Insectes Sociaux

Review article

Worker connectivity: a simulation model of variation in worker communication and its effects on task performance

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Abstract. We develop a simulation model of worker connectivity to analyze how variation in worker communication can influence task performance. The model generates predictions about how colony demography, worker communicative behavior, and worker cognition will affect the rate of recruitment of workers to a new task. The model explores some mechanisms for modulating the recruitment of workers. Under the conditions of our model– probabilistic interactions that lower worker's response thresholds to tasks– worker recruitment follows a logistic growth pattern. The rate of recruiting workers increases exponentially toward an inflection point when 50% of the available force has been activated, then decreases toward the upper asymptote (all workers recruited). Many relevant features of colony design and worker behavior, including group size, probability of interacting, and strength of interaction effects on receivers, show a positive but decelerating effect on the rate of worker recruitment. We also identify features of worker cognition that can influence task recruitment, focusing on the time course of worker's memories about previous interactions. Both learning (e.g., sensitization) and forgetting about previous interactions can influence the rate of worker recruitment to a task. The model suggests that worker cognition may be shaped by natural selection on task performance at the colony level. Forgetting about interactions may be especially costly, because it leads to unpredictable patterns of worker recruitment. We also show that social inhibition, when coupled with excitatory interactions, can effectively modulate worker recruitment at the colony level.

Keywords: Cognition, division of labor, network models, polyethism, recruitment, task allocation.

Introduction

Task allocation is the process of assigning workers in a colony to perform different duties, and this process is thought to be critical to colony fitness (Oster and Wilson, 1978; Gordon, 2003). Therefore, we can expect task allocation to evolve in response to natural selection on colonies. Patterns of task allocation can be affected by intrinsic characteristics of the workers, and by information about the relative levels of need for different tasks (O'Donnell and Bulova, 2007). There is increasing interest in analyzing task allocation in insect societies by applying tools from social network analysis, and other network approaches (Page and Mitchell, 1998; Beshers and Fewell, 2001; Fewell, 2003; Newman, 2003). Network models focus on the transmission of information within a group, such as an insect colony, and on the ability of group members (nodes) to affect each other's behavior.

In social insects, network models generally treat the workers as nodes, which are connected to each other via communicative interactions (edges), although Fewell (2003) recently suggested that tasks can also be treated as nodes (also see Gorelick and Bertram, 2007). Previous network models of task allocation have assessed how a colony's workers can be effectively distributed among several different tasks. These models emphasize that worker information sharing plays an important role in the allocation of labor among tasks (Gordon et al., 1992; Pacala et al., 1996; Page and Mitchell, 1998; Detrain et al., 1999; Naug and Gadagkar, 1999). However, the earlier models do not explore how the characteristics of information transfer among workers affect the recruitment of workers to tasks. In this paper we extend these models by analyzing the variable nature of worker communication itself. Where appropriate, we use terminology from the network analysis literature (Newman,
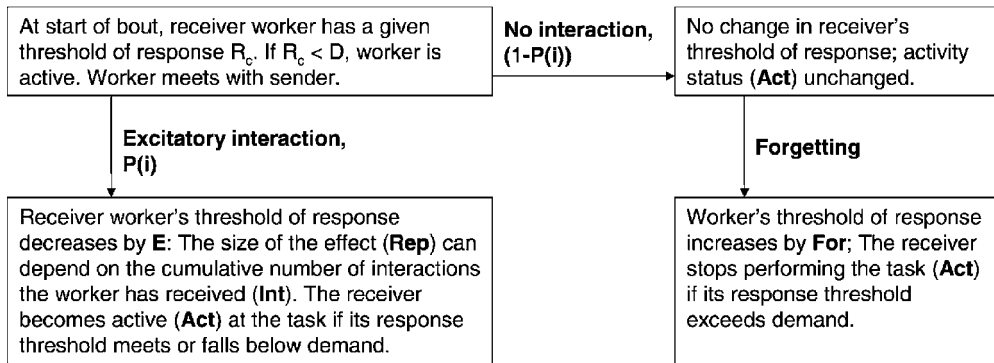
| At start of bout, receiver worker has a given threshold of response R_c. If $R_c < D$, worker is active. Worker meets with sender. | **No interaction, (1-P(i))** | No change in receiver's threshold of response; activity status (**Act**) unchanged. |

Excitatory interaction, P(i)

Forgetting

| Receiver worker's threshold of response decreases by **E**: The size of the effect (**Rep**) can depend on the cumulative number of interactions the worker has received (**Int**). The receiver becomes active (**Act**) at the task if its response threshold meets or falls below demand. | | Worker's threshold of response increases by **For**; The receiver stops performing the task (**Act**) if its response threshold exceeds demand. |

Figure 1. Flow diagram, and list of parameters and parameter values for simulation model of worker connectivity.

