

Social Insects: A Model System for Network Dynamics

Daniel Charbonneau, Benjamin Blonder, and Anna Dornhaus

Abstract Social insect colonies (ants, bees, wasps, and termites) show sophisticated collective problem-solving in the face of variable constraints. Individuals exchange information and materials such as food. The resulting network structure and dynamics can inform us about the mechanisms by which the insects achieve particular collective behaviors and these can be transposed to man-made and social networks. We discuss how network analysis can answer important questions about social insects, such as how effective task allocation or information flow is realized. We put forward the idea that network analysis methods are under-utilized in social insect research, and that they can provide novel ways to view the complexity of collective behavior, particularly if network dynamics are taken into account. To illustrate this, we present an example of network tasks performed by ant workers, linked by instances of workers switching from one task to another. We show how temporal network analysis can propose and test new hypotheses on mechanisms of task allocation, and how adding temporal elements to static networks can drastically change results. We discuss the benefits of using social insects as models for complex systems in general. There are multiple opportunities emergent technologies and analysis methods in facilitating research on social insect network. The potential for interdisciplinary work could significantly advance diverse fields such as behavioral ecology, computer sciences, and engineering.

D. Charbonneau (✉)

Graduate Interdisciplinary Program in Entomology & Insect Science, University of Arizona, Biological Sciences West, 1041 East Lowell, Room 235, Tucson, AZ 85721, USA
e-mail: charbonneau.daniel@gmail.com

B. Blonder · A. Dornhaus

Department of Ecology and Evolutionary Biology, University of Arizona, 1041 E Lowell St., Tucson, Arizona 85721, USA
e-mail: bblonder@email.arizona.edu; dornhaus@email.arizona.edu

1 Introduction

1.1 *Social Insect Biology*

There are currently over 1.7 million described species on earth and 1 million of these are insects. Insects can be found in nearly all habitats and the earliest insects are thought to have evolved 400 million years ago [39, 96]. Within this exceptional group there exists an even more exceptional group: the social insects. Though they only represent 2% of insect species, social insects may constitute up to 80% of insect biomass and in total outweigh vertebrates by 7 to 1 [41, 89, 104]. They are known to be one of the most ecologically successful groups in nature, dominating most terrestrial habitats. Division of labor is often cited as a primary reason for their ecological success, particularly in ants [42, 72, 90, 103].

Social insects, including particularly termites, ants, bees and wasps, live in family groups of up to millions of members, called colonies. Colonies contain only one or few “queens”, who lay eggs and ensure colony reproduction. The rest of the colony is primarily composed of workers and sometimes males. Workers ensure the maintenance and growth of the colony. When a colony matures, it produces sexuals, male drones and female queens, which leave the colony to mate and establish new colonies.

The reproductive division of labor between queens and workers is an essential component of eusociality or “true sociality”. Although workers do not reproduce themselves, they gain indirect fitness through the queen because queens and workers share a large proportion of their genes. This leads to extreme cooperation between individuals within a colony and thus group-level optimization of colony features.

1.2 *Information Exchange Networks in Social Insects*

Social insect societies are complex self-organized systems. They display sophisticated problem-solving that emerges from relatively simple individual behaviors. For example, ant and bee colonies can select the best among several nest sites that differ along multiple dimensions by a consensus-decision-making process that resembles a voting procedure. They also demonstrate division of labor, which involves individual workers adaptively allocated to different tasks (e.g. caring for eggs, larvae, and pupae or brood care; building; foraging; defense; etc.), in a way that is robust to change in demand and to individual failure or even to loss of large numbers of workers. Many of these processes are regulated by interactions between the individual agents within the colony. As such the structure and dynamics of the network of interactions will affect overall colony functioning.

Information-sharing between nestmates is thus necessary for the coordination of social insect colonies. The most commonly known means of communication among social insects are pheromone trails. However, social insects use a wide range of types

of communication including visual, acoustic, tactile, vibration, and chemical cues other than pheromone trails [37, 42]. Each of these modalities of communication has properties that could affect information flow in complex ways. For example, broadcast cues like volatile pheromones will likely have a greater range than an individual-specific cue like antennation (touching with antennae, which contain sensory organs). Broadcast cues also travel faster, though less reliably than contact signals. The type of communication will fundamentally affect network structure, as it affects how many links a single communication event creates and how connected the network will be. It also affects network dynamics by changing the speed and reliability of information flow. As such, we might expect that the structures and properties of the interaction networks for each of these methods of communication could be different and optimized for different constraints.

For example, different species of ants are optimized for different environments. When workers in mass-recruiting ants find a new food source, they lay pheromone trails on the return trip to the colony. These pheromones serve to both recruit new workers to exploit the food source as well as guide these foragers to it. Successful foragers typically add to the pheromone trails on the return trip. This creates a feedback loop where the better the food source, the more foragers will be recruited to exploit it, allowing the ants to quickly and efficiently exploit resources. In addition, this enables ants to find the shortest path to a food source through a self-organized process [7, 19]. However, studies have shown that, although pheromone laying ant species are capable of quickly exploiting food sources, they cannot quickly switch to a new, better food source because they get locked into exploiting the food source with the existing pheromone trail [8, 19, 54]. There is evidence suggesting that this phenomenon, linked to symmetry-breaking, could be explained by non-linearity of individual choice behaviors in response to signal strength [54]. This suggests that mass-recruiting species are better suited to less variable environments.

Other species have developed different means of recruitment and communication about food source locations. For example, some species engage in “tandem-running,” where a worker who finds a food source returns to the colony and recruits a second individual which then follows the leader back to the site by maintaining antennal contact. Such recruits, having learned the location of the resource, can then return and recruit more individuals in turn, thereby creating a feedback loop which increases the total number of individuals having knowledge of the food site location and who can contribute to its exploitation. Studies have shown that this means of recruitment is much better suited to exploiting sporadic and ephemeral food sources because any time an individual forager returns from a new food source, it is able to immediately recruit other workers to it [33, 83].

1.3 Why Should We Care About Social Insects?

Social insects must also balance many simultaneous constraints, such as efficient communication and movement within the colony with nest defense and limited

disease propagation. This is particularly interesting because man-made networks are also often faced with multiple constraints and social insects could serve as good model systems. For example, balancing efficient movement in termite colonies with limiting disease spread [76, 77] can easily be applied to efficient data transmission in computer networks while limiting the potential for spreading viruses or other harmful programs. Furthermore, balancing efficient movement and communication within the colony with effective nest defense could have military applications.

Colonies are sometimes spatially organized such that workers show fidelity to certain areas of the nest [44, 92]. There are often relationships between spatial location of individual workers and their task specialization [82, 92], age [91], and/or body size [44]. Although it is unclear whether spatial location is driving these relationships, it is clear that the spatial location of interacting workers will change the structure of interaction networks [10, 80]. The physical nest structure itself can also affect information flow by constraining interactions, thus limiting global and enhancing local information flow.

Many biological networks, including social insect networks, are thought to approximate scale-free networks [3, 4, 31]. Specifically, the connectivity (or degree) of biological networks often follows a power law distribution. Scale-free networks share certain properties that make them particularly interesting to study. They are typically composed of several hubs, or more central nodes, and a large number of nodes with few connections. They also belong to a class of networks known as small world networks, which have the property of rapid communication between nodes throughout the network. Lastly, scale-free networks are often robust or resilient to the removal of random nodes.

Although many biological networks have been shown to be scale-free (metabolic networks, [47]; protein–protein interactions networks, [60]; gene expression networks, [70]; gene interactions, [98]), there is still some question as to how prevalent scale-free networks are in biological systems [52]. In the case of social insect networks, there is yet to be a clear answer. Because the size of social insect colonies is often small (naturally limited to no more than a few hundred individuals), natural scales may emerge in a network and also limit the power of model-selection approaches to detecting scale-free phenomena.

In Sect. 2, we review the current literature and show that degree distribution in social insect can depend on colony size. However, when social insect networks are found to be scale-free, it is possible to transpose methods and results from these to other scale-free networks, such as computer, social or business networks, and vice versa [3].

Social insects are particularly interesting to network scientists in all fields because they are an evolved (and thus optimized) system in which the interacting parts can be individually tracked and manipulated (Fig. 1). The same cannot be said for many other model network systems, such as primate social networks [95]. This is particularly interesting because experiments can be conducted on social insect networks that might not be possible in networks in other fields. We can map many of social insect adaptive functions on to functions of interest to humans. That is, they are a simulacrum of our engineered world.

Fig. 1 Individually marked ants of the species *Temnothorax rugatulus*. Photo by Alex Wild



1.4 Role and Types of Networks in Social Insects

Most research to date has focused on interaction networks, i.e. ones where individual workers are nodes and edges are defined as interaction events between workers. The relevant interactions used as network edges can be of different types such as spatial proximity [45, 73], physical contact (usually with antennae, “antennation”) [10, 67, 80], a food exchange event [15, 68, 69, 93], or specific communication signals [38, 56]. Such studies may investigate questions relating to the propagation of disease or information through the colony, and may test specific hypotheses concerning speed of transmission, whether all individuals are equally likely to be reached by the disease/information, or whether particular individuals or subgroups of the network (e.g. foragers or the queen) will transmit information/diseases more or less quickly than the rest of the colony.

