J Bioecon (2015) 17:207–216
DOI 10.1007/s10818-015-9207-2

Social Biomimicry: what do ants and bees tell us about organization in the natural world?

Jennifer H. Fewell[1]

Abstract The social insects serve as exemplars for social biomimicry, the search for social design inspiration from the natural world. Although their group members are individually much simpler than humans, social insect colonies provide elegant tutorials on the large-scale outcomes that can be achieved by social interactions and self-organizational processes. These range from complex physical structures built by collective effort; to exemplars of flexible work organization; to effective consensus building in group decisions. This special issue highlights examples of the lessons to be learned from the bees and ants, providing ways to think about how humans can (and in some cases should not) borrow from social insect rules of organization and their collective outcomes.

Keywords Social biomimicry · Social insects · Self-organization · Collective behavior

1 Introduction

Biomimicry is the search for design inspiration from the natural world (Benyus 1997; Passino 2005). A wealth of organismal design features have served as inspiration for technological design, from the adhesive foot pads of wall-climbing geckos (Autumn et al. 2000, 2006), to the limb and tail balance of bounding kangaroos (reviewed in Chevallereau et al. 2013). Innovation at the *social* scale also represents a biomimicry frontier, especially as we accelerate into the unique challenges of modern

---

✉ Jennifer H. Fewell
j.fewell@asu.edu

[1] School of Life Sciences and Center for Social Dynamics and Complexity, Arizona State University, Tempe, AZ 85287-4501, USA

technologically-driven and interconnected societies. This new social world requires effective ways to communicate across large networks, and innovative organizational approaches to generate effective social outcomes at the community to global levels.

The question of how large groups can effectively organize themselves is, of course, not unique to human societies. Eusocial insects, especially the ants, termites and honey bees, have been living in large complex societies for almost 200 million years (Hölldobler and Wilson 2009). The degree of size and social complexity varies dramatically in social insect colonies. Ant colonies range in size from a few dozen individuals to millions; they may include several queens who behave both cooperatively and in competition with each other, or consist of a single reproducing queen and thousands of workers (Hölldobler and Wilson 1990; Bourke and Franks 1995). Importantly, across this diversity, social insect societies use a consistent generalized set of organizing principles that are applicable to a range of human organizational problems. These are: (1) that large scale societies can organize up effectively from diverse local interactions, rather than being imposed via external or centralized commands (i.e. they function as distributed systems); (2) the cumulative effects of these local interactions, or social dynamics, generate nonlinear changes in social behavior (self-organization), and (3) these effects scale up into group-level effects, allowing the emergence of group level products that are much more than a summation of individual abilities (Bonabeau et al. 1997; Camazine et al. 2001).

This issue presents four examples of how research on the organization of insect societies can inform social biomimicry. Charbonneau and Dornhaus (2015) synthesize the organizing mechanisms behind the systems of task allocation and division of labor for which social insects are exemplars. This discussion gives special consideration to one of the most puzzling aspects of colony organization: the presence in functional colonies of what appear to be lazy individuals. Grüner et al. (2015) discuss the mechanisms by which a heterogeneous group (the honey bee colony) evaluates information from diverse sources, and coordinates to collectively decide on a single outcome. They then consider how the rule sets generating consensus in bees might inform voting processes in human social constructs. Examining the structural outcomes of self-organizational processes, Tschinkel (2015) provides an overview of the diversity of subterranean nest architectures generated by ant colonies, ranging from small and simple nests to harvester ant colonies, whose nests are constructed as a cascade of chambers extending several feet into the ground. From Cassill et al. 's (2015), we learn about the emergency "life rafts" constructed by fire ants in response to flooding. These rafts are created as an amalgam of worker bodies, designed to carry the queen and brood to safety. This feat combines the self-organizational processes inherent in group assembly, with the physical ability of some ants to link their bodies together and create larger group structures. The juxtaposition of these very different structures—one a physical space and the other a raft made of bodies—provides a concrete example of how variation in simple iterative rule sets can generate a world of diversity in functional design.

