Temporary Queens in Metapolybia Wasps: 
Nonreproductive Helpers Without Altruism?

Abstract. In Metapolybia aztecoidea some mated females produce only workers, losing in competition with other similar egg-layers before producing either males or queens. Worker production by these ultimately nonreproductive females may incidentally benefit others without lowering individual fitness (without "altruism"). It could be a by-product of mutualism rather than of kin selection or parental manipulation.

The social insects are of special interest to evolutionary theorists because they live in groups containing nonreproductive individuals (workers) that help rear the offspring of others (queens). Young colonies of the neotropical social wasp Metapolybia aztecoidea (I) observed near Cali, Colombia (4°N, 915 m elevation), contain an additional kind of helper—mated egg-layers that produce workers but which are eventually forced to leave the colony to become workers before producing males or queens. These temporary queens resemble workers in that they make no direct contribution to the genetic composition of future generations and they help (by worker production) maintain a colony used by other females to produce sexual brood. In this report, I describe the circumstances giving rise to temporary worker-producing queens in Metapolybia and discuss their possible evolutionary basis.

The colony cycle and behavior at the nest in M. aztecoidea was observed in an undisturbed colony and in two of its offspring colonies during the 18-month period (23 February 1974 to 1 September 1975) encompassing their development from initiation to abandonment. Brood development was monitored by periodically recording cell contents on maps of the combs; 905 females were marked for individual identification with quick-drying enamel. These three colonies were observed for 260 hours with special attention to the functional roles of the marked individuals. The representativeness of the data was checked by observations and dissections of 20 additional colonies of the same species.

There are no dependable morphological means of distinguishing the castes of living females in M. aztecoidea, although an old queen's abdomen is usually swollen by ovarian eggs, and (even in young egg-layers) extended rather than inclined ventrally during locomotion (see cover). However, egg-layers are recognizable because (i) they perform a characteristic aggressive "bending display" (cover); (ii) they usually cluster at one edge of the comb; and (iii) workers perform a distinctive shaking "dance" toward them as they move about on the comb. These behavior patterns unequivocally distinguish queens (egg-layers) from workers (nonegg-laying females seen building or foraging).

Young colonies of M. aztecoidea alternate between multiple queen (polygynous) and single queen (monogynous) phases (2) (Fig. 1A). As in most other tropical social wasps, nests are founded by swarms containing numerous workers and usually several egg-layers. The number of egg-layers then gradually declines: some queens leave with swarms; some cease laying eggs and become workers when workers are scarce; and some are forced off the nest by aggressive workers and queens (2), and fail to return. Sometimes there is only one egg-layer for several months (Fig. 1A). If such a lone reproductively disappears, a number of young females immediately (within a few hours) begin to elicit the workers' dance. This cycle of alternating polygyny and monogyny can apparently be repeated indefinitely until, in large colonies producing males as well as females, polygyny becomes permanent (3). This report concerns only small, temporarily polygynous or monogynous colonies, in which male production was not observed.

The initial functional caste of a young M. aztecoidea female depends largely on conditions in the colony soon after her emergence as an adult; if a queen or group of queens is present, she is likely to become a worker; if not, she is likely to mate and, at least temporarily, become a queen. Of the 840 female offspring marked on long-term observation nests, only 82 were known to lay eggs, and all of these were marked between 17 February and 30 March—they were newly emerged when the lone queen of the preceding 6 months disappeared on 18 March (Fig. 1). Of 96 newly emerged females marked during this critical period, 78 (81 percent) were behaviorally recognized as queens. In contrast, none of the more than 700 female offspring marked at other times on these nests were ever seen to lay eggs or evoke dancing on ei-
Both workers and queens are active in eliminating some queens from reproduction. The dance of workers toward queens is performed with extra intensity during episodes of queen elimination, and appears to function as a test of queen dominance; if the danced-to queen adopts a crouching, subordinate posture or offers regurgitated fluid (also a subordinate gesture) the worker attacks her; if she acts dominant (solicits fluid, avoids the worker, or simply stands her ground) she is not attacked. Queens sometimes push attacked individuals from resting clusters, and chase them off the comb. When attacked persistently, queens eventually either fail to return to the nest, or change caste (become workers), and are eliminated from reproduction. It appears that eliminated queens are subordinate compared to persistent queens. They may, therefore, be females of inferior reproductive capacity, since the degree of dominance and of ovarian development are known to be associated in social wasps (7). If the elimination of some queens is desirable (in order to augment the supply of workers or reduce wasteful competition among egg-layers), it might be to a worker's advantage to eliminate those likely to be inferior (7). It is also possible that dancing workers may distinguish between their mothers and their aunts (or other peripheral relatives) who might be laying eggs on the nest, because of the superior genetic payoff of rearing the mother's offspring (siblings) (8).

