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Altruism and Relatedness at Colony Foundation in Social Insects

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Cooperative nest initiation in social insects is most easily explained when cooperating females are relatives, as is common in polistine wasps. However, recent research has revealed that unrelated ant queens also initiate colonies together. Reproductive dominance hierarchies are absent among unrelated foundresses, which contrasts with the rigid dominance hierarchies found among related foundresses. New field studies of joint nest founding among non-relatives show that cooperation is favored where colonies are clumped and brood raiding is common, so that attaining a large worker force quickly is critical to colony survival. These studies enrich our understanding of the role of relatedness in social groups.

Social insect colonies are initiated by a solitary, mated queen, or by a group of two or more mated queens. In some species workers accompany these queens. Species where cooperative colony foundation is typical have been the focus of much research on the evolution of altruism because the queens appear to have the option of beginning a nest alone and yet they do not[1]. Instead, females contribute to the reproductive success of a single queen either by rearing her eggs and laying no eggs of their own, or by laying eggs themselves only early in the colony cycle when all eggs are destined to become workers[2,3]. Understanding why these females give up personal reproduction is of special interest: if we can understand these relatively simple systems, we may approach an understanding of the factors that selected for group living and subsequent sterile castes in the first place.

The special insights of Hamilton[4] on the interaction of genetic relatedness and altruism have helped us to understand why related females cooperate. Hamilton predicted that subordinates would give up egg-laying opportunities to help a relative when it increased their inclusive fitness. The inclusive fitness effect of a behavior is $rB-C$, where r is the relatedness between subordinate and egg layer, B is the number of extra progeny reared as a result of the subordinate's assistance, and C is the cost, measured in terms of progeny that the subordinate would have reared had she reproduced independently[4]. Cooperative colony foundation by relatives can be advantageous to all group members as compared to independent colony foundation, at least for small groups of polistine wasps[1,5].

Less clearly understood is why individuals join non-relatives and ultimately sacrifice their egg-laying opportunities, as has been recently reported in ants with cooperative colony founding[2,6–10]. Since group members are not related to each other, they cannot propagate their genes by rearing relatives other than their own progeny, and losers in the battle for queenship do not have progeny. Therefore, these groups are expected to differ from groups of relatives in several important ways. Females cooperating together must not be able to predict which female will become the eventual egg layer (and win all the fitness of the group) when they first join the group, or at any time when leaving the group and reproducing independently is still a viable option. Otherwise, females that are unlikely to become the reproducing individual will leave the group. Advantages to group nesting need to be great enough to make up for the probability that the individual will be the loser in the battle for queenship and will pass on no genes. Also, there must be few opportunities to found nests with relatives, as this would normally be a more advantageous strategy than nesting with non-relatives. It

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Fig. 1. Cooperating foundresses of *Polistes annularis*. Photo by Joan Strassmann.

appears that these conditions have been met most frequently in various ant taxa[10].

Occurrence of cooperative colony initiation

Cooperative colony foundation is not restricted taxonomically or ecologically. It has arisen a number of times in a variety of habitats and latitudes in many social insect taxa. In wasps (e.g. Fig. 1), group nest initiation occurs mainly in primitively eusocial taxa where workers and queens are not morphologically distinct (C.R. Hughes, PhD thesis, Rice University, 1987). Cooperative colony initiation occurs in a number of ant species[10] (e.g. Fig. 2); ants with group nest initiation are not consistently among the most advanced or the most primitive taxa, and they also occur in a variety of habitats[2,10]. In bees, cooperative colony initiation occurs most frequently where the natal nest is re-used, and is largely restricted to halictid and allodapine species that lack morphological castes[11-13]. Cooperative colony foundation has also been reported in termites[14]. This review focuses on the differences in cooperative colony initiation between wasps and ants, and is restricted to those taxa in which queens are not accompanied by workers at colony initiation since the efforts of the accompanying workers are likely to obscure cooperative efforts of multiple queens.

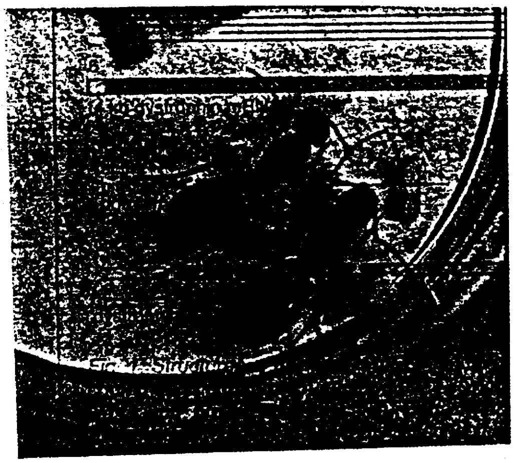

Fig. 2. Cooperating foundresses of *Camponotus vicinus*. Photo: Alex Mintzer.

