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The economics of brood raiding and nest consolidation during ant colony founding

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Summary

The most dangerous time for an ant colony is during the founding stage when the small colony is vulnerable to predation and competition. Colonies can grow more rapidly when multiple queens cooperate in raising the first worker brood (pleometrosis) or by raiding other incipient colonies for their brood. This brood raiding has been proposed to be the primary force selecting for pleometrosis, i.e. multiple-queen colonies may have a considerable advantage in destroying neighbours by aggressively stealing their brood. An alternative hypothesis is that incipient nests are part of a larger, interconnected population structure and that brood raiding reflects cooperative pleometrosis with subdivided colonies. A simple mathematical model supports the second hypothesis: workers of incipient colonies are especially favoured to peaceably abandon their nest and join with other colonies if the queens are related or queens from raided colonies can infiltrate the raiding colony. The latter condition is often met in ant species that brood raid and particularly exemplified in fire ants (*Solenopsis invicta*), where brood raiding involves little mortal combat and combines with pleometrosis to rapidly increase colony size. It is proposed that the term nest consolidation should replace brood raiding to more accurately reflect the relatively non-aggressive and potentially apparently cooperative nature of interactions between incipient ant colonies.

Keywords: ants; brood raiding; colony founding; competition; cooperation; nest consolidation

Introduction

The most common way ant colonies are initiated is by females (queens) flying from their natal colony, mating, finding a suitable nest site and then raising their first brood of workers by metabolizing their own tissues as food for the larvae (Hölldobler and Wilson, 1990). Ant queens can perform this process entirely alone (haplometrosis) or two or more queens can cooperate in nesting and raising the first brood (pleometrosis). The prevalence of pleometrotic behaviour varies across species and explaining why this variance exists has attracted a fair measure of attention (see Rissing and Pollock, 1988; Hölldobler and Wilson, 1990). This interest in pleometrosis arises because it showcases a dynamic interaction of forces favouring competition and cooperation between individuals that are probably not kin.

The advantages of cooperative colony founding for queens can include more offspring in the initial broods (Waloff, 1957; Mintzer, 1979, 1987; Bartz and Hölldobler, 1982; Tschinkel and Howard, 1983; Nonacs, 1990), more efficient nest construction (Peeters and Andersen, 1989), earlier maturation of workers (Waloff, 1957; Taki, 1976; Rissing and Pollock, 1987) and queens losing less weight during the provisioning of the first brood (Waloff, 1957). However, pleometrosis has one serious fitness consequence counterbalancing the listed benefits: generally only one queen survives within a nest (Rissing and Pollock, 1988). Such intracolony competition between queens for reproductive preeminence predicts that queens should prefer to join females that are likely to be eventually competitively dominated (Nonacs, 1989). Choice experiments

with *Lasius pallitarsis* support this prediction in that large queen size and good physical condition correlates significantly with joining (Nonacs, 1992).

Recently, however, Rissing and Pollock (1988, 1991) have de-emphasized the importance of within-colony factors in the evolution of pleometrosis in favour of between-colony interactions. They note that often many more incipient colonies are in close proximity than can survive to maturity. In such a situation, a colony may have to aggressively eliminate its neighbours to reach adult size. In several species this destruction appears to occur soon after the first workers mature by those same workers raiding or collecting brood from less well-developed neighbouring colonies (Bartz and Hölldobler, 1982; Tschinkel and Howard, 1983; Rissing and Pollock, 1988). It is proposed, therefore, that evolutionarily, brood raiding precedes and selects for pleometrosis. Colonies started by multiple queens will have more workers and, thus, be more successful at raiding their neighbours and preventing raids upon themselves. This hypothesis generates several behavioural predictions: (1) queens will join others and show few preferences in this joining behaviour because group size is much more important than group composition, (2) strong between-colony competition selects for little within-colony competition because of the need to maximize overall colony productivity and (3) multiple-queen incipient colonies will be differentially successful at destroying single-queen colonies.

