More Fun Than Fun: Plants Also Have Their Social Lives and Family Disputes

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Lord Howe Island. View on Mount Lidgbird and Mount Gower from Mount Eliza.
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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.

Titles of research papers usually don't surprise us, but this one did. It is called *Primitive eusociality in a land plant?*. The reason for the surprise is that eusociality, so far as we know, is restricted to the animal kingdom. Many animals live in social groups of varying degrees of complexity. The most complex of these is called 'eusocial', meaning 'truly social'. Members of eusocial colonies belong to multiple generations, exhibit cooperative care of the offspring, and only some reproduce, while others merely work for the welfare of the colony.

Now, Kevin Burns, a professor of biology at the Victoria University of Wellington, New Zealand, and his colleagues claim that they have discovered a eusocial plant. Burns's research takes him, among other places, to Lord Howe Island, a small volcanic island located between Australia and New Zealand. Just over 14 sq. km wide, it was found and claimed by the British in 1788. It is currently administered by the state of New South Wales in Australia, and harbours stunted tropical dry forest, coral reefs and some mountains, with many endemic species of plants and animals, in addition to a resident human population of 328 people and a floating population of 400 tourists.


Kevin C. Burns, a field biologist interested in a wide range of topics involving the ecology and evolution of plants and animals and who regularly takes concepts, hypotheses and methodologies that were developed on animals and apply them to plants, and vice versa. Photo: Kevin Burns

A eusocial fern?

The object of Burns's study is the epiphytic fern *Platycerium bifurcatum*. Epiphytes are plants that live on plants, but they are non-parasitic – they germinate on other plants but do not take nourishment from them. Surprising as it may seem, epiphytes derive all their nutrition from the air and rainwater. Such an austere lifestyle suggests interesting innovations that deserve greater attention from evolutionary biologists.

Ferns are vascular plants – those with xylem and phloem tissues to transport water and food – but they lack seeds or fruits. When I was in high school, ferns were called pteridophytes, but the pteridophytes have turned out to be a bunch of loosely related plants, and hence the true ferns now go by the more fancy name polypodiophyta. They have stems and leaves and produce their own food by photosynthesis, but reproduce with spores.

Though their eusociality is a new discovery, *Platycerium bifurcatum* itself is a well-known plant. Commonly known as elkhorn fern or the staghorn fern, because its leaves are forked like the antlers of deer, it is commonly cultivated as an ornamental plant in gardens and homes. It is easy to mount on wooden boards and needs little care.

A colony of the epiphytic staghorn fern Platycerium bifurcatum is seen in the foreground. Photo: Kevin Burns

Burns and his team found that *Platycerium bifurcatum* never occurred solo but was always clustered in distinct colonies, with 6 to 58 individuals per colony, well separated from other colonies.

The fern, as is well-known, produces two kinds of leaves, technically called fronds. The so-called 'strap fronds' are long, narrow and photosynthetically active. Some of them are also reproductively active. The other kind, called 'nest fronds', are reproductively inactive. The function of the non-reproductive nest fronds appears to be to absorb water and nutrients and share them with the reproductively active strap fronds.

Burns and his colleagues have provided two additional lines of evidence that are suggestive of eusociality. First, they find that the per-capita reproductive effort increased with colony size. Second, they found through DNA sequencing that although eight colonies were clones, at least two colonies consisted of unrelated individuals.

If all the individuals in a colony are clones of each other, they might simply be thought of as a single plant. But if some of the members are unrelated, they would have to be regarded as a colony, with the non-reproductive fronds being altruistic towards the reproductive fronds inasmuch as they share water and nutrients.

In another paper, Burns makes a strong argument for the evolution of eusociality and division of labour in *Platycerium bifurcatum* in response to ecological stress. His arguments are essentially indistinguishable from the arguments zoologists make for the evolution of eusociality and division of labour in their taxa.

It is entirely possible that purists will raise red flags and demand more stringent evidence for overlap of generations, cooperative brood care and reproductive caste differentiation – the three diagnostic characters of eusociality. To be fair to Burns and his colleagues, they frame the title of their paper as a question to be answered by their readers or by future work.

They also display admirable caution in their prose: "Here, we explore whether a major evolutionary transition to eusociality has occurred in plants…". Nevertheless, this is already an exciting finding that should broaden the scope of eusociality or near-eusociality. More importantly, it should bring eusociality to the doorstep of the plant kingdom.

Why is that so significant? Let's look at some history.