Relatedness among foundresses

If individuals in the group are related, they may increase their inclusive fitness by helping each other. The importance of this factor can be seen in the large numbers of groups that are composed of relatives. The importance of relatedness has been indicated further by the sophisticated abilities of a number of social taxa at recognizing relatives[15,16].

If relatedness among co-foundresses is high, cooperation will be favored even if cooperating leads to only a few more young being raised. However, the difficulties in measuring relatedness[17,18] have resulted in a dearth of precise measurements of relatedness among foundresses. One of the best ways to measure relatedness is to use genetic markers[17]. This method requires genetic variation, and the implementation of laboratory techniques to identify that variation, and is therefore not always a practical accompaniment to a field study. Observations of the behavior of marked individuals can also give an indication of relatedness among nestmates. If females that emerged from the same natal nest begin a new nest together, they are very likely to be related, often as sisters (daughters of the same queen), half-sisters (daughters of the same multiply-mated queen) or cousins (daughters of sisters that began the nest together). Observation of reproductive behavior of females on nests can give estimates of the average relatedness among females in spring if the females begin nests only with nestmates[19]. Additional techniques can be used to infer absence of relatedness. For example, if females naturally begin nests with whatever other individuals settle close to them out of a mating swarm, it is unlikely that they are related.

Relatedness has been measured recently for a number of social insect taxa. Relatedness is high among most wasps beginning nests together in genera including *Polistes* and *Mischocyttarus*[19,20]. Relatedness values of 0.31–0.80 in these two genera indicate that females frequently join full sisters (Strassmann *et al.*, Ref. 36).

Ant co-foundresses are unlikely to be related because they begin nests together with females that leave the mating swarms in the same area, rather than returning to natal nests or other locations where they would be likely to meet relatives[10]. When queens from different locations are put together, they nest cooperatively – a further indication that relatedness is not necessary for co-founding[6,10,21]. Allozyme studies indicate that foundresses are unrelated in *Veromessor pergandei*, *Acromyrmex versicolor*[22] and *Solenopsis invicta*[7]. Thus, it is unlikely that co-founding queens are related in those ant taxa so far studied.

Behavior of foundresses before worker emergence

Foundress behavior before worker emergence is expected to reveal much about why foundresses begin nests in groups, since this is the time when additional females can have the greatest impact on the nascent colony. Later on, their importance for many tasks will be diluted by the presence of workers.

In *Polistes* and *Mischocyttarus* wasps, females begin new nests with natal nestmates in close proximity to their natal nest. The females are all mated, and begin the season with developed ovaries. On the new nest they fight with each other, chewing on each other's cuticle and sometimes attempting to sting each other. A linear dominance hierarchy is established soon after or along with colony initiation, and the dominant female lays most of the eggs. Since size and order of arrival at the nest are the two most critical factors in determining female rank[23,24], it is likely that a given female has a good idea of her rank very soon after joining a nest.

Behavior in a newly founded ant colony is very different from that in a wasp colony[6,8,21,25]. A multiple-female ant colony is typically begun by two or more mated females that have detached their wings and are about to begin a nest in a chamber underground or in a hollow twig, acorn or gall. This chamber is closed in most ants, and larvae are fed exclusively from the metabolites of the flight muscles, which are made available to the larvae when the queen feeds them eggs. Typically, all founding queens lay eggs and they do not fight[6,8,25]; and although in *Myrmecocystus mimicus* the queens have been observed to arrange themselves along the tubular chamber in an order, with one female consistently closest to the brood[6], this behavior is very different from the dominance hierarchy and differential reproduction found in polistine wasps. Some ants may still forage during this stage, as in *Acromyrmex versicolor*, a desert ant with fungus gardens[26]. Foragers in pre-emergence colonies of *A. versicolor* do not differ in size or ovarian development from non-foragers[26] and, like the ants that begin colonies in closed chambers, no aggression occurs in multiple-foundress colonies of this species[26].

Fate of foundresses after worker emergence

Worker emergence is a critical time for foundresses; after workers emerge, extra foundresses are no longer so essential to the colony. At this time the fate of co-foundresses varies even among wasp taxa[3,27,28]. In *Polistes*, the subordinate foundresses of five out of seven species disappear within a couple of weeks after worker emergence, either because they are expelled from the colony, or because they increase working efforts[3]. The other two species have very high colony failure rates due to adult mortality, so subordinates continue to be critical to the colony[3]. Because subordinates usually disappear shortly after worker emergence, the main reproductive efforts of these females are expressed early in the colony cycle when they are helpers.

