How to Design Experiments in Animal Behaviour

3. How Do Ants Find the Shortest Path?

Raghavendra Gadagkar

In this article, I will describe how a simple, curiosity-based experiment to understand how ants are smart enough to choose the shortest path led the exploration of self-organization and swarm-intelligence and resulted in major applications in computer science and optimization algorithms. The focus will be on curiosity, simplicity, interdisciplinarity, and being un-mindful of immediate applications.

1. The Usefulness of Useless Knowledge

In a 1939 influential essay entitled ‘The Usefulness of Useless Knowledge’, Abraham Flexner, Founding Director of the Institute for Advanced Study in Princeton, and one who recruited the likes of Albert Einstein and gave them the freedom to do what they wished, said “A poem, a symphony, a painting, a mathematical truth, a new scientific fact, all bear in themselves all the justification that universities, colleges and institutes of research need or require” [1]. In a brilliant companion essay written for the new reprint of Flexner’s essay in book form, Robert Dijkgraaf, the current Director of the Institute for Advanced Study in Princeton, says “Just as in Flexner’s time, the progress of our modern age, and of the world of tomorrow, depends not only on technical expertise, but also on unobstructed curiosity and the benefits—and pleasures—of traveling far upstream, against the current of practical considerations.” [2]. Nevertheless, we often hear from misguided politicians, bureaucrats, and (sadly) from scientists who happen to be doing the so-called applied research, that taxpayers’ money cannot be wasted on basic, or blue-sky research, especially in a developing country like India. This, I have come to accept as arising from political and selfish motives, rather than

Raghavendra Gadagkar is
Year of Science Chair
Professor at the Centre for
Ecological Sciences, Indian
Institute of Science,
Bangalore, Honorary
Professor at JNCASR, and
Non-Resident Permanent
Fellow of the
Wissenschaftskolleg (Institute
for Advanced Study), Berlin.
During the past 35 years he
has established an active
school of research in the area
of animal behaviour, ecology
and evolution. The origin and
evolution of cooperation in
animals, especially in social
insects, such as ants, bees and
wasps, is a major goal of his
research.

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from ignorance. What I am more concerned about is the genuine and often very touching need, almost a moral imperative, felt by many young people to do good to the society through their scientific research. We cannot find fault with this. Unfortunately, the problem, however, is that we cannot usually predict what kind of research will do the maximum good to society. It is the unpredictability of the possible uses of knowledge that makes it necessary that we pledge to do good research of all kinds, whether its ultimate use is currently obvious or not. We must keep adding nuggets of the highest quality to the well of collective human knowledge so that we can proceed rapidly when the utility of any kind of knowledge becomes obvious, and feasible to apply, to the problems of society. How then should we choose our research topic? I will make two points. First, I think we will have a natural advantage if we follow our curiosity and work on the topics that we most love. Second, we are more likely to succeed if we choose, from among the topics we love, those that present the least external obstacles to achieving the best of our potential. For these reasons, I have chosen to illustrate the theme of how to design experiments, with examples of experiments that attempt to answer intrinsically interesting questions and at the same time require almost nothing in terms of money, equipment and other facilities. In the third article of this series, I will have the opportunity to also illustrate the usefulness of useless knowledge.

In a classic 1989 paper [3] that started it all, published in a somewhat obscure journal, Jean-Louis Deneubourg and his colleagues, begin by observing that “It is evident that finding the shortest route is extremely important not only for Roman road builders, thirsty rugby men and applied mathematicians working on this very problem, but also for any animal that must move regularly between different points. How can an animal with only limited and local navigational information achieve this?” So, they asked how ants find the shortest path to food – as good an example of blue-sky research as any.

2. Ants

Ants are probably the most familiar social insects, occurring everywhere – from the arctic tree line to the tip of South Africa and Tasmania. They are especially familiar because they walk about on the ground, often in intriguingly disciplined moving columns. Some 13,000 species of ants have been catalogued, named and described by scientists who call themselves myrmecologists, although this number is expected to be no more than a half or a third of the number of ant species out there, waiting for you. Finding new ants without having a scientific name yet and describing them and thus adding to the well of collective human knowledge is a charming hobby, easily cultivated and one that can be especially rewarding in a poorly studied place like India. Wondering how and why they (named or not yet) move about in columns and do so many other amazing things can be equally fascinating and rewarding, enough to prevent you from ever growing out of your hobby and pursuing other ‘traditional careers’. There are many charming accounts of ant watchers that can entice you into such an adventurous life [4, 5].

