Effects of social group size on information transfer and task allocation

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Summary

Social animals exchange information during social interaction. The rate of interaction and, hence, the rate of information exchange, typically changes with density and density may be affected by the size of the social group. We investigate models in which each individual may be engaged in one of several tasks. For example, the different tasks could represent alternative foraging locations exploited by an ant colony. An individual's decision about which task to pursue depends both on environmental stimuli and on interactions among individuals. We examine how group size affects the allocation of individuals among the various tasks. Analysis of the models shows the following. (1) Simple interactions among individuals with limited ability to process information can lead to group behaviour that closely approximates the predictions of evolutionary optimality models, (2) Because per capita rates of social interaction may increase with group size, larger groups may be more efficient than smaller ones at tracking a changing environment, (3) Group behaviour is determined both by each individual's interaction with environmental stimuli and by social exchange of information. To keep these processes in balance across a range of group sizes, organisms are predicted to regulate per capita rates of social interaction and (4) Stochastic models show, at least in some cases, that the results described here occur even in small groups of approximately ten individuals.

Keywords: information transfer; social interaction; group size; task allocation

Introduction

One important feature of social groups is that individuals engage in a variety of tasks. The diversity of tasks is as great as the diversity of social taxa, but some broad categories of tasks are common, such as foraging, vigilance for predators, territorial interactions with conspecifics and care of juveniles. Each individual pursues a single task at any one time, but an individual changes tasks, in response to interactions with its environment and in response to interactions with other individuals.

Here we investigate some models of social groups, to explore how the simple behaviour of individuals can allow groups to adjust the allocation of individuals into various tasks. We define the behavioural state of a social group as the vector describing the distribution of a societies' members among tasks. The group's behaviour is determined by the balance between two kinds of forces: task switching caused by each individual's interaction with its environment and task switching caused by social interactions. Because the rate of social interactions may change with group size, the balance between these two forces and, hence, the behaviour of a society, may change as a function of group size. In this paper, we focus on the effects of group size on group behaviour. When designing the models we used social insects as our primary biological reference. Nonetheless, the models are sufficiently general that they may be employed to study other kinds of social groups (e.g. fish schools or ungulate herds) and other arrays of behaviours or tasks.

Empirical studies of social insects show that colony size affects the allocation of workers to various tasks (Tschinkel, 1988; Nonacs and Dill, 1990; Wolf and Schmid-Hempel, 1990). In harvester ants, task allocation in larger colonies is more stable and consistent when environmental conditions change in comparison with smaller colonies (Gordon, 1987). In disputes with neighbours over foraging area, smaller, younger colonies are more persistent and combative than older, larger ones (Gordon, 1991, 1992). Territorial behaviour involves some assessment of the relative sizes of the colonies involved (Holldobler, 1981; Adams, 1990).

Early models of social insect behaviour were concerned with societies made up of specialized individuals, i.e. individuals that consistently perform a single task (Oster and Wilson 1978). Subsequent work has shown that task switching is pervasive in social insects (Calabi, 1988; Gordon, 1989; Robinson, 1992). Other work has shown that activity levels vary greatly among individuals (Jaisson et al., 1988; Schmid-Hempel, 1990) and among task groups (Gordon, 1986). Whether an individual changes tasks may depend on how successful it is at its current task (Cartar, 1992). The general picture that has emerged from empirical work in social insects is that as conditions change, individuals decide whether or not to be active and which task to perform. All these individual decisions generate the dynamics of group behaviour, the numbers actively engaged in each task at any moment.

Recent theoretical work on social insects has provided new insight on the dynamics of group- or colony-level behaviour. Most of this work explores how individuals are allocated to different components of a single task, including the allocation of foragers to food sources that differ in quality (Seeley et al., 1991) or to food sources in different locations (Deneubourg et al., 1986; Pasteels et al., 1987; Deneubourg and Goss, 1989) or the allocation of workers to various aspects of nest construction (Jeanne, 1986). Other studies model how individuals are allocated to a variety of different tasks (Gordon et al., 1992). These models differ in many ways but share the basic features of those we present here: an individual's behaviour depends in part on some assessment it makes of its environment (e.g. assessment by a honeybee forager of the quality of its nectar source in Seeley et al. 1991) and in part on its interactions with other individuals (e.g. following the trail pheromone laid by another individual in Deneubourg et al. 1990).

Theoretical studies of social insect behaviour have not yet addressed the question of colony size. More generally, it is well known that group size affects vigilance rates (Caraco, 1980) and foraging success (Packer et al., 1990) and a large body of work explores how the benefits of large groups are balanced by the costs of sharing resources (Pulliam, 1973; Brown, 1982; Giraldeau and Gillis, 1985; Kramer, 1985). A basic principle underlying this work is that interaction rates depend on densities and densities may change with group size (Waser, 1984).

If interactions among individuals were a consequence of random collisions, like particles in Brownian motion, then the total number of encounters among n individuals enclosed within an arena of constant size would increase as n^2. However, empirical studies of social insects show that individuals can regulate their encounter rate (Gordon et al. 1993). Encounter rates in ants were measured at a range of densities, by housing several different group sizes in arenas of varying size. Total numbers of encounters (measured by counting antennal contacts) did not increase as n^2. Instead, at low densities, individuals aggregated into a small portion of the arena. By elevating the local density about each ant, the ants increased the per capita rate of contact. In contrast, at high densities ants were evenly spaced and resisted contact with nearby individuals. As a result, the contact rate levelled off as the density increased (Fig. 1). Why do ants regulate the rate of social interaction? We present theoretical results that show how the capacity to regulate interaction rates may contribute to the efficiency with which large colonies or groups adjust task allocation to changing conditions.

The remainder of this paper is divided into two sections. In the first, we introduce deterministic models that illustrate how extremely simple behaviours of individuals can permit a colony to operate efficiently. We compare the distribution of workers among tasks with the predictions of simple evolutionary optimality models. An analysis of the effects of colony size on this distribution shows (1) the efficiency with which a colony's behaviour tracks a changing environment may increase with colony size and (2) regulation of the per capita rate of social interactions (as in Fig. 1) will permit efficient behaviour by a colony despite changes in colony size.

In the second section, we examine Markovian models of the stochastic processes that underpin the deterministic models, to determine how large a social group must be before the deterministic approximation is reasonable. We show that the deterministic models typically provide close approximations for social groups with more than 100 members. Interestingly, the deterministic approximation is sometimes useful with ten or fewer members and thus, simple deterministic models may be appropriate for social species that live in small groups.

Deterministic model of task switching

State variables

Suppose that, at any one time, organisms can either be inactive or engage in one of Q tasks and let X_i be the number of individuals engaged in task i. The models in this paper describe how
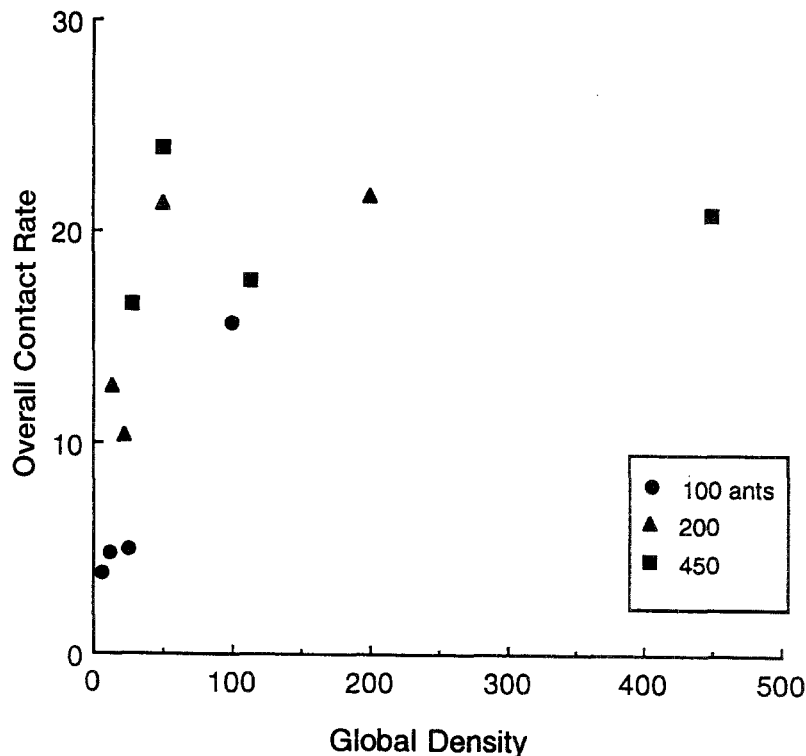

Figure 1. Per capita interaction rates for the ant species *Lasius fuliginosus* as a function of the number of ants per unit area from Gordon *et al.* (1993). The horizontal axis is labelled 'global density' to distinguish it from the local density within the arena which the ants controlled by aggregating at low densities and spacing evenly at high densities.

interactions among individuals, together with each individual's assessment of its local environment, control the allocation of individuals among tasks. The models thus focus on the dynamics of the vector $\mathbf{X} = \{X_1, X_2, \ldots, X_Q\}$. There is abundant evidence that in social insects, worker allocation is rapidly adjusted to changes in food supply (Seeley, 1986, 1989), predation (Nonacs and Dill, 1990, 1991) and nest structure (Gordon, 1986, 1987).

For simplicity, we model interactions among individuals as simple collisions. The rate at which an individual engaged in task i encounters individuals engaged in task j, is simply proportional to D_{ij} – the mean local population density of task j individuals about a task i individual. Also, for simplicity, we assume that each individual has only a very limited ability to assess the environment. An individual can be in one of only two behavioural states. Either it views the environment as profitable, in which case the individual is in the successful state, or it views the environment as unprofitable, in which case it is in the unsuccessful state. Let s_i be the probability that an individual engaged in task i is in the successful state and let $\mathbf{s}$ be the vector $\{s_1, s_2, \ldots, s_Q\}$. We must specify the processes that govern the dynamics of $\mathbf{s}$ if we are to model how task allocation ($\mathbf{X}$) responds to environmental changes.

In what follows, we first review some evolutionary reasoning that helps in understanding the behavioural models. We then introduce the equations that govern $\mathbf{X}$ and finally discuss the dynamics of $\mathbf{s}$.

Evolutionary rationale

Let R_i be the abundance of the resource that is the focus of task i. If task i were foraging, then R_i might be either the abundance of prey in location i or the abundance of prey of type i. If task i were nest maintenance, then R_i might be the amount of debris present on the nest. Also, let the function $f_i(R_i)$ be the rate of resource capture by an individual engaged in task i, but scaled in units of fitness benefit. Finally, let ξ_A and ξ_I be, respectively, the cost of engaging in a task and the cost of inactivity (cost of being in the inactive class). We define the differential cost of activity as $\Delta_c = \xi_A - \xi_I$.

The ESS distribution of individuals among tasks, assuming that evolution maximizes individual (as opposed to group) fitness, is given by the well-known ideal free distribution (Fretwell and Lucas, 1970). Individuals should distribute themselves among tasks such that no animal can increase its fitness by switching activities. The ESS is characterized by two classes of tasks. Tasks that are performed must yield equal fitness benefits, $f_i(R_i) = f_j(R_j)$ if $X_i > 0$, and $X_j > 0$, and these benefits must exceed or equal the cost of activity, $f_i(R_i) \geq \Delta_c$ if $X_i > 0$. Tasks that are not performed must yield lower benefits than those performed: $f_i(R_i) > f_j(R_j)$ if $X_i > 0$ and $X_j = 0$.

In contrast, if evolution maximizes colony-level fitness, then a different ESS is obtained. The social group's fitness (W) is given simply by its total net rate of resource capture:

$$W = \sum_{i=1}^{Q} X_i(f_i(R_i) - \xi_A) - \left[N - \sum_{i=1}^{Q} X_i\right]\xi_I$$

where N is the number of individuals in the colony and the term in the square brackets is the number of inactive individuals. The optimal distribution of individuals from the point of view of the colony is obtained by differentiating W with respect to each X_i. The ESS is again characterized by two classes of tasks. Tasks that are performed must yield equal *marginal benefits*, $d[X_if_i(R_i)]/dX_i = d[X_jf_j(R_j)]/dX_j$ if $X_i > 0$, and $X_j > 0$, and these marginal benefits must exceed or equal the cost of activity, $d[X_if_i(R_i)]/dX_i \geq \Delta_c$. Tasks that are not performed must yield lower marginal benefits than those performed: $d[X_if_i(R_i)]/dX_i > d[X_jf_j(R_j)]/dX_j$ if $X_i > 0$ and $X_j = 0$.

An intuitive understanding of this result can be obtained by ignoring temporarily the cost of activity. Imagine a colony directing workers to a sequence of tasks beginning with the most

profitable (task 1 with less profitable tasks ranked 2, 3, . . ., Q). If there is no density dependence in the capture rates of individuals engaged on the best task (i.e. R_1 is a constant that does not depend on X_1), then colony fitness is maximized by allocating all workers to this task. However, if there is density dependence then colony returns from task 1 may be sufficiently depressed that $dW/dX_2|_{x_2=0} \geq dW/dX_1$ and the colony is selected to switch some workers to task 2 until $dW/dX_1 = dW/dX_2$. If at this stage $dW/dX_3|_{x_3=0} \geq dW/dX_1 = dW/dX_2$, then allocation to the third task is favoured. This process goes on until $dW/dX_i|_{x_i=0} = 0 \leq dW/dX_1 = dW/dX_2 .. = dW/dX_{i-1}$ tasks 1 to i-1 are now all performed with an equal marginal return and all less profitable tasks are not performed. We are not, of course, suggesting that the optimum task allocation is arrived at sequentially, just that this is a means of visualizing the ESS.

One difficulty with behavioural optimization models is that proximal behavioural mechanisms that lead to an optimum may be difficult to imagine. The mechanistic equations governing **X** and **s**, which are described in the following sections, were designed to produce patterns of task allocation that approximate ESSs. The system governing **X** is constructed from simple rules controlling individual behaviour. Although no single individual is able to compute much of anything, in a social group the simple rules both equalize the success probabilities (the s_i) of all tasks performed and ensure that only those tasks yielding the highest success probabilities are performed. Similarly, the equations governing **s** embody simple behavioural rules that cause the success probabilities to mirror either individual returns (e.g. s_i 'measures' $f_i(R_i)$) or marginal returns (e.g. s_i 'measures' $d[X_i f_i(R_i)]/dX_i$).

Dynamics of task switching

To define the model of task allocation, we specify the rules that govern how individuals switch from one task to another and switch between activity and inactivity. Consider a collision between two active individuals. We make the simple assumption that an interaction between two successful or two unsuccessful individuals results in no net change in behaviour. In contrast, an interaction between a successful and an unsuccessful individual causes the latter to engage in the former's task. Because of our assumption that interactions occur like random collisions, the rate at which interactions occur between successful task i individuals and unsuccessful task j individuals is proportional to $X_i s_i D_{ij} (1-s_j)$ (or equivalently $X_j (1-s_j) D_{ji} s_i$). Similarly, the rate at which interactions occur between unsuccessful task i individuals and successful task j individuals is proportional to $X_i (1-s_i) D_{ij} s_j$. To keep the notation as simple as possible, in what follows we subsume the constant of proportionality within the symbol for local density (within D_{ij}).

Now consider the behavioural transitions from active to inactive and vice versa. We assume that an unsuccessful individual will become inactive in a small time interval Δt, with probability $q \Delta t$ and that an inactive individual is recruited to perform task i if it interacts with a successful individual engaged in task i. Thus, the rate of loss of task i individuals to the inactive pool is qX_i $(1-s_i)$ and the rate of gain of task i individuals from the inactive pool is $(N - \sum X_j) D_{Ii} s_i$, where D_{Ii} is the mean local density of task i individuals about an inactive individual.

With these specifications, the model is

$$\frac{dx_i}{dt} = x_i (1 - s_i) q + \left[\sum_{j=1}^{Q} x_i s_i D_{ij} (1 - s_j) - \sum_{j=1}^{Q} x_j s_j D_{ji} (1 - s_i) + (N - \sum_{j=1}^{Q} x_j) D_{Ii} s_i \right] \quad (1)$$

$i = (1,2, . . .,Q)$. Equation 1 gives change (the left-hand side) as a function of four terms on the right-hand side: (1) individuals who cease task i and become inactive because they are unsuccessful, (2) individuals from other tasks who are actively recruited to task i, (3) individuals

who are recruited from task i to other tasks and (4) inactive individuals who are recruited to task i.

To complete the model of task dynamics, we must define the relationship between the numbers of individuals (the X_i's) and the local densities (the D_{ij}'s). This is complex because local densities may depend on the host of factors determining spatial distributions and patterns of movement (Adler and Gordon, 1992). However, a variety of simple mechanisms would cause D_{ij} to be proportional simply to X_j/N. For example, random collisions among nest workers might occur throughout a nest whose volume is proportional to the number of individuals in the colony or among foragers moving randomly throughout a foraging territory whose size is proportional to N. This scenario is the extreme of perfect regulation, because, in it, densities and per capita rates of social interaction remain constant despite changes in group size (providing that the fractions of individuals engaged in each task remain constant). Note that interaction rates would also be independent of group size if each individual were to regulate its own encounter rate at a constant value. Both of these mechanisms – regulation of densities and regulation of contact rates independent of densities – are responsible for the constant per capita interaction rates of *Lasius fuliginosus* (Fig. 1, abundances ≥ 50).

A variety of simple mechanisms could also produce the opposite extreme of no regulation of contact rates. In this extreme, D_{ij} is simply proportional to X_j and interaction rates increase linearly with group size (see the interaction rates in Fig. 1 for abundances < 50). For example, interactions among foragers might occur in some subset of the habitat (e.g. in the vicinity of a nest entrance for social insects) that does not expand in size as a group grows, or the physical space corresponding to some tasks might be constrained by factors such as the availability of food or the presence of competitors that prevent territorial expansion.

