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Minireview

Do unicolonial wood ants favor kin?

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Abstract

Vast supercolonies of interconnected nests formed by unicolonial ant species are the largest cooperative groups of animals known. Research published recently in *BMC Evolutionary Biology* reveals that a supercolony can be more genetically structured than previously thought, comprising several extended families. Surprisingly, the families coexist peacefully, even though they seem to recognize each other as non-kin.

The supercolonies formed by so-called 'unicolonial' ant species are huge cooperative groups - networks of interconnected nests that exchange individuals and share territory peacefully over extensive areas [1]. In extreme cases, a whole population can comprise a single supercolony; for example, the largest supercolony discovered, the Mediterranean Argentine ant supercolony, covers 6,000 kilometers of Southern European coastline, and individuals accept each other as colony-mates all the way from Italy to the Spanish Atlantic coast [2]. A feature of supercolonies compared with the more usual family-based colonies of social insects is the free movement of individuals between nests, and the fact that each nest contains several queens. Consequently, the relatedness between nestmates approaches zero in the Argentine ant and many other species, both invasive and non-invasive [1]. In other words, individuals that share a nest are no more similar genetically than would be individuals chosen at random from the whole population.

Ant supercolonies, a dilemma for social evolutionary theory

The evolution and persistence of unicoloniality poses a dilemma for the widely accepted theory of kin selection as an explanation for social evolution [1]. In all colonial insects, including the unicolonial ants, the success of the colony depends on so-called 'altruistic' behavior of non-reproductive individuals - the workers - who build the nest, collect food for the sexually reproducing queen and care for the larvae (brood rearing) without any apparent benefit to themselves in terms of maximizing their own reproduction, their 'fitness'. Kin selection theory proposes that such altruism can evolve and persist if the altruists, such as the ant workers, direct help only to individuals that are genetically related to them. In family-based social insect colonies, which usually have a single queen per colony, this will be their mother queen and her brood. So, even though the workers do not reproduce, their cooperative altruistic behavior increases the chance that genes identical to their own will be transmitted to the next generation; in other words, altruism increases the 'inclusive fitness' of the individual worker - the overall reproductive fitness of itself and its close relatives. In such situations, production of both queens and workers, in addition to males, is in the interest of the workers, queens, and the developing larvae.

By this logic, altruism should not persist in a supercolony, where the receivers of help - the nestmate queens - may be

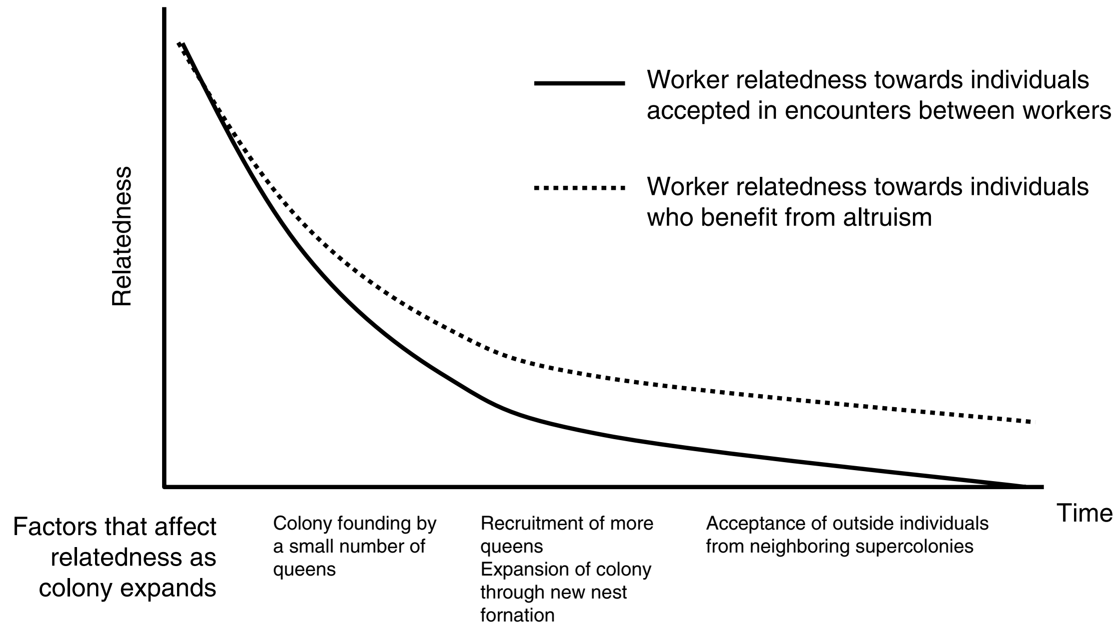

Figure 1
A hypothetical scheme of the life of a supercolony. In a young colony, relatedness between individuals is high as a result of the small number of founder queens. Relatedness decreases as the colony grows and expands. But even if relatedness between individuals who do not behave aggressively to each other drops to zero, relatedness to individuals who benefit from worker altruism remains above zero. Factors that increase relatedness between individuals in altruistic interactions include: limited dispersal of sexuals, context-specific discrimination and variation in kin structures over worker life-time.

