

MONOGYNY IN "POLYGYNOUS" SOCIAL WASPS

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One of the oldest surviving generalisations about social insects has to do with the social organisation of wasp colonies. It states that there are two distinct kinds of social wasps: the monogynous (single-queen, or "haplometrotic") species, having only one fertilized, egg-laying female per colony with colonies founded by a lone female; and the polygynous (multiple-queen, or "pleiometrotic") species, always having more than one fertilized, egg-laying female and colonies founded by swarms containing more than one queen. (R. von Ihering, 1905). Monogyny is the rule among temperate-zone social wasps: the four major genera of vespids widespread in temperate regions - Polistes, Vespula, Vespa and Provespa - all have primarily single-queen colonies, and none form nests by swarms. In most tropical genera, on the other hand, nests are generally thought to be founded by polygynous swarms and to characteristically contain several queens in all stages.

The existence of multiple-queen colonies poses a special problem for current theories of the evolution of insect sociality. All of the major theories, whether based on kin selection (Hamilton, 1963; 1964ab), "maternal control" (Alexander, in press), or a history of cooperation due to predator and parasite pressure (Michener, 1958; Lin & Michener, 1972) are applied primarily to explain the evolution of the matri-filial colony - a colony consisting of a single mother queen and her offspring, some of whom are sterile workers. All presently involve the idea that a colony is - one could even say "must be"- composed of close relatives (the "semisocial" colonies discussed by Michener and Lin & Michener may contain non-relatives, but are seen as a pre-adaptation to eusociality). None deals directly and successfully with the polygynous societies of tropical wasps and of some ants (see Wilson, 1971) which, since they contain numerous egg-laying females, must be genetically diverse unless a high degree of inbreeding is assumed. How are we to explain the persistence of a sterile worker caste in such colonies, either from the worker's or the mother queen's point of view, when a worker's relatedness with the brood being reared approaches the low levels indicated for polygynous colonies in Figure 1? Obviously pure kinship considerations cannot account for such a situation. Before attempting to evaluate other possible explanations or to dismiss completely an explanation involving kin selection we should consider some new information about polygynous societies, especially my own findings on the neotropical genus Metapolybia.

Metapolybia is a genus of small (9-11 mm. long) wasps which build a simple nest consisting of a single comb of cells attached directly to a smooth surface (rock, board, tree-trunk or leaf) and covered over by a thin envelope containing tiny transparent patches or "windows"

(see Rau, 1933). Various characteristics of these wasps facilitate their study. Most are singularly unaggressive, and on the rare occasions when they attack seem unable to penetrate the skin with their tiny stings. The delicate nest envelope is easily removed with only a momentary disruption of normal colony activity, and the entire colony can then be observed at once. Although moving queens and workers are not usually distinguishable by conspicuous markings or morphological features, living queens can be unequivocally identified because workers perform a distinctive "dance" toward them whenever they are encountered walking about the comb. Males have conspicuous white markings when seen from the front. Individuals can be marked for identification with coloured model-airplane paint.

Metapolybia has traditionally been considered a genus of polygynous social wasps (e. g. by Ducke, 1910; Rau, 1933). Indeed, I have found as many as 36 queens (fertilized females with large eggs present in the ovary) in a colony (43% of 84 females present). However, a study of living colonies has led to the conclusion that both of the two species common in Western Colombia - M. docilis and M. aztecoides - are to be regarded as periodically monogynous, with polygyny occurring during certain stages of the colony cycle.

The colony cycle in Metapolybia begins with new nests founded by swarms containing a number of workers and from one to 14 queens; one to three is most common. There is evidence that the swarm containing 14 queens was formed after the invasion of a nearby colony by army ants. As pointed out by Richards & Richards (1951) the interpretation of data on swarm composition is complicated by the fact that a swarm can originate, either as a reproductive offshoot of a mature colony, or as the result of colony disruption at any stage. In the latter case the swarm may be composed of all the survivors of the original colony who move en masse to a new site. Such an "emergency swarm" would have a variable number of queens depending on the stage of the disrupted nest.

Once the new comb is partially constructed and numerous eggs have been laid the number of functional queens in a polygynous group is reduced: colonies containing young brood prior to emergence of the first adult offspring usually contain only one queen. The others may be forced to be non-reproductive or to leave the nest by the workers: in one colony whose initiation was observed in detail workers began attacking certain queens 2-3 days after initiation of the comb and after numerous eggs had been laid but before the envelope had been laid down. Workers, sometimes singly and sometimes in groups, repeatedly made ferocious biting attacks on four of the 16 marked queens, pulling at their wings and legs, often chasing them some distance off the comb. Workers sometimes solicited strongly from these queens in a manner resembling dominance behaviour in Polistes (Pardi, 1944), once taking 18 large drops of regurgitated fluid from a persecuted queen in one hour. Two of the queens began to behave like workers, occasionally adding pulp to cells and sitting among workers