To permit a range of possible dependencies of interaction rates on group size, we assume that each D_{ij} is equal to $X_j[I(N)/N]$ where $I(N)$ is formally the *per capita rate of social interaction as a function of group size*. Note that, for simplicity, we assume a single $I(N)$ function common to all pairs of tasks (rather than considering the intractable general case of separate functions for each pair of tasks). We expect that in most cases $I(N)$ will fall between the extremes of no regulation and perfect regulation. Suppose, for example, that $I(N)$ is proportional to N^z. Then, the extreme of no regulation of per capita interaction rates corresponds to $z = 1$ and the extreme of perfect regulation of per capita interaction rates corresponds to $z = 0$.

For algebraic reasons, it is useful to express Equation 1 in terms of the fractions of individuals in each task (signified by the lower case x_i rather than the number X_i). After replacing D_{ij} by $X_j[I(N)/N]$, D_{Ii} by $X_i[I(N)/N]$ and D_{Ii} by $(N-\Sigma X_j)[I(N)/N]$, dividing both sides by N and algebraic rearrangement we have

$$\frac{dx_i}{dt} = -x_i\, q\, (1 - s_i) + x_i\, I(N)\, \left[s_i - \sum_{j=1}^{Q} x_j\, s_j \right] \tag{2}$$

$i = (1, 2, \ldots, Q)$.

The system in Equation 2 shows that the dynamics are influenced by two forces, each described by a separate term on the right-hand side. The first describes the experience of each individual with its environment. An individual is more likely to cease its task and become inactive if it is unsuccessful. The second describes the information transfer and resultant task switching caused by social interaction. Observe that interactions among individuals will cause a net inflow into task i if s_i is greater than the mean success rate (the sum on the right-hand side assuming a success rate of zero for inactive individuals), and a net outflow from task i if s_i is less than the mean success rate. Observe also that direct effects of colony size occur *only* in the second term. Because $I(N)$ is likely

to be a non-decreasing function of group size (i.e. proportional to N^z with $O \leqslant z \leqslant 1$), the effects of social interaction relative to individual experience will typically increase with colony size.

Dynamics of success

Suppose that an individual captures and processes a unit of resource (R_i) during the small time interval Δt, with probability $k(R_i/\alpha_i)\Delta t$, where α_i is the area over which the task is performed $(R_i/\alpha_i$ is the resource density) and k is the slope of the linear functional response. We assume that resource capture causes an unsuccessful individual to switch its behavioural state to successful. This type of behavioural transition causes the number of successful individuals to increase during Δt by $(1-s_i)x_ik(R_i/\alpha_i)\Delta t$ and thus the fraction of task i individuals in the successful state to increase by $(1-s_i)k(R_i/\alpha_i)\Delta t$. We also assume that an individual in the successful state will switch to the unsuccessful state with probability $\tau\Delta t$, if it does not capture any resource during Δt. This causes the fraction of successful individuals to decrease by $[1-k(R_i/\alpha_i)\Delta t](\tau\Delta t)s_i = \tau s_i\Delta t$ plus a term of order $(\Delta t)^2$. Putting these two rates together and passing to the limit of infinitesimal Δt, we have

$$\frac{ds_i}{dt} = -\tau s_i + k\frac{R_i}{\alpha_i}(1 - s_i) \qquad (3)$$

The equilibrium of Equation 3 is $s^\varepsilon_i = f_i(R_i)/(f_i(R_i) + \tau)$, where $f_i(R_i)$ is the per capita rate of resource capture, $k\,R_i/\alpha_i$. Note that s^ε_i is a monotonically increasing function of an individual's rate of resource capture. Thus, if the dynamics of Equation 3 are sufficiently fast, then s_i will provide an accurate mirror of the *fitness benefit of task i to the individual* (see 'Evolutionary rationale' above).

In some circumstances, we expect that the abundance of the resource will be largely unaffected by the activities of the social species. For example, seed abundance may be determined primarily by plant yield, the dynamics of seed burial and germination and seed predation by rodents, fungi, weevils and birds, and so be largely unaffected by the activities of a granivorous ant species. However, in other circumstances, the profitability of a task will be affected by the activities of the social species. For example, suppose that R_i is deposited at rate Γ_i and removed by agents other than our social species at rate μ. Then, the dynamics of R_i is governed by

$$\frac{dR_i}{dt} = \Gamma_i - \mu R_i - k\frac{R_i}{\alpha_i}x_i \qquad (4)$$

and, at equilibrium, R_i is a decreasing function of X_i:

$$R_i^\epsilon = \frac{\Gamma_i}{\left[\mu + k\frac{x_i}{\alpha_i}\right]}$$

In this paper, we consider three different classes of functions for the s_i.

(1) Class I – s_i is a monotonically increasing function of the per capita returns from task i and per capita returns are independent of X_i (e.g. capture rates are unaffected by foraging). The example yielding this class is Equation 3 with fast dynamics (s is always in equilibrium relative to X because the dynamics of s are faster than the dynamics of X) and Equation 4 with $k << \Gamma_i$ and $k << \mu$. s_i measures the fitness benefit of task i to the individual as well as the marginal fitness benefit to the group, because $f_i(R_i) = d[X_if_i(R_i)]/dX_i$ if $f_i(R_i)$ is independent of X_i.

(2) Class II – s_i is again a monotonically increasing function of the per capita returns available from task i, but s_i is now also a monotonically decreasing function of X_i (e.g. capture rates are affected by foraging). The example yielding this class is equations 3 and 4 with fast dynamics (the dynamics of s_i and R_i are faster than the dynamics of X_i. Thus, s_i is given approximately by the equilibrium of Equation 3 (s_i^ε), with $f_i(R_i)$ evaluated at the equilibrium of Equation 4 (R_i^ε). s_i measures the fitness benefit of task i to the individual.

To motivate class III, we add within-task avoidance of crowding to equation 3 by introducing a single new term. Suppose that individuals engaged in the same task interact at random (following random collisions) and that each interaction causes an individual in the successful state to switch to the unsuccessful state with some probability. Because random collisions increase proportionately with population density, we have

$$\frac{ds_i}{dt} = -\tau s_i + k\frac{R_i}{\alpha_i}(1 - s_i) - \theta\frac{X_i}{\alpha_i}s_i \tag{5}$$

where θ is the constant of proportionality.

At the equilibrium of Equations 4 and 5

$$s_i^\varepsilon = \frac{\frac{k}{\alpha_i}R_i^\varepsilon\left[\dfrac{1}{\tau + \theta\frac{X_i}{\alpha_i}}\right]}{1 + \frac{k}{\alpha_i}R_i^\varepsilon\left[\dfrac{1}{\tau + \theta\frac{X_i}{A_i}}\right]}$$

In the special case in which the parameter θ is set equal to $k\tau/\mu$, the above expression becomes

$$s_i^\varepsilon = \frac{\left[\dfrac{dXf_i(R_i^\varepsilon)}{dX_i}\right]}{\tau + \left[\dfrac{dXf_i(R_i^\varepsilon)}{dX_i}\right]} \tag{6}$$

where $f_i(R_i^\varepsilon) = kR_i^\varepsilon/\alpha_i)$. Note that s_i^ε is a monotonically increasing function of the *marginal benefit of task i to the social group* (the derivative in square brackets).

(3) Class III – s_i is a monotonically increasing function of marginal rate of return from task i and a monotonically decreasing function of X_i. The example yielding this class is Equations 4 and 5 with fast dynamics (the dynamics of s_i and R_i are faster than the dynamics of X_i) and with θ tuned (presumably by evolution) to be equal to $k\tau/\mu$. In this class, s_i measures the marginal fitness benefit of task i to the group.

The assumption of fast dynamics underpinning classes I–III allows us to dispense with dynamical equations for the s_i and R_i and to focus exclusively on the dynamics of task allocation (Equation 2). This greatly simplifies the presentation. However, with a single exception (which is noted below in the text), all results obtained using classes I–III, can also be obtained without the assumption of fast dynamics, by repeating the analyses for the system composed of Equations 2, 3 and 4 or the system composed of Equations 2, 4 and 5.

Analysis of the model of task allocation – equilibria

By inspection of Equation 2, the equilibrium fraction x_i^* must either equal zero or satisfy

$$s_i^* - \frac{q(1 - s_i^*)}{I(N)} = \sum_{j=1}^{Q} x_j^* s_j^* \tag{7}$$

where s_i^* signifies s_i evaluated at the equilibrium x_i^* and s_j^* signifies s_j evaluated at x_j^*. Now assume that the equilibrium fraction is non-zero for two tasks, task a and task b and consider Equation 3 for each task (Equation 3 with $i = a$ and $j = b$). Because these equations have the same right-hand side, we may set the left-hand sides equal to one another and simplify the result to produce $s_a^* = s_b^*$. Thus, at equilibrium, all tasks that are performed *must have equal success rates*: $s_i^* = s_j^*$ if $X_i^* > 0$ and $X_j^* > 0$. Clearly, this result accords with the predictions of the ESS models. In what follows, s^* designates the success rate common to all tasks that are performed at equilibrium and s_i^0 designates the success rate for the ith task when no individuals pursue it (when $x_i = 0$). Note that s_i^0 is also the maximum success rate for the ith task, because s_i is a non-increasing function of x_i (see the definitions of classes I–III).

Let x_I^* be the fraction of individuals that are inactive at equilibrium. We use the fact that $\sum x_j^* s_j^* = s^* \sum x_j^*$ to re-express Equation 7 as

$$x_I^* = 1 - \sum_{j=1}^{Q} x_j^* = \frac{q}{I(N)} \left[\frac{1}{s^*} - 1 \right] \tag{8}$$

Figure 2 shows the relationship between success rate and the fraction of inactive individuals predicted by Equation 8. Recall that our ESS models also make a prediction about this relationship (because of the interchangability of success rates with fitness benefits or marginal fitness benefits). To simplify the discussion, it is best to scale the differential cost of activity, Δ_c, in units of success rate. The ESS models predict a step function $x_I^* = 1$ if $s^* < \Delta_c$ and $x_I^* = 0$ if $s^* > \Delta_c$.

The curves in Fig. 2 show that the dynamical model of task allocation predicts a reasonable approximation of a step function. For each curve, $x_I^* = 1$ if $s^* < q/(q + I(N))$ and x_I^* declines to values near zero as s^* increases beyond $q/(q + I(N))$. Thus, if evolution were to tune the value of $q/(q + I(N))$ to equal Δ_c (or a value slightly less than Δ_c), then the dynamical model and ESS models would have quantitatively similar predictions about levels of inactivity. Note that the correspondence between the ESS and dynamical models would be best in the likely case of small Δ_c (the bottom curve is closest to a step function).

The three curves shown were produced using the assumption of zero regulation of the per capita interaction rate ($I(N)$ increases proportionately to N), to demonstrate the necessity of regulation. If $I(N)$ were not regulated, then evolution could not tune $q/(q + I(N))$ to be approximately equal to Δ_c. Instead, the threshold success rate at which a group becomes active would change markedly with group size, as shown in Fig. 2. This is clearly suboptimal because Δ_c does not change with group size. The obvious way around this problem is to regulate $I(N)$ at a constant value (e.g. Fig. 1, abundances ≥ 50).

Analysis of the model of task allocation – stability

We first examine the stability of the trivial equilibrium $x_i^* = 0$ for all i. By inspection of equation 2, the trivial equilibrium is stable if and only if $s_i^0 < q/[q + I(N)]$ for all i. An inactive group will become active if at least one task is sufficiently profitable. Inspection of Fig. 2 and Equation 8 shows also that the existence of a non-trivial equilibrium implies the instability of the trivial equilibrium.

Turning now to equilibria in which at least some individuals are active, we find that the eigenvalues governing the stability of a non-trivial equilibrium can be divided into two groups. First, for each unperformed task i ($x_i^* = 0$) in an equilibrium ($\underline{x}^* = (x_1, x_2^*, \ldots, xQ^*)$), there exists a corresponding eigenvalue:

$$\lambda_i = [q + I(N)] \; [s_i^o - s^*] \tag{9}$$

Thus, an equilibrium is unstable if the success rate for any unperformed task (s_i^0) is greater than the success rate common to all performed tasks (s^*). A necessary condition for stability is that only the most profitable tasks are performed. Also, it is easy to show with Equation 9, that there is at most a single stable non-trivial equilibrium (use the fact that s_i is a non-increasing function of x_i).

These results are sufficient to demonstrate the tight correspondence between the ESSs described in the 'Evolutionary rationale' section and a stable equilibrium of the task allocation model. At a stable equilibrium: (1) tasks that are performed must yield equal success probabilities, (2) tasks that are not performed must yield lower success probabilities than those performed and (3) success probabilities of tasks that are performed must exceed the threshold value of $q/(q + I(N))$. With $q/$
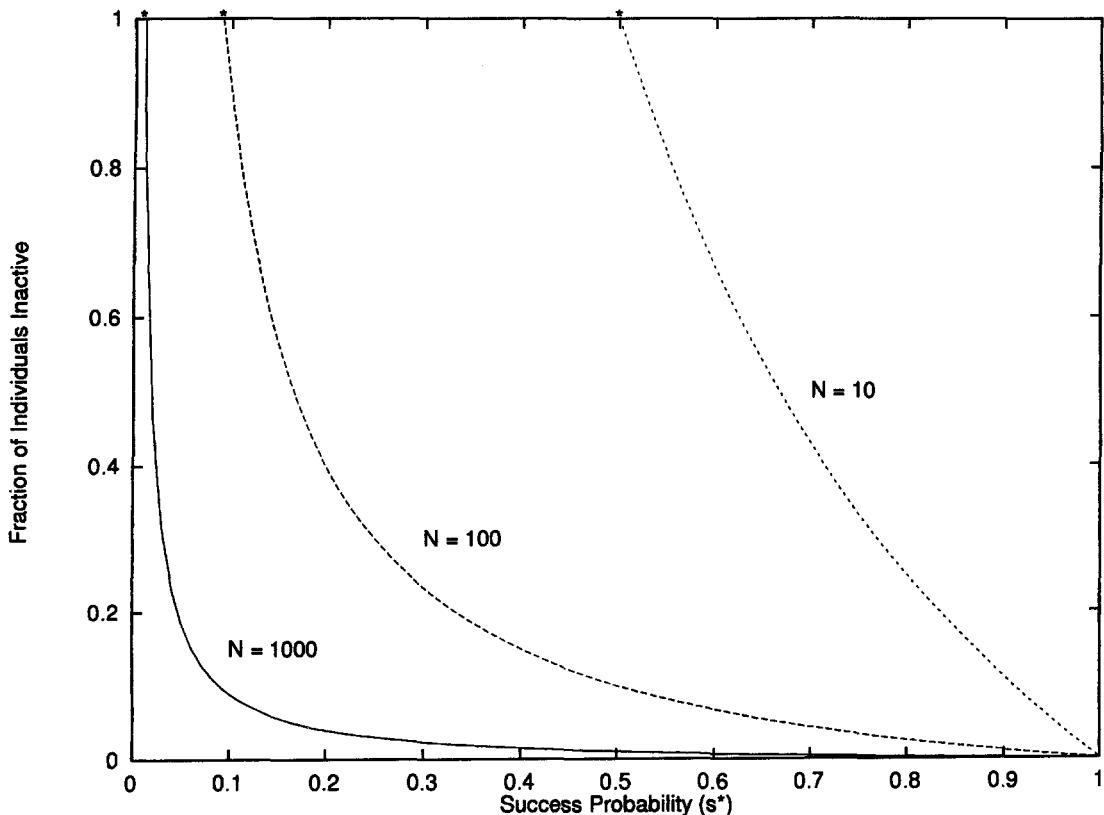
Figure 2. Equation 8 – the fraction of inactive individuals at equilibrium in the model in Equations 1 and 2 as a function of the success rate of the most profitable task (s^*) and colony size (N). Parameters: $a = 0.01$, ($I(N) = aN$) and $q = 0.1$. For each colony size (N) shown, the fraction of inactive individuals is approximately a step function – the fraction equals 1 until the appropriate (for the colony size) asterisk at the top of the figure and then follows the curve descending from the asterisk.

$(q + I(N))$ tuned by evolution to equal Δ_c and success probabilities in classes I or II, a stable equilibrium of Equation 2 is almost identical to the ESS that maximizes individual fitness. If success probabilities are in classes I or III, then a stable equilibrium of Equation 2 is equally similar to the ESS maximizing group fitness. In either case, the sole discrepancy between the predictions of the evolutionary and behavioural models is in the fraction of inactive individuals. This discrepancy is the difference between the step function predicted by the ESS and the approximation to a step function predicted by Equation 8.

The one remaining chore of the stability analysis is to consider the eigenvalues not given by Equation 9 (those associated with the tasks that are performed at equilibrium). If any of these eigenvalues had a positive real part, then task allocation would oscillate perpetually. We can prove that these eigenvalues have negative real parts only if we place an additional restriction on the functional forms of the s_i. This is the sole portion of the analysis that we cannot complete if we relax the assumption(s) of fast dynamics used to motivate classes I–III, and analyse directly Equations 2, 3 and 4 or Equations 2, 4 and 5.

We now assume that $d(X_i s_i)^*/dX_i \geq 0$ for all i, where the asterisk indicates that the derivative is to be evaluated at equilibrium. It is important to understand that this new restriction does not affect cases in which the s_i are constant and still permits cases in which individual success probabilities are negatively density dependent. The restriction is met by the equilibrium of Equations 3 and 4 used to motivate class II. It is also met by the equilibrium of Equations 5 and 4 used to motivate class III, if τ is sufficiently small. With this assumption, all remaining eigenvalues are real and negative (see Appendix 1). A non-trivial equilibrium in which only the most profitable tasks are performed is locally stable. Moreover, numerical solutions of cases that violate the restriction (e.g. with s_i given by the equilibrium of Equations 4 and 5 with large τ) invariably also exhibited stable dynamics. This confirms that $d(X_i s_i)/dX_i \geq 0$ is sufficient, but not necessary, to ensure that the remaining eigenvalues (those not given by Equation 9) have negative real parts.