Interaction networks can be directed, i.e. interactions may have a defined directionality. This can be the case in food flow networks, where one worker gives food to another worker. Given that only a fraction of the colony is out foraging at any time, successful foragers need to be able to share food, which they can store in their crop, with other workers and brood. The process by which this food is regurgitated and shared is called trophallaxis. Food flow networks are comprised of individual ants as network nodes and edges as trophallaxis events. The duration of a trophallaxis event tends to correlate with the amount of food being transferred [21], and edges may be weighted by duration of this interaction. Food flow networks can answer questions such as: what is the mean degree of separation between foragers and nurses (individuals who care for the immature brood)? Is food channeled to particular individuals preferentially (nurses, queen)? What elements of the network structure are necessary to achieve these things? Are networks structured to increase food distribution while simultaneously decreasing disease spread?

Worker–worker contact (interaction) networks can also be used to answer important questions. However, many key questions can only be answered by looking beyond networks constructed from mere physical contacts between individuals. In ecology, plant–pollinator networks (bipartite networks between pollinator communities and plant communities) have been the focus of much research. Pollinator communities are often composed primarily of social insects [22]. These types of

networks can be used to look at the resilience of plant–pollinator communities to the disappearance of one or many pollinator species [28, 29, 43, 62, 94] and temporal variation in plant–pollinator interactions [1, 5, 78].

Beyond these networks, other extremely interesting possibilities of non-interaction networks exist. For example, it is possible to create worker–task bipartite networks where each worker is linked to the set of tasks it performs, and each task is linked to the set of workers that perform it. Research using worker–task networks would enable investigation of worker specialization and individual variation of worker specialization as well as questions of network resilience to worker loss or failure.

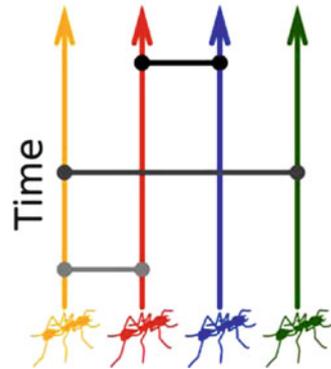
Alternatives to interaction networks include task–task networks, in which interactions are weighted and directed by the number of workers switching from one task to another [31]; worker–nest area networks, which could help investigate spatial fidelity within the nest and even nest area–nest area networks which could yield information about the movement patterns of individuals within colonies.

In this chapter, we make the case that looking beyond the worker–worker interaction networks is a necessary new direction for social insect network research. Further developing alternative network types will allow researchers to pose and answer new kinds of questions, and keep the field dynamic and exciting. Integrating networks at different organizational levels could be used to develop unified models [55]. In the following sections we review a selection of worker–worker interaction networks covering classic questions explored by these types of networks as well as two alternative network types that look at the temporal stability of bipartite plant–pollinator networks and the temporal dynamics of nest construction. We then present a worked example with original data of a task–task network in an ant colony to showcase the potential of exploring new types of networks.

2 Network Dynamics Applied to Social Insects

In recent years, networks have become increasingly popular in social insect research. Here we survey previous network research on topics that include interaction network resilience, flow (information, disease, and food), temporal stability of species interactions (plant–pollinator systems), and temporal dynamics of nest construction. Recently, researchers have focused on adding temporal elements to existing models and investigating the properties of network dynamics. Temporal networks on their own can provide insight into dynamic patterns within social insect colonies (e.g. network stability), and including a temporal dimension to static networks can yield surprising results and even invalidate conclusions drawn from static networks. The topics discussed in the following section (resource flow, group structure, task allocation, multi-species interactions) are actually dynamic processes, and as such are ideally suited to be studied from a dynamic perspective.

Fig. 2 Representation of a time-ordered network. Reproduced with permission from [10]



2.1 Worker–Worker Interaction Networks

2.1.1 Information Flow

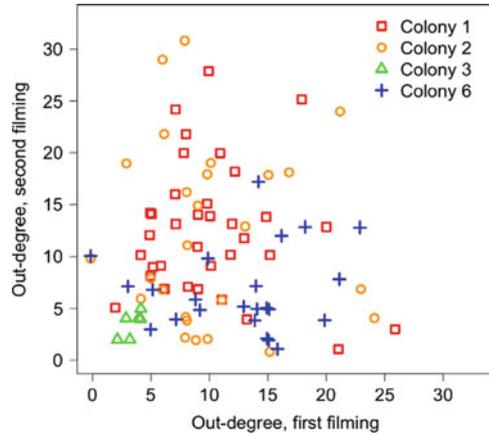
Social insect interaction networks have been described in different ways: worker interaction networks (e.g. [80]), network motifs (e.g. [100]), and temporal dynamic networks (e.g. [11]). Many complex interaction networks are adapted to inhibit or promote the transmission of disease, resources, or information between individuals. However, interactions between individuals occur over time, may be repeated, and are stochastic. These temporal dynamics are certain to affect network function, and are not captured by static network analyses. There is currently a trend in the literature to incorporate temporal dynamics into established static models and to apply methods that directly take the dynamic nature of interactions into account.

In a recent paper, Blonder and Dornhaus [10] investigated constraints on information flow in colonies of the ant *Temnothorax rugatulus*. They employed a “time-ordered network” (Fig. 2) which directly incorporates the timing of interaction events, and thus allows the tracing of possible pathways of information flow through time. The observed network of ant antennation interactions (physical touching with antennae) was compared to a diffusion model in which all individuals interact like kinetic gas particles. They compared the number of individuals reached by a message propagated from a random individual within a set time interval in the diffusion model with the observed ant interaction network. This measure can be thought of as an upper bound to information flow, as it was not determined whether each interaction actually involved transmission of information.

They found that, at large time-scales, information flow was significantly slower in ant networks than that predicted by the diffusion model, but that at small time-scales information flow was faster than predicted. This suggests that the structure of the ant network is optimized to facilitate local information flow, but also underlines the importance of using an appropriate time-scale as results may vary.

The absence of a relationship between the number of individuals a focal ant touches (out-degree) in one bout of filming compared to the next (Fig. 3) suggests

Fig. 3 Individual out-degree between the first and second observation of all colonies. Reproduced with permission from [10]



that individual ants did not consistently hold central roles within the network. This is especially interesting as many scale-free networks show consistent individual specialization.

Since this lack of individual consistency in interaction pattern was not found in other studies [45, 80], it is likely that these network properties differ between different ant species with different ecology and life history (colony size, nest types, etc.), whose individual and collective behavior is optimized for different conditions and constraints.

2.1.2 Resilience of Colony Function to Perturbation

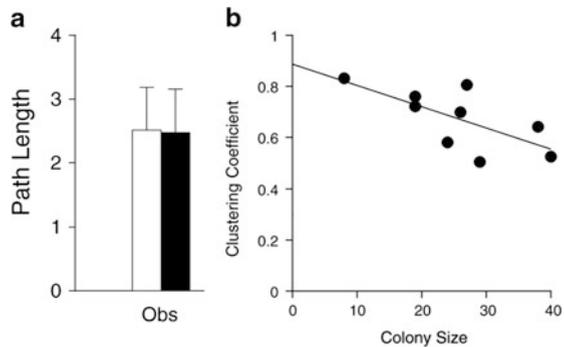
Network resilience can be broadly defined as the ability of a network to retain or restore its function after perturbation [35, 65, 106]. In the case of a computer network, this means being able to provide and maintain an acceptable level of service in the face of faults. For ecological networks such as between plants and their pollinators, this may mean having a limited extinction of plant species should several species of pollinators disappear. For social insect interaction networks, this may mean maintaining an acceptable level of function when individuals fail, either by making errors or by disappearing.

In a study looking at the resilience of a colony to the death of workers, Naug [67] assembled undirected worker–worker contact networks weighted by the frequency of interactions before and after removal of random workers from colonies of the social wasp *Ropalidia marginata* (Fig. 4). By comparing the intact and reduced networks, he showed that path lengths were maintained, thus preserving information flow throughout the colony (Fig. 5a). The wasps achieved this by an increase in connectivity amongst remaining individuals attained through an increase in the rate of interactions. As such, his results showed that interaction networks within this wasp species were resilient to the removal of random workers.

Fig. 4 The social wasp *Ropalidia marginata* (*top*) and its nest (*bottom*). *Top*: by School of Ecology and Conservation/CC-BY-2.5. *Bottom*: by Abhadra/CC-BY-2.5



Fig. 5 (a) Path length before (*white*) and after (*black*) removal of random workers. (b) Clustering coefficient decreases as colony size increases. Reproduced with permission from [67]



Naug [67] also looked at the effect of colony size, i.e. the number of individuals in the group, on network structure and properties. His results showed that smaller colonies tended to have more homogeneously connected individuals while larger colonies tended to have more heterogeneously connected individuals (Fig. 5b). Uniform connectivity in small colonies may allow all workers to have access to information about what work needs to be done. This might lead to more generalist workers in smaller colonies (if workers frequently switch tasks). On the other hand, workers in larger colonies only have access to partial information, potentially leading to behavioral specialization. This is in accord with the prevailing view in the literature that group size often correlates with task specialization ([34, 46, 50, 97], although see [26]).