The Rissing and Pollock hypothesis is supported by several studies. Preference for nesting with kin has not been found in any ant species that exhibits pleometrosis (Hagen *et al.*, 1988; Nonacs, 1989) although *L. pallitarsis* does exhibit size-based preferences in joining others (Nonacs, 1992). Support for (2) comes from observations that *Messor (Veromessor) pergandei* queens in pleometrotic associations are non-aggressive towards each other until worker emergence (Rissing and Pollock, 1987) and that in *Acromyrmex versicolor* pleometrotic associations, one queen 'voluntarily' assumes the dangerous role of foraging (queens in this species need to collect vegetable matter for their fungus gardens during colony founding) without any apparent aggression or size-based dominance hierarchy forming (Rissing *et al.*, 1989). Finally as predicted in (3), multiple-foundress colonies in *M. pergandei* are more successful at brood-raiding than are single-foundress colonies in laboratory situations (Rissing and Pollock, 1987).

However, recent field work by Tschinkel (1992a,b) and Pfennig (submitted), suggests a different relationship between pleometrosis and brood raiding. Instead of being aggressive competition, brood raiding may be a much more peaceable phenomenon where 'losing' colonies quite often incorporate en masse (workers and queens included) into the 'winning' colonies. As such, brood raiding is an extension of cooperative pleometrosis. In this paper, I will show under which conditions brood raiding is advantageous for both the raiding and the raided colony. I will also discuss details of the new data on *Solenopsis invicta* to illustrate how pleometrosis and between-colony brood consolidation are synergistic processes that rapidly move incipient colonies through their most vulnerable life stage.

The model

I start with the assumption that several colonies are being initiated in close proximity to each other. For simplicity, I assume that all founding colonies prior to any joining have only one queen (for the evolution of pleometrosis itself, see Nonacs, 1989). Therefore, the initial case models the conditions under which two colonies, symmetrical in size, should join, i.e. should one colony allow itself to be brood-raided? If the answer to this question is yes, then eventually an asymmetrical population develops, with larger and smaller colonies. The question then becomes under what conditions does a smaller colony join a larger one.

Symmetrical colony size

Workers can show allegiance to their nest site and never join another colony or allow themselves to be brood-raided. The expected fitness for workers in such a colony would therefore be:

$$S_a r_a \quad (1)$$

where S_a is the expected survivorship of colony A given its worker number. The survivorship per colony is small and no more than one colony can survive to maturity. The variable r_a is the mean relatedness of the queen's eventual sexual brood to the workers ($= 0.5$, assuming single-mating by the queen and a 1 : 1 sex ratio). The expected fitness for colony A's workers abandoning their colony and joining colony B is

$$(S_{ab} \alpha r_a + [(S_{ab} - S_b (1 - \alpha) r_b)]) \quad (2)$$

where S_{ab} is the survivorship of a colony with a combined workforce, α is the probability that the raided colony's queen will successfully relocate to colony B and become the surviving queen ($0 =$ never, $0.5 =$ survivorship equal to that of colony B's queen) and r_b is the mean relatedness of the offspring of the colony B queen to colony A's workers. Thus, given that $S_b = S_a$, joining is favoured when

$$S > [0.5 + r_b (1 - \alpha)] / [0.5\alpha + r_b (1 - \alpha)] \quad (3)$$

where $S = S_{ab} / S_a$. Figure 1 evaluates this relationship for $r_b = 0.19$ (queen B is a full sister of queen A), 0.10 (the queens are half sisters) and 0 (the queens are unrelated). Three interesting points emerge. First, when queens are unrelated, α must be positive (i.e. $S > 1/\alpha$) and workers are never favoured to abandon their queen if she has no chance of entering the raiding colony, irrespective of how much a combined workforce may increase survivorship. Second, when queens are related, workers can be selected to join another nest even when $\alpha = 0$, if they sufficiently increase survivorship of the joined nest (i.e. $S > (r_b + 0.5)/r_b$). Finally, if $\alpha = 0.5$ (both queens have equal survivorship), the combined nest survivorship has to be merely doubled for joining to be equally favoured under the most extreme circumstance of unrelated queens (and substantially less for related queens).

