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Review article

Worker connectivity: a review of the design of worker communication systems and their effects on task performance in insect societies

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Abstract. Within-group communication is a fundamental feature of animal societies. In order for animal groups to function as adaptive units, the members must share information such that group mates respond appropriately to each others' behavior. One important function of social communication is to affect the allocation of tasks among group members. Theoretical and empirical findings on a diverse array of social insect taxa show that interactions among workers often play important roles in structuring division of labor. We review worker interactions that regulate division of labor in insect societies, which we refer to as *worker connectivity*. We present a framework for synthesizing and analyzing the study of worker connectivity. The widespread reliance on worker connectivity among eusocial insect taxa and the diversity of communicative mechanisms used to recruit workers suggest that the nature of worker interactions has evolved by natural selection. We suggest that colony-level selection acting on variation in task allocation has been an important force in the evolution of mechanisms for worker connectivity. We also propose that there are important links between individual worker cognition and task allocation at the colony level. Evolutionary changes in the cognitive aspects of worker responses may affect task allocation as much as changes in the communicative signals themselves.

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

Introduction

At any point in time, an insect colony is confronted with an array of distinct tasks that need to be performed, including foraging, brood care, and nest maintenance. Division of labor among the workers in eusocial insect colonies involves individual specialization on tasks. However, because colonies and their environments are dynamic, task needs change over time, and adaptive division of labor must accommodate worker behavioral flexibility. To meet new labor demands, workers that are already active at a given task can adjust their rate of performance. New workers can also be recruited to perform a task, either from inactivity or away from other tasks. Summed across the worker population, the amount of worker effort allocated to different tasks is expected to track changes in colony needs (Oster and Wilson, 1978; Seeley, 1989).

Workers that take on new tasks may perceive an increased colony need for those tasks directly (Pratt, 1998, 2004). Alternatively, communication among workers can transmit information about colony needs for tasks (Sachs, 2004). There is increasing interest in analyzing communication in animal groups using social network approaches (Gordon, 1996, 2003; Bonabeau et al., 1997; Fewell, 2003). Insect colonies often exhibit "swarm intelligence": adaptive decisions are made by the group, rather than the individual, and these decisions are based largely on worker interactions (Schmickl and Crailsheim, 2004). O'Donnell (2006) proposed the term *worker connectivity* to refer to communicative interactions that link a colony's workers in a social network and affect task performance. The goal of this review is to synthesize recent research on worker connectivity, with the aim of identifying relevant features of worker communication that affect task performance at the group or colony level.

Connectivity may not be inherently advantageous, and in fact, it may entail some costs relative to the workers relying on direct perception of task needs. Signaling itself can incur costs to senders, such as time, energy, and metabolically expensive chemicals (Detrain et al., 1999; Dechaume-Moncharmont et al., 2005). Erroneous information transfer may impose additional costs to colonies. For example, senders may incorrectly assess the level of colony need for a task, and activate other workers to perform unneeded labor. Selection on worker connectivity should lead to an adaptive balance between the colony's fitness costs of worker communication on the one hand, and its fitness gains from more efficient or reliable division of labor on the other.

What are the adaptive advantages of connectivity? Why might we expect workers to rely on communication, rather than on their own direct assessment of colony need for labor? We propose that there are three major classes of adaptive advantages to worker connectivity.

(1) Connectivity can allow the sharing of information among more workers, and across greater distances, than direct perception of task stimuli. Direct worker experience of a task stimulus is not necessary when workers can communicate. Information can propagate across space and time via sequential worker interactions. The signals and displays that workers use to communicate with nestmates may be able to transmit farther, faster, or to more individuals than the cues used in direct perception of task needs. Connectivity can be especially valuable if there is task partitioning, when a complex task involves subroutines that are performed by different workers (Jeanne, 1986a; Seeley and Tovey, 1994; Anderson and Ratnieks, 1999a, 2000). Communication among the workers that are performing the different subroutines of a partitioned task may be necessary for efficient completion of the job (Jeanne, 1996; Anderson and Ratnieks, 1999b; Karsai and Wenzel, 2000; Grüter and Farina, 2007). Similarly, performance of certain tasks (for example, foraging away from the nest) can remove some workers from the stimuli for other task needs. Communication with nestmates may be necessary to alert these occupied workers of changes in colony needs (Schmickl and Crailsheim, 2004).