However, colony sizes in this study ranged from 8 to 40 individuals which form relatively small interaction networks. Samples across more orders of magnitude would provide greater insight into the effects of colony size on network properties, but there are often natural and practical limitations to these studies. For example,

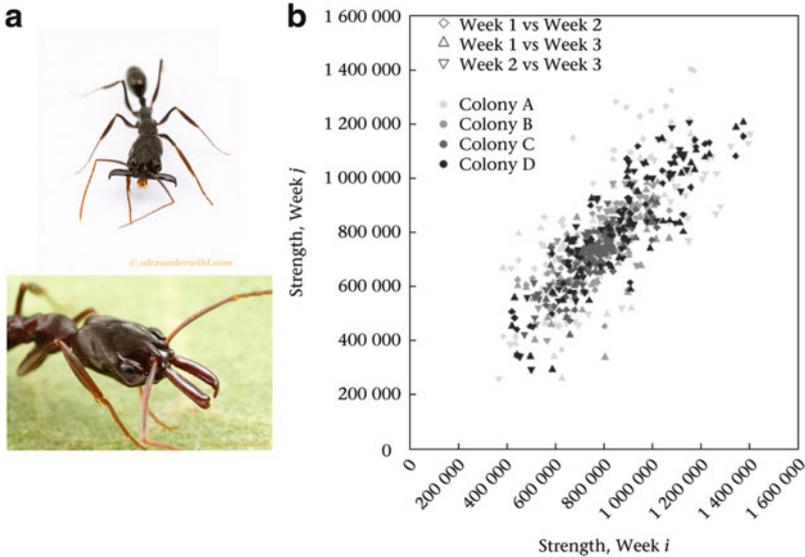


Fig. 6 (a) Ants of the genus *Odontomachus* with mandibles open at 180° and resting in closed position. These ants hold the record for fastest moving predatory appendages within the animal kingdom [75]. Photos by Alex Wild. (b) Strength of associations between workers at different times. Reproduced with permission from [45]

colonies of *Ropalidia marginata* (the wasp species used in the Naug study) typically hold no more than 200 workers and the amount of work required to collect these data increases exponentially with colony size. Thus the application of scale-free network concepts may be less relevant in these naturally small systems.

A related study looked at the stability of interaction networks and their resilience to queen removal in ants of the genus *Odontomachus*, often called “trap-jaw ants” because of their unusual mandibles (Fig. 6a). In this study, Jeanson [45] used passive microtransponders superglued to the ants to track their spatial position over a 3 week period. By assuming that ants who came in close proximity were interacting, the author created a dynamic worker–worker interaction network. His results showed that the interaction networks were stable over time and resilient to the removal of the queen, but that inter-individual differences were important in connectivity patterns (Fig. 6b). Specifically, some workers formed stronger long-lasting interactions with a smaller group of nestmates while other workers did not have privileged relationships and interacted uniformly with their nestmates.

2.1.3 Disease Transmission

Social insects, like humans, are particularly susceptible to disease because of high population density, genetic homogeneity within colonies, and high interaction rates

[105]. As such, social insects may have evolved strategies which mitigate the effects or limit the transmission of diseases.

If interaction networks are scale-free, interactions should not be uniformly distributed amongst individuals. A small number of workers should be more central and most workers should be directly connected only to a subset of the colony. One effect of this organization is that networks are particularly resilient to the random loss of some individuals [67]. It has also been shown that that highly clustered subgroups and short average path lengths, which are characteristics of scale-free networks and incidentally small world networks, should maximize efficient communication [101]. As such, we might expect that disease transmission would equally be maximized.

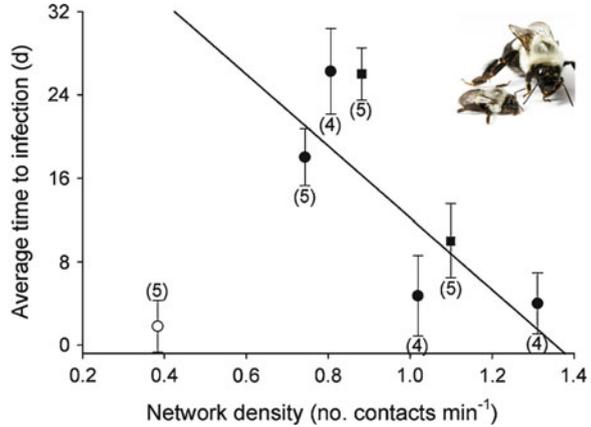
However, there could also be some evolutionary pressure to limit the spread of disease within social insect colonies. Certain features of colony organization help limit the spread of disease [67] and infection period plays an important role in the spread of disease in social insect colonies [69], as it does in human societies [51]. Indeed, one effect of clustered subgroups is that the network is partitioned which, combined with short infection periods, can result in a limited spread of disease throughout the colony because portions of the colony will die out before the disease can spread to the majority of the colony. Indeed, in an agent-based modeling study, Pie et al. [79] show that even minimal spatial segregation tends to slow the spread of disease. On the other hand, if the infection period is long, then the highly efficient communication of the network will ensure that most if not all of the colony will be infected.

A study investigating colony properties and their effects on the transmission of a contagious pathogen (*Crithidia bombi*) in bumblebee colonies (*Bombus impatiens*) used automated video tracking of uniquely identified bees to measure worker-worker contact (spatial proximity) networks within the colony and quantified the actual spread of the pathogen [73]. They showed that across colonies, rates of infection were mostly dependent on network density (average contacts per minute) where higher densities lead to higher rates of infection (Fig. 7). Furthermore, the rate of contact for individuals predicted the likelihood of infection for that individual.

Similarly, using weighted trophallaxis networks (undirected food sharing networks weighted by transfer duration) to emulate the transmission of orally transmitted pathogens rather than those transmitted simply by contact, Naug [68] shows that disease transmission in honeybee colonies is more widespread when colony interaction networks have lower clustering coefficients (degree to which nodes in a graph are clustered together). Interestingly, lower clustering coefficients and high network densities are typically associated with network resilience, which suggests a tradeoff in clustering between colony resilience to losing workers and limiting disease transmission. Both of these empirical results are supported by Pie et al. [79] who use agent-based modeling to show a nonlinear interaction between worker density and the probability of disease transmission.

A surprising fact about social insects is that a significant proportion (as much as 60 %) of colony workers is inactive at any time [27, 85]. One reason for this may be that reduced activity slows disease transmission, presumably because interaction

Fig. 7 The average time of infection from *Crithidia bombi* decreases with increasing network density (average contacts per minute) in colonies of *Bombus impatiens*. Reproduced with permission from [73]



rates in less active colonies would be lower ([79], Fig. 8). Interestingly, an empirical study found no effect of individual activity on the risk of infection [73]. Naug [68] also suggests that the location of younger individuals both within the colony and the network could have the effect of limiting their exposure to diseases.

2.1.4 Food Flow

Sendova-Franks et al. [93] looked at the network structure of trophallaxis interactions and its progression in time in the ant *Temnothorax albipennis* (Fig. 9). They also compared colonies in normal feeding situations with colonies that had been starved for 48 h. Note that this ant genus is highly starvation resistant: colonies have been shown to survive up to eight months of complete starvation [88]. Within the first 30 min, as much as 95 % of ants from starved colonies (Fig. 10, full circles) were fed, versus less than 50 % of ants in fed colonies (Fig. 10, empty circles). Increased efficiency in food distribution resulted from increased movement of internal workers away from the brood piles (eggs larvae, and pupae which are typically at the colony center) and movement of foragers carrying food further into the nest. Indeed, both the number of recipients per donor and the number of ants participating in trophallaxis increased in starved colonies. Furthermore, the distance of a vector from the centroid of internal workers to the centroid of external workers (or foragers) was shorter after starvation than in the control and the direction of this vector was parallel to that of a line going between the nest entrance and the center of the brood pile. This is particularly interesting because workers have shown spatial fidelity according to their tasks where internal workers are essentially segregated from external workers, a phenomenon which was observed in the fed colonies, but not in the starved colonies. After starved colonies had been sated, spatial segregation resumed.