The origin of the concept

Suzanne Batra coined the term 'eusocial' in a paper entitled 'Nests and Social Behavior of Halictine Bees of India', published in the *Indian Journal of Entomology* in 1966. While researching sweat bees (family *Halictidae*) for her PhD at the University of Kansas, she married the Indian botanist Lekh R. Batra, and visited India and studied Indian halictine bees.

Batra was piqued that her wonderful bees were generally referred to as 'primitively social insects' while the unqualified label of 'social insects' was reserved for the more complex societies of honey bees, ants and termites. So she coined the term 'eusocial' for her less complicated but no less fascinating halictine bees. But then she became the victim of success.

People liked the term 'eusocial', which also meant 'truly' social, so much that they usurped it for all social insects, including the halictines, ants, bees, wasps and termites. Her professor, Charles Michener, in his influential article *Comparative Social Behavior of Bees* (1969), and E.O Wilson, in his monumental *The Insect Societies* (1971), further popularised the term 'eusocial'.

Snapshot from a recording of Jay Evans' tribute to Suzanne Batra – click on the image to see the video (https://youtu.be/3QS7pjjMLEw)

But the ants, honey bees and termites are, of course, more complex societies, as Batra had argued in the first place. Ironically, and to her frustration, her halictine bees and other less complex societies, such as those of the paper wasps we study in my lab, were dubbed back as 'primitively eusocial'!

Many others are also unhappy with this state of affairs. Some have suggested that eusociality be reserved only for complex societies of ants, honey bees and termites. Others like me have suggested that it should be expanded to include cooperatively breeding birds and mammals, which are closer in their social life to primitively eusocial bees and wasps than to honey bees, ants and termites.

But I think that the term has stuck, and I doubt we can change its usage now. Scientific terminology is often the victim of historical contingency – precedent trumps accuracy!

The evolution of eusociality studies

Be that as it may, the march of eusociality has continued unabated, well beyond the ants, bees, wasps and termites.

In 1977, the Japanese scientist Shigeyuki Aoki discovered a sterile soldier caste in an aphid species, suggesting that eusociality was present even *outside* the insect orders *Hymenoptera* (ants, bees and wasps) and *Isoptera* (termites). Aphids are small sap-sucking plant bugs belonging to the insect order *Hemiptera*.

Subsequent research has shown that in addition to altruistic soldiers, aphids can also have altruistic workers who perform housekeeping tasks required for the welfare of their colony. I remember the great excitement of going on an expedition to Japan in 1991, along with W.D. Hamilton, Mary Jane West-Eberhard and Yosiaki Itô, to see Aoki's aphid soldiers.

In search of Aoki's soldier aphids in Japan. Left to right: W.D. Hamilton, the author, Yosiaki Itô, Norio Arakaki and Mary Jane West-Eberhard. Photo: R.G. Lab collection

In 1992, two more insect orders were brought into the eusocial fold. Bernard Crespi of the Simon Fraser University in Canada discovered eusociality in Australian gall thrips (insect order *Thysanoptera*). Kent and Simpson at the Forestry Commission in New South Wales in Australia discovered eusociality in the Ambrosia beetle *Austroplatypus incompertus* (insect order *Coleoptera*) that lives on eucalyptus trees.

Close on the heels of these two range extensions of eusociality, J. Emmett Duffy at the Virginia Institute of Marine Science, in Virginia, demonstrated eusociality in a coral reef shrimp in 1996. The shrimps brought eusociality outside the class *Insecta* and into the class *Crustacea*, in the phylum *Arthropoda*.

Scientists have vigorously researched all the newly discovered eusocial groups. Shrimp eusociality, for example, reached new heights of sophistication with the discovery that social life can have interesting feedback on genome evolution and architecture. And beetle eusociality has gathered new momentum by unravelling the nuances of their agriculture (including fungus-farming).

The vertebrate barrier

Perhaps the greatest excitement to date was the discovery of a eusocial mammal, the naked mole rat, by Jennifer Jarvis in South Africa, as early as 1981. Part of the excitement was because eusociality had crossed over to the vertebrates, and to a mammal no less.

But the excitement was heightened because Richard Alexander, a cricket biologist at the University of Michigan, had made an uncannily accurate prediction: that if ever a eusocial mammal were discovered, it would be "a completely subterranean rodent that feeds on large tubers and lives in burrows inaccessible to most but not all predators, in a xeric tropical region with heavy clay soil".

People often ask me whether we can consider humans to be eusocial. After all, we humans live in highly sophisticated societies and our social behaviour is at the heart of our successful conquest of the planet (whether it should be called 'success' is another matter).

