Social Science at the Crossroads

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Cover illustration: From the Age of Anxiety series by Alexander Polzin. Mixed media on wood.

Library of Congress Cataloging-in-Publication Data

Names: Institut international de sociologie. World Congress (38th : 2008 : Budapest, Hungary) | Randeria, Shalini, 1955- editor. | Wittrock, Björn, editor.
Title: Social science at the crossroads / edited by Shalini Randeria, Bjorn Wittrock.
Description: Leiden ; Boston : Brill, 2019. | Series: Annals of the international institute of sociology, ISSN 1568-1548 ; Volume 13 | Includes bibliographical references and index.
Identifiers: LCCN 2018049136 (print) | LCCN 2018051237 (ebook) | ISBN 9789004385122 (E-Book) | ISBN 9789004224261 (hardback : alk. paper)
Subjects: LCSH: Social sciences--Congresses. | Sociology--Congresses.
Classification: LCC H22 (ebook) | LCC H22 .156 2008 (print) | DDC 300--dc23
LC record available at https://lccn.loc.gov/2018049136

Typeface for the Latin, Greek, and Cyrillic scripts: "Brill". See and download: brill.com/brill-typeface.

ISSN 1568-1548 ISBN 978-90-04-22426-1 (hardback) ISBN 978-90-04-38512-2 (e-book)

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What Can We Learn from Insect Societies?

Raghavendra Gadagkar

Introduction¹

1

Many species of insects such as ants, bees, wasps and termites live in societies paralleling, if not bettering, our own societies, in social integration, communication, division of labour and efficient exploitation of environmental resources. What indeed can we learn from insect societies? The short answer, which I will state up-front, is that we can learn a great deal, but there is also a great deal that we cannot/should not learn. Let me begin with an anecdote.

Because I work on insect societies and people easily relate to this topic, I often get invited to lecture to high school students. On one such occasion, when I was describing the life of the honeybee, I explained how a colony of bees gives rise to a new colony. A colony of honey bees consists of many thousands of workers, a small number of drones and only one queen. While the drones do nothing except mate, and die in the process, all the tasks involved in nest building, cleaning, maintenance and guarding, food gathering and processing, as well as nursing thousands of larvae, are performed by the workers. Under normal situations, the queen is the sole reproducer of the colony, laying thousands of eggs per day – fertilizing them with sperm she has gathered from numerous drones from foreign colonies and stored in her body, to make new daughters and withholding the flow of sperm into the oviduct and laying unfertilised eggs that develop parthenogenetically into sons. To make a new colony, the bees will have to first rear a new queen, and this they do by building special large-sized cells and feeding the larvae in them with a special royal jelly, which directs their development into fertile queens rather than sterile workers. When a new queen completes development, there is a potential problem - the colony now has two queens, the mother and the daughter. But since each colony can only have a single queen, one of them has to leave. It is an invariant "tradition" in honey bees that it is the mother who leaves with a fraction of the workers, to undertake the

Based on the plenary talk delivered in June 2008 during the 38th World Congress of the International Institute of Sociology (IIS) in Central European University, Budapest. This chapter is a modified version of Gadagkar 2011, and we are grateful for the permission to include it in this volume [Editors' note].

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risky mission of building a new home in a new location and start brood production all over again. The daughter inherits the ready-made old nest with most of the workers and indeed, with all the honey, brood and wax that comes with it.

Before I could proceed further with my description, the kindly teacher, addressing her students more than me, interrupted to exclaim how much we humans have to learn from the honey bees. This was rather embarrassing to me, because what I was going to say next would embarrass the teacher. My next point was that, if the mother queen has for some reason not departed when the daughter queen emerges, they may fight unto death. It is also true that, often more than one daughter queen is produced and while all may swarm and produce additional daughter colonies, they will also fight unto death if two or more of them fail to leave the parent colony in time. Surely, these are not lessons that we would like to learn!