Responses to environmental changes

Suppose now that environmental change alters the success rate of a task (i.e. by changing Γ_i in Equation 4). The above results imply that the distribution of individuals in different tasks will readjust, eventually reaching a new equilibrium corresponding to the altered conditions. What effect does colony size have on the efficiency of this environmental tracking? To answer this question, we perform a perturbation experiment. Suppose that a colony is close to a stable non-trivial equilibrium when a single success rate, s_i^*, suddenly changes to the new value, $s_i^* + \Delta s$. We Taylor-expand the right-hand side of Equation 2 about the equilibrium and retain the first non-zero term:

Case 1 – $x_i^* > 0$

$$\frac{dx_i}{dt} \approx \Delta s x_i^* [q + I(N)(1 - x_i^*)]$$

$$\frac{dx_j}{dt} \approx -\Delta s x_j^* x_i^* I(N); \text{ if } x_j^* > 0$$

$$\frac{dx_j}{dt} \approx -\Delta s I(N) x_i^* x_j + \lambda_j x_j; \text{ if } x_j^* = 0$$

$$(10)$$

Case II – $x_i^* = 0$

$$\frac{dx_i}{dt} \approx \Delta s [q + I(N)] x_i + \lambda_i x_i$$

$$\frac{dx_j}{dt} \approx -\Delta s I(N) x_j^* x_i + T_j; \text{ if } x_j^* > 0$$

$$\frac{dx_j}{dt} \approx \Delta x_j \lambda_j; \text{ if } x_j^* = 0$$

where λ_i and λ_j are given by Equation 9 and T_j is the right-hand side that would result for task j from a first-order Taylor expansion with $\Delta s = 0$ (see Appendix 1 for this Taylor expansion).

Because Δs in Equation 10 is invariably multiplied by the per capita rate of social interaction ($I(N)$), the rapidity of response to environmental changes increases with $I(N)$. Large social groups should respond more quickly than small groups whenever $I(N)$ is an increasing function of N (as it will be in most cases, see above). If $I(N)$ increases with N, then large groups will track an ESS more efficiently than will small groups.

The generality of this conclusion is clouded somewhat in cases where success rates are functions of the X_i (rather than constant), because then, the s_i may also depend on colony size. This complication does not affect the first or second equation in Equation 10 because the s_i do not appear in these. Also, it is easy to show that dependence of s on N can only further speed the dynamics of large colonies in the fourth equation and the third and fifth equations are obviously unaffected at least for sufficiently large Δs. Finally, the effects of group size will be smaller in the sixth equation than in the other equations if Δs is sufficiently large, because there is no effect (to first order) of the environmental change on the sixth equation.

The effects of group size on the rate at which a colony can track a changing environment are illustrated in Fig. 3. To produce this figure we assumed that $I(N) = aN$, where a is a constant (corresponding to the extreme of no regulation) and that s_i was given by the equilibrium of Equations 3 and 4. To simplify the notation, we define m_i as $k\Gamma_i/(\alpha_i\tau\mu + k\Gamma_i)$ and c_i as $\tau k/\alpha_i$, yielding $s_i = m_i/(1 + c_i Nx_i)$, where m_i is the success rate for task i when it is unexploited (when $x_i = 0$) and c_i is a constant governing how fast s_i decreases as the number of individuals engaged in the task increases. The numerical simulations involved a colony whose workers were engaged in up to three tasks. At the beginning of the simulations, 10% of the individuals were occupied at each task and 70% were inactive. We set the initial unexploited success rates to $m_1 = 0.3$, $m_2 = 0.4$ and $m_3 = 0.01$, but at time $= 4$, the value of m_3 was changed to 0.6. We explored the response of three sizes of colony: $N = 1000$ (Figs. 3a and b), $N = 100$ (Figs. 3c and d) and $N = 50$ (Figs. 3e and f).

As predicted by the behavioural model, the colony in Fig. 3a equilibrated so that only the two most profitable tasks were performed before time $= 4$, while all three were performed thereafter. Moreover, the allocation of labour converged to the ideal free distribution, yielding equal success rates for all tasks performed (Fig. 3b). The two remaining numerical solutions exhibited qualitatively similar behaviour (Figs. 3c–f). However, the rate of convergence was an increasing function of colony size (slower in Figs. 3c and d than in Figs. 3a and b and slower still in Figs. 3e and f). Note that task 3 was adopted by the largest colony very soon after the value of m_3 increased (by time $= 5$ in Fig. 3a). In contrast, the adoption of task 3 took considerably more time in the smaller colonies (approximately time $= 7$ in Fig. 3d and time $= 9$ in Fig. 3f). As predicted by Equation 10, a colony's ability to track a changing environment increased with its size.

The success probabilities used to produce Fig. 3 are in class II and thus correspond to per capita rates of resource capture and the ESS in which individual fitness is maximized. Figure 4 contains

Figure 3. Effects of colony size on resource tracking in a changing environment in the model in Equations 1 and 2. In each of the three cases shown the profitability of task 3 jumped suddenly at time 4 (from $m_3 = 0.01$ to $m_3 = 0.6$). Colony sizes (a) and (b) were $N = 1000$, (c) and (d) $N = 100$, and (e) and (f) $N = 50$. Figs. 3(a), (c) and (e) show the fractions of the colonies engaged in each of the three tasks, while (b), (d) and (f) show the success rates (the s_i). Note that (a), (c) and (e) illustrate the fact that only the most profitable tasks are pursued at equilibrium and (b), (d) and (f) the ideal free distribution (equal success rates for tasks pursued at equilibrium). Also, observe that the rate of adjustment to environmental change increases with colony size. The remaining parameters were $a = 0.1$, $q = 0.1$, $c_1 = c_2 = c_3 = 0.02$, $m_1 = 0.3$ and $m_2 = 0.4$.
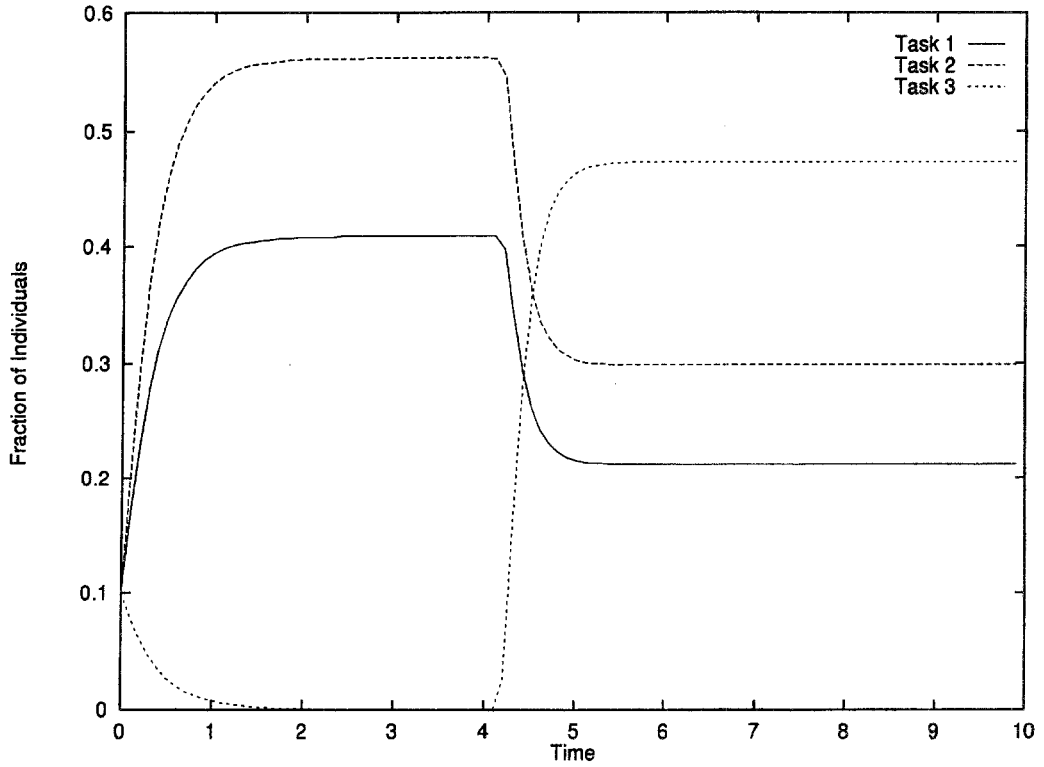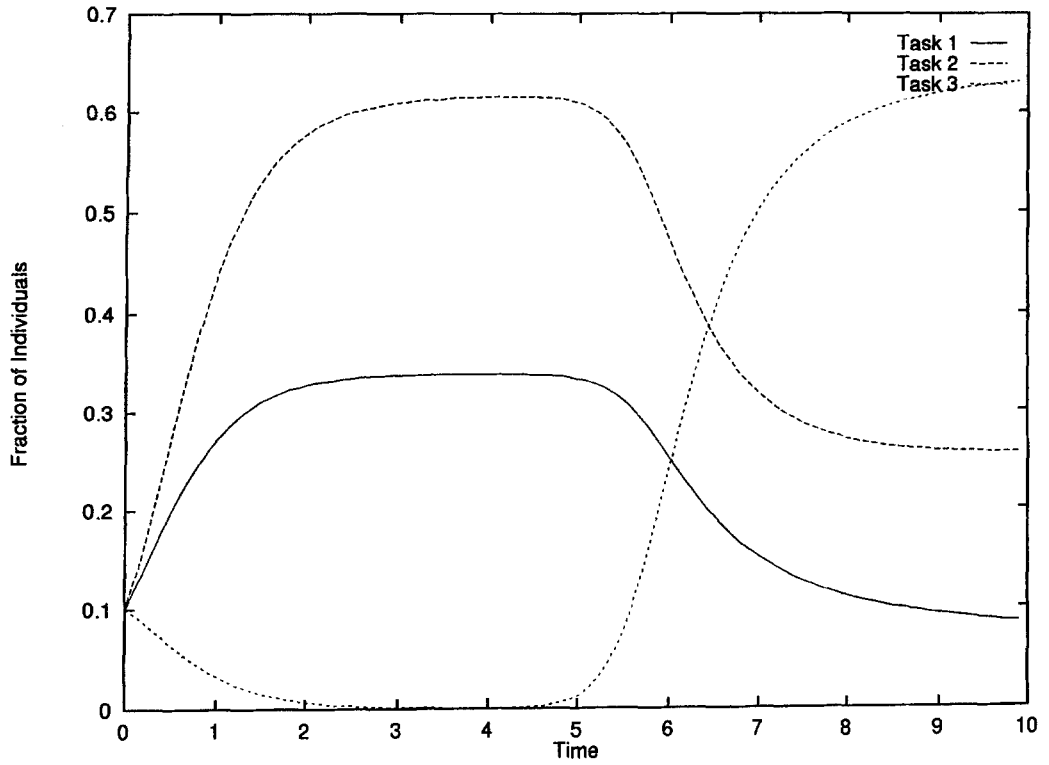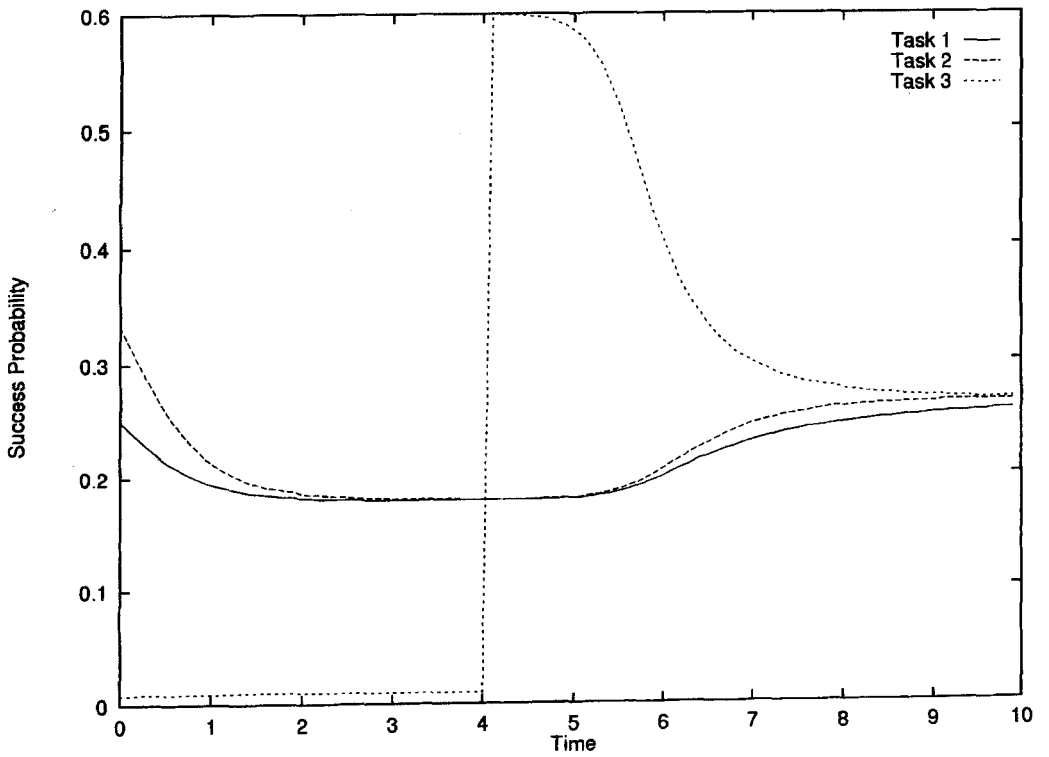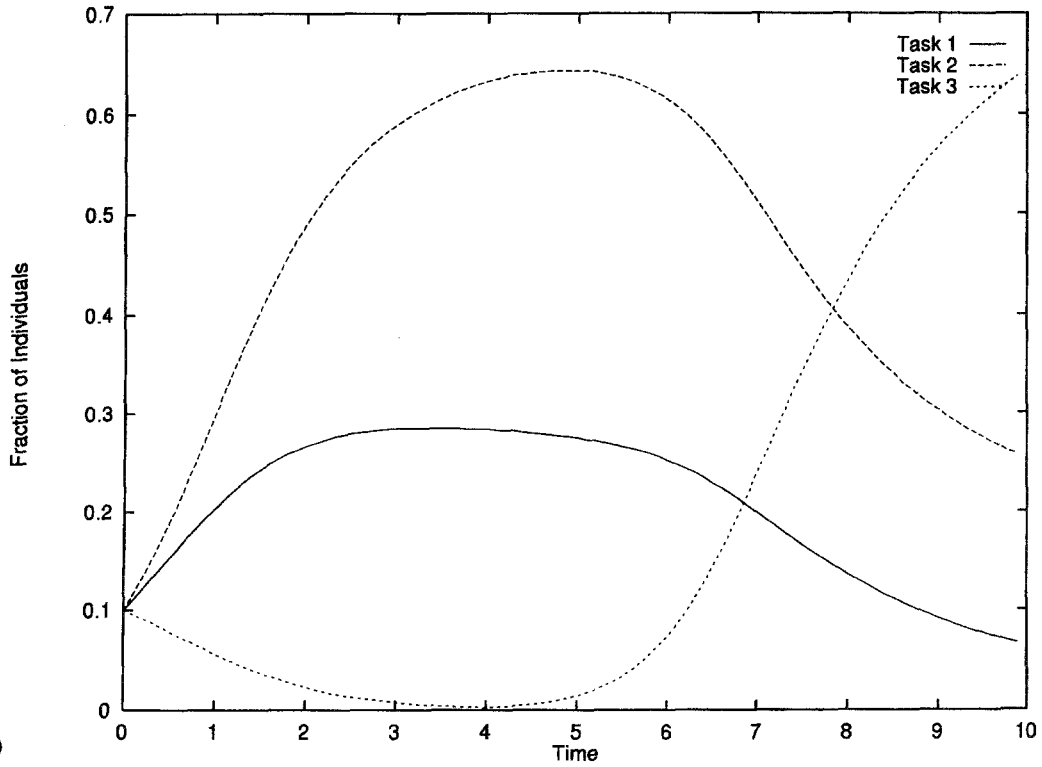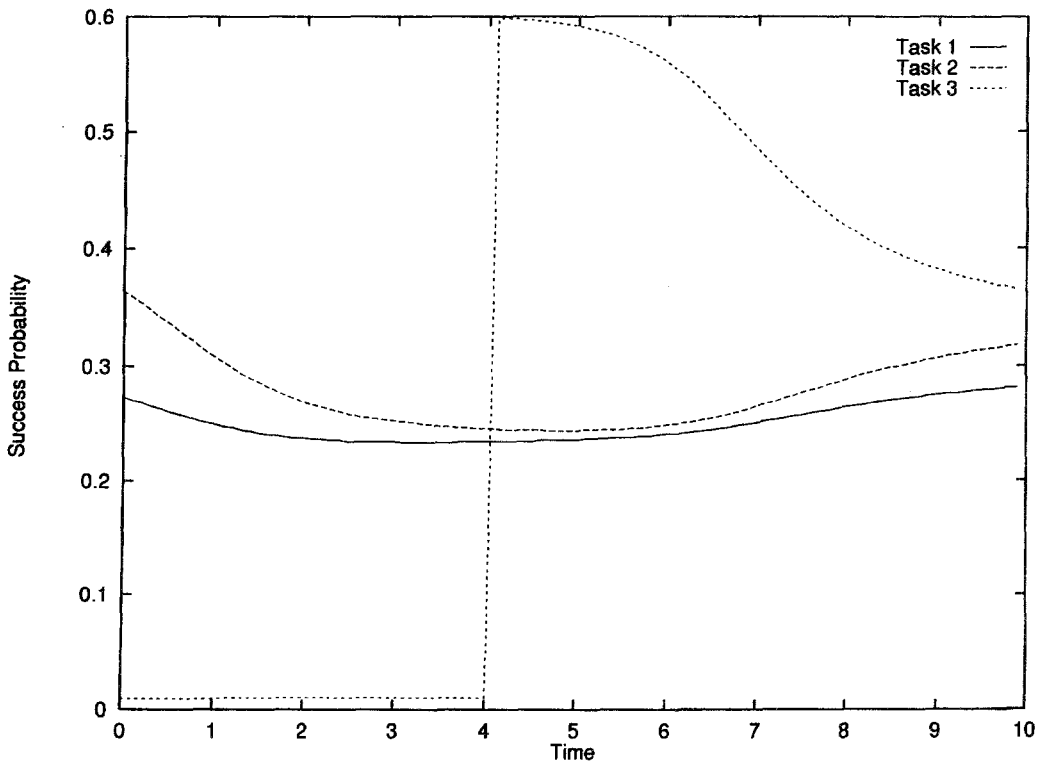
(a)
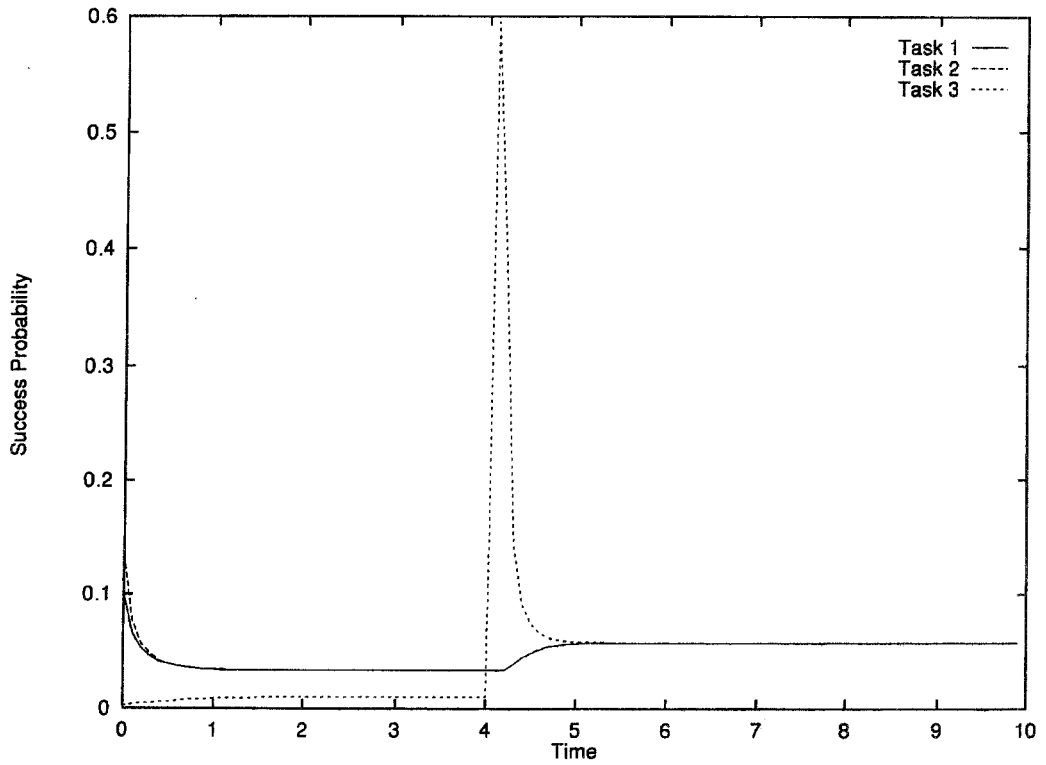
(b)

