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Research article

Division of labor among a cohort of young individuals in a primitively eusocial wasp

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Summary

Age polyethism has recently been demonstrated in the primitively eusocial wasp *Ropalidia marginata*, and it has been shown that workers allocate tasks based more on their relative age rather than on their absolute age, thus providing flexibility to division of labor. The flexibility of division of labor and the respective roles of absolute and relative ages is further evaluated here by creating colonies of only young individuals (young-cohort colonies). The results show that workers in young-cohort colonies can forage at an earlier age, in larger numbers and with a higher probability and frequency. This confirms that division of labor in the colony can indeed be independent of absolute age. The results also show that relative age governs the probability of task performance while absolute age governs the frequency of task performance. The constraints posed by absolute age in the organization of work in an insect colony and the flexibility lent to it by relative age are discussed.

Introduction

Adult workers of most species of social insects change tasks as they grow older, ordinarily progressing from intranidal tasks to extranidal ones (Wilson, 1971; Oster and Wilson, 1978). It has been repeatedly established that such temporal polyethism is to some extent flexible, so that the ontogeny of task performance can be adjusted to meet colony requirements. A limited ability of young workers to perform, in a contingency, the tasks that are normally performed by old workers, and vice versa has been demonstrated in various studies (Winston and Punnett, 1982; Calabi and Traniello, 1989; Robinson et al., 1989, 1992; Page et al., 1992; Huang and Robinson, 1996).

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In the primitively eusocial wasp, *Ropalidia marginata*, age was recently found to have a definite correlation with division of labor (Naug and Gadagkar, 1998). Individuals performed different tasks in a distinct sequence in their life with successive tasks being initiated at significantly older ages. The probability of performance of a given task relative to other tasks (PTP) and absolute rates at which tasks were performed per unit time (FTP) both showed clear age-dependent patterns, confirming the association of age with division of labor. Compared to absolute age, relative age (ranked age) could explain a higher amount of variation both for PTP and FTP. Although this superiority of relative age was more marked for PTP than it was for FTP, it suggests that division of labor in these wasps is based on relative rather than absolute age, allowing work organization to be flexible.

Studying division of labor in colonies with only young individuals (young-cohort colonies) allows one to test if division of labor can indeed be responsive to changes in the age structure of the colonies. To test the respective roles of absolute and relative ages it is necessary to control for the effect of one while letting the other vary. While both these are highly correlated in natural colonies, the young-cohort colonies allow one to weaken this correlation.

Methods

Five queenright, young-cohort colonies of *R. marginata* were created by removing all workers older than seven days before behavioral observations began and also those that eclosed subsequently until the end of the observations, resulting in a seven-day cohort of individuals. Behavioral observations were conducted on these colonies for eight days during the following 2–3 weeks during which the absolute ages of the cohort of individuals ranged from 1–24 days. Behavioral observations consisted of recording every occurrence of Feed Larva and Build (Intranidal tasks) and Bring Pulp, Bring Food and Bring Liquid or Bring Nothing (Extranidal tasks). All sampling sessions were randomly chosen between 0830 and 1630 hours with each sampling day having two sessions of two hours each. Observations were made on colonies DN2 (colony size: 9–15 wasps) between May 19 and June 2, 1996, DN3 (17–21 wasps) between April 29 and May 16, 1996, L65 (10–16 wasps) between February 19 and March 7, 1996, N264 (13–23 wasps) between April 23 and May 9, 1996 and N360 (15–19 wasps) between May 22 and June 4, 1996, each of these five colonies yielding 32 hours of data.

All wasps were classified into one-day age groups based on their absolute or relative age. Relative age is the ranked age of a wasp and is a measure of its position in the age distribution of the colony (Naug and Gadagkar, 1998). Using the number of times extranidal tasks were performed during the 150 min of sampling in a day, the probability of performing the task relative to other tasks (PTP) and the rate of performing the task (FTP) for each individual of a given age was calculated (Naug and Gadagkar, 1998). The rationale for analyzing the performance of only extranidal tasks is that it is an atypical task for such young individuals. Mean absolute ages and proportions of foragers (defined as individuals performing extranidal tasks) on each day of observation were also computed.