A more than two-fold doubling in colony survivorship with a doubling in worker number is likely for small ant colonies which tend to show a non-linear type IV survivorship curve (most mortality occurs on young, small colonies, Wilson (1971)). When nest joining increases colony survivorship with a slope greater than one and queens can either successfully enter the raiding colony or the colony-founding queens are related, then joining between colonies is likely to be favoured (Fig. 2).

As a final consideration, if for some reason S_a should go to zero (i.e. the incipient colony is located in a nest site that will never allow it to survive to maturity), then any non-zero S_{ab} value may favour joining. In this case, joining will be favoured as the best of a bad situation whenever $r_b > 0$ or $\alpha > 0$, regardless of how marginal the increase in survivorship might be.

Asymmetrical colony size

Once several colonies have joined, however, colony expected survivorship will become reasonably high ($S_b \approx 1$) and the addition of more workers will have rapidly diminishing returns ($S_{ab} - S_b \approx 0$) (see Fig. 2). Therefore, the second term in Equation 2 goes to zero and Inequality 3 simplifies to:

$$\alpha > S_a \quad (4)$$

for joining to be favoured. The simplicity of Inequality 4 is that relatedness of queens no longer

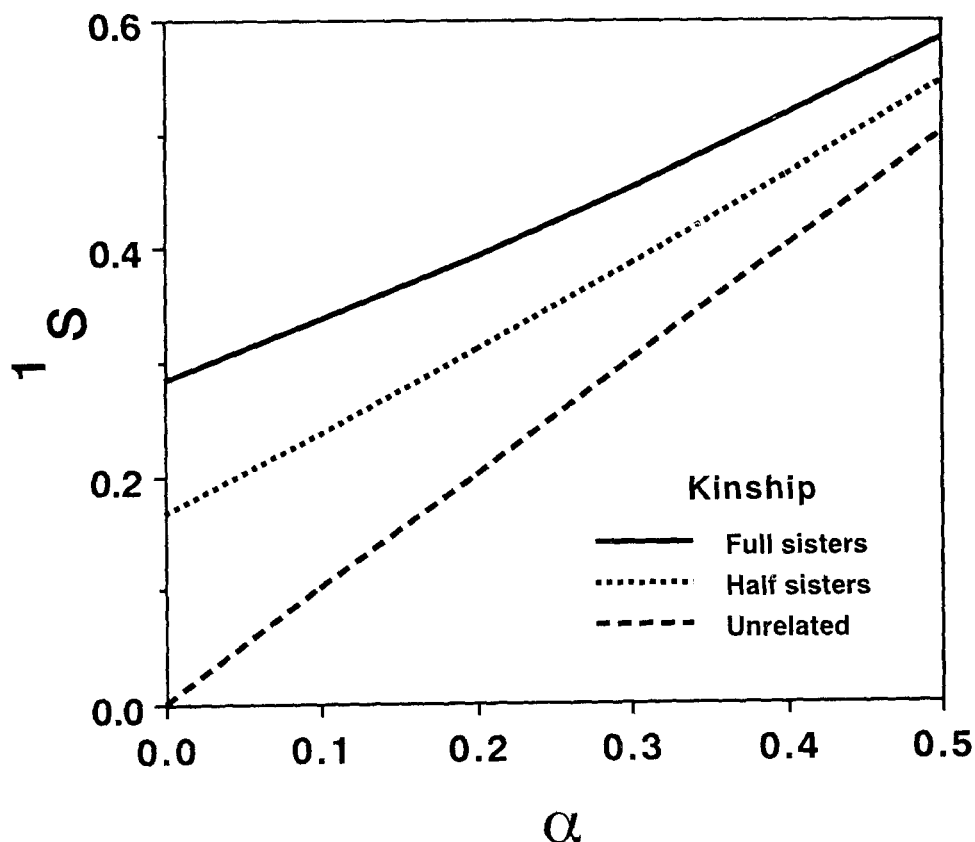


Figure 1. Joining behaviour as a function of colony survivorship, ability of queens to infiltrate other colonies and kinship of colony queens. Joining (or allowing one's colony to be brood raided) is favoured in the regions below the lines (given by inequality 3), which are calculated assuming that queens in the different nests are either full sisters, half sisters or unrelated. $1/S$ equals the ratio of the survivorship of a colony that is not joined (S_a) divided by the survivorship of a colony with a combined workforce (S_{ab}) and α is the likelihood that a queen, whose colony is raided successfully, moves into the raiding colony.

