

Evolution of Natural and Artificial Swarms

Project for Animal and Machine Intelligence

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Abstract

Ideas from the biology of Social Insects and Computation have had many fruitful interactions. This paper examines Social Insects, the models used to understand them, and how those models in turn influence Computation. Evolution in Social Insects is studied in particular, and in this light, suggestions are made for future interaction of ideas.

1 Introduction

Social insects have long been the subject of intense fascination and equally intense puzzlement. Hives and colonies behave with sophistication and “intelligence”, in tasks like resource gathering, defense of the community, and nest construction; yet understanding of the methods by which individual organisms act in accordance with complex group level goals has only recently made great headway. Decades of intense field work, plus a general fundamental shift in approach to studying emergent levels of organization, has led to a detailed understanding of many behaviors in social insects. In parallel, social insects have served as both a high level inspiration for computational techniques, and as a quite specific model for solving optimization problems.

There still remain many open questions, on the mechanics of these species, as well as the larger question of how it is possible that such unusual species evolved at all. Mathematical and computational models have been successfully employed in the process of research on behavior of social insects, but hardly at all on the question of how those behaviors came about. Research employing evolutionary modeling techniques may address open questions, or perhaps lead to new questions asked. Likewise, evolutionary techniques may lead to further advances in social insect inspired optimization algorithms.

2 The Social Insects

Social behavior has a precise definition against which behavior of insects, or any animals, can be measured. Any degree of social behavior beyond sexual interactions is categorized as presocial, and three specific behaviors are as follows. Individuals cooperate in caring for the young. Practically sterile individuals, whether physiological or behaviorally, work on behalf of other individuals which are reproducing. Multiple generations coexist and contribute to the colony, so that offspring assist parents. These traits are seen individually and in combination in species of insects, and if all are present, that species is classified as eusocial. Eusociality is what is commonly expressed by the term Social Insects[4].

Eusociality is observed in species of ants, bees, wasps, and termites. Careful taxonomy study, inferred from both phylogenetic and behavioral data, plus investigation of the fossil record, has led to the theory of common ancestry of ants, bees, and wasps, in ancient wasp species, all within the order Hymenoptera. Ants have been likened to wingless wasps, living at ground level and burrowing through soil to take advantage of the abundant resources below the surface. The adaptation has led to ants being the most widely distributed, numerically abundant, and diverse of the eusocial insects. Bees can be considered as wasps that collect and feed their young pollen, rather than insect prey.

The relatedness of these species might make for a relatively simple story of social insects, if not for two things. First, of course, is that termites belong to a separate order of insects, Isoptera, more closely related to cockroaches. Second, the vast majority of bees and wasps are solitary species. Yet, all ants are eusocial, like the termites (the one possible exception is a parasitic ant, *Teleutomyrmex schneideri*, which rides on the abdomen of the host queen and “tricks” the host colony into caring for its young). The basis for eusociality can therefore not be strictly found in genetic or physiological similarities, and leaves open the intriguing possibility that eusociality has its own independent principles of organization.

Though they are not strictly included in the definition of social insects, a few characteristics stand out as typical in these species. A single colony of insects will be divided into multiple castes, with different morphology and behaviors. In some cases, like the wasps *Evylaeus marginatus*, the differentiation is the minimal required by the definition of eusocial; that is, into a single reproducing queen, and a group of non-reproducing “worker” females. At the other extreme, species of termites can have several types of

reproductive castes, worker and soldier castes. The queen of *Macrotermes subhyalinus* can grow thousands of times larger than workers, her abdomen bloated with ten thousands of eggs. In many cases, the development of a member of a particular caste is dependent on nutritional variances during the development process.

Another typical characteristic is highly structured nests. Again this can vary, from occupying an abandoned nest of another animal, to the large mounds of *Macrotermes*, with distinct structural elements of the royal chamber, brood chambers, fungus gardens, and ventilation ducts. A third common characteristic is highly developed communication systems. These range from dominance hierarchy behaviors in wasps, to the information rich waggle dance of honey bees. Particularly interesting is stigmergy, defined as indirect communication through the physical environment, which includes the variety of behavioral responses in *Macrotermes* to the emerging structures during nest building and the pheromone trails of foraging ants.

