Understanding Change

Models, Methodologies, and Metaphors

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Exporting Metaphors, Concepts and Methods from the Natural Sciences to the Social Sciences and *vice versa*

Raghavendra Gadagkar

How could a biologist react to Jeffrey Nugent's excellent chapter in this volume? Since I have studied insect societies it should come as no surprise that I will be looking for parallels, real or apparent, in the world of social insects. Relative to our understanding of human economic institutions, our understanding of insect societies is woefully inadequate. But the little that we do know about them convinces me that there are fascinating parallels waiting to be explored to the mutual benefit of insect sociology and human economics. Let me briefly describe three of the many possible examples.

The honey bee dance language

Honey bees live in populous colonies consisting of tens of thousands of individuals. Each colony consists of a single queen, a small number of males (drones) while the rest of the colony consists of nearly sterile female worker bees. Because the drones do not contribute to colony labour and the queen merely lays eggs, all domestic duties are the responsibility of the workers. Worker bees have elaborate adaptations to undertake various tasks required for the welfare of the colony. After spending about half their life (which totals about 40 days) working inside the nest, worker bees fly out of their nests in search of food (nectar and pollen), which they bring back to the nest. To aid in this process of stocking up the nest with nectar and pollen, forager bees recruit other bees, which are idle in the nest (Gould J. L. and Gould C. G., 1988). Recruitment is not achieved by leading naive bees to new sources of food but, as the Austrian zoologist Karl von Frisch discovered in the 1940s, it is done by providing naive bees with abstract information about the distance and direction of the food sources discovered by the forager bees (Frisch, 1967). The information transfer is accomplished by means of a dance language that is a unique form of symbolic communication not witnessed in any other non-human animal. When the food is within about 100 metres form the nest, returning foragers perform a 'round' dance which conveys no specific information about the location of the food. But, having been alerted to the presence of food near their nest and having a good idea of what they should be looking for, which they get by smelling the dancing bee and by partaking drops of regurgitated nectar provided by the dancer, dance followers are able to successfully locate the source of food. When the food source is at greater distances, returning forager bees perform a 'waggle' dance, which additionally encodes information about direction and distance as well. Many different aspects of the honey bee dance language are under intense scientific investigation by dozens, perhaps hundreds of researchers (Seeley, 1995).

Many of the questions being investigated bear a remarkable resemblance to the kinds of questions that Nugent and others ask about human institutions: How are the dances of different bees different from one another? How are the dances related to the quality and quantity of food found by the dancer? How are the characteristics of the dances related to success in recruitment? How do bees in the nest respond to multiple dancers, advertising different sources of food, perhaps of differing quality and quantity and of differing value to the nest? How do bees balance short-term and long-term needs of the nest? How do bees deal with competition from neighbouring nests, which must also depend on the same sources of food? Is the recruitment system based on the dance language more efficient in some environments and less so in others? Can we find or breed bees, which recruit/get recruited more efficiently than other bees? The parallels with human institutions are hard to miss. I cannot believe that there isn't much to be gained by cross-fertilization of ideas between those of us who study insect or other animal social institutions and those of you who study human institutions.

Ant agriculture

Human agriculture which is believed to have originated some 10,000 years ago has rightly been considered the most important development in the history of our species. Virtually all the plants 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. The impact of agriculture on the further development of human societies has been profound – high rates of population growth, urbanisation and economic surpluses – all of which were pre-requisites for the development of modern civilization – were made possible with the advent of agriculture. Impressive as all this is, 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 are, ants belonging to the tribe Attini, macrotermitine termites and certain wood-boring beetles. While the beetles in this group are few and not of comparable importance, the fungus growing ants in the new world and fungus growing termites in the old world are ecologically very dominant. With a few exceptions, all fungus-growing ants are leaf cutters – 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 so grown and not from the leaves themselves. There are some 200 species of ants that do not know any other form of life style other than fungus farming. Because of their ecological dominance and their insatiable hunger for leaves, leafcutter ants are major pests in the new world. These ants can devastate forests and agricultural fields alike – they may maintain ten or more colonies per hectare and a million or more individuals per colony. Where they occur, leafcutter ants consume more vegetation than any other group of animals. 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. 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. On the other hand, growing pure cultures of some of these fungi in the laboratory has proved difficult or impossible for us humans. How ants manage to achieve this remarkable feat remains poorly understood. Not surprisingly, they manure their fungus gardens with their own faecal pellets. When a colony is to be founded, the new queen receives a 'dowry' from her mother's nest – a tuft of mycelia carried in her mandibles! Thus these ants appear to have asexually propagated certain species of fungi for millions of years (Hölldobler and Wilson, 1990).

