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ORIGINAL ARTICLE

Adam Tofilski

Influence of age polyethism on longevity of workers in social insects

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Abstract Age polyethism is widespread among social insects and, as a rule, safe tasks are performed by workers earlier in life than are risky ones. Mathematical models were used to compare expected longevity of workers in colonies with and without age polyethism. The results of the models suggest that if aging does not depend on activity then age polyethism is profitable when safer tasks are performed earlier in life. If, however, aging depends on activity, age polyethism is profitable when safer tasks are performed earlier in life and if they are associated with higher aging-related mortality. On the other hand, age polyethism is not profitable if safer tasks are performed later in life, and if they are associated with lower aging-related mortality. Furthermore, if there is no aging, then age polyethism does not bring any benefits. Electronic supplementary material to this paper can be obtained by using the Springer Link server located at http://dx.doi.org/10.1007/s00265-001-0429-z

Keywords Division of labor · Age polyethism · Life span · Social insects · Aging

Introduction

In most social insects, the workers perform different tasks at different times of their lives (Wilson 1971). This division of labor is known as age polyethism. The tasks can be associated with different mortality rates. Usually, tasks performed inside a colony such as feeding larvae are much safer than foraging, which is performed outside the colony (Sakagami and Fukuda 1968; Winston and Katz 1981). As a rule, safe tasks are performed earlier in life than are risky ones (Seeley 1982; Schmid-Hempel and Schmid-Hempel 1984). Jeanne (1986) demonstrated that this sequence of tasks is profitable because it increases the life expectancy of workers. The problem of age polyethism was also explored by Woyciechowski and Kozlowski (1998a), who demonstrated that risky tasks should be performed by workers that have a shorter life expectancy. The profitability of age polyethism has been suggested to depend on the pattern of aging (O'Donnell and Jeanne 1995).

There are two kinds of worker mortality: (1) mortality independent of aging, for example that caused by predators, and (2) mortality related to aging. The latter mortality is explained by two major ultimate mechanisms: antagonistic pleiotropy (Williams 1957) and accumulation of deleterious mutations (Medawar 1946). Apart from ultimate causes, many proximate causes of aging have been proposed (for a review see Rose 1991). For example, flying has been suggested to reduce the life span of workers because it causes wing wear (Cartar 1992) or degeneration of carbohydrate metabolism (Neukirch 1982). On the other hand, aging has also been suggested not to depend on activity (Guzman-Novoa et al. 1994). In this case, the observed shorter life span of workers spending more time in flight can be explained by mortality independent of aging.

The distinction between activity-dependent and activity-independent aging is particularly important in social insects, because different tasks can be divided among different individuals. Here, a comparison is made between the expected longevity of workers in colonies with and without age polyethism. Such a comparison allows prediction of the conditions under which age polyethism can evolve in colonies of social insects.

Simplified model

To estimate the profitability of age polyethism, a mathematical model is used. I assume that there are two sets of

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A. Tofilski (✉)
Bee Research Department, Agricultural University,
29 Listopada 52, 31425 Kraków, Poland
e-mail: rotofils@cyf-kr.edu.pl
Tel.: +48-12-4173443

tasks, A and B, which are associated with different mortality rates. In the simplified model, the term mortality corresponds to aging-independent mortality. A-type tasks are associated with mortality m_A, and B-type tasks are associated with 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). In the model, A-type tasks can be safer than B-type tasks and vice versa. If more time is spent on brood care, more time has to be spent on foraging because rearing brood requires the gathering of food. I assume that the relationship between the amounts of time spent on tasks A and B is linear and that in the colony, a fixed proportion of time f is devoted to A-type tasks. I also assume that workers do not reproduce, and that there are no conflicts among colony members. In the model, the fitness of workers depends on the reproductive success of their colony, and the higher the expected longevity of workers the higher their fitness. The rates of fitness gain are assumed equal for the tasks A and B.

