that implantation with cyclic AMP induces such differentiation. Measurements of ATP and extracellular cyclic AMP levels under aerated and unaerated conditions would be of interest in this regard.

It is possible that these considerations are relevant to the normal control of morphogenesis and differentiation. No measurements of oxygen concentration in different regions of the slug are available. If, however, increased oxygen permeability through the more fluid sheath at the slug tip created an increased rate of respiration in this region, heightened ATP and cyclic AMP levels could explain the differentiation of pre-stalk and stalk cells and the occurrence of stalk morphogenesis in this part of the slug. The question of the involvement of metabolic gradients in the establishment of polarity and pattern is of general interest in the formulation of developmental models.

IRA N. FEIT
GEORGE A. FOURNIER*
ROBERT D. NEEDLEMAN†
MARA Z. UNDERWOOD‡
Franklin and Marshall College,
Lancaster, Pennsylvania 17604

References and Notes

1. J. T. Bonner, *The Cellular Slime Molds* (Princeton Univ. Press, Princeton, N.J., ed. 2, 1967); W. F. Loomis, *Dictyostelium discoideum, A Developmental System* (Academic Press, New York, 1975).
2. T. M. Konijn, J. G. C. van de Meene, J. T. Bonner, D. S. Barkley, *Proc. Natl. Acad. Sci. U.S.A.* **58**, 1152 (1967); T. M. Konijn, D. S. Barkley, Y-Y. Chang, J. T. Bonner, *Am. Nat.* **102**, 225 (1968); D. S. Barkley, *Science* **165**, 1133 (1969).
3. P. Pan, J. T. Bonner, H. J. Wedner, C. W. Parker, *Proc. Natl. Acad. Sci. U.S.A.* **71**, 1623 (1974).
4. A. M. Malkinson and J. M. Ashworth, *Biochem. J.* **134**, 311 (1973).
5. J. T. Bonner, *Proc. Natl. Acad. Sci. U.S.A.* **65**, 110 (1970).
6. W. K. Chia, *Dev. Biol.* **44**, 239 (1975).
7. J. T. Bonner, *J. Exp. Zool.* **110**, 259 (1949).
8. _____, *ibid.* **106**, 1 (1947).
9. Fixed overnight in Carnoy's Fixative (acetic acid and ethanol, 1:3) at 10°C. Dehydration and embedding in Epon-araldite [L. M. Lewis, E. R. Witkus, G. M. Vernon, *Protoplasma* **89**, 203 (1976)], sectioned (3 μm) on Porter-Blum MT2-B ultramicrotome with glass knives, stained with 1 percent toluidine blue for 30 seconds.
10. J. Sternfeld and J. T. Bonner, *Proc. Natl. Acad. Sci. U.S.A.* **74**, 268 (1977).
11. Supported in part by an institutional grant from Franklin and Marshall College. We acknowledge the helpful suggestions of Drs. Richard A. Fluck and David B. King of Franklin and Marshall College, and express our gratitude to Dr. Larry M. Lewis and Millersville State College for technical assistance and use of facilities.

* Present address: Johns Hopkins University School of Medicine, Baltimore, Md. 21205.

† Present address: Hershey Medical College of Pennsylvania State University, Hershey 17033.

‡ Present address: Temple University School of Medicine, Philadelphia, Pa. 19140.

1 November 1977

Temporary Queens in *Metapolybia* Wasps: Nonreproductive Helpers Without Altruism?

Abstract. *In* Metapolybia aztecoides *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 aztecoides* (*1*) 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 or 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. aztecoides* 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. aztecoides*, although an old queen's abdomen is usually swollen by ovarial 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. aztecoides* 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 reproductive 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. aztecoides* 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-

0036-8075/78/0428-0441$00.50/0

ther the parent or the swarm-founded offspring nests (the latter were observed for about 50 hours). This critical period for caste determination may correspond to a brief ovary-developed phase known to occur commonly in young unmated females of *Metapolybia*, and other social wasps, soon after they emerge (*4, 5*). Females that are in this phase when the colony becomes queenless are evidently those that begin to lay eggs (*4, 5*).

