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The social behavior of *Leptothorax allardycei* (Hymenoptera, Formicidae): time budgets and the evolution of worker reproduction

Blaine J. Cole

Department of Biology, University of Virginia, Charlottesville, Virginia 22901, USA

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Summary. The use of time by workers of the ant *Leptothorax allardycei* (Mann) is examined. Theoretical predictions are developed concerning the maximal lowering in colony reproductive output that is consistent with the evolution of worker production. Measurements are made of the effect of aggression on colony efficiency. Analysis of time budgets indicate that a typical ant spends a large fraction (0.55) of its time quiescent and another large fraction of time (0.32) involved in undifferentiated activity. Dominance activity and brood care together make up about 11% of the total time. The amount of time spent on dominance activity is negatively related to the amount of time spent on brood care, but positively related to the amount of time that an ant is active. The amount of time that an ant has available for brood care which is actually spent on brood care declines with the amount of time spent on dominance activity. The amount of time that a worker spends feeding liquid food to larvae is a function of hierarchy rank; alpha spends the most time, beta less and gamma still less. The spread of the trait of worker reproduction is examined theoretically, with particular regard to the associated costs to colony reproduction. Worker reproduction can spread through a population, under a variety of formulations, provided the cost to colony reproduction is less than some critical value in the neighborhood of 0.17–0.22 of the total colony output. The cost of worker reproduction in *L. allardycei* is estimated in two ways: as a time cost and as a reduction in the total number of brood tended per unit time. The two estimates of cost are 0.15 and 0.13 respectively. The reproductive options of the worker caste and the division of reproductive labor vary considerably between species. Reproduction by workers yields fitness differences between workers and results in competition among workers with the result that colony efficiency is affected.

Introduction

Reproductive division of labor among social insects in one of the features of social insects that has captured the attention of evolutionary biologists. In large part they have focused on the question: under what circumstances does one expect a non-reproductive caste to evolve? This concentration has obscured an equally interesting question: under what circumstances does one expect the normally non-reproductive caste to reproduce? One might rephrase this question as: what are the reproductive options available to the worker caste of a eusocial species?

In order to construct answers to these questions it is first important to explore, in a more detailed manner, the behavior of individual workers within colonies. It is necessary to observe individual workers in order to get some idea of individual differences in behavior which may result in fitness differences. Secondly, it is necessary to make detailed measurements of the effect of one individual on other members of the colony.

In this paper I shall first describe the use of time by workers of *Leptothorax allardycei* and show the relationship between brood care and dominance activity. Second I shall build some models for the evolution of reproduction in the social hymenoptera. Finally I shall relate measurements of the effect of dominance activity on brood care to the theoretical predictions.

Methods

Observations were made of ants in naturally occurring queenless colonies. Approximately 20% of *Leptothorax allardycei* colonies lack a queen, (Cole 1984). Colonies were housed and maintained as described in Cole (1984). An outline of the social behavior is to be found in Cole (1981). Six individuals, the top three ranking ants of two colonies were chosen for intensive study; colony 798 had 22 workers and colony 795 had 24 workers. Approximately 10 h of observation, in one hour blocks, were made of each of the six ants. The position and activity of the ant was continuously recorded. This allowed a time budget to be constructed for each ant.

When an individual worker tended one or more immature ants, either eggs, larvae or pupae, the sequence of tending was referred to as a bout of brood care. Individual workers were observed from the onset of a brood care bout until the bout was terminated. Termination either came about as a result of normal cessation of brood care activities or as a result of truncation by dominance activity. The ant taking care of the brood might either be the dominant or the subordinate in the interaction that truncated brood care activity.

Results

The amount of time engaged in each of various activities is shown in Table 1 and Fig. 1. Of the categories of behavior, the amount of time engaged in brood care, dominance activity and self-grooming require little explanation. Several categories of behavior e.g. licking eggs, feeding larvae or carrying pupae (see Cole 1980, 1983, in preparation) are lumped together in brood care. Dominance activity includes time spent both as a dominant and as a subordinate in a dominance interaction. Self-grooming is the most frequent behavior even though each bout of self-grooming does not last very long.