Each of the articles also asks us to consider social insect collective behavior from newer viewpoints. Charbonneau and Dornhaus (2015) offer an important take-home message from their consideration of task allocation mechanisms. Effective colony function is not an analogy for "optimization"; it necessarily also includes the ability of colonies to adapt flexibly and quickly to a changing environment. Cassill et al. 's (2015) experimental analyses move from elements of the construction process to individual costs of survival in these structures. Her discussion, along with that of Grüner et al. (2015), reminds us that social insects and humans vary fundamentally in their consideration of the importance of the individual versus the group in decision making, and in answering the question of "what is effective colony function?"

2 Self-organization and emergence as the building blocks for colony organization

The diverse examples of behavioral coordination in this issue all emerge from self-organizational processes. Thus, it is useful to remind ourselves what this fundamentally means. Individual workers in a colony generally operate around relatively simple rule sets for behavior. Instead of being directed from a central or external controller, they behave in response to information they receive from their local environment and/or the other ants around them. A social insect colony therefore operates as a distributed, rather than a centralized system (Anderson and McShea 2001). The cumulative outcomes of local interactions among workers can generate escalating effects on individual and group level behaviors. These self-organizational effects minimally require two components: (a) iteration, or a repeating pattern of interactions, coupled with (b) positive feedback loops, which produce the escalation effects from those interactions (Bonabeau et al. 1999; Jeanson and Deneubourg 2009). A classic example occurs when ant foragers make decisions about which of two alternate routes to choose. Foragers initially choose either path randomly when offered no information to differentiate them. However, once trail pheromone is deposited by a successful first forager, the choice of subsequent foragers is weighted towards the marked trail. As successive ants choose that path and deposit additional trail pheromone, that signal is amplified (via positive feedback), and the colony converges on a single resource (Beckers et al. 1993; Sumpter and Beekman 2003).

Most functional self-organizational processes require a combination of positive coupled with negative feedback, to allow flexible moderation of outcomes. In the above example, positive feedback leads to a single food source, but the addition of negative feedback rules allow the colony to switch quickly away from resources as they deplete or become over-crowded (Grüter et al. 2012; Czaczkes et al. 2013). With this combination of simple rule sets incorporating amplification effects and modulation, social insect "teams" perform an array of complex activities required for successful social life, from resource collection to house construction, colony maintenance, and offspring care, as well as coordinating in nest defense or even in attacking other nests. Models inspired by social insect design have already proven extremely useful for a range of computing and network applications, including as a few examples: routing algorithms for transportation and communication networks, or programming robotic systems for autonomous exploration, and/or task coordination (Bonabeau et al. 1999; Kube and Bonabeau 2000; Garnier et al. 2005; Passino 2005; Şahin 2005; Karaboga and Akay 2009).

To be mimetic and biologically relevant, algorithms of social organization must capture social complexity without being too complex. How small can individual rule sets be, and still produce meaningful patterns of behavior? As one example, the patterns of trail formation in army ants build from a “golden seven-rule set”, including components in which individuals follow a trail (positive feedback) unless that trail is too crowded (negative feedback; Camazine et al. 2001; Franks et al. 2009). These rules, coupled with speed of movement and recruitment, allow foragers to move quickly and efficiently along intricate trail systems and most efficiently retrieve prey. Slight quantitative variations in the rule set produce recognizable species-specific trail architecture, adaptable to the type and distribution of prey they hunt. These types of detailed biological studies identify minimum individual complexity and the associated mechanisms for interaction. Similarly, social insects can serve as inspiration for human building design (Ben-Alon et al. 2014). Likely, the rules of excavation for ant nests begin with: excavate where there is evidence of a tunnel. From this, species differences in rule sets likely generate a diversity of subterranean nests, varying in number of chambers, connections between tunnels, and the types of activities performed within separate regions of the nest. Until recently, little was known about the functional and evolutionary diversity in these underground nest structures. The work of Tschinkel and colleagues in dissecting and reconstructing nest architecture, beautifully summarized in this issue, provides a wealth of information from which to model their construction processes.