(2) Connectivity may function to push workers into undesirable tasks, or to overcome task inertia. In species where direct reproduction is an option for workers, the workers may tend to avoid performing tasks that reduce their direct fitness (West Eberhard, 1981). There can be dominance aspects to connectivity in these species (O'Donnell, 1998a,b; Markiewicz and O'Donnell, 2001). Dominance interactions may induce workers to perform tasks that are costly to their survival or energy stores (O'Donnell and Jeanne, 1995; Toth and Robinson, 2005). For example, foraging often entails high energy expenditure and elevated risk of mortality, and subordinate workers often forage (Reeve and Gamboa, 1987; Doorn, 1987; Heinze and Oberstadt, 1999; Powell and Tschinkel, 1999). However, even in species where worker reproductive conflict is weak or absent, there may be a need to overcome task inertia. Task inertia may occur for two opposing reasons. First, successful task performance can favor repetition of that task, in a positive feedback pattern akin to job satisfaction (Plowright and Plowright, 1988). Task fixation may increase workers' efficiency at performing a task, but fixated workers may be resistant to switching to new tasks (Johnson, 2002). These workers may need to be recruited via worker interactions. Conversely, in a pattern that might be termed task burnout, workers may tend to become inactive after repeatedly performing the same task, possibly due to physiological stress. As a plausible example, *Polybia occidentalis* foragers sometimes become inactive, apparently taking days off from foraging although they are rarely observed performing other tasks (Jeanne et al., 1988; O'Donnell and Jeanne, 1992). Worker interactions may be necessary to induce task switching for fixated nestmates, or to maintain activity after extended task repetition, respectively.

(3) There may be supervisory or catalytic individuals that possess relatively complete information about colony-wide labor demands (Fewell, 2003). Although it is often assumed that insect societies are not hierarchically organized, empirical evidence suggests that certain individuals can be in a position to more accurately assess colony needs for certain tasks, or to more accurately assess the relative needs for different tasks. Queens in smaller colonies, or workers that patrol the nest or its surroundings in larger colonies, may assess the level of need for one or more tasks (Reeve and Gamboa, 1987; Breed et al., 1992; Hughes and Goulson, 2001; Gordon, 2002). When this is the case, the better informed individuals can play a catalytic role (Robson and Traniello, 1999), interacting with nestmates and increasing the likelihood that their less informed nestmates will respond appropriately to changing colony needs.

In this paper we review empirical examples of aspects of worker connectivity. We identify some aspects of connectivity that are poorly understood and should be targets for future research. We identify some of the key variables that influence the patterns of information flow within colonies. Where appropriate, we use terminology from the network analysis literature (Newman, 2003), and we propose new terminology for some characteristics of worker connectivity.

Key variables that influence worker connectivity

Degree

In network models, the interacting individuals are referred to as nodes. In models of insect colonies, the workers are usually treated as nodes (but see Fewell, 2003). 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. Newman (2003) illustrates some patterns of the degree of connectivity in real and model social networks.

One important factor in the degree of connections in an insect colony is the probability that workers will interact with each other. The probability of interaction in an insect colony could be adjusted by changes in the general activity level and movement rate of the workers (Cao et al., 2007), or by changes in the speed or distance of signal transmission through the nest. Empirical and theoretical work on ants suggests that rates of worker contact can have profound effects on task performance (Pacala et al., 1996; Gordon and Mehdiabadi, 1999). By changing worker densities in laboratory arenas, Gordon et al. (1993) found that overall interaction rates changed less than expected as density increased. They suggested that the ants might modify their behavior so as to maintain their rates of interaction, perhaps by adjusting the directionality of their travel through the environment (Adler and Gordon, 1992). Alternatively, limits on interaction rates may be an automatic by-product of changes in density. For example, if workers that are already engaged in interactions are unable to serve as receivers in additional interactions, and interactions take time, then interaction rates will not increase linearly with worker density (Nicolis et al., 2005). In any case, worker interaction rates may be robust to changes in group size or density in some species (Pacala et al., 1996).

