cells needing cleaning. (Because honeybee queens lay eggs in patches, brood emerges in fairly synchronous patches, thus there are large patches of recently vacated cells requiring cleaning.) In other words, the constraint of task location efficiency may be relaxed in this case, only task performance efficiency matters, and so, as would be predicted by the hypothesis, the bees specialize on the easily-found task. Alternatively, developmental constraints on the timing of nervous system maturation or muscle development, or both, may limit 1-day-old bees to the single task of cell cleaning.

Throughout this paper I have implicitly assumed that the spatial layout of the honeybee's nest set the stage for the evolution of the age polyethism schedule, rather than that the labor schedule evolved prior to or simultaneously with nest architecture. My justification for this assumption is that primitively eusocial bees, such as bumblebees, spatially segregate cells for brood rearing and food storage, despite their lacking age polyethism for the tasks occurring inside the nest (Free and Butler 1959; Michener 1964, 1974; Alford 1975). I suspect that spatial segregation of broodnest and food storage regions was initially advantageous because it facilitates brood incubation. In later stages of social evolution, it probably also helps economize in nest construction, for identical adjacent cells in a comb permit the construction of truly economical combs of perfectly-packed polyhedrons, such as occur in the nests of honeybees.

One product of this research has been the precise definition of the caste structure in honeybee colonies. It is now clear that there are 5 female castes in a honeybee colony: the queen (reproductive caste) plus 4 age subcastes among the workers (cell cleaning caste, broodnest caste, food storage caste, and forager caste). Actually, the caste structure depicted in Fig. 1 was essentially revealed in 1953 by Sakagami's study of honeybee age polyethism, though his study techniques did not bring the caste structure into sharp focus. In the terminology of Wilson (1976), the age subcastes of worker honeybees are 'discretized', that is, workers are organized into just 4 distinct age ensembles, each of which handles a set of tasks. Such a caste system closely resembles that found by Wilson (1976) for the ant *Pheidole dentata,* despite the fact that honeybees and *Pheidole* ants are phylogenetically remote and possess radically different nests – wax combs in tree cavities vs subterranean galleries, respectively. What both species share is a complex nest structure, one in which different nest regions serve different functions. This correlation between structurally complex nests and discretized age caste systems in two phylogenetically remote species suggests that among the social insects in general, age polyethism schedules will prove to be functionally related to nest architecture. The premier candidates for further exploration of this hypothesis are probably the stingless bees (tribe Meliponini). Numerous species in this group form colonies composed of many thousands of individuals, apparently possess complex age polyethism schedules (Bassindale 1955; Hebling et al. 1964; da Cruz Landim and Ferreira 1968; reviewed by Michener 1974) and, most importantly, construct complex nests with marked spatial separation of functionally different parts, such as the broodnest and food storage areas (Wille and Michener 1973).

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