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3. The Experiments

Jean-Louis Deneubourg (*Figure 1*), one of the protagonists of this article is a theoretical chemist but has always been interested in animal behaviour. He was registered for a PhD in the Université de Bruxelles in Belgium, with the famous Viscount Ilya Romanovich Prigogine, physical chemist and Nobel laureate, famous for his work on complex systems, and sometimes called the ‘Information Philosopher’. But Jean-Louis wanted to work on ants! So he teamed up with, to use his own words, “three brilliant biologists: J M Pasteels who was the Head of our university lab working on social insects, one of his PhD students S Aron, and a British biologist working in our university S Goss. One result of our discussions is the paper Goss *et al.*” [3]. Deneubourg, being a chemist rather than a field biologist (there is room for everyone’s curiosity), was more intrigued by the columns of moving ants

Figure 1. Jean-Louis Deneubourg (1951–).

Deneubourg and his colleagues conducted laboratory experiments to understand how Argentine ants choose the shorter of two available paths.

rather than their diversity. He chose to study the Argentinian ant, then known as *Iridomyrmex humilis* (more recently renamed as *Linepithema humile*), that has become notoriously invasive in Europe and other places, having been inadvertently introduced there by humans (*Figure 2*). Deneubourg and his colleagues decided to conduct laboratory experiments to understand how these ants choose the shorter of two available paths. Deneubourg says he was interested in shortcuts because he thought “time is money”, and that must be true for the ants too. Biologists would say, for ants, time is Darwinian fitness.

Thus, they put an ant colony in one box and some food in another box and connected the two boxes with a bridge with two branches – a long one and a short one – and let the ants forage. You will get an idea of the experimental setup that Deneubourg and his colleagues used from *Figure 3* (which shows the setup that my undergraduate students Ankan and Jadeera used in trying to repeat this experiment). As expected, the ants began by randomly using either branch but soon, nearly all the traffic was on the shorter branch. How did the ants manage to achieve this feat? A reasonable line of inquiry, and one that I think a biologist is more likely to have made is to assume that the ants measure and compare distances and that natural selection would have selected for ants that choose the shortest path. Ants and bees can indeed measure distances, and this will be the subject of the next article in this series. But being a chemist, Deneubourg appears to have

Figure 2. Argentine ants *Linepithema humile* (previously known as *Iridomyrmex humilis*). (Image purchased from Shutterstock: <https://goo.ggl/BPa6UT>)

Figure 3. Experimental setup used by my undergraduate students Ankan and Jadeera to study if ants can choose the shorter of two paths provided between their nest and the food source.

Photo credit:

Dr. Thresiamma Varghese

followed his natural instinct to pursue a physicochemical explanation, rather than a biological one, and to his credit, he appears to have persuaded his two biologist colleagues to give it a shot.

It is well known that many ant species including the Argentine ants deposit volatile chemicals, known as ‘pheromones’, as they walk from their nest to the food and from the food to the nest. This behaviour scent marks the route taken by the ants so that other naïve ants can follow the trails laid by the successful ants. This is the method by which scout ants recruit naïve ants from their colonies to efficiently transport food that they may have found, back to the nest. Deneubourg built up a logical argument (hypothesis) that did not involve any intelligence or abil-

ity to measure or compare distances. Instead, it required the ants to obey only two simple rules, unconnected to the lengths of the branches – (i) lay trail pheromones as you walk and (ii) follow the trails of others. A crucial clue to build such an argument comes from a preliminary experiment, a kind of null experiment in which they had both branches of equal length. Now, the question was whether half the ants will use one branch and the other half will use the other branch, or whether one branch will nevertheless win over and get all the traffic. These two possible outcomes will lead us to very different logical paths of hypothesis construction.

