

Implications of senescence patterns for the evolution of age polyethism in eusocial insects

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Division of labor based on age, with workers delaying performance of risky tasks, evolved in all major lineages of eusocial insects, raising questions about possible selective advantages of this pattern. We present a model showing that patterns of senescence in workers can have profound implications for the evolution of age polyethism in insect societies. Controversy exists over the relative importance of programmed versus rate of living senescence in determining the longevity of animals. If programmed senescence occurs in eusocial insects, workers that delay performance of risky tasks until later in life have greater expected longevity and therefore perform more labor per unit production cost. If senescence does not occur or if the age of senescent death is determined solely by rate of living effects, then worker longevity is not increased by delayed performance of risky tasks. Several lines of indirect evidence suggest that high rates of work have negative effects on worker longevity, supporting the rate of living hypothesis. Critical empirical data on patterns of senescence in eusocial insect workers are lacking, however, particularly with respect to the occurrence of programmed senescence. Furthermore, programmed senescence may operate in conjunction with rate of living effects. In this case, a negative relationship between work rate and longevity will be evident in highly active workers, while longevity of inactive workers will reach an upper plateau and will not be related to differences in work rate. If programmed senescence is demonstrated in eusocial insect workers, then increased worker longevity may have favored the evolution of age polyethism with delayed performance of risky tasks. *Key words:* age polyethism, division of labor, eusocial insects, programmed senescence, rate of living hypothesis. [*Behav Ecol* 6:269–273 (1995)]

Age polyethism, or division of labor among workers based on age, has evolved in all major lineages of eusocial Hymenoptera (reviewed by Wilson, 1971) and is a central organizing feature of colony activity (Robinson, 1992). In nearly all cases of age polyethism, performance of tasks exposing workers to high risk of mortality (such as foraging and colony defense) are delayed until late in worker life (e.g., O'Donnell and Jeanne, 1992 for wasps; Schmid-Hempel and Schmid-Hempel, 1984 for ants; Winston and Katz, 1981 for honey bees). Previous models for the evolution of this pattern focused on efficient worker behavior and external risks of mortality (Jeanne 1986; Seeley, 1982; West Eberhard, 1981). Here we present a model showing that the nature of worker senescence has implications for the evolution of age polyethism.

Jeanne's (1986) model demonstrated that colony-level selection could account for the near ubiquity of age polyethism. When maximum worker longevity was fixed at 50 days, expected (mean) worker longevity was greater in colonies where workers delayed performance of riskier tasks until late in life. Assuming that the cost of producing workers does not change with the evolution of age polyethism, longer-lived workers would perform more labor relative to the cost of their production. In Jeanne's (1986) model, an increase in labor output of workers per unit production cost, resulting in increased colony energetic efficiency, is the selective advantage of age polyethism.

In this article we extend this model and show that patterns of worker senescence determine whether age polyethism increases expected worker longevity. Two competing hypotheses explain patterns of senescence in animals (Austad and Fischer, 1991), the programmed senescence hypothesis (Hamilton, 1966; Partridge and Barton, 1993) and rate of living

hypothesis (Davies, 1991; Sohal, 1986). Under programmed senescence, maximum longevity is set by the accumulation of deleterious alleles with age-specific effects. This occurs either because selection against deleterious genes acting late in life is weak (mutation accumulation) or because selection on life history characteristics favors genes with positive effects early in life and correlated negative effects later in life (antagonistic pleiotropy) (Partridge and Barton, 1993). Through both evolutionary pathways, an equilibrium is reached between expected age of last reproduction and genes promoting early senescence, and senescent death is selected to occur at a programmed age within populations (Sauer et al., 1986; but see Abrams, 1993).