In the simplified model, 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 (Jeanne 1986; Schmid-Hempel et al. 1985). I assume that aging depends on activity and a worker cannot expend more than the maximum resources available for its entire life k. In this situation, maximum longevity depends on the rate of expenditure of resources during tasks A and B: c_A and c_B, respectively. Those rates describe the aging-related mortality associated with the tasks. The higher the rates of expenditure of resources, the shorter the life span. If aging is activity-independent, the two rates are equal (c_A=c_B). Two strategies are considered here: (1) a worker alternates between tasks A and B, as in colonies without polyethism, and (2) a worker performs A-type tasks first and B-type tasks afterwards, as in colonies with age polyethism. The aim of the model is to calculate the expected longevity of a worker in colonies with and without age polyethism.

The expected longevity of a worker is represented by a surface under the survivorship curve of the worker (Fig. 1). It can be calculated as an integral of the survival function from the beginning of life to the moment of resource depletion. If there is no age polyethism, the rate of expenditure of resources equals the mean rate of expenditure of resources during tasks A and B. Then the resources available for an entire life become exhausted after $k/[c_A f+c_B(1-f)]$ units of time. The rate of mortality equals the mean rate of mortality during tasks A and B, and the expected longevity of workers is:

$$p_0 = \int_0^{\frac{k}{c_A f+c_B(1-f)}} \exp\left[-\left(m_A f+m_B(1-f)\right)t\right]dt \quad (1)$$

When age polyethism is present, the workers perform A-type tasks first, but after time t_s they switch to B-type tasks. Then, the survivorship of the worker is represented by two curves, because the tasks are associated with different mortality rates. The expected longevity of workers, p_a, equals the sum of expected longevity during A-type tasks, a_A, and expected longevity during B-type tasks, a_B: p_a=a_A+a_B (Fig. 1a). Expected longevity during A-type tasks is given by:

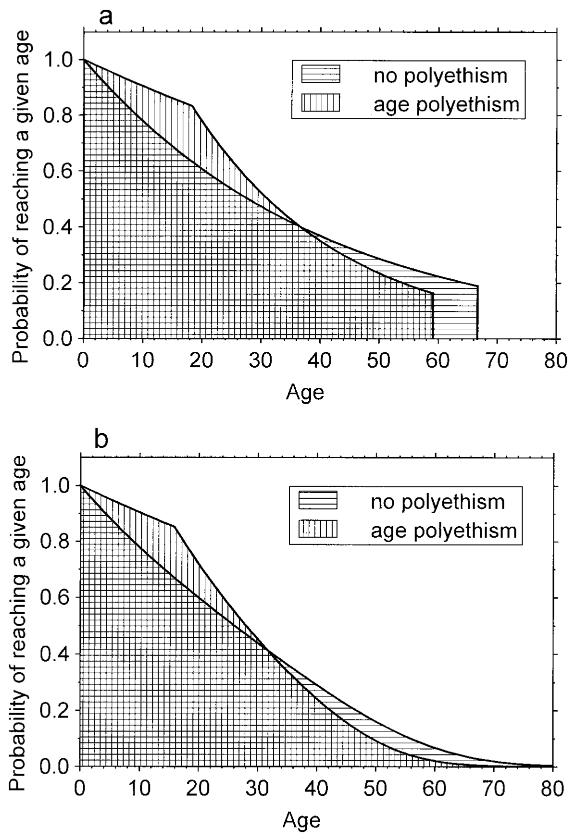

Fig. 1 Expected longevity of workers from a colony with age polyethism and without polyethism, according to the simplified model (**a**) and more realistic model (**b**) (c_A=2, c_B=4, k=200, f= 0.5, m_A=0.01, m_B=0.04, α_A=10^{-7}, α_B=10^{-6}, β=3)

$$a_A = \int_0^{t_s} \exp(-m_A t)dt \quad (2)$$

and expected longevity during B-type tasks is:

$$a_B = \exp(-m_A t_s) \int_0^{\frac{k-t_s c_A}{c_B}} \exp(-m_B t)dt. \quad (3)$$

Because mortality differs during tasks A and B, a correction term $\exp(-m_A t_s)$ has to be used. It adjusts survivorship at the beginning of the B-type tasks period to that at the end of the A-type tasks period. The proportion f of time devoted to A-type tasks is fixed:

$$f = \frac{a_A}{a_A + a_B} \quad (4)$$

and the switching time, t_s, can be calculated using Eqs. 2, 3, and 4. The model can be solved by analytical

