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Influence of caste polyethism on longevity of workers in social insect colonies

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Abstract

Different patterns of division of labor can affect the expected longevity of social insects workers. It has been earlier suggested that when tasks performed inside and outside colony are equally risky then the expected longevity of workers in colonies with caste polyethism is greater than that in colonies without polyethism. To verify these predictions I used a model assuming two sets of tasks, associated with different mortality rates. In the colony without polyethism the workers preformed safe and risky tasks in turn, while in the colony with caste polyethism the workers specialized in only one set of tasks. The outcomes suggest that the expected longevity of workers in colonies with caste polyethism cannot be greater than that in colonies without polyethism. Only if there is no aging and under some special and rare conditions are there no differences in expected longevity between colonies with and without caste polyethism. If aging is independent of activity, caste polyethism does not shorten longevity when all tasks in the colony are equally risky. The results can explain why caste polyethism is not as widespread among social insects as age polyethism.

Keywords: Division of labor; Caste polyethism; Longevity; Aging

1. Introduction

Workers of some social insects specialize in particular tasks and perform them during greater part of their lives than other workers do. When the specialization is associated with morphological adaptations it is called caste polyethism (Wilson, 1971). More recently the term "physical caste" has been applied to a group of workers specializing in a particular task and morphologically distinct (Oster and Wilson, 1978). For example, in *Pheidole pallidula* there are two casts of workers: majors (called soldiers) and minors. Majors are much bigger than minors and they are equipped with strong mandibles. Majors specialize in killing enemies, while minor ones do not specialize in any particular task (Detrain and Pasteels, 1992). There are also cases of specialization among morphologically similar individuals. For example, some honeybee workers specialize in collecting water (Robinson et al., 1984). In this paper I consider caste polyethism as an age-independent division of labor in which workers, with or without morphological adaptations, specialize in particular tasks during most of their lives.

Caste polyethism may be adaptive because it increases efficiency (Oster and Wilson, 1978). However, to assess the profitability of caste polyethism not only the benefits but also costs have to be considered. Jeanne (1986) remarked that caste polyethism can affect the expected longevity of workers. He assumed that there is no mortality during tasks performed inside colony and used simulations to find longevity of workers for different mortalities outside colony. Jeanne (1986) did the calculations both for colonies with and without caste polyethism. His results presented as a figure suggest that when the mortality outside colony is low then the expected longevity of workers in colonies with caste polyethism is greater than that in colonies without

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polyethism. The opposite was true when the mortality outside colony was high (Jeanne, 1986).

In this paper the influence of caste polyethism on worker longevity is verified more strictly. I use a mathematical model which is modification of the model comparing longevity of workers in colonies with and without age polyethism (Tofilski, 2002). The results show that, unlike age polyethism, caste polyethism in most cases reduces the expected longevity of workers. The conclusions can help explain the evolution of division of labor in social insects.

2. The model

As in the age polyethism model (Tofilski, 2002) I assume that workers do not reproduce and that there are no conflicts among colony members. Fitness of a worker has no direct component and depends solely on reproductive success of the queen, its mother. The success of the queen is determined, among others, by efficiency of work organization in the colony. As a measure of the colony efficiency I used expected longevity of workers.

All resources in the colony can be expressed in amount of time spent by workers to obtain them. To produce a new worker the colony has to spend working time of present workers and other resources, e.g. food and space in a nest. The other resources can be expressed in currency of working hours of workers collecting the food and enlarging the nest. The profitability of investment in a new worker can be calculated as a difference between amount of time spent to produce the new worker and the amount of time the newly produced worker will work for the colony in future. If costs of worker production are the same for all workers, maximum efficiency will be achieved by maximizing average longevity of the workers. Workers of social insects with caste polyethism often differ in size and amount of time required to produce them. However, in this model I consider moment of origin of the caste polyethism when all workers in colony are identical and require the same amount of time to be produced.

I assume that there are two sets of tasks, A and B, associated with different mortality rates. A-type tasks are associated with aging-independent mortality m_A and B-type tasks are associated with aging-independent mortality m_B . Tasks associated with lower mortality are called safe and tasks associated with higher mortality are called risky. In social insects the safe tasks are those performed within the nest (e.g. brood care) and risky tasks are those outside the nest (e.g. foraging). High mortality during foraging in comparison to mortality inside colony was found in honeybees (Sakagami and Fukuda, 1968) and stingless bees (Biesmeijer and Toth, 1998).