Figure 3 (continued)

(c)

(d)

Figure 3 (continued)

(e)

(f)

Figure 3 (continued)

an example using success probabilities in class III and thus corresponding to marginal rates of return and the ESS in which group fitness is maximized. To produce the figure, we assumed that s_i was given by the equilibrium of Equations 4 and 5. Three tasks were included and the initial condition was the same as in Fig. 3 (10% in each task and 70% inactive). At the beginning of the run, $\Gamma_1 = 0.3$, $\Gamma_4 = 0.4$ and $\Gamma_3 = 0.01$, but at time $= 10$, the value of Γ_3 was changed to 0.6. Also, $\mu = 1.0$, $k = 0.02$, $\tau = 0.02$ and $\alpha_1 = \alpha_2 = \alpha_3 = 1.0$. The results show that the colony devoted most of its effort to the most profitable tasks (Fig. 4a) and did not equalize the resource capture rates of individuals in tasks 1–3 (Fig. 4b), but did equalize the marginal rates of return from the three tasks (Fig. 4c).

Summary of results from the model of task allocation

We have demonstrated the following four results about the model (Equation 2).

(1) Result 1. The simple behavioural rules that underpin Equation 2 cause an equilibrium pattern of task allocation that is remarkably close to the evolutionary optimum. With success probabilities
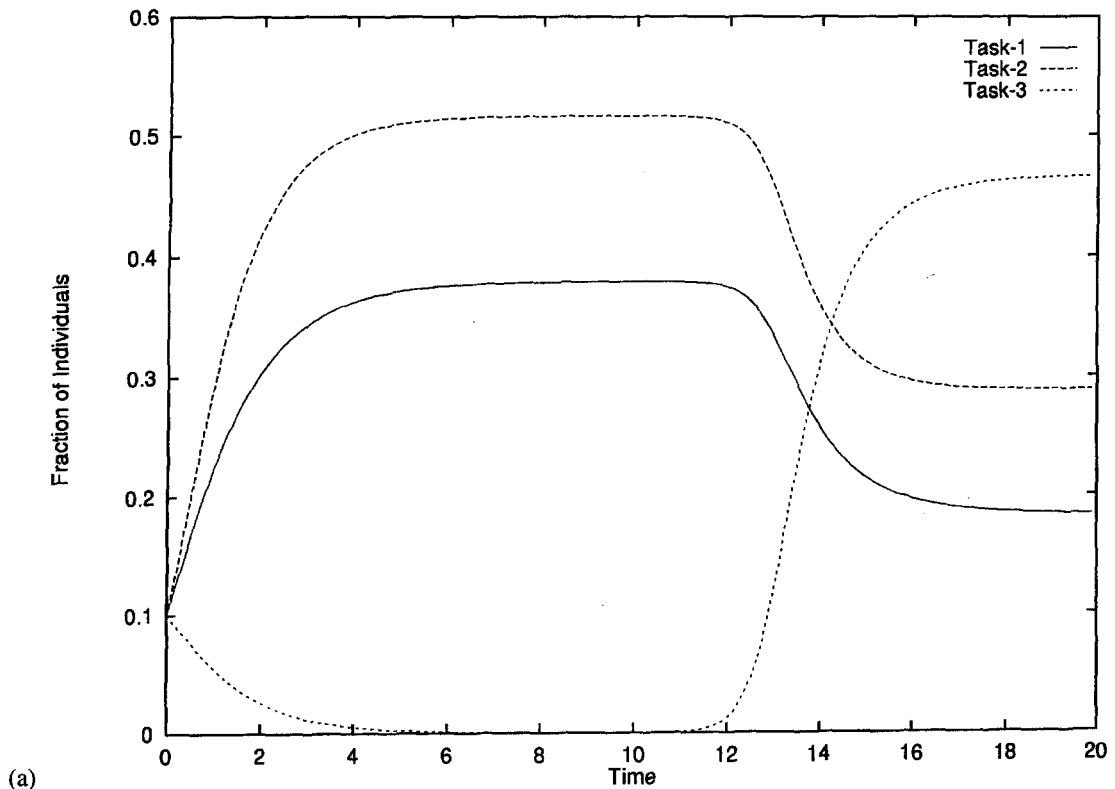

(a)

Figure 4. Interactions that equalize marginal rates of return: a numerical solution of the model in Equations 1 and 2 with class III success rates given by the equilibrium of Equations 4 and 5. Three tasks were included and the initial condition was 10% of the group engaged in each task (with 70% inactive). At the beginning of the run $\Gamma_1 = 0.3$, $\Gamma_2 = 0.4$ and $\Gamma_3 = 0.01$ but at time 10, the value of Γ_3 was changed to 0.6. Also, $I(N) = 0.1N$, $N = 100$, $k = 0.02$, $q = 0.1$, $\mu = 1.0$, $\tau = 0.02$ and $\alpha_1 = \alpha_2 = \alpha_3 = 1.0$. (a) The colony devoted must of its effort to the most profitable tasks, (b) did not equalize the prey capture rates of individuals in tasks 1–3, (c) but did equalize the marginal rates of return from the three tasks.
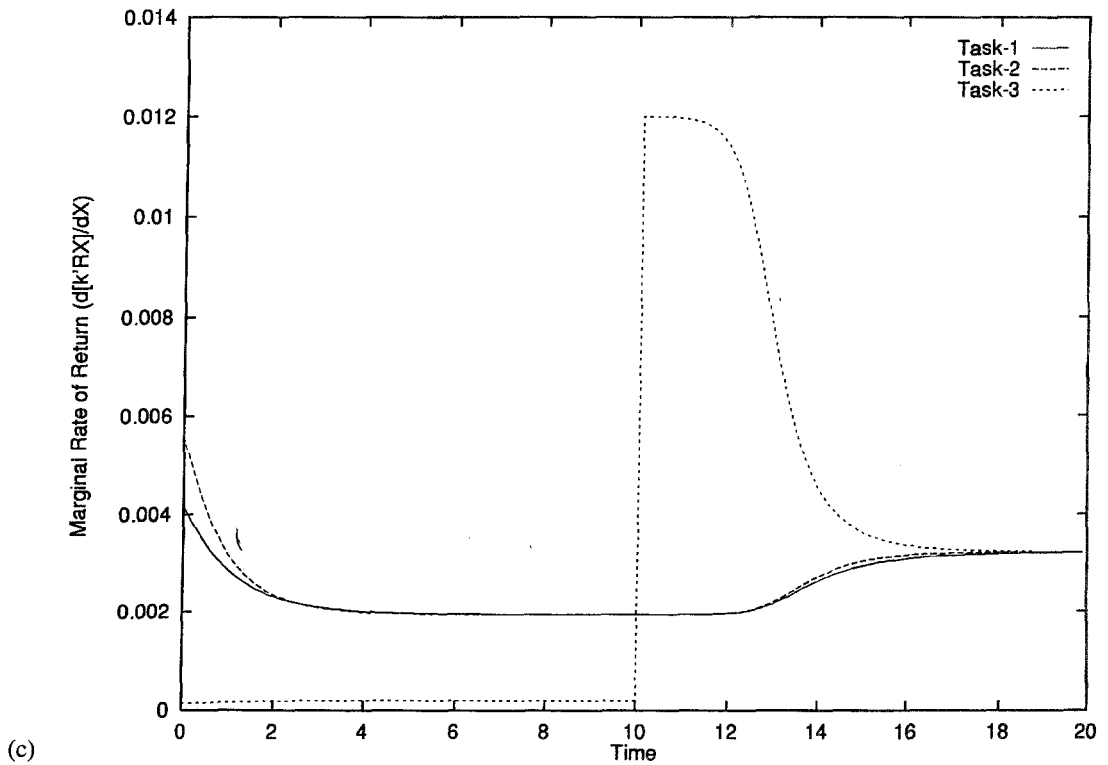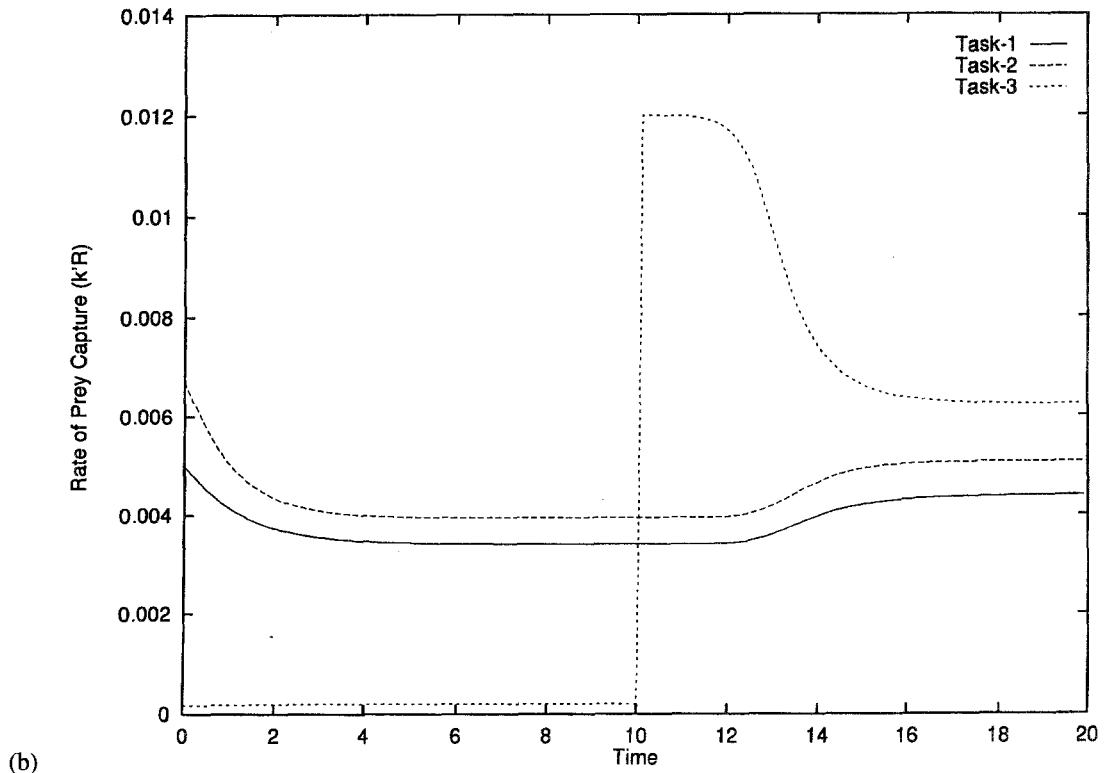
(b)

(c)

Figure 4 (continued)

in classes I or II, the task allocation approximately maximizes individual fitness and with success probabilities in classes I or III, the task allocation approximately maximizes group fitness.

(2) Result 2. If the per capita rate of social interaction increases with colony size, then large colonies generally will track a changing environment more efficiently than will small colonies. This is because increased interaction provides faster dissemination of information about new environmental conditions.

(3) Result 3. If per capita rates of social interaction increase with group size, then individuals in large groups will remain active in less profitable environments than will individuals in small groups. This dependence of activity threshold on group size is maladaptive.

(4) Result 4. The regulation of per capita rates of social interaction shown in Fig. 1 confers the advantages of large groups while diminishing the costs. The function will allow rapid response to a changing environment in colonies of even moderate size because its slope is large at small values of N. Also, because it reaches an asymptote at relatively small colony sizes, the function will permit all but the smallest colonies to cease activity at approximately the same minimum success rate, despite developmental or environmentally induced changes in colony size.

Alternative models

The model (Equation 1) is general in the sense that it may be interpreted also as a model of many different kinds of activity. Still, it is only one of an infinite number of similar models. How robust are the conclusions that we have drawn from it? In Appendix 2, we briefly outline three of the alternatives that we have investigated. The first is a model of foraging that is designed to be as applicable to some social vertebrates (i.e. colonially nesting swallows) as it is to eusocial insects. The second two are models of ants interacting via pheromonally marked foraging trails. The findings from two of the alternatives in Appendix 2 illustrate that our conclusions are robust to some changes in mathematical structure and biological mechanism. The findings from the third alternative illustrate the bounds on this claim.

Stochastic models

Many social insect colonies contain thousands of workers and it is easy to believe that deterministic models are appropriate for such large groups. How small does a group have to be before deterministic models are wildly inaccurate? Are models such as Equations 1 and 2 and the models in Appendix 2 restricted to very large groups or might they sometimes apply to groups of 100 or even ten?

To answer these questions, we examine the stochastic processes that govern groups of finite size and lead, in the limit of large colony size, to simple deterministic models like those studied above. The stochastic models are continuous-time Markov processes that describe the temporal dynamics of $P(\mathbf{X})$, the probability at time t of observing the distribution of activity $\mathbf{X}$.

For simplicity, assume first that $\mathbf{X}$ has a single element, X, describing, say, the number of active as opposed to dormant individuals. Then

$$\frac{dP(X)}{dt} = 5 = dt = P(X\text{-}1)\,F(X\text{-}1) + P(X+1)B(X+1) - P(X)\,[F(X) + B(X)];$$

$$X = (0, 1, 2, \ldots, N) \tag{11}$$

Here, $\Delta t F(X)$ and $\Delta t B(X)$ are, respectively, the probabilities that, within the time interval Δt, a colony with X active individuals moves *forward* into the $X + 1$ class or *backward* into the $X - 1$ class.

Generalizing to Q different tasks requires some additional notation. $F(X_v)$ refers to the probability of moving forward from $\mathbf{X} = (X_1, X_2, \ldots X_v, \ldots, X_Q)$ to $\mathbf{X} = (X_1, X_2, \ldots, X_v + 1, \ldots,$

X_Q). $B(X_v)$ refers to the probability of moving backward from $\mathbf{X} = (X_1, X_2, \ldots, X_v, \ldots, X_Q)$ to $\mathbf{X} = (X_1, X_2, \ldots, X_v - 1, \ldots, X_Q)$. Finally, $S(X_v, X_w)$ refers to the probability of switching from $\mathbf{X} = (X_1, X_2, \ldots, X_v, \ldots, X_w, \ldots, X_Q)$, to $\mathbf{X} = (X_1, X_2, \ldots, X_v - 1, \ldots, X_w + 1, \ldots, X_Q)$.

