The Nature of Ant Colony Success

In an interesting study, Cole and Wiernasz (1) recently showed that for the ant *Pogonomyrmex occidentalis*, colonies with high genetic diversity had a much greater growth rate and survival than did colonies with low genetic diversity. This was taken as evidence that multiple mating by queens (polyandry) and low relatedness increase colony fitness. An alternative explanation seems possible, however. Polygyny (multiple queens per nest) is common in ants and, like polyandry, reduces within-colony relatedness (2, 3).

Polyandry and polygyny can be distinguished by reconstructing maternal and paternal genotypes from the genotypes of many offspring per colony. Cole and Wiernasz genotyped only six offspring per colony and analyzed their data with an algorithm that only estimates the average relatedness among nestmates. The authors state that primary polygyny is extremely rare but provide no evidence that secondary polygyny (adoption of queens by established colonies) does not occur. Because polygyny mostly arises through secondary polygyny in ants (2, 3), reduced within-colony relatedness might result also from the presence of multiple queens per nest. If decreased relatedness were only due to multiple mating, the observed relatedness ($r = 0.32$) would require an effective number of matings by queens of 7.1 (4)—a value greater than the average ($N_e = 1.16$, $n = 19$) (5) and maximal ($N_e = 3.9-6.3$) (6) values yet reported for ants.

Polygyny has been shown to be associated with greater colony size and higher productivity in several ant species (7–9). Moreover, the presence of multiple queens should also lower the rate of colony mortality because the risk of loss of all egg-layers is reduced. Hence, it remains to be seen whether the greater growth rate and higher survival of *P. occidentalis* colonies with higher genetic diversity is simply due to the presence of several queens rather than any selective advantage of low relatedness.

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Response: We argued (1) that differences in colony fitness arise from differences in within-colony relatedness levels due to polyandry. The alternative explanation—that our results were due to the possibility that colonies with multiple queens may have higher productivity, growth, and survival, and also lower relatedness, than colonies with a single queen—requires that polygyny be relatively common. Although polygyny is theoretically possible in *P. occidentalis*, we consider it highly unlikely. All investigations of *Pogonomyrmex*, which has been extensively studied (2–10), have reported that single queens are, without exception, found in the genus. Observations of multiple mating, by contrast, are common (4, 5). In more than 2000 observations of founding queens of *P. occidentalis*, we have never observed multiple foundresses that were successful; founding queens are extremely aggressive to one another (4, 5). Of the 33 *P. occidentalis* colonies that have been excavated (3, 10), not one has revealed more than a single queen.

Genetic and morphologic considerations likewise offer little support for the multiple-queen hypothesis. One of our protein electrophoretic loci, Amylase, has five alleles. An observation of either three different homozygotes in the same colony, two different homozygotes and one heterozygote without a matching allele, or one homozygote and two different heterozygotes without a matching allele would require the assumption of more than one queen. No colony in our sample ($n = 1492$) fell into these categories. (Because of the low genetic power of our electrophoretic locus, however, this should not be regarded as definitive.) Morphologically, in contrast to the dramatic variation in male dry mass, there is less within- or between-colony variation in queen size. Polygynous queens are often smaller than their monogynous counterparts (11), so the lack of size variation is suggestive. Additionally, the queen-worker thorax volume ratio is 12. In all cases in which this ratio has been greater than 5.1, the species was monogynous (12).

Because there is substantial evidence that colonies are not founded by multiple queens, the only possibility consistent with polygyny is that a colony could have multiple queens secondarily—that is, queens are added to colonies sometime later in the life cycle. During nine colony-founding episodes, we have never observed queens cofounding or attempting to enter established colonies, nor has this behavior been observed in other members of the genus (2, 3). On the contrary, we frequently have observed queens being excavated from their burrows and killed by workers from other colonies (4, 5). If secondary polygyny did occur, we would expect the intracolony relatedness to be greater in first-year colonies (that have workers from a single queen) than from older colonies; no such pattern was observed. If colonies adopt queens at some point during their life cycle, producing lower relatedness, cohorts of first-year colonies should not show an inverse correlation of relatedness and growth rate; instead, that pattern should be exhibited only by older colonies (that can be polygynous). We found, however, that the association of fast growth and low relatedness was not tied to particular cohorts or years [figure 3 of (1)].

Although none of these lines of evidence is decisive in itself, in the aggregate they suggest that the standard for positing multiple queens in a colony must be high; it is not enough simply to point out their logical possibility. In view of the lack of positive evidence for the existence of polygyny—and the abundant evidence of multiple mating within this species and across the genus—we thus conclude that polygyny is an unlikely explanation for the results we observed.

Fjerdingstad and Keller also reason that because the number of effective matings by queens is greater than the number of effective matings in other monogynous species, it is unlikely that *P. occidentalis* forms colonies with a single queen. Given the population intracolonial relatedness ($r = 0.324$), the effective number of times that the queens mate (under the assumption of a single queen) is 6.76, not 7.1, as Fjerdingstad and Keller suggest (13). As Fjerdingstad and Keller note, the highest value obtained previously is 6.3 matings, based on relatedness of 0.33 in *Acromyrmex octospinosus* (14). The estimate of relatedness for *P. occidentalis* is strikingly similar to the estimate of relatedness obtained for *A. octospinosus* ($r = 0.326$ for 22 field colonies) (14), and the standard errors on these estimates (0.012 and 0.044, respectively) indicate that there is no statistical

difference between the two. The application of sensitive genetic techniques to more species will determine whether these two species are unusual extremes or represent a category which is relatively unstudied.

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13. The result of 6.76 also differs from our originally reported figure of 3.75, as noted in a subsequent correction. See B. J. Cole and D. C. Wiernasz, *Science* **286**, 49 (1999).
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