More Fun Than Fun: Experienced Ants Lead and Teach, Naïve Ants Follow and Learn

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Two men on a tandem bicycle. Photo: State Library of Victoria.

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This article is part of the 'More Fun Than Fun' column by Prof Raghavendra Gadagkar. He will explore interesting research papers or books and, while placing them in context, make them accessible to a wide readership.

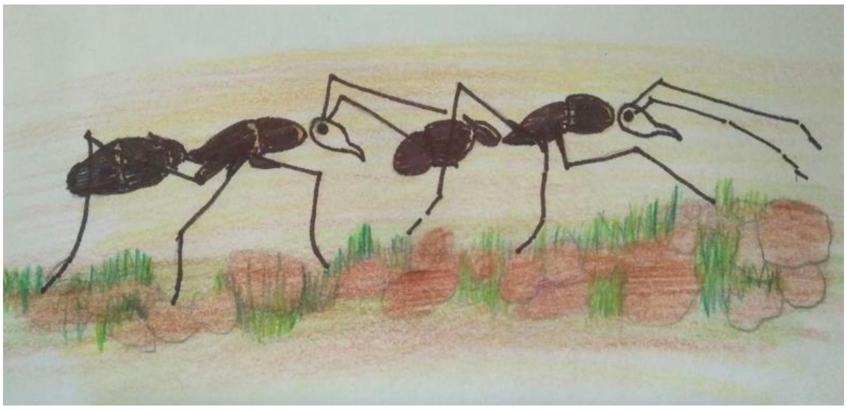
Maj. Richard William George Hingston (1887-1966) was an Irish doctor who served in the Indian Medical Service from 1910 to 1927, and returned to India on military duty from 1939 to 1946. A passionate naturalist, he spent all his spare time collecting and studying the Indian fauna, mostly insects and spiders. Based on his studies in the Himalayan valley of Hazara (now in Pakistan), Hingston published *A Naturalist in Himalaya* (1920).

Recording what is perhaps his most famous observation, made on the common Indian ant *Camponotus sericeus*, he wrote in his *Problems of Instinct and Intelligence* (1928):

> This ant nests on the ground and goes up trees in search of food. Its plan of communication is very simple, and, being so simple, is highly instructive. All that happens is that one ant leads another to the place where spoil has been found. One ant discover spoil. It returns to the nest, finds a comrade and leads it to the required place. The two go off over the ground. The leader keeps in front; the led ant follows. Number two keeps in number one's footsteps, and repeatedly touches its tail. The leader moves particularly slowly in order not to lose connection with its follower. If number two happens to get out of touch, then the leader halts and waits until number two regains its place.

Harvard University professor and arguably the world's most famous ant biologist Edward O. Wilson rediscovered this behaviour while studying another ant, *Cardiocondyla venustula*, in Puerto Rico in 1959. Wilson christened this behaviour tandem running – simply because it involves the movement of a pair of ants running in tandem, not unlike a tandem bicycle.

In most species however, experienced ants guide their naïve sisters to new sources of food or a new place to build their nest by marking their path with volatile chemicals called trail pheromones. And yet, many ants, especially those that live in small colonies, communicate without trail pheromones. Instead, they use tandem-running to guide their naïve sisters to new locations.



A drawing of tandem-running ants by Sumana Annagiri. Photo: Author provided

Because it involves more dynamic behaviour and considerable intelligence, I am always more impressed by tandem-running ants than by those who rely on their glands spewing out some chemicals – or perhaps that's just my prejudice. But maybe some others share my sentiments. Elizabeth L. Franklin, Nigel Franks, and their colleagues at the University of Bristol have studied the ant *Temnothorax albipennis* to make tandem running a favourite tool for ant-researchers to investigate communication, collective decision-making, learning and teaching. I will have more to say about teaching later.

In recent years, Annagiri Sumana and her students at the Indian Institute of Science Education and Research, Kolkata, have had great fun studying the ant *Diacamma indicum*, which live on their institute campus in large numbers. This ant belongs to the rather unusual group of ants that no longer make queens: over evolutionary time, the workers have stopped rearing some larvae into future queens. Instead, the workers have learnt to manage their affairs on their own.

One of the workers mates and becomes the sole egg layer of the colony. She is called a 'gamergate' – literally 'married worker'. My friend and one-time collaborator Christian Peeters, and S. Higashi, discovered that the gamergate maintains her reproductive monopoly in a bizarre way. She promptly bites off little appendages called gemmae of all female ants at birth, thus effectively castrating them. Devoid of their gemmae, they cannot produce the pheromones needed to attract males. And remaining virgins, they pose no threat to the gamergate's reproductive monopoly. When the gamergate dies, there is no one to bite the gemmae of the next to be born, who therefore becomes the next gamergate, and she in turn mutilates all who are born after her.

A colony of Diacamma indicum ants in the lab, with individual markers for identification, ready for an experiment. Photo: Thresiamma Varghese

Sumana and her students have studied tandem running in *Diacamma indicum* in the context of nest relocation, or house-hunting. When their nest becomes unsuitable due to flooding or any other reason, these ants have to move to another more suitable place and build a new nest. This is no mean task, given that they have to walk (being wingless they can't fly) and transport their brood, and ensure all of them reach the new place without getting lost or falling prey to lurking predators. Sumana and her students are studying this process by experimentally inducing them to abandon their old nests and seek a new nesting site.

