Usurping the queen

Michael D. Breed¹

Published online: 4 February 2017

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In this issue of *Insectes Sociaux*, Saga et al. (2017) present a fascinating long-term study of nest usurpation and social parasitism in *Vespula* wasps. Reproduction based on usurpation is relatively rare in vespine wasps and outcomes are often only anecdotally reported. *Vespula flaviceps* and *V. shidai* can each have colonies with normal reproductive strategies, but some queens in each species usurp nests of either their own species (intraspecific usurpation) or the other species (interspecific usurpation). Saga et al. (2017) focus on interspecific usurpations. In an 8-year study they documented ten cases of interspecific usurpation. In nine of these the resulting colony had a *V. shidai* queen and in the remaining one the queen was *V. flaviceps*. The workers in these colonies were predominantly *V. flaviceps*, but the gynes and males produced were nearly all *V. shidai*. This suggests that *V. shidai* has a selective advantage in this relationship and raises the interesting question of whether facultative social parasitism can provide a route to the evolution of obligate parasites.

Facultative social parasitism differs from obligate relationships in that facultative usurpers exploit the nest as a resource but can also produce their own workers. In facultative parasitic wasps, the usurped colony may ultimately contain a blend of host and parasite workers or may consist of only parasite workers. Obligately parasitic social wasps, on the other hand, must always exploit the workers of the host species, as they only produce sexuals, not their own workers.

Based on the observations that *V. flaviceps* nests usurped by *V. shidai* produced sexuals of *V. shidai*, these facultative

social parasites present provocative questions in understanding animals' reproductive choices. Among the social wasps, three types of social parasitism are known: intraspecific facultative nest usurpation, interspecific facultative usurpation, and obligate social parasitism (e.g. *sulcopolistes* species group of *Polistes* (Cervo 2006), *Dolichovespula arctica* (= *adulterina*)) but whether the former two are evolutionary stops on the road to obligate social parasitism are unknown.

Facultative social parasites seem to make a reproductive choice to usurp a nest, rather than establish one on their own. The choice of host species usually follows Emery's rule that a socially parasitic species exploits its taxonomic sister species. However, this is not always true, and relatively closely related species, with similar social behavior and communication, are pre-adapted to exploit each other by virtue of possessing the "keys to the kingdom", a repeated theme in the discussion of the evolution of social parasitism (Breed 2016). Thus, social parasites often belong to the same genus as their hosts.

But little is known about the genetics that underlies social parasitism in wasps, and possibly differing reproductive strategies reflect underlying genetic divergences within populations. Within-species sympatric divergence—Emery's rule strictly applied—is very rare and seems an unlikely route to obligate parasitism. Facultative social parasitism can be an evolutionarily stable strategy, rather than a step towards obligate parasitism (Lowe 2002). However, in relationships such as the one described by Saga et al. (2017) one species could gain the upper hand in competition among free-standing nests while the other could evolve superior parasitic strategies. In that case the outcome could be the evolution of obligate parasitism by the species that is the superior parasite but inferior independent competitor.

✉ Michael D. Breed
michael.breed@colorado.edu

¹ University of Colorado, Boulder, USA

Vespula flaviceps and *V. shidai* are already distinct species. Saga et al. (2017) fill out a more complete picture of the outcomes of facultative social parasitism among similar species; their work has high value in adding to our understanding of these intriguing relationships.

Michael D. Breed

Editor-in-Chief.

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