In the Wild, There's More Than One Way to Find a Mate

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Darwin proposed the theory of sexual selection to account for extravagant secondary sexual characters in males, such as the peacock's train. Photo: Kelly Sikkema/Unsplash.

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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.

The importance of Darwin's theory of evolution by natural selection to biology and indeed to every aspect of our life can't be overstated. "Nothing in biology makes sense except in the light of evolution," said the Ukrainian-American geneticist Theodosius Dobzhansky. The Brazilian-British biologist Peter Medawar wrote, "For a biologist, the alternative to thinking in evolutionary terms is not to think at all."

Despite a recent one-off anomaly, we can be justly proud that the Government of India issued a postage stamp in honour of Charles Darwin, on May 18, 1983, to mark the centenary of his death. Most of this eulogy is based on, and adequately justified by, Darwin's most famous book, *On the Origin of Species* (1859).

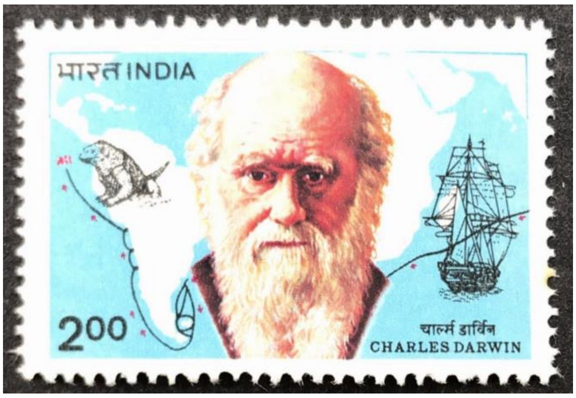


Photo: V. Rajarajan, Chief Postmaster General, Kerala

But Darwin wrote many more books. Perhaps his second most famous book was *The Descent of Man and Selection in Relation to Sex* (1871). In this book, Darwin not only proposed his theory of human evolution from primate ancestors but also proposed yet another. Arguing that his theory of natural selection couldn't by itself explain some features of the natural world, he proposed the theory of sexual selection to account for extravagant secondary sexual characters in males, such as the train of the peacock.

As do all his books, this one too contains many hidden insights that we are only now beginning to appreciate and explore. One such insight concerns why males in some species have two or more different ways of getting a mate. In some species, for example, males come in two very different sizes. The large males, often endowed with additional weapons and fighting devices, use their size and strength to their advantage in competing for females. The small males who stand no chance against the large males use alternative tactics: they may sneak in without being noticed or fool the large males by pretending to be females.

The presence of such alternate strategies presents an evolutionary puzzle. Let's explore why.

Any kind of variation within a species – in morphology, physiology or behaviour – is of great interest to evolutionary biologists. Variation is the raw material on which natural selection acts. Different variants have different abilities to survive and reproduce in a given environment. Some variants are selected and come to prevail while others are disfavoured and are eliminated from the population. Without variation, there can be no evolution.

But variation – which arises from random mutations – should quickly disappear as natural selection gets to work. When variation persists, it needs a special explanation. Why should natural selection allow multiple strategies to persist? Whichever is the inferior of the two, however small the difference, should be eliminated by natural selection in the long run. Darwin presciently surmised that the variants might persist because they may achieve nearly equal success, albeit by different tactics. This remained a mere surmise for the next 101 years!

The first proof for Darwin's idea came in 1972, when a 30-year-old young scientist from the Maharashtra Association for the Cultivation of Science, Pune, published a paper entitled 'Male Dimorphism as a Consequence of Sexual Selection' in the noted journal *The American Naturalist*. The young scientist was none other than Madhav Gadgil, who has gone on to become India's most famous ecologist and conservation biologist.

Ecologist Madhav Gadgil (right) with ornithologist Salim Ali at the Maharashtra Association for the Cultivation of Science, Pune, in 1972. Photo: Madhav Gadgil

Using a simple cost-benefit model, Gadgil demonstrated that males who have invested the most energy in developing competitive superiority might leave behind no more offspring than those who have saved all that energy and used it for better survival. The rest, as they say, is history.

Alternative reproductive tactics are now the subject of intense study and many research papers, books and monographs. It is a matter of pride to see most of these studies begin by paying tribute to Gadgil's courageous and insightful paper.

It is also a matter of history that, in addition to *writing* courageous and insightful papers, Madhav Gadgil also showed foresight and fortitude in founding the Centre for Ecological Sciences at the Indian Institute of Science, Bengaluru, where more young scientists have continued to conduct similar studies. I will focus on some of the work of Professor Rohini Balakrishnan and her students, who conduct exciting research in field ecology.

