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HIGHLIGHTED ARTICLE

Socially polymorphic bees as model organisms for studying the evolution of eusociality

M. H. Richards[1]

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The evolutionary transition from solitary to social behaviour has long been one of the central obsessions of social insect biologists. A difficulty with studying this transition is that in many social insect lineages, transitions to sociality took place tens of millions of years ago, obscuring the behavioural changes involved in these transitions. The eusocial sweat bees used to be considered an exception to this rule, because we thought that eusociality was quite recent and that there were many origins of eusociality in this group. Alas, phylogenetic research since then has conclusively demonstrated that sweat bees, like other social insect lineages, made the transition to eusociality too long ago to regard current behaviour as representing the first stages of social transitions (Brady et al. 2006; Gibbs et al. 2012). Fortunately, over the past few decades, behavioural researchers have uncovered many examples of socially polymorphic sweat bees, in which solitary or eusocial behaviour is facultatively expressed within or between populations, starting with the discovery of reversion to solitary behaviour in a high altitude population of *Lasioglossum calceatum* (Sakagami and Munakata 1972). Social polymorphism has now been identified in multiple species of sweat bees, small and large carpenter bees, and orchid bees, allowing biologists to compare both causes and consequences of solitary and eusocial behaviour, shedding empirical light on what would, otherwise, remain purely theoretical studies on the origin of social behaviour.

The social behaviour of the tropical sweat bee, *Megalopta genalis*, has, in recent years, been so extensively studied, that it is on its way to becoming a “model organism” for research on bee social evolution. *Megalopta* are crepuscular or nocturnal foragers with very large eyes from which they derive their names. They dig linear burrows in rotting branches suspended in tropical vegetation, forage rather rarely compared to temperate sweat bees, and just seem to live slowly (I think of them as the sloths of the sweat bee world). Females found nests solitarily, and it is not until they lay their first eggs, that their subsequent social behaviour can be discerned. The first offspring of solitary foundresses are male, while the first offspring of eusocial foundresses are females that will become workers. Thus, within populations, there are three types of females, large solitary foundresses that remain solitary, large solitary foundresses that become queens, and small daughters that become workers.

A crucial requirement of social living is the ability of group members to tolerate living in close proximity. Many solitary animals, including solitary sweat bees, are largely intolerant to conspecifics, whereas mutual tolerance is necessary for group-living. It follows, then, that in encounters between unfamiliar individuals of socially polymorphic bees, pairs of solitary individuals should exhibit less tolerance and more aggression than pairs of social individuals. On the other hand, bees that live in caste-based societies often use aggression to establish and maintain dominance hierarchies; in particular, sweat bee queens are often aggressive towards workers (Kapheim et al. 2012).

In this issue, Smith et al. (2019) analyse the behaviour of pairs of solitary foundresses, queens, and workers of *M. genalis*, using circle tubes, a simple apparatus in which two bees are forced to interact in a tubular environment not unlike the tunnels of their nests. As predicted, social females, both queens and workers, are more tolerant of unknown conspecifics than solitary females. In contrast, the results for aggression did not support the original prediction. Instead, solitary foundresses and social queens had similar, relatively high rates of aggression, whereas workers were less aggressive. As pointed out by Smith et al., the latter results support the idea that workers represent an evolutionarily novel phenotype. One might speculate, then, that in both evolutionary and developmental terms, solitary foundresses and queens represent a kind of default phenotype.

✉ M. H. Richards
mrichards@brocku.ca

[1] Department of Biological Sciences, Brock University, St. Catharines, ON, Canada

Queens can convert their daughters into workers through nutritional adjustments to larval provisions, completing the process by aggressive interactions post-eclosion. It would be interesting to repeat these experiments with worker-destined females that were removed from maternal influence prior to eclosion, the prediction being that their circle tube behaviour would then look like that of solitary foundresses or queens.

Whether we call species like *M. genalis* socially polymorphic, facultatively social, or facultatively solitary, they are incredibly valuable subjects for studying the evolutionary origins of sociality, including the origins of structured societies. They provide us with the empirical data that allow us to examine alternative behavioural strategies, which illuminate the processes by which sociality might evolve and devolve in differing ecologies, times, and places. And they are incredibly fun to study!

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