More Fun Than Fun: Weaving with Silk, the Ant Way

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Bert Hölldobler during field work in Arizona around 1976. Photo: © Bert Hölldobler

RAGHAVENDRA GADAGKAR

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.

- *Ants in the genus Oecophylla produce silk but don't spin cocoons for themselves. Instead, they donate all their silk for the communal nests of their colonies.*
- *How did the ants attain this level of perfection through evolutionary time? And why do the larvae donate their silk?*
- *The evolution of altruism is a paradox that Charles Darwin and all his successors have had to grapple with.*

For those of us living in the tropics, in Africa, Asia and Australia, the arboreal nests of weaver ants are iconic. For the sociobiologist, their method of building nests makes them even more special. As Bert Hölldobler and Edward O. Wilson noted, "One of the most remarkable social phenomena among animals is the use of larval silk by weaver ants of the genus *Oecophylla* to construct nests".

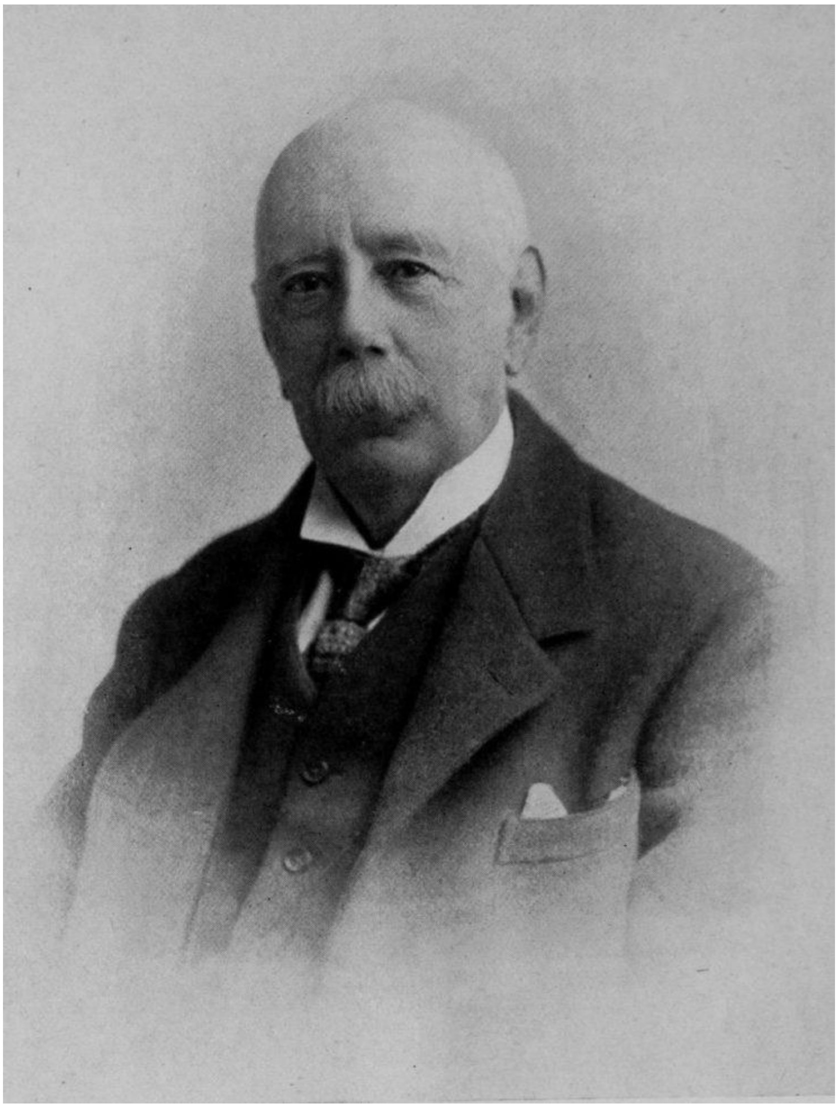
Weaver ants belong to the genus *Oecophylla*, which in turn belongs to the large subfamily of ants, the Formicinae – named for their unique habit of using formic acid to capture prey and for defence. In nearly all ants in Formicinae, larvae produce silk and spin protective cocoons around themselves before becoming pupae. Ants in the genus *Oecophylla*, however, produce silk but don't spin cocoons for themselves. Instead, they remain naked and donate all their silk for the communal nests of their colonies.