Insect societies understandably capture the imagination of people as few other topics do. Since the time of Aristotle, all manner of people have drawn upon honey bees and other insect societies to learn and teach good behaviour and morals. This has been particularly true in economic and political matters. And of course, we are familiar with the Biblical injunction "Go to the ant, thou sluggard; consider her ways, and be wise [Proverbs 6:6]. My two favourite examples are those of Francis Bacon and John Knox. Francis Bacon compared empiricists to ants that only collected materials from outside, and philosophers to spiders who only spun from within, but preferred the bees that collected materials from outside and then transformed them, as a worthy model for intellectuals. While Francis Bacon was inspired by the worker bees, John Knox was inspired by the queen bee; but there is a cruel twist to the latter tale. Perhaps because people (men) could not imagine that the beehive could be headed by a female bee, the queen was long thought to be a male bee and was referred to as the king. It was only in the 17th century that the Dutch anatomist Jan Swammerdam demonstrated that the "king" bee contained ovaries with eggs, although he nevertheless could not bring himself to use the word queen. Efforts to draw upon bees to embellish political debates often led to absurd situations before the true sex of the "leader of the hive" was established. John Knox published a treatise in 1558 entitled "First Blast of the Trumpet against the Monstrous Regiment of Women" in which he argued against the rule of women such as Queen Elizabeth, on the grounds that "Nature hath in all beasts printed a certain mark of dominion in the male, and a certain subjugation in the female." Peter Burke (1997) gives these two and many other examples of the fables of the bees in Western cultures, and shows how desired "social arrangements were projected onto nature, and this socialised or domesticated nature was in turn invoked to legitimate society by 'naturalising' it." I would therefore argue that we should

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not turn to nature to decide *what* we should do, because we will find everything in nature – the good, the bad and the ugly. It is easy to justify any desired course of action by drawing upon the appropriate examples from nature. And yet, I submit that there is a great deal that we can learn from nature in general and insect societies in particular. Having decided *what* we wish to do, independently of nature, it might often be profitable to turn to nature for lessons on *how* to do what we wish to do. In the rest of this essay I will describe two examples of the "how" lessons that we can certainly learn from insect societies.

2 Ant Agriculture

Human agriculture, which has been estimated to have originated some 10,000 years ago, has rightly been considered the most important development in the history of mankind. Virtually all the plants, which we consume today, are derived from cultivars that have been bred and modified by humans for thousands of years. There has also been extensive exchange of cultivated crops from one part of the globe to another. While consuming plants and their products, we tend to forget that the cultivation of coffee originated in Ethiopia, that of tobacco around Mexico, tomato and potato in South America, rice in South East Asia and so on. The impact of agriculture on the further development of human societies has been profound – high rates of population growth, urbanization, economic surpluses and providing people with free time – all of which were pre-requisites for the development of modern civilization, including arts, literature and science.

Impressive as all these are, our achievements are surely humbled by the lowly ants, which appear to have invented agriculture – and as we shall see below a fairly sophisticated type of agriculture – almost 50 million years before we did. Three different groups of insects practice the habit of culturing and eating fungi. They include some ants, some termites and some beetles. Agriculture arose nine times independently in insects, once in ants some 45–65 million years ago, once in termites some 24–34 million years ago and seven times in beetles some 20–60 million years ago, and there are no known examples of any insect lineages having reverted back to non-agricultural life. (By a curious coincidence, human agriculture has also been estimated to have arisen on nine independent occasions, but between 5000–10,000 years ago.) Here I will restrict my attention to ant agriculture and will base my description on studies by and the ideas of a large number of ant biologists and especially Ulrich Mueller, Ted Schultz and Cameron Currie (Mueller et al. 2005). With a few exceptions, all fungus-growing ants are also leafcutters – they cut pieces of

leaves, bring them to the nest and use them as substrata to grow fungi. The ants derive their nutrition only from the fungi grown in this manner and not from the leaves themselves. There are some 220 species of ants that do not know any life style other than fungus farming. Because of their ecological dominance and their insatiable hunger for leaves, leafcutter ants are major pests in some parts of world. These ants can devastate forests and agriculture alike – they may maintain ten or more colonies per hectare and a million or more individuals per colony. Where they occur, the leafcutter ants consume more vegetation than any other group of animals.