Worker production by females destined to lose out reproductively (by being eliminated as egg-layers before producing brood giving rise to sexual adults) could increase the inclusive fitness of those individuals if it contributes sufficiently to the reproductive success of their sisters, whose female offspring (nieces) are genetically almost as valuable as daughters (9). Or selection on persistent queens could favor the production of the mixture of workers, temporary queens, and persistent queens, among descendants, that is most conducive to their individual reproductive success (10).

A more conventional explanation, in terms of the individual reproductive success of the temporary queens, also seems to apply: cooperative worker production (continued egg-laying, and tolerance of ovipositing nest mates) early in the colony cycle may be essential to preserve a resource (the established nest and worker staff) that is absolutely necessary for the potential queen's future reproduction (nesting by a single female without workers is unreported in Metapolybia). A young queen's own egg-laying capacity may initially be too small to quickly produce enough workers to maintain the colony. Her subordinate companions can also serve as a reserve work force when the worker population approaches extinction prior to the emergence of the first worker offspring: in the colony of Fig. 1, the last swarm worker disappeared 11 days before the initiation of foraging by worker offspring, and the "workerless" colony was maintained by working former queens. Such preemergence labor crises are probably common in newly founded colonies since the average time needed to produce a foraging worker (55 days) is considerably greater than the average worker life-span (28 days) (II). The rarity of male production in small colonies (3) may also reflect the likelihood of worker scarcity early in the colony cycle (males do not work). Con-
tinued egg-laying, rather than parasitic waiting while others produce workers, probably also contributes to a female’s chances of eventually becoming dominant since, in social wasps, persistent oviposition commonly leads to ovarian development, increased egg-laying capacity, and dominance (failure to oviposit leads to ovarian regression and subordinance) (5, 12).

Later, when worker production is under way and each queen’s ovaries are more developed [as evidenced by the increasingly swollen abdomens of older queens (see cover)], competition among queens (aggressive bending and eating of each others’ eggs) increases until only one queen is left. At that stage the single persistant queen is able to produce workers at a rate equaling or even surpassing that of a group of young queens (Fig. 1); and, at least on a small nest, she is able to inhibit all reproduction by nest mates (13).

The dominant queen wins a colony largely built and maintained by the offspring of others: in the case of the lone queen of Fig. 1, an estimated 89 percent (14) of the workers that emerged before and during her tenure as queen were offspring of other females of the founding swarm that produced neither egg-layers nor males on that nest. Some of the losers (those that leave with swarms) have a chance of reproducing on a new nest. Those exiled without swarms and those becoming workers probably have little or no chance of reproducing (none were observed to lay eggs subsequently). They are effectively sterilized in competition with nest mates.

This “mutantivorous loser” hypothesis (the suggestion that increasing competition among temporarily cooperating group members might impose reduced fertility on some individuals) solves the conundrum of how a mutualistic society, which implies activity benefiting others without reduced reproductive success (fitness), could give rise to drastically reduced fitness in some helpers with no parental manipulation or benefit to kin, a problem that has been a principal objection to mutualistic theories of helper evolution in the past (10, 15).

In general, sterile helpers can be maintained in a population by mutualism if the average reproductive brood size of active mutualists (group-living helpers), including those sterilized through competition, is greater than that of solitary individuals or idle group members (16). All the necessary conditions (16) appear likely to hold for worker production by temporary queens in young colonies of M. azteoides. However, mutualism may not account for the performance of worker duties by some former queens, since they may not remain capable of reproduction after helping, as required by this hypothesis (16). In a completely selfish case (pure mutualism with no opportunity for indirect payoff by means of benefits to kin) subordinate egg-layers would be expected to fight to the death in the attempt to take over the colony, unless the small chance of reproduction by a worker or exile is greater than that of an all-out fighter (17, 18).

Worker-producing temporary queens are likely to occur in other temporarily polygynous species in which the colony passes through a monogynous stage before producing a sexual brood (19). In newly founded colonies of Polistes fuscatus, ultimately nonreproductive mated females occasionally lay worker-producing eggs, in a situation closely parallel to that of young Metapolybia colonies: solitary nest founding is rare; once spring nest building is under way; egg laying auxiliaries are subordinate to those aided and often lose out (are ultimately sterilized) in competition; subordinate egg layers retain the ability to oviposit (are hopeful reproducitives) for a prolonged period (18). As in M. azteoides, P. fuscatus cofoodresses are close relatives, probably often sisters (18, 20); thus, their behavior may likewise be explained in terms of kin selection or maternal manipulation, as well as by the mutualism hypothesis outlined above. The difficulty of distinguishing which of these three hypotheses applies in nature is compounded by the fact that all three modes of selection could operate simultaneously to produce helping behavior among kin.