The Q task model consists of a separate equation for each behavioural state of the group (each way to place N individuals, regardless of order, into $Q + 1$ categories (Q tasks and one dormant state)). Each of these equations has the form

$$
\begin{aligned}
\frac{dP(\mathbf{X})}{dt} = &\sum_{v=1}^{Q} [-F(X_v) \, P(\mathbf{X}) - B(X_v) \, P(\mathbf{X})] \\
&\sum_{v=1}^{Q} F(X_v - 1) \, P(X_1, X_2, \ldots, X_v - 1, \ldots, X_Q) \\
&\sum_{v=1}^{Q} B(X_v + 1) \, P(X_1, X_2, \ldots, X_v + 1, \ldots, X_Q) \\
&\sum_{v=1}^{Q} \sum_{w=1}^{Q} S(X_v, X_w) \, P(\mathbf{X}) \\
&\sum_{v=1}^{Q} \sum_{w=1}^{Q} S(X_v + 1, X_w - 1) \, P(X_1, X_2, \ldots, X_v + 1, \ldots, X_w - 1, \ldots, X_Q
\end{aligned}
\tag{12}
$$

Clearly, the general model (Equation 12) is intractable unless either Q or N is small. In this section we focus exclusively on two simple stochastic counterparts of model (Equations 1 and 2). The first includes one active and one dormant state and the second includes two active and no dormant states. We caution that the results which follow must be interpreted in this limited context. Nonetheless, our analysis does show that deterministic models of the kind considered in the previous sections are appropriate, at least in some cases, for colonies as small as ten individuals.

Stochastic model 1

As in Equations 1 and 2, we assume that an active individual will abandon its task in time interval Δt with probability $\Delta t q(1-s)$ and that an inactive individual will be recruited with probability $\Delta t X s I(N)/N$. In the examples that follow, $I(N)/N$ equals a constant, a, as is appropriate for purely random interactions in an arena of fixed size (the extreme of no regulation). We also introduce one new feature: an inactive individual may find the stimulus to do a task, such as forage at a new food source, on its own with probability $\Delta t f$. This new feature is essential in a stochastic model because colony-wide inactivity is otherwise an absorbing state that would trap colonies in perpetual inactivity.

With these specifications, the forward and backward probabilities in Equation 11 are

$$
\begin{aligned}
F(X) &= f(N - X) + sX(N - X) a & (X = 0,1,2,\ldots,N-1) \\
F(N) &= 0 \\
B(X) &= q(1 - s) X & (X = 1,2,3,\ldots,N) \\
B(0) &= 0
\end{aligned}
\tag{13}
$$

and the corresponding deterministic model is

$$
\frac{dX}{dt} = -q(1-s)X + f(N-X) + sX(N-X)a
\tag{14}
$$

Stochastic model 2

Suppose now that there are two active classes and no inactive class and let X measure the number engaged in task 1. Also, let $\Delta t f_1$ be the probability that an unsuccessful task 2 individual independently finds (without being recruited) the task 1 stimulus, such as a new food source and switches to task 1 and let $\Delta t f_2$ be the corresponding probability for a task 1 individual finding the task 2 stimulus. Task switching caused by recruitment works exactly as in Equations 1 and 2 (unsuccessful individuals are recruited by successful individuals). Then, the forward and backward probabilities in Equation 11 are

$$
\begin{aligned}
F(X) &= f_1 (1 - s_2) (N - X) + a s_1 X (1 - s_2) (N - X) & (X = 0,1,2,....,N-1) \\
F(N) &= 0 \\
B(X) &= f_2 (1 - s_1) X + a (1 - s_1) X s_2 (N - X) & (X = 1,2,3,...,N) \\
B(0) &= 0
\end{aligned}
\tag{15}
$$

and the deterministic model is

$$
\begin{aligned}
\frac{dX}{dt} = f_1 (1 - s_2) (N - X) - f_2 (1 - s_1) X \\
+ a s_1 X (1 - s_2) (N - X) - a (1 - s_1) X s_2 (N - X)
\end{aligned}
\tag{16}
$$

Analysis

If M is the mean number of active workers in the first stochastic model, then by the definition of the mean

$$
\frac{dM}{dt} = \sum_{X=0}^{N} X \frac{dP(X)}{dt}
\tag{17}
$$

Substituting Equation 11 into Equation 17, some straightforward, but tedious, algebra leads to

$$
\frac{dM}{dt} = -q (1 - s) M + f (N - M) + sM (N - M) a - a s \sigma^2
\tag{18}
$$

where σ^2 is the variance in the number of active workers. Note that Equation 18 is identical to Equation 14 if we make the substitution $X = M$, except for the presence of a variance term. One arrives at precisely this same result if one repeats these steps for the second stochastic model. The question of the accuracy of the deterministic models, Equations 14 and 16, is thus a question of the magnitude of the effect of the variance terms.

We have examined this problem numerically and have discovered that these terms have surprisingly little effect in either model, even when colony size is small. This finding is illustrated by the numerical results in Figs 5–7.

Figure 5(a) shows typically close correspondence between the dynamics exhibited by the first stochastic model (Equations 11 and 13, solid line) and corresponding deterministic model (Equation 14, dashed line). In this example, the colony size is 100. Although the variance predicted by the stochastic model (dotted line = standard deviation of number of active individuals) is initially high because $P(X)$ was initialized with a uniform distribution, the variance collapses over time and apparently has little effect on the mean, even initially. The distribution of X in the stochastic model at equilibrium is the black histogram in Fig. 5b.

The equilibrium or stationary distribution of Equation 11 is found by setting $dP(X)/dt = 0$ for all X and rearranging to show that

$$P^*(1) = \frac{F(0)}{B(1)} P^*(0)$$

$$P^*(X+1) = \frac{1}{B(X+1)} [P^*(X) [F(X)+B(X)] - P^*(X-1) F(X-1)] \tag{19}$$

$$X = (1,2,...,N-1)$$

The stationary distribution is calculated by assuming arbitrary $P(0)$, using the recursion in Equation 19 to calculate $P^*(1)$ through to $P^*(N)$ and then normalizing so that $\Sigma P^*(X) = 1$. It is important to understand that the stationary distribution is both the *temporal* distribution of a single colony followed for a long time and the *instantaneous* distribution, after a long period of time, of a large ensemble of colonies.

Figure 5(c) shows how the equilibrium mean fraction of foragers changes as a function of colony size, using the parameter values corresponding to the dark histogram in Fig. 5b. The equilibria predicted by the first stochastic (solid line) and deterministic (dotted line) models are similar, even for a colony size of ten, despite the high equilibrium variance (dashed line = coefficient of variation (CV)). Figure 5(d) provides a similar set of relationships corresponding to the white histogram in Fig. 5b.

Finally, Figs 6 and 7 show results analogous to those in Fig. 5, but for the second stochastic model (Equations 11 and 15) and corresponding deterministic model (Equation 16). These results generally support the patterns in Fig. 5 and also illustrate one new phenomenon.

The dashed line in Fig. 6a shows that the decay of the variance in the stochastic model is slow (it eventually equilibrates at the adjacent dark square). The reason for this is that a small fraction of colonies become 'fixed' on the less profitable task. In time, individuals that are unsuccessful at this task will encounter the more profitable task and then, via social interactions, the whole colony will quickly flip to the alternative source. Note that if the two tasks are taken to represent two food sources, then this mechanism will produce the same pattern of foraging as the simultaneous stability of boundary equilibria in deterministic models such as alternative model 3 in Appendix 2 (see Fig. 9). The difference is that the pattern is temporary if caused by the stochastic mechanism.

The decay of the variance is virtually halted in the example in Fig. 7a, because the two food sources are almost equally profitable ($s_1 = 0.9$ and $s_2 = 0.89$) and the richer source is 60 times more difficult to find ($f_1 = 0.01$ and $f_2 = 0.6$). The bimodal stationary distribution (Fig. 7b) demonstrates that temporary fixation on the less profitable food source persists indefinitely at a relatively high frequency. Even in this extreme example, however, there is close correspondence between the predictions of the stochastic and deterministic models for colony sizes ≥ 100 (Fig. 7a and c).

A casual inspection of Equation 18 might lead one to predict a substantial effect of variance, especially at small colony sizes where stochastic effects should be strong. Nonetheless, the examples that we have examined show that simple deterministic models sometimes remain useful at group sizes on the order of ten individuals. This suggests that future studies of simple deterministic dynamical models of group behaviour might profitably be applied to social animals that, unlike most eusocial insects, live in small groups.

Discussion

Models of task allocation and models of interaction rates are widespread in behavioural ecology. Here we combine the two, showing how interaction rates can determine task allocation. Such models have been put to diverse uses, from studies of interspecific competition (Waser, 1984) to
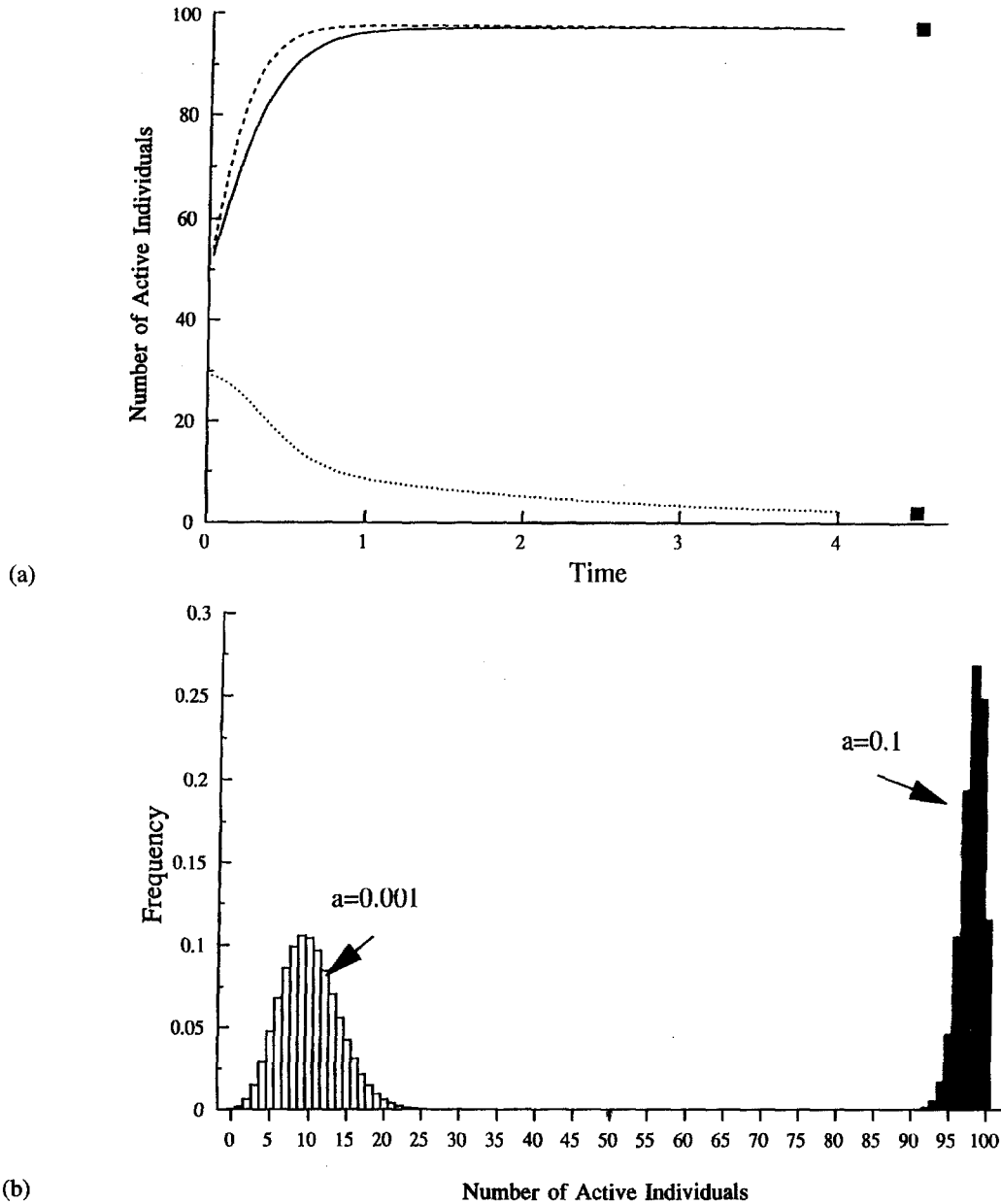
(a)

(b)

Figure 5. Dynamics of the first stochastic model (Equations 11 and 13) and corresponding deterministic model (Equation 14). In all cases $s = 0.3$, $q = 0.1$ and $f = 0.005$. (a) Solid line, stochastic model mean; dotted line, stochastic model standard deviation; dashed line, deterministic model; top solid square, equilibrium mean for both models; bottom solid square, equilibrium SD for stochastic model; N = 100; a = 0.1; stochastic models; bottom solid square, equilibrium SD for stochastic model; N = 100; a = 0.1; stochastic model initialized at a uniform distribution over [0, N]. (b) Task allocation at equilibrium (the stationary distributions given by Equation 19) for two values of a and $N = 100$. (c) Equilibria of the models as a function of colony size: solid line, stochastic model; $a = 0.1$. (d) Same as in (c) except $a = 0.001$. In all cases, note the close correspondence between the deterministic model and the mean of the stochastic model.
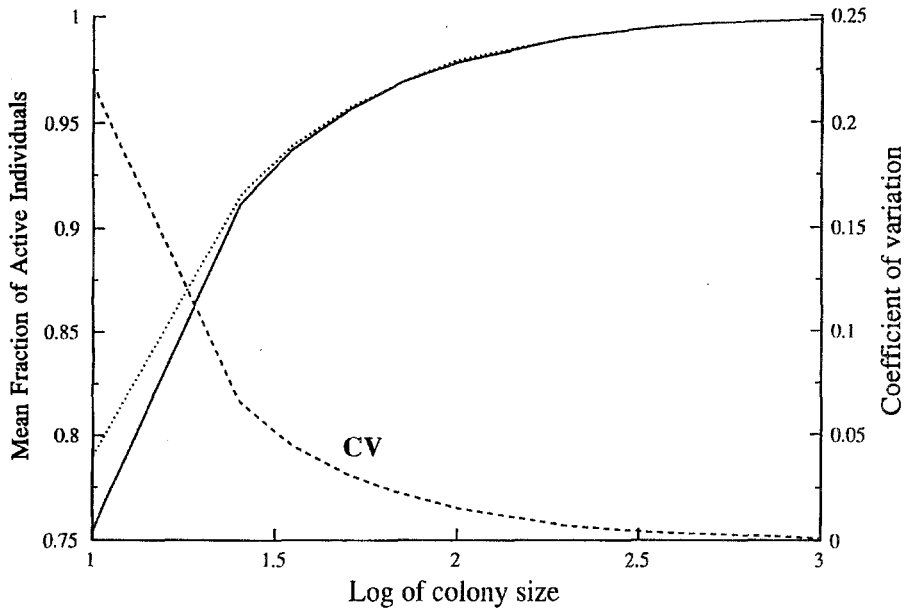
(c)
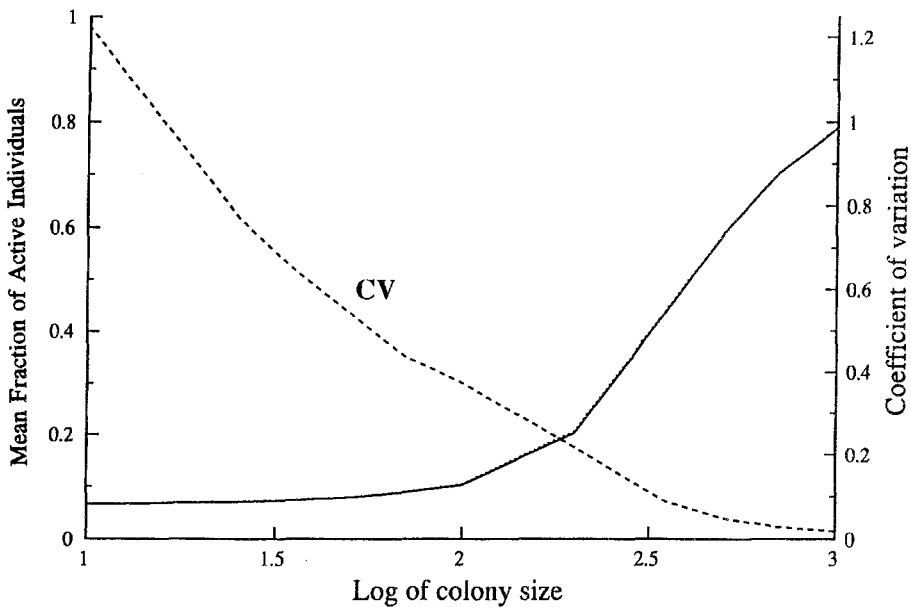
(d)

Figure 5 (continued)

studies of detailed time budgets of foragers (Caraco, 1979). Because of this diversity, it may not be generally realized how much such models have in common. Recognizing this can broaden our understanding of the dynamics of any system in which individual decisions depend in a simple way both on environmental stimuli and on interaction among individuals.

Within the literature on social insects, various models of task allocation are still viewed as unrelated because they are used to describe different behaviour. Here we show, for example, that

existing models of foraging on different food sources (Seeley *et al.*, 1991) or trail-following in an ant colony exposed to multiple food sources (Deneubourg *et al.*, 1990), are analogous to the simple model presented in the first section.