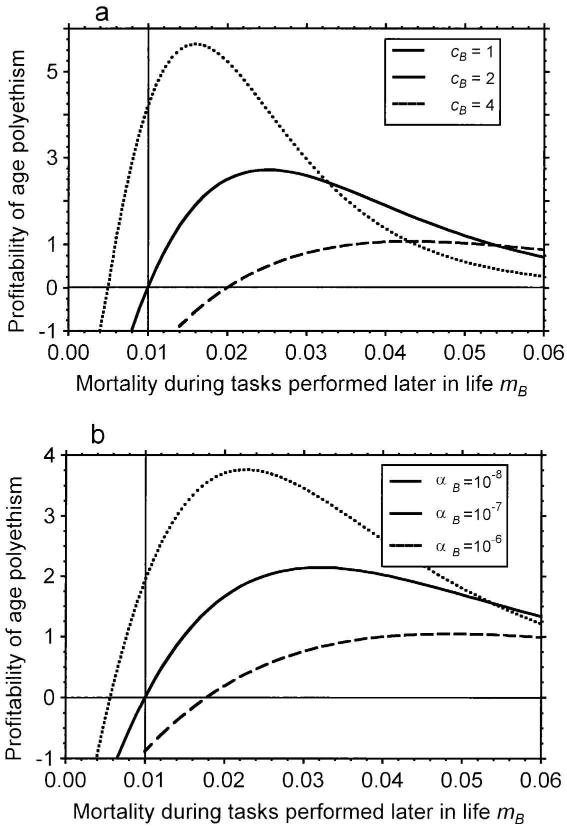

Fig. 2a, b Profitability of age polyethism calculated as the difference between longevity in colonies with and without age polyethism for different values of aging-independent mortality during tasks performed later in life, m_B. When aging-related mortality is constant through life (*solid line*), age polyethism is profitable if aging-independent mortality during tasks performed later in life, m_B, is higher than that earlier in life, m_A. Also indicated is the profitability of age polyethism when aging-related mortality during tasks performed later in life is lower (*dotted line*) and higher (*dashed line*) than aging-related mortality earlier in life. The *vertical line* indicates the same aging-independent mortality during tasks performed earlier and later in life (c_A=2, k=200, f=0.5, m_A=0.01, $\alpha_A=10^{-7}$, β=3). **a** The simplified model. **b** The more realistic model

means for the special case where $m_A c_B = m_B c_A$. In this special case, the expected life span of the workers in a colony with age polyethism is the same as in a colony without polyethism (for details see the Appendix; available online at http://dx.doi.org/10.1007/s00265-001-0429-z). For other cases, numerical methods must be used. The calculations suggest that age polyethism is profitable only if $m_A c_B < m_B c_A$. Otherwise, the lack of polyethism is more profitable (Fig. 2a).

The situation in which aging is not dependent on activity constitutes a special case of the prior model. In this instance, the rate of expenditure of resources is the same during tasks A and B ($c_A = c_B$) and age polyethism is profitable if $m_A < m_B$. Similarly, in a hypothetical situation in which mortality is the same during both tasks ($m_A = m_B$), tasks associated with higher aging-related mortality should be performed earlier in life ($c_A > c_B$). This sequence of tasks is profitable because survivorship is higher earlier in life and the proportion of life span, t_s, devoted to tasks associated with greater aging-related mortality is shorter. In effect the moment of resource depletion is delayed.

If there is no aging ($c_A = c_B = 0$), the maximum life span is infinity. Then, in a colony without polyethism the expected longevity is:

$$p_{00} = \int_0^\infty \exp[-(m_A f + m_B(1-f))t]dt \qquad (5)$$

In a colony with age polyethism, the expected life span of workers during A-type tasks is the same as in the earlier model (Eq. 2), and the expected longevity during B-type tasks is:

$$a_{B0} = \exp(-m_A t_s) \int_0^\infty \exp(-m_B t)dt \qquad (6)$$

It can be proved analytically that if there is no aging, the expected longevity of workers in a colony with age polyethism is the same as in a colony without polyethism (for details see the Appendix; available online at http://dx.doi.org/10.1007/s00265-001-0429-z).