rather than in clusters of queens as they had done before. Workers no longer performed the "queen dance" towards them. Unfortunately this colony was attacked by ants only six days after nest initiation and I was unable to trace its further development. Although it was not clear what cues provoked the attacks on some queens while others were left alone, there are indications that the attacked queens were the only ovipositing challengers for the queenship. All the unattacked, marked queens were identified as queens because they were danced to by workers, and sat together with ovipositing females in a "queen cluster". However, during 22 hours of observation none of them laid eggs. On the other hand, all except one of the four observed egg-layers were attacked at least once, and two of them were among those frequently attacked; presumably the one unattacked egg-layer was the "accepted" queen. Of the four frequently attacked queens two were not observed ovipositing, but this may have been a consequence of the attacks. It would be interesting to investigate the possibility that unpersecuted queenlike females have less developed ovaries than persecuted queens.

Potential queens from the swarm who ultimately do not reproduce may sometimes remain on the nest for some time, as indicated by the fact that in dissections of mature monogynous colonies one sometimes finds fertilized females with obviously degenerate ovaries.

All the late post-emergence colonies so far observed have had more than one queen. One event that can lead to polygyny is removal of the monogynous queen. When I experimentally removed the lone queen from a monogynous colony of M. docilis, then one month later, I found several females laying eggs and being treated as queens by workers. Dissection showed the presence of 36 queens, at least some of whom must already have been present but not laying eggs or being danced to by workers, when the colony was originally observed. I am indebted to O. W. Richards for explaining how to estimate the relative age of adult wasps by noting the pigmentation of the transverse apodeme across the hidden base of each sternite (increasingly dark with advancing age). I suspect that in the normal colony cycle disappearance or reproductive decline of the original queen leads to polygyny and subsequent colony multiplication. I have never observed or dissected a Metapolybia colony having a well developed "old" queen along with a number of young queens with the less developed ovaries indicating that absence of the old queen is a condition for polygyny.

There is behavioral evidence that reproductive competition develops among the polygynous queens, and this may eventually lead to colony multiplication. It is well known that in some species of the monogynous genus Polistes one form of competition among potential queens is differential oophagy (Gervet, 1964). In such a species, P. fuscatus, egg-laying females remain near the egg in a post-oviposition vigil lasting up to one hour which may reduce the chances of the newly-laid egg being eaten and replaced by that of another female (West Eberhard, 1969). A species (P. canadensis) lacking differential oophagy likewise lacks a post-oviposition vigil (West Eberhard, 1969).

In parallel fashion, monogynous queens of both Metapolybia docilis and M. aztecoides, having no competing nestmates, show no post-oviposition vigil, whereas polygynous queens in colonies having several "well-developed" egg-laying females (with one or more mature oocytes and ten or more discernible developing oocytes) have very long post-oviposition vigils, in one case lasting three hours. Newly polygynous colonies, in which the several queens all have only rudimentary ovarian development, have no post-oviposition vigils, suggesting that competition among polygynous queens may develop gradually with the increasing reproductive development of queens. Evidently future queens lay eggs for a time during the polygynous stage preceding colony multiplication, for the queens found in swarms have "well-developed" ovaries, though less developed than those of monogynous queens from established nests.

On the basis of the presently available information the colony cycle in Metapolybia seems to be as follows: following nest foundation by a monogynous or polygynous swarm, the number of queens in the new colony is reduced to one, who lays most of the eggs producing the next generation of queens. Following her death, disappearance, or reproductive senility the colony enters a polygynous stage: daughter queens begin ovipositing in the parental nest and, when their ovaries are well-developed, colony multiplication by swarming occurs, with some daughters remaining to maintain the old nest. For instance, one colony of M. aztecoides has persisted beneath the porch of a building near the Pacific coast of Colombia (Anchicaya) for more than three years. Metapolybia societies, then, are alternately polygynous and monogynous, monogyny occurring early in the history of each new colony.

There is evidence of periodic monogyny in many topical Polybini, particularly in the widespread neotropical genus Polybia. Among the Polybia colonies in which all females were dissected by Richards and Richards (1951) there was at least one monogynous colony for five different Polybia species (P. micans, P. bistriata, P. bicyttarella and P. catillifex); and Robert L. Jeanne (pers. comm.) has found monogynous colonies of Polybia chrysothorax and P. occidentalis in Brazil. My own studies of Colombian wasps have indicated that a Metapolybia-like colony cycle involving a monogynous stage is possible in Polybia ignobilis: a swarm of this species contained 45 queens, while a young post-emergence colony contained just one very well-developed queen (162 oocytes) and three young, probably daughter, queens (having light apodemes and only 9-27 oocytes each). The queens of the swarm had ovaries intermediate between those of the old and young queens of the mature colony (30-111 oocytes, $\bar{x} = 67.2$). I have also found monogynous colonies of Protopolybia scutellaris and in a Charterginus sp., and Jeanne found a single-queen colony of a Clypearia species in Brazil. However, some of the polybiines are almost certainly permanently polygynous, e.g., Protopolybia pumila (Naumann, in press) and other Protopolybia species examined by Richards and Richards (1951). We can conclude, then, that there are at least two general kinds of social organization among the so-called polygynous social wasps:

1. Permanent polygyny - several (usually many) queens in swarms

and in all other stages of the colony cycle, with no one queen showing marked reproductive dominance.

and

2. Temporary polygyny (periodic monogyny) - swarms containing one or more queens of which one becomes the primary or sole egg-layer on the new nest, with a return to polygyny prior to colony multiplication (swarm formation).

Regularly occurring monogyny may raise the relatedness among colony members sufficiently to make an explanation of polygyny involving kin selection feasible. Although Hamilton's theory is commonly misinterpreted as requiring extraordinarily high relatedness of worker ("altruist") and queen, e.g., the 3/4 relatedness in monogamous Hymenoptera, the same theory can be applied to groups of more distant relatives (see West Eberhard, in press). What is required is that the worker gain in terms of "inclusive fitness" through helping one or various near or distant relatives sufficiently so that the personal cost (in terms of individual classical fitness) is more than compensated for by the gain in genes, like the worker's produced by the aided relatives (the kinship component of inclusive fitness; inclusive fitness = classical fitness + the kinship component) (see Hamilton, 1964a, West Eberhard, in press). Obviously, the more distantly related the aided relatives, the higher must be the gain:loss ratio for advantageous altruism to occur. Figure 1 shows that in Metapolybia relatedness, while fluctuating, would be maintained at a high level by periodic monogyny, relative to the low levels found in permanent polygyny without inbreeding. Another argument in keeping with the "genetic (kin selection) theory" is that Metapolybia workers are probably irreversibly sterile, "hopeless" reproductives with little or nothing to lose, and everything to gain, by helping even fairly distant relatives (see West Eberhard, in press). In hundreds of dissections I have not yet found "workers" (unfertilized females) with mature eggs or a degree of ovarian development suggesting that they might sometimes lay eggs.

Still, it is clear that an explanation in terms of kin selection alone is not complete, since in those terms monogyny would always tend to become permanent. Independent of kin selection there must be some advantage to having many queens instead of just one, either temporarily (temporary polygyny) or permanently (in permanent polygyny). In the case of temporary polygyny one must explain both the temporary willingness of individual queens to cooperate and share workers and the subsequent "willingness" of all but one to be eliminated as queens, also a kind of altruism on the part of those eliminated. As pointed out by Alexander (in press), although kin selection may often be applicable to such situations, it may sometimes be simpler and more correct to consider them products of selection operating on mothers - in this case the monogynous queens. In Metapolybia, for example, selection must act to maximize the number of successful new colonies formed by the brood of each monogynous queen. A period of polygyny on the maternal nest may function to allow ovarian development in