Parameters and values of the simulation model of worker connectivity.
Parameter values for the example analyses shown in the figures are given in parenthesis, and were constant unless noted otherwise.

Global (colony) Variables	Definition/description
N_t	Total number of workers; size of the task group or colony (Nt=25)
T	Elapsed number of bouts of interaction; limit is set at start of run (Limit=100 for figures)
N_a	Number of workers active at the end of bout T
D	Level of demand for task in arbitrary units (D=50)
G	Number of groups of workers, with a set number of workers assigned to each group

Individual (worker) Variables	Definition/description
R_i	Initial threshold of response for workers in each group in arbitrary units, the same units as for demand D (R_i=75)
R_c	Worker's current threshold of response within a bout
P(i)	Probability of interacting when in the sender role (P(i)=2%)
E	Interaction effect, when worker is in the receiver role, amount its response threshold is reduced by an interaction, in arbitrary units, the same units as for demand D and threshold R (E=1). Note that when interactions are inhibitory, the threshold is increased by this amount.
Act	Binary variable: whether worker is active at the task in a given bout; worker is active when $R_c < D$
Int	Cumulative number of communicative interactions worker has experienced
Rep	Amount by which E changes upon repeated interactions
For	Forgetting; amount by which worker's response threshold increases if it does not interact in a given bout, in arbitrary units, the same units as for demand D, threshold R, and Interaction effect E.

2003). Through a simulation model, we predict how variation in some major characteristics of information transfer will affect task performance. We discuss the predictions of the model in light of empirical findings on worker communication and task performance (O'Donnell and Bulova, 2007) and we use the predictions to identify new areas of research on worker connectivity.

A simulation model of worker connectivity

We treat insect colonies as networks, where nodes (workers) are connected to each other through edges (social interactions). Much of the network modeling literature focuses on developing metrics that describe complex networks. Our major aim is different: to contribute to the understanding of how colony (network) behavior will be affected by the properties of its edges and nodes. This has been identified as a major remaining goal of network analysis (Newman, 2003). Our model explicitly quantifies the effects of varying the patterns of information transfer on task performance (Fig. 1). The model explores how variation in communication influences one important aspect of task allocation: the rate of recruiting workers to a task. We assume that this would affect colony fitness, because it would influence the amount of work done per unit time, and/or the probability that a given task would be completed within a certain time window (Myerscough and Oldroyd, 2004; Thomas and Framenau, 2005).

We employed a response thresholds approach to simulating worker behavior (Bonabeau et al., 1996;

Theraulaz et al., 1998; Beshers et al., 1999; Myerscough and Oldroyd, 2004). For each worker, the response threshold is the colony's level of demand for task performance to which the worker will respond by performing the task. If the colony's task demand is below a worker's threshold, it will be inactive at that task; if the demand equals or exceeds a worker's threshold, the worker will become active and perform the task. Factors that lower a worker's threshold consequently increase the probability that it will perform the task. In our model, workers are active as long as their thresholds are lower than or equal to task demand. Response thresholds in workers are thought to include a combination of intrinsic, relatively static components such as genetic effects (Robinson and Page, 1989; Mailleux et al., 2005), and flexible components (Beshers et al., 1999; Fewell and Bertram, 1999; Weidenmueller, 2004). We assume that worker communicative interactions influence their group mates' response thresholds. We use the model to explore how changes in response thresholds affect variation in work output at the individual and colony levels.