Additional limits on interaction rates can be imposed by task performance itself. Foragers that are absent from the nest collecting materials, and more generally workers that are already engaged in tasks, may not be available to participate in social interactions. In honey bees, experimental changes in the rate of nectar flow affected the amount of time that foragers spent at food stations in the field, and consequently affected the rate of information transfer to potential recruits in the nest (Fernandez et al., 2003). Although most worker connectivity probably occurs in or near nests, workers that depart from the nest can still participate in some communicative interactions. Eusocial bee workers can either facilitate or impede grouping with their nestmates by signaling at food sources away from the nest (Fernandez et al., 2003; Slaa et al., 2003).

Rates of worker interaction have strong effects on labor when there is task partitioning. Task partitioning means that the subroutines of a complex job are performed by different individuals. One common form of task partitioning occurs when the foragers collect a material, such as food or building supplies, that they then pass on to nestmates that work with the material. If there are not enough recipients to take the foragers' loads, the foragers can experience queuing delays while they search for a ready recipient. Excessive queuing delays can decrease colony efficiency. Models and empirical studies show that these delays generally decrease with social group size (Jeanne, 1986b, 1996; Anderson and Ratnieks, 1999a). However, queuing delays can also provide information about the colony's level of need for a given material. Failure to transfer a load of material is a type of information that a forager can use in deciding whether to continue collecting that material. The quality of the information improves if the forager can assess queuing delays across multiple attempted transfers (Ratnieks and Anderson, 1999; Karsai and Balazsi, 2002). Foragers can also adjust their responses to queuing delays based on their own perception of resource quality. Honey bee foragers use queuing delays to assess their colony's food needs (Seeley and Tovey, 1994), but they make more offering contacts with nest bees when the quality of the food they are collecting increases (Fernandez et al., 2003).

The degree of connections in a colony can be further affected by *modularity:* the existence of spatio-temporal breaks in the flow of information within the labor force. Sets of nodes that are connected to each other are referred to as components in a network (Newman, 2003), and insect colonies may often comprise multiple components. Modularity of insect colonies may be influenced by nest architecture. Workers in different parts of large or complex nests may rarely contact each other, and communication among them may be restricted; thus, they belong to different components (Murakami et al., 2000; Hinze et al., 2002; Tschinkel, 2004). Polydomy is the occupation of multiple nest sites by a single colony (usually in ants), and polydomy may often be associated with marked modularity (Debout et al., 2007; Wilgenberg and Elgar, 2007). Components could also be delineated by castes, for example, if certain castes of workers avoid interacting with other castes. Large-bodied major workers of the ant *Pheidole pubiventris* avoid making contact with minor workers, and are thereby prevented from performing certain tasks (Wilson, 1985). In the leaf cutter ant *Atta colombica*, workers avoid contact with those nestmates that perform waste removal tasks, possibly to avoid contact with pathogens (Hart and Ratnieks, 2002).

Size of the component

The demography of the interacting adults in a colony can have strong effects on communication. Group size is a fundamental feature of demography that shapes and constrains the expression of an array of social characteristics (Bourke, 1999). Mature eusocial insect colonies range in size over several orders of magnitude among species. For example, eusocial paper wasps (Vespidae) range in colony size over six orders of magnitude, from several interacting adults to millions (Jeanne, 1991).

The size of the interacting group can also change dramatically over the course of insect colony development, particularly in those species where colonies are founded by a lone female or pair, or a small social group. Mailleux et al. (2003) showed that the ant *Lasius niger* relies more heavily on recruitment to food sources, rather than solitary foraging, as colony size increases. By manipulating colony size, they showed that colony and worker age had little additional effect on recruitment. We predict that worker interaction rates, and/or the strength of interaction effects, will change over the course of insect colony development. These changes may be necessary to stabilize the dynamics of task recruitment within colonies. Colony size does not change as dramatically in swarm-founding species, where new colonies consist of a relatively large group of workers and reproductives. We suggest that reduced variation in the patterns of information transfer during colony development is an adaptive advantage to the swarm-founding mode of colony initiation.