3 The social insect colony as a model for the organization of work

Just as self-organizational processes can lead to behavioral convergence, they can also lead to divergence. Division of labor, in which the different workers of a colony specialize on different tasks, is a hallmark of eusocial insects. Many activities, such as nest construction or recruitment to food, generally involve only a subset of the workforce. Others, such as house hunting or building life rafts, occur only periodically, thus requiring shifting of individuals between tasks. The self-organizing principles driving division of labor provide one of the most directly relevant social biomimicry exemplars for human societal organization.

The organization of work within a colony is based on the need for individuals to self-sort across the different tasks required for colony function. The most recognized mechanisms underlying this task allocation are morphological or age differences among workers that channel them with some bias into different tasks (reviewed by Hölldobler and Wilson 1990, 2009). However, as in humans, these are actually somewhat limited in their occurrence across social insect taxa. Further, as nicely discussed by Charbonneau and Dornhaus, mechanisms such as morphological castes that reduce individual flexibility can constrain social groups from adjusting flexibly to changes in task need.

Like other colony functions, the allocation of workers across tasks is actively dependent on self-organizing mechanisms. Models for these often include the assumption of response thresholds, in which each worker has an innate set-point, and is biased towards performing a task when stimulus levels exceed that threshold (Bonabeau et al. 1998; reviewed by Beshers and Fewell 2001). In these models, thresholds generate divergence in individual task choices, although individuals retain the ability to perform other task when colony need becomes high. Response threshold models can be integrated with reinforcement, in which individuals become more specialized as they increasingly perform a task (Theraulaz et al. 1998), and with spatial parameters, such as fidelity to areas of the nest in which certain tasks occur, or with progressive changes in location and thus tasks performed (Sendova-Franks and Franks 1995; Tschinkel 1999). These models make two important points. First, a distributed system such as a social insect colony can maintain group-level flexibility while achieving a useful level of individual specialization. Second, diversity across individuals can be extremely important to group-level success (Oldroyd and Fewell 2007). When models lack such mechanisms for generating individual-level variation in task preference, successful division of labor becomes difficult to achieve (Myerscough and Oldroyd 2004; Jeanson et al. 2007).

Social insects also make excellent empirical systems in which to "ground truth" organizational models. In other words, does an optimized model of task organization reflect the real world? As a challenge to the answer of "yes", studies of worker task performance and activity raise an intriguing and quite counter-intuitive point for task allocation models. As Charbonneau and Dornhaus discuss, a large minority (and sometimes a majority) of workers at any given time are inactive. Some are so consistently inactive that they can be categorized as "lazy". What, if any function do these workers serve? Are they a reserve population, available for when the colony needs an extreme worker force? Perhaps, they instead represent a natural outcome of variation—a colony that requires a distribution of task thresholds must tolerate some individuals with high thresholds for all tasks. In other words, they are a necessary fallout of an otherwise useful system. Charbonneau present an alternative possibility, that they help colonies regulate task performance consistently, even with temporal and/or stochastic fluctuations in workload.

4 Coming to consensus in social insect and human societies

Social insects serve also as an important comparison and counterpoint to modern and large-scale human societies (Gowdy and Krall 2015; Wilson and Gowdy 2015). Of all animal societies, only the social insects match modern urban societies in scale. They face similar issues in scaling of resource and energy flow, in organization of labor, and in the challenges of reaching consensus. Highly eusocial colonies have become a point of interest for their analogy to human voting processes (Seeley 2010). House hunting in ant and bee colonies requires a series of processes from information gathering, to assessment and consensus (Franks et al. 2002; Seeley 2003). This begins when the colony sends out scouts, who return with incomplete information on the location and quality of nest sites. The colony as a whole receives more complete information, presented as competing recruitment signals for choosing individual sites. The components of this voting process involve multiple critical features. First, the recruitment intensity (or number recruiting) varies according to quality of nest site; this requires that individual scouts have their own internal assessment of quality. As a result, high quality nest sites receive higher intensity than a low quality one (Franks et al. 2002, 2003b; Seeley 2003). Second, and an important lesson for human social consensus, individual signaling for less popular options must decrease in frequency (Seeley et al. 2012), so that recruitment for lower quality sites decays. Finally, there has to be an end to the voting process. Both honey bees and house hunting ants achieve a transition point, a quorum, in which they shift from voting to consensus and the actual process of moving begins. Achieving a quorum does not require 100% consensus for a single option before it is achieved; however, once that transition occurs, the colony moves as an entirety to that single location (Pratt 2005; Sumpter and Pratt 2009).