Methods

Model design

The original computer code is available upon request from the authors. The model is individual based, and the simulated workers are characterized as either active or inactive at a task (Fig. 1). Changes in the number of active workers in the social group is tallied as a measure of recruitment of workers to a task. As the model runs, workers encounter their nest mates one at a time, with one worker acting as a potential information sender and the other as a receiver during each encounter. The simulation runs in discrete time steps or bouts. During a bout, the model cycles through all of the potential senders in a fixed order. When they are active as senders, the workers communicate at random, with a fixed probability, with the nest mates they encounter. Not all encounters result in communication. When communication does occur, the senders lower the receiver's threshold of response by a set amount; in other words, senders increase the probability of task performance by receivers. We set limits on the range of changes in thresholds of response, such that communicative interactions cannot cause workers' thresholds to fall below zero.

At the start of the simulation, a fixed level of task need is designated for the group of workers (Fig. 1). This constant represents the level of demand for a given task, against which workers' response thresholds are compared. The number of workers in the group is set. Each simulated worker is assigned to a behavioral category. The group can include a single category of workers wherein all act as senders, or there can be two categories of workers with one category acting as senders, and the other only as receivers, of information. Because the colony level of work demand is constant, changes in worker behavior are caused only by communicative interactions among workers, or by forgetting about previous interactions.

During a bout, inactive workers can remain inactive, or they can become active as a result of communicative interactions with nestmates. Worker communication is assumed not to affect task performance. In the simplest form of the model, the workers that are already performing the task remain active. This form of the model simulates only the process of recruitment to a task, and is used to analyze factors that affect the rate of recruitment. We explore other processes by which workers' thresholds can increase, leading them to cease task performance, later in the paper. At the end of each bout, the model tallies and reports the number of workers that are performing the task, i.e., the

number of workers whose response thresholds are at or below the work demand. The main dynamic output variable of the model is the number of workers performing a task during a given time interval.

To simulate forgetting, when a worker failed to interact during a bout, its threshold was raised by a set amount, counteracting the excitatory effects of previous interactions. We limited the effects of forgetting, such that a workers' threshold of response could not exceed its initial set value. Forgetting effects were set to zero for most all runs of the model.

We explore the effects of manipulating key model parameters on the rates of activating workers. We present the results of these manipulations and the predictions they generate about recruitment to tasks in real colonies, and we discuss features of real insect colonies that the model parameters could represent. For each level of each parameter that we varied, we ran the model ten times, and we calculated the mean and SD of model output values. We analyzed the fit of model output data to various functions using the regression wizard tool in Sigmaplot 9.0.1 software (SYSTAT Software Inc., Richmond, CA). Significance tests for differences in model output were made using SAS 9.1.2 software (SAS Institute, Cary, NC).

Results and discussion

Key variables that influence worker connectivity

Colony design: size of the component

In social network models, a component is a group of interacting individuals. In our model, the component can represent an entire colony. Alternatively, it can represent a subset of the worker force that is more likely to communicate with each other about task needs. Examples of components within colonies include morphological or age castes, or the workers that occupy an isolated area of the nest. The model predicts that the number of workers in the component will dramatically affect worker recruitment (Fig. 2). All else being equal, the transmission of information about task needs proceeds more rapidly in larger interacting groups because interacting with more potential senders in a given bout increases the chances that a receiver's threshold of response will be reduced. Similar conclusions about colony size effects were drawn from network models of task switching (Pacala et al., 1996).

A general finding of our model is that the rate of worker recruitment to tasks has a logistic (sigmoidal) growth form. For example, in the analysis of colony size effects, all three values of colony size plotted in Fig. 2 (for n=25, 20, and 100 workers: all $R^2 \geq 0.998$, all p<0.0001) conform to a three parameter logistic growth model of the form:

$$y = a/1 + e^{-(x-xo/b)}$$

where:

y = Cumulative number (or proportion) of workers recruited to the task

a = Asymptote, usually the total number of workers available in the group

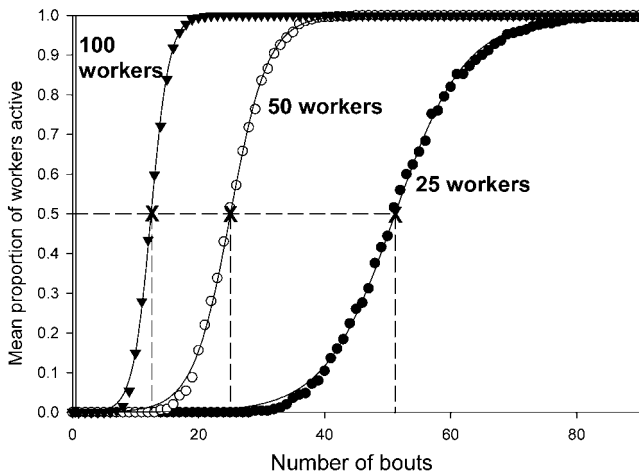b = Curve shape/slope parameter

Figure 2. Workers are recruited to the task more rapidly as colony size increases. For each value of group size, the mean proportion of the workers that have been recruited to the task is plotted for successive time intervals (bouts of interactions in the model). The estimated logistic growth model parameters were, n=25 workers: b=5.5, xo=51.1; n=50 workers: b=3.0, xo=25.1; n=100 workers: b=1.4, xo=12.5. The dashed horizontal line represents 50% worker recruitment, and vertical dashed lines indicate the value of logistic function parameter xo, the inflection point at which half of the workers have been recruited.

xo = Inflection point of curve; point where 50% of available workers have been recruited

The rate of recruiting workers to a new task (workers activated/bout) increases exponentially up to the inflection point xo, then the rate of recruitment begins to decelerate as the asymptote (all workers recruited) is approached. As group size increased, the time to reaching the inflection point (50% worker recruitment) decreased, and the curve rose more steeply (i.e., the logistic curve shape parameter b decreased) (Fig. 2). For the analysis of other model parameters we use the time (in bouts) to reaching the inflection point, when 50% of the workers are recruited, as an index of relative overall rates of worker recruitment under different model conditions.

Worker behavior: degree- the number of edges per node

In network models, degree refers to the number of edges (connective links) that a node makes with other nodes (Newman, 2003). If degree is *sparse*, any given worker interacts with only a small proportion of its nestmates. When degree is *extensive*, workers interact with most or all of their nestmates. In our model, degree is affected by two parameters. One is the proportion of the worker force that act as senders. The other is the probability that a sender will interact with nestmates in a given time bout.

The model predicts that rates of worker activation will be higher when interaction probabilities increase (Fig. 3). The increase in recruitment rate with interaction strength declines as interaction strength goes up (R^2=0.996,

$p < 0.0001$). This means that recruitment rate is affected more strongly by changes in interaction strength at low values. The decrease best fits an inverse first order function, with the formula $y = y_0 + a/x$, where y_0 is the limit of the minimum time to recruiting 50% of the workers. The second order term was not significant when added to the model, and the fit to a negative exponential model was significantly poorer (results not shown). Along with the logistic pattern of worker recruitment, the positive but decreasing (inverse first order) effect of connectivity variables on the recruitment rate was seen in all parameter manipulations, and is a general prediction of our model.
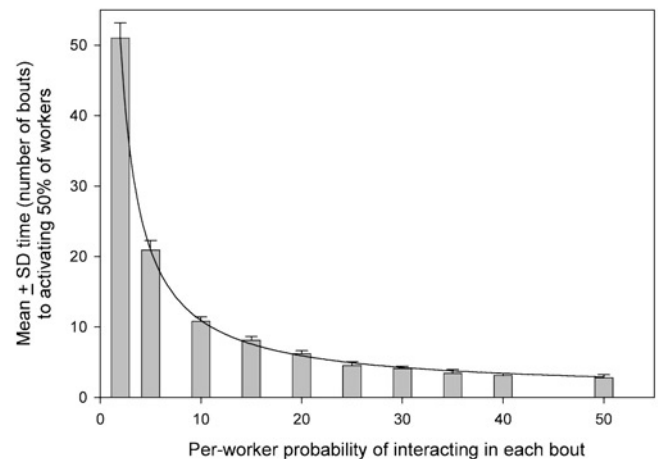

Figure 3. Workers are recruited more quickly when the probability of interacting increases. The bar graph presents the mean + SD time (number of bouts of interactions) elapsed to recruiting at least 50% of the worker force. The line graph plots the first order inverse function of the effect of interaction probability on rate of worker recruitment, fitted to the simulation data, illustrating the decreasing magnitude of the effect of interaction probability on recruitment. All similar graphs in the paper use the same format.