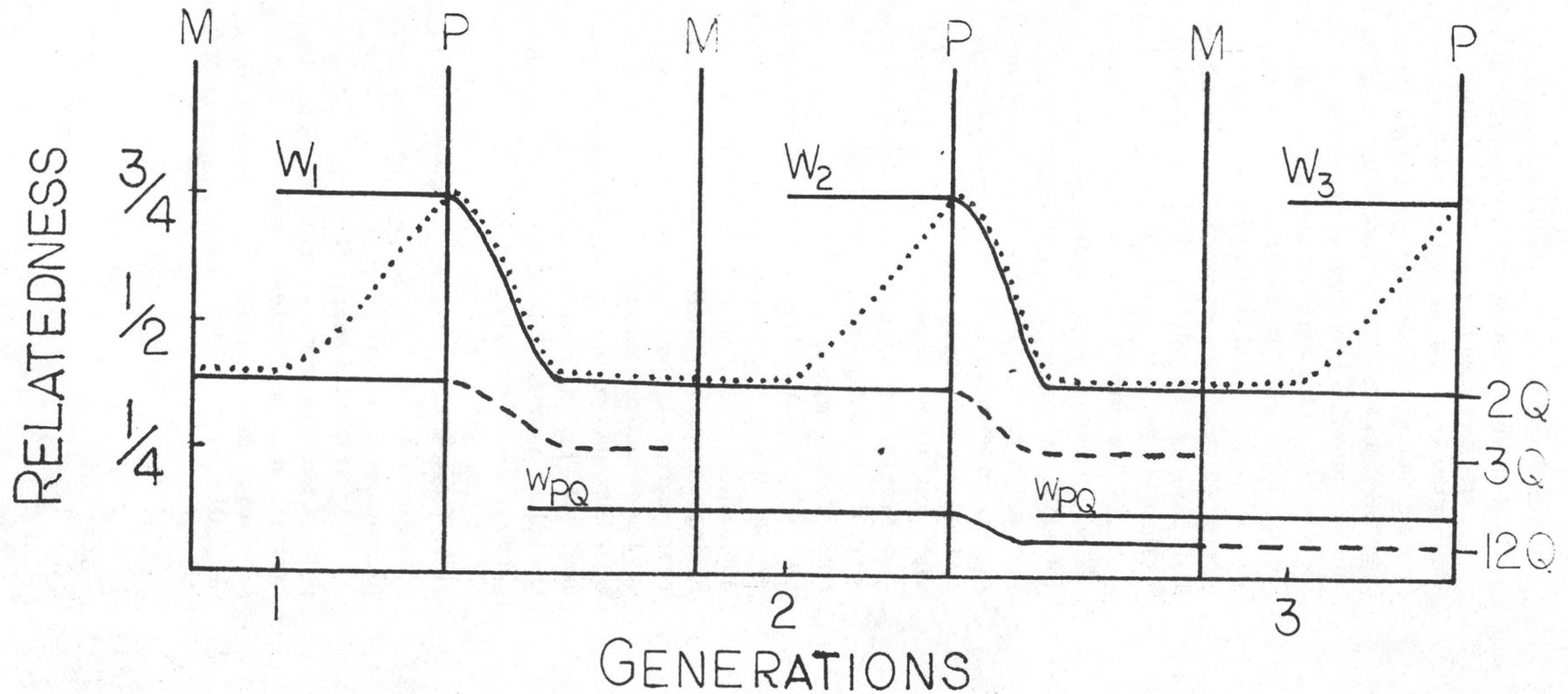
daughters prior to swarming, thus enhancing the likelihood of successful and rapid foundation of new colonies; when polygynous swarms occur they must increase the likelihood of successful colony multiplication during the high-risk period of swarm migration and nest initiation, when a monogynous swarm might lose its only queen and hence represent a large loss of reproductive effort on the part of the mother queen. The return to monogyny indicates that once the nest is established the single-queen system is more advantageous. It may be that in the absence of factors favouring polygyny, monogyny is preferable from the mother's point of view, because it prevents the decline of relatedness among brood members in her descendents, and thus insures that selfish mutants among workers will be selected against in terms of inclusive fitness (see West Eberhard, in press).

Temporary polygyny may have been a stage in the evolution of the permanent polygyny found in species having a permanent need for multiple queens, e.g., in cases where a constant high egg-production rate is selected for and exceeds the capacity of a single queen, or when the colony cannot afford a monogynous stage in which it would not be prepared to send off polygynous swarms (e.g. if disruption were common in all stages of colony development). Or permanent polygyny may be the product of a different breeding structure: if inbreeding is the rule, colonies are clonelike and many queens could coexist with little reproductive (genetic) competition (see Hamilton, 1972). When (if ever) inbreeding is the basis of a polygynous social organisation one would expect little evidence of competition among queens. On the other hand, in outbreeding species having permanent polygyny, we might sometimes find signs of reproductive competition among queens, for example, spatial separation of queens and/or their broods within the nest (e.g. on separate combs), or ability of a worker to discriminate her own mother and/or siblings among the brood. In such cases it may be more accurate to regard the colony as an aggregate of competing monogynous females for whom group living (cooperation) is individually advantageous in some context(s), rather than as a single polygynous unit. Alternatively, it could be viewed as a group of somewhat competitive sisters on whom cooperation has been imposed by selection operating on the mother (à la Alexander, in press).

At least it seems clear that "polygyny" among social wasps is not a uniform phenomenon to which any one single evolutionary explanation can be applied. Many so-called polygynous species may prove to be fundamentally monogynous with polygyny occurring only facultatively, or during certain stages of the colony cycle.

Figure 1. Hypothetical pattern of fluctuation in average worker-brood relatedness with periodic monogyny (Metapolybia). M = time of initiation of monogynous stage. P = time of initiation of polygynous stage. Dotted line shows average worker-brood relatedness given the colony cycle hypothesized in the text. Solid lines represent average relatedness for workers (W_1 , W_2 , W_3) produced by successive monogynous queens and (W_{PQ}) by polygynous queens. Dashed portions of these lines represent values reached only by extremely long-lived workers. Numerical values of relatedness assume single mating and outbreeding; parallel fluctuations would occur (at a lower level) with multiple mating and (at a higher level) with inbreeding. Levels of worker-brood relatedness approached in permanently polygynous colonies having 2, 3, and 12 queens are indicated on the left.

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