There are at least three questions of interest. How do the ants build their nests and enlist the help of the larvae? How did the ants attain this level of perfection through evolutionary time? And why do the larvae donate their silk?

How weaver ants build their nests

There are only two species of *Oecophylla* in the world. *Oecophylla smaragdina* occurs in India and Sri Lanka in South Asia, throughout Southeast Asia, northern Australia and Melanesia. *Oecophylla longinoda* occurs in the African tropics.

The weaver ants' remarkable habit of building nests by stitching leaves together with larval silk was discovered in *O. smaragdina*, simultaneously and independently by two English naturalists, H.N. Ridley in Asia and William Saville-Kent in Australia.



Henry Nicholas Ridley (1855-1956). Photo: British Colonial Government of the Straits Settlement of Singapore, public domain

Born in Norfolk county in South East England in 1855, Ridley went on to become an accomplished botanist and director of the gardens and forests of the Straits Settlements in Singapore. Ridley's long life, spanning 101 years, was rich in natural history expeditions and discoveries, especially in South and Southeast Asia. Ridley didn't restrict himself to the study of botany but collected many different animals and plants. Although he probably misnamed his species, he provided perhaps the first description of nest building in *O. smaragdina* in 1890, in the *Journal of the Straits Branch of the Royal Asiatic Society*.

Because it is so old and so clear, I will quote an abridged passage from Ridley rather than paraphrase him.

> "When a nest is to be built, a number of ants seize one edge of a leaf in their jaws and by sticking the claws of the hind legs into an adjoining leaf steadily draw the two edges together. If the edges of the two leaves are still too far apart, and one ant cannot reach both edges, a chain is made. One ant grasps one edge with its jaws, seizes him gently but firmly by the notch above the abdomen in its jaws. A third repeats the operation on the second and holds the second leaf by its hind claws. In this manner leaves are gradually pulled together till the edges almost entirely meet. In a few minutes, others come up and commence to sew the leaves together with silk. One or two ants come from interior of the nest, each bearing a larva in its mouth, the tail of the larva pointing outwards. They then commence by plying the tail end of

the grub to the edge of one leaf irritating it by quivering the antennae over and upon it. The grub emits a thread of silk which is fixed apparently by the antennae of the ant to the leaf-edge. The sewer then runs across to the other leaf drawing the thread from the grub and fixing it there, thus it goes backwards and forwards from leaf-edge to leaf-edge till a strong web of silk binds the two leaves together."

William Saville-Kent was born in Devon in southwest England in 1845, and became an accomplished marine biologist and commissioner of fisheries for Western Australia. Saville-Kent was best known for "his sumptuous work on the Great Barrier Reef of Australia". His passion for marine biology didn't prevent him from discovering the weaving habits of *O. smaragdina* any more than his passion for botany prevented Ridley.

There is a remarkably similar description of nest building in Saville-Kent's *The Naturalist in Australia* (1897):

> "That the green ants should be capable of spinning silk seemed such an anomaly that the elucidation of their *modus operandi* attracted the writer's attention on more than one of the occasions of his visit to the north. It was, finally, when examining the nests of these ants and their ways in the bush a little way out of Cooktown, in July 1890, that the enigma was solved. It was then found that the ants in their matured state took no distinct part in the weaving, though they were at the same time instrumental in requisitioning their immature grubs or larvae to fulfil the task."

William Saville-Kent (1845-1908). Photo: Waterlow & Sons; negative by Maull & Fox, public domain

Much of the rest of what we know today comes mainly from the extensive studies of the Harvard biologists Bert Hölldobler and Edward O. Wilson, of *O. longinoda* in Africa and *O. smaragdina* in Australia. They and others have added interesting details to Ridley's and Saville-Kent's memorable descriptions of nest-building. Many of these details reinforce the idea that the larvae donate silk in an act of evolutionary 'altruism', for the good of the colony.