Active workers fail to communicate

Additional limits on interaction rates can be imposed by task performance itself. For example, foragers that are absent from the nest collecting materials, and more generally workers that are engaged in performing tasks, may not be available to participate in social interactions to communicate task needs. We modeled this limitation on communication by preventing the active workers from interacting as senders in the simulation. Doing so led to a decrease in the rate of recruitment of workers to the task. This is one means by which recruitment to a task could be regulated at the colony level (Fig. 4).

The model also predicts that the proportion of workers that function as senders will positively affect the rate of activating nestmates (Inverse first order regression; R^2=0.997, $P < 0.0001$; Fig. 5). However, in the extreme case, even a single catalytic adult can transmit information effectively throughout the colony (Fig. 6). The rate of
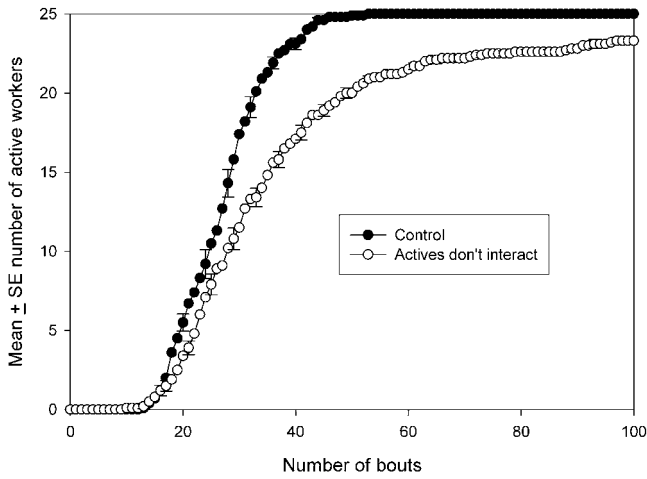
Figure 4. Preventing the active workers from interacting modulates the rate of recruitment of workers. The graph plots the mean ± SD cumulative number of active workers during successive time intervals (bouts of interactions). All similar graphs in the paper use the same format.

worker activation by a single catalytic nestmate depends on both the strength and probability of its interactions with its nestmates (results not shown). With a fixed number of senders, the time to recruit 50 % of the workers is constant across colony sizes ($F_{1,38}=1.08$, $p=0.31$; Fig. 6). This suggests that larger colonies can achieve comparable rates of worker recruitment (relative to colony size) without investing in greater numbers of senders, as long as the senders can transmit information effectively. A constant proportion of senders leads to faster recruitment of workers in larger colonies (Fig. 2).
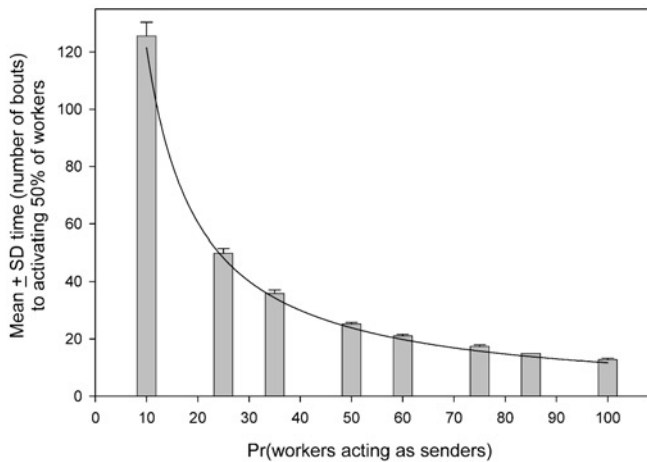

Figure 5. Workers are recruited more quickly if a larger proportion are acting as information senders. In this simulation there are two groups of workers, only one of which interacts as senders (the sender group represents a varying proportion of the colony).
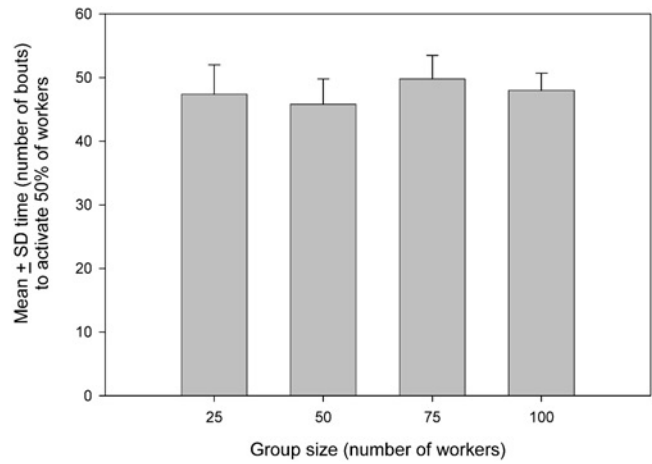

Figure 6. Given a constant number of senders, the mean time required to recruit 50 % of the workers is constant across colony sizes.

