SOCIAL INSECTS

All for one, one for all, that is our device

Jon Seger

SOCIAL insects have played a unique role in the development of the theory of natural selection, ever since Darwin noted[1] that sterile workers pose a "special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory". Darwin saw in outline how selection might be "applied to the family, as well as to the individual", an idea that eventually gave rise to the modern theory of inclusive fitness[2]. Inclusive fitness is a general concept that applies to all situations in which relatives interact, but the motivation to develop it (and in particular, its connections with sex-ratio theory[3,4]) came largely from social insects. Theories of group selection[5] have also been inspired by insect sociality, and may soon receive new impetus from the same source.

On page 420 of this issue[6], Rissing and colleagues show that unrelated females of the desert leaf-cutting ant *Acromyrmex versicolor* seem to participate voluntarily in an unequal division of risk and labour during the establishment of new colonies.

Several different patterns of colony formation are found among social insects of the order Hymenoptera, and most have evolved more than once[7]. In some ants and bees, for example, a fraction of the parent colony's worker force departs with a newly produced female reproductive (gyne) who becomes the principal egg-layer (queen) of the resulting daughter colony. But in most social Hymenoptera, each gyne departs alone and attempts to establish a new nest and to raise a first generation of workers without any help at all. In either case a colony has a single queen, and the relatedness of nestmates tends to be high.

The new colony may also be established by several or many gynes, without an initial worker force. This pattern is common among social wasps. Dominance hierarchies form among the cofoundresses, such that one or several high-ranking individuals monopolize reproduction, and subordinates act as workers. The average relatedness of nestmates varies widely, but cofoundresses seem to be significantly related in most species[8].

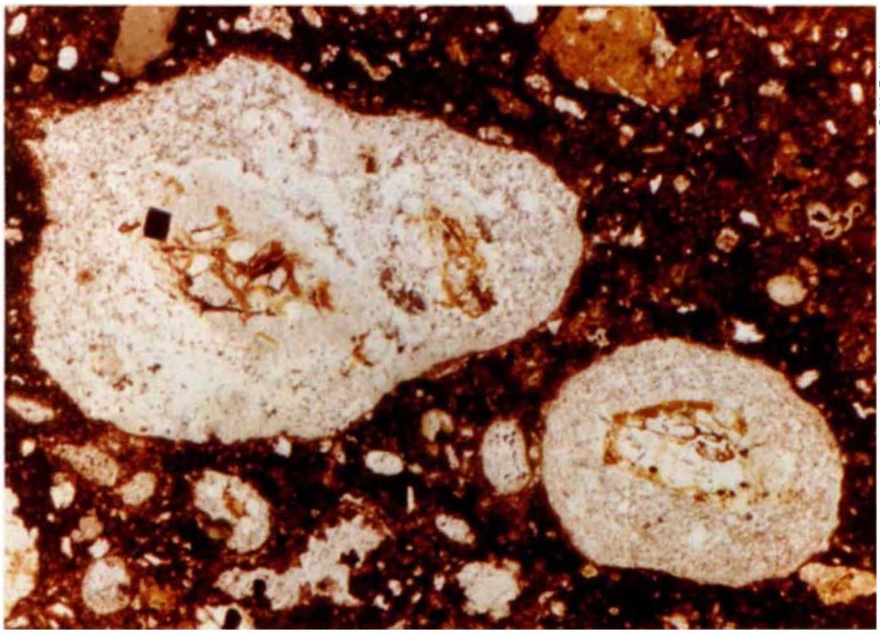
Multiple foundresses also occur in some species of ants; by analogy to social wasps, one would expect them to be relatives. In 1910, the great myrmecologist William Morton Wheeler[9] assumed "without doubt" that two cofounding females "were sisters that had accidentally met . . . and had renewed the friendly relations in which they had lived before taking their nuptial flight". Only in the past decade has it been learned that, in ants, cofoundresses are usually unrelated. The first evidence came from behavioural studies showing that gynes readily team up with each other independent of the distance between their natal colonies (and thus presumably independent of their relatedness)[10,11]. Recent genetic studies of relatedness within colonies of *Solenopsis invicta*[12], *Veromessor pergandei*[13] and *A. versicolor*[13] show that cofoundresses are indeed no more closely related than random individuals drawn from the population at large.

In the laboratory, gynes have survived better in groups than alone[10], and foundress groups of moderate size have produced more first-generation workers, more quickly, than have smaller or larger groups[10,11]. Species that frequently found nests cooperatively often engage in reciprocal brood raiding, with small colonies tending to be eliminated by their larger neighbours[10,11]. Thus at high population densities, cooperative founding may greatly increase the probability that a given nest will survive long enough to produce reproductives.

An alliance may improve survival, but given survival, it dilutes the expected reproductive success of each foundress. Conflict between foundresses or between workers and foundresses often begins soon after the emergence of the first workers[10,11,14], and such conflict often leads to the expulsion or killing of one or more foundresses; in many species with multiple foundresses this process goes to completion and the mature colony is monogynous[11].

In most ant species, foundresses raise the first workers on secretions derived metabolically from flight muscle and fat[7], and they never leave the nest. *A. versicolor* is unusual in that one found-

Life imitates (experimental) art



THE white globules in this micrograph are chilled droplets of a carbonate melt, set in a groundmass of carbonate-rich volcanic ash. There has been much controversy as to whether such 'carbonatite' magma can form directly by partial melting of the mantle, or whether a two-stage process, involving modification of a mantle melt at shallower, crustal levels, is required. Recently, Margaret Wallace and David Green (*Nature* 335, 343–346; 1988; see also the accompanying News and Views article by J. Gittins) reported the experimental formation of a carbonatite melt by melting a mantle peridotite composition at mantle pressures and temperatures, lending support to the idea that carbonatites can be primary melts from the mantle. Now Ken Bailey on page 415 of this issue reports the existence of a close natural analogue to this experimental melt — the droplets pictured above, from the Rufunsa volcanoes in Zambia. Although these carbonatites have been known for some time, the similarity of their composition to that produced in the experiments, together with the discovery by Bailey of inclusions of mantle-type chromium-rich spinel (such as the black diamond-shaped grain in the larger droplet) now provides evidence that they are the long-searched-for primary carbonate melts. Field of view is 3.4 mm wide.

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