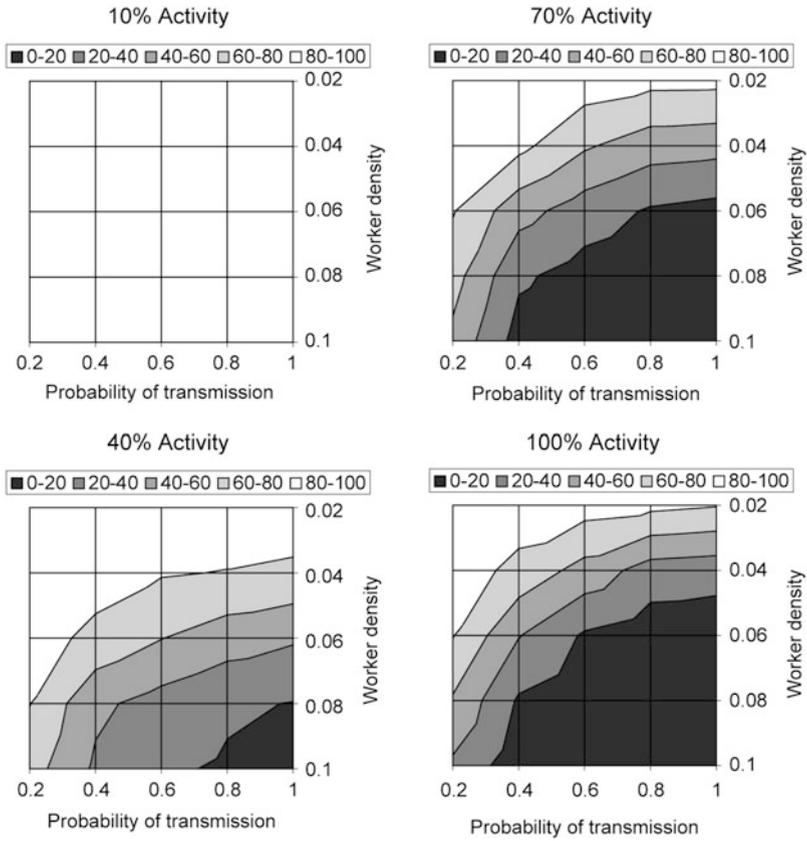


Fig. 8 Relationships between worker density, probability of transmission and colony activity obtained from an agent-based model. Reproduced with permission from [79]



Fig. 9 Nest of *Temnothorax albipennis* ants surrounded a wall of colored sand grains built by the ants. Photo by Anna Dornhaus

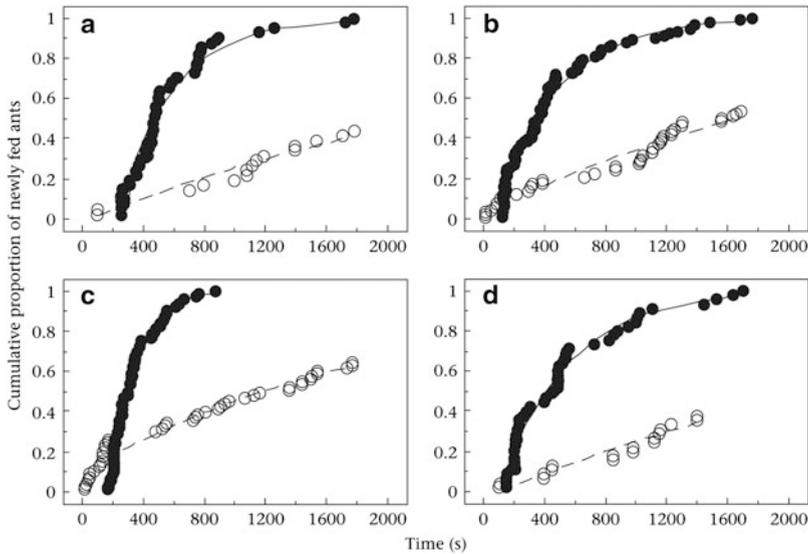


Fig. 10 The cumulative proportion of the colony fed for colonies A (a), B (b), C (c) and D (d) when that were starved for 48 h before feeding (*full circles*) and during regular feeding. Reproduced with permission from [93]

After starvation, some workers stored food rather than pass it on to other ants. They suggested that these ants are living “silos” and they may also act as food testers for the rest of the colony. Essentially, by storing large amounts of newly acquired food in these individuals the colony can test whether the food contains any toxins. If there were, only the “silo” worker would die, thus saving the rest of the colony. Otherwise, if the “silo” ant seems healthy, then the food would likely be safe. However the long-term network dynamics of food and disease flow were not directly investigated in this study.

2.2 Beyond Worker–Worker Interaction Networks

2.2.1 Temporal Stability of Species Interaction Networks

Different types of animals and plants often interact with each other in beneficial or harmful ways. For example, there is a long history of studying plant–pollinator systems, in which different species of plants are pollinated by different species of animals, usually insects [58, 86]. These interactions among different species can be thought of as plant–pollinator networks. Studies on such networks make use of theory developed in food web networks [28, 29, 43, 94]. These have allowed researchers to address questions relating to the resilience of such species networks to changes in biological community composition [62], the effects of invasive plants

on plant–pollinator networks [57], and the disruption of pollination networks due to global warming [61].

Resilience is tested by simulating a perturbation, typically by removing network nodes, and examining its effects on network topology and function. Plant–pollinator networks have been shown to be fairly resilient to removals [28, 29, 43, 94]. It is thought that resilience in pollination networks might stem from a redundancy in pollinators per plant as well as from the nested topology of the networks [62].

In the last 20 years, the question of specialists vs. generalists in plant–pollinator systems has been the subject of active debate. The idea that interactions between plants and pollinators tend toward specialization, or that plants and pollinators will coevolve towards increased fidelity, has long been widely accepted [2, 40]. However, in an extensive review, Waser et al. [99] showed evidence that perhaps generalists might be equally important and prevalent. Within the last decade, due to advances in network theory and an increasing awareness of networks, researchers have been using network approaches to address this question. Some work focused on characterizing the network properties of plant–pollinator systems such as the distribution of specialists to generalists [6, 103]. Although this work is important in understanding plant–pollinator network structure, it does leave the question of how these networks might vary in time. Indeed, research has shown that relationships between specialists and generalists are complex and that plant–pollinator networks are both asymmetric (interaction rates are not equal in each direction) and nested (species with few links have a sub-set of the links of other species), but until recently we did not know how stable these interactions were over time. A few recent studies explicitly address this issue [1, 30, 71, 78].

These studies showed that pollination network topology varied through time. Indeed, both the number and identity of interaction partners varied in time. This suggests that the relationships between plants and their pollinators may not be as strong or exclusive as expected. Indeed, within a single year of plant–pollinator interactions, a large portion of plants and pollinators seem to be specialists, but over a longer timescale interactions that were strong one year are not necessarily strong the next year (Fig. 11).

While the precise network topology of pollination networks varied through time, overall structural parameters of the network (e.g. degree centralization, connectance, nestedness, average distance, and network diameter) remained fairly constant. A large scale study spanning a wide range of latitudinal gradients shows similar results [30]. These studies are particularly interesting because they show how different patterns can appear at different timescales.

2.2.2 Temporal Dynamics of Nest Construction

Many social insects build complex nests which both constrain and facilitate collective organization. Nests often consist of multiple chambers connected by tunnels, and these have garnered much attention from researchers interested in networks. The networks created by social insect nest architecture are particularly interesting

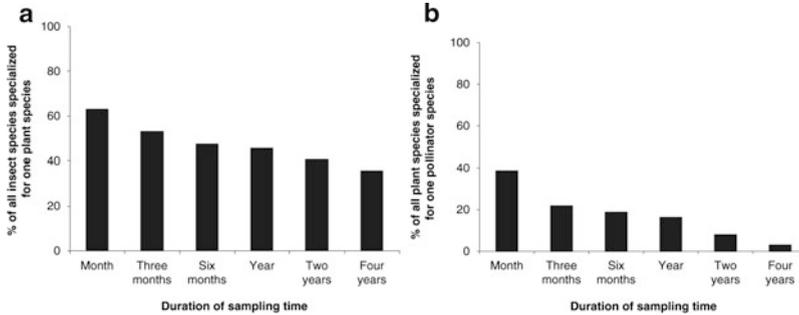


Fig. 11 Time dependence of “apparent specialization” of (a) pollinators and (b) plants. Reproduced with permission from [78]

because they show how self-organized networks can solve problems with multiple complex constraints, such as the need for efficient movement within the colony while making the nest defensible to attacks.

Over the last decade, with increasing accessibility to sophisticated computer and imaging tools and the interest in applying network approaches to biological systems, we have seen a progression of increasing complexity and detail in the studies investigating the network structure of nest architecture. Early studies focused on two-dimensional nest architecture and looked at the network properties of nest architecture such as the effects of group size on nest architecture [16], the efficiency and robustness of nest networks [18], and the relationship between topology and structural properties of nest networks [17].

More recently, researchers looked at nest networks in three-dimensional space, which better represents nest architectures of many species. Using computer tomography (CT) scanning to build three-dimensional models (Fig. 12) of nest architecture, Perna et al. [76, 77] looked at the transportation efficiency in termite nests and found that it is significantly higher than random, but below optimal transportation efficiency (Fig. 13). They proposed that this was a compromise between multiple constraints, such as efficient connectivity inside the nest, defense and resilience to attacking predators, and spatial constraints.

Recently, Minter et al. [63] investigated the temporal dynamics of nest building. Using microcomputer tomography at multiple time points over a 24 h period, they were able to track tunnel and chamber construction in time (Fig. 14).

In this study, they showed how features of the environment, specifically the presence of planes between sediment layers, would influence nest construction. When ants met with a new sediment layer, they tended to excavate more horizontally along the planes and over longer periods before continuing to tunnel downwards. They suggested that it is in fact not the planes they are responding to, but rather local heterogeneities in sediment compaction. This suggests that the importance of local information outweighs that of global information in determining individual nest construction behavior which in turn leads to the emergent phenomenon of nest structure.