Worker behavior: strength of interaction effects on receivers

The model shows that the strength of interactions can affect the recruitment of workers to perform tasks. Stronger interactions recruit workers to tasks more rapidly (Inverse first order regression, $R^2=0.989$, $p<0.001$; Fig. 7). We know of no data on eusocial insects that address how workers' responses to a recruitment stimulus change when the stimulus is repeated, but these results suggest that cognitive factors that affect worker responses are important to understanding task allocation. Some relevant considerations are whether interaction effects increase when they are repeated (sensitization), and if so, how the effects are compounded over time and across repetitions (Anderson and Ratnieks, 1999b; Fernandez et al., 2003). When a receiver experiences sequential interactions, are the effects on behavior constant, additive (linear increase in effect), or multiplicative (geometric increase in effect)? To model this, we compared rates of worker recruitment under three conditions. (1) All interactions were equal in intensity. (2) For a given receiver, each subsequent interaction increased in effect by one unit, to simulate linear sensitization. (3) For a given receiver, each subsequent interaction was multiplied by the number of interactions, to simulate geometric sensitization. Predicted recruitment rates were affected by receiver sensitization ($F_{2,27} = 48.2$, $p<0.0001$; Fig. 8), and our model therefore implicates receiver cognition in worker recruitment. We predict that cognitive mechanisms that set the time course of worker responses to task-related communication will be under colony-level selection.
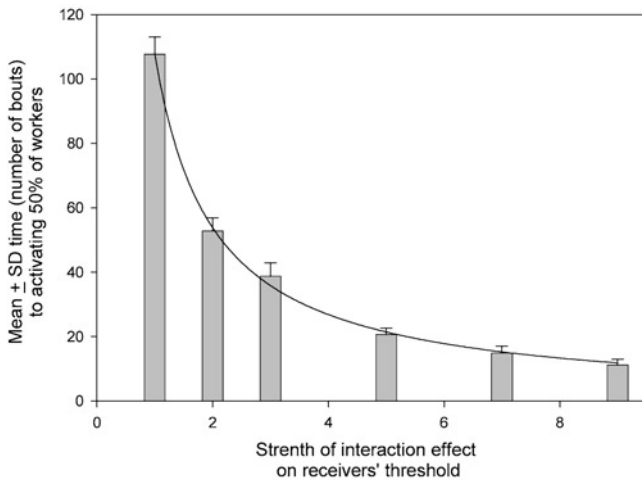
Figure 7. Workers are recruited more quickly when the strength of the recruitment signal increases.
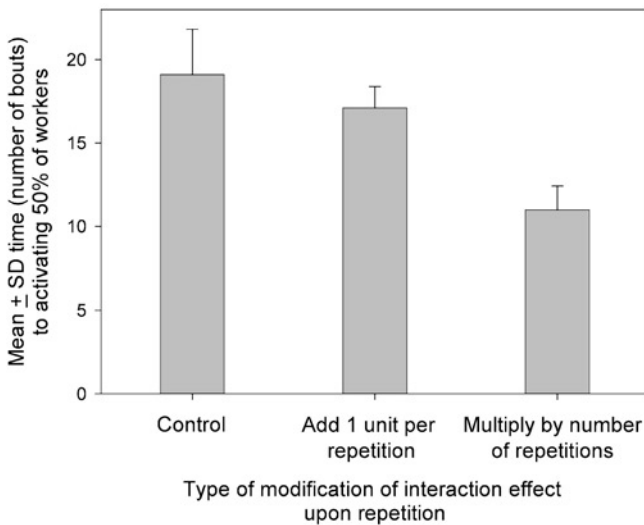

Figure 8. The process of sensitization: the strength of interaction effects on receivers increases as they experience repeated interactions. Sensitization leads to faster recruitment of workers to a task, and multiplicative sensitization effects are stronger than additive effects. In this example interaction effect = 5.