The rate of living hypothesis assumes that life span is limited by non-renewable physiological resources or non-regenerating morphological structures. These resources are consumed, or morphological structures are worn out, as an individual ages (Sohal, 1986). Depletion of the resource, or concomitant accumulation of physiological or morphological damage, leads to physical degradation and eventually to senescent death. When the rate of consumption or damage accumulation depends upon activity level, more active individuals will have shorter life spans. Therefore, the rate of living hypothesis predicts that individual longevity will correlate negatively with an appropriate measure of activity and that senescence will not occur at a fixed age within populations.

In this article we show that patterns of worker senescence in eusocial insects determine whether worker longevity is greater in colonies with age polyethism. Age polyethism increases expected longevity only when programmed senescence occurs, that is, when workers begin to senesce at a fixed age independently of their activity level. If worker senescence is caused solely by rate of living effects, then expected longevity is equal in colonies with and without age polyethism. We review evidence on the proximate causes and patterns of senescence in workers and conclude that empirical studies are needed to assess whether the evolution of age polyethism could have been favored because it increased worker longevity and thereby led to greater colony efficiency.

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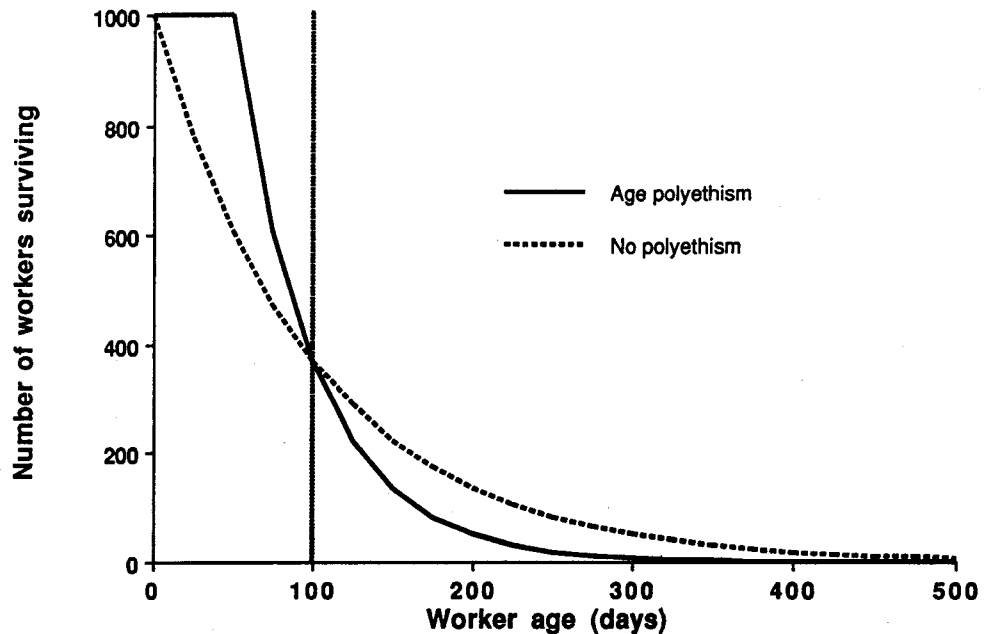


Figure 1
Expected distributions of worker longevities in days for eusocial insect colonies with (solid line) and without (dashed line) age polyethism. In this case, original population size $N_0 = 1000$; risk associated with safe task $r_1 = 0$; risk associated with dangerous task $r_2 = 0.02$; age of switching $t_s = 50$ days. Mean (expected) longevity = 100 days with and without polyethism, as indicated by the dotted vertical line.

THE MODEL

The model explores the effects of age polyethism on expected worker longevity. We incorporated into the model two alternative mechanisms of senescence (programmed versus rate of living) that could operate on eusocial insect workers. The assumptions of our model (detailed below) are similar to those of Jeanne (1986), except that we derived distributions of worker longevities numerically, rather than through simulation.