Silk production and utilisation in weaver ants are quite distinct from the corresponding phenomena in other ants – where silk serves the 'selfish' purpose of protecting the individual producers of silk.

Nest construction by the weaver ant (Oecophylla longinoda). Clockwise: worker ants seizing the edges of a leaf in their mandibles, attempting to align the edges of two leaves, using a larva to bind the leaves with silk threads, and a completed nest. Photos: © Bert Hölldobler

Weaver ants preferentially choose their early final instar larvae for silk donation duties – whereas in species where the larvae spin silk for making their *own* cocoons, it is done by late final instar larvae.

As I mentioned earlier, weaver ant larvae never make cocoons for themselves – the silk is entirely for communal use. The larvae are used as passive dispensers of silk, and all the appropriate body movements required for efficient use of the silk fibres, for binding leaves together, are performed by the larva-bearing adult ants. Hölldobler and Wilson, therefore, consider the larvae in *Oecophylla* societies as an additional 'auxiliary caste'.

This is one of the few examples I know of the immature stages serving as a specialised worker caste in ants, bees and wasps, though it is well known in termites and has recently been discovered in ambrosia beetles as well.

A high level of perfection

How indeed could such an elaborate and impressive method of nest construction, quite unique to the genus *Oecophylla*, have evolved by natural selection? As Hölldobler and Wilson have documented in impressive detail, the nest-building behaviour of the weaver ants is "complicated, precise and distinctive", involving several adaptations of the adult ants as well as the larvae.

The larvae have lost the habit of spinning cocoons for themselves but haven't lost the habit of producing silk. The adults have to identify larvae at the suitable stage of development to donate silk, and make very precise body movements – both to align the leaves and to induce the larvae to begin to yield silk.

The stage of development of the larvae that is suitable to donate silk for nest-building is not the same as is typical for producing silk for making their own cocoons (in other species). And the larvae have to be quite passive during nest construction and refrain from making such body movements as are appropriate for spinning their own cocoons. How could all this have come together?

Any elaborate, seemingly well-designed structure or behaviour raises the same question. The most notorious example is the vertebrate eye, whose very perfection has sometimes been used to doubt the power of natural selection and even deny evolution altogether. The root of the misunderstanding is to think of natural selection as a random process and to imagine that the perfect final product suddenly springs up fully formed.

No one has argued more persuasively than Richard Dawkins (see his books *The Blind Watchmaker*, 1986, and *Climbing Mount Improbable*, 1996) that natural selection can produce the most complex structures or behaviours imaginable. The correct argument is that although mutations are random, natural selection is by no means random. Instead, natural selection is the very slow, *non-random* selection of small variations eventually culminating in the final product. Besides, apparent perfection is attained over a long time, through a process of sequential selection over many generations.

The argument that natural selection can thus climb even the "most improbable mountain" is sound. But the problem – and one that requires a great deal of patient research – is to identify the possible intermediate stages, each one better than its predecessor, that must have been traversed on the way to perfection. And this is what Hölldobler and Wilson have painstakingly unearthed, with extensive studies of nest-building in different ant species.

An instructive example of a possible intermediate stage in communal nest-building among ants is a species in the genus *Polyrhachis* that Hölldobler studied in Australia. These ants also build communal nests with leaves and twigs using silk from their larvae. However, they don't make chains of ants as *Oecophylla* do. Indeed, they don't even seem to bend the leaves.

The larvae they use are closer to the stage of development suitable for spinning individual cocoons, and the body movements of the larvae themselves appear to be much more important in the weaving process compared to *Oecophylla*. However, even in *Polyrhachis*, the larvae donate all their silk, and their pupae, like those of *Oecophylla*, are naked.