These voting processes serve as interesting examples for human consensus processes, because the colony as a group of voters achieves a level of consensus that matches very accurately to the options available. Colony decisions are not perfect. House hunting ants, for example, are much more likely to make mistakes under conditions when it is important to make a decision quickly, suggesting that the process suffers from speed-accuracy trade-offs (Franks et al. 2003a). However, colonies are generally extremely good at choosing the best nest site among options, although the information provided by any individual scout is always limited. The ongoing process of changing numbers of individuals "competing" via signaling allows colonies to select the better option, even when an individual has incorrect information or gives inaccurate information on the value of their site (Franks et al. 2015). Colonies thus can make rational nest decisions even when individual ants have sub-optimal biases (Sasaki and Pratt 2011; Franks et al. 2015).

Humans engage in similar consensus building, for example when using iterative and anonymous voting procedures. (We come to similar convergence informally when social media affect our choices of the latest products to buy!). Both individual humans and individual ants or bees are also faced with limited information during decision making; we all have bounded rationality (Simon 1982, 1986). Imagine being offered a choice between two options that vary in different ways such that there is no generally correct choice. If a third option is presented that is similar to, but worse than one of the first two options, individual ants and humans are both biased towards the original option that they can most easily compare to this "decoy". Retailers use the decoy effect on humans to great advantage. Ant colonies, however, are not fooled by the decoy—they choose rationally (Sasaki and Pratt 2011).

Our increasingly technology-driven societies may allow us to more easily use the kinds of consensus systems seen in social insect colonies. However, as noted by Grüner et al. (2015) human consensus processes are often considerably less optimized. One key difference between human and insect models may be in the individual complexity of the decision process. Human social consensus is often made around social considerations (Engel 2011; Ensminger and Henrich 2014). We are much more willing, for example, to acquiesce because of established friendship relationships, or to choose around variation in individual personality and dominance status. For a human social group, the actual achievement of consensus itself can be more important than the need to agree on the best option. Alternatively, as noted by Grüter et al. (2012) we may trust our own information over that of others. Highly eusocial insect societies, such as a honey bee colony have none of these complicating factors and thus base decision making on the cumulative changes in information flow, as options are compared and re-compared (Franks et al. 2002, 2015; Seeley 2010).

This leads to the consideration of group versus individual rationality. The assumption of individual optimization forms the basis of rationality models for humans; the economic or fitness outcome for me is more important than that of the group (Simon 1986). This assumption, however, ignores the commonality across social systems that success of the individual is, in fact, intimately bound into the success of the group. The degree of consilience between individual and group fitness is undoubtedly higher for a social insect colony. Although the complexity of human social organization makes us unique in the biological world, humans are still biologically primates. Unlike social insect colonies, primate societies are comprised of individuals who vary considerably in their degree of common interest and cohesion (Harcourt and De Waal 1992; Muller and Mitani 2005). The goals of individual group members can run counter to each other and members may alternatively cooperate and compete with each other on a daily basis (Boesch 1994; De Waal 2000). We see this difference clearly in the structure of human versus ant social networks. Human social networks (and likely those of most cooperative animal societies) are constructed around mutually beneficial connections, and the resulting network graphs can be reduced to densely interconnected "social cliques" (Milo et al. 2002). Ant colonies are not built this way; the network connections between individual ant workers are ephemeral, and the network itself is built around information flow (Waters and Fewell 2012).

5 Conclusion: but ants are not humans

The organizational structure of the eusocial insect colony generates a wealth of ideas for human organizational constructs. But there is a caveat. As noted above, human organizations and social insect colonies operate around different principles of individual versus group worth. In a highly eusocial ant colony, we expect that (as eloquently noted by Mr. Spock in *The Wrath of Khan*, *Paramount* 1982) "the needs of the many outweigh the needs of the one". Cassill et al. offer an intriguingly polemic discussion of whether this is always the case, using the example of fire ants constructing life rafts to escape flooding. The rafts are built to transport queen and brood, but they are also important to the survival of smaller workers. However, they are constructed to include larger workers, who themselves survive equally well on a raft or alone. The case is first illustrative of what should be a general principle of social insect collective behavior: that diversity is important to group success. However, Cassill et al. also raise the question of whether the processes of building and exiting these rafts actually rely on individuals behaving to save themselves first.