Sometimes a colony of social insects is referred to as a Superorganism, likening the individuals in a colony to the cells in a single organism. Social insects are divided into reproductive and non-reproductive members, as a body consists of reproductive and other cells. A colony goes through a process of development, usually from a single queen or reproductive pair, to a large differentiated colony capable of reproduction of the entire colony. Social insects display homeostasis, particularly in thermoregulation of the nest. For example, individual honey bees align themselves in different geometric configurations according to ambient temperature. Still this designation serves as a more inspirational and conceptual guide, rather than a precise scientific idea.

3 Models and Measurement of Social Insects

Of all the complex behaviors of social insects, the most deeply studied and understood is nectar foraging in honey bees. A colony of honey bees must efficiently choose among multiple nectar sources, to exploit the most rewarding, and redistribute workers as the quality of sources changes. The task is highly impressive when it's considered that each individual bee acts only on its own local information, with no global coordination. It has been suggested in the past that there must be some bees among the thousands in the colony with understanding and leadership. However, the experimental evidence confirms that forager allocation is a result of the interactions of the colony as a whole [3].

The key advantage of studying "Superorganisms" over typical organisms is the possibility of introducing variables into the system, without fatal results. For example, insect colonies can be divided, queens can be substituted, and individuals can be labeled for careful, detailed observation. Seeley built observation hives, labeled individuals with a combination of colors and numbers, carefully manipulated food sources, and took very detailed records. This data supported the construction of a mathematical model, which was then tested for predictive ability against new experimental situations.

One experiment consisted of examining the distribution ratios of foragers among two nectar sources. The equidistant feeders contained sugar solutions of different concentrations, and therefore of different quality to the hive. At noon, the quality of the feeders was reversed. The number of foragers visiting each feeder, and the rates of recruitment and abandonment were recorded. As a whole, the colony responded with a sensible strategy of deploying the majority of foragers to the more profitable source, but still deployed a few foragers to the other source. This strategy enabled the hive to quickly adapt to the changing conditions of the experiment, or, of course, in natural settings.

The key to this flexible strategy is the presence of employed and unemployed foragers. Employed for-

agers collect nectar from a source, return to unload in the hive, and based on the profitability of that source to the hive, either attempt to recruit unemployed foragers with a waggle dance or abandon the source and become unemployed themselves. The waggle dance, encoding information on the direction and distance of the source, has duration relative to profitability of the source. Each unemployed forager has a probabilistic threshold for responding to the dance. Therefore a dance of longer duration has a higher probability of recruiting more foragers, but a forager dancing for a lower quality source still has a chance of recruiting a few foragers. The profitability of the source is judged individually by the forager, by quality of the source, the distance to the source, and the time it takes to unload nectar to a food-storer bee, an indication of the nutritional needs of the hive.

From this theoretical model, a complex set of differential equations were derived, incorporating probabilities of the different responses in employed and unemployed bees, duration of different activities, and number of bees employed to each of the food sources, or not at all. Under similar conditions, the differential equations accurately predicted the observed colony level behavior in the feeder swapping experiment.

4 Social Insects as a Model for Computing

The model of social insects, of individuals with limited local information acting on simple rules, coupled in a large community that behaves with “intelligence” and adaptability, has been very influential in computer science. The metaphor of the Swarm has been applied to multiple agent simulation systems, and even more widely to any sort distributed computation. Chris Langton, the “founder” of Artificial Life, developed a popular multi-agent simulation software package, and named it Swarm.

Recently, the behaviors of social insects have been applied in a more direct way, in the new sub-field of Swarm Intelligence. Applications range from task scheduling optimization to programming of cooperative autonomous robots, with great success in communication network routing. This technique of Ant Colony Optimization has even spawned a series of conferences [1].

ACO takes its inspiration from trail creation and following behavior in foraging ants. Individuals returning from a food source lay down a pheromone trail, which recruits other ants to follow back to that source. A food source closer to the ants’ nest will be discovered more quickly, so pheromone will be deposited to that source before others, recruiting more ants faster and reinforcing the trail. Once the food source is exhausted, pheromone laying behavior from that source will cease, and previously deposited pheromone will eventually evaporate.

The ability to find the shortest distance between multiple points suggested the initial application of this technique to the Traveling Salesman Problem. A team of ants is programmed to complete a tour of nodes on a network. Each ant keeps track of which nodes it has visited, and at each step, chooses an edge from its current location to another node, with weighted probability depending on the length of those edges. This would make for a simple greedy algorithm, if not for the presence of a virtual pheromone trail. On the completion of a tour, the path an ant took is updated with an amount of pheromone dependent on the performance of the ant. The amount of pheromone of each edge is factored into the trail determination probability function. To avoid solution stagnation and sub-optimal trail reinforcement, pheromone has a limited lifetime. This solution performed well on problems of limited size, but hit a limit on larger problems. Modifications, giving the ants more flexibility and heuristics in exploring the network, and more conservative pheromone trail updates, gave results on par with the best known algorithms.