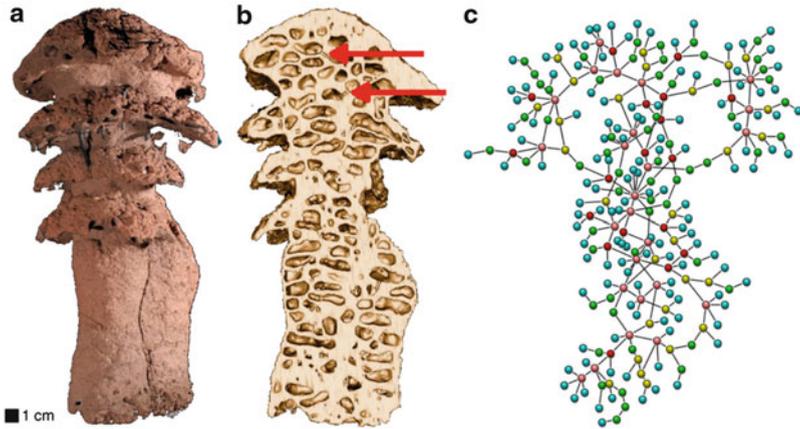


Fig. 12 (a) Above ground mushroom shaped termite nest. (b) tomographical cut of the same nest (the *arrows* indicate two of the corridors between chambers). (c) representation of chambers and galleries as a network. Nodes are chambers in the nest and edges are corridors. Reproduced with permission from [77]

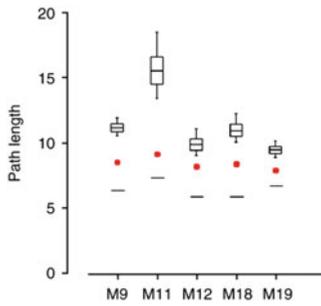


Fig. 13 Average topological path length for random spanning subgraphs (*black*), optimized spanning subgraphs (*horizontal lines*), and real gallery networks (*red circles*). Reproduced with permission from [77]

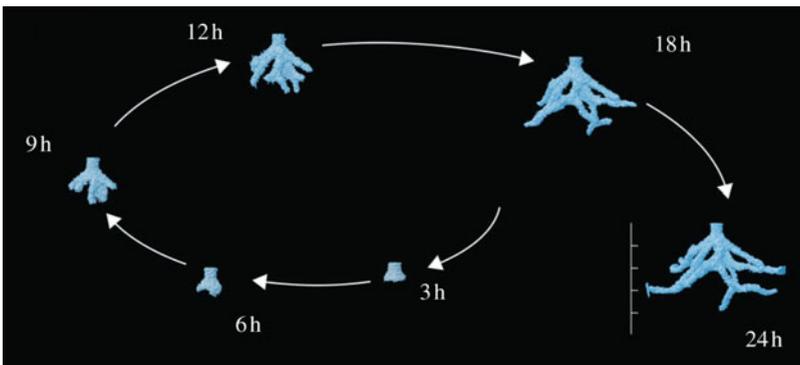


Fig. 14 Example of the progression of three-dimensional nest structure through time. Reproduced with permission from [63]

3 Even Further Beyond Worker–Worker Networks: A Task–Task Network

Networks play a role in several aspects of collective behavior in social insects. In Sect. 2 we presented a selection of the network types that have been most studied so far, including worker–worker interaction networks as well as other network types (bipartite plant–pollinator networks and nest architecture networks). We made the case for looking beyond networks of individual interactions, and employing network theory more broadly to other types of complex interacting processes. In support of this idea, we present original data worked into an example of a task–task network, i.e. defining the different tasks performed by workers in an insect colony as nodes, and each case of a worker switching between tasks as linking these nodes.

The process of allocating workers to the different jobs (“tasks”, such as foraging or nest-building) in a colony is both difficult and important to colony performance [9, 13, 36]. There is no consensus in the literature on how this is achieved in the face of changing demand for tasks and possible worker failure. To investigate this issue, we performed a temporal network analysis of the dynamics of task switching, asking if certain switching patterns were particularly common and whether the patterns of switching were stable over time. We hypothesized that workers would often rotate through certain “hub” tasks before switching to other tasks, and that flow through other tasks would be consistently low.

We collected a colony of *Temnothorax rugatulus* ants consisted of 41 workers and 2 queens in the Santa Catalina Mountains, outside of Tucson, Arizona USA in a pine forest at an altitude of approximately 8,000 ft. The collected ants were kept in the lab in artificial nests made of a piece of cardboard sandwiched between two glass slides ([27], see Fig. 15a). In the field, these ants typically nest in small rock crevices and artificial nests emulate these [32].

The ants were then painted with unique combinations of four paint spots, one on the head, one on the thorax and two on the abdomen so that they could be individually identified and tracked (Fig. 15b). Videos (5 min long) of normal colony activity were taken at four time points throughout the day: 8 am, 4 pm, 8 pm and 4 am (Fig. 15c). For each ant, the task it performed was recorded every second by an observer (see Table 1 for task list).

We first constructed a time-ordered network for each 5-min interval, creating a node for each task and an edge for each instance of a worker switching between tasks. Time-ordered networks are structures that provide a complete record of the timing of all observed interactions [11]. Here an example is shown for the first 5-min interval, qualitatively demonstrating extensive switching involving the tasks “wandering inside” (wi), “self-grooming” (sg), and “brood care” (bc), and some involving rotating through inactivity (i) (Fig. 16).

We used established techniques [11] to transform these time-ordered networks to a series of time-aggregated networks, with the aim of applying network methods in a temporal context. We chose a window size of 60 s but in this case results are robust to the choice of window size. Time aggregated networks constructed from

Fig. 15 Artificial *Temnothorax rugatulus* nest composed of a piece of cardboard sandwiched between two glass slides (a). Individually marked ants. The larger ant is a queen (b). Video recording setup of HD cameras equipped with servos filming an ant colony (c). Photos by Daniel Charbonneau

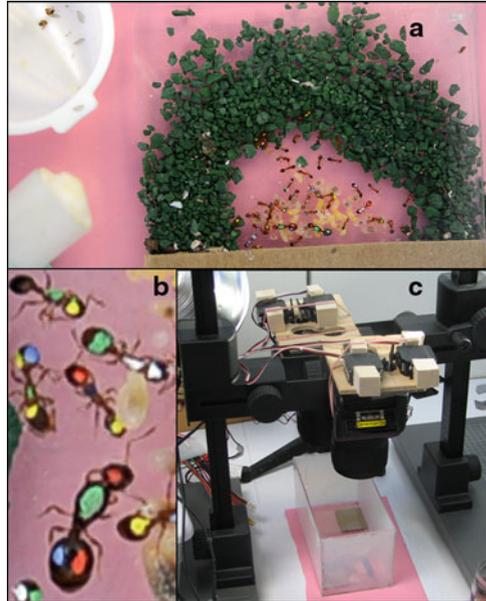


Table 1 List of possible tasks observed during video analysis and their associated codes

Code	Task
b	Nest building
f	Foraging
wo	Wandering outside nest
bc	Brood care
sg	Self-Grooming
go	Grooming other (giver)
og	Grooming other (receiver)
t	Trophallaxis
fd	Eating
wi	Wandering inside nest
i	Inactive

the first 5-min interval are shown below. These networks qualitatively demonstrate consistent patterns of flow between tasks (Fig. 17).

To quantitatively test whether workers return to a “hub” task before switching to new tasks, we measured betweenness for each task for every time-aggregated network during every interval (Fig. 18). The “wandering inside” (wi) task has the highest betweenness over nearly every time interval, demonstrating that it is a hub task. Most other tasks had consistently low betweenness. We then tested for temporal stability in the task flow by assessing trends in the betweenness of “wandering inside” (wi) over time. Within each interval, we found no significant increase or decrease (ANOVA; all $p > 0.12$). However across all intervals, there was a significant increase and then decrease in betweenness (ANOVA with linear and quadratic terms; both $p < 0.02$).

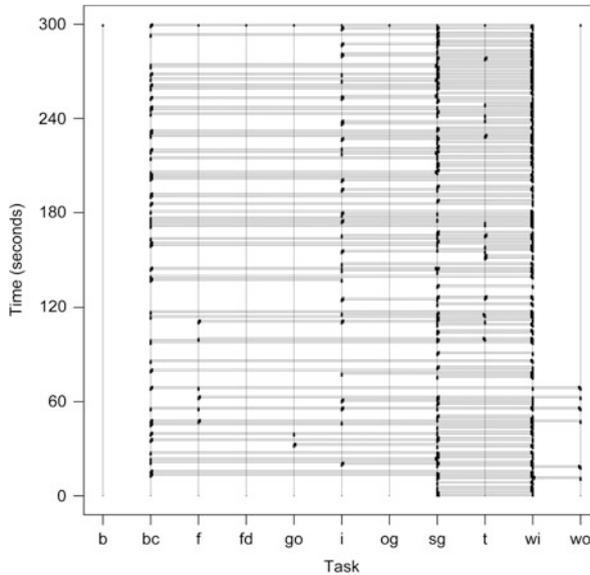


Fig. 16 Example of a time-ordered network for the first 5-min interval. Explanations of task abbreviations can be found in Table 1

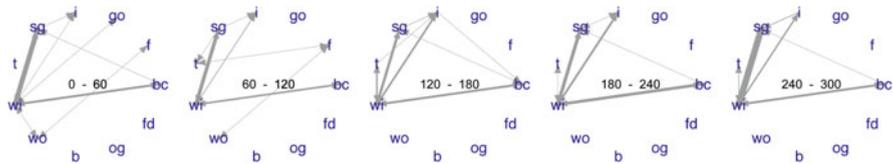


Fig. 17 Example time aggregated networks for the first 5-min interval. The numbers in the center of each network indicates the time interval in seconds. Explanations of task abbreviations can be found in Table 1

This temporal network analysis therefore indicates that there is minute-scale stability in task flow but hour-scale variation, and that most variation in task assignment is mediated through temporary assignment of workers to “wandering inside” (wi) tasks.