Alternatively, in a classic example of "colony needs coming first", in age-based division of labor, older workers transition from in-nest tasks to the much riskier activities of foraging (Seeley 1982, reviewed by Giraldo and Traniello 2014 and discussed by Charbonneau and Dornhaus, this issue). Ants within a nest may live a year or more, but foragers survive only for about two weeks (Porter and Jorgensen 1981). Colonies thus partition workloads to place higher costs on those individuals with lower future contribution (Woyciechowski and Kozlowski 1998). This serves as a lesson. We can learn a tremendous amount from the eusocial insects about the organization of work, the mechanisms underlying collective behavior, and how to integrate from simple individual rules and local information exchange to the global construction of products, ideas and consensus. However, ants and humans deviate significantly in the value placed by the society on the individual. We may learn from the ants, but we do not necessarily want to become them.

References

Anderson, C., & McShea, D. W. (2001). Individual versus social complexity, with particular reference to ant colonies. *Biological Reviews of the Cambridge Philosophical Society*, *76*, 211–237.

Autumn, K., Dittmore, A., Santos, D., Spenko, M., & Cutkosky, M. (2006). Frictional adhesion: A new angle on gecko attachment. *Journal of Experimental Biology*, *209*, 3569–3579.

Autumn, K., Liang, Y. A., Hsieh, S. T., Zesch, W., Chan, W. P., Kenny, T. W., et al. (2000). Adhesive force of a single gecko foot-hair. *Nature*, *405*, 681–685.

Beckers, R., Deneubourg, J. L., & Goss, S. (1993). Modulation of trail laying in the ant Lasius niger (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *Journal of Insect Behavior*, *6*, 751–759.

Ben-Alon, L., Sacks, R., & Grobman, Y. J. (2014). Similarities and differences between humans' and social insects' building processes and building behaviors. In: Construction Research Congress 2014: Construction in a Global Network (pp. 51–60). American Society of Civil Engineers. doi:10.1061/9780784413517.006.

Benyus, J. M. (1997). *Biomimicry*. New York: William Morrow.

Beshers, S. N., & Fewell, J. H. (2001). Models of division of labor in social insects. *Annual Review of Entomology*, *46*, 413–440.

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48*, 653–667.

Bonabeau, E., Dorigo, M., & Theraulaz, G. (1999). *Swarm intelligence: From Natural to Artificial Systems*. Oxford: Oxford University Press.

Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S., & Camazine, S. (1997). Self-organization in social insects. *Trends in Ecology & Evolution*, *12*, 188–193.

Bourke, A. F., & Franks, N. R. (1995). *Social evolution in ants*. Princeton: Princeton University Press.

Camazine, S., Deneubourg, J., Franks, N. R., Sneyd, J., Theraulaz, G., Bonabeau, E. (2001). *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.

Cassill, D. L., Casella, A., Clayborn, J., Perry, M., & Lagarde, M. (2015). What can ants tell us about collective behavior during a natural catastrophe? *Journal of Bioeconomics*, *2015*, 1–16. doi:10.1007/s10818-015-9195-2.

Charbonneau, D., & Dornhaus, A. (2015). When doing nothing issomething. How task allocation strategies compromise betweenflexibility, efficiency, and inactive agents. *Journal of Bioeconomics*. doi:10.1007/s10818-015-9205-4.

Chevallereau, C., Bessonnet, G., Abba, G., & Aoustin, Y. (2013). *Bipedal robots: Modeling, design and walking synthesis*. New York: Wiley.

Czaczkes, T. J., Grüter, C., & Ratnieks, F. L. (2013). Negative feedback in ants: Crowding results in less trail pheromone deposition. *Journal of the Royal Society Interface*, *10*, 20121009.

De Waal, F. B. (2000). Primates-a natural heritage of conflict resolution. *Science*, *289*, 586–590.