Other categories of behavior consume very short periods of time involving an average of 0.6% of the total time. For several rare activities, antennal tipping, defecation and egg-laying it is impossible to obtain a reliable measure of duration. Antennal tipping is a behavior whose function is unknown. The ant bring the tips of its antennae together in front of its mandibles, jerking spasmodically, opening the mandibles, bringing the gaster forward between the legs, rising on its legs and occasionally even falling on its side. This behavioral sequence is followed by a period of quiescence and often preceeded by one as well. It is difficult to draw the line between the end of antennal tipping and quiescence so I did not attempt to do so. Defecation only takes a period of several seconds, however the worker actively moves through the nest for some prior period of time. The worker explores areas of the nest that normally does not move about in. It is not possible to assess objectively the onset of activity involved in defecation. Egg-laying similarly begins somewhat cryptically, becoming observable only when the egg begins to appear. All of these activities together could make a difference of only a small fraction of one percent.

Table 1. Time budget of an average worker ant. Data based on the activity of the three highest ranking ants from each of two colonies. Each activity is described in the text. The fraction of time spent active is divided into the categories below

"Activity"	Fraction of time
Quiescent	0.55
Active	0.45
Dominance activity	0.068
Brood care	0.043
Self-grooming	0.020
Other	0.006
Undifferentiated (Activity)	0.32

Time spent quiescent occupies a large fraction of the total time of an ant (on average 55%). When an ant is quiescent it is completely stationary; it does not even move its antennae. Because the onset of quiescence is difficult to determine an ant was defined as quiescent only when it was inactive during an entire observation minute and quiescence had to last a minimum of two minutes. This results in an underestimate of the actual time spent quiescent and an overestimate of the undifferentiated activity period. Quiescence lasts an average of 17 min and occurs on average 1.9 times per one hour observation period.

Undifferentiated activity involves activity that cannot be assigned to a discrete category of behavior. Moving through the nest is the largest component in this category. It is possible that this movement is associated with brood care or with dominance activity if it carries the ant between piles of brood or between subordinate workers. However, it is impossible to assign, with any confidence, a purpose to the activity. This category is probably homologous to what Lindauer (1978) calls patrolling. Since that term suggests purposive activity, I prefer the more non-committal phrase undifferentiated activity.

The time budgets for individuals ants do not reveal details about functional relations of various activities. The amount of time spent by a worker ant on dominance activity is inversely related to the amount of time spent on brood care activities. A Bartlett's three group method regression on 59 one-hour observation periods is shown in Fig. 2. The average total time involved in both brood care and dominance activity is only 11% of the total one hour observation period. Therefore the two quantities are very nearly independent of one