To interpret these results, we must first discuss the observed tasks. These fall into three separate categories. The first category, which includes all tasks with the exceptions of “wandering inside” and “inactive”, represents observable tasks that are thought to contribute to colony fitness (e.g. brood care or foraging). The second category (inactivity) is a conservative estimate of the time at which and duration during which individuals are inactive. The last category (anytime workers are wandering inside the nest but without performing an identifiable task) is less interpretable. We do not know whether they are simply being inactive, whether they are in fact performing some other yet to be identified task, whether they are simply between tasks, or whether they are looking for work to do. Some evidence in

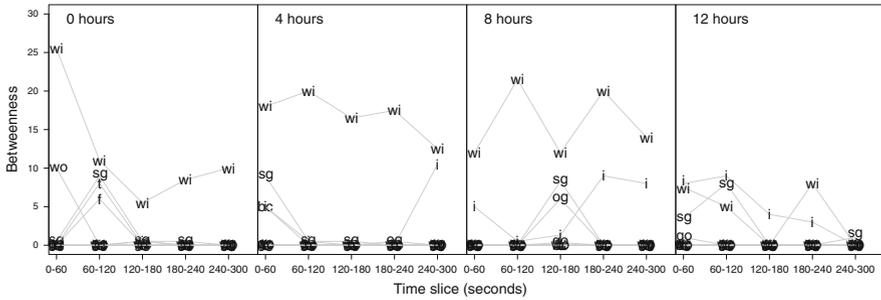


Fig. 18 Betweenness for each task for every time-aggregated network during each 60 s interval for all time points. Explanations of task abbreviations can be found in Table 1

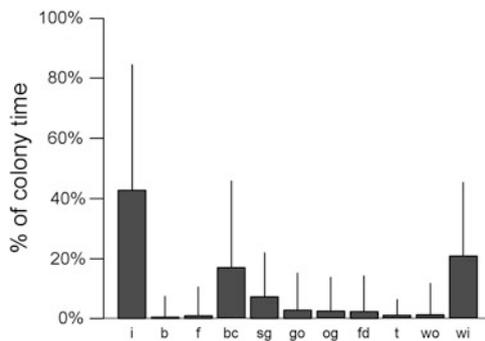


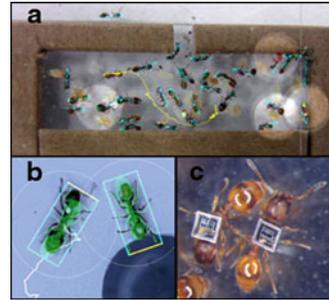
Fig. 19 Mean proportion of time spent in each task

honeybees indicates that they may be “patrolling”, i.e. collecting information about demand for work in different tasks [49].

The fact that the “wandering inside” (wi) task is a hub task (highest betweenness over nearly every time interval) suggests that the latter two possibilities are likely. Indeed, it seems as though “wandering inside” (wi) is an intermediate state between being engage in a task. We’ve shown that there is extensive switching between the tasks “wandering inside” (wi), “self-grooming” (sg), and “brood care” (bc), and some involving rotating through inactivity (i). This is likely because these are by far the tasks which workers spend most of their time doing (Fig. 19).

The temporal network approach lets us test new types of hypotheses and has identified a key behavior that deserves future study as it plays a key role in mediating between other tasks. Our task–task network quantifies the role of wandering in worker task switching in a new way as compared to other studies [48, 49]. It seems that ants must wander throughout the nest between tasks rather than awake from inactivity or directly switch from one active task to another.

Fig. 20 (a) Examples of the ant tracking tools being developed in Dr. Shin’s laboratory and (b) by Quitmeyer and Balch. (c) *Temnothorax albipennis* ants with RFID tags



4 Future Challenges and Opportunities

Many complex systems (e.g. social groups, neural networks, macro/micro-economics, etc.) can be studied with a network perspective, but these are often limited by constraints such as difficulty in acquiring high quantities of data or lack of an ethical or cost-effective way to do experiments. Social insects do not have these issues and thus provide a good model for other systems.

Because social insects are thought to employ relatively simple algorithms to achieve sophisticated group-level behaviors [19], they have been used as inspiration for the design of many artificial systems [12, 66]. Insect-inspired solutions have already been derived from foraging behavior [25], spatial sorting [59], or task allocation [13], and are used in job-shop scheduling [23], “traveling salesman” problems [24], software “agents” [74, 102], optimization of communication networks [20], and collective robotics (e.g. for planetary exploration: [14, 53]). Given the existence of a variety of methods for experimentation on social insects and that the research can be transposed to so many other fields, we expect this list to keep growing.

Although social insect colonies are tractable to observation and manipulation and offer a means of gathering real data relatively quickly, the many steps and processes required for acquiring data are still fairly time- and work-intensive. In many cases, social insect networks are created from spatial information and advances in tracking software have helped reduce the workload of acquiring this type of data. For example, Dr. Shin’s lab at the University of North Carolina Charlotte has developed a tracking tool (Fig. 20a) that can highly reliably track individual ants (96% + accurate) [81], but there are other tracking tools being developed as well (e.g. [84], Fig. 20b). The miniaturization of electronics has made it possible to use of radio-frequency identification (RFID) chips to both uniquely identify individuals and track individual movement ([64, 87], see Fig. 20c). Lastly, rapidly emerging analytical methods are being developed by social insect scientists (e.g. the R package “timeordered” that was used in the worked example. See [11] for a review).

Applying network approaches to social insect research is an emerging area and many studies are only just getting off the ground. Initial datasets were so hard to obtain that authors are reluctant to publish them completely. However, with new methods of obtaining data (e.g. video tracking) and new traditions in science (it is

becoming more common and often required by journals and NSF to publish full datasets) this is likely to change. Furthermore, there is a strong interest from social insect scientists to collaborate and share their data with network researchers and theoreticians. Indeed, social insect researchers often have the data and the biological questions which could be answered by network analyses, but lack the know-how to answer them appropriately.

The development of new network analysis tools can advance our understanding of social insect networks, but also of general organizational principles. We can transpose many social insect adaptive functions on to functions of interest to humans such as organizational structures, social and computer networks as well as physics and engineering. Social insect networks have been optimized by evolution to deal with multiple simultaneous constraints and principles derived from social insect systems can be used to find optimal network structures for multiple functions or under specific constraints.

Nonetheless, there are future challenges that need to be addressed in order for the use of the network framework to move forward. More and more the importance of including a temporal element to static networks is becoming evident. These can have drastic effects on results and even yield completely inverse results as in the case of specialist vs. generalist pollinators in pollination networks (See Sect. 2.2.1).

Furthermore, simply including a temporal element is insufficient. Finding and using an appropriate timescale is equally essential in drawing out accurate conclusions. In ant interaction networks, Blonder and Dornhaus [10] show that at small timescales, degree distribution is heterogeneous and some individuals are more central than others, but that at larger timescales degree distribution flattens out and becomes more uniform (See Sect. 2.1.4). If we only looked at the smaller timescale, we would conclude that some individuals are more central and perhaps act as communication hubs.

In this chapter, we have made the case for moving beyond worker–worker networks. This is an exciting avenue of network research that will open the possibility of answer novel questions. The framework surrounding bipartite networks will be especially important in advancing this burgeoning area of research.

Emerging technologies are facilitating the way social insect researchers gather and analyze data, but their development is also fostering a desire for interdisciplinary collaboration. Indeed, the need to develop time-saving technologies as well as the possibility of transposing research between fields is bringing together biologists, computer scientist, engineers, physicists, mathematicians, to name a few, and creating a synergism in research that we feel will be very exciting in years to come.