When they disturb the nest, they observe that a few ants come out and explore the surrounding area for a suitable place to build a new nest, or at least as a temporary abode before they can find a more permanent home. Returning from their trips, some of these explorers spontaneously become tandem leaders and begin to tandem-run the rest of the colony members to the new place they have chosen. Some of the followers who are successfully led to the new location, and have learnt how to get there, return and become new leaders and tandem-run others. Some of the followers transport brood by carrying eggs, larvae and pupae in their mandibles as they follow the leaders. In this way, the entire colony, including the brood, is efficiently transported to the new site – entirely by tandem-running.

This is such a beautiful study system that even without knowing much about ants, anyone can begin to ask important questions, and indeed, almost anyone can begin to answer these questions. Which ants become explorers, and why? Which among them become leaders and why? Which followers return to become new leaders and which stay put in the new place? Who transports brood and why? How do they agree on a single new location as multiple explorers may have found many possibilities? Do they converge on the best new site among those available? What happens if the colony gets divided into two parts? What dangers do they face while relocating their nest? Will their brood get stolen on the way?

Sumana is leading and an army of her students are following. Together, they are continuously answering these and many other questions by performing simple and clever experiments, both in the laboratory and in nature. I impatiently await and consume each of their new findings as they come, hot off the press. You can do the same by keeping an eye (or your cursor) on the website of Sumana's Ant Lab.

My favourite pick from their experiments thus far is one where they show that even during the crisis of relocation, and while tandem-running to transport the entire colony and brood to safety, the ants are mindful of their paths. In a recent paper entitled 'Path minimisation in a tandem running Indian ant in the context of colony relocation', Snigdha Mukhopadhyay, Manish Kumar Pathak and Sumana Annagiri reported the results of their study of 4,100 tandem runs performed by 450 different tandem-runners. They showed that both explorers and tandem leaders chose the shorter of the two or more paths provided.

This discovery assumes importance because such path minimisation was hitherto known only in ants that use trail pheromones. In 1989, Jean Louis-Deneubourg and his colleagues at the University of Brussels conducted a landmark experiment: they showed that trail-laying ants choose the shorter of two paths, but not by individual intelligence. Individual ants initially choose one of the two paths randomly, but the ants using the short path make more trips per unit time (simply because of the shorter distance). Naturally, more pheromone gets deposited on the shorter path as compared to the longer one. This makes the short path more attractive to new ants – not because it is shorter but because it has more pheromones. Very quickly, all ants begin to use only the short path.

Thus, an 'intelligent' outcome of using the shorter of two paths is made without any intelligence. This was one of the pioneering experiments that led to researchers realising that insect societies rely on such *collective*, or swarm, intelligence. The two simple rules – follow the trails of others and lay your own pheromone trail – when followed by a large number of individuals leads to the emergence of unexpected and unplanned outcomes, without the need for any planning, leader or top-down control.

(L-R) Manish Kumar Pathak, Sumana Annagiri and Snigdha Mukhopadhyay work with a simple apparatus to test the ability of ants to choose the shortest path available. Photo: Subhasis Halder

Such decentralised self-organisation among ants has inspired the development of the academic discipline of ant colony optimisation, with applications in computer programming, telecommunication, internet traffic and much more.

However, Sumana's tandem-running ants don't have the luxury of pheromone-based emergence of intelligence. The individual ants have to figure out, using old-fashioned intelligence, which path is the shorter and should have the intelligence to choose it instead of the long one. I'm not surprised that the ants are capable of this feat even in the absence of pheromones. We still don't know how they manage it. But Sumana and her students have already begun their sleuthing, checking out the roles of visual and other stimuli. So, let's keep an eye on the Ant Lab website!

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I now return to teaching. Can we say that in the tandem-running ants, the leaders are teaching and the followers are learning? For reasons that I don't sympathise with, there is often strong resistance to attributing 'exalted' phenomena such as teaching, intelligence or consciousness to animals, especially 'lower' animals such as ants. This 'anthropo-supremacy' is neither necessary nor tenable.

Tim Caro and Mark Hauser, then at the University of California, Davis, asked "Is there teaching in nonhuman animals?" in a fascinating review of the literature on 'teaching' in animals. They argued that "adherence to conventional, narrow definitions of teaching, generally derived from of human adult-infant interactions, has caused many related but simpler phenomena to go unstudied or unrecorded, and severely limits further exploration of this topic". They then set out a simple working definition of teaching:

> "An individual actor A can be said to teach if it modifies its behaviour only in the presence of a naive observer, B, at some cost or at least without obtaining an immediate benefit for itself. A's behaviour thereby encourages or punishes B's behaviour, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all."

In her review of the literature on tandem running, Elizabeth Franklin provides convincing evidence – mostly from her own experiments – that tandem-running ants satisfy all the criteria set out in this definition. She explains how leaders provide followers an opportunity to learn how to get to the new site, rather than teach them a particular route to be followed blindly. The followers seem to be learning about landmarks along the way and making their own measurements of distances travelled and turns made, so that they can work out a route by themselves.

I find it curious that some people continue to object to calling this teaching on the grounds that tandem-leaders are not transferring all the needed information to the followers but are merely giving them an opportunity to learn. I think that is what human teachers should do in the first place!

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