Workers specializing in safe task can survive for longer than workers specializing in risky task. However, both safe and risky tasks need to be done because colony would not benefit from workers performing brood care without workers performing foraging. The relationship between the amounts of time, summed over all workers, spent in colony as a whole on tasks A and B, t_A and t_B respectively, is taken to be linear, and in the colony a fixed proportion of time f is devoted to A-type tasks:

$$f = \frac{t_A}{t_A + t_B}. \tag{1}$$

Two strategies are considered here: (1) a worker performs tasks A and B in turn, as in colonies without polyethism, and (2) some workers, called caste A, perform only A-type tasks during the whole life, and other workers, called caste B, perform only B-type tasks during the whole life, as in colonies with caste polyethism. The proportion of workers from caste A f_w needs to be adjusted in such a way that caste A performs fraction f of the total working time performed in the colony. If expected longevity of workers from caste A w_A is shorter than expected longevity of workers from caste B w_B then more workers from caste A is needed to recompense differences in longevity and in effect $f_w > f$. The proportion of workers from caste A is given by

$$f_w = \frac{\frac{t_A}{w_A}}{\frac{t_A}{w_A} + \frac{t_B}{w_B}}. \tag{2}$$

As in simplified version of the age polyethism model (Tofilski, 2002) I assume that aging does not affect worker mortality until a certain age is reached, at which time all workers die. Similar assumptions are made in models concerning foraging and longevity in social insects, although not explicitly (Schmid-Hempel et al., 1985; Jeanne, 1986; Schmid-Hempel, 1987). I assume that a worker cannot expend more than the maximum resources available for whole life k. When the resources become exhausted the worker dies (Tofilski, 2000). A worker's life span can be limited by non-regenerating morphological structures (Cartar, 1992) or non-renewable physiological resources (Neukirch, 1982). The maximum life span depends on the rate of resource expenditure during tasks A and B: c_A and c_B, respectively. If the rates are equal ($c_A = c_B$) then aging does not depend on the activity. If the rates are not equal, the maximum longevity of workers depends on the amount of time devoted to tasks A and B. For example, it is suggested that workers spending a longer time in flight live shorter (Neukirch, 1982).

The expected longevity of a worker can be represented as the area under the survival curve. The probability of surviving to a given age decreases due to aging-

independent mortality until the maximum life span is reached. The area under the survival curve can be calculated as a definite integral of the survival function, given by $\exp(-m_A\ t)$, from the beginning of life to maximum life span. The maximum life span of a worker from caste A is k/c_A, and its expected longevity is

$$w_A = \int_0^{k/c_A} \exp(-m_A t)\,\mathrm{d}t. \quad (3)$$

The expected longevity of a worker from caste B is given by a similar equation. Only the rate of resource expenditure and aging-independent mortality are different:

$$w_B = \int_0^{k/c_B} \exp(-m_B t)\,\mathrm{d}t. \quad (4)$$

The expected longevity of workers in colony with caste polyethism p_w is given by

$$p_w = w_A f_w + w_B(1 - f_w). \quad (5)$$

In a colony without polyethism, the expected longevity of workers is given by the same equation as in the model for age polyethism (Tofilski, 2002):

$$p_0 = \int_0^{k/(c_A f + c_B(1-f))} \exp[-(m_A f + m_B(1-f))t]\,\mathrm{d}t. \quad (6)$$

There are no simple analytical solutions of the equation $p_0 = p_w$. It can be, however, showed analytically that the expected longevity of a worker in a colony with caste polyethism is the same as in a colony without polyethism when $m_A c_B = m_B c_A$. The way in which the problem was solved does not imply that there is only one solution, so the equations were solved numerically. The calculations confirmed the analytical solution and showed that if $m_A c_B m_B c_A$ the expected longevity of workers in colonies with caste polyethism is less than that in colonies without polyethism (Fig. 1).

The situation when aging is independent of activity constitutes a special case of the prior model. In this instance the rate of resource expenditure is the same during tasks A and B ($c_A = c_B$), and caste polyethism does not entail any costs if $m_A = m_B$.

If there is no aging ($c_A = c_B = 0$) the maximum life span is infinity. Then in a colony with caste polytheism the expected life span of workers from caste A is given by

$$w_{0A} = \int_0^{\infty} \exp(-m_A t)\,\mathrm{d}t \quad (7)$$

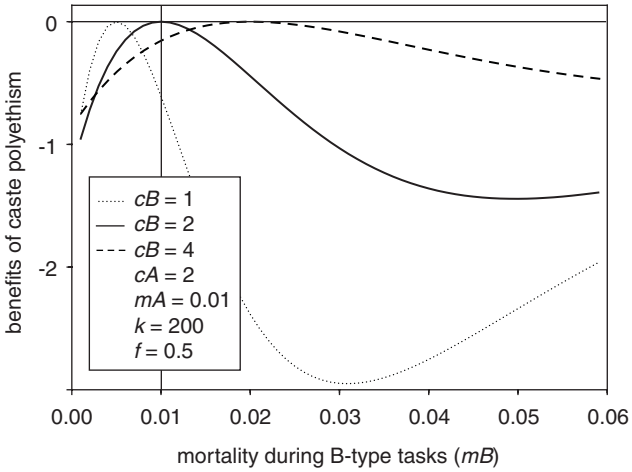

Fig. 1. Benefits of caste polyethism are calculated as the difference in longevity between colonies with and without caste polyethism for different values of aging-independent mortality during B-type tasks m_B. When aging-related mortality is constant through life (solid line), caste polyethism is not associated with any costs if aging-independent mortality during tasks A and B is the same ($m_A = m_B$). Also indicated are the costs of caste polyethism when aging-related mortality during B-type tasks is lower (dotted line) and higher (dashed line) than that during A-type tasks. The vertical line indicates the same aging-independent mortality during tasks A and B.

and the expected longevity of workers from caste B is given by

$$w_{0B} = \int_0^{\infty} \exp(-m_B t)\,\mathrm{d}t. \quad (8)$$

In a colony without polyethism the expected longevity is

$$p_{00} = \int_0^{\infty} \exp[-(m_A f + m_B(1-f))t]\,\mathrm{d}t. \quad (9)$$

It can be proved analytically that the average longevity of workers in a colony with caste polyethism is the same as in a colony without polyethism if there is no aging.