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As it happened, one of the two branches always won over the other so that in most trials of the experiment, most of the traffic was restricted to one of the two branches, even though both branches were of the same length (*Figure 4*). *Figure 4* may seem a bit confusing so let us go over it carefully. Percentage of traffic is counted on any one of the branches, chosen randomly, say the left branch. The tall bar on left shows that 0–20% of the traffic was on the left branch in 50% of the experiments. This means that 80–100% of the traffic was on the right branch. Thus, most of the traffic in 50% of the experiments was largely restricted to one of the two branches, namely the right branch. In other words, one of the branches (the right one) had won over the left branch, even though the two branches were of the same length. The short bar in the middle shows that 40–60% of the traffic was on the left branch in only 8% of the experiments, meaning that the traffic was roughly equally divided between the two branches. The relatively tall bar on the right shows that in 42% of the experiments, 80–100% of the traffic was restricted to the left branch (the one we are counting) meaning that only 0–20% of the traffic was on the right branch. In other words, most of the traffic was restricted on one branch (the left one) in 42% of the experiments. In summary, most of the traffic was restricted to one of the two branches (either the right or the left) in 92% of the experiments while the traffic was distributed roughly equally between the two branches only in 8% of the experiments.

Figure 4. When Argentine ants are given a bridge with two equal branches, most of the traffic in most of the experiments is on or the other branch and on both branches in only a few experiments (see text for a detailed description). Adapted by permission from Springer Nature Customer Service Centre GmbH, Springer, *Naturwissenschaften*, Self-organized Shortcuts in the Argentine Ant, S Goss, S Aron, J-L Deneubourg, and J M Pasteels, 76, pp.579–581, 1989.

So, we must look for a mechanism by which one branch wins over the other even when the two branches are of equal length. This makes us think very differently because we are no longer thinking of the biological advantage of choosing the shorter of the two paths. Deneubourg and his colleagues imagined the following scenario. In the very beginning, the ants choose randomly between the two branches. In course of time, as the ants begin to move between the nest and the food and back, repeatedly, and keep laying pheromone all the time, pheromone concentrations build upon both the branches. Due to small stochastic variations in the amount of traffic on one of the two branches, there will be small stochastic variations in the amount of pheromone on the two branches. Now, the branch with the slightly higher concentration of pheromone will be slightly more attractive to the ants leading to slightly more traffic on that branch. This will result in even higher pheromone concentration on that branch and the process will runaway due to positive feedback resulting in that branch winning completely over its counterpart. Which of the two branches will win, however, is completely random. Now let us consider the experiment in which one branch is shorter than the other. As in the previous experiment, the ants will choose one of the two branches randomly in the beginning. In this experiment, there will, of course, be more traffic per unit time on the shorter branch because ants choosing the shorter branch will

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Figure 5. When Argentine ants are given a bridge with two unequal branches, most of the traffic in most of the experiments is on the shorter branch (see text for a detailed description). Adapted by permission from Springer Nature Customer Service Centre GmbH, Springer, *Naturwissenschaften*, Self-organized Shortcuts in the Argentine Ant, S Goss, S Aron, J-L Deneubourg, and J M Pasteels, 76, pp.579–581, 1989.

reach the food sooner and return sooner and thus make more trips per unit time. Here there will be more pheromone build up on the shorter branch and through a similar positive feedback, the shorter branch will win over the longer branch. See from *Figure 5* that 80–100% of the traffic was on the shorter branch in 97.5% of the experiments and only in 2.5% of the experiments, was there less traffic on the shorter branch, but even here there was 60–80% traffic on the shorter branch and only 20–40% of the traffic on the longer branch. Thus, the ants can choose the shorter of the two available paths merely by each individual ant choosing two simple rules unrelated to the final outcome – lay pheromone and follow the trails of others.

Impressive, no doubt! But we have a result and we have a hypothesis that can explain the observed result. There is a correlation between the prediction of the hypothesis and the behaviour of the ants. However, correlation is not always evidence of cause and effect. There is always the possibility that the behaviour of the ants was caused by some mechanism other than what we have postulated. We, therefore, need better evidence to prove that the mechanism we postulate is indeed at work. Deneubourg and his colleagues marshalled two further lines of evidence in support of their hypothesis. First, they built a stochastic mathematical model of differential equations which defined the probability that an ant

Figure 6. Percentage of ants passing on the winning branch (Y-axis) as a function of the total number of ants passing on the two branches put together. 20 experiments, in colonies of 150–1200 workers. The green curve represents the average values calculated for every 100 ant passages. The red curve represents the average of 200 Monte Carlo simulations, with $n = 2$ and $k = 20$. Adapted by permission from Springer Nature Customer Service Centre GmbH, Springer, *Journal of Insect Behaviour*, The Self-organizing Exploratory Pattern of the Argentine Ant, J-L Deneubourg, S Aron, S Goss, and J M Pasteels, Vol.3, pp.159–168, 1990.