As may be imagined, the process of fungus cultivation is a complicated business. In the field, leaves are cut to a size that is most convenient for an ant to carry them back. In the nest, the leaf fragments are further cut into pieces 1-2 mm in diameter. Then the ants apply some oral secretions to the leaves and inoculate the fragments by plucking tufts of fungal mycelia from their garden. The ants maintain a pure culture of the fungus of their choice and prevent bacteria and other fungi from contaminating their pure cultures. Growing pure cultures of some of these fungi in the laboratory has proved difficult or impossible for scientists. How the ants achieve this remarkable feat remains poorly understood. Not surprisingly, they manure their fungus gardens with their own faeces. When a colony is to be founded, the new queen receives a "dowry" from her mother's nest – a tuft of mycelia (the vegetative part of the fungus that can be used to propagate it) carried in her mandibles. Thus, these ants appear to have asexually propagated certain species of fungi for millions of years.

What kind of fungi do these ants cultivate? Do all ants cultivate the same type of fungi? As in the case of human beings, have there been multiple, independent events of domesticating wild species? Like humans, do the ants exchange cultivars among themselves? Until recently, it was not easy to answer any of these questions. Today, with the advent of powerful DNA technology, answers to many of these questions can be found. We now know that there have been at least four independent domestication events rather than a single domestication followed by long-term clonal propagation. Even more interesting, we now have evidence that ants occasionally exchange fungal cultivars among themselves so that different nests of the same species of ants may contain different cultivars. Whether the ants deliberately borrow fungal cultivars from their neighbors or whether the horizontal transfers occur accidentally is however not known. But there is good evidence that new cultivars have been added to the ant fungal gardens from time to time.

But does ant agriculture suffer from pests like ours does? Yes, of course. The fungus gardens are often infected with a potentially devastating pest, which is another kind of fungus called *Escovopsis*. And how do ants deal with the

menace of pests? Exactly as we do – they use pesticides. The only difference is that their pesticide is an antibiotic produced by a bacterium. In other words, ant agriculture is more like our organic gardening. But what is even more fascinating is that the antibiotic producing bacterium grows on the bodies of the ants, deriving its nutrition form the ants themselves. This close coevolution of ant, fungus, *Escovopsis* and antibiotic producing bacterium has persisted for some 50 million years. What effect such agriculture (including perhaps "economic surpluses" thus generated and spare time thus available to the ants) had on the evolution of the ants themselves? Like in the humans, the advent of agriculture appears to have significantly affected the evolution of leafcutter ants. Today the leafcutter ants are among the most advanced and sophisticated social insects.

How should we react to the knowledge of such sophisticated achievements by the lowly ants? I would like to believe that this knowledge will generate some amount of modesty about our own achievements and make us more tolerant of other forms of life on earth. I would also like to believe that, as a civilized and cultured species, we will support and encourage some members of our species to devote their lives to the study of the achievements of insects and other lowly creatures. Although sheer intellectual pleasure is in my opinion more than adequate compensation for such study, it is clear that there is far more to be gained by studying ant agriculture and comparing it to human agriculture.

The great efficiency of both ant and human agriculture depends upon the cultivation of monocultures. But this comes at a significant cost in the form of loss of genetic variability in the cultivars and their consequent heightened disease susceptibility. Unlike most human agriculturists who depend almost exclusively on the use of pesticides to solve these problems, ants use a complex mix of strategies and this is where we may have much to learn. First, by being subterranean farmers, the ants largely insulate their crops from disease-causing pathogens. This is of course possible for them because they cultivate fungi and not angiosperms. It is therefore probably not a very promising solution for us, although I am not yet convinced that we cannot cultivate at least some fungi or other easily protected crops.

Second, ants engage in intense, manual monitoring of crops and removal of pathogens. This can easily be dismissed as prohibitively expensive for us. But a little reflection is in order. By relying almost exclusively on pesticides humans have got used to the huge surplus of food and time that agriculture can provide for most of us to indulge in other activities. It is possible that when and where pesticide based crop protection becomes truly unsustainable on account of damage to the environment, the investment of additional manual labour will be considered worthwhile.

Third, and most remarkably, ants maintain and retain access to a reservoir of crop genetic variability. This is achieved by periodically borrowing cultivars from other populations and also by periodically acquiring new free living, sexually reproducing strains. I believe that there is great scope for humans to adopt this strategy even at the cost of some loss of efficiency compared to the cultivation of a single super-variety of crop. It will of course require humans to re-work the trade-offs between short-term efficiency and long-term sustainability.

