

# Behavioral Plasticity: Levels of Sociality in Bees

## Dispatch

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**The evolution of sociality was fundamental to the tremendous ecological success of humans and some insects. The degree and type of sociality varies greatly across species. A new type of social polymorphism uncovered in bees provides useful information on the routes toward sociality.**

Sociality has evolved repeatedly and is at the root of the tremendous ecological success of several taxa, notably humans and social insects. Social insects — termites, ants and some bees and wasps — have a wide range of social organisations, ranging from species where individuals facultatively cooperate to form large colonies. In some species, colonies may contain up to a million workers which are completely sterile and specialise in tasks such as nest building, collecting food, rearing the young and defending the colony. Social organisation can also vary within species: for example, some bees and wasps facultatively express solitary or social behaviour in different environments. A recent study [1] has revealed a new type of social polymorphism in the halictine sweat bee *Halictus sexcinctus* (Figure 1). In this species, some nests are initiated by a single female and sociality emerges after the daughters eclose and remain with their mother; alternatively, several females of the same generation may join to initiate a new colony. This social polymorphism provides important insights into the factors promoting social evolution.

Sweat bees are significant model organisms for studying the evolution of altruism and social behaviour because of their astonishing range of social behaviour. Species can be solitary, with females constructing a nest and raising their own brood. Other species exhibit two main types of social organisation. In communal species, several females of the same generation join to start a colony together. Within colonies, all females contribute more or less equally to reproduction. In eusocial species a single female (the queen) initiates a colony and sociality emerges when the daughters (workers) eclose and help their mother. In contrast to communal nesting, eusocial colonies are generally characterized by high reproductive skew and strong aggression toward foreign females trying to join the colony.

A striking aspect of halictine social variation is the mutual exclusivity of communal and eusocial types of colony social organisation within the same species: these two types of social behaviour are usually characteristic of different genera and subgenera [2]. The discovery of the coexistence of communal and eusocial nests in *H. sexcinctus* is thus unanticipated and of great interest. The two types of social organisation were

discovered during a detailed study of nesting behaviour in a population in Greece. Richards *et al.* [1] first observed that about 500 nests were each initiated in a cliff by single females. A few weeks later, a second set of nests was started on road beds within 2 meters of the cliff by groups of females. As has been observed across halictid species exhibiting these two alternative modes of colony founding, nests started by a single female became eusocial with the mother queen monopolising most of the reproduction. By contrast, reproduction was more equally shared in communal nests and there was no aggression between females. Morphological observations also revealed significant differences. In eusocial nests, queens were significantly larger than workers. The size of females in communal nests ranged between that of eusocial queens and workers. Importantly, however, communal females had proportionally shorter wings than either eusocial queens or workers, showing that these females followed a different developmental pathway.

Might the difference between the two types of nest be due to the presence of two cryptic species? After all, this would be the most parsimonious explanation, given that previous studies showed that communality and eusociality are mutually exclusive types of colony social organisation in halictine bees. To address this possibility, Richards *et al.* [1] compared mitochondrial DNA sequences for two sections of the cytochrome oxidase I gene. Their analysis revealed that the communal and eusocial sequences are intermingled and more similar to each other than to those of conspecifics from elsewhere in Europe. The authors thus conclude that the two social forms are members of the same species and population. Although this is the most parsimonious explanation, a definitive answer would require an analysis of nuclear genes. For example, the comparison of allele frequencies between the two social forms would allow us to determine whether there is ongoing gene flow which would definitively demonstrate that the two social forms are part of a single species.



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Figure 1. A eusocial foundress of the bee *Halictus sexcinctus* returning to her nest following a pollen-foraging trip. The orange mark on her thorax allows her to be individually recognized. (Photograph courtesy of Miriam Richards.)

A related important issue is whether the morphological and behavioural difference between the communal and eusocial females has a genetic basis or whether it results from phenotypic plasticity with an environmentally induced developmental switch during the larval stage, perhaps as a result of differential feeding by queens. Richards *et al.* [1] favour the latter possibility because previous studies have shown that morphological polymorphism in other halictine species is environmentally induced [3]. But while it is true that caste determination in social insects is usually the result of environmentally induced differences in gene expression, several cases of genetic polymorphisms have been recently discovered. Thus, a fundamental social polymorphism is under simple genetic control in the fire ant *Solenopsis invicta* [4–6]. In the monogyne form, colonies invariably contain a single queen, whereas in the polygyne form colonies contain anywhere between 2 and 200 queens. This fundamental difference in social organisation, as well as morphological differences between queens of the two social forms, is completely associated with variation at the gene *Gp-9*. In the same vein, two cases of genetically determined caste differentiation have recently been found in harvester ants [7–9]. This unusual system evolved following complex events of historical hybridization between two parental species [10]. Whether or not the social polymorphism in *H. sexcinctus* has a genetic basis remains an open question until detailed genetic studies or breeding experiments have been carried out.

Whatever the exact underlying proximate mechanism, the existence of mixed social strategies in *H. sexcinctus* sheds light on the sequence of steps leading to eusociality. The finding that colonies are either eusocial or communal, and that there is no transition from one form to the other, fails to support the view that communal breeding might be a transition to eusociality [11]. Similarly, it is now clear that co-founding between queens of the same generation almost never leads to stable colonies in ants and wasps [12]. Rather, stable colonies with clear reproductive division of labour, the hallmark of complex insect societies, almost invariably occur in species where colonies are initiated by single females and then develop with the daughters produced. This is the pattern predicted by theoretical analyses showing that a high reproductive skew and the evolution of specialized morphological castes should occur almost exclusively in mother–daughter associations [13]. In short, both empirical and theoretical studies now support the view that communal breeding is not a route to eusociality and complex social organization.

A final and important message emerging from the work of Richards *et al.* [1], as well as some other recent studies, is that social polymorphisms are probably more common than generally assumed [14]. Important progress in this area has been possible with the advent of molecular tools, thus making it feasible to rule out the possibility that alternative social forms are merely cryptic species. Molecular tools have also been instrumental in demonstrating the genetic basis of several of these polymorphisms. One of the most fascinating

challenges in behavioural genetics will now be to determine how frequently social polymorphisms are genetically based, to identify the genes involved and, importantly, to elucidate the exact nature of the interaction between genes and social environment.

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