References

1. Alarcón, R., Waser, N.M., Ollerton, J.: Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos* **117**, 1796–1807 (2008). doi: 10.1111/j.0030-1299.2008.16987.x

2. Baker, H.G., Hurd, P.D.: Intrafloral ecology. *Annu. Rev. Entomol.* **13**, 385–414 (1968)
3. Barabási, A.L., Albert, R.: Emergence of scaling in random networks. *Science* **286**, 509–512 (1999)
4. Barabási, A., Bonabeau, E.: Scale-free networks. *Sci. Am.* **288**, 60–69 (2003)
5. Bascompte, J., Jordano, P.: Plant–animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **38**, 567–593 (2007)
6. Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M.: The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* **100**, 9383 (2003)
7. Beckers, R., Deneubourg, J.L., Goss, S.: Trails and U-turns in the selection of a path by the ant *Lasius niger*. *J. Theor. Biol.* **159**, 397–397 (1992a)
8. Beckers, R., Deneubourg, J.L., Goss, S.: Trail laying behaviour during food recruitment in the ant *Lasius niger* (L.). *Insect. Soc.* **39**, 59–72 (1992b)
9. Beshers, S.N., Fewell, J.H.: Models of division of labor in social insects. *Annu. Rev. Entomol.* **46**, 413–440 (2001)
10. Blonder, B., Dornhaus, A.: Time-ordered networks reveal limitations to information flow in ant colonies. *PLoS ONE* **6**, e20298 (2011)
11. Blonder, B., Dornhaus, A., Wey, T.W., et al.: Temporal dynamics and network analysis. *Methods Ecol. Evol.* **3**, 958–972 (2012)
12. Bonabeau, E., Dorigo, M., Theraulaz, G.: *Swarm Intelligence: from Natural to Artificial Systems*. Oxford University Press, Oxford (1999)
13. Bonabeau, E., Sobkowski, A., Theraulaz, G., Deneubourg, J.L.: Adaptive task allocation inspired by a model of division of labor in social insects. *Biocomput. Emergent Comput.* 36–45 (1997)
14. Brooks, R.A., Flynn, A.M.: Fast, cheap and out of control. DTIC document (1989)
15. Buffin, A., Goldman, S., Deneubourg, J.L.: Collective regulatory stock management and spatiotemporal dynamics of the food flow in ants. *FASEB J.* **26**, 2725–2733 (2012). doi: 10.1096/fj.11–193698
16. Buhl, J., Gautrais, J., Deneubourg, J.L., Theraulaz, G.: Nest excavation in ants: group size effects on the size and structure of tunneling networks. *Naturwissenschaften* **91**, 602–606 (2004a)
17. Buhl, J., Gautrais, J., Louis Deneubourg, J., et al.: The growth and form of tunnelling networks in ants. *J. Theor. Biol.* **243**, 287–298 (2006). doi: 10.1016/j.jtbi.2006.06.018
18. Buhl, J., Gautrais, J., Solé, R.V., et al.: Efficiency and robustness in ant networks of galleries. *Euro. Phys. J. B Condens. Matter Complex Syst.* **42**, 123–129 (2004b)
19. Camazine, S., Deneubourg, J.L., Franks, N.R., et al.: *Self-Organization in Biological Systems*. Princeton University Press, Princeton (2003)
20. Di Caro, G., Dorigo, M.: AntNet: distributed stigmergetic control for communications networks. *J. Artif. Intell. Res.* **9** (1998)
21. Cassill, L.D., Tschinkel, W.R.: Regulation of diet in the fire ant, *Solenopsis invicta*. *J. Insect Behav.* **12**, 307–328 (1999)
22. Chapman, R.E., Bourke, A.F.G.: The influence of sociality on the conservation biology of social insects. *Ecol. Lett.* **4**, 650–662 (2001)
23. Cicirello, V.A., Smith, S.F.: Wasp-like agents for distributed factory coordination. *Auton. Agent. Multi-Agent Syst.* **8**, 237–266 (2004)
24. Dorigo, M., Gambardella, L.M., others: Ant colonies for the travelling salesman problem. *BioSystems* **43**, 73–82 (1997)
25. Dorigo, M., Stützle, T.: *Ant Colony Optimization*. MIT, Cambridge (2004)
26. Dornhaus, A., Holley, J.A., Franks, N.R.: Larger colonies do not have more specialized workers in the ant *Temnothorax albipennis*. *Behav. Ecol.* **20**, 922–929 (2009)
27. Dornhaus, A., Holley, J.A., Pook, V.G., et al.: Why do not all workers work? Colony size and workload during emigrations in the ant *Temnothorax albipennis*. *Behav. Ecol. Sociobiol.* **63**, 43–51 (2008)
28. Dunne, J.A.: *The Network Structure of Food Webs. Ecological Networks: Linking Structure to Dynamics in Food Webs*, pp. 27–86. Oxford University Press, Oxford (2006)

29. Dunne, J.A., Williams, R.J., Martinez, N.D.: Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* **5**, 558–567 (2002)
30. Dupont, Y.L., Padrón, B., Olesen, J.M., Petanidou, T.: Spatio-temporal variation in the structure of pollination networks. *Oikos* **118**, 1261–1269 (2009). doi: 10.1111/j.1600-0706.2009.17594.x
31. Fewell, J.H.: Social insect networks. *Science* **301**, 1867–1870 (2003)
32. Franks, N.R., Mallon, E.B., Bray, H.E., et al.: Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* **65**, 215–223 (2003)
33. Franks, N.R., Pratt, S.C., Mallon, E.B., et al.: Information flow, opinion polling and collective intelligence in house-hunting social insects. *Phil. Trans. R Soc. Lond. B* **357**, 1567–1583 (2002). doi: 10.1098/rstb.2002.1066
34. Gautrais, J., Theraulaz, G., Deneubourg, J.L., Anderson, C.: Emergent polyethism as a consequence of increased colony size in insect societies. *J. Theor. Biol.* **215**, 363–373 (2002)
35. Gordon, D.M.: *Interaction Patterns and Task Allocation in Ant Colonies*. Birkhäuser Verlag, Basel, Switzerland (1999)
36. Gordon, D.M.: The organization of work in social insect colonies. *Nature* **380**, 121–124 (1996)
37. Gordon, D.M.: *Ant encounters: Interaction Networks and Colony Behavior*. Princeton University Press, Princeton (2010)
38. Greene, M.J., Gordon, D.M.: Interaction rate informs harvester ant task decisions. *Behav. Ecol.* **18**, 451–455 (2007)
39. Grimaldi, D.A., Engel, M.S.: *Evolution of the Insects*. Cambridge University Press, Cambridge (2005)
40. Hodges, S.A., Arnold, M.L.: Columbinas: A geographically widespread species flock. *Proc. Natl. Acad. Sci. USA* **91**, 5129 (1994)
41. Holden, C.: Entomologists wane as insects wax. *Science* **246**, 754–756 (1989). doi:10.1126/science.2814497
42. Hölldobler, B., Wilson, E.O.: *The Ants*. Belknap Press of Harvard University Press, Cambridge (1990)
43. Ings, T.C., Montoya, J.M., Bascompte, J., et al.: Review: ecological networks – beyond food webs. *J. Anim. Ecol.* **78**, 253–269 (2009). doi: 10.1111/j.1365-2656.2008.01460.x
44. Jandt, J.M., Dornhaus, A.: Spatial organization and division of labour in the bumblebee *Bombus impatiens*. *Anim. Behav.* **77**, 641–651 (2009)
45. Jeanson, R.: Long-term dynamics in proximity networks in ants. *Anim. Behav.* **83**, 915–923 (2012). doi: 10.1016/j.anbehav.2012.01.009
46. Jeanson, R., Fewell, J.H., Gorelick, R., Bertram, S.M.: Emergence of increased division of labor as a function of group size. *Behav. Ecol. Sociobiol.* **62**, 289–298 (2007)
47. Jeong, H., Tombor, B., Albert, R., et al.: The large-scale organization of metabolic networks. *Nature* **407**, 651–654 (2000)
48. Johnson, B.R.: Global information sampling in the honey bee. *Naturwissenschaften* **95**, 523–530 (2008)
49. Johnson, B.R.: A Self-organizing model for task allocation via frequent task quitting and random walks in the honeybee. *Am. Nat.* **174**, 537–547 (2009)
50. Karsai, I., Wenzel, J.W.: Productivity, individual-level and colony-level flexibility, and organization of work as consequences of colony size. *Proc. Natl. Acad. Sci.* **95**, 8665 (1998)
51. Keeling, M.J., Rohani, P.: *Modeling Infectious Diseases in Humans and Animals*. Princeton University Press, Princeton (2008)
52. Khanin, R., Wit, E.: How scale-free are biological networks. *J. Comput. Biol.* **13**, 810–818 (2006)
53. Krieger, M.J.B., Billeter, J.B., Keller, L.: Ant-like task allocation and recruitment in cooperative robots. *Nature* **406**, 992–995 (2000)
54. Lanan, M.C., Dornhaus, A., Jones, E.I., et al.: The trail less traveled: individual decision-making and its effect on group behavior. *PLoS ONE* **7**, e47976 (2012). doi: 10.1371/journal.pone.0047976