Distribution of senders in the social group

A key feature of many networks is the distribution of edges among nodes. In many network systems, some of the nodes make relatively few connections, while other nodes are heavily connected. These high-degree nodes individuals are often important to overall network behavior and stability (Fewell, 2003; Newman, 2003). In insect colonies, if the distribution of edges is *diffuse*, then all workers are more equally likely to interact. In contrast, a *concentrated* distribution would involve a subset of the workers that act as senders in communicative interactions. An extremely concentrated distribution would involve a single catalytic individual, which would be in a position to play a supervisory role. Examples of concentrated interactions are found both in small and large insect societies. In small *Polistes fuscatus* colonies, the queen plays a central role in inciting workers to forage (Reeve and Gamboa, 1987). In *P. instabilis* colonies, one or two dominant workers appear to play a similar role in inducing nestmates to forage (O'Donnell, 1998a). In the much larger colonies of honey bees, the scouts comprise a small proportion of the forager force on any given day. Scouts locate new food resources or nest sites and recruit nestmates to them (Winston, 1987; Anderson, 2001).

Worker interactions are often diffuse in ant colonies, with many workers contacting each other as they forage and perform other tasks (Gordon et al., 1993; Dussutour et al., 2007). These brief worker contacts can have dramatic effects on task performance patterns. Information transfer can occur during brief encounters with nestmates, which are summed over time by the receivers and used to estimate nestmate densities and task performance rates. In the ant *Temnothorax albipennis*, colonies can be induced to choose among several potential new nest sites in the laboratory. Workers' rates of encounters with nestmates at potential new nest sites lead to individual decisions, and eventually to colony decisions, about which new site to choose (Pratt, 2005; Dornhaus and Franks, 2007). Recent empirical work suggests that complex information can be transmitted during these brief encounters. Greene and Gordon (2003) showed that harvester ant workers recognize the task specializations of their nestmates based on the cuticular hydrocarbon profiles on their body surface. Idle foragers can be stimulated to activity when they contact patrollers, which have a distinct hydrocarbon signature. Foragers were also activated when they were exposed to artificial models coated with the hydrocarbon blends that are typical of the patrolling workers.

Strength of interaction effects on receivers

Social displays vary widely in the strength and time course of their effects on recipient's task performance. Receiver's reactions to displays range along a continuum from nearly deterministic, immediate responses to alarm pheromones, to modulatory interactions whose effects on receivers are probabilistic and gradual (i.e., releaser *versus* primer effects: Hölldobler, 1984, 1995).

Interaction strength could evolve by adjustment of either the senders' displays, or by adjustment of the receivers' responses to those displays.

Senders' communicative actions could evolve through ritualization to become enhanced or exaggerated. For example, the concentration or absolute amount of a work-inducing pheromone could be adjusted up or down (Hölldobler, 1995). Changes in the form and intensity of honey bees' dance language are a likely example of signal ritualization from the tactile/vibratory mode of communication (Dyer, 2002). On the receiver side, cognitive evolution could influence the strength of the effects of a given signal. Several features of receiver's cognitive information processing abilities can affect interaction strength. Sensory organs could change in their sensitivity to senders' displays. Although little studied in eusocial insects, evolutionary changes in insect sensory capabilities can occur rapidly, and have major effects on ecology and behavior (Boeckh, 1984; Lai and Orgogonzo, 2004). It is also plausible that changes in receiver sensitivity result from the evolution of more central cognitive processing of task related signals in the worker's brains (Beshers et al., 1999).