chooses branch A (for e.g.) as:

$$(k + A_i)^n / [(k + A_i)^n + (k + B_i)^n],$$

where A_i and B_i are the numbers of ants that have previously chosen the branch A and B respectively. The parameters k and n are meant to decide how slowly or quickly one branch wins over the other and they determined that $k = 20$ and $n = 2$ best described the rate at which the short branch won over, in their experiments. Using this equation, they used Monte Carlo simulations to obtain the rate at which traffic on the short branch should increase gradually, starting from about 50% (random) to plateau at some 80–100%. This rate closely matched the corresponding rate observed in the experiments (*Figure 6*) [6]. Although the values of k and n were empirically determined from the experiments, the close fit between the results from the simulation of the model and the behaviour of real ants gives confidence that the simple mechanism envisaged in the model is sufficient for the ants to choose the shorter of the two branches. This is encouraging but not quite sufficient.

Their clinching evidence came from another simple but really clever experiment. They modified the original experiment in such a way that the mechanism we have in mind will fail, and then they

Figure 7. When Argentine ants are given a bridge with two unequal branches, but the short branch is opened 30 minutes after the ants have been using the long branch. Now the ants fail to choose the short branch (see text for a detailed description). Adapted by permission from Springer Nature Customer Service Centre GmbH, Springer, *Naturwissenschaften*, Self-organized Shortcuts in the Argentine Ant, S Goss, S Aron, J-L Deneubourg, and J M Pasteels, 76, pp.579–581, 1989.

checked whether the ants also failed to choose the short branch. They argued that if they opened the long branch first and allowed the ants to forage using only this branch for some 30 minutes before they opened the short branch, then so much pheromone would have been built upon the long branch by the time the short branch was opened, that it would not be able to win over the long branch. This idea was also supported by their model, which showed that the short branch would not win if it was opened 30 minutes later [6]. This is precisely what they also found when they did the experiment accordingly. See from *Figure 7* that when the short branch was opened 30 minutes later, there was less than 50% of the traffic on the short path in more than 79% of the experiments (sum of the two left-most bars). This is clinching evidence [3].

Thus, a colony of ants can choose the shorter of two branches available, a task that at first appears to be cognitively challenging, by nothing more than individual ants following two simple rules, with no apparent connection to the ultimate goal. This process has come to be known as ‘self-organization’. Other telling phrases that are often used to describe such phenomena include emergent properties, bottom-up control, distributed intelligence and swarm intelligence [7, 8]. The last phrase comes from ‘a swarm of bees’, the name given to an aggregation of bees; bees,

of course, are also social insects which provide many similar instances of complex behaviour arising through self-organization. Self-organization is today the preferred explanation for a variety of phenomena including, pattern formation in slime moulds and bacteria, feeding aggregations of bark beetles, synchronized flashing among fireflies, fish schooling, nectar source selection by honey bees, trail formation in ants, the swarm raids of army ants, colony thermoregulation in honey bees, comb construction by honey bees, wall building by ants, termite mound building, construction algorithms in wasps, and dominance hierarchies in paper wasps [8]. Self-organization, with its distributed intelligence and bottom-up control, appears to have permitted social insects, in spite of their small brains, to accomplish extremely complex tasks. It is perhaps for this reason that they have achieved unprecedented ecological dominance and evolutionary success – some three-quarters of all animal biomass in some tropical forests is made up by ants and termites.

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4. Enter Marco Dorigo

Marco Dorigo, now Director of IRIDIA (*Figure 8*), the Artificial Research Intelligence Laboratory in the University of Brussels, was a young student pursuing his PhD when Deneubourg and his colleagues were performing these, now classic, experiments about how ants choose the shorter of two paths. Marco Dorigo realized that the mechanism proposed by Deneubourg and his colleagues for the efficient behaviour of their ants lends itself to an application in developing efficient computer algorithms for solving many discrete optimization problems. The simple mechanism by which ants choose the shorter of two paths, discovered by Deneubourg and his colleagues, has since been put to mind-boggling practical use, the extent of which is hard to believe, for a biologist, even after the fact. Inspired by the behaviour of real ants as discovered by Deneubourg and colleagues, Dorigo and colleagues considered the problem of how artificial ants can move around on graphs of varying complexity, and find the shortest path between any two points. Although the behaviour of real ants is