Many recent studies of social insect behaviour draw on models that involve interaction rates, though again, this common theme may not be generally recognized. Seeley's (1989) study shows that a honey bee forager's decision whether to leave the nest in search of nectar is based on the time elapsed between its arrival back at the hive from a foraging trip and its first contact with a nectar storer. Schneider's (1986) studies show that bees circulate around the hive, performing a vibration dance with other individuals they encounter and such encounters stimulate higher activity levels. In army ants, when the interaction between mature adults and young, callow workers reaches a threshold, the younger workers join in emigration (Topoff and Mirenda, 1978). Jeanne's (1987) studies of nest building in wasps show that rates of interaction among workers affect an individual's decision whether to continue building. The existence of activity cycles in the ant *Leptothorax* suggests that waves of brief interaction spread across entire colonies (Franks *et al.*, 1990; Cole, 1992), and that interactions among ants are temporally patterned, leading to 25 min cycles of movement. Robinson's studies of age polyethism (e.g. Huang and Robinson, 1992) suggest that interactions between old and young honey bees determine which tasks a worker performs.
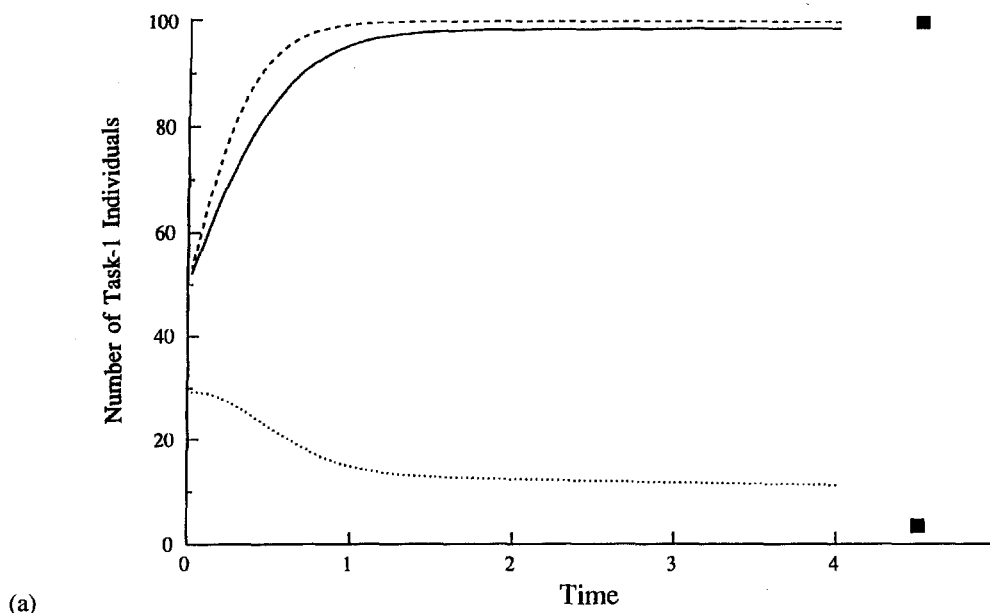

(a)

Figure 6. Dynamics of the second stochastic model (Equations 11 and 15) and corresponding deterministic model (Equation 16). In all cases $a = 0.5$, $s_1 = 0.9$, $s_2 = 0.8$ and $f_1 = f_2 = 0.005$. (a) Solid line, stochastic model mean; dotted line, stochastic model standard deviation; dashed line, deterministic model; top solid square, equilibrium mean for both models; bottom solid square, equilibrium sd for stochastic model; $N = 100$; stochastic model initialized at a uniform distribution over $[0, N]$. (b) Task allocation at equilibrium (the stationary distribution given by Equation 19; $N = 100$. (c) Equilibria of the models as a function of colony size: solid line, stochastic model mean; dotted line, deterministic model; dashed line, coefficient of variation of stochastic model. In all cases, note the close correspondence between the deterministic model and the mean of the stochastic model.

Social behaviour that depends on interaction rates can be divided into two categories: (1) an interaction leads to information transfer, affecting the decisions of individuals involved in the interaction and (2) an interaction has some inevitable, physiological effect on the participants. Of course, it is possible to find examples of behaviour at the boundary of the two types, but there are many obvious cases of the extremes. When a female worker termite interacts with a reproductive
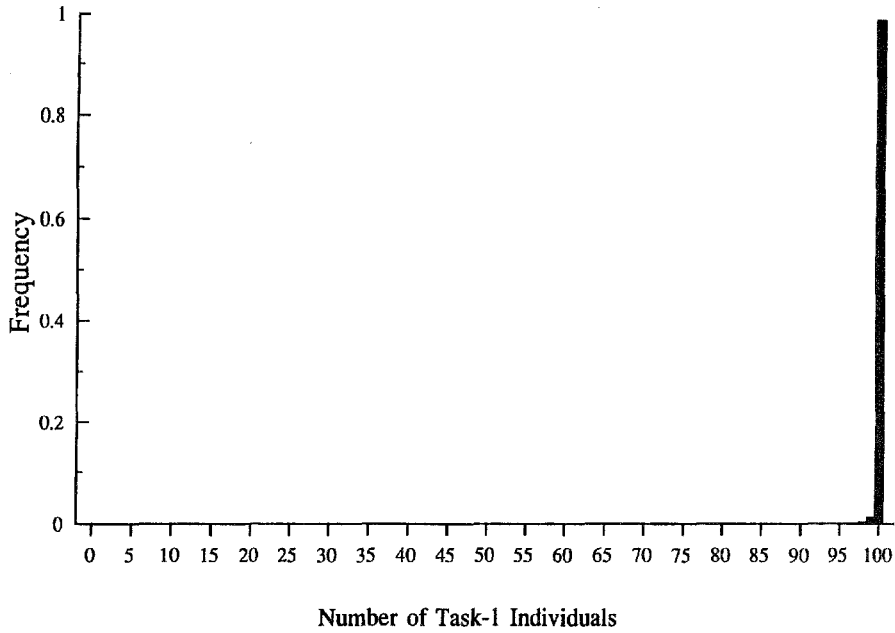
(b)
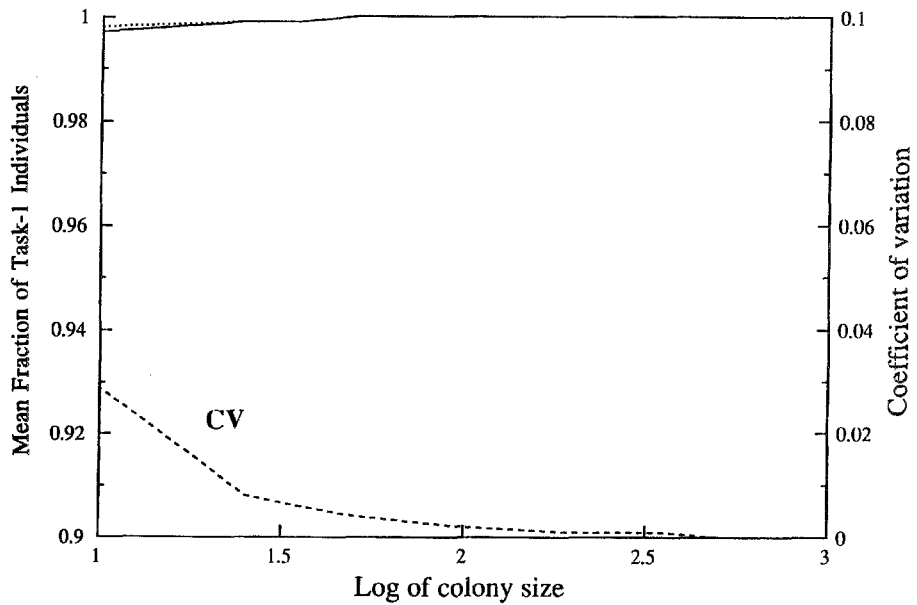
(c)

Figure 6 (continued)

female, her own reproductive system is inhibited, due to the transfer of a primer pheromone; there is an inevitable, physiological effect. In models of social behaviour that depend on interaction rates, this distinction is often built in. For example, recent models of foraging and patrolling behaviour refer to information transfer during interactions (Seeley *et al.*, 1991; Adler and Gordon, 1992); others on age polyethism suggest there may be physiological effects of substances transmitted during interaction (Huang and Robinson, 1992).

The work presented here suggests this distinction may be irrelevant to the dynamics of the group's behaviour. We may describe an exchange of information or of a physiologically active substance. Encounters may affect participants through a huge variety of perceptual, hormonal or cognitive events. We do not wish to deny the importance of understanding these events. However, the dynamics they produce will depend only on the rate of interaction and the relation of response to interaction and response to other environmental stimuli.

A general feature of a social system in which group behaviour depends on interaction rates and environmental stimuli, is that its dynamics depend on density, which in turn depends on group size. Group size has been shown to determine allocation of individuals to different tasks, such as foraging and vigilance, but this work has been concerned with finding the optimal group size to
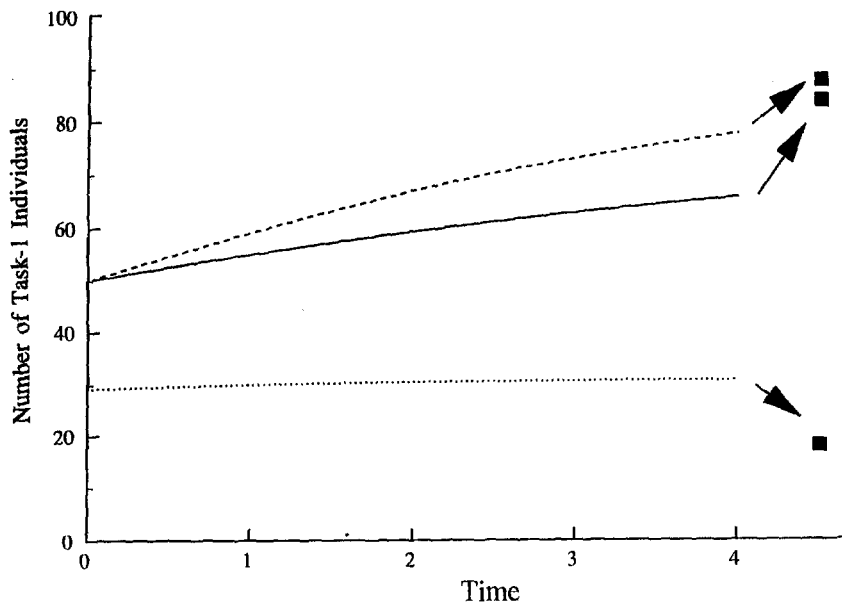

(a)

Figure 7. Dynamics of the second stochastic model (Equations 11 and 15) and corresponding deterministic model (Equation 16). In all cases $a = 0.5$, $s = 0.9$, $s_2 = 0.89$, $f_1 = 0.01$ and $f_2 = 0.6$. (a) Solid line, stochastic model mean; dotted line, stochastic model standard deviation; dashed line, deterministic model; top solid square, equilibrium of deterministic model; middle solid square, equilibrium mean for stochastic model; bottom solid square, equilibrium SD for stochastic model; $N = 100$; stochastic model initialized at a uniform distribution over $[0, N]$. (b) Task allocation at equilibrium (the stationary distribution given by Equation 19; $N = 100$. (c) Equilibria of the models as a function of colony size: solid line, stochastic model mean; dotted line, deterministic model; dashed line, coefficient of variation of stochastic model. Note the considerable difference between the deterministic model and the mean of the stochastic model for small colony sizes and the large coefficients of variation.
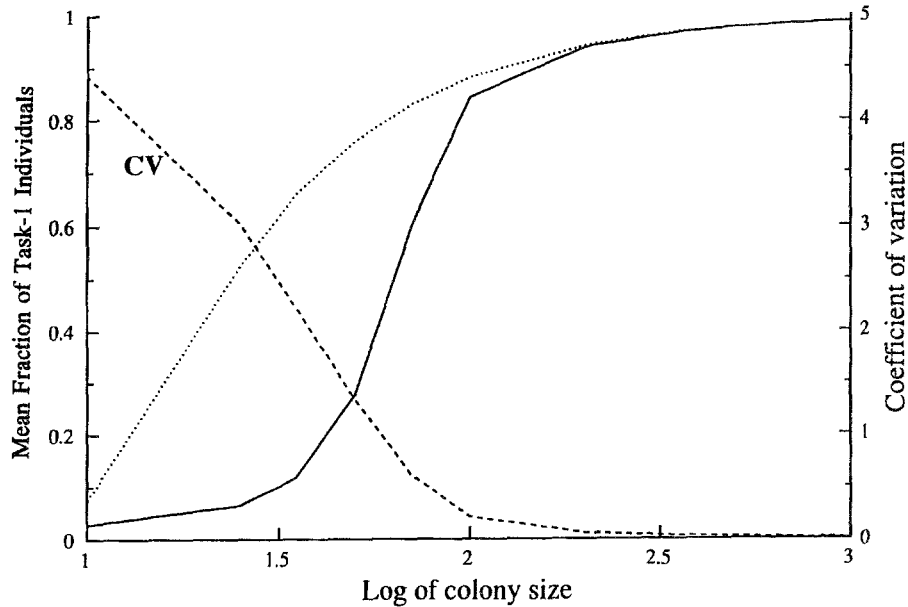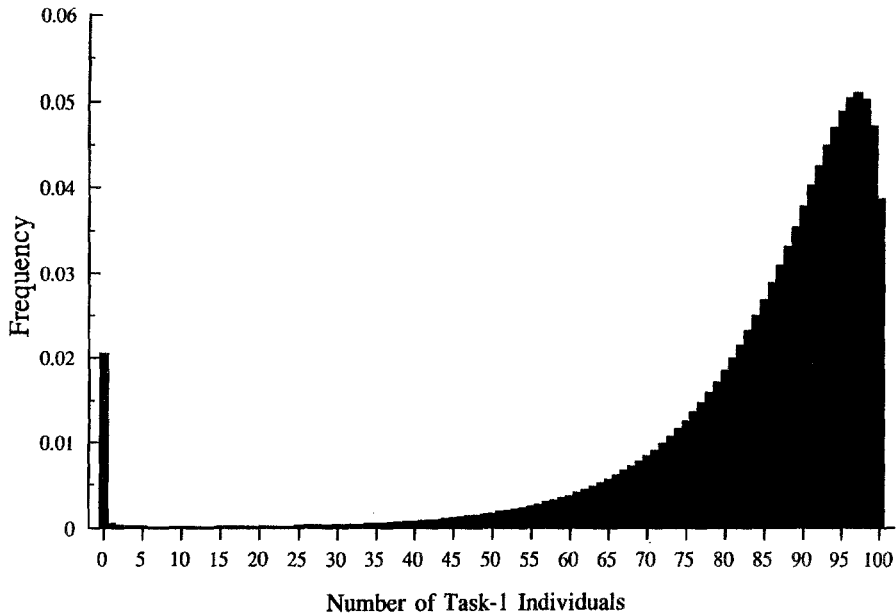
(b)

(c)

Figure 7 (continued)

maximize the intake of food by individual foragers. Here we consider how group size and density affects a group's ability to track a changing environment by changing task allocation.

Our first result about group size (result 2) is that larger groups can be more efficient than smaller ones at tracking a changing environment. If interaction rates increase with group size, then

information about new environmental conditions will be disseminated more readily in large than in small groups (see Fig. 2). In addition, as a group gets larger, the probability increases that when there is a new event, some individual will encounter it soon after it occurs (as in the first and second stochastic models). It follows that the larger the group, the more quickly it will respond to a changing environment. Assuming that the time scale of environmental change is somewhat slower than that of the group's adjustment, a larger group will more quickly tend to reach an equilibrium state in which individuals are distributed into tasks exactly as the environment requires.

However, our second result about group size (result 3) shows that large groups may experience a disadvantage. High interaction rates and more rapid information transfer may cause a large group to maintain unprofitable activities more readily than a small one. In our models, an individual's tendency to perform a task depends in part on its encounters with other individuals engaged in the task. If an unsuccessful or inactive individual encounters a worker that is successfully performing a task, it will begin to perform the task. But its tendency to continue performing the task depends on its encounters with environmental stimuli (i.e. successful location of food or failure to locate food). If interaction rates increase with group size, then, as group size grows large, the probability of encountering successful individuals increases relative to the probability of encountering an environmental stimulus. That is, as group size increases, there will be a point at which social
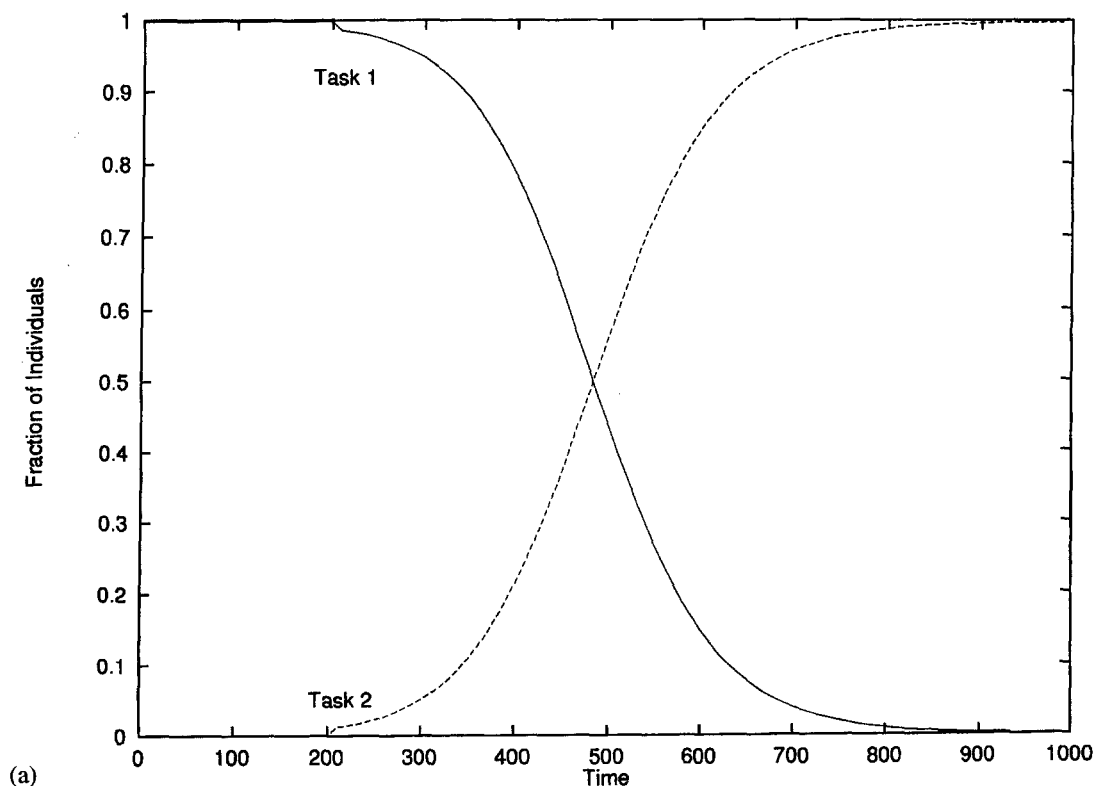