What kinds 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 cultivating 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 are being attempted (Mueller *et al.*, 1998). Recent studies suggest that there have been at least five independent origins of fungal cultivation by ants, rather than a single event as was supposed previously. Even more interesting, recent results suggest that ants occasionally exchange fungal cultivars among themselves because different nests of the same species sometimes contain different cultivars. Whether the ants deliberately borrow fungal cultivars from their neighbours or whether the horizontal transfer occurs accidentally is however not known. How do ants deal with pests and parasites of their agriculture? What has been the impact of agriculture (including perhaps the economic surpluses thus generated) on the evolution of the ants themselves? These and other similar questions are now engaging the attention of researchers (Currie *et al.*, 1999). But again the parallels with human institutions are uncanny. Remarkably similar studies have been made using pretty much the same techniques and posing the same sorts of questions but concerning human domestication of plants and animals. For example, sixteen highly regarded wine grapes of northeastern France, including 'Chardonnay', 'Gamay noir', 'Aligoté', and 'Melon', all bred and cultivated since the middle ages, have now been shown to have DNA markers consistent with the possibility that they are all the progeny of a single pair of parents, 'Pinot' and 'Gouais blanc' (Bowers *et al.*, 1999). In contrast, analysis of DNA from today's domestic horses and samples from archaeological sites suggest that the horse was repeatedly domesticated over an extended period of time throughout the Eurasian range (Lister *et al.*, 1998; Vila *et al.*, 2001). The parallels between ant agriculture and human agriculture and other human institutions go far beyond questions of origin and evolution. Indeed they concern economics in the most direct manner. In the context of the leaf cutting, fungus-growing ants, e.g. what are the economic principles governing leaf harvesting and fungus production? There are issues concerning the optimum numbers of harvesting individuals, optimum sizes of the cut leaves, selection of patches of vegetation to be harvested in terms of species of the plant, distance from the nest, long-term, possibly sustainable use of resources and effective competition with neighbours who are all attempting to optimize the same variables. There has been some work along these lines but it barely scratches the surface. It is crucial for biologists to pay attention to parallel situations in humans and their study by economists and crucial for economists dealing hitherto only with *Homo sapiens* not to underestimate the potential sophistication of the adaptations and capabilities of the ants.

The division and organization of labour

Division of labour is a fundamental characteristic of insect societies. First there is the division into reproductive and non-reproductive labour. In almost all insect societies, only one or a small number of fertile individuals are responsible for reproduction while the remaining individuals in the colony (referred to as workers) are engaged only in non-reproductive tasks. In most social insects (i.e. ants, bees and wasps), colonies are headed by one or a small number of fertile females referred to as queens and there are no kings (except in the termites) as the males usually mate and die (Wilson, 1971). Apart from such reproductive division of labour, workers in many insect societies divide non-reproductive tasks among themselves by certain individuals specializing in certain tasks. Thus the colony's needs are fulfilled only because of the coordination between several individuals accomplishing sub-components of larger tasks (Oster and Wilson, 1978). For example, a returning nectar forager in a honey bee colony, has to wait in a queue to be unloaded and, depending on how quickly or how slowly she is unloaded, she will decide whether to bring more nectar or perhaps something else (pollen or water) that may be in greater demand in the colony. In addition to the mechanisms that help the insects achieve effective division of labour, there are questions concerning the organization of work – how does an individual insect that plays only a small part in a complex task, know what to do when? This problem seems to have been solved in at least two different ways. In relatively primitive insects societies, such as those of many species of bees and wasps, where colony sizes are small (less than one hundred individuals), the queen is the most active and physically dominant individual in the colony. She constantly interacts with her workers and by means of these physical interactions, she suppresses any attempts by the workers to take on reproductive roles and also regulates their non-reproductive tasks – more or less, telling that what to do when. The queen in such primitive, small societies has been called a central pacemaker. If the queen is removed, the workers stop working for the welfare of the colony and may start reproducing. If the queen is retuned soon, they abandon attempts at reproduction and get back to work. Centralized control by a single leader is thus the solution that these societies have come up with. The relatively more advanced societies, such as those of honey bees, many ants and termites, where colony sizes can be very large (thousands if not millions of individuals), have arrived at a different solution. Here it is of course impossible for a single pacemaker to control her colony by physical interaction with all the workers. A fairly sophisticated form of decentralized control thus replaces centralized control in the large, complex societies. Control of worker reproduction is still largely centralized and is achieved by the queen using a chemical weapon to inhibit worker reproduction. But even this may be thought of as somewhat decentralized. There are two reasons for this. First, it appears that the chemical weapon produced by the queen is more likely to be an honest signal that the workers find in their own interest to obey. Second, workers in some situations actually assist the queen by policing errant workers. However, the regulation of non-reproductive activities of the workers is entirely decentralized and self-organized. The principles of self-organization, using distributed intelligence and simple local rules to produce complex global patterns, are just beginning to be studied and the questions that biologists can potentially ask are rich and varied (Camazine *et al.*, 2001). In my own research for example, I study two primitive wasp societies (Gadagkar, 2001). One of them, *Ropalidia cyathiformis* is relatively more primitive than the other, *Ropalidia marginata*. As expected, *R. cyathiformis* has a queen who is physically active and dominant and centrally regulates both worker reproduction as well as their non-reproductive activities. An *R. marginata* queen on the other hand, is behaviourally docile and inactive and appears to use a chemical to regulate worker reproduction, leaving it to the workers themselves to self-organize their foraging in a decentralized manner. I believe that a comparative study of this pair of contrasting species will help understand the evolutionary transition from centralized control of worker activity to decentralized control and indeed, the evolutionary transition from relatively primitive to relatively advanced social organization.