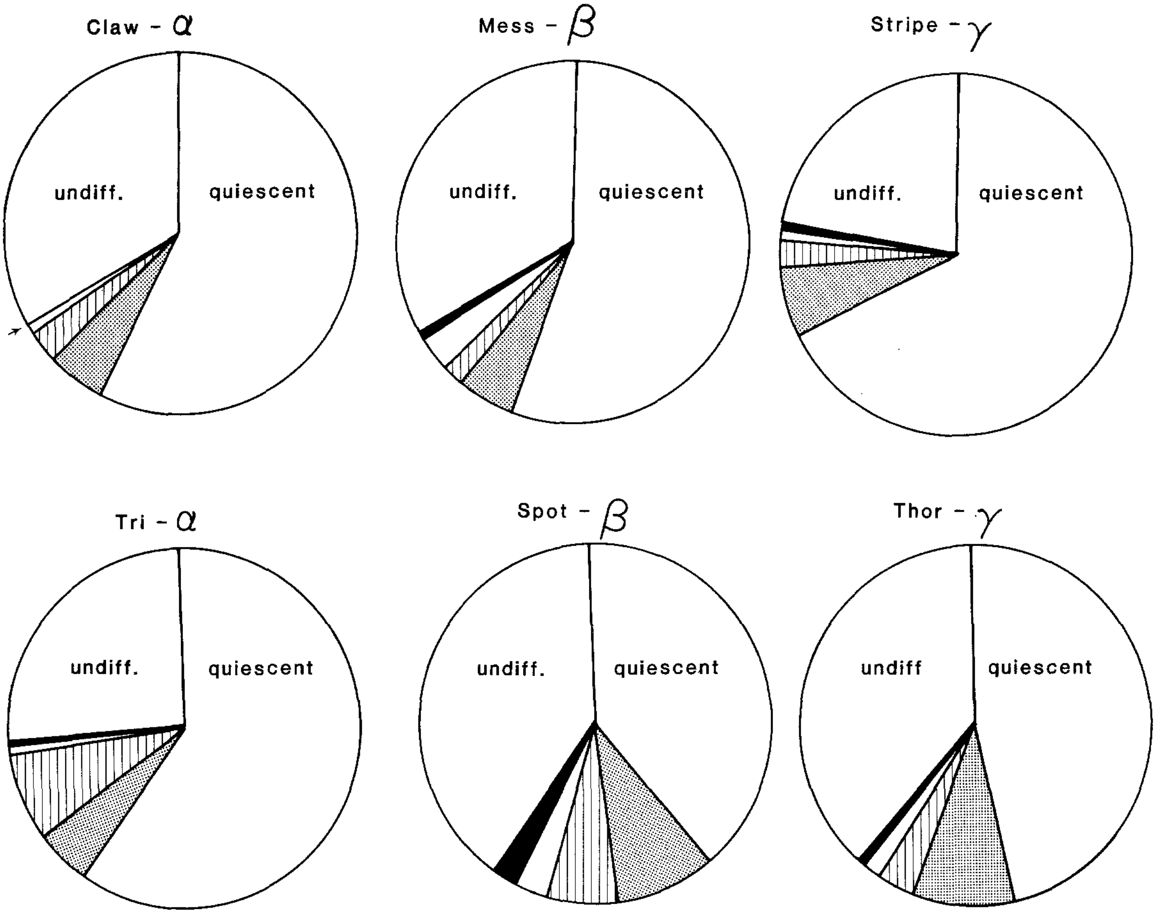

Fig. 1. Individual time budgets for the top three ranking ants of two colonies. Quiescent refers to time inactive. Undiff. refers to undifferentiated activity. Dominance activity is shown in stippling, brood care activities are cross-hatched, self-grooming is the open area. All other activities are indicated by the solid section. For claw, the other activities are indicated by the arrow

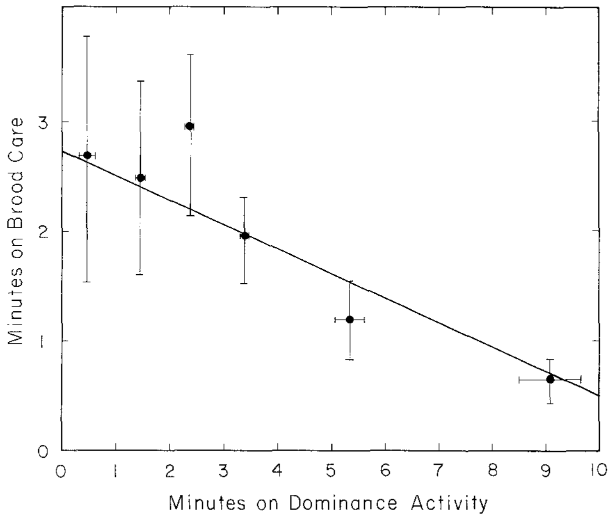

Fig. 2. The relationship between time spent on brood care and time spent on dominance activity for 59 one-hour observation periods. The points are the mean amount (±SE) of time spent on broad care for 0–1, 1–2, 2–3, 3–4, 4–7 and more than 7 min on dominance activity. The line is the Bartlett's three group method model II regression on all data points

another. However one may object that the two variables are not completely independent of one another. If one plotted the amount of time spent on dominance activity against the fraction of the remaining time spent on brood care, one would find a relationship virtually identical to that of Fig. 2.

The amount of time active, in any one-hour period, is a function of the amount of time that a worker spends on dominance activity. There is a significant ($t = 3.56$, $P < 0.001$) positive relationship, (slope 1.29) between the amount of time spent on dominance activity and the amount of active time not involved in dominance activity. For every minute added to dominance time there is an additional 1.3 min added to active time of an ant, time that would be available for brood care or other activities.