no more closely related to the workers in that nest than they are to the rest of the supercolony. One might expect a complete breakdown of co-operation in such circumstances, with individuals behaving antagonistically towards non-relatives, and natural selection no longer favoring worker traits. Furthermore, in the absence of genetic relatedness, 'selfish' queens could maximize their fitness by producing larvae that develop into females and males rather than workers - in which case the supercolony, and the trait of unicoloniality, would eventually die out [1].

But unicoloniality seems to be going strong, and not only in invasive species. The paradox has been investigated by Laurent Keller and colleagues in a series of papers on native European wood ants of the genus *Formica* [3-6]. In their most recent paper, published in *BMC Evolutionary Biology* (Holzer *et al.* [3]), Keller and colleagues have looked more closely at the genetic structure of supercolonies of the wood ant *Formica paralugubris*. They find that supercolonies that appear to behave as single units in fact harbor genetic substructure and consist of several extended families living side by side. Such structuring may help to explain the evolutionary maintenance of unicoloniality [1,3], while the peaceful coexistence of potentially competing families can also teach us lessons about behavioral adaptations.

Even if supercolonies are problematic for kin selection theory when they have grown to cover whole populations, the behavioral rules that underlie their development can be understood through inclusive fitness principles [1]. A supercolony starts from a family group that extends its network of nests and retains more and more queens (Figure 1), competing against other such colonies. This is often a successful strategy for monopolizing resources over a large area, and can be favored by kin selection. But when this successful family-based strategy continues for a long time and the colony grows larger and larger, it paradoxically dilutes the relatedness between individuals and eventually leads to a situation where individual workers may no longer be helping kin. Worker behavior is no longer favored by selection, but because workers lack the means to assess the decline in relatedness they continue to behave according to the previously successful rules. Formation of supercolonies with extremely low relatedness is especially easy for foreign invasive species, whose colonies grow unhindered by conspecific competitors and native parasites, and can extend over hundreds of square kilometers. But in evolutionary terms, supercolonies are thought to be evolutionary dead-ends as the link between genetic relatedness and behavior has been lost [1].

Are supercolonial wood ants indiscriminate cooperators?

In contrast to the Argentine ant, supercolonies of indigenous European ants, such as certain species of *Formica* wood ants, are found in stable habitats such as boreal or alpine forests and are non-invasive. But like their invasive counterparts, these supercolonies cover large areas, and workers from distant parts of the supercolony behave unaggressively, like nestmates, towards each other [4]. Holzer *et al.* [3] made a detailed genetic and behavioral study of three *F. paralugubris* supercolonies in the Swiss Jura mountains, which revealed that the supercolonies are not as genetically heterogeneous as expected, but consist of cryptic genetically related clusters of nests [3]. These clusters define groups of individuals that are genetically similar at a level comparable to cousins, with the proportion of genes shared approximating to 0.125. These extended families are not sharply delineated, but can exchange individuals and genes.

Holzer *et al.* [3] suggest that such family substructures might enable workers to direct help to their relatives, and that this might help to maintain the trait of unicoloniality, in line with kin selection theory. However, the presence of genetically differentiated subunits raises the question of why there is no aggression within the supercolony, and why the clusters keep exchanging individuals. In theory, workers should exclude non-kin from sharing resources and receiving altruistic help. In other supercolony-forming species studied, within the supercolony aggression seems to be minimized by workers being unable to recognize whether an ant is close kin or not, but *F. paralugubris* workers behave unaggressively in artificial bioassay encounters even though they do seem able to recognize non-nestmates [4]. In contrast to most supercolonial ants, aggression is rare in *F. paralugubris*, even towards individuals from other supercolonies. The workers seem to treat most conspecifics amicably, even if recognized as 'outsiders'. Does this mean that the potential inclusive fitness payoffs from the family structuring are not in fact realized? Is it possible that the peaceful strategy