The model generated distributions of life spans for eusocial insect workers assigned to perform two sets of tasks, the simplest form of division of labor (Jeanne, 1986). Workers performed safe tasks such as brood care with a low constant probability of mortality, r_1 , and risky tasks such as foraging with some higher constant probability of mortality, r_2 . Differences in the probability of mortality for the task sets are associated with exposure of workers to different levels of external risk (non-senescent death), for example predation or getting lost. On the colony level, worker populations were required to devote equal total effort to each task set (safe and risky).

Using the model, we compared two categories of division of labor among workers (polyethism). First, to represent colonies without age polyethism, all workers performed both tasks with equal probability from the beginning of their adult lives; therefore, they were assigned a constant probability of mortality equal to the mean mortality risk of the safe and dangerous tasks combined, given by $(r_1 + r_2)/2$ when equal effort is devoted to each task set.

Second, to represent colonies with age polyethism, all workers first perform the safe task with mortality risk r_1 , then switch to performing the dangerous task with risk r_2 . The fixed age of switching between tasks for all workers, t_s , was set such that the population of workers under age polyethism devoted equal effort to each task (as did workers without age polyethism). If the safe task has no associated risk ($r_1 = 0$; see Results, below), then $t_s = 1/r_2$. For colonies with and without age polyethism, the number of workers alive at time t (N_t) was calculated using an exponential decay model:

$$N_t = N_0 e^{-rt}$$

where N_0 is the original population size.

Programmed senescence, represented by a fixed maximum

longevity, was incorporated into the model by imposing a fixed age of senescent mortality. All surviving workers die at this age, as in Jeanne's (1986) model. We varied the age of programmed senescence and compared the effects of this variation on expected worker longevity in colonies with and without age polyethism. We assumed that overall colony labor requirements would not change with the evolution of age division of labor. Therefore, the age of switching from safe to risky tasks (t_s) in colonies with age polyethism was adjusted downward when programmed senescence was imposed to maintain the requirement that equal total effort was devoted to each task by the worker populations. This was done by calculating the switching age (t_s) where the area under the longevity distribution curve before switching equalled that after switching.

RESULTS

To fully explore the implications of patterns of senescence for the evolution of age polyethism, we examined the greatest possible difference between colonies with and without age polyethism. The greatest difference in worker longevity distributions between the two types of colonies results if the safe task has no associated risk, $r_1 = 0$. Distributions of worker longevities generated for age polyethism and no polyethism colonies when $r_1 = 0$ are shown in Figure 1. The area under the distribution of worker longevity curves represents the total amount of labor performed (worker-days) by the worker population. In colonies without polyethism, this area is $N/[(r_1 + r_2)/2]$. Under age polyethism, the total area consists of two additive components: before the age of switching, when the safe task ($r_1 = 0$) is performed exclusively, the area component is $N_0(t_s)$; after the age of switching, when the risky task is performed exclusively, the area component is N_0/r_2 . Although life expectancy (mean longevity) of workers is equal in colonies with and without age polyethism, note that more workers have longevities greater than the mean longevity in colonies without age polyethism (Figure 1).

When maximum worker longevity is fixed by programmed senescence, colonies with age polyethism achieve higher expected worker life spans (Figure 2). This is true because a