The three groups of individuals that were compared are (1) individuals in the young-cohort colonies, (2) individuals of corresponding absolute ages (1–24 days) in the normal colonies and, (3) all individuals of all absolute ages in the normal colonies. To represent normal colonies, data from the earlier study (Naug and Gadagkar, 1998) were used. One-way ANOVAs followed by multiple comparison of means by Tukey-Kramer test were used to study the effect of age distribution on task performance. For each individual, increase in absolute age and difference in its relative age on each day of observation from the first day of observation (Day 1) as well as changes in its PTP and FTP during the corresponding period were calculated to explore the relationship between absolute and relative age and their roles in division of labor. For both normal and young-cohort colonies, data were pooled from five nests each since there was no qualitative difference among the colonies.

Results

The absolute age of individuals in the five young-cohort colonies ranged between 1–24 while the range was 1–89 in normal colonies. The age distribution of the normal and young cohort colonies significantly influenced (one-way ANOVA, $p < 0.05$) the mean absolute and relative ages of the individuals in them (Fig. 1 a, b). The mean absolute age of individuals in the young-cohort colonies (12.03 ± 5.12 days) was marginally lower ($p < 0.05$) than that of the 1–24 day old individuals in normal colonies (12.76 ± 6.44 days) and significantly lower ($p < 0.01$) than that of the entire normal colonies (24.97 ± 17.38 days). However, as expected, the mean relative age of individuals in the young-cohort colonies (51.17 ± 30.17) was significantly higher ($p < 0.05$) than that of the 1–24 day old individuals in normal colonies (38.40 ± 21.62) although it was not significantly different ($p > 0.05$) from the mean relative age of the entire normal colonies (53.52 ± 26.94).

The mean absolute age and proportion of foragers was significantly influenced (one-way were ANOVA, $p < 0.05$) by the age distribution in the colony (Fig. 1 c, d). The mean absolute age of foragers in the young-cohort colonies (12.04 ± 4.88 days) was not only significantly lower ($p < 0.05$) than that of foragers in the entire normal colonies (31.54 ± 12.01 days) but was also significantly lower than that of 1–24 day old foragers in the normal colonies (14.94 ± 4.71 days). The mean proportion of foragers in young-cohort colonies (0.42 ± 0.18) was significantly higher ($p < 0.05$) than that among the 1–24 day old individuals in normal colonies (0.33 ± 0.23) but was not significantly different ($p > 0.05$) from the proportion of foragers in the entire normal colonies (0.45 ± 0.19).

Age distribution also significantly influenced (one-way ANOVA, $p < 0.05$) the probability and frequency of foraging (Fig. 1 e, f). Individuals in young-cohort colonies had a mean probability of foraging (0.44 ± 0.42) that was significantly higher ($p < 0.05$) than that of 1–24 day old individuals in normal colonies (0.33 ± 0.37) but not significantly different from that of all individuals in normal colonies (0.43 ± 0.40). Similarly, individuals in the young-cohort colonies had a mean frequency of foraging (0.40 ± 0.58/hr) that was significantly higher ($p < 0.05$) than that of 1–24 day old individuals in normal colonies (0.31 ± 0.39/hr) but not significantly different from that of all individuals in normal colonies (0.37 ± 0.43/hr).