Modulating worker recruitment: the effects of forgetting or signal decay

Forgetting is another cognitive process that could affect connectivity. The process of forgetting in our model can be interpreted as representing a cognitive process, or alternatively as representing decreases in the effectiveness of the communicative signals themselves over time (e.g., the evaporation of a volatile pheromone). The simulation predicts that forgetting will have strong but variable effects on worker recruitment (Fig. 9). In general, workers are recruited more slowly as the strength of forgetting increases, but the output of the model was unstable, especially at higher forgetting strengths. In

several runs, all of the workers were temporarily inactivated, although work demand remained constant. We predict that reliance on forgetting will lead to unpredictable patterns of worker recruitment, and that forgetting by itself is unlikely to be employed to adjust the colony's worker recruitment.
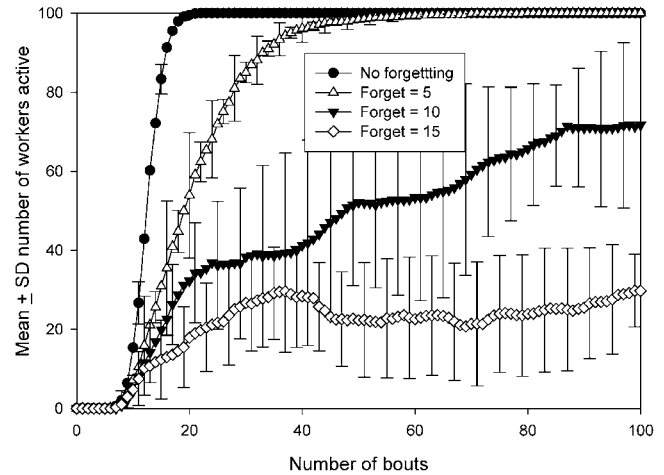

Figure 9. Forgetting about previous interactions modulates the rate of worker recuitment, and can prevent the entire worker force from being recruited. In this example colony size = 100.

Modulating worker recruitment: social inhibition

Social inhibition refers to communicative interactions that decrease, rather than increase, task performance in recipients. We simulated social inhibition by the recruited workers that are actively performing the task. When the active workers are senders in the social inhibition version of the model, they raise (rather than lower) the recipient's threshold of response, while the workers that are not performing the task can still act as excitatory senders. The simulation shows that inhibition by active workers can be an effective means of regulating worker recruitment to tasks (Fig. 10). When we increased the strength of inhibition relative to the strength of excitatory interactions, the rate of worker recruitment declined. Not all workers were recruited when the active workers inhibited task performance. Similar patterns of regulation of recruitment were seen when workers experienced forgetting, but forgetting effects were relatively erratic (compare the width of the error bars in Figs. 10 and 11). Based on these results of our model, we predict that regulation of worker recruitment is more likely to be achieved by inhibitory interactions among workers than by the cognitive decay of interaction effects within workers. Organization of multiple tasks at the colony level probably requires negative feedback, such as social inhibition, to brake recruitment to each task (Bonabeau et al., 1997).
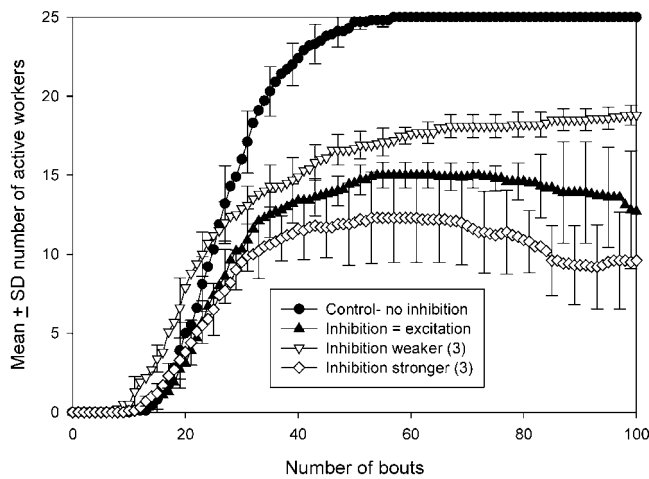
Figure 10. When active workers inhibit task performance in the nestmates they communicate with, they modulate the rate of recruitment of workers and can prevent the entire worker force from being recruited.