The persistence of effects of a single interaction on a worker's task performance decisions is relevant when the communicative interactions are modulatory and require repetition. Important questions are whether interaction effects sum when they are repeated, and if so, how the effects are compounded over time and over repetition (Anderson and Ratnieks, 1999b; Fernandez et al., 2003). We predict that cognitive mechanisms that set the time course of worker responses to task-related communication will be under colony-level selection. Because most insect learning and memory occurs in the brain, these aspects of worker connectivity are likely to have a CNS basis (Beshers et al., 1999). The ways in which interaction effects might change over repetition in social insects are little known, but could be addressed empirically. By following focal individuals and recording successive interactions, it could be determined whether and how task performance changes following repeated interactions.

Modulating worker recruitment: the effects of forgetting or signal decay

Forgetting about interactions is another cognitive process that could affect task performance. Forgetting after communicative interactions may be difficult to avoid, particularly if maintaining memories about communicative interactions is costly to receivers (Dukas, 1999; Mery and Kawecki, 2005). However, cognitive plasticity and decision making when workers assess task needs directly can also incur costs. Workers may be confronted with stimuli from several tasks at the same time, and animals making decisions in the face of competing stimuli risk expending time, making errors, and even failing to act at all (Bernays, 1999). Communicative interactions can lower the potential costs of direct assessment of task needs, by directing workers more quickly to make choices about appropriate task performance.

Modulating worker recruitment: social inhibition

Not all worker communicative interactions are excitatory; some worker interactions inhibit task performance by nestmates. Previous work on social inhibition largely addresses developmental effects, and workers affecting each others' rates of behavioral development (Naug and Gadagkar, 1999; Beshers et al., 2001). In honey bees, active foragers inhibit the developmental onset of foraging in younger workers (Huang et al., 1998). The labor activities, or the results of active workers' labor, may inhibit nestmates. A model of foraging recruitment in ants suggested the interesting possibility that workers would forage more efficiently by producing and responding to inhibitory chemical signals, as well as activating recruitment pheromones (Strickland et al., 1999).

The mechanisms of social inhibition have been studied in a few systems. Honey bees use a piping or stop signal to help deactivate nectar foragers that are visiting poor-quality resources (Anderson and Ratnieks, 1999b; Thom et al., 2003). *Monomorium* ants produce a volatile pheromone that inhibits workers from walking on paths that lead to unprofitable resources (Robinson et al., 2005). In honey bees, inhibition of the developmental onset of foraging requires contact among the workers, suggesting the involvement of a nonvolatile inhibitory chemical signal (Leoncini et al., 2004). The interplay between activation and inhibition may fine tune the rate of recruitment of workers into tasks more often than is currently recognized (Anderson and Ratnieks, 1999b).

Specificity of the elicited response

The information communicated by senders about task needs may be specific, directing receivers toward performing a single task, or it may be more general. One form of non-specific response to communicative interactions is simply to change the receiver's activity level (Savoyard et al., 1998; Dornhaus and Chittka, 2001; Schneider and Lewis, 2004). Active workers may be more likely to encounter task stimuli directly. Therefore, performance of a number of tasks may be initiated in response to non-specific communication that induces activity.

Alternatively, the performance of specific tasks may be elicited or affected by worker interactions (Dornhaus and Chittka, 2004; Lopes et al., 2004). In *Polistes* paper wasps, subordinate workers often depart from the nest to forage soon after receiving aggression from nestmates (Reeve and Gamboa, 1987; O'Donnell, 1998a,b). Similar responses to biting interactions are seen in *Polybia* paper wasp workers (O'Donnell, 2001, 2006). Nest departure may be derived from fleeing behavior, and represents a task-specific response to aggressive interactions. Chemical displays often elicit particular responses. For example, workers of many ants have a diverse array of exocrine glands that produce distinct blends of compounds. These gland products often serve discrete functions such as orientation or recruitment pheromones, or alarm pheromones. In some cases, different chemical products from a single gland elicit subtly different responses from nestmates (reviewed in Hölldobler and Wilson, 1990).

Other species and task differences

The relative urgency of completion of different tasks will favor different, possibly hierarchically organized worker communication networks for distributing workers among tasks. We expect the above characteristics of worker connectivity to differ among tasks for any given species, as well as likely showing species specificity.