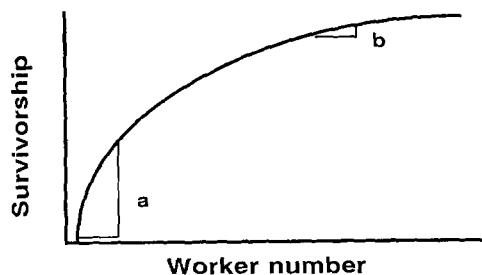


Figure 2. The colony survivorship benefits for adding workers. (a) When worker number is low (the symmetrical colony stage), a doubling in worker number more than doubles colony survival. (b) When worker number is large (the asymmetrical colony stage), a few additional workers only marginally increases colony survivorship.

affects whether or not colonies should coalesce: as long as the probability that their mother can infiltrate the larger colony exceeds the expected survival rate of the smaller colony, workers should switch allegiance.

Given that small colonies may be selected to join larger colonies, why should larger colonies accept them when the benefits are small (colony survivorship is minimally increased) and the potential costs are high (a foreign queen may invade with the added workers)? The answer is two-fold: most workers would gain little or nothing by preventing further joinings and even those workers that would gain, may not be able to recognize that they are being joined. Both points are based on the realization that the large colony will have become large by the joining of many smaller entities. Therefore, the colony is a genetic polyglot and most of the workers may not be more related to the resident queen than to any given invading queen. Expelling an invading queen that does not want to be expelled can be a dangerous activity for a worker (see Bartz and Hölldobler, 1982) that holds no inclusive fitness benefit if the resident queen is unrelated. Obviously, some of the workers are likely to be the offspring of the resident queen and would gain by exclusion of other queens. However, in a highly genetically-diverse colony, it may be impossible to form a template that can discriminate between kin and non-kin invaders, so that all workers and all queens are acceptable (see reviews of nestmate recognition in Hölldobler and Carlin (1987) and Hölldobler and Wilson (1990)). It may not be until well after the colony-founding time period when one or more queens have established reproductive dominance that a colony 'identity' can appear.

The model as derived here, predicts that small colonies should exhibit a high proclivity to join each other. If this true, it might be argued that rather than coalescing through brood raiding, time and effort would be saved if all the queens initially aggregated into one, large pleometrotic group at the very beginning. There are several reasons, however, why scattering queens across many sites may be adaptive. The first is that searching for colony sites is rather dangerous for ant queens (Nonacs, 1989). If all queens kept searching for the common site while avoiding suitable empty sites, mortality rates would greatly increase. Furthermore, the use of many sites allows a process of site selection to operate during the brood-raiding phase. Workers can evaluate the best site (i.e. the site with the best microclimate, food availability, protection from predators, etc.) and defect with their queen to that site. Second, there is evidence that colony productivity actually decreases with too many queens in one nest at the same time, possibly due to disease or inefficiency in brood tending (Wilson, 1966; Bartz and Hölldobler, 1982; Tschinkel and Howard, 1983). Finally, a large aggregation of queens in one place might be highly apparent and attractive to predators. Starting colonies in multiple sites is a form of bet hedging in that the likelihood of all the nests being found by predators is minimized.

The above models begin with the assumption that all colonies initially contain one queen (no pleometrosis). The effect of pleometrosis would be to reduce r_a by some amount depending on the number of queens and their variance in reproductive output. As far as the model's predictions are concerned, pleometrosis makes no difference in the asymmetrical colony size stage because all relatedness values cancel out. In the symmetrical colony size stage, pleometrosis would increase brood raiding and the abandonment of natal colonies by workers because it reduces the genetic relatedness of brood in their natal colony without much affecting the relatedness to other colonies (which is probably already low).