In the colony of Fig. 1, all of the new queens, after the disappearance of the lone queen, were probably sisters, since the former queen was almost certainly the only female ovipositing on the nest from 3 January to 13 February when the eggs producing these females had been laid (*6*). Thus, periodic monogyny, if it lasts long enough for all replacement egg layers to be offspring of the single queen, maintains high genetic relatedness within the colony (*2*).

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 toleration 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 subordinant 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) (*11*). 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-

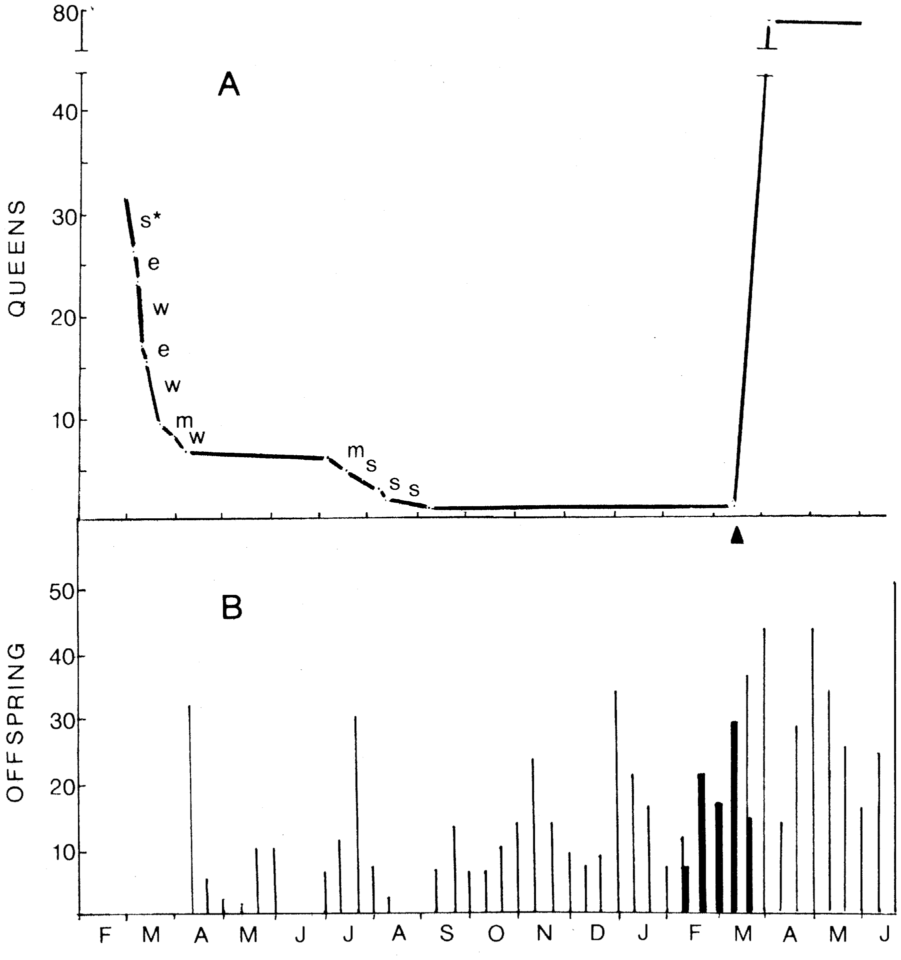

Fig. 1. (A) Changes in number of queens present in a colony of *Metapolybia aztecoides* after observation of preswarming behavior (*s*), conversion to worker behavior (*w*), and eviction from the nest following attacks (*e*). A few queens were missing (*m*) for unknown reasons. The solid triangle indicates the time of disappearance of the monogyne; *S** was 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.

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 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*).

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 "mutualistic 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. aztecoides*. 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) subordinant 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 reproductives) for a prolonged period (*18*). As in *M. aztecoides*, *P. fuscatus* cofoundresses 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.

