RELATEDNESS IN NEO-TROPICAL POLYGYNOUS WASPS

Colin R. Hughes, David C. Queller and Joan E. Strassmann
Department of Ecology and Evolutionary Biology, Rice University,
P.O. Box 1892, Houston, Texas, 77251, U.S.A.

Many neo-tropical wasp colonies are founded by large swarms which contain many queens. Mature colonies contain hundreds or thousands of individuals, often with little or no morphological caste differences. In these colonies, there are often as many as 10 queens and sometimes even hundreds.

High queen number makes the maintenance of eusociality in this group difficult to explain because it is expected to lead to lowered relatedness between workers and the brood they rear. With just ten singly mated, outbred queens contributing eggs equally to the brood, relatedness is expected to fall below 0.1, requiring a benefit to cost ratio greater than five to explain continued helping by the workers. Hamilton himself recognized this difficulty and suggested that it may not exist in nature due to the asynchronous production of sexuals within a population and limited dispersal of swarms[1]. This, he reasoned, could lead to significant inbreeding and thereby, higher intracolony relatedness. West Eberhard suggested a second resolution after observing a *Metapolybia* nest[2]. She documented a decline in queen number starting soon after swarming that ended when just one queen was left; at this point a reproductive brood was produced and queen number rose. This "cyclical monogyny" would be reflected in cyclical variation in relatedness with reproductives being produced when intra-colony relatedness peaked.

We measured levels of intra-colony relatedness in 4 species of this enigmatic group of wasps (*Polybia occidentalis*, *Polybia sericiea*, *Polybia emaciata*, and *Parachartergus colobopterus*) in order to detail just how difficult it is to explain their continued sociality and to evaluate the above hypotheses. Females were collected from their nests at two field sites in Venezuela then kept frozen until analyzed using standard starch gel electrophoresis techniques. Relatedness values were calculated from individual phenotypes at polymorphic loci using the method of Queller and Goodnight[3].

Relatedness (±S.E.) varied from a high of 0.34 ± 0.05 in *Polybia occidentalis* (21 colonies, 197 individuals) to a low of 0.10 ± 0.07 in one of two populations of

Parachartergus colobopterus (15 colonies, 161 individuals) that were sampled[4]. In no population of any species studied was there any indication of inbreeding.

Relatedness within colonies of polygynous tropical wasps is not as low as had been expected from knowledge of queen number alone. This makes the problem of explaining the maintenance of sociality in these wasps less difficult. However, in at least some species, most notably here in *Parachartergus colobopterus*, relatedness is quite low. Four explanations seem possible to explain why workers in such colonies do not reproduce directly. First, the benefit to cost ratio could be high enough to explain worker behavior in the absence of any other special factors. Second, workers may actually be a sub-fertile caste, less able than queens to lay eggs. Third, it is possible that the relatedness value we measured is not the true value of importance to the workers; it is conceivable that workers could aid more closely related brood preferentially, as has been suggested recently in honey bees[5]. Fourth, relatedness among colony mates may not always be as low as we measured; a situation which would arise if West Eberhard's cyclical monogyny hypothesis[2] is applicable.

We investigated these questions in more detail in one population of *Parachartergus colobopterus*. Morphometric analyses of queens (females whose ovaries contained at least one mature oocyte) and workers revealed that there were no differences between these two groups in head width, length of scape, or number of hamuli. Further, there was no correlation between the head width and the number of mature oocytes in the ovary. This strongly suggests that this species has no morphological castes and that workers are not physically unable to perform reproductive functions.

Relatedness among a random sample of females from this population was higher than that found at our other field site; $r \pm S.E. = 0.32 \pm 0.11$ (24 groups, 375 individuals). The most intriguing finding was that relatedness among queens was significantly higher than relatedness among the random sample[6]. This higher relatedness largely resolves the disparity between the relatedness value calculated from queen number and that calculated from allozyme variation. High relatedness among queens is also compatible with West Eberhard's hypothesis that reproductive individuals are produced when only one queen is left in the colony[2]. However, analysis of the number of queens in new, young, mature and declining colonies failed to provide any support for the cyclical monogyny hypothesis. There was no decrease in queen number as colonies aged[6].

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