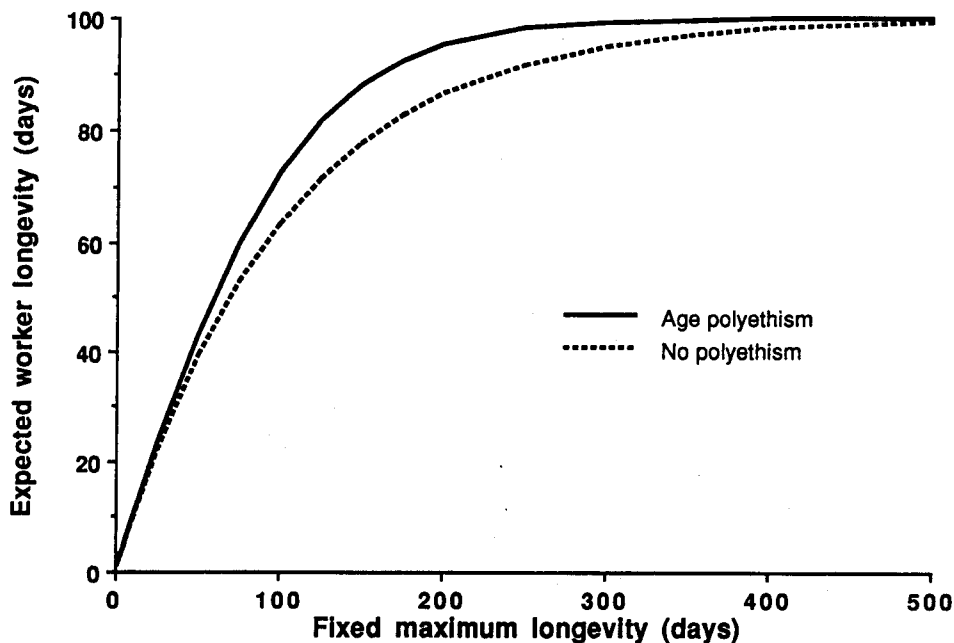


Figure 2
Expected worker longevities in colonies with (solid line) and without (dashed line) age polyethism when a fixed age of mortality (representing programmed senescence) is imposed. Age in days at which workers undergo programmed senescence is shown on the x-axis. Parameters of the model as in Figure 1.

fixed age of mortality truncates the life span distribution of colonies without polyethism to a greater degree than those with age polyethism (Figures 1 and 2); the strength of this effect is less pronounced when programmed senescence occurs at very young and very old ages, but age polyethism is always favored (Figure 2). Under programmed senescence, expected labor output relative to the cost of producing workers is therefore higher in colonies with age polyethism.

On the other hand, if longevity is determined solely by an individual's rate of work and programmed senescence is absent, as expected under the rate of living hypothesis, there will be no difference in expected life span between colonies with and without age polyethism. Any increased mortality due to some individual's high work rates can be incorporated into the mortality risks associated with the tasks (by increasing the population parameters r_1 and/or r_2). Doing so does not change the relationship between the distributions of worker longevities in colonies with and without age polyethism (Figure 1) as long as the changes in worker activity level are equal in the two types of colonies. Similarly, productivity gains due to increases in worker activity would be equal in age polyethism and no polyethism colonies.

DISCUSSION

Implications of the model

Patterns of senescence in eusocial insect workers determine whether increased worker longevity can serve as a selective advantage to colonies with age polyethism over those without polyethism. If programmed senescence occurs, worker death should occur at a population-mean age, and maximum longevity should be independent of an individual's rate of work. In this case, age polyethism yields a greater expected worker longevity than does non-polyethism (Figure 2).

However, to the extent that worker longevity is determined only by rate of living effects, age polyethism does not increase the expected longevity of workers. To assess the validity of the hypothesis that increased worker longevity favored the evolution of age polyethism, it is necessary to establish which mechanism(s) of senescence operate in eusocial insect workers.

Patterns of senescence in eusocial insect workers

Adult insects are enclosed in a non-regenerating solid cuticle, and their cells are post-mitotic; therefore, they lack capacities thought to be critical in the repair of physiological degradation leading to senescence (Cartar, 1992; Cutler, 1976). When physiological and morphological wearing processes are accelerated by task performance, senescent degradation of workers conforms to predictions of the rate of living hypothesis.

Two experimental studies examined tradeoffs between work loads and longevity in honey bee (*Apis mellifera*) workers. Both produced results inconsistent with a direct tradeoff between rate of work and longevity. Manipulations that decreased time spent foraging or increased forager weight had little effect on longevity; however, longevity was negatively related to work rate within treatment groups in the foraging time experiment (Schmid-Hempel and Wolf, 1988; Wolf and Schmid-Hempel, 1989). Wolf and Schmid-Hempel (1989) posited that natural selection favors a weak relationship between worker longevity and work load over the usual range of labor output and that only extreme (low or high) work loads will have a measurable effect on worker longevity.

