

And now... eusocial thrips!

Raghavendra Gadagkar

Eusocial insects (the only truly social insects, by definition) are defined as those that possess all of the three fundamental traits of eusociality namely, (a) cooperative brood care, (b) differentiation of colony members into fertile reproductive castes (queens or kings as the case may be) and sterile non reproductive castes (workers) and (c) an overlap of generations such that offspring assist their parents in brood care and other tasks involved in colony maintenance^{1,2}. When this definition was formulated, eusociality was known to be restricted to the class Insecta and even there to just two orders namely Isoptera (termites) and Hymenoptera (ants, bees and wasps). While all known termites are eusocial, the distribution of eusociality in the Hymenoptera is curious. The suborder Symphyta, consisting of several families of free-living phytophagous species is devoid of eusociality. In the other suborder Apocrita, the subgroup Terebrantia consisting of several families of parasitoid species is also completely devoid of eusociality. It is

only in the subgroup Aculeata that eusociality is seen. But even here, while all ants are eusocial, most bees and wasps are not eusocial. Nevertheless eusociality is believed to have originated at least eleven times independently within the Aculeata².

In recent times, eusociality has been demonstrated in another order of insects namely Homoptera (in the aphids)³⁻⁵. There is also an unsubstantiated claim of a eusocial spider⁶ and a clear demonstration of eusociality in a mammal, the naked mole rat^{7,8}. The discovery of eusociality in any species of animal outside the Isoptera and Hymenoptera has come to be regarded as sensational, usually warranting a report in *Nature* or *Science*^{7,9} but claims and counter-claims about whether something should be classified as eusocial continue^{5,10}.

And now Bernard J. Crespi¹¹ of the Simon Fraser University in Canada has demonstrated eusociality in two species of Australian gall thrips *Oncothrips tepperi* Karny and *O. habrus* Mound.

(For general information about thrips and their galls, see refs. 12, 13). The thrips Crespi describes seem tailor-made for the evolution of eusociality. Galls (the equivalent of single foundress nests in eusocial Hymenoptera) are initiated by single inseminated macropterous (fully winged) females in spring. After fighting off other similar females over possession of a presumably valuable young growing phyllode tissue of *Acacia oswaldii* and *A. melvillei* respectively, the foundress oviposits inside the gall. Her offspring hatch, feed, develop and eclose inside this gall. She produces four kinds of offspring: macropterous females (like her), macropterous males, micropterous (short-winged) females as well as micropterous males. The term micropterous is somewhat distracting for, the important feature of micropterous adults is their enlarged and armed forelegs specialized for fighting. Sure enough micropterous adults (both females and males) eclose earlier than macropterous females and males. Notice the analogy with the first batch of brood becoming workers and subsequent batches becoming future reproductives in social Hymenoptera.

Crespi has convincingly demonstrated that in both species, micropterous adults attack and attempt to kill *Koptothrips* spp. (inquiline thrips that invade galls of other species, kill the gall formers, and breed inside), lepidopteran larvae and *Iridomyrmex humilis* ants and do so more often than foundresses (the macropterous offspring of the foundress had not yet eclosed at the time of the experiment). He has also provided evidence that *Koptothrips* spp. form a real threat to the *Oncothrips* and that the micropterous offspring provide a substantial benefit of protection to the foundresses. The micropterous adults are therefore termed 'soldiers'. Dissection of foundresses and micropterous adults show that although many soldiers had developing oocytes, their ovarian development was clearly inferior to that of the foundresses. Besides, Crespi points out that "there is simply insufficient space in the gall for micropterous females to produce as many adult offspring as do foundresses". Thus *O. tepperi* and *O. habrus* appear to satisfy all the three criteria required to label them as eusocial. There is overlap of generations, the morphological specialization and defensive behaviour of the

micropterous females and its consequence for the survival of the foundresses certainly implies cooperative brood care and there is some level of reproductive caste differentiation or at least sub-fertility on the part of the micropterous adults. Notice however that, unlike in the Hymenoptera, the soldiers (workers) can be of either sex.

As Crespi¹¹ remarks "Australian gall thrips provide remarkable new opportunities for analysing the causes of the evolution of eusociality". A particularly fascinating aspect of Crespi's discovery of eusociality in yet another order of insect is that Thysanoptera are also haplodiploid. The evolution of eusociality in diploid aphids, naked mole-rats and termites is thought to be linked to their living and feeding inside a "highly valuable, persistent habitat that they have created" and which is "defensible primarily by individuals specialized with weaponry and behaviour for heroic acts^{11,14}". On the other hand eusociality in the Hymenoptera is usually thought to be linked to the genetic asymmetries created by haplodiploidy and the ability of mothers to produce female-

biased sex-ratios due to parthenogenesis^{2,15-19}. The gall thrips have both sets of conditions. Nevertheless, unless future research proves otherwise, eusociality in gall thrips, like in the Hymenoptera, Aphids and naked mole-rats, appears to be restricted to a just a few species while the vast majority of related species apparently endowed with the same set of adaptations have failed to evolve eusociality. The plot thickens!

1. Michener, C. D., *Annu. Rev. Entomol.*, 1969, **14**, 299-342.
2. Wilson, E. O., *The Insect Societies*, Harvard University Press, Cambridge, Massachusetts, USA, 1971.
3. Aoki, S., *Kontyu, Tokyo*, 1977, **45**, 276-282.
4. Ito, Y., *TREE*, 1989, **4**, 69-73.
5. Benton, T. G. and Foster, W. A., *Proc. R. Soc. London*, **B**, 1992, **247**, 199-202.
6. Vollrath, F., *Behav. Ecol. Sociobiol.*, 1986, **18**, 283-287.
7. Jarvis, J. U. M., *Science*, 1981, **212**, 571-573.
8. Sherman, P. W., Jarvis, J. U. M. and Alexander, R. D., *The Biology of the Naked Mole-Rat*, Princeton University Press, Princeton, New Jersey, 1991.

9. Matthews, R. W., *Science*, 1968, **160**, 787-788.
10. Holldobler, B. and Wilson, E. O., *The Ants*, Springer-Verlag, Berlin, Heidelberg, 1990.
11. Crespi, B. J., *Nature*, 1992, **359**, 724-726.
12. Ananthakrishnan, T. N., *Thrips: Biology and Control*, Macmillan, India, 1973.
13. Ananthakrishnan, T. N. and Raman, A., *Thrips and Gall Dynamics*, Oxford and IBH Publishing Co. New Delhi, 1989.
14. Alexander, R. D., Noonan, K. M. and Crespi, B. J., in *The Biology of the Naked Mole-Rat* (eds. Sherman, P. W., Jarvis, J. U. M. and Alexander, R. D.), Princeton University Press, New Jersey, 1991, pp. 3-44.
15. Hamilton, W. D., *J. Theor. Biol.*, 1964a, **7**, 1-16.
16. Hamilton, W. D., *J. Theor. Biol.*, 1964b, **7**, 17-52.
17. Trivers, R. L. and Hare, H., *Science*, 1976, **191**, 249-263.
18. Gadagkar, R., *Proc. Indian Acad. Sci. (Anim. Sci.)*, 1985a, **94**, 309-324.
19. Gadagkar, R., *Proc. Indian Acad. Sci. (Anim. Sci.)*, 1985b, **94**, 587-621.

Raghavendra Gadagkar is in the Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India