What I like most about their research is that it involves asking intelligent questions arising out of deep knowledge of the literature, and answering them with simple but innovative experiments, often conducted on the institute campus or in villages nearby. Their work essentially requires passionate, back-breaking fieldwork and sleepless nights, rather than fancy technology. And luckily for our present discussion, some of their work concerns alternative reproductive tactics.

Rohini Balakrishnan is well-known for her research on crickets, and crickets are well-known for their courtship songs. Male crickets don't quite sing because they do not vocalise, but they produce the sounds that we are all familiar with by rubbing their forewings together, a process called stridulation. Males call to attract females, and such courtship songs help female crickets identify suitable mating partners and find them.

But as one might expect, in the complex web of nature, courtship songs also help predators and parasites to identify and locate suitable prey and hosts. Therefore, these songs extract both an energetic cost of song production and also the cost of mortality due to predation or parasitism. Some males, therefore, attempt to avoid these costs altogether by seeking mates without singing at all. Instead, they listen to the calling males, move towards them and intercept females who are moving toward the calling males. Such males are termed non-calling or satellite males, and exemplify an alternative reproductive tactic.

The Centre for Ecological Sciences building, with a magnificent specimen of the tropical liana (Entada pursaetha) from the Western Ghats. Photo: Nutan Karnik

The best-known example of alternative reproductive tactic in crickets is in the field cricket *Gryllus integer*, studied by Michael Cade of the University of Texas, Austin. In the field, satellite males benefit from the fact that a parasitic fly, *Euphasiopteryx ochracea*, locates calling male crickets (or loudspeakers broadcasting recorded male songs) and deposit their larvae on them. The fly larvae burrow though the crickets' bodies and consume the interiors.

Non-calling, satellite males don't pay this cost, nor the energetic cost of singing. The calling and non-calling tactics have a strong genetic basis, meaning that some males are born as high-probability callers and others are born as low-probability callers. As Gadgil showed, both callers and non-callers can persist in the population if they are present in such a ratio that both the calling and the non-calling reproductive tactics yield equal mating success.

Balakrishnan and her students study the tree cricket (*Oecanthus henryi*). Rather than a fly parasitising them, calling tree crickets may be located and eaten by the green lynx spider (*Peucetia viridans*). In this species also, some males attract females by calling, and others may locate females silently. But I find what these crickets can do to be more impressive because the alternative tactics are not genetically determined.

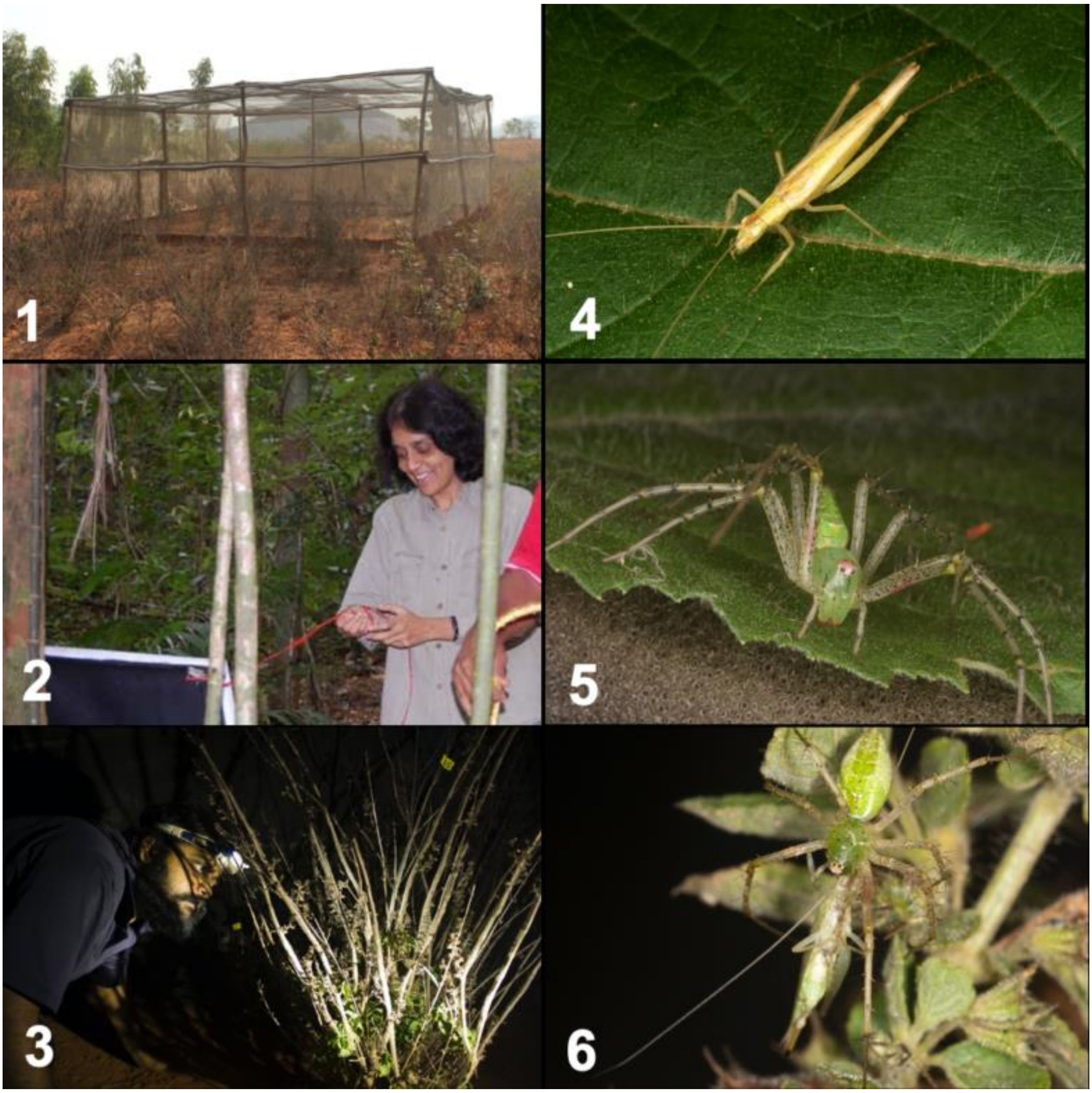
Individual males have to decide which tactic to use and when to switch from one tactic to another as appropriate. Such flexible switching between tactics is more demanding from the crickets. They have to sense various aspects of their environment continuously, assess the prevailing probabilities of predation and mating, and alter their behaviour accordingly. At the same time, such a species offers many more opportunities for us to investigate sensory perception, cognition and behavioural decision-making.