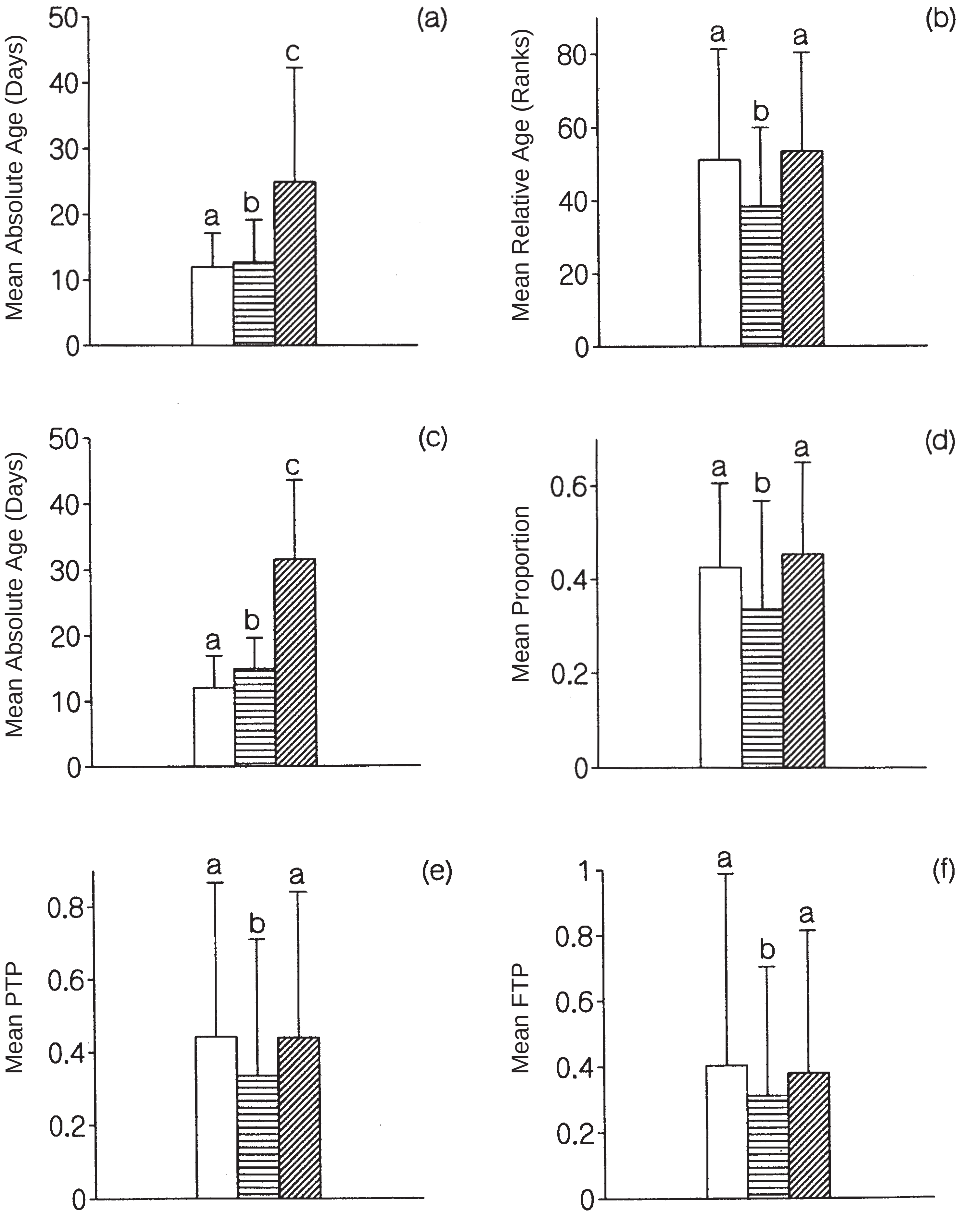

Figure 1. Mean (± SD) (a) absolute ages of all individuals, (b) relative ages of all individuals, (c) absolute age of foragers, (d) proportion of foragers, (e) PTP of all individuals and (f) FTP of all individuals, in the young-cohort colonies (open bars), the corresponding age group in normal colonies (horizontal hatches) and the entire normal colonies (diagonal hatches). One-way ANOVA followed by multiple comparisons of means by Tukey-Kramer method was used to test the effect of age distribution on the above parameters. Within each graph, bars with different alphabets are significantly different from each other ($p < 0.05$) while those with similar alphabets are not significantly different ($p > 0.05$)