A very successful application of this technique has been applied to routing in telecommunications networks, including British Telecom. Each node in a telecommunications network maintains a routing table,

giving the probabilities of following one of the edges of its neighbors on route to another destination node. The problem is that network demands vary and are unpredictable, so the most optimal route between any two points is a dynamic function of the current network traffic. ACO is successful at this problem, because the ants, laying evaporating pheromone, are able to adapt to changing conditions. Ants are placed on the network, with the goal of traversing from start to end point. In a similar way to the traveling salesman problem, the routing tables are updated based on the success of the traversal.

5 Evolution of Social Insects

The social insects posed a problem of great difficulty for even Charles Darwin. How could a species evolve to produce predominantly sterile and altruistic individuals? It seemed to contradict the primary argument of evolution by natural selection. Darwin suggested treating an entire colony as a unit of selection. With a high degree of relatedness among individuals in a colony, all members of the colony share a close genetic destiny. Sterile, altruistic individuals could evolve if it is beneficial to the entire colony, through improved defense of the nest, improved homeostasis, or improved labor [4].

Individuals in colonies of Hymenoptera are indeed more closely related to each other than usual, due to the peculiar sex determination process. Fertilized eggs produce females, and unfertilized produce males. Females form from diploid eggs, males from haploid eggs, giving this situation the name haplodiploidy. Daughters of the queen receive half of their chromosomes from their father, and half from their mother. Since the father has only half as many chromosomes, every sister shares all those genes in common. And on average, they share one half of the genes received from their mother. In total, two sisters share three quarters of their genetic makeup. In comparison, if these daughters were to reproduce, they would share only one half of their genes with their daughters. The expression of this mathematical relationship in the altruism of members of a colony seems beyond elegance. Yet, eventually with this genetic relationship, the development of colonies with sterile, altruistic individuals would be more successful.

The theory is not without problems. The queens of many species of Hymenoptera mate with more than one male. The relatedness of the sisters drops to below half in this situation, seemingly invalidating the theory, yet there are possible explanations. The males may be closely related to each other, so that the genetic relationship of their young is still above one half. Also possible is that multiple matings is an adaptation evolved after the irreversible formation of a sterile, worker caste. Another problem is that termites are not haplodiploidy. However, there is a high incidence of inbreeding in termites, and with repeated inbreeding the relatedness of a colony of termites might even exceed that of Hymenoptera. Interestingly, the difference in sex determination is expressed in the behavior of males in these two orders. Hymenoptera males are only one quarter related to their sisters, and as a result contribute little labor to the colony, while males of highly inbred termites do contribute to colony labor.

Still, there are some examples where a more immediate need underlies eusociality. In *Evyllaenus marginatus*, the castes are entirely based on reproductive behavior. However, if the current queen is removed, the workers rapidly undergo ovarian development. As well, after five years, some of the workers will mate and depart to form their own nests. In this case, it seems that the protection provided by sharing a nest is the primary motivation for eusociality. The workers have a chance of inheriting it, without the added energy expenditure of building their own nests, and always have a later possibility of reproducing.

It is estimated that eusociality evolved separately as many as eleven times. There are also several examples of individual species evolving back from eusocial to presocial or solitary species, perhaps because whatever threat led to cooperative nest defense have left the environment. Most research on the precise progression on social behaviors in insects is taxonomic, especially examining the conditions under which

intermediate levels of eusociality form.

More speculatively, this paper offers two ideas on the evolution of social insects which have seemingly received no coverage, and are subtle, inexact, and possibly incorrect propositions. The first concerns the particular ecological niche that ants occupy. Ants serve a great ecological function in forests, clearing dead organic matter from the forest floor and aerating the soil by building extensive nests. Only because of small size and huge numbers can they perform this service with such magnitude. So, as an alternative perspective, the evolution of a eusocial species was necessary to increase the efficiency in this ecological niche.