I was undecided whether humans are eusocial until I read a paper in 2005 entitled *A new eusocial vertebrate?*. This paper was written by Kevin R. Foster of the Department of Ecology and Evolutionary Biology at Rice University, and Francis L. W. Ratnieks of the Department of Animal and Plant Sciences at the University of Sheffield.

We should not fail to notice that this paper's title is also a question, not an answer – as it should be for an argumentative paper. It is well known that humans are almost unique in that women survive long after they stop having children, a phenomenon known as menopause.

Specifically, menopause is the programmed, sudden and irreversible cessation of reproduction accompanied by distinct physiological changes. There is growing evidence that menopause increases the reproductive fitness of women. There is data from some human societies to show that post-menopausal women enhance the ability of their offspring to reproduce more by being available to assist them ('mother' effect) and also enhance the survival of their grandchildren ('grandmother' effect).

Humans are well known to display overlap of generations and cooperative offspring care, satisfying two of the three conditions of eusociality. If post-menopausal women can be compared to sterile worker castes in social insects, in terms of Darwinian fitness, then humans can also be said to satisfy the third and most important criterion of eusociality: reproductive caste differentiation.

The inclusion of humans in the roster of eusociality is in tune with the spirit of expanding the scope of eusociality to include all animal taxa that display similar fitness-maximising strategies.

Enter plants

As we saw at the beginning of this essay, Kevin Burns and his colleagues are attempting to breach the barrier of the animal kingdom and bring eusociality to the plant kingdom. This is even more radical than painting humans with the eusocial brush. Why? Because we usually don't think of plants as capable of behaviour, let alone social or altruistic behaviour. But this is merely a matter of semantics.

In the 1980s and 1990s, I was part of an informal group of young evolutionary biologists passionate about all things evolutionary, particularly of the new fields of sociobiology and behavioural ecology. We were excited by the prospect of finding evolutionary explanations for social behaviour, selfishness and altruism, parent-offspring conflict, sibling rivalry, infanticide and the like.

Most of us studied animals of one sort or another, from bees and wasps to deer and elephants. But two of us, rather one pair among us was bold enough to attempt to apply these concepts to plants: R. Uma Shaanker at the Department of Crop Physiology and K. N. Ganeshaiah at the Department of Genetics and Plant Breeding, both at the University of Agricultural Sciences, Bengaluru.

Uma Shaanker and Ganeshaiah were unusual in several ways. They always worked together; their work on plant evolutionary biology was a hobby and quite outside the scope of their day jobs. They also stood out in our group because of their extraordinarily sharp minds, penchant for debate and undeniable rustic charm.

(Ganeshaiah is also an acclaimed Kannada novelist and short story writer, with at least 25 literary works to his credit.)

R. Uma Shaanker (left) and K.N. Ganeshaiah. Photos: Uma Shaanker and Ganeshaiah

The duo fed us on a regular diet of "though plants can neither sing nor dance, they indulge in sibling rivalry, fratricide, and kin cooperation as intensely as animals do". There were, of course, people who decried the application of such "highly anthropomorphic sociobiological hypotheses to plants", and some people continue to do so today.

This is the result of an unfortunate misunderstanding. When we say a seed behaves selfishly by taking more than its share of nutrients, it's just a convenient shorthand. The cumbersome longhand would be: "if a gene in the seed enabled it to draw more nutrients, such a gene might increase its proportional representation in the population's gene pool, relative to alternative gene forms that do not enable the seed to draw more nutrients".

We are not claiming that the seed makes a conscious decision to behave selfishly. Indeed, we do not claim deliberate or conscious selfish or altruistic behaviour even for animals, nor even for humans. So there is no reason that the logic of natural selection should be any different for plants.

In addition to their fascinating studies of plant behaviour, Uma Shaanker and Ganeshaiah have written many expository articles published in India and abroad. One of their best-known articles, co-authored with K.S. Bawa, is *Parent-Offspring Conflict, Sibling Rivalry, and Brood Size Patterns in Plants*. Another is called *Conflict between parent and offspring in plants: Predictions, processes and evolutionary consequences*. As they have convincingly argued, "these 'highly anthropomorphic, sociobiological hypotheses' which were suggested to be 'best not applied to plants', have indeed been helpful in providing a new framework to view the evolution of plant reproductive strategies."

One of their many remarkable original studies concerned how plants reduce competition between seeds in a developing fruit. There is a rather unusual tissue called the endosperm in many plants, which acts as a conduit for the flow of nourishment from the mother plant to the developing seeds. It has been suggested that the endosperm, which contains two copies of the mother's genes and one copy of the father's genes, acts as an arbiter in the quarrels between seeds.