3. Discussion

The model shows clearly that the expected longevity of workers in a colony with cast polyethism cannot be greater than that in a colony without polyethism. In most cases caste polyethism significantly shortens it. Jeanne (1986) obtained different predictions. The results of his simulations, presented as a figure, suggest that the expected longevity of workers in a colony with caste polyethism could be greater than that in a colony without polyethism if the mortality during foraging is low. Verbal description of the simulations (Jeanne, 1986) is not precise enough to indicate cause of the discrepancy.

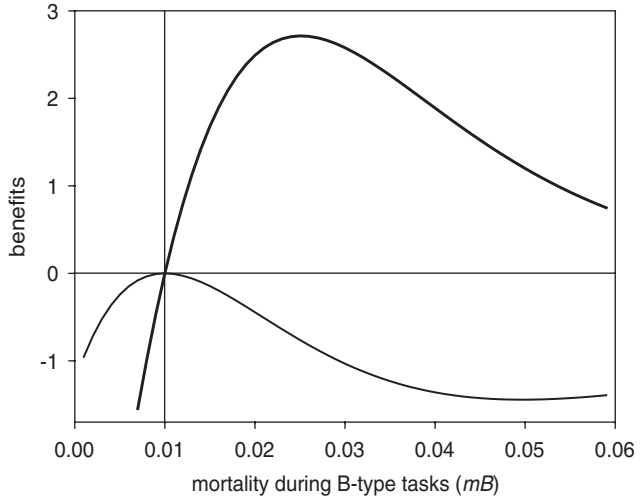

Fig. 2. Benefits of caste polyethism (thin line) and age polyethism (thick line). The benefits are calculated as difference in longevity between colony with caste or age polyethism and colony without polyethism. At one point ($m_A\ c_B = m_B\ c_A$) all three strategies are associated with the same expected longevity. In all other cases the best strategy is age polyethism because it allows sequence of task to be chosen in such a way that $m_A\ c_B < m_B\ c_A$. ($m_A = 0.01$, $c_B = c_A = 2$, $k = 200$, $f = 0.5$).

In some special circumstances ($m_A\ c_B = m_B\ c_A$; Fig. 1) the expected longevity of workers in colonies with caste polyethism is the same as in colonies without polyethism. Under the same condition age polyethism is equally beneficial as lack of polyethism (Tofilski, 2002, Fig. 2). Using the transitive property of equality it can be proved that in those rare circumstances all three ways of division of labor are associated with the same workers longevity. However, in all other cases age polyethism, with risky tasks performed later in life, is the best strategy (Fig. 2). The conclusions do not require detailed knowledge of life history parameters; they are valid as long as there is mortality and aging.

The comparison of the expected longevity of workers in colonies with different ways of division of labor can explain why age polyethism is much more widespread among social insects than caste polyethism. Age polyethism is common among eusocial bees (Michener, 1974), wasps (Jeanne, 1991) and ants (Hölldobler and Wilson, 1990). It was also found in termites although number of studies is limited in this group (Crosland et al., 1998; Hinze and Leuthold, 1999 and references cited therein). Lack of age polyethism has been found only in one species of termites *Zootermopsis angusticollis* (Traniello and Rosengaus, 1997) and one species of ants *Amblyopone pallipes* (Traniello, 1978; Traniello and Rosengaus, 1997). On the other hand caste polyethism with morphologically specialized workers is common only in termites (Haverty, 1977). In ants it is rare (Hölldobler and Wilson, 1990) and in wasps and bees it is absent (Wilson, 1971).

Reduced longevity of workers is not the only factor affecting evolution of caste polyethism. It has been suggested that lack of flexibility in changing environment can constrain the evolution of caste polyethism (Schmid-Hempel, 1992). However, this does not agree with mathematical models showing that unpredictable changes of environment promote evolution of multiple casts (Oster and Wilson, 1978, pp. 205–217). Evolution of caste polyethism can be constrained also by: ergonomic costs, environmental dispersion, behavioral plasticity, task overlap and individual level selection (Oster and Wilson, 1978, pp. 188–193) but there is not enough theoretical and empirical evidence to verify significance of those factors.

I showed here that different ways of division of labor can affect expected longevity of workers. In most cases age polyethism prolongs the longevity but caste polyethism shortens it. This can explain why in social insects age polyethism is much more widespread than caste polyethism.

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