Returning to the theme of this essay, the parallels with human institutions and their modes of organization and sources of efficiency and inefficiency are obvious. How do centralized and decentralized modes of regulation differ in their ability to promote efficiency under different conditions – conditions relating to group size, modes of communication and perhaps most important, the levels of motivation of the individuals to strive for the common good. The last point is perhaps better understood in the context of insect societies where there is a clear correlation between decentralized regulation and high 'motivation' among the individuals to work for the common good; interestingly, this high 'motivation' is created by the queen by foreclosing nearly all selfish option for the workers.

Exporting metaphors, concepts and methods

Now I wish to make some general remarks about exporting metaphors, concepts and methods from the natural sciences to the social sciences and *vice versa*. I would like to argue that exporting methods is easy and even essential, exporting concepts is desirable and exporting metaphors is difficult and may even be dangerous. Let me begin with that which I consider easy and desirable.

Exporting methods

One area in which I would like to see a significant unification of the natural and social sciences concerns research methodology. There are two fundamental differences in studying humans on the one hand and other animal or plant species on the other. One is that humans speak while other species don't. Thus, research on human systems can be based on what the humans involved have to say about the matter while research on other species has to necessarily depend on our using observation and experiment to find our facts. The second is that in the social sciences the researchers and the objects of research usually belong to the same species while that is not usually the case in the natural sciences. I believe that these two special features of research in the social sciences make it all the more important that, even though there is a simple option of 'asking' your subjects what they think of the matter, social scientists should increasingly adopt observations and experiments to gather their data. I would like to see many more studies of human institutions that depend on data gathered by direct observations using observational and sampling methodology so commonly used in studying animals. The most striking example of the pitfalls of not using direct observations and depending too much on what the human subjects have to say about themselves is the 'Fateful Hoaxing of Margaret Mead' in her *Coming of Age in Samoa* (Mead, 2001 [1928]; Freedman, 1983, 1998). Supplementing what humans have to say about themselves with what a relatively objective outsider can observe and infer for himself will surely reduce the probability of such errors.

Exporting concepts

Exporting concepts is not always necessary but can be useful and never particularly harmful. My impression is that here natural sciences, particularly the study of insect societies, has much to gain by importing concepts from human sociology, psychology and economics. Division of labour, the adaptive significance of castes, market economy, the relationship between demand and supply, group benefits versus individual interests, egalitarian versus despotic systems of control, private property *versus* common property, are some of the many concepts that come to mind as having potential application in the study of both human economic institutions and insect societies.

Exporting metaphors

Metaphors play a useful role in both human and animal research. But metaphors can be potentially dangerous if misunderstood and that danger is especially great when metaphors are exchanged across disciplines. The reason for this is that metaphors are specially defined for a particular context and are usually understood by the parishioners of a field and easily misunderstood by outsiders who are unaware of the restricted usage. Borrowing metaphors for one field into another without understanding such restricted meanings has caused endless debate and controversy. In the study of insect and other animal societies, it is quite common to use such terms that originally belong to human institutions as royal, king, queen, police, soldier, army, caste, labour, selfish, altruistic, nepotistic, egalitarian, despotic, democratic, revolt, loyal, rebel, rape … the list is long. When used in the context of insect and other animal societies, these terms are defined in very specific ways that strip them of much of the connotation that is inevitably tied to their usage in the human context. Consider some of the more controversial ones – selfish, altruistic and nepotistic. A selfish act by an insect is defined as any interaction that increases its own genetic fitness at the cost of the fitness of the recipient of that interaction. Conversely, altruism is defined as any interaction that reduces the genetic fitness of the actor while increasing that of the recipient. Nepotism is defined as any behaviour that enhances the fitness of genetic relatives of the actor. There is no implication of any associated moral or ethical values or of conscious awareness on the part of the actors. But when a biologist says that natural selection usually favours selfish or nepotistic behaviour, it is immediately interpreted by those outside the field to mean that biologists defend and condone and even encourage selfishness and nepotism. What is the solution to this problem? There are two. One is to insist that biologists should coin new terms (more jargon?) that have no chance whatsoever of being associated with the value system of humans. The other is to respect the restricted, metaphoric use of terms by biologists and not borrow metaphors 'illegitimately' from one field to another. I certainly prefer the latter solution. I don't believe that inventing new words would help either the cause of animal behaviour or of human ethics. Instead, it would make communication of science to non-specialists, and, indeed, even communication among specialists, more difficult and it would not necessarily prevent anybody from justifying any kind of human behaviour they wish to encourage (Gadagkar, 1997).

Exporting metaphors, concepts and methods between the natural and social sciences is useful if done with care but can be dangerous, especially with metaphors, if done without adequate understanding of their original function in the field from which they are being imported.

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