Uma Shaanker and Ganeshaiah, along with their students K.V. Ravishankar and S.G. Hegde, argued that if this hypothesis is correct, there should be less conflict between seeds in species with well-developed endosperm.

To put this idea to the test, they gathered information on 1,113 species from the *Flora of the Presidency of Madras*, a well-known compendium prepared by an Englishman named J.S. Gamble between 1915 and 1934. They showed that the endosperm was better developed and persisted longer in species that had many developing seeds per fruit – a situation needing conflict control. Conversely, the endosperm was usually absent or short-lived in species with a single seed per fruit, a situation with no scope for a rivalry between the seeds.

They also found that among the species that had multiple seeds per fruit, in species where the endosperm was present or persistent, there were fewer instances of seed abortion. Thus, the endosperm was more likely to be present when there was scope for rivalry and that the endosperm brought the rivalry under control.

I am fascinated every time I read this paper. It is, of course, a beautiful test of an elegant theory – but it is also much more. What facilities did Uma Shaanker and Ganeshaiah need to do this work? Bright ideas, impeccable logic, passionate students and access to a widely available book are all they needed. I wonder why we still keep complaining that we cannot do cutting-edge research due to the lack of funds and access to sophisticated laboratories?

Uma Shaanker and Ganeshaiah also inspired another member of our group, N.V. Joshi, to construct population-genetic models to explore sibling rivalry in seeds. Joshi's model predicted that rivalry should be most intense in two-seeded fruits and then decrease with increasing numbers of seeds per fruit. This is consistent with the observation that while one and many-seeded fruits are relatively common, two-seeded fruits are rather rare in nature.

The story of the endosperm recently took an even more exciting turn in the hands of another pair of my friends, David Queller and Joan Strassmann, professors of biology at Washington University in St Louis, US. Queller and Strassmann are best known for their work on the sociobiology of wasps and slime molds. But Queller began his career as a graduate student with some very influential work on plants, modelling kin selection and conflict during seed development, in the 1980s.


Katherine S. Geist flanked by her PhD mentors David Queller (left) and Joan Strassmann. Photo: Joan Strassmann

In a new paper tellingly entitled *Family quarrels in seeds and rapid adaptive evolution in Arabidopsis*, Queller and Strassmann, along with their graduate student Katherine S. Geist, now a postdoc at Iowa State University, have shown through clever analysis that quarrels continue on a small scale despite endosperm.

It is possible to estimate the rates of adaptive evolution by comparing changes in gene sequences and estimating the proportion of changes that result in a change in the amino acid sequence of the corresponding protein (non-synonymous changes) and changes that result in no such change (synonymous changes). Synonymous changes occur because of the redundancy in the genetic code – i.e. more than one codon specifies the same amino acid. Thus, a high proportion of non-synonymous changes mean more adaptive evolution.

Their study found that there have been more adaptive changes in genes active in the seeds compared to other organs. More pertinent, they find more adaptive evolution in genes active in maternal tissues and the endosperm than in the embryo itself. This finding is consistent with the hypothesis that the endosperm has taken over the role of the mediator between parent (plant) and offspring (seed).

To paraphrase the authors of this paper, "despite the conflict-reducing role of kinship and the mediating role of the endosperm, plants can engage in slow but steady tortoise-like arms races."

At first glance, one might imagine that this research was expensive, but the truth is that it cost them next to nothing. Taking a leaf out of Uma Shaanker and Ganeshaiah's book, they analysed already published data sets! Queller told me in an email:

> "It came about when I saw there was going to be a seminar by John Harada at the Danforth Plant Sciences Center. It looked sort of interesting … but it's hard to tell from the seminar announcement. But I took a chance and went, and he talked about this amazing dataset. I chatted with him afterwards to sound out a possible collaboration and he just said that it's published, the data are publicly available, so do what you want with it."

I think there should be a special prize for new research that uses already existing data. Imagine how much wisdom must lie in all the published data waiting for someone to pry open with new ideas and new questions – the cleverest way of doing cutting-edge research at trifling cost.

Plants remain woefully understudied in evolutionary and sociobiological terms; their selfish quarrels and altruistic sacrifices are locked up, not just in the plants but probably in the data sets already compiled. Why is almost no one filling this gap in India? It will be a pity if the reason is fear of anthropomorphism – worse if the reason is because of the erroneous perception that we do not have the funding and facilities required.

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