Finally and most importantly, ants use biological control to deal with unwanted pathogens and parasites. But their brand of biological control is unlike ours. It does not simply involve suddenly bringing in an exotic biological enemy of the currently most devastating parasite. Instead, it involves the continuous selection, engineering and cultivation of a whole consortium of microorganisms resulting in integrated pest-management in the true sense of the term. Such a strategy is neither impractical for humans nor do we lack the relevant technical knowledge. It is however, a sobering thought that in our efforts at selecting for the most high-yielding varieties of crops we may have actually selected against the very genes in our cultivars that make coexistence with microbial consortia and sustainable agriculture possible. We really need to reassess the economics of our agricultural operations and settle for a relatively smaller profit in exchange for long-term sustainability.

There is a rather interesting contrast between ant agriculture and human agriculture that is worth reflecting upon. In the course of the co-evolution of ants and their cultivars, the farming ants have undergone major evolutionary changes themselves while they appear to have caused rather few reciprocal evolutionary changes in the species they cultivate. In contrast, humans have themselves undergone relatively few evolutionary modifications in response to their farming practices while we have effected very significant evolutionary changes in our cultivars. In other words, the humble ants have adapted themselves to their cultivars while we arrogant humans have attempted to change and dominate our cultivars. I suspect that this contrast holds the key to understanding the reasons for the long-term sustainability of ant agriculture and the striking lack of sustainability of human agriculture.

In my experience, there is a significant aspect of human behaviour that may prevent or at least delay our learning these lessons from ants. I alluded above to my hope that the knowledge about ant agriculture will generate some modesty in us about our own achievements. I now focus on a particularly dangerous form that our lack of modesty often takes. On many occasions, I have attempted to share our growing knowledge of the capabilities of social insects to colleagues in the social sciences and humanities. This has sometimes been a frustrating experience because many people, especially those engaged in scholarly studies of human societies have a mental block about making comparison between humans and insects. Their argument is that terms such as selfishness, altruism, language and even agriculture, cannot be borrowed from humans and used for insects because this is pure anthropomorphism. Their main argument is that while humans are conscious of their actions, insects cannot be said to be conscious. Take the example at hand – agriculture. Even if we grant that ants do not inoculate, manure, clean and harvest their crops consciously as humans might do, should that preclude our labeling ant agriculture as such? I am often told to go find another word, which makes no sense in the human context and therefore carries no pre-conceived connotations. The failure to use the term agriculture or to substitute it with gibberish will make it even more unlikely that we will benefit from the profound insights that ant agriculture is certain to provide us. It is my hope that the convincing demonstration of the benefits of comparing ant and human agriculture will deflate persistent arguments against anthropomorphizing insect behaviour. Incidentally, some may grudgingly agree to call insect agriculture as protofarming but this will be unacceptable and indeed absurd. Outside the three groups of agricultural insects, namely ants, termites and beetles mentioned earlier, there are hundreds of species that practice relatively primitive kinds of fungal cultivation, and they may indeed be collectively referred to as protofarmers. The beetle, termite and especially ant agriculture is truly advanced by insect standards and, I would argue, even by human standards.

We can only ignore the study and emulation of ant agriculture at our own peril. And there will be a touch of irony in the ensuing peril – leaf-cutting ants are today among the most devastating marauders of human agricultural farms in many parts of Central- and South America!

3 Ant Colony Optimization and Swarm Intelligence

In the late 1980's and early 1990's Jean-Louis Deneubourg and his colleagues at the University of Bruxelles were engaged in some simple curiosity driven experiments on ants. Their interest was to study the methods used by ants to find sources of food and to return to their nests. It was of course already well known that many ants lay a pheromone trail that guides them and other ants in their navigation. Using one such trail-laying ant, the so-called Argentine ant, *Iridomyrmex humilis*, they presented the ants with the following problem. Two bridges connected their nests with the source of food. Initially both bridges were used but soon there was an abrupt preference for one of the two bridges. When both bridges were of equal length, one of the two bridges came to be preferred randomly. However when one bridge was longer than the other, the shorter bridge often, but not always, became the preferred one.