Characteristics of colony founding and brood raiding in ants

The model developed above predicts that workers will abandon their natal nest if they can substantially increase the survivorship of a related queen's colony. However, queens in several

species show no discrimination in joining kin rather than non-kin (review in Nonacs, 1989) and natural associations of queens are random with respect to kinship (Hagen *et al.*, 1988; Rissing *et al.*, 1989). Therefore, the above models seem to be most realistically examined using values of r_b close to zero and their validity would then seem to rely on whether α , the probability of queens successfully moving between colonies, is non-zero. In the best-studied brood-raiding species, *Solenopsis invicta*, field data reveal that queens abandoning their nests can infiltrate other colonies and are as successful in becoming the dominant reproductive in a surviving colony as are queens that remain in their nests (Tschinkel, 1992a; see below).

The evidence is more mixed from other species. In *Myrmecocystus mimicus* colonies raid each other and workers from the losing colony amicably join the winning colony (Bartz and Hölldobler, 1982). Queens from the losing colony also attempt to enter the winner, but are repulsed by the workers. Founding *Messor pergandei* colonies readily raid each other with very little worker mortality and both workers and queens from the losing colonies will join with the winning colony (Rissing and Pollock, 1987: in four of 17 pairings of nests, the 'losing' nest's queens were found in the 'winning' nest with one instance of the 'losing' queen being the sole survivor). Interestingly, brood raiding between founding *M. pergandei* colonies appears to be rare or absent in the field and pleometrotic colonies have no survivorship advantage over haplometrotic colonies (Pfennig, submitted). Nest-founding females also tend to clump near established colonies, which seems paradoxical if brood raiding were a major mortality factor to be avoided (*sensu* Rissing and Pollock, 1991). Most young colonies were eventually raided by a nearby adult colony, which led Pfennig to propose that the young colonies might peaceably fuse with the mature colony. If the mature colony's queen has recently died or is senescent, the foundress queen may inherit a rather large workforce. A similar phenomenon may occur in *Iridomyrmex purpureus* where mature colonies tolerate and even protect queens initiating colonies near them (Hölldobler and Carlin, 1985). Finally, Rissing *et al.* (1989) observed that *Acromyrmex versicolor* colonies engage in aggressive brood and food raids and that workers retained nest fidelity during raids. However, they did not report the stage of colony development at which their observations were taken and the fate of the workers and queen(s) from the 'losing' colony. In *A. versicolor* one queen in a pleometrotic group becomes a foraging specialist prior to the emergence of the workers, which is assumed to put her at a fitness disadvantage (Rissing *et al.*, 1989). It would be interesting to test whether this disadvantage is moderated by an increased knowledge of the state of the surrounding colonies and therefore an increased probability of defection to a 'winning' site after brood raiding.

The fire ant, Solenopsis invicta

Solenopsis invicta is an introduced species to the southern United States that does extremely well in disturbed habitats and populations often reach quite high densities (Porter *et al.*, 1988). There are two social morphs: in the first, adult colonies are strictly monogynous (single-queened) and colonies are founded by one or several cooperative queens; in the second, adult colonies are polygynous and new colonies appear to be founded solely through colony fission (Vargo and Porter, 1989). In this paper, I will restrict the discussion to the colony initiation behaviour of the monogyne morph.

Multiple *S. invicta* queens are often found in the same incipient colony in the field and the percentage of pleometrotic nests correlates positively with local densities of queens (Tschinkel and Howard, 1983; Tschinkel, 1992a,b). Young nests are spatially clumped, but the densities of adult nests suggests that most die prior to maturity (Tschinkel and Howard, 1983). In an experimental study, an initial population of 80 founding nests at the beginning of the summer, left two survivors at the end of the summer (Tschinkel, 1992b). A major cause accounting for at least

60% of the nest failures was brood raiding which began with the first appearance of workers and continued over a period of several months (Tschinkel, 1992a,b).