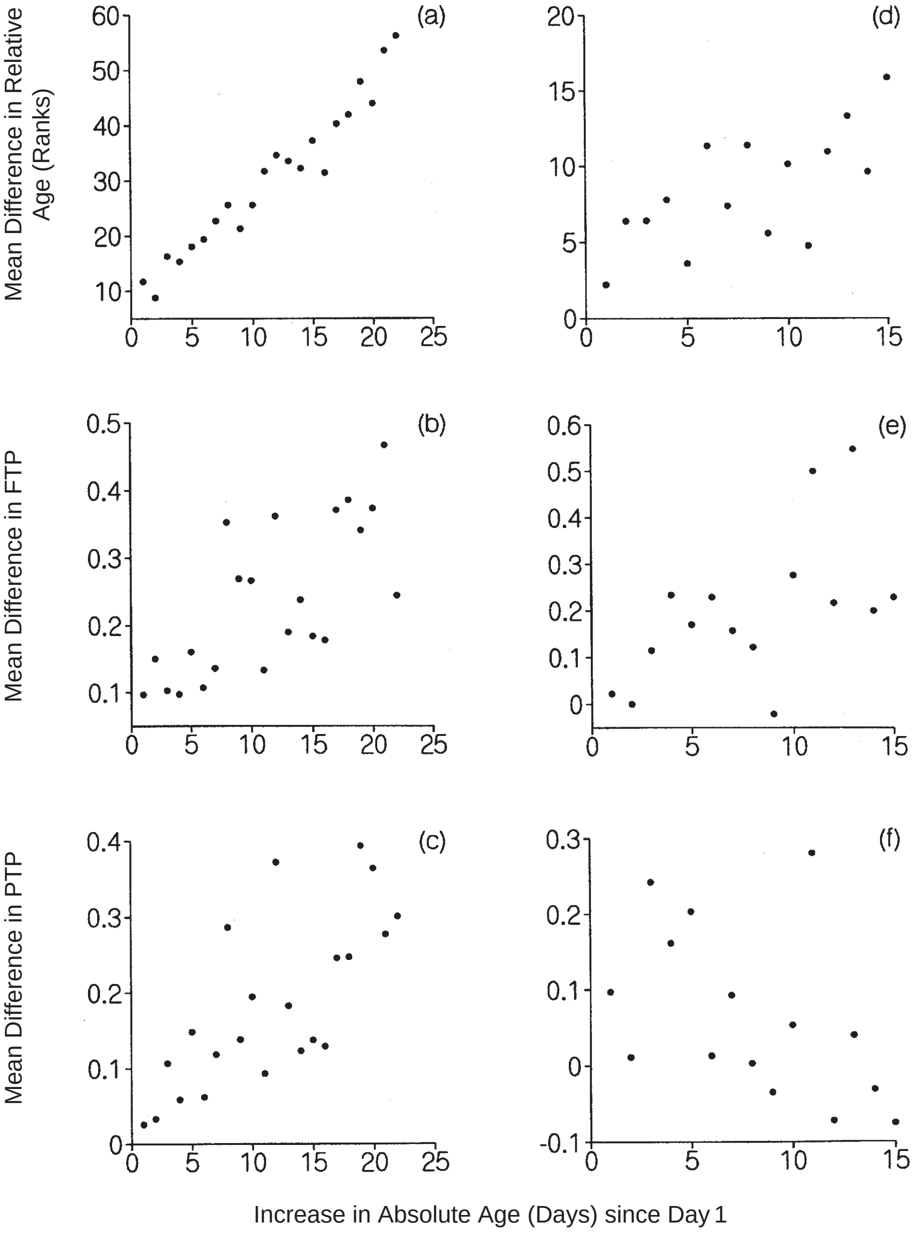

Figure 2. Scatter plots showing the relationship between increase in absolute age since Day 1 and (a) difference in relative age ($r = 0.97$, $p < 0.01$), (b) difference in FTP ($r = 0.71$, $p < 0.05$) and (c) difference in PTP ($r = 0.73$, $p < 0.05$) in normal colonies ($N = 22$); and (d) difference in relative age ($r = 0.67$, $p < 0.05$), (e) difference in FTP ($r = 0.56$, $p < 0.05$) and (f) difference in PTP ($r = 0.45$, $p > 0.05$) in young-cohort colonies ($N = 15$)

In both normal and young-cohort colonies, the increase in absolute age of individuals since Day 1 and the change in relative age during the corresponding period were positively correlated ($p < 0.05$, Fig. 2 a, d). However, this correlation was significantly greater ($t_s = 3.47$, $p < 0.01$) in the normal colonies ($r = 0.96$) than that in the young-cohort colonies ($r = 0.59$). While increase in absolute age of the individuals was accompanied by increase in both frequency and probability of extranidal tasks in normal colonies (Fig. 2 b, c), only frequency and not probability of extranidal tasks increased significantly with increase in absolute age in young-cohort colonies (Fig. 2 e, f).

Discussion

Wasps in young-cohort colonies forage earlier in their life compared to foragers among individuals of similar ages in normal colonies, showing that behavioral development in young-cohort colonies is faster. The foragers in young-cohort colonies can therefore be referred to as precocious foragers. The existence of such precocious foragers has also been reported in empirical studies of honey bees (Winston and Punnett, 1982; Robinson et al., 1989; Page et al., 1992; Huang and Robinson, 1996). That behavioral development is faster in young-cohort colonies is also supported by the result that a higher proportion of 1–24 day old individuals forage in young-cohort colonies compared to that in normal colonies. Thus, the young-cohort colonies respond to the loss of older individuals by a decrease in the mean absolute age of foraging and an increase in the proportion of individuals participating in foraging duties. That precocious foragers forage at an atypical absolute age demonstrates that task performance, when governed by relative age, can be independent of absolute age. It is interesting to note that the proportion of foragers in the young-cohort colonies is not significantly different from that in the entire normal colonies. This shows that by a suitable adjustment in the number of individuals performing different tasks, the young-cohort colonies are able to compensate for the loss of older individuals.