They modeled the behaviour of the ants with the following assumptions. Ants initially select one of the two bridges randomly but as they mark their trails with pheromone, the shorter bridge accumulates more pheromone because it gets traversed more (because the ants reach the food and their nest sooner and thus make more trips in the same time period). Now if the ants are sensitive to the amount of pheromone and simply choose bridges in accordance with the intensity of their smell, the shorter bridge would automatically get preferred most of the time. This model predicts that the probability with which the shorter bridge becomes preferred should be proportional to the difference in lengths of the two bridges. It also predicts that if the shorter bridge is added after the longer bridge is already in use, the ants should not be able to switch to the shorter one. It was easy enough for them to verify these predictions and gain confidence in their model. Thus ants could perform a seemingly intelligent and evolutionarily adaptive task of choosing the shorter of two paths without ever having made any measurements of their path lengths and without "knowing," by instinct or intelligence, that shorter paths are better (Goss et al. 1989; Deneubourg et al. 1990).

Marco Dorigo, a PhD student at Politecnico di Milano in Italy, decided to learn from the ants and developed an algorithm for computers (or for artificial intelligence in general) that has come to be known as Ant Colony Optimization (ACO). Dorigo had his "agents" (or artificial ants) behave as the model predicted the ants to behave. Soon he was free to relax some of the assumptions in the model even beyond what is biologically reasonable. After all, he was not modeling the ants but using the ant inspired algorithm to solve problems. For example, he was interested in a simple and efficient algorithm to find the shortest of alternative paths. Today ACO algorithms are among the most powerful and popular algorithms and have been applied to a number of academic problems including the traveling salesman problem, vehicle routing problem, group shop scheduling problem and the like. More impressively ACO (Ant Colony Optimization) algorithms are being used in real life applications such as deciding setup times, capacity restrictions, resource compatibilities and maintenance calendars in reservoirs, routing of vehicles, management and optimization of heating oil distribution with a non-homogeneous fleet of trucks etc. (Dorigo and Stützle 2004).

It is now being increasingly recognized that insect societies are selforganized and display emergent properties. This means that the collective group of individual insects can perform tasks beyond the capability of any member of the group, making the whole literally greater than the sum of its parts. By following simple rules, modifying, and being modified by their local environments, social insects display global properties that can be extremely impressive. The metaphor Swarm Intelligence (also referred to as distributed intelligence) has become a powerful way of expressing our new conception of insect societies (Bonabeau, Dorigo, and Theraulaz 1999). Trail following is not the only behaviour that has inspired artificial intelligence algorithms. Cooperative transport of materials by ants has begun to find industrial applications including in the handling of cargo by airlines and managing traffic in the telecommunication industry and in the internet. Similarly, optic flow based distance estimation by honeybees has potential applications in the design of unmanned aircraft (Srinivasan et al. 2004). An interesting article in *Harvard Business Review* (Bonabeau and Meyer 2001) concluded that "possible applications of swarm intelligence may only be limited by the imagination."

4 Concluding Remarks

I wish to conclude this essay by reflecting on the contrast between the two examples I have cited. Computer scientists have explicitly and eagerly drawn upon the wisdom of insect societies and made great progress in solving practical problems in their own domain. There is no hint in any of their writings that ants are "primitive" relative to humans. Indeed, there is persistent praise for what ants and other social insects can teach us. On the other hand, it is not the same story in the realm of ant agriculture. Here I suspect that agricultural scientists are much more skeptical about learning from the ants, and even when they draw upon the wisdom of the ants, it is less likely that their acknowledgement of the source of their wisdom will match the generosity of computer scientists. Many useful details about ant agriculture have been known for a long time but it was only in 2005 (in the papers cited above) that we witnessed the first attempt to articulate the benefits to human agriculture of learning from insect agriculture, and that too came from myrmecologists (ant researchers) and not from agricultural scientists or economists. In contrast, the crucial paper on self-organized behaviour in ants was published in 1989 (Gross et al 1989) and ACO was developed in 1992 and has since grown into a major enterprise, retaining the explicit reference to the ants in its nomenclature. Why this difference – I wonder!²

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² My research is supported by the Department of Science and Technology, Department of Biotechnology, Ministry of Environment and Forests and Council of Scientific and Industrial Research, Government of India.

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