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References and Notes

1. Specimens identified by O. W. Richards and deposited at the Natural History Museum, London. Additional voucher specimens can be found at Universidad del Valle, Cali.
3. So far as observed, all nests of this species that contain adult males have been relatively large (900 cells or larger) and polygynous. All of the ten monogynous colonies observed have lacked males or else have been relatively small. All very large colonies observed were polygynous. The same situation obtains in a large portion of the species under study in Costa Rica although one small monogynous colony did produce males (A. Forsyth, personal communication).
4. Such temporary ovary development in workers has been found in Polistes gallicus (5) and in my own dissection of M. azteoides, Prototombus ebeninus, Polybia bromelina, and Pseudochartergius sp.; in M. azteoides seven new (replacement) queens, dissected 3 days after experimental queen elimination, were young unmated females with slight ovarian development [mean ovarian swellings (oocytes plus nurse-cell clusters) was only 3.8 compared to 23 for the removed queen; the largest oocyte was 0.23 mm as compared to 0.8 in the removed queen; C. B. Bernard, Cepedesa 4, 245 (1975), for methods of determining relative age and ovarian development]. Replacement queens evidently leave the nest to mate; those dissected 1 month after queen removal in M. decorus had full spermathecae, and those of a long-term experiment (Fig. 1) laid female-producing (fertilized) eggs, although males were never seen on nests.
6. She was the only female observed ovipositing, doing aggressive bending, or eliciting the workers’ dance during that period. Dissections of females of other monogynous colonies show that the single queen is present containing mature or nearly mature oocytes.
8. R. D. Alexander, personal communication. The average fractional relatedness (by descent) of a worker and her sisters is 0.25; for her daughters it is no higher than 0.12. For a discussion of inclusive fitness and kin selection see M. J. West-Eberhard, Q. Rev. Biol. 50, 1 (1975), and references therein.
10. The time for producing a foraging worker is equal to eggo-adult developmental time (45 days) plus average age at first observed foraging (10 days), or 55 days. Estimates of average worker lifespan, based on complete life histories of the first 15 offspring of a new founded colony (Fig. 1) during a period when no workers left with swarms, ranged from 7 to 52 days. This, even for relatively long-lived workers of a founding swarm probably disappear before the emergence of the first workers.
13. Based on the data in (10) the assumption that all queens contributed equally to the worker-producing eggs laid during the time that the queens were present. (12).
15. This requires that (i) group living is likely to be much more advantageous to reproduction; (ii) helping is more advantageous (in terms of future reproductive success) than not helping; (iii) helping appears to result in reproductive increase if given the chance; and (iv) some group members lose out (are actually sterilized) in competition with others.
16. I have not observed overt fighting among queens in M. azteoides, but it occurs in M. coagulata (A. Forsyth, Psyche 82, 299 (1975)). In Polistes it can lead to severe injuries (unpublished observation) and arrest of reproduction (5).
18. In certain ants, Formica exsecta, Lasius flavus and Solenopsis saevissima (E. O. Wilson, The Insect Societies (Belknap, Cambridge, Mass., 1971)) colonies are founded by several queens that fight when the brood emerges, until the colony is monogynous. Many tropical social wasps (Polistes) have both monogynous and polygynous stages (5), but the durations and timings are unknown.

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Fig. 1. (A) Changes in number of queens present in a colony of *Metapolybia aztecoide* after observation of preswarming behavior (s), conversion to worker behavior (w), and eviction from the nest following attacks (e). A few queens were missing (m) for unknown reasons. The solid triangle indicates the time of disappearance of the monogyne; S* gives a premature swarm caused by overheating of the nest. (B) Adult offspring produced (number of vacated full-term pupal cells during the preceding 10-day period). Dark bars denote the queen-producing period. This nest was abandoned in June.
continued egg-laying, rather than parasitic waiting while others produce workers, probably also contributes to a female’s chances of eventually becoming dominant since, in social wasps, persistent oviposition commonly leads to ovarian development, increased egg-laying capacity, and dominance (failure to oviposit leads to ovarian regression and subordination) (5, 12).

Later, when worker production is under way and each queen’s ovaries are more developed [as evidenced by the increasingly swollen abdomens of older queens (see cover)], competition among queens (aggressive bending and eating of each others’ eggs) increases until only one queen is left. At that stage the single persistent queen is able to produce workers at a rate equaling or even surpassing that of a group of young queens (Fig. 1); and, at least on a small nest, she is able to inhibit all reproduction by nest mates (13).

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8. R. D. Alexander, personal communication. The average fractional relatedness (by descent) of a worker and her sisters is 0.74, four times as high as that with her cousins (30).
9. The fractional genetic relatedness by descent of a niece is 0.38, that of daughters is 0.25, and of a son is 0.12. For a discussion of inclusive fitness, natural selection, SEE M. J. West-Eberhard, Q. Rev. Biol. 50, 1 (1975), and references.
11. The time for producing a foraging worker is equal to egg-to-adult developmental time (45 days) plus average age at first observed foraging (10 days), or 55 days. Estimates of average worker lifespan, based on complete life histories of the first 15 offspring of a newly founded colony (Fig. 1) during a period when no workers left with swarms, ranged from 7 to 52 days. Thus, even relatively long-lived workers of a founding queen probably do not live through the period of helping behavior.
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