A wide array of sensory modalities is employed in worker connectivity, including direct physical contact (Gordon et al., 1993; O'Donnell, 2001, 2003; Schneider et al., 2004), chemical signals (Pankiw et al., 2004), and substrate-borne vibratory signals (Connetable et al., 1999; a similar system may exist in eusocial rodents: Narins et al., 1997). Even within functionally similar task classes, species can differ in the mechanisms of worker connectivity. Foraging is an excellent and well-studied example. In some cases, simple contact with other workers can apparently influence workers' foraging decisions (Gordon, 2002). In others, ritualized worker interactions affect the probability of foraging in recipients (O'Donnell, 2006; Schneider et al., 2004). Signals that are transmitted via different sensory modalities show inherent variation in the time course of the action, and in their persistence after the sender ceases providing information (Bradbury and Vehrencamp, 1998). Within chemical communication, signals can vary in rapidity of detection and in duration depending on the volatility of the pheromone mixture (Bradshaw et al., 1975). For example, the gradual evaporation of trail pheromones shapes patterns of foraging recruitment in ants (Strickland et al., 1999). In social insects, alarm pheromones are often highly volatile, and their effects dissipate quickly once they stop being released (Jeanne, 1981; Hölldobler and Wilson, 1990; Breed et al., 2004).

Tempo, the notion of species variation in the general activity level and rapidity of movement (Oster and Wilson, 1978; Hölldobler and Wilson, 1990), may affect worker connectivity via effects on the probability of worker interactions. Ant species differ dramatically in their mean contact rates among nestmates when the workers are at the same density (ants/unit area) in an arena (Gordon et al., 1993). Tempo may have evolved, in part, as a means of adjusting rates of worker communicative interactions that affect task performance.

Within colonies, growth and development and other changes in colony demography may influence worker connectivity. Major developmental changes include increases in colony size, and increases in the diversity of worker castes present (Wilson, 1983). Growing colonies of many species exhibit greater complexity and compartmentalization of their nest architecture (Thorne and Haverty, 2000; Tschinkel, 2004). The modularity of worker communication is likely to increase over the course of colony development. We predict that the extent of coverage will decrease with colony size because the chances of all workers meeting each other goes down as colony size goes up. Increasing nest compartmentalization will compound this pattern. Colonies may often develop into a collection of partly autonomous network components.

Conclusions

Individual differences in the probability of responding to tasks are widespread in insect societies, and evidence that thresholds of response contribute to these differences has been found in a wide diversity of species (Ants: Detrain and Pasteels, 1991; Paper wasps: O'Donnell, 1998a; Honey bees: Page et al., 1998; Bumble bees: O'Donnell and Foster, 2001; Weidenmueller, 2004). In some species, morphological worker castes differ in their thresholds of response to communicative signals such as recruitment trail pheromones (Traniello and Busher, 1985; Detrain and Pasteels, 1991). From a mechanistic perspective, it is largely unknown how interactions might affect workers' thresholds of response. This will depend in part on the mechanisms that set the threshold values in the first place. Beshers et al. (1999) posited that thresholds reside in the central nervous system, but we suggest that peripheral (e.g., sensory) cognitive changes could also affect thresholds.

It is important to note that there is not a single optimal design to a system of worker communication. For example, the most rapid possible recruitment of workers to any one task is not necessarily adaptive, a point also made by Pacala et al. (1996). Colony-level selection should alter the mechanisms of worker communication for each task such that colony fitness is optimized. For communication about a given task, the appropriate sensory modality and signal design, and possibly the associated cognitive mechanisms, will depend in part on the severity and immediacy of the task need. Some tasks might require rapid responses by much or all of the worker force, for example, defense against predators that pose a risk of colony destruction (Chadab, 1979). Other tasks may require gradual or finely attuned responses, such that appropriate numbers of workers are recruited, and other tasks are not disrupted (O'Donnell and Jeanne, 1990; Anderson, 2001). The latter task category could include nest thermoregulation and foraging. The tuning of features of connectivity such as interaction rates and strengths, and the patterns of summation of interaction effects on recipients, should evolve to a level that is appropriate for each task.

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