More realistic model

The assumption that aging does not affect mortality until a certain age is reached simplifies the model. A more realistic assumption is that the mortality rate r increases exponentially with age t (Fig. 1b). To describe this phenomenon, the Weibull equation is used ($r = m + \alpha t^\beta$), because it separates aging-independent mortality, m, and aging-related mortality computationally (Ricklefs 1998). In this equation, aging-related mortality is described by two parameters: α, controlling the magnitude of this mortality, and β controlling the shape of the curve depicting changes in aging-related mortality with age. I assume that the parameter β describing the shape of the relationship between age and mortality is the same during tasks A and B. Only the parameter describing the magnitude of this relationship during A-type tasks, α_A, differs from that during B-type tasks, α_B.

The model was solved numerically [for details see Appendix (available online at http://dx.doi.org/10.1007/s00265-001-0429-z) and Fig. 2b]. The results of the more realistic model are similar to those of the simplified model. If aging is independent of activity, that is, if aging-related mortality is the same during tasks A and B ($\alpha_A = \alpha_B$), age polyethism is profitable when safe tasks (associated with lower aging-independent mortality) are performed earlier in life ($m_A < m_B$). If aging-related mortality differs between tasks A and B, age polyethism is profitable when safe tasks are performed earlier in life and if they are associated with higher aging-related mortality ($m_A < m_B$ and $\alpha_A > \alpha_B$). On the other hand, age polyethism is not profitable when risky tasks are performed earlier in life and if they are associated with lower aging-related mortality ($m_A > m_B$ and $\alpha_A < \alpha_B$). In other situations (e.g., $m_A > m_B$ and $\alpha_A > \alpha_B$), precise values of the parameters have to be known to predict the profitability of age polyethism.

Discussion

Age polyethism in social insects has been extensively studied, and there are a great number of hypotheses to explain it (reviewed by Calderone 1998). Only a few explanations consider the costs and benefits of age polyethism in terms of fitness (Jeanne 1986; Seeley 1982; Oster and Wilson 1978; West-Eberhard 1981). Jeanne's (1986) idea is very convincing. He suggests that safe tasks should be performed earlier in life because this prolongs worker longevity. However, the age polyethism is profitable only when programmed senescence occurs and not when aging is caused by rate-of-living effects (O'Donnell and Jeanne 1995). Concepts of programmed senescence and rate-of-living theory are vague and reflect a rather outdated view of aging (for critical review see Rose 1991). Moreover, the assumptions of O'Donnell and Jeanne's model (1995) are not clear. They assumed that if aging is determined by rate-of-living effects, then the mortality of workers will be constant throughout life. This is in conflict with the concept of aging as a decrease in both the age-specific survival rate and the age-specific reproductive rate (Hamilton 1966; Charlesworth 1980). Workers, as a rule, do not reproduce but spread their genes by helping relatives (Hamilton 1964). In this case, aging can be defined as an increase in the mortality rate. When the mortality of workers does not change in time, as O'Donnell and Jeanne (1995) assumed, aging is absent. In fact, O'Donnell and Jeanne (1995) unintentionally demonstrated that age polyethism is not profitable when aging is absent.

The models presented in this paper show how age polyethism affects the longevity of workers in different circumstances. The models are more accurate than the simulation of Jeanne (1986) and clarify the erroneous prediction of O'Donnell and Jeanne (1995). I demonstrate here that if aging does not depend on activity, then age polyethism is profitable only when safe tasks are performed earlier in life, which is consistent with Jeanne's (1986) findings. If aging depends on activity then age polyethism is profitable if safe tasks are performed earlier in life and if they are associated with higher aging-related mortality. This differs from the predictions of O'Donnell and Jeanne (1995), but their assumptions are not appropriate, as mentioned earlier. I confirm, however, that age polyethism is not profitable if there is no aging, as O'Donnell and Jeanne (1995) unintentionally demonstrated.

Data concerning aging of social insects is scarce (Cartar 1992; Guzman-Novoa et al. 1994; Neukirch 1982; Tofilski 2000; Woyciechowski and Kozlowski 1998b). It confirms that workers of social insects undergo aging, as do all organisms. However, whether aging depends on activity or not, is not clear. This information is crucial for understanding the evolution of the division of labor in social insects.

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