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Figure 8. Marco Dorigo (1961–).

the starting point, the behaviour of the artificial ants can be made progressively more complicated as per the needs of the task. We know that even real ants can behave in more complex ways if required. For example, when presented with two different qualities of food at the same distance, ants can efficiently choose the better of the two, by a slight modification of their behaviour namely laying more pheromone when exploiting the better food source [9]. Real ants may have evolved many other additions to their behaviour, but the initial discovery of Deneubourg and colleagues was enough to set computer scientists on a path of exploration of their own by making their artificial ants increasingly complex as per the needs of their problems. Indeed, one can imagine a sort of competition between the designing of artificial ants and the discovery of the behaviours of different real ants – a healthy competition between nerds and naturalists!

Dorigo and colleagues realized that using difference equation with discrete time steps, while mimicking the behaviour of Deneubourg's ants and their differential equations, are more amenable for further development of their algorithms. The main reason for this is that while the continuous model reflects the stochastic behaviour of individual ants, the discrete model describes the average behaviour of a finite number of ants. Thus, they first developed an algorithm they called a 'simple ant colony optimization' or

S-ACO and used to understand in detail, how ant colony optimization works. For a biologist, it is pleasing to see how much of the ant metaphors they have retained in exploring the workings of S-ACO. Before meaningful application, they (and by now many more computer scientists had jumped in) had to develop an ant colony optimization metaheuristic. A heuristic is a kind of self-learning strategy based on trial and error or on some very simple rules, and a metaheuristic is a master strategy that guides individual heuristics. The ‘ant colony optimization metaheuristic’ and related ant, wasp or bee-based algorithms have since been used to solve a number of real-life problems. In a remarkable lucid and reader-friendly textbook (even reprinted as an inexpensive ‘Eastern Economy Edition’ for the Indian market) [10], Marco Dorigo develops the idea of ACO from its historical roots beginning with the experiment by Deneubourg and his colleagues all the way to its development as an everyday application and shows us how ACO-based algorithms are outperforming other routing methods for the internet and telecommunication and how ant-based models have been used by South West Airlines for example, for efficient routing of their air-cargo. In *Table 2.1* of this book, they list more than 30 real-life problems including the travelling salesman problem, adaptive routing in communication networks, distributed algorithms for data clustering, dynamic resource sharing, graph colouring, machine scheduling, vehicle routing, sequence learning, and machine learning for which ACO has been applied [10]. There are also a number of other useful and very accessible accounts of this story, going from mere curiosity to real-life applications [11].

ACO-based algorithms are outperforming other routing methods for the internet and telecommunication, and ant-based models have been used by South West Airlines for efficient routing of their air-cargo.

5. Reflection

What are the general lessons one learns from this experiment? Clearly, the spotlight is on curiosity, simplicity, interdisciplinarity, and being unmindful of immediate applications.

Curiosity: How ants choose the shortest path is the kind of curiosity-based question that any person should be able to ask; it does not

take training of any kind. Indeed, it takes training not to ask such questions or at least think that it is pointless to ask such questions and to believe and make others believe that there are better, more useful and responsible ways to spend one's time. That is the kind of training that we must try to eliminate, students can do so by staying away from such training, and educators must find ways of abolishing such training.

Simplicity: There is so much social prestige these days in sophisticated and complicated scientific research that simplicity has become unfashionable. Instead, we must create prestige for simple, inexpensive experiments, of the kind that anyone can do and anyone can understand. We must once again make it fashionable to say that simple is beautiful.

Interdisciplinarity: Another feature of modern science is that it has become very specialized, leading to the mistaken belief that it is essential to become an expert in the subject, and gain mastery of all that is already known, before you can discover new things. This is not always true. Some of the best discoveries are made precisely because of being naïve in the field one is dabbling in.

Practical Utility: Perhaps the biggest lesson we learn from these experiments is that apparently, useless knowledge can have unexpected uses. Who would have thought that understanding how ants find the shortest path can lead to a revolution in computer science! The more we make our research simple and low-cost, the more we can avoid the need to guarantee practical utility.

Suggested Reading

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Address for Correspondence
 Raghavendra Gadagkar
 Centre for Ecological Sciences
 Indian Institute of Science
 Bangalore 560 012, India.
 Email: ragh@iisc.ac.in