Dominance activity and brood care are negatively related even though there is an absolute increase in the amount of time available for brood care. In order to correct for difference in the

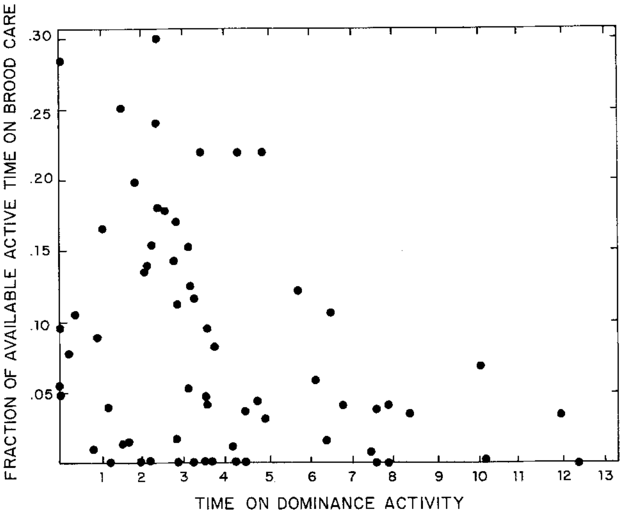

Fig. 3. The relationship between the amount of time spent on dominance activity as a function of the fraction of active time that is available for brood care which is spent on brood care

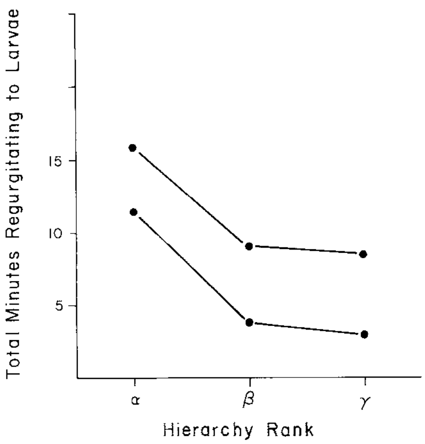

Fig. 4. The amount of time spent feeding liquid food to larvae over 10 h of observation on each of the three highest ranking for two colonies

amount of time available one can consider the fraction of active time that is spent on brood care. Figure 3 shows a plot of the amount of time spent on dominance activity as a function of the fraction of available active time spent on brood care (time on brood care: (total active time − dominance time)).

The number of pieces of brood tended when brood care is and is not interrupted by dominance activity differs significantly. The average number of brood tended per bout of brood care is 2.3 when dominance activity does not intervene and 1.1 when dominance activity causes the truncation of a bout of brood care. Taking the number of brood tended when dominance activity does not intervene as the expected value, the two distributions are different ($\chi^2 = 8.83$, $df = 2$, $P < 0.025$). The distribution of pieces of brood tended in truncated bouts of brood care closely approximates a zero-truncated Poisson distribution ($\chi^2 = 0.26$, $df = 3$, $P > 0.9$).

The amount of time spent in feeding larvae was the only activity that showed an interpretable relation to hierarchy rank. Figure 4 shows the total time which a worker spent regurgitating to larvae for ten hours of observation on each ant. Alpha is significantly more likely to feed larvae liquid food during a one-hour observation period than is beta or gamma (percentage test, $t = 3.0$, $P < 0.01$).

Evolution of worker reproduction

In this section I shall consider some simple models for the evolution of reproduction by workers of social haplodiploids. I shall first consider one particular formulation of the phenomenon of worker reproduction, and then consider modifications to the model involving cost allocation, sex ratio, and multiple mating. In the next section I shall attempt to test the predictions of the models that are discussed in his section.

The evolution of reproduction by workers of a social insect has been considered by a number of investigators (e.g. Abugov 1981; Alexander and Sherman 1977; Aoki and Moody 1981; Charnov 1978a, b; Craig 1979, 1980; Hamilton 1972; Trivers and Hare 1976; West Eberhard 1975). The general conclusion is that workers that can reproduce have a selective advantage over those workers that cannot reproduce and that worker reproduction is expected to evolve.

An implicit assumption in past attempts to model the evolution of worker reproduction is that this trait does not have negative effects on the colony as a whole. In *Leptothorax allardycei* this assumption seems clearly to be violated. There exists routine aggression that is organized in dominance hierarchies, workers avoid one another and liquid food flow is constrained (Cole 1981). There are constraints placed on movement patterns and space use patterns as a function of dominance hierarchy rank (Cole 1985). There is also a negative relation between the amount of time spent on dominance activity and brood care and reduction in the number of pieces of brood tended in a bout of brood care when dominance activity intervenes.

It seems likely that worker reproduction is not independent of colony function as assumed previously. It is worthwhile to consider under what conditions the trait of worker reproduction might

Table 2. Outline of a genetic model for the evolution of worker reproduction. The frequency of the mutant allele is e_1 in males and e_2 in females. When the alleles is rare the frequency of wild type mating can be taken to be approximately one. Events occurring with frequency e^2 or less can be ignored when the allele is rare. Workers with allele A produce sons; colonies with such workers suffer a cost of aggression, c

Colony type	Frequency in population	Worker genotype		Reproductives produced
$aa \times a$	1	aa	rY	aa
			$(1-r)Y$	a
$aa \times A$	e_1	Aa	$r(Y-c)$	Aa
			$1/2(1-r)(Y-c)$	A
			$1/2(1-r)(Y-c)$	a
$Aa \times a$	e_2	$1/2aa$	$1/2r(Y-c)$	Aa
			$1/2r(Y-c)$	aa
			$1/2(1-r)(Y-c)$	A
			$1/2(1-r)(Y-c)$	a
		$1/2Aa$	$1/2r(Y-c)$	Aa
			$1/2r(Y-c)$	aa
			$1/2(1-r)(Y-c)$	A
			$1/2(1-r)(Y-c)$	a

spread if there was a cost to overall colony functioning. The genetic models that I will consider below are similar in their structure. I consider a population of a haplodiploid social species in which there is no reproduction by workers in the wild type colonies. Introduced into this population is the trait worker reproduction. The workers produce males only and suffer some reduction in the total reproductives that they produce. The purpose of this theoretical analysis is to determine the conditions under which the trait of worker reproduction will increase in frequency when rare.

An outline of the model is shown in Table 2. When the worker reproduction allele is rare we can limit discussion to the three types of colonies shown. The first is the wild type colony. This colony has a frequency of very nearly one. All of the workers produced in the colony are, of course, wild type. Each worker is responsible for the production of Y reproductives a fraction r of which are diploid females and a fraction $1-r$ of which are haploid males. In colony type two, which occurs with frequency e_1, the male carries the trait. All of the workers in such a colony also carry the trait. The workers are each responsible for the production of $Y-c$ reproductives, where c is the cost of worker reproduction. A fraction r of the reproductives are from fertilized eggs produced by the queen and a fraction $1-r$ of the reproductives are males produced from unfertilized eggs laid by the workers. In colony type three, which occurs with frequency e_2, the queen carries the allele. In this colony half of the workers are wild type and allow the queen to reproduce as in colony type one. The other half of the workers express the worker reproduction trait and reproduce as in colony type two. The same cost as in colony type two is assessed against colony type three workers.

The production of wild type males and females from colony types two and three is insignificant in comparison to production of wild type males and females from colony type one. We can thus focus exclusively on the production of mutant males and females from colony types two and three. Gathering together like genotypes we find:

$\# \; aa = rY$

$\# \; a = (1-r)Y$

$\# \; Aa = e_1 r(Y-c) + \frac{1}{2} e_2 r(Y-c)$

$\# \; A = \frac{1}{2} e_1 (1-r)(Y-c) + \frac{1}{2} e_2 (1-r)(Y-c).$

The frequency of the mutant alleles in the males of the next generation is thus:

$$e_1 = \tfrac{1}{2} e_1 \left(1 - \frac{c}{y}\right) + \tfrac{1}{2} e_1 \left(1 - \frac{c}{y}\right) \tag{1}$$

and the frequency of the mutant alleles in the females of the next generation is:

$$e_2 = e_1 \left(1 - \frac{c}{y}\right) + \tfrac{1}{2} e_2 \left(1 - \frac{c}{y}\right). \tag{2}$$

If we define the relative cost of worker reproduction, c/Y as c' we have two equations that describe the frequency of the allele in males and females of the next generation in terms of the frequencies on the previous generation. Writing Eq. 1 and 2 in matrix form:

$$\begin{pmatrix} e_1 \\ e_2 \end{pmatrix} \begin{pmatrix} \frac{1}{2} & \frac{1}{2}(1-c') \\ (1-c') & \frac{1}{2}(1-c') \end{pmatrix} = \begin{pmatrix} e_1 \\ e_2 \end{pmatrix}. \tag{3}$$

The characteristic equation for Eq. 3 is:

$$\lambda^2 - \lambda(1-c') - \tfrac{1}{4}(1-c')^2 = 0.$$

Solving for the dominant eigenvalue, $\lambda_{\max}$, we find:

$$\lambda_{\max} = 1.21\,(1-c'). \tag{4}$$

This is shown in Fig. 5. When the dominant eigenvalue is greater than one, $(c > 0.17)$ the allele is increasing in frequency and when the dominant eigenvalue is less than one $(c > 0.17)$ the allele is dying out of the population.

There is a critical maximal cost that is consistent with evolution of the worker reproduction. If the trait of worker reproduction arose in a popu-

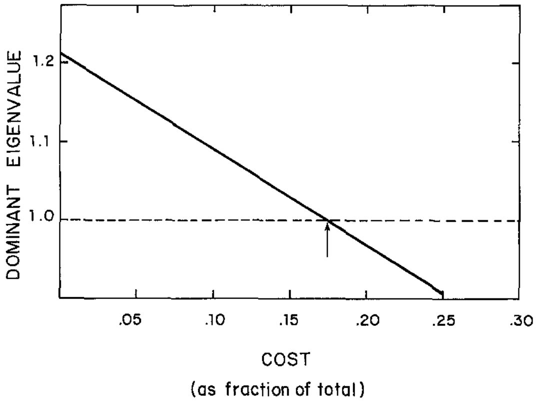

Fig. 5. A plot of the dominant eigenvalue of the relation in Eq. (3). If the cost is less than 17% of the total reproductive output, the dominant eigenvalue is greater than 1 and the worker reproductive allele will spread

lation, described by the situation outlined in Table 2, with the concommitant effect of causing total colony reproduction to decline by 15% the worker reproduction allele would increase in frequency. Note that when there is no cost of worker reproduction the selective advantage to worker reproduction is 21% when rare. This reclaims the conclusion of previous workers who showed a great advantage to worker reproduction.

Note that the result does not depend upon the sex ratio, that is on who controls investment. However the model assumes that sex ratio in the colonies is the same before and after worker reproduction. This assumption is made in order to avoid implicit assumptions about linkage between sex ratio control and worker reproduction.

The allocation of cost can also be altered from that presented in Table 2. There are perhaps two extremes. The cost can be assessed only against those workers that possess the trait or it can be spread evenly among all workers in the colony. If the cost is incurred only by those workers that possess the trait then all workers in type two colonies are assessed a cost but only the carriers of the trait in type three colonies are assessed a cost. In this case the characteristic equation is:

$$\lambda^2 - \frac{\lambda}{4}(4-3c') - \frac{1}{8}(1-c')(2-c') = 0 \qquad (5)$$

and the condition for spread of the allele is $c' < 0.228$. If the cost is proportional to the fraction of workers that possess the trait, then the cost in type two colonies will be twice as great as the cost in type three colonies. In this case the characteristic equation is:

$$\lambda^2 - \frac{\lambda}{2}(2-3c') - \frac{1}{4}(1-c')(1-2c') = 0$$

and the condition for spread of the trait is $c' < 0.114$. If the frequency of type two and type three colonies is equal the critical cost is $c' < 0.17$.

Multiple matings have no effect on the spread of a worker reproductive allele. It is only in type two colonies that any difference occurs. Here the cross, $aa \times A \times a_{n-1}$, of a female that mates n times occurs with frequency ne_1 because the carrier male can be any of the n males to mate with the female. A fraction $(n-1)/n$ of the workers are aa and each produce $1/nr(Y-c)Aa$. A fraction of the workers $1/n$ are Aa and each produce $1/nr(Y-c)Aa$ and $1/2(1-4)(Y-c)A$. The total number of mutant females is: $ne_1(n-1)/n)(1/n)r(Y-c)+ne_1 1/nr(Y-c)=e_1 r(Y-c)$. The total number of males produced is: $ne_1 1/n\, 1/2(1-r)(Y-c)=1/2e_1(1-r)(Y-c)$. Each of these totals is the same as produced by colony type two in Table 2. The reduction in production of mutant males and females by each colony is exactly offset by the increase in the frequency with which mutant males can mate.

The above analysis is appropriate only when the frequency of the mutant allele is very low. As

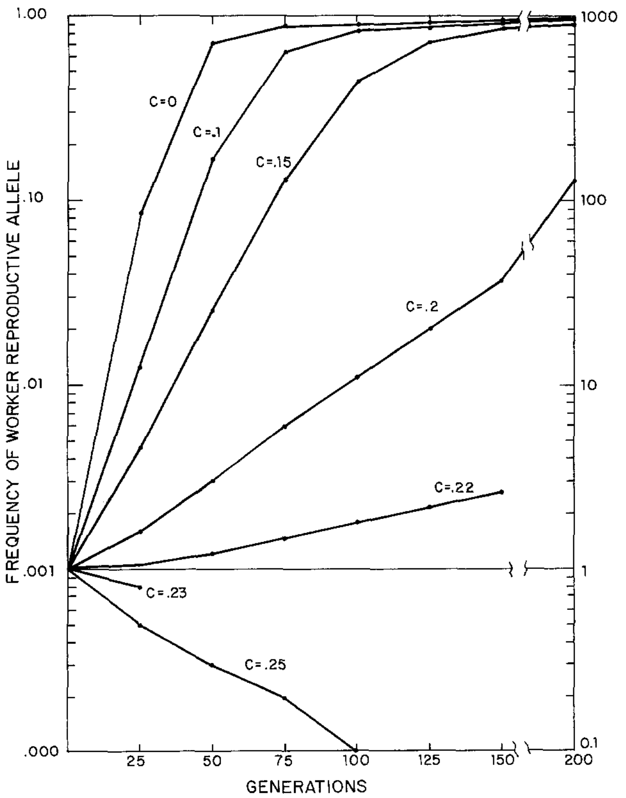

Fig. 6. The frequency of the worker reproductive trait in a population as a function of the number of generations. The frequency of the allele is started at 0.001 in males and females. If the cost is 0.22 or less the allele goes to fixation

the allele increases in frequency it is no longer possible to ignore events taking place with frequency e^2 or less and to assume that the frequency of wild type colonies is approximately one. One must perform computer calculations on the production of reproductives by all six possible mating types. Figure 6 shows the global fate of an allele for worker reproduction. The underlying model used is one in which the cost is assessed only against the workers that carry the allele as given by Eq. (5) above. The frequency of the worker reproductive allele was started at 0.001 for both males and females. The result of the local stability analysis was that the allele would increase in frequency if the cost was less than about 0.22. The results of the local stability analysis are reclaimed in the global calculation; the allele declines in frequency with a cost of 0.23 or more. In addition, the worker reproductive allele appears to go to fixation as long as the dominant eigenvalue in the local analysis is greater than one. Thus worker reproduction is an evolutionarily stable strategy (ESS) provided the cost is less than some critical value. Non-reproductive workers are an ESS if the cost is greater than this critical value.

The cost of worker reproduction

The cost of worker reproduction in the foregoing models was an important factor in determining the fate of worker reproductive alleles. If the cost is less than a critical value of 0.17–0.22 worker reproduction should go to fixation. If the cost is greater than this value worker reproduction should not evolve.

The results presented earlier in this paper allow two independent estimates of the cost of worker reproduction, the first a time cost and the second as a reduction in the number of brood tended. Earlier (Figs. 2 and 3) I showed that the amount of time spent on dominance activity and brood care were negatively related. By using this relation one can estimate the amount of time that would be spend on brood care if there was no dominance activity in the nest (2.73 min/h). The average amount of time spent on brood care in a queenright colony (with 2.2-fold less time on dominance activity Cole 1981) is 2.33 min/h. This translates into a 15% reduction in the amount of time spent on brood care in colonies with dominance activity over colonies without dominance activity.

The second method of calculating the cost of worker reproduction is based on the truncation of a brood care bout. When dominance activity truncates a bout of brood care there is a reduction of approximately one piece of brood tended. Furthermore, the care of the piece of brood being tended when dominance activity intervened is also interrupted. The number of pieces of brood tended in truncated bouts is described by a zero-truncated Poisson suggesting that dominance activity is intervening without regard to the length of the brood care bout. This lends support to the assumption that dominance also halves the amount of care that a piece of brood gets if it is being tended when dominance activity intervenes. Some 13% fewer pieces of brood are tended per unit time as a result of the interruption of brood care by dominance activity within the nest.

Discussion

The time budgets for *Leptothorax allardycei* and *L. ambiguus* (Herbers 1983) and *L. longispinosus* (Herbers and Cunningham 1983) are fairly concordant. In each case a large fraction of the time is spent motionless and the second greatest amount of time is spent in what is termed undifferentiated activity (this study) or movement through the nest. The two sets of time budgets are not completely comparable, however, due to the focus on specific ants of high rank in this study.

More comparable are the results of Lindauer (1978) on the time budget of a single honeybee worker. Lindauer found that the fraction of time spent resting and patrolling was 0.40 and 0.32 of the total. The fraction of time that a *L. allardycei* worker spends quiescent and in undifferentiated activity is 0.55 and 0.32 of the total. While there is a close correspondence between the fraction of time spent in movement of undiscernable function it must be pointed out that this is a larger fraction of the active time for *L. allardycei* than for *Apis mellifera*.

It is clear that worker *L. allardycei* spend a large fraction of their time doing nothing (55%) and a remarkably large fraction of time engaged in activity whose exact function is unclear (87%). Lindauer attributed function to these activities by calling them resting and patrolling and, perhaps that is exactly what they are. He suggested that certain activities are only acutely needed (e.g. colony defense) and a standing crop of a large number of individuals must be maintained in order to meet these contingencies. It may also be possible that the periods of inactivity serve some recuperative physiological function.

In queenless *L. allardycei* colonies it is remarkable that approximately one and one-half times as much time is spent on dominance activity as is spent on care of the brood. It is clear that there is substantial importance placed upon establishing and maintaining a high hierarchy rank. Of course dominance activity is an investment in personal reproduction is opposed to investment in the offspring of relatives. It is clear that the resolution of the conflict between the two may pose a significant problem in this species.

The fact that the highest ranking ants spend more time regurgitating liquid food to larvae may be an indication of nepotistic behavior. The highest ranking ants have the greatest ovarian development and lay the most eggs. Whether they actually redistribute food to the larvae that they have produced is unknown. However, they are distributing a resource to a group of individuals (the larvae) to whom they are disproportionately related. However this is weak evidence of nepotism. Since high ranking ants receive a disproportionate share of liquid food in the nest (Cole 1981) they may simply be altering the worker from which the liquid food comes without altering the eventual destination of the liquid food.

The tradeoff between increased personal reproduction by a eusocial insect worker and decreased reproduction by the queen is resolved in favor of worker reproduction as long as the cost is less than some critical value. This value, in a variety of formulations, is in the neighborhood of a 15–20% reduction in colony output of reproductives. In two estimates of cost, values were obtained of 13% and 15%. These two estimates clearly are not direct measures of fitness. However, they are measures of quantities time spent on brood care and the number of brood tended per unit time, that probably reflect the efficiency of colony function. There are no studies that show the effect of any aspect of ant behavior directly on the reproductive output, however it has been argued that colony efficiency is related to colony fitness (Oster and Wilson 1978; Wilson 1980a, b).

Since the observed cost estimates are near the maximal theoretical levels it is worth asking if there is a reason for this. If worker reproduction has a cost associated with it, there is no necessity that the cost be near the maximum, only that it be less than the maximum. If an allele for worker reproduction arose with the result that there was a 10% reduction in reproductive output, such an allele should go to fixation. It is simple to show that any other allele for worker reproduction will invade a population in which the workers already reproduce as long as an additional cost is less than the critical value. Theoretically there seems to be no limit to the reduction in fitness that can accompany this process. However only alleles which do not produce a cost in excess of the critical value for spread of worker reproduction in a non-reproducing population will be resistant to invasion by non-reproductive social insect workers.

The reproductive options of the worker caste of ants are far more diverse than is generally presumed. In some species the ovaries of the worker caste have disappeared (e.g. *Solenopsis*). In a large number of other species reproduction by workers can occur in the absence of a queen. This reproduction can be limited solely to male production (many species) or may include thelytokous production of female reproductives (see Wilson 1971 for review).

In other species there is reproduction within queenright colonies. This sort of reproduction inevitably results in variability in fitness and may generate overt signs of conflict of interest between workers (as in *L. allardycei, L. pastinifer* and *L.* (near) *schwarzi* pers. obs. and in *Harpagoxenus americanus* Franks and Scovell 1983). Finally the morphological workers may mate and become gynes, either the sole female reproductives in the species or in some combination with morphological queens (Ward 1983). It is perhaps a mistake to identify one particular social organization as paradigmatic when the cataloguing of diversity has only begun.

Each of the above reproductive options of social insect workers has certainly evolved more than once. It would thus be important to try to identify ecological or phylogenetic patterns for the loss of ovaries, occurrence of thelytoky, reproduction in the presence of the queen and loss of a morphological queen. Each of the variety of reproductive options has concomitant effects on the pattern of conflict in insect societies. The existence of routine aggression between workers as seen in *L. allardycei* or *Harpagoxenus americanus* (Franks and Scovell 1983) is an expression of this conflict of interest. The pattern of conflict, in turn, affects the direction and speed of response of subsequent behavioral evolution.

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