Limitations of the simulation model

In our model, worker activation does not affect the level of demand for the task. The model is therefore most appropriate to understanding the early stages of recruitment of workers to meet a new task demand, or recruitment to a task where the level of demand persists after workers are recruited. An alternative way of interpreting the model is that worker interactions change the internal state of readiness of workers to perform a task, altering the size of the pool of workers that are available to perform the task. This interpretation of worker activation was employed by Gordon et al. (1992, also see Beshers et al., 1999). In this case worker recruitment would be a two stage process, requiring social interaction followed by exposure to the task need. Alarm recruitment in some aculeate Hymenoptera follows this pattern. Alarm pheromone sensitizes or alerts the workers, which then attack and sting if exposed to relevant visual stimuli from natural enemies (Breed et al., 2004).

The model does not treat the relationships among tasks, and it does not distinguish workers that are recruited away from other tasks from the activation of idle workers. In real colonies, worker effort that is recruited to one task may affect the performance of other tasks. At the individual worker level, the model does not address how thresholds for various tasks interact (Beshers et al., 1999). Labor linkages among tasks may be a central component to understanding colony-wide task dynamics (Fewell, 2003; Gordon, 2003).

All changes in response thresholds are dependent on worker interactions, and therefore the model does not accommodate the possibility of learning and other forms of self-reinforcement following repeated task performance (Plowright and Plowright, 1988). Communicative interactions occur as a random process in the model. There are few data to assess whether this is a reasonable reflection of real interaction patterns. Naug and Gadagkar (1999) developed a model of division of labor in paper wasp colonies that was based on random interactions. The model accurately predicted the flexible, age-related division of labor that is observed in *Ropalidia marginata* colonies. However, some interactions are likely to be directed toward particular classes of receivers in insect colonies. An obvious example is dominance interactions, which are by definition directed preferentially to certain nestmates. Dominance interactions are widespread in insect societies, and often affect division of labor (Doorn, 1987; Hillesheim et al., 1989; O'Donnell, 1998; Heinze and Oberstadt, 1999; Powell and Tschinkel, 1999). In *Polybia* paper wasps, some workers are targeted for biting by nestmates more often than expected by chance, and biting induces foraging behavior in recipients (O'Donnell, 2001, 2006).

Workers in real colonies may alter their behavior so that they are more likely to be recruited, for example, by moving to areas where they are likely to contact senders. In some species with complex nest architecture, certain areas of the nest serve as locations for worker interactions. Honey bee foragers unload food materials to nestmates, and recruitment dances are usually performed near the nest entrance. Potential dance followers congregate in this location (Winston, 1987).

Conclusions

A fundamental pattern of worker recruitment in our model is that the rate of worker activation has a logistic growth form. If connectivity has the properties that are simulated in our model– iterative, probabilistic interactions that lower recipient's response thresholds to tasks– then we predict that the rate of worker recruitment should follow a logistic pattern for a wide range of tasks in many species.

We also found evidence that several modifications of worker communication (active workers failing to recruit and social inhibition), and of worker cognition (forgetting about previous interactions), can limit the recruitment of workers to tasks. This shows that competition for labor among tasks is not necessary to modulate the rate of worker recruitment, or to limit the number of workers to a task.

How does connectivity evolve? We have shown that a number of factors- group size, the degree of connection among workers, and the strength of interaction effects- can independently affect the rate of recruitment of workers. There are multiple evolutionary pathways by which worker cognition, colony demography, or nest architecture could change to affect division of labor among workers. Whether and how these different aspects of connectivity interact is a comparative question that has received little attention, and whether these factors are free to vary independently in real colonies is poorly understood. Our model suggests that each of these factors

shows positive but exponentially decreasing effects on the overall rate of recruitment. At high variable values, this pattern may buffer colonies from undesirable changes to the rate of worker recruitment. However, once high values are achieved, further adjustments to the rate of worker recruitment will be difficult to attain without altering another variable. It is important to bear in mind that increasing the rate of recruitment to a task is not always adaptive (Pacala et al., 1996). Some tasks may be better addressed by a gradual build up, or require few workers. Rapid recruitment to one task may disrupt the performance of another. We expect the components of worker connectivity that we identify to be optimized for each task within a species, at levels that produce task-appropriate worker activation rates.

Acknowledgements

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