Engel, C. (2011). Dictator games: A meta study. *Experimental Economics*, *14*, 583–610.

Ensminger, J., & Henrich, J. (2014). *Experimenting with social norms: Fairness and punishment in cross-cultural perspective*. New York: Russell Sage Foundation.

Franks, N. R., Dornhaus, A., Fitzsimmons, J. P., & Stevens, M. (2003a). Speed versus accuracy in collective decision making. *Proceedings of the Royal Society of London B*, *270*, 2457–2463.

Franks, N. R., Dornhaus, A., Marshall, J. A. R., & DeChaumeMoncharmont, F.- X. (2009). The dawn of a golden age in mathematical insect sociobiology. In J. Gadau & J. H. Fewell (Eds.), *Organization of Insect Societies: From Genome to Sociocomplexity* (pp 437–459). Cambridge, Harvard University Press.

Franks, N. R., Mallon, E. B., Bray, H. E., Hamilton, M. J., & Mischler, T. C. (2003b). Strategies for choosing between alternatives with different attributes: Exemplified by house-hunting ants. *Animal Behaviour*, *65*, 215–223.

Franks, N. R., Pratt, S. C., Mallon, E. B., Britton, N. F., & Sumpter, D. J. (2002). Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philosophical Transactions of the Royal Society of London B*, *357*, 1567–1583.

Franks, N. R., Stuttard, J. P., Doran, C., Esposito, J. C., Master, M. C., Sendova-Franks, A. B., et al. (2015). How ants use quorum sensing to estimate the average quality of a fluctuating resource. *Scientific Reports*, *5*, 11890.

Garnier, S., Jost, C., Jeanson, R., Gautrais, J., Asadpour, M., Caprari, G., et al. (2005). Aggregation behaviour as a source of collective decision in a group of cockroach-like-robots. In W. Banzhaf, T. H. Christaller, P. Dittrich, J. T. Kim, & J. Ziegler (Eds.), *Advances in artificial life* (pp. 169–178). Heidelberg: Springer.

Giraldo, Y. M., & Traniello, J. F. (2014). Worker senescence and the sociobiology of aging in ants. *Behavioral Ecology and Sociobiology*, *68*, 1901–1919.

Gowdy, J., & Krall, L. (2015). The economic origins of ultrasociality. *Behavioral and Brain Sciences*, *22*, 1–63.

Grüner, S., Fietz, A., & Jantsch, A. (2015). Float like a butterfly, decide like a bee. *Journal of Bioeconomics*. doi:10.1007/s10818-015-9204-5.

Grüter, C., Schuerch, R., Czaczkes, T. J., Taylor, K., Durance, T., Jones, S. M., et al. (2012). Negative feedback enables fast and flexible collective decision-making in ants. *PLoS One*, *7*(9), e44501.

Harcourt, A. H., & De Waal, F. B. (1992). *Coalitions and alliances in humans and other animals*. Oxford: Oxford University Press.

Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge: Harvard University Press.

Hölldobler, B., & Wilson, E. O. (2009). *The superorganism: The beauty, elegance, and strangeness of insect societies*. New York: WW Norton & Company.

Jeanson, R., & Deneubourg, J. L. (2009). Positive feedback, convergent collective patterns and social transitions in arthropods. In J. Gadau & J. H. Fewell (Eds.), *Organization of insect societies: From genome to socio-complexity* (pp. 460–482). Cambridge: Harvard University Press.

Jeanson, R., Fewell, J. H., Gorelick, R., & Bertram, S. M. (2007). Emergence of increased division of labor as a function of group size. *Behavioral Ecology and Sociobiology*, *62*, 289–298.

Karaboga, D., & Akay, B. (2009). A survey: Algorithms simulating bee swarm intelligence. *Artificial Intelligence Review*, *31*, 61–85.

Kube, C. R., & Bonabeau, E. (2000). Cooperative transport by ants and robots. *Robotics and Autonomous Systems*, *30*, 85–101.

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science*, *298*, 824–827.

Muller, M. N., & Mitani, J. C. (2005). Conflict and cooperation in wild chimpanzees. *Advances in the Study of Behavior*, *35*, 275–331.