Viraj R. Torsekar and Rohini Balakrishnan have recently exploited these opportunities to further our understanding of alternative reproductive tactics. They did some of their work in the natural habitat of tree crickets and their predatory spiders near Ullodu village, in the Chikkaballapur district of Karnataka. To observe the behaviour and interactions of the crickets and spiders, they constructed large enclosures measuring 6 × 6 × 2.2 metres using wooden stakes and stainless-steel mesh around naturally growing bushes (of *Hyptis suaveolens*). Next, they collected crickets and spiders from the surrounding area and released predetermined numbers of both into each enclosure.

They marked all their crickets with quick-drying, non-toxic paint for individual identification and tagged and numbered each bush inside the enclosure. As an important precaution, they also looked for and removed any pre-existing crickets or spiders on the bushes inside the enclosures.

The crickets are most active, calling and mating between 7 pm to about 9:30 pm, and Torsekar got active at the same time. He noted the position of every cricket, whether it was calling and whether a spider was present on its bush, once every 10 minutes.

By varying the relative numbers of crickets and spiders in their enclosures and by observing the behavioural response of individually identified crickets, Balakrishnan and Torsekar have taken the study of alternative reproductive tactics to a new level. They set up three kinds of experimental enclosures: 'no predation', with zero spiders; 'low predation', with 15 spiders; and 'high predation', with 120 spiders. In each enclosure, they introduced 15 male and 15 female crickets. They confirmed that the probability that the crickets would find a spider on their bush increased with the number of spiders introduced in the enclosure.



1. The study site in Ullodu showing a large field enclosure with crickets and spiders; 2 & 3. Rohini Balakrishnan and Viraj Torsekar conducting observations; 4. the tree cricket; 5. the green lynx spider; 6. the spider in the act of eating a cricket. Photos: Provided by Viraj Torsekar and Rohini Balakrishnan

In doing so, they were able to assess the predation risk faced by each cricket, and not just some average value for the whole population in the enclosure. Next, they observed the behavioural response of the crickets to varying predation risk that they individually experienced.

As we might expect, males called less often when their predation risk was high than when their predation risk was low. Their research provides clear evidence that male crickets respond to predation risk they experience and behave accordingly. As the predation risk increased, male crickets reduced their calling behaviour. Such reduced calling would, of course, decrease the chances of the males getting a mate since females find males who are calling more easily.

But males experiencing high predation risk showed more movement, suggesting that the crickets experiencing high predation risk moved closer to other calling males. This would reduce their predation risk, because calling males have presumably not seen a spider in their bush, but it would also increase their chances of mating by intercepting females who may be moving toward the calling males.

Thus, the presence of predatory spiders made male crickets switch from their primary mating tactic to an alternative one. Balakrishnan and Torsekar have also discovered many interesting facts about what female crickets do, but that's another story. This experimental paradigm holds great potential for understanding what crickets are capable of doing, and how natural selection has fashioned their behaviour and thus confirm or refute Darwin's surmise and Gadgil's theory.

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