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Development of colony phenotype in social insects controlled by frequency-dependent thresholds among workers

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ABSTRACT

The frequency of workers adopting different behaviours often depends on thresholds. If too few workers are foraging, for example, then those workers with relatively low foraging thresholds begin to collect food. The regulation of colony phenotype is controlled by frequency-dependent feedback among worker threshold values. I show that, for a given average threshold value among workers, variability in thresholds influences the frequency of workers that adopt a particular behaviour. This conclusion applies whenever the tendency of a developmental unit to adopt a particular phenotype depends on the frequency of other units with that phenotype. Social insects are unusual, however, because the distribution of thresholds among developmental units (workers) depends on the number of times the queen has mated.

Keywords: foraging, multiple mating, ontogeny, regulatory network.

INTRODUCTION

Workers often adopt one of two behavioural roles within a colony. For example, an individual may forage or stay within the nest. Each individual's decision depends on its threshold for switching from one role to the other. The frequency of other workers in each role often influences whether or not an individual switches its own behaviour. This frequency-dependent feedback may often be indirect – mediated, for example, by the supply of food relative to the number of developing larvae (see reviews by Page and Robinson, 1991; Robinson, 1992).

The frequency of workers in each role defines the colony phenotype. The essential determinants of colony phenotype take the following form. Each individual has a particular threshold for switching from one role to the other. That threshold is determined by the individual's genotype, its environmental experience, and stochastic factors. At any point in time, the workers as a group will have some distribution of threshold values. The colony phenotype – the frequency of workers in each role – depends on the frequency-dependent interaction among the workers mediated by the distribution of threshold values.

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The development of colony phenotype is, as often noted, much like the development of metazoan form. Genotype determines the attributes of the individual cells – the units of development. Interaction among the cells determines phenotype. The workers of a colony are like cells, but they may differ genetically and they have greater independence and flexibility. Development, in both cases, follows this pathway: genotype and environment determine the distribution of rules among the developmental units; interaction among the units with variable rules determines phenotype; and selection sorts among phenotypes to change how the distribution of rules is specified. The phenotype may be the frequency of foragers versus workers that stay on the nest or the frequency of different cell types within a tissue.

I demonstrate the following point about a phenotype determined by frequency-dependent interaction among developmental units: to achieve some optimum frequency of alternative behaviours, the required average threshold of units depends on the variability in thresholds among units. I also comment on the fact that, in social insect colonies, the distribution of threshold values depends on the number of times the queen has mated.

THE FREQUENCY OF ALTERNATIVE BEHAVIOURS WITHIN A COLONY

I first define the basic assumptions and notation. I then derive the equilibrium switch point in a colony at which an individual with a particular threshold is indifferent between two alternative behaviours. That switch point allows one to calculate the frequency of the two behaviours in the colony.

Suppose a worker can adopt one of two alternative behaviours, A or B. The frequency of workers performing behaviour A is p, and the frequency performing B is $q = 1 - p$. Workers vary in their threshold tendency to switch between behaviours. Denote the threshold of a worker by the variable x, and let the distribution of threshold values in a colony be $f(x)$. Define a threshold in the following way. If the frequency of behaviour B is greater than an individual's threshold value, then that individual adopts behaviour A. To repeat the same condition with symbols, if $q > x$, then an individual adopts behaviour A, otherwise the individual adopts behaviour B.

These assumptions are illustrated in Fig. 1. The frequency of individual threshold values, x, is given by the curve, $f(x)$. For now, let us assume that there exists some individual threshold level, $\alpha = x$, such that individuals with lower thresholds adopt behaviour A and individuals with higher thresholds adopt behaviour B. This is reasonable, because the condition for an individual with threshold x to adopt behaviour A is that the frequency of B is greater than x, that is, $q > x$.

The frequency of the A types is, from Fig. 1, the area under the curve $f(x)$ between 0 and α. In particular, the frequency of A is:

$$p = \int_0^\alpha f(x)\,\mathrm{d}x = F(\alpha)$$

where $F(x)$ is the area under the curve of $f(x)$ up to the point x. The function $F(x)$ is, by convention, called the cumulative distribution function.

We can think of the point α as an equilibrium switch point under frequency-dependent feedback control. In particular, α is a stable switch point only when an individual with threshold $x = \alpha$ is indifferent between adopting behaviour A or behaviour B. This can be proved as follows.

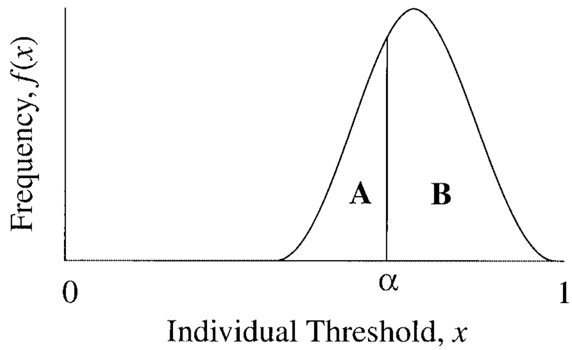

Fig. 1. Thresholds of individual workers, x, have distribution $f(x)$ within the colony. A switch point, α, exists such that individuals with lower thresholds adopt behaviour A and individuals with higher thresholds adopt behaviour B.

An individual with threshold α is indifferent between the two behaviours only when $q = \alpha$; that is, the frequency of the B types is equal to the threshold. This is true because, by definition, an individual with threshold α would adopt A if $q > \alpha$, but would adopt B if $q < \alpha$. The point $q = \alpha$ is a stable switch point because individuals with higher thresholds, $x > \alpha$, satisfy the condition $q < x$ and are therefore stably maintained as B types, as shown in Fig. 1 for individuals with thresholds above α. Similarly, individuals with lower thresholds, $x < \alpha$, satisfy the condition $q > x$ and are therefore stably maintained as A types. Any perturbation from $q = \alpha$ causes individuals to switch their behaviours until the system returns to this stable configuration.

Thus we have the stability condition $q = \alpha$, which can be expanded as

$$q = 1 - p = 1 - F(\alpha) = \alpha$$

or $F(\alpha) = 1 - \alpha$. This can be visualized in Fig. 1, where the area under the curve up to the point α, the frequency of the A types, is equal to the distance between α and 1.

VARIABILITY OF THRESHOLDS AND THE FREQUENCY OF ALTERNATIVE BEHAVIOURS

The threshold, α, at which individuals switch between behaviours is typically different from the average threshold of the group. Figure 2 illustrates this with a symmetrical distribution of thresholds. That distribution has an average value, μ. Because the distribution is symmetrical, $F(\mu) = 0.5$. The average value can be a stable switch point only when $F(\mu) = 1 - \mu$, which is true only when $\mu = 0.5$. This can be seen in Fig. 2 by noting that, for the area under the curve up to the point α to equal the distance $1 - \alpha$, the switch point α must be lower than the average value, μ.

Figure 3 shows that, in general, α will be closer to 0.5 than the median, m, of the distribution of individual thresholds, $f(x)$. The distance, $|m - \alpha|$, between the median threshold and the equilibrium switch point tends to rise as the median moves away from 0.5 and as the variability in the distribution increases. A quantitative analysis of magnitudes requires explicit assumptions about the shape of the individual threshold distribution, $f(x)$. From a mathematical point of view, one should use an example such as the beta

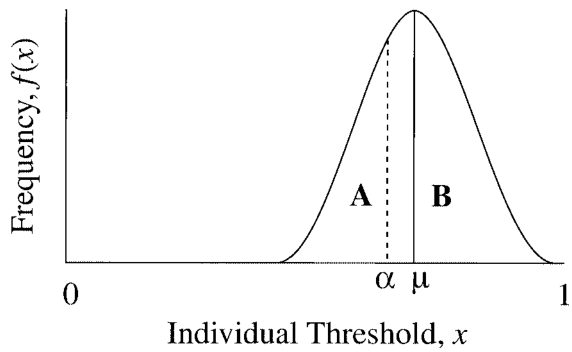

Fig. 2. The equilibrium switch point, α, will typically differ from the average threshold value, μ.

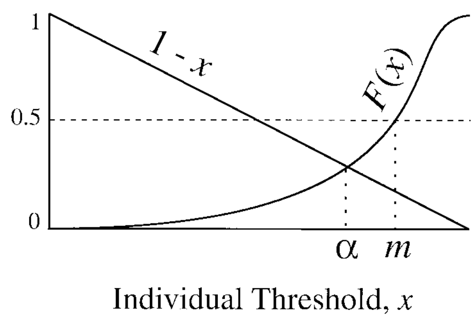

Fig. 3. The condition for the equilibrium switch point, α, is $F(\alpha) = 1 - \alpha$. The median of the distribution is m, determined by $F(m) = 0.5$. The figure demonstrates geometrically that if the median of the distribution is greater than 0.5, then the switch point is less than the median; that is, if $m \geq 0.5$, then $0.5 \leq \alpha \leq m$. Similarly, if $m \leq 0.5$, then $0.5 \geq \alpha \geq m$.

distribution defined on the interval (0, 1), or use a distribution over the real numbers for a transformed variable such as $\log[x/(1 - x)]$ and transform back onto the interval (0, 1).

Both of these methods for specifying a distribution work well. But one loses the simple intuition of how particular magnitudes of variability, measured by standard deviation, affect the switch threshold, α, and the frequency of workers that adopt behaviour A. Thus I use a normal distribution with mean μ and standard deviation σ. Figure 4 shows the frequency of the A behaviour in the colony, p, as functions of the mean and standard deviation of the distribution of individual thresholds. As the standard deviation approaches zero, p converges to the mean of the distribution. As the standard deviation increases, p moves from the mean, μ, towards 0.5. The dashed lines show, for example, that a frequency of $p = 0.25$ is obtained when the mean threshold is 0.2 and the standard deviation is approximately 0.075.

MULTIPLE MATING AND COLONY FITNESS

Colony phenotype develops by interaction among the workers. The workers vary genetically; the distribution of traits among workers depends on the queen's genotype and on the genotypes of her mates.

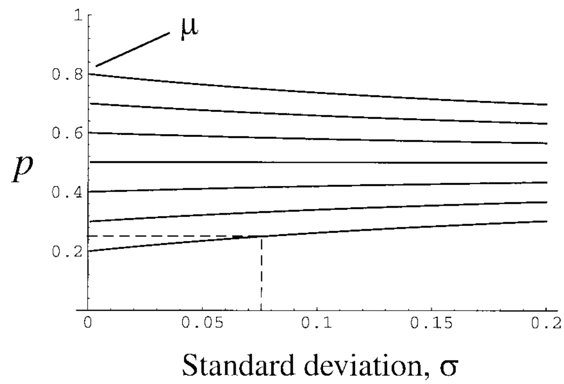

Fig. 4. Quantitative effect of threshold variability on the frequency, p, of workers adopting behaviour A.

Suppose that selection favours some optimum frequency, p^*, of workers adopting behaviour A. The queen's genotype would, by itself, probably generate a distribution of worker thresholds and colony phenotype that differ by at least a small amount from the optimum. Deviations occur because genetic variability is likely to be maintained by mutation–selection balance.

The number of times a queen mates has complex effects on colony phenotype and fitness. More mates increase genetic variability among workers, shifting the colony phenotype. But additional mates also move the average threshold among workers closer to the average threshold in the population, because multiple mating provides a broader sample of the genetic diversity in the population. It would be interesting to study the joint evolution of multiple mating, genetic variability in the specification of threshold, colony phenotype, and colony fitness.

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