55. Linksvayer, T.A., Fewell, J.H., Gadau, J., Laubichler, M.D.: Developmental evolution in social insects: regulatory networks from genes to societies. *J. Exp. Zool. B Mol. Dev. Evol.* **318**, 159–169 (2012). doi: 10.1002/jez.b.22001
56. Linksvayer, T.A., Fondrk, M.K., Page, R.E.: Honeybee social regulatory networks are shaped by colony-level selection. *Am. Nat.* **173**, E99–E107 (2009). doi: 10.1086/596527
57. Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R., Memmott, J.: The impact of an alien plant on a native plant–pollinator network: an experimental approach. *Ecol. Lett.* **10**, 539–550 (2007)
58. Lovell, J.H.: *The Flower and the Bee: Plant Life and Pollination*. C. Scribner's sons, New York (1918)
59. Lumer, E.D., Faieta, B.: Diversity and adaptation in populations of clustering ants. In: *From Animals to Animats. Proceedings of the 3rd International Conference on the Simulation of Adaptive Behavior*, pp. 501–508 (1994)
60. Maslov, S., Sneppen, K.: Specificity and stability in topology of protein networks. *Science* **STKE** **296**, 910 (2002)
61. Memmott, J., Craze, P.G., Waser, N.M., Price, M.V.: Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* **10**, 710–717 (2007)
62. Memmott, J., Waser, N.M., Price, M.V.: Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 2605–2611 (2004)
63. Minter, N.J., Franks, N.R., Robson Brown, K.A.: Morphogenesis of an extended phenotype: four-dimensional ant nest architecture. *J. R. Soc. Interface* **9**, 586–595 (2011). doi: 10.1098/rsif.2011.0377
64. Moreau, M., Arrufat, P., Latil, G., Jeanson, R.: Use of radio-tagging to map spatial organization and social interactions in insects. *J. Exp. Biol.* **214**, 17–21 (2011)
65. Najjar, W., Gaudiot, J.L.: Network resilience: A measure of network fault tolerance. *IEEE Trans. Comput.* **39**, 174–181 (1990)
66. Nakano, T.: Biologically inspired network systems: a review and future prospects. *IEEE Trans. Syst. Man Cybern. C Appl. Rev.* 1–14 (2011)
67. Naug, D.: Structure and resilience of the social network in an insect colony as a function of colony size. *Behav. Ecol. Sociobiol.* **63**, 1023–1028 (2009). doi: 10.1007/s00265–009–0721-x
68. Naug, D.: Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behav. Ecol. Sociobiol.* **62**, 1719–1725 (2008)
69. Naug, D., Smith, B.: Experimentally induced change in infectious period affects transmission dynamics in a social group. *Proc. R. Soc. B Biol. Sci.* **274**, 61–65 (2007)
70. Van Noort, V., Snel, B., Huynen, M.A.: The yeast coexpression network has a small-world, scale-free architecture and can be explained by a simple model. *EMBO Rep.* **5**, 280–284 (2004)
71. Olesen, J.M., Bascompte, J., Elberling, H., Jordano, P.: Temporal dynamics in a pollination network. *Ecology* **89**, 1573–1582 (2008)
72. Oster, G.F., Wilson, E.O.: *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton (1979)
73. Otterstatter, M.C., Thomson, J.D.: Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia* **154**, 411–421 (2007)
74. Parunak, H.V.D.: “Go to the ant”: Engineering principles from natural multi-agent systems. *Ann. Oper. Res.* **75**, 69–102 (1997)
75. Patek, S.N., Baio, J.E., Fisher, B.L., Suarez, A.V.: Multifunctionality and mechanical origins: ballistic jaw propulsion in trap-jaw ants. *Proc. Natl. Acad. Sci. USA* **103**, 12787–12792 (2006). doi:10.1073/pnas.0604290103
76. Perna, A., Jost, C., Couturier, E., et al.: The structure of gallery networks in the nests of termite *Cubitermes* spp. revealed by X-ray tomography. *Naturwissenschaften* **95**, 877–884 (2008a)
77. Perna, A., Valverde, S., Gautrais, J., et al.: Topological efficiency in three-dimensional gallery networks of termite nests. *Phys. A Stat. Mech. Appl.* **387**, 6235–6244 (2008b). doi: 10.1016/j.physa.2008.07.019
78. Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., et al.: Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network

- structure and implications for estimates of specialization. *Ecol. Lett.* **11**, 564–575 (2008). doi: 10.1111/j.1461-0248.2008.01170.x
79. Pie, M.R., Rosengaus, R.B., Traniello, J.F.A.: Nest architecture, activity pattern, worker density and the dynamics of disease transmission in social insects. *J. Theor. Biol.* **226**, 45–51 (2004). doi: 10.1016/j.jtbi.2003.08.002
80. Pinter-Wollman, N., Wollman, R., Guetz, A., et al.: The effect of individual variation on the structure and function of interaction networks in harvester ants. *J. R. Soc. Interface* **8**, 1562–1573 (2011). doi: 10.1098/rsif.2011.0059
81. Poff, C., Nguyen, H., Kang, T., Shin, M.C.: Efficient Tracking of Ants in Long Video with GPU and Interaction (2012)
82. Powell, S., Tschinkel, W.R.: Ritualized conflict in *Odontomachus brunneus* and the generation of interaction-based task allocation: a new organizational mechanism in ants. *Anim. Behav.* **58**, 965–972 (1999)
83. Pratt, S.C., Sumpter, D.J.T.: A tunable algorithm for collective decision-making. *PNAS* **103**, 15906–15910 (2006). doi: 10.1073/pnas.0604801103
84. Quitmeyer, A., Balch, T.: Biotrack Pack 1.5. In: Bio-Tracking. <http://www.bio-tracking.org/biotrackpack/>
85. Retana, J., Cerdá, X.: Social Organization of *Cataglyphis cursor* Ant Colonies (Hymenoptera, Formicidae): Inter-, and Intraspecific Comparisons. *Ethology* **84**, 105–122 (1990). doi: 10.1111/j.1439-0310.1990.tb00788.x
86. Robertson, C.: Flowers and Insects: Lists of Visitors to Four Hundred and Fifty-Three Flowers. C. Robertson. National Center for Ecological Analysis and Synthesis Interaction, Carlinville, IL (1929). Web Database: http://www.nceas.ucsb.edu/interactionweb/html/robertson_1929.html. Keywords: Lists plant–pollinator interactions for 456
87. Robinson, E.J.H., Smith, F.D., Sullivan, K.M.E., Franks, N.R.: Do ants make direct comparisons? *Proc. R. Soc. B* (2009). doi: 10.1098/rspb.2009.0350
88. Rueppell, O., Kirkman, R.W.: Extraordinary starvation resistance in *Temnothorax rugatulus* (Hymenoptera, Formicidae) colonies: Demography and adaptive behavior. *Insect. Soc.* **52**, 282–290 (2005). doi: 10.1007/s00040-005-0804-2
89. Samways, M.J.: Insects in biodiversity conservation: some perspectives and directives. *Biodivers. Conserv.* **2**, 258–282 (1993)
90. Schwander, T., Rosset, H., Chapuisat, M.: Division of labour and worker size polymorphism in ant colonies: the impact of social and genetic factors. *Behav. Ecol. Sociobiol.* **59**, 215–221 (2005)
91. Seeley, T.D., Kolmes, S.A.: Age polyethism for hive duties in honey bees — illusion or reality? *Ethology* **87**, 284–297 (1991). doi: 10.1111/j.1439-0310.1991.tb00253.x
92. Sendova-Franks, A.B., Franks, N.R.: Spatial relationships within nests of the ant *Leptothorax unifasciatus* (Latr.) and their implications for the division of labour. *Anim. Behav.* **50**, 121–136 (1995)
93. Sendova-Franks, A.B., Hayward, R.K., Wulf, B., et al.: Emergency networking: famine relief in ant colonies. *Anim. Behav.* **79**, 473–485 (2010)
94. Sole, R.V., Montoya, M.: Complexity and fragility in ecological networks. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 2039–2045 (2001)
95. Sueur, C., Jacobs, A., Amblard, F., et al.: How can social network analysis improve the study of primate behavior? *Am. J. Primatol.* **73**, 703–719 (2011)
96. The World Conservation Union: IUCN red list of threatened species. Summary Statistics for Globally Threatened Species (2010)
97. Thomas, M.L., Elgar, M.A.: Colony size affects division of labour in the ponerine ant *Rhytidoponera metallica*. *Naturwissenschaften* **90**, 88–92 (2003)
98. Tong, A.H.Y., Lesage, G., Bader, G.D., et al.: Global mapping of the yeast genetic interaction network. *Science STKE* **303**, 808 (2004)
99. Waser, N.M., Chittka, L., Price, M.V., et al.: Generalization in pollination systems, and why it matters. *Ecology* **77**, 1043–1060 (1996). doi: 10.2307/2265575

100. Waters, J.S., Fewell, J.H.: Information processing in social insect networks. *PLoS ONE* **7**, e40337 (2012). doi: 10.1371/journal.pone.0040337
101. Watts, D.J., Strogatz, S.H.: Collective dynamics of “small-world” networks. *Nature* **393**, 440–442 (1998)
102. Weiss, G.: *Multiagent Systems a Modern Approach to Distributed Artificial Intelligence*. MIT, Cambridge (1999)
103. Wey, T., Blumstein, D.T., Shen, W., Jordán, F.: Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* **75**, 333–344 (2008)
104. Wilson, E.O.: *Ants*. Bull. Am. Acad. Arts Sci. **45**, 13–23 (1991)
105. Wilson-Rich, N., Spivak, M., Fefferman, N.H., Starks, P.T.: Genetic, individual, and group facilitation of disease resistance in insect societies. *Annu. Rev. Entomol.* **54**, 405–423 (2009). doi: 10.1146/annurev.ento.53.103106.093301
106. Wuchty, S., Ravasz, E., Barabási, A.L.: The architecture of biological networks. *Complex Syst. Sci. Biomed.* 165–181 (2006)