The readjustment in the organization of work in the young-cohort colonies is also reflected in the behavioral profiles of the individuals. In the young-cohort colonies, the probability and frequency of foraging are comparable to the corresponding values for the entire normal colonies but significantly higher than those for the 1–24 day old individuals in the normal colonies. Such an increase in the levels of task performance has been reported earlier for honey bee colonies lacking older or younger individuals (Kolmes and Winston, 1988). These results reemphasize the fact that a work organization based on relative age rather than absolute age can be flexible.

The significantly lower mean absolute age of foragers in the young-cohort colonies compared to the 1–24 day old individuals in the normal colonies ($p < 0.01$) may be partly attributed to the fact that the individuals in the young-cohort colonies were also marginally younger than the 1–24 day old individuals in the normal colonies ($p < 0.05$). However, the significantly higher proportions of foragers in the young-cohort colonies and their significantly higher PTP and FTP compared to 1–24 day old individuals in normal colonies, in spite of the fact that the former were marginally younger than the latter, strengthens the conclusion that behavioral development is faster in these colonies.

In the young-cohort colonies, individuals advance in absolute age but their relative age is more or less constant since all new individuals eclosing were removed and the only possible means by which the relative age of an individual could change was through the loss of one or more wasps. Therefore, the correlation between the absolute and relative ages of an individual in the young-cohort colonies is significantly weaker than what is found in normal colonies. In the absence of a strong correlation between absolute and relative ages, an increase with absolute age, in FTP but not in PTP, shows that relative age is what determines PTP and absolute age is what determines the FTP of an individual.

Absolute age might well be important in determining the total work budget of an individual since the amount of work an individual can perform depends on its physical condition which can be expected to be correlated with its absolute age. However, given such a constraint on work organization posed by absolute age, insect societies could attain flexibility by a mechanism such that the probability of performing a task is determined by relative age. Calderone and Page (1991) have argued in a similar vein that the age-specific probability of performing a task can be acted upon by selection independently of the temporal pattern of task performance.

It may be possible to meet small changes in colony work profile brought about by small changes in age structure with changes in FTP that are small enough to be permissible without any change in absolute age of the individuals. However, if there is a major perturbation to the colony age structure, the remaining individuals cannot compensate adequately by altering their FTP since such a large change in FTP may not be permissible without a substantial change in absolute age. Since such large perturbations are generally accompanied by large changes in the relative ages of the individuals, it is possible for them to appropriately alter their PTP because it is governed by relative age, independent of absolute age. The graded response of insect colonies to changing conditions (Kolmes and Winston, 1988; Robinson, 1992) can be explained by such a mechanism. A work organization in which different parameters of task performance, such as PTP and FTP, are acted upon by different parameters of the worker age, such as absolute and relative, can therefore be suitably flexible and reliable.

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References

Calabi, P. and J.F.A. Traniello, 1989. Behavioral flexibility in age castes of the ant *Pheidole dentata*. *J. Ins. Behav. 2*: 663-677.

Calderone, N.W. and R.E. Page, 1991. Evolutionary genetics of division of labor in colonies of the honey bee (*Apis mellifera*). *Am. Nat. 138*: 69–92.

Huang, Z. and G.E. Robinson, 1996. Regulation of honey bee division of labor by colony age demography. *Behav. Ecol. Sociobiol. 39*:147–158.

Kolmes, S.A. and M.L. Winston, 1988. Division of labour among worker honey bees in demographically manipulated colonies. *Insectes soc. 35*:262–270.

Naug, D. and R. Gadagkar, 1998. The role of age in temporal polyethism in a primitively eusocial wasp. *Behav. Ecol. Sociobiol. 42*:37–47.

Oster, G.F. and E.O. Wilson, 1978. *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton. 352 pp.

Page, R.E., G.E. Robinson, D.S. Britton and M.K. Fondrk, 1992. Genotypic variability for rates of behavioral development in worker honey bees (*Apis mellifera* L.). *Behav. Ecol. 3*:173–180.

Robinson, G.E., R.E. Page, C. Strambi and A. Strambi, 1989. Hormonal and genetic control of behavioral integration in honey bee colonies. *Science 246*:109–112.

Robinson, G.E., R.E. Page, C. Strambi and A. Strambi, 1992. Colony integration in honey bees: mechanisms of behavioral reversion. *Ethology 90*:336–348.

Wilson, E.O., 1971. *The Insect Societies*. The Belknap Press of Harvard University Press, Cambridge. 548 pp.

Winston, M.L. and E.N. Punnett, 1982. Factors determining temporal division of labor in honeybees. *Can. J. Zool. 60*:2947–2952.

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