

Wasp who would be queen: A comparative study of two primitively eusocial species

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***Ropalidia marginata* and *Ropalidia cyathiformis* are two Old World, primitively eusocial, tropical polistine wasps that exhibit perennial, aseasonal, indeterminate nesting cycles. Queens are periodically ousted and replaced by one of the workers, whom we refer to as the potential queen. Here we identify the characters of the potential queens by experimentally removing queens from several colonies of both species. Potential queens in *R. marginata* are unspecialized, worker-like individuals, not unique in their dominance ranks. In contrast, potential queens in *R. cyathiformis* are queen-like individuals and unique in always holding the top dominance rank among the workers. We suggest that this striking difference in the behaviour of the potential queens of the two species has to do with the very different mechanisms that queens of the two species use to suppress worker reproduction. In regard to their ovarian development, potential queens of neither species are unique and they are only one among several individuals with partially developed ovaries. This may have to do with the fact that queen replacements are frequent in tropical, aseasonal climates, making it adaptive for several individuals to be prepared to take over the position of the queen at short notice.**

Keywords: Dominance behaviour, potential queen, primitively eusocial wasps, queen succession, *Ropalidia cyathiformis*, *Ropalidia marginata*.

HYMENOPTERAN societies may be regarded as feminine monarchies because their colonies consist of one or a small number of fertile queens and a large number of sterile workers, while the males typically do not participate in social life¹. In any monarchy, the identity of the successor to the king/queen is of obvious interest. In highly eusocial insects, where caste determination is pre-imaginal and queens and workers are morphologically differentiated, new queens are produced by an elaborate process of differential larval nourishment². On the other hand, in primitively eusocial insects, where caste determination is post-imaginal, queens

and workers are morphologically identical and where most individuals are totipotent, adult workers can replace their queens^{1,3,4}. In newly founded colonies of primitively eusocial species that follow annual nesting cycles in temperate regions, subordinate cofoundresses may, after some period of working, challenge and replace the dominant cofoundress (queen)⁵⁻⁹. Queen replacement is not restricted to the founding stage; occasionally some of the eclosing female wasps can also take over the role of a queen if the original queen dies. These females mate with early-produced males and can lay diploid eggs^{10,11}. However, eclosing daughters who stay back on their natal nests may often be unable to become replacement queens either due to intrinsic physiological limitations or due to the absence of mating opportunities at the appropriate time¹².

The most widespread opportunities for workers to kill or drive away existing queens and take over their positions are to be found in primitively eusocial species in the tropics, especially those that follow aseasonal, perennial, indeterminate nesting cycles¹³⁻¹⁵. *Ropalidia marginata* and *Ropalidia cyathiformis* are two examples that fit the above description. Frequent queen turnover has been observed in natural colonies of both these species. Because these colonies can be long-lived and undergo successive queen replacements, working for sometime and then replacing the existing queen may be as common or more common a strategy to become queens than founding a new colony¹⁴. As might be expected from the high frequency of queen replacements, there is little disruption in colony activity, foraging and brood care, following queen replacements^{16,17}. *R. marginata* and *R. cyathiformis*, therefore, offer an excellent opportunity to understand the characters of workers who successfully replace their queens.

Materials and methods

Behaviour

Behavioural observations were made on 12 *R. marginata* and 12 *R. cyathiformis* post-emergence colonies during February 2000 and April 2001 (Figure 1). All adult wasps

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