Bert Hölldobler (left) and the author posing in front of a portrait of Edward O. Wilson at the National Portrait Gallery in Washington, D.C., May 2016. Photo: Geetha Gadagkar

Another species, *Camponotus senex*, that occurs in south and central America, appears to represent a possible earlier stage in the evolutionary trajectory of nest-building technology. In *C. senex*, nest-building is similar to that in *Polyrhachis* – except that the larvae donate only some silk for the communal nest and use the rest to build protective cocoons for themselves.

An even simpler form of communal nest construction is represented by yet another ant, belonging to the genus *Dendromyrmex*, which occurs in Brazil. In this species, larvae donate silk to the communal nest but do so by themselves, without the adults holding them and binding the leaves together.

It is easy to imagine that *Dendromyrmex*, *Camponotus senex*, *Polyrhachis* and *Oecophylla* represent the sequential development of an increasingly complex communal nest-building practice, with the help of larval silk. We don't claim, of course, that these species evolved from each other. The claim merely is that useful and increasingly adaptive intermediates are conceivable so that we don't have to rule out gradual natural selection as the mechanism by which complexity evolves.

Why do larvae donate their silk?

The 'why' question has a particular connotation in evolutionary biology, and needs a bit of explaining to the uninitiated.

When we wish to understand what causes some behaviour, we ask two distinct questions – a proximate one and an ultimate one.

The proximate question, also called the 'how' question, concerns the mechanism by which organisms accomplish a task. How do ground-nesting wasps find their nests among others? How do honey bees estimate the distance flown? How do animals know who their relatives are? How do birds know that it is time to migrate to warmer regions? How do germinating seedlings know that their shoots should grow above-ground and their roots below-ground?

Answers to these proximate questions usually take the following form. Ground-nesting wasps locate their nests by learning the configuration of landmarks around their nests. Honey bees estimate the distance flown by measuring the extent of image motion on their eyes. Many animals assess genetic relatedness by using prior familiarity as a proxy. Birds respond to the hormones secreted by their pineal glands to understand changing day-length. Cell division and tissue growth in germinating seedlings respond differentially to the production of the hormone auxin in response to the direction of sunlight.

Ultimate questions, also called 'why' questions, on the other hand concern the adaptive advantage over evolutionary time, conferred by accomplishing tasks. Their answers usually take the following form. By learning and memorising landmarks and identifying their nests, wasps avoid provisioning the nests of *other* wasps. By measuring image motion and estimating distance accurately, honey bees can return to a profitable food source and also convey this information to other bees.

Using familiarity as a proxy for relatedness provides many animals with a convenient and inexpensive way of avoiding inbreeding. By migrating to warmer regions at the onset of winter, birds avoid high mortality for themselves and their offspring. By directing the growth of photosynthetic parts towards the Sun and water-harvesting parts towards the earth, plants use water and sunlight more efficiently.

The form of the 'why' questions and answers can be misleading at first. We don't imply conscious-decision on the part of animals or plants. When animals avoid inbreeding, they don't do so by a conscious process. That birds migrate to warmer regions at the onset of winter to avoid mortality doesn't mean birds are conscious of the costs and benefits of migrating. It is simply our convenient shorthand for the longer, more cumbersome way of saying: "a mutant bird that migrates and breeds in warmer regions leaves behind more surviving offspring than the non-mutant variety that stays put in the cold regions and attempts to breed there itself".

Using the convenient shorthand of asking 'why do birds migrate?', knowing that we don't mean they do so consciously, has become second nature to evolutionary biologists. To avoid being misunderstood by an unfamiliar audience, we have the responsibility of making the intended meaning of our 'why' questions very clear – as I am doing here.

In the context of nest-building with larval silk, Hölldobler and Wilson asked the obvious 'why' question. Why should larvae donate their silk to the communal nest instead of keeping it to themselves, and using it to make a protective cocoon? I hope the cumbersome longhand form of this question is clear. Is it possible that a mutant larva that donated all its silk for the communal nest gained more Darwinian fitness (number of offspring produced) than the alternative form that kept its silk to itself?