Secondly, the species of army ants of the genus *Eciton* display different foraging behaviors, dependent on the spatial distribution of their prey. Both column-like and branching raid patterns are seen, and models show that the same individual level behavior can produce both. However, through evolution, each species has diverged in the level of pheromone deposits during the raid, possibly restricting their potential pattern repertoire. This may be considered an example of the Baldwin effect in the phenotype of the entire colony, though much experimental work would be required to validate this idea.

6 Simulation and Evolution of Social Insects

Despite being a core inspiration for agent-based simulations, there have been few biologically plausible attempts at modeling social insects with this technique. In his suggestions for a course toward a theoretical unified sociobiology, Wilson enumerates many of the core parameters necessary in development of an agent-based model. Primarily, the evolutionary history of a species and the environmental niche open to the species are chief determinants of the expressed superorganism behavior, yet also the most difficult to incorporate in a model. Populations are governed by reproductive cycles and population densities, and individuals have a degree of relatedness to each other. Individuals have a repertoire of behaviors and methods of communication, depending on caste. From this emerge group level conditions, like the size of a colony, division of time and labor among castes, and the possible adaptive responses to the environment [4].

In other words, these parameters lay a ground work for investigating the “solution space” of social insect organizations. There are many large questions that could eventually be addressed by the agent-based approach. What are the organizational and energetic constraints of observed mathematical relationships in social insects, such as the ratio of caste populations? What effects do changes in specific thresholds of behavior in individuals have at a colony level? How would the evolution of more intelligent individuals affect colony efficiency, and at what energetic cost?

Large questions indeed, so what of more tractable research problems. The construction of wasp nests, through evolutionary search techniques, has made some progress [2]. Construction seems to take place via stigmergy, in that the construction behavior of an individual wasp is governed according to the different phases of construction, as well as the particular local configuration. Models represented this governing by an individual level template, employed in a similar way to a cellular automata update rule. Individuals were evolved according to abstract measures of the final hive architecture, such as cohesiveness and internal space. Incorporation of physical constraints during the construction process, like gravity and material strength, is one suggestion for future research.

Honey bee foraging seems a likely candidate for extension from differential equation models, for deeper investigation into the individual level functioning in foraging, as well as a starting platform for more complicated questions of evolution, such as how haplodiploidy encourages altruistic behavior. The evolution of two separate populations could be simulated, one with a standard genetic relationship between

individuals and the other with a haplodiploidy relationship. Fitness would be based on a simple task of collecting resources. Any cooperation in collecting resources would result in a necessary sharing of that resource. So, if a cooperative strategy resulted in more efficient resource gathering than a solitary one, expectations would be for that strategy to evolve. The task could be constructed with this explicitly in mind. This experiment could then examine if haplodiploidy resulted in quicker evolution of the cooperative strategy.

7 Evolution of Social Insect Algorithms

Devising and tuning a social insect inspired algorithm is not straightforward. The inherently complicated relationship between algorithms of individuals and the group level behavior makes it particularly difficult to predict the results of variations in population size, individual behaviors, and parameters, such as the persistence of artificial pheromone in ACO.

Evolutionary techniques seem a good strategy to address this problem. If the parameters of even a portion of behavior can be suitably quantified for a genetic algorithm, then evolution could effectively search the space of possible swarms. No research has been published in using evolution to optimize swarm intelligence systems.

The entire algorithm determining individual behavior may also be suitable for evolution. Genetic Programming has had just limited success in solving optimization problems, perhaps due to the fairly complex algorithms needed. In contrast, the algorithms of swarm computing can be relatively simple, as the complexity arises from interaction of these simple algorithms. Genetic Programming could find some application here.

Another untried inspiration from insects is the use of behaviorally and phenotypically differing castes. The evolution of different castes, into specific population ratios, could have application in the development of cooperative robotics.

8 Conclusion

Evolution, computation, and social insects in combination have a very high potential, but are no means a certain success.

Biologically, advances in theory and observation are necessary for any advances in computational models. Theoretical advances are highly speculative. Wilson's efforts towards a unified theory of sociobiology are not universally supported. Seeley, with so much practical direct experience studying honey bees, warns "it is probably an exercise in futility to seek grand principles of colony functioning". Perhaps the intricacies of such physically dependent solutions, embedded in immensely complex ecosystems, are beyond the grasp of computational methods.

Social insect inspired computation has had notable early success, but it is still early days. There is still much to study in these algorithms without adding the additional complications of evolution.

It will be exciting to see if these ideas reproduce themselves and swarm the landscapes of our thinking.

References

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