Until recently, all reports on ants indicated that all but one queen was killed at worker emergence, either by the victorious queen or possibly by the workers[2,6,9]. In *Veromessor pergandei*, for example, one queen kills the other queens; in other taxa, including *Solenopsis invicta* (monogyne form) and *Myrmecocystus mimicus*, the workers appear to kill one of the queens[6,29]. There is controversy over whether workers execute queens that are wounded or take the initiative and kill otherwise healthy queens[10]. Recent reports on *Atta texana*[8] and *Acromyrmex versicolor*[26] indicate that foundresses are not eliminated upon worker emergence. In these species, both queens continue to contribute eggs to a common brood pile and aggression does not increase among queens after worker emergence.

Advantages to cooperative nest initiation

The nature of the advantage that cooperative colony foundation confers varies among taxa. The advantages include earlier production of brood[9,30], increased defense against predators, parasites[11] and usurping conspecifics[31], better recovery from predation[32], lower adult mortality[20] and the assurance that brood will be reared by another if one female dies[5]. In some ants, foundress groups rapidly exaggerate their numeric advantages over solitary foundresses by stealing pupae from less advanced colonies[6,9]. The workers that arise from the stolen pupae work for their host colony. Since ants often begin nests in an environment restricted by the presence of mature, perennial, territorial colonies that would quickly eliminate a new colony, the openings for new colonies are often restricted[33]. Competition for nesting in such locations is intense among new queens. *Veromessor pergandei* is further restricted to nesting in sandy desert ravines[34], and *Acromyrmex versicolor* nests only in areas where there is sufficient shade to protect the brood from excessive temperatures[35].

Relatedness and foundress behavior

Several ant taxa appear to meet the conditions necessary for foundress groups to be selected in the absence of relatedness. The first condition is that it should be hard to predict the eventual queen in ants, especially as compared to wasps. This is consistent with the lack of a dominance hierarchy, and cooperation in egg laying in ants.

The second condition is that these groups produce many more brood than solitary queens. A multiple-foundress colony may be the only one to survive in a patch appropriate for nesting[6,9]. However, this advantage applies mainly to territorial ants that nest in dense patches, and there are foundress associations in ants that nest under other circumstances, where the advantages of the types discussed above are not exaggerated by brood raiding[10].

The third condition is that relatives are not readily available. Recent studies support this claim too. Ant foundresses are highly vulnerable to predation, and must dig a nest chamber very quickly after mating. They are usually found away from their natal colony since a new colony could not compete with an extant colony. Thus, relatives will be difficult to find.

The absence of relatedness among foundresses apparently causes major behavioral differences between wasps and ants. However, there are also other possible causes of these differences. Wasp queens that form cooperative foundress associations are able to forage for the nascent colony while most ant queens are not. Perhaps the inability of ant queens to help the colony by foraging means that they will continue to lay eggs long past the point when some wasp foundresses would have begun foraging and their ovaries would have atrophied; even so, queens of *Acromyrmex versicolor* forage and yet they do not give up egg-laying rights[26]. Another difference is that ants walk to a new colony site after nest destruction, while wasps fly there[2]. This means that wasps cannot metabolize their flight muscles to feed the first brood of workers in the safety of a closed burrow and therefore may have a greater need for auxiliary foundresses that will forage. This argument may predict a greater frequency of multiple-foundress associations in wasps if mortality while foraging is great, but it is not clear that it should also predict dominance hierarchies in wasps and not in ants.

Ants also differ from wasps in their perennial colonies and their territoriality. Therefore, new ant colonies may endure greater competition for nest sites, which can favor group nesting. In fact, in a vacant area where new nests are clumped, brood raiding results in only one colony per clump surviving[9]. Wasp colonies are not territorial and are strictly annual in temperate regions. However, it is not apparent that this difference would result in equal egg laying by queens followed by fights to the death. Colonies with a division of labor are likely to be better able to compete for nest sites than are egalitarian colonies.

It has been suggested that dominance is unlikely to evolve in a closed system because such competition would diminish the fitness of groups with fighting members as compared to groups with cooperating members[25]. Furthermore, in a closed system the queens can monitor the numbers of eggs that each lays. However, *A. versicolor* colonies are not closed systems, and yet they have no dominance hierarchies or aggression among queens (who all lay eggs)[26]; thus it is more likely that relatedness is the variable of importance, rather than whether the system is open or closed.

Cooperative colony initiation occurs in many social insects. Where foundresses are related, as in wasps, a reproductive division of labor arises, perhaps because relatives are more exploitable than non-relatives due to the indirect pay-offs that relatives receive when they rear related young. Where foundresses are not related, as is the case in ants, all foundresses reproduce initially. After workers emerge, all but one foundress is eliminated (either by the queen or by workers) in most ant taxa; in other taxa all continue to lay eggs. Evidence to date favors the view that the differences in behavior of foundresses are predicted by the differences in relatedness.

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