In the evolutionary sense, devoid of conscious choice or motives, the act of a larva keeping all its silk to make its own cocoon is said to be a 'selfish' act. Conversely, the act of donating its silk for the communal good and foregoing the chance to build a protective cocoon for itself is an act of 'altruism'.

How did such larval selfishness evolve through the process of natural selection?

The evolution of altruism is a paradox that Darwin and all his successors have had to grapple with. This is because an act of altruism appears to lower the actor's fitness and increase the recipient's fitness. How does a gene that reduces the fitness of its bearer spread in the population?

The English biologist W.D. Hamilton proposed an elegant solution to this paradox, and that is now the subject of intense study and some controversy, too. Hamilton argued that altruism could also evolve by natural selection if the survival of genetic *relatives* more than compensates for the cost of altruism due to the loss of offspring. This is because, like offspring, we also share copies of our genes with our relatives. This form of natural selection has come to be known as 'kin selection'. Thus, natural selection should favour altruism towards close relatives rather than towards distant relatives.

Such a prediction is usually difficult to test – but the weaver ants provide a unique opportunity.

Ants, bees and wasps belonging to the insect order Hymenoptera display a peculiar mode of reproduction. Males develop from unfertilised eggs by parthenogenesis, and therefore have only one set of genes (from their mother). Like in all other animals, females develop from fertilised eggs and therefore have two sets of genes (one set from their mothers and another from their fathers). As a consequence of this so-called haplodiploid genetics, sisters share three-quarters of their genes with each other (more than half, as in humans, for example), whereas males share only one-quarter of their genes with their sisters (less than half, as in humans).

Thus, female larvae in *Oecophylla* are more related to the rest of the colony than are the male larvae. The theory of kin selection predicts that female larvae should thus be more likely to donate silk for the communal good than the male larvae. In a study, Wilson and Hölldobler tested this prediction. In their words:

> "In the course of the evolution from cocoon spinning to nest building, a conflict between individual-lineage and kin selection seems inevitable. Every unit of protein converted into silk and contributed to nest construction is a unit withdrawn from personal growth. Where male and worker destined larvae coexist and kin selection prevails, current theory predicts that the males will have more of an incentive to "cheat" – to hold back on the production of silk and allow the female larvae to carry a greater per capita share of the burden because the latter individuals are subject to more intense kin selection."

Wilson and Hölldobler conducted remarkably simple laboratory experiments to assess the levels of altruistic silk donation by female and male larvae. Consistent with the predictions of kin-selection theory, they found that female larvae had silk glands that were three-times larger than the glands of male larvae. Female larvae were also 4.3-times more likely to donate silk than male larvae.

The conclusion is that female larvae are more altruistic when it comes to donating silk for the communal nest than male larvae. By implication, the answer to the question 'why do larvae donate silk' is that the personal cost of their act of altruism is likely to be offset by their greater relatedness to the rest of the colony members.

Indeed, "one of the most remarkable social phenomena among animals is the use of larval silk by weaver ants of the genus *Oecophylla* to construct nests". But *Oecophylla* offers us much more: the genus would make an extraordinary model for a comprehensive study of behaviour and evolution. There are only two species, and both are abundant, conspicuous and widely distributed over large geographical areas. While they are very similar, the two species diverged from each other over 10 million years ago, giving us more opportunities to observe evolutionary differentiation.

Oecophylla has also proved a valuable agent of biological control of pests, and is used as food in some places. The pioneering research of Hölldobler and Wilson, monumental though it is, has just scratched the surface and served to whet our appetite.

If I could start my career all over again, *Oecophylla smaragdina* might well be my *Ropalidia marginata*. However, I am happy to say that Neelkamal Rastogi of the Banaras Hindu University, Varanasi, and Himender Bharti of Punjabi University, Patiala, have independently begun to shower local populations of *Oecophylla smaragdina* with their attention. I hope they persist.

Raghavendra Gadagkar is a Department of Science and Technology (DST) Year of Science Chair Professor at the Centre for Ecological Sciences at the Indian Institute of Science, Bengaluru.

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