MARY JANE WEST-EBERHARD
Departamento de Biología, Universidad del Valle, Cali, Colombia, and
Smithsonian Tropical Research Institute, Balboa, Canal Zone

References and Notes

1. Specimens identified by O. W. Richards and deposited in the British Museum of Natural History, London. Additional voucher specimens can be found at Universidad del Valle, Cali.
2. M. J. West-Eberhard, in *Proceedings of the 7th International Congress of the International Union for Study of Social Insects, London* (1973), p. 396.
3. So far as observed, all nests of this species that contain newly emerged males have been relatively large (900 cells or larger) and polygynous. All of the ten monogynous colonies observed have lacked males and have occupied relatively small nests. All very large colonies observed were polygynous. The same situation obtains in a large population of this species under study in Costa Rica although one small monogynous colony did produce males (A. Forsythe, personal communication).
4. Such temporary ovary development in workers has been found in *Polistes gallicus* (*5*) and in my own dissections of *M. aztecoides*, *Protopolybia scutellaris*, *Polybia ignobilis*, *Polybia scrobalis*, and *Pseudochartergus* sp.; in *M. aztecoides* seven new (replacement) queens, dissected 3 days after experimental removal of the queen, were young unmated females with slight ovarian development [mean ovarian swellings (oocytes plus nurse-cell clusters) per ovariole was only 3.8 compared to 23 for the removed queen; the largest oocyte was 0.23 mm as compared to 80 in the removed queen] [see M. J. West-Eberhard, *Cespedesia* **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. docilis* had full spermathecae, and those of a long-term observation colony (Fig. 1) laid female-producing (fertilized) eggs, although males were never observed on that nest.
5. L. Pardi, *Physiol. Zool.* **21**, 1 (1948).
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 the only female present containing mature or nearly mature oocytes.
7. M. J. West-Eberhard, *Science* **157**, 1584 (1967), and references therein.
8. R. D. Alexander, personal communication. The average fractional relatedness (by descent) of a worker and her sisters is 3/4, four times as high as that with her cousins (3/16).
9. The fractional genetic relatedness by descent (*r*) of niece is 3/8, that of daughters is 1/2. For a discussion of inclusive fitness and kin selection see M. J. West-Eberhard, *Q. Rev. Biol.* **50**, 1 (1975), and references.
10. For a discussion of parentally imposed helping behavior see R. D. Alexander, *Annu. Rev. Ecol. Syst.* **3**, 193 (1974).
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 swarm probably disappear before the emergence of the first worker offspring.
12. S. Flanders, in *Proceeding of the 6th International Congress of the International Union for the Study of Insects Bern* (1969), p. 47 (1969).
13. M. J. West-Eberhard [in *Proceedings of the 8th International Congress of the International Union for Study of Social Insects, Wageningen* (1977)] discusses the maintenance of reproductive dominance in social wasps.
14. Based on the data of Fig. 1 and the assumption that all queens contributed equally to the worker-producing eggs laid during the time that the queens were present on the nest.

→ W. D. Hamilton, *J. Theor. Biol.* **7**, 17 (1964); *Annu. Rev. Ecol. Syst.* **3**, 193 (1972); W. Lin and C. D. Michener [*Q. Rev. Biol.* **47**, 131 (1972)] outline a mutualistic theory of insect sociality.

16. This requires that (i) group living is likely to be much more advantageous than solitary reproduction; (ii) helping is more advantageous (in terms of future reproductive success) than not helping; (iii) helpers remain capable of reproduction if given the chance; and (iv) some group members lose out (are eventually sterilized) in competition with others.
17. I have not observed overt fighting among queens in *M. aztecoides*, but it occurs in *M. cingulata* [A. Forsythe, *Psyche* **82**, 299 (1975)]. In *Polistes* it can lead to severe injuries (unpublished observation) and arrested colony development (*18*).
18. M. J. West-Eberhard, *Misc. Publ. Mus. Zool. Univ. Mich.* **140**, 1 (1969).
19. In certain ants, for example, *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 (Polybiini) have both polygynous and monogynous stages (*3*), but the durations and timing are unknown.
20. R. Metcalf, thesis, Harvard University (1975).

21. I thank R. D. Alexander, M. Breed, W. G. Eberhard, A. Forsythe, E. Leigh, C. D. Michener, K. Noonan, J. Pickering, N. Smith, E. O. Wilson and D. Windsor for critiques of an early version of this manuscript. Drs. Alexander, Eberhard, Leigh, and Michener made detailed and helpful comments at several stages. Discussion with M. Litte clarified particular points.

14 December 1976; revised 23 August 1977