Myerscough, M. R., & Oldroyd, B. P. (2004). Simulation models of the role of genetic variability in social insect task allocation. *Insectes Sociaux*, *51*, 146–152.

Oldroyd, B. P., & Fewell, J. H. (2007). Genetic diversity promotes homeostasis in insect colonies. *Trends in Ecology & Evolution*, *22*, 408–413.

Passino, K. M. (2005). *Biomimicry for optimization, control, and automation*. Berlin: Springer Science & Business Media.

Porter, S. D., & Jorgensen, C. D. (1981). Foragers of the harvester ant, pogonomyrmex owyheei: A disposable caste? *Behavioral Ecology and Sociobiology*, *9*, 247–256.

Pratt, S. C. (2005). Quorum sensing by encounter rates in the ant Temnothorax albipennis. *Behavioral Ecology*, *16*, 488–496.

Şahin, E. (2005). Swarm robotics: From sources of inspiration to domains of application. In E. Şahin & W. M. Spears (Eds.), *Swarm robotics* (pp. 10–20). Berlin: Springer.

Sasaki, T., & Pratt, S.C. (2011). Emergence of group rationality from irrational individuals. *Behavioral Ecology*, arq198.

Seeley, T. D. (1982). Adaptive significance of the age polyethism schedule in honeybee colonies. *Behavioral Ecology and Sociobiology*, *11*, 287–293.

Seeley, T. D. (2003). Consensus building during nest-site selection in honey bee swarms: The expiration of dissent. *Behavioral Ecology and Sociobiology*, *53*, 417–424.

Seeley, T. D. (2009). *The wisdom of the hive: The social physiology of honey bee colonies*. Cambridge: Harvard University Press.

Seeley, T. D. (2010). *Honeybee democracy*. Princeton: Princeton University Press.

Seeley, T. D., Visscher, P. K., Schlegel, T., Hogan, P. M., Franks, N. R., & Marshall, J. A. (2012). Stop signals provide cross inhibition in collective decision-making by honeybee swarms. *Science*, *335*, 108–111.

Sendova-Franks, A. B., & Franks, N. R. (1995). Spatial relationships within nests of the ant *Leptothorax unifasciatus* (Latr.) and their implications for the division of labour. *Animal Behaviour*, *50*, 121–136.

Simon, H. A. (1982). *Models of bounded rationality: Empirically grounded economic reason* (Vol. 3). Cambridge: MIT press.

Simon, H. A. (1986). Rationality in psychology and economics. *Journal of Business*, *59*, S209–S224.

Sumpter, D. J., & Beekman, M. (2003). From nonlinearity to optimality: Pheromone trail foraging by ants. *Animal Behavior*, *66*, 273–280.

Sumpter, D. J., & Pratt, S. C. (2009). Quorum responses and consensus decision making. *Philosophical Transactions of the Royal Society of London B*, *364*(1518), 743–753.

Theraulaz, G., Bonabeau, E., & Deneubourg, J. N. (1998). Response threshold reinforcements and division of labour in insect societies. *Proceedings of the Royal Society of London B*, *265*, 327–332.

Tschinkel, W. R. (2015). The architecture of subterranean ant nests: beauty and mystery underfoot. *Journal of Bioeconomics*. doi:10.1007/s10818-015-9203-6.

Tschinkel, W. R. (1999). Sociometry and sociogenesis of colonies of the harvester ant, Pogonomyrmex badius: Distribution of workers, brood and seeds within the nest in relation to colony size and season. *Ecol Entomol*, *24*, 222–237.

Waters, J. S., & Fewell, J. H. (2012). Information processing in social insect networks. *PLoS One*, *7*, e40337.

Wilson, D. S., & Gowdy, J. M. (2015). Human ultrasociality and the invisible hand: Foundational developments in evolutionary science alter a foundational concept in economics. *Journal of Bioeconomics*, *17*, 37–52.

Woyciechowski, M., & Kozlowski, J. (1998). Division of labor by division of risk according to worker life expectancy in the honey bee (*Apis mellifera* L.). *Apidologie*, *29*, 191–205.