(a)

Figure 8. Effects of colony size on resource tracking in a changing environment in the model in Equation A5 of Appendix 2 (alternative model 1). In each of the three cases shown the profitability of task 2 jumped suddenly at time 200 (from $s_2 = 0.25$ to $s_2 = 0.35$). There were two tasks and colony sizes were (a) $N = 1000$, (b) $N = 100$ and (c) $N = 10$. Observe that the rate of adjustment to environmental change is approximately independent of colony size. The remaining parameters were $a = 0.1$, $q = 0.1$ and $s_1 = 0.3$.
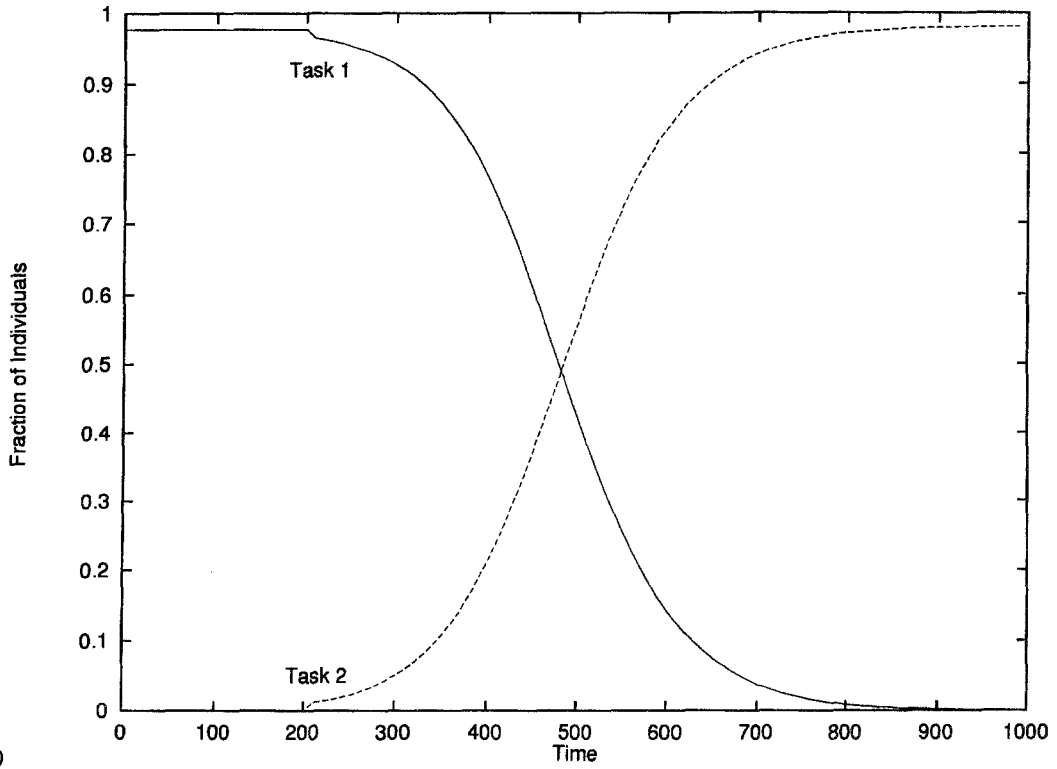
(b)
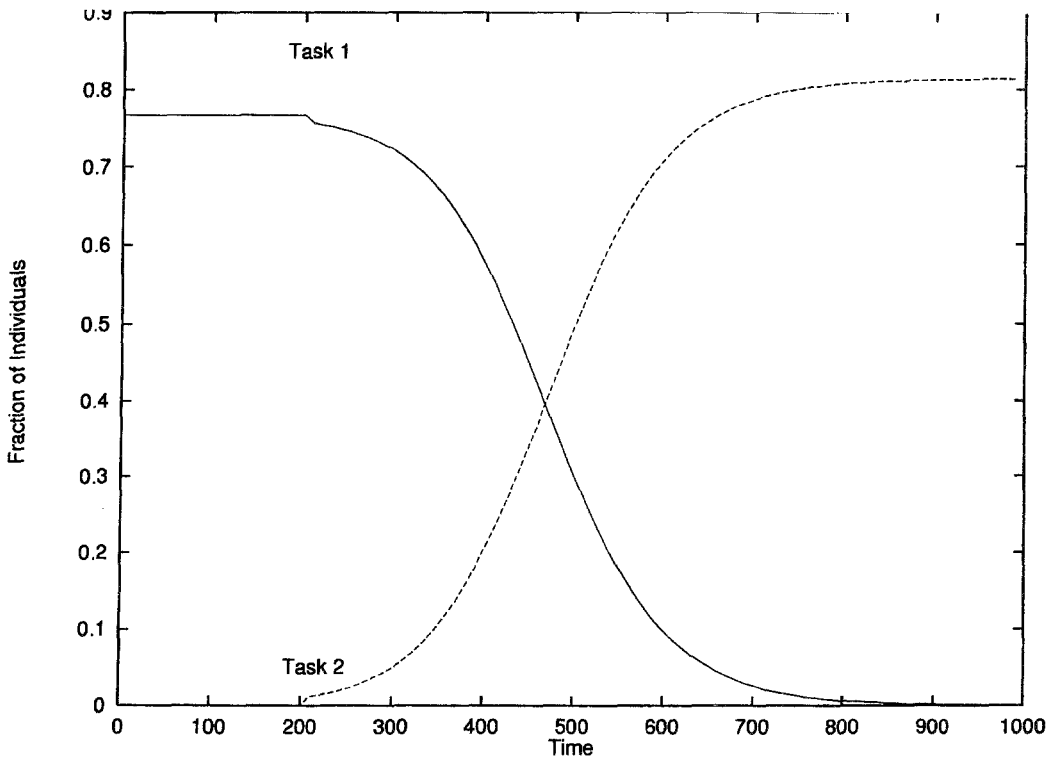
(c)

Figure 8 (continued)

encounters overwhelm environmental stimuli. At this point, individuals may be rendered active, even when they should abandon their task. For this reason, we predict that individuals should regulate interaction rates (as in Fig. 1).

An alternative to regulating interaction rates would be to develop compensating social interactions. For example, interactions with unsuccessful workers that increase one's tendency to abandon a task could balance interactions with successful workers that increase one's tendency to continue the task. A disadvantage of this system is that individuals in large groups with high interaction rates would either switch rapidly between activity and inactivity or would need to develop the ability to process information about the relative rates of different kinds of social interactions (e.g. relative rates of interaction with successful and unsuccessful individuals). In contrast, the regulation of interaction rates provides a simple and direct solution to the general problem of balancing environmental stimuli and information transfer.

A third result on group size comes from stochastic models, analogous to the deterministic ones of the first section. It might be expected that stochastic variation in the sequence and timing of encounters would dominate the outcome in small groups. However, our numerical results show surprisingly small stochastic effects. It appears that the dynamics described here occur even in small groups in the order of ten individuals. A full explanation of this will require further analytical work.

In a social insect colony, group size is a feature of ontogeny. As a colony grows older, it contains more workers. Thus, if group size affects the efficiency with which the colony responds to its environment, this efficiency will change during the life history of the colony. In temporary social groups, such as winter-feeding flocks of passerine birds, group size may depend on ephemeral conditions, such as the distribution of food. Here the effect of changing group size on task distribution will operate on a much shorter time scale. Social insect colonies and feeding flocks of birds may represent extremes; there is enormous diversity in the biological context of group size and density and in the ways that group sizes change in time and space. But many social groups may have in common similar constraints of group size on task allocation. Further investigation may show that a relatively simple principle of the dynamics of group behaviour is ecologically important: large groups can track a changing environment efficiently, but may need to regulate interaction rates.

Conclusion

The models presented here illustrate how group size affects the allocation of individuals into different tasks, when individual decisions depend both on environmental stimuli and interaction among individuals. Tasks and social interactions include (but are not restricted to) foraging on multiple food sources, nest maintenance, direct exchange of information among individuals that encounter one another, simple following of individuals by one another and trail following in ant colonies.

Figure 9. Suboptimal behaviour indicated by Equation A9 for the model of foraging trails in ant colonies (alternative model 3 of Appendix 2). There were two tasks with success rates $s_1 = 0.3$ and $s_2 = 0.4$. Initial abundances for tasks 1 and 2 were, respectively, 0.8 and 0.2 in (a) and (c) and 0.2 and 0.8 in (b) and (d). The colony sizes were larger in (a) and (b) ($N = 250$) than in (c) and (d) ($N = 100$). Note that the more profitable task is abandoned in (a) and (c) and that abandonment proceeds more quickly in the larger colony. Remaining parameters: $b = 0.1$, $q = 0.1$, $v = 1.0$, $\Phi = 1.0$ and $w = 2$.
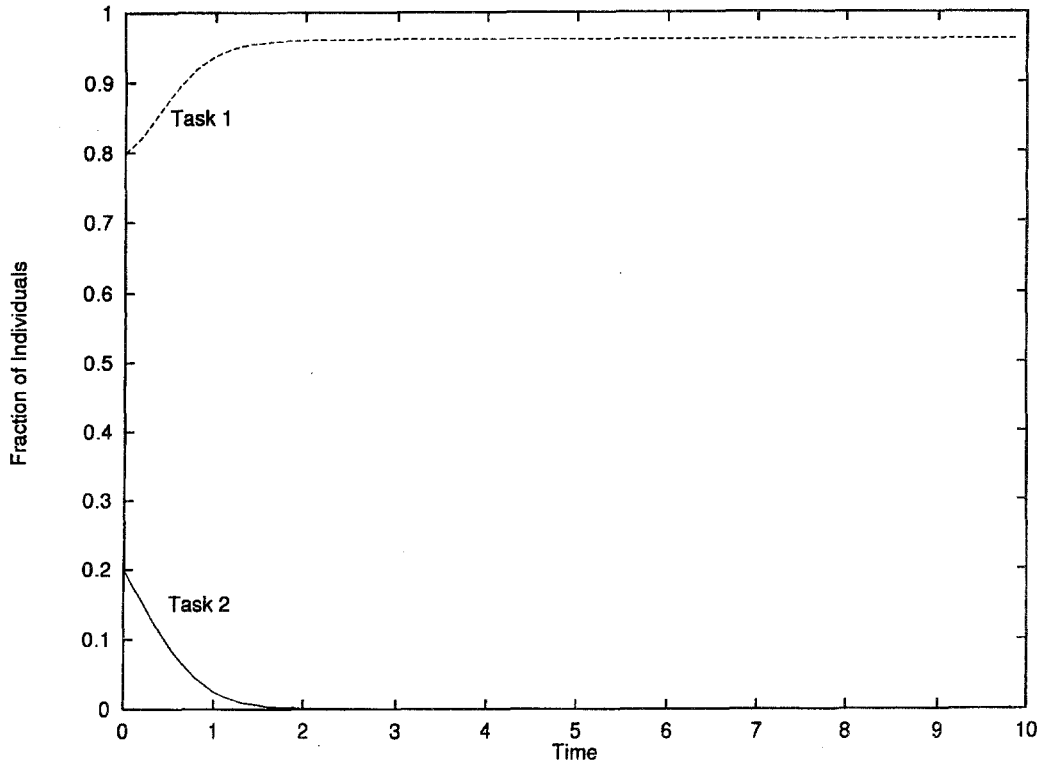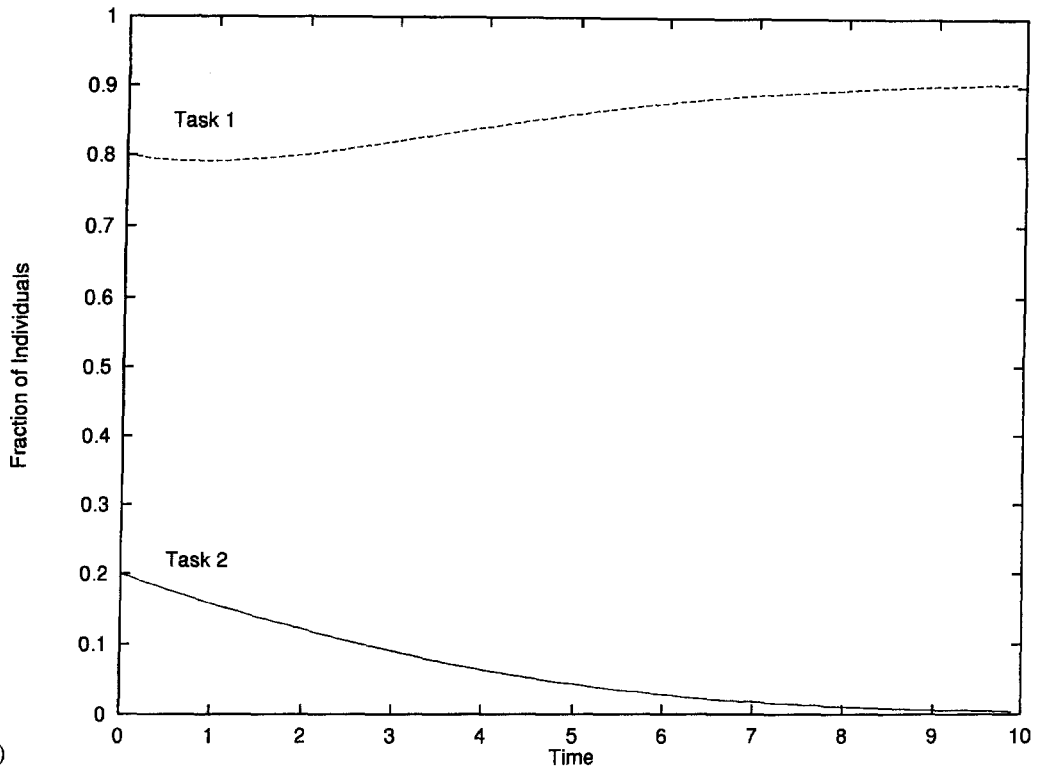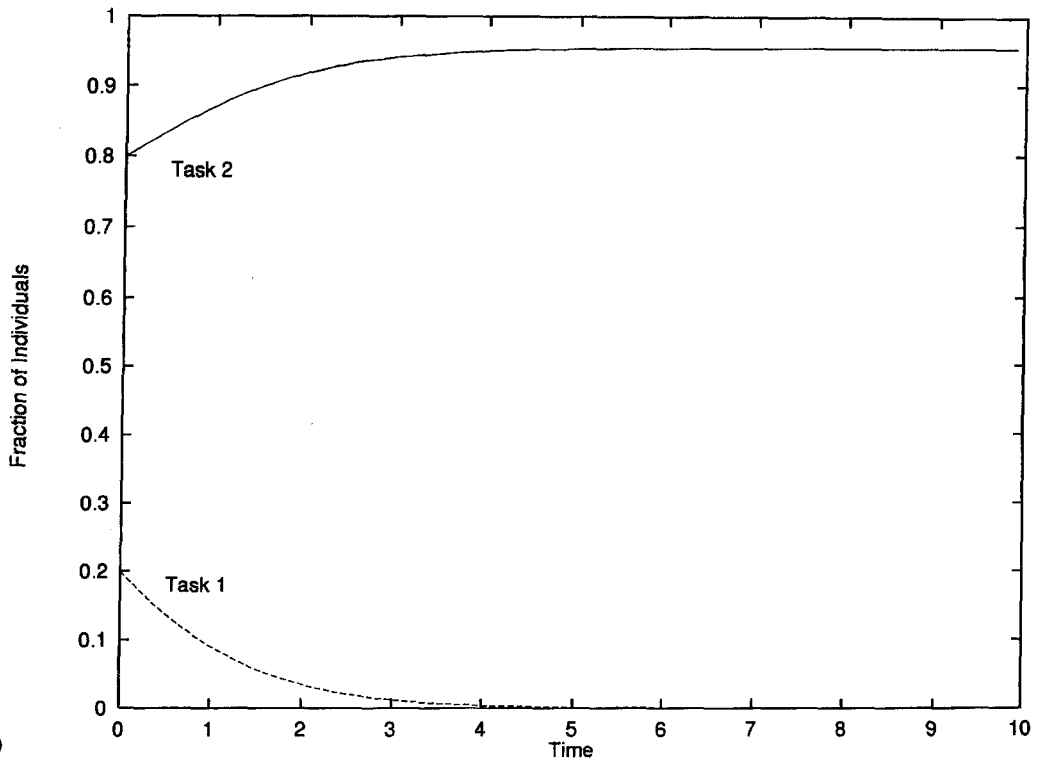
(a)
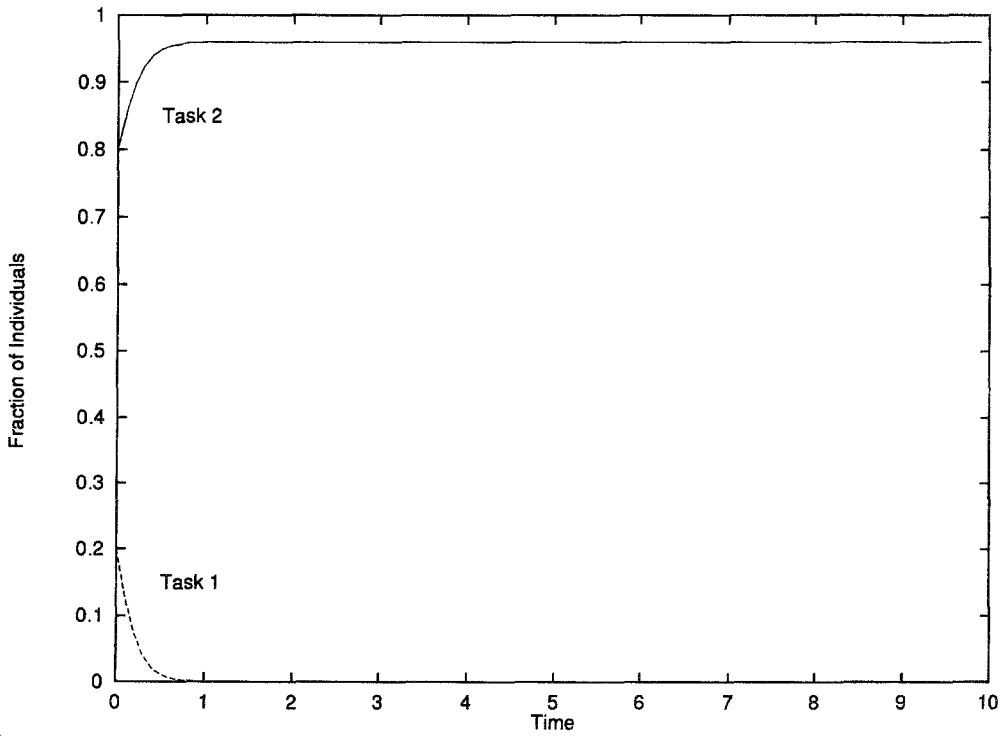
(b)

Figure 9 (continued)

(c)

(d)

Figure 9 (continued)

Analysis of the dynamics of these models shows the following.