However, although sites may survive the brood-raiding phase, it is not always the original queen that survives with the site. Tschinkel (1992a) isolated 960 queens in 200 incipient nests and followed the fate of queens and their nest sites. Censuses after 29–39 days revealed that of the 30 surviving nests, 23 had or were likely to have a surviving queen that was initially in the nest, with the remaining seven probable survivors being queens that had emigrated from another (now dead) nest. As Tschinkel's experimental design bounded the founding nests with a moat, a large number of queens (89% of those that left their nest) died in the moat. Therefore, the experiment likely underestimated the success rate of emigrating queens from losing colonies.

In sum, when many young *S. invicta* colonies coalesce through brood raiding, colony growth rate can be greatly accelerated beyond the brood-rearing capacity of a single queen and her first worker brood. By the end of a colony's first summer it can reach the size of a mature colony, a size that without brood-raiding might not be otherwise achieved for more than a year (Tschinkel, 1992b). Nest-consolidation in *S. invicta* seems very effective in increasing colony survivorship by rapidly 'growing' the colony through its most vulnerable life stage. Thus, Tschinkel (1992a) suggests that queens and their workers are not acting like competing colonies but, instead, like members of a single colony sharing multiple nest sites (a phenomenon known as polydomy for adult colonies).

Conclusions

Pleometrosis and brood raiding both appear to increase the survivorship of young colonies by rapidly increasing worker numbers. The hypothesis (Rissing and Pollock, 1991) that destructive brood raiding is the prime factor favouring the evolution of the pleometrosis is not well-supported. Rather Tschinkel's (1992a) proposal that young colonies can be considered a polydomous population appears more accurate: queens initially cooperate in pleometrotic groups, followed by workers cooperatively coalescing the many small colonies into larger, more survivable units. The simple models developed in this paper show that this behaviour can be evolutionarily favourable for all parties involved if the initial local grouping of queens is related or, more importantly, if queens are able to move from nests that lose brood to nests that gain brood. The majority of studies on brood raiding species show that such movement by queens is possible and quite often successful. Conversely, if pleometrosis has evolved because of intercolony competition (Rissing *et al.*, 1989; Rissing and Pollock, 1991), 'defeated' queens should have been excluded from 'victorious' colonies at all cost. In sum, the data suggest dropping the rather bellicose and quite probably misleading term of 'brood raiding' for the colony-founding process. Also brood raiding has been used in the social insect literature to describe interspecific interactions where brood are actually taken as food or as future slaves (Hölldobler and Wilson, 1990). Obviously, these relationships are not mutualistic, but are entirely exploitative. As an alternative, nest consolidation may more aptly encompass both the possible mutualism and the competition involved in colony founding.

The proposed synergistic relationship between pleometrosis and nest consolidation in increasing colony size makes several interesting predictions.

(1) Species that found colonies pleometrotically need not always also exhibit nest consolidation. In many species low population densities or high predation risks may make nest consolidation prohibitively costly.

(2) However, nest consolidation will not occur in the absence of pleometrosis. Any selective

advantage that favours between-colony cooperation should favour within-colony cooperation even more strongly. This predicts that evolutionarily, pleometrosis precedes nest consolidation and, thus, is exactly in reverse order of the Rissing–Pollock hypothesis.

(3) In species that nest consolidate, a high level of mortal aggression between incipient colonies should not occur. Certainly, larger colonies could kill smaller colonies and take their brood. However, if workers of the smaller colony fight to the death, the gains from consolidation (some more brood) may be outweighed by the costs (loss of a significant number of adult, foraging workers).

The mild resistance by defending workers in all species of ants where nest consolidation has been reported supports the third prediction. Testing the first two predictions, however, will require a larger data set than currently available. It is hoped that the ongoing interest in the evolution of cooperation and competition will continue to find fertile ground in studies of ant colony initiation and will soon provide more examples.

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