Several other lines of evidence, however, suggest that rate of work affects eusocial insect worker longevity. In temperate and seasonal tropical habitats, both honey bee and stingless bee worker life spans vary greatly with seasonal shifts in colony-wide activity in a manner consistent with a tradeoff between rate of work and longevity (Roubik, 1982; Winston, 1987). Neukirch (1982) found that time spent in flight strongly affected honey bee worker longevity and that total flight performance by workers had an upper limit caused by diminution of metabolic enzyme activity. Similarly, field studies of eusocial wasps (*Polistes exclamans* and *Polybia occidentalis*) showed that hazard function values, which index age-specific risks of mortality, increased with the number of days spent foraging, suggesting that total duration of foraging activity is limited for workers (O'Donnell and Jeanne, 1992; Strassmann, 1985). Lighton (1989) observed that the minimum sensitivity of O_2 consumption rate to temperature in an African species of carpenter ant (*Camponotus*) occurred around the temperatures at which foragers were most active in the

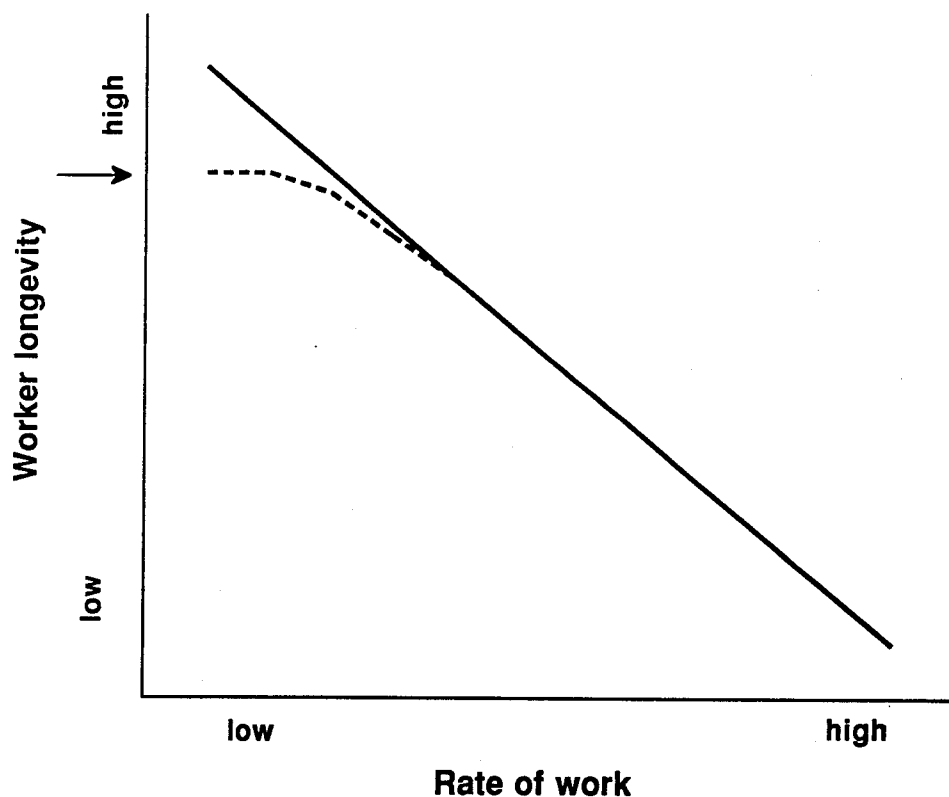


Figure 3

Predicted relationships of rate of work with longevity for eusocial insect workers when a tradeoff exists between work rate and life span, as posited by rate of living models of senescence. The solid line represents a species without a fixed maximum longevity (representing senescence caused by rate of living effects only); the dashed line represents a species with a fixed maximum longevity at the age indicated by the arrow on the y-axis (representing combined rate of living and programmed senescence).

field, providing evidence for selection on metabolic efficiency of workers and suggesting that elevated worker metabolic rates impose some selective cost on the colony.

A striking difference between eusocial insects with cursorial workers (ants) and those with flying workers (wasps, bees) is that energy expenditure rates are much higher for flying workers because flight is relatively energy-expensive per unit time (Fewell, 1988; Lighton and Bartholomew, 1988; Nielsen and Baroni-Urbani, 1991). Foraging honey bees appear to be more sensitive to changes in metabolic rate than to time invested when making foraging decisions (Waddington, 1990; Wolf and Schmid-Hempel, 1989). This suggests that physiological costs are more important in honey bee foraging decisions than exposure to predation risk while away from the nest. In contrast, ants require little energy expenditure to retrieve food materials (Baroni-Urbani and Nielsen, 1991; Fewell, 1988). Consistent with this difference, harvester ants (*Pogonomyrmex occidentalis*) are more sensitive to net energetic gain rate (maximizing gain/unit time) than to energetic efficiency (maximizing gain/unit energetic cost) when foraging (Fewell, 1988).

The preceding observations suggest a comparative test between the rate of living and the programmed senescence hypotheses of longevity in eusocial insect workers. Because flight is metabolically much more costly per unit time than walking or running (Nachtigall et al., 1989; Rothe and Nachtigall, 1989), if rate of living senescence operates strongly on workers, longevity will be more variable and will depend more directly on amount of foraging in flying than in cursorial eusocial insects.

Few studies have measured longevities of eusocial insect workers, and data on more species are clearly needed for a valid comparison. Ant workers are often long-lived under laboratory conditions, with longevities ranging from 10 weeks to over 3 years (reviewed by Hölldobler and Wilson, 1990). However, Miranda and Vinson (1981) found that foraging workers

had reduced life spans compared to non-foragers in laboratory colonies of fire ants (*Solenopsis invicta*). Fire ant workers lived longer in colony fragments without queens and brood, further suggesting a relationship between labor output and life span in some species of ants (Calabi and Porter, 1989). Large differences in body size among ant workers, absent in flying eusocial insects, can affect individual metabolic rates and load carrying efficiency (Calabi and Porter, 1989; Lighton et al., 1987; but see Nielsen, 1986). Interactions of body size with metabolic rate and activity level must be accounted for in studies of worker longevity in polymorphic ant species. Further studies that carefully examine the effects of foraging activity on longevity (Neukirch, 1982; Schmid-Hempel and Wolf, 1988) are needed.

Few data are available to address the question of whether programmed senescence occurs in eusocial insect workers. Guzman-Novoa et al. (1994) found weak evidence for programmed senescence in honey bees (*Apis mellifera*): foraging tenures were longer in workers that began foraging at younger ages. Foraging tenure did not vary with age at first foraging in *Polybia occidentalis* wasps; therefore, age of mortality does not appear to be fixed in this species (O'Donnell and Jeanne, 1992). However, demonstrating decreased longevity with increased activity in workers does not necessarily rule out a genetically programmed age of death (Hamilton, 1966). For example, it is possible that strong rate of living effects on longevity may be superimposed on programmed senescence in eusocial insect workers. Hypothetical distributions of workers' longevities that might be expected in insect societies where performance of work affects life span, with and without the occurrence of programmed senescence, are shown in Figure 3. To critically test for increased worker longevity through the evolution of age polyethism, it will be necessary to ascertain whether or not worker mortality rates increase with age independently of the amount of work performed. As seen in Figure 3, examination of longevity of relatively inactive work-

ers is most likely to indicate the operation of programmed senescence.

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