(1) Simple interactions among individuals with limited capacity to process information can lead to group behaviour that closely approximates the ideal free distribution or the equivalent distribution that maximizes colony fitness.

(2) Larger groups can be more efficient than smaller ones at tracking a changing environment, if per capita rates of social interaction increase with group size (i.e. Figs 3 and 8).

(3) Group behaviour is determined both by each individual's interaction with environmental stimuli and by social exchange of information. To keep these processes in balance across a range of group sizes, organisms are predicted to regulate per capita rates of social interaction as in Fig. 1. Failure to do so can cause unprofitable behaviour. For example, without such regulation, high interaction rates could cause a large group to pursue unprofitable tasks more readily than a small one (i.e. Figs 2 and 9).

(4) Stochastic models show that, at least in some cases, the dynamics described here occur even in small groups on the order of ten individuals (i.e. Figs 5–7).

(5) Our results suggest that very simple mechanistic interactions between individuals are sufficient to allow the colony to maximize food intake and other quantities related to fitness. In a sense, our model colonies achieve this end by parallel processing, but it is parallel processing of a very simple kind, without the need to invoke abstract principles of the self-organization of complex dynamical systems.

Acknowledgements

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Appendix 1

In this appendix, we examine the local stability of the equilibria of Equation 2. In what follows, the subscript 'i' refers to a task that is not performed at equilibrium ($x_i^* = 0$) and 'j' refers to a task that is performed at equilibrium ($x_j^* > 0$). We suppose that there are Z tasks in the former category and Y tasks in the latter category ($Y + Z = Q$). Moreover, we label the tasks so that $j = (1, 2, \ldots, Y)$ and $i = (Y + 1, Y + 2, \ldots, Q)$.

Because the quantity $\partial(dx_j/dt)/\partial x_j$ is invariably zero when evaluated at equilibrium, the Q by Q Jacobian matrix governing the stability of the boundary decomposes into two blocks: a Y by Y block in the upper left-hand corner governing the tasks that are performed at equilibrium and a Z by Z diagonal matrix in the lower left-hand corner governing the tasks that are not performed at equilibrium. Thus, Z of the eigenvalues are simply given by the Z elements of the diagonal matrix (Equation 4 in the text).

The remaining Y eigenvalues are found as roots of the characteristic equation for the matrix in the upper left-hand corner:

$$|J| = 0 = \begin{vmatrix} A_1 + B_1C_1 & B_1C_1 & . & . & B_1C_Y \\ B_2C_1 & A_2 + B_2C_2 & . & . & B_2C_Y \\ . & . & . & . & . \\ . & . & . & . & . \\ B_YC_1 & B_YC_2 & . & . & A_Y + B_YC_Y \end{vmatrix} \tag{A1}$$

where

$$A_k = x_k^* \frac{ds_k^*}{dx_k} [q + I(N)] - \lambda$$

$$B_k = -x_k^*$$

$$C_k = I(N) \left(s_k^* + x_k^* \frac{ds_k^*}{dx_k} \right)$$

and λ signifies an eigenvalue.

We now indulge in two algebraic tricks. We first subtract B_k/B_Y times the last row in J from each kth row ($k = 1, 2, \ldots, Y\text{-}1$). We then reverse the order of the subscripts so that the subscript Y becomes 1,1 becomes Y, Y-1 becomes 2 and so on. The result is the characteristic equation

$$
0 = \begin{vmatrix} A_Y & 0 & . \; . & 0 & 0 & -\frac{A_1 B_Y}{B_1} \\ . & . & . \; . & . & . & . \\ . & . & . \; . & . & . & . \\ 0 & 0 & . \; . & A_3 & 0 & -\frac{A_1 B_3}{B_1} \\ 0 & 0 & . \; . & 0 & A_2 & -\frac{A_1 B_2}{B_1} \\ b_1 C_Y & B_1 C_{Y-1} & . \; . & B_1 C_3 & B_1 C_2 & A_1 + B_1 C_1 \end{vmatrix} \tag{A2}
$$

Now, let D_i be the determinant of the i by i sub-matrix in the lower left-hand corner of Equation A2. Thus, $D_1 = A_1 + B_1 C_1$, $D_2 = A_2 D_1 + A_1 B_2 C_2$, $D_3 = A_3 D_2 + A_1 A_2 B_3 C_3$ and

$$
D_Y = A_Y D_{Y-1} + \left[\prod_{i=1}^{Y-1} A_i \right] B_Y C_Y
$$

After expanding the above expression, we may use it to write Equation A2 as

$$
0 = A_1 A_2 \ldots A_Y + B_1 C_1 A_2 A_3 \ldots A_Y + \\ A_1 B_2 C_2 A_3 \ldots A_Y + \ldots + A_1 A_2 \ldots A_{Y-1} B_Y C_Y \tag{A3}
$$

We now divide both sides of Equation A3 by $A_1 A_2 \ldots A_y$ and rearrange:

$$
1 = \sum_{j=1}^{Y} \frac{b_j}{a_j + \lambda} \tag{A4}
$$

where $a_j = -A_j - \lambda$ and $b_j = B_j C_j$. Note that a_j and b_j are independent of λ.

Note that $a_j > 0$ unless the success rate, s_j, is independent of x_j (in which case prey availability is not affected by foraging and $a_j = 0$). Also, the b_j are non-negative unless increased numbers of individuals engaged in the jth task results in a decreased amount of the task being accomplished. This kind of over-exploitation is unlikely because it typically occurs on a time scale longer than that considered here (see the text). Thus, in most cases we expect $b \leq 0$ because $d(s_j x_j)/dx_j \geq 0$.

Case 1: $b_j \leq 0$ for all j. By inspection of Equation A3, for each $b_j = 0$, there is a corresponding eigenvalue equal to $-a_j$. Each such eigenvalue is strictly negative (see the definitions of A_k, B_i and C_k above). Now consider the remaining Ψ eigenvalues. Let us label the Ψ remaining tasks in Equation A4 (for which the b_j are non-zero) in increasing order of the values of the a_j's, so that a_1 is the smallest and a_Ψ is the largest. Note that in all generic cases, there is at most one a_j equal to zero; all others are strictly positive. Two such values would imply *constant* and *equal* success rates. By inspection of the denominators in Equation A4, the right-hand side of this equation will decrease monotonically from positive to negative infinity as λ decreases from $-a_j$ to $-a_{j+1}$ ($j = 1, 2, \ldots, \Psi - 1$). Also, the right-hand side will decrease from positive infinity to zero as λ decreases from $-a_\Psi$ to negative infinity. Thus, the remaining Ψ roots of Equation A4 are real and negative and the largest is between $-a_i$ and $-a_2$. In the important special case in which all success rates are constant, the single eigenvalue given by Equation A4 is simply equal to b_j (note that $b_j < 0$ if $a_j = 0$).

Case 2: $b_j > 0$ for at least one j. Following an argument identical to the one above leads to the conclusion that roots may be complex depending on the functional forms of the s_j. Further analytical progress is impossible (at least for us) without specifying functional forms.

Appendix 2

In this appendix, we present three alternatives to the model (Equations 1 and 2).

Alternative 1: following without direct information exchange

Suppose that, at any one time, an individual can either be inactive or can forage in one of Q places or on one of Q kinds of prey. After capturing prey, an individual returns temporarily to a central nest or colony. Let the success rate s_i be the fraction of individuals foraging on the ith food source who have recently captured prey. Also, suppose that individuals periodically cease foraging if unsuccessful, return to the nest *and then follow a forager chosen at random*. Note that this simple scenario may be applicable to some social birds or mammals (e.g. colonially nesting swallows).

A model of this scenario is

$$\frac{dx_1}{dt} = -q(1 - s_1)x_i + \left(1 - \sum_{j=1}^{Q} x_j\right)I(N)x_i s_i \tag{A5}$$

The first term on the right-hand side is identical to the 'ceasing' term in Equation 1, and the second describes the influx of new recruits into food type i. This influx is simply proportional to the fraction of potential recruits in the nest (the term in brackets) and the number of individuals returning to the nest from source i with captured prey (see Seeley *et al.* (1991) for a model of a similar scenario).

Following the same steps used to analyse Equations 1 and 2 above, it is straightforward to show that Equation A5 has exactly the same equilibria as Equations 1 and 2, each with precisely the same qualitative local stability. Thus, a very simple process of ceasing and following with no overt exchange of information about foraging success can lead to exploitation corresponding to the predictions of evolutionary optimality models. Of course, this process works because there is indirect exchange of information. Individuals in the nest are more likely to have left food sources with low rather than high success rates. Individuals that are followed are more likely to be exploiting food sources with high rather than low success rates because individuals with high success rates return frequently to the nest with captured prey.

Despite the identical equilibria of Equations 1, 2 and A5, the indirect exchange of information in Equation A5 is a poor substitute for the direct exchange in Equations 1 and 2. To see this, observe that $I(N)$ is not the per capita rate of social interaction in Equation A5, because active individuals do not interact with one another. Instead, at equilibrium, each individual engages in $q(1-s^*) - q^2(1 - s^*)^2/[s^*I(N)]$ interactions (following) per unit time, where s^* is the success rate common to all food sources pursued at equilibrium ($x_i^* > 0$). This function climbs with increasing $I(N)$ from zero at $I(N) = q(1/s^* - 1)$ to the asymptote $q(1 - s^*)$. Thus, the interaction rate is capped at a value less than $q(1 - s^*)$, no matter what the value of $I(N)$. The cap effectively prevents the rapid exchange of information that is possible in the model in Equations 1 and 2 for large groups with unregulated $I(N)$ or for any group in which $I(N)$ is regulated at a high value. The cap on information exchange occurs in Equation A5 because ceasing rates alone determine interaction rates whenever there are sufficient numbers of foragers to ensure that ceasers do not wait long in the nest before finding a successful forager to follow. Because, over a broad range of N, interaction rates are approximately *independent of colony size* (e.g. capped at the asymptote $q(1 - s^*)$), we expect little direct effect of colony size on the rate at which a colony can track a changing environment.

An analysis of the dynamics of Equation A5 following a sudden, environmentally induced change in the success rate s_i^* confirms that this is true. For example, the equations corresponding to the first and fourth equations in Equation 10 are

$$\frac{dx_i}{dt} \approx \Delta s \frac{q}{s^*} \left[1 - \frac{q\ (1 - s^*)}{s^* I\ (N)}\right] y_i^*;\ \text{if}\ x_i^* > 0$$

$$\frac{dx_i}{dt} \approx \Delta s \frac{q}{s^*} x_i + q \left[\frac{s_i^*}{s^*} - 1\right] x_i;\ \text{if}\ x_i^* = 0 \tag{A6}$$

where y_i^* is the fraction of active foragers pursuing the ith food source ($y_i^* = x_i^*/\Sigma x_j^*$) and, as before, s^* is the success rate common to all food sources such that $x_j^* > 0$. Equations corresponding to the second, third, fifth and sixth equations in Equations 10 are independent of the environmental perturbation. In contrast to Equations 10, Equations A6 shows little effect of colony size. Note that the first equation in Equations A6 reaches an asymptote as $I(N)$ increases, while the second equation does not contain $I(N)$.

Figure 8a–c illustrates three numerical solutions of Equation A5 with different colony sizes ($N = 1000$ in Fig. 8a, $N = 100$ in Fig. 8(b), and $N = 10$ Fig. in 8(c)) and $I(N) = aN$. There were two food sources present with $s_1 = 0.3$ and $s_2 = 0.25$ prior to time 200, and $s_1 = 0.3$ and $s_2 = 0.35$ thereafter. Although each colony was able to track the most profitable food source, there was no apparent effect of colony size on the rate of tracking. Note also the dynamics in Fig. 8 are two orders of magnitude slower than the dynamics in Fig. 3.

Alternative 2: foraging trails

Many species of ants recruit new foragers to a food source using pheromonally marked trails (Wilson, 1971). Typically, ants mark a trail when returning to the nest from a food source. The more heavily marked a trail is, the more recruits are stimulated to follow (Wilson, 1962).

Let s_i be the rate of prey capture in location i and suppose that s_i is constant (s_i is in class I). Also, let the concentration of the marking pheromone (P) on the trail to the ith food source (task) be governed by

$$\frac{dP}{dt} = M\ (X_i,\ s_i) - vP \tag{A7}$$

where $M(X_i,\ s_i)$ is the rate at which the pheromone is deposited by returning foragers and v is the rate at which the pheromone volatilizes. The deposition rate is a function of s_i and X_i simply because the pheromone is deposited by successful foragers on their way back to the nest.

For simplicity, assume that the time scale of pheromonal deposition and volatilization is faster than the time scale at which the X_i change. Then, the pheromonal concentration is simply given by the equilibrium of Equation A7: $P(X_i,\ s_i)^* = M\ (X_i,\ s_i)/v$. Further suppose that a fraction $U(s_i)$ of ants are unsuccessful and become inactive at rate $qU(s_i)$ and that inactive and unsuccessful ants periodically test trails at random and follow a trail (adopt a new foraging task) with a probability proportional to its pheromonal concentration. Then the model is

$$\frac{dX_i}{dt} = X_i\ qU\ (s_i) + bP\ (X_i,\ s_i)^* \left[\sum_{j=1}^{Q} x_j\ U\ (s_j) + \left(N - \sum_{j=1}^{Q} X_j\right)\right] - X_i\ bU\ (s_i) \sum_{j=1}^{Q} P\ (X_j,s_j)^* \tag{A8}$$

where b is a constant.

To see how similar this model is to Equations 1 and 2, note that the two are identical if we make the substitutions $U(s_i) = 1 - s_i$ and $M(X_i,\ s_i) = \Phi X_i\ s_i$, where Φ is a constant and $I(N) = \Phi bN/v$. Thus, the model Equations 1 and 2 and all results derived from it, also apply to at least some models of recruitment to foraging trails.

Alternative 3: foraging trails with non-linear recruitment

In an extensive series of papers, Deneubourg, Goss and co-workers (e.g. Deneubourg *et al.*, 1986, 1990; Deneubourg and Goss, 1989) have investigated models similar to Equation A8 but that have unstable internal equilibria and simultaneously stable boundary equilibria. In these models, a trail's attractiveness to potential recruits increases faster than linearly with the pheromonal concentration on the trail. Once a food source is connected to the nest by a heavily marked trail, it will continue to be exploited because the trail itself is attractive, even if richer food sources become available. The richer sources, in turn, will remain unexploited. Pasteels *et al.* (1988) have empirical evidence that this kind of what appears to be suboptimal behaviour can occur in at least some species.

For example, consider the special case of the model in Equation A8 mentioned at the end of the previous section (with $U(s_i) = 1 - s_i$, $M(X_i, s_i) = \Phi X_i s_i$ and $I(N) = \Phi b N / v$). We now replace the assumption that a potential recruit follows a trail with a probability proportional to the pheromonal concentration, $P(X_i, s_i)^*$, with the assumption that this probability is proportional to $[P(X_i, s_i)^*]^w$, where w is > 1. Thus, the attractiveness of a trail increases super-linearly with the concentration of pheromone.

Now consider the eigenvalue, analogous to Equation 9, that governs the adoption or abandonment of a task that is nearly unexploited in the vicinity of a boundary equilibrium (e.g. task i with $X_i^* = 0$). This eigenvalue is

$$\lambda_i = -q\,(1 - s_i) - bs_i \sum_{j=1}^{Q} (x_j^* s_j)^w\, [N\,\Phi\,/\,v\,]^w \tag{A9}$$

Because the above eigenvalue is negative, the *i*th food source will never be exploited no matter how rich it is, if a colony has first become fixed on an alternative food source. Moreover, because the eigenvalue in Equation A9 decreases as colony size increases, this clearly suboptimal tendency will often proceed at a greater rate in large rather than in small colonies.

Figure 9(a)–(d) illustrates the behaviour of Equation A9 for the case of two food sources with success rates $s_1 = 0.3$ and $s_2 = 0.4$ and colony sizes $N = 250$ (Fig. 9a and b) and $N = 100$ (Fig. 9c and d). Initial abundances on food sources 1 and 2 were, respectively, 0.8 and 0.2 in Fig. 9(a) and (c) and 0.2 and 0.8 in Fig. 9(b) and (d). Note that the richer food source is abandoned in Fig. 9(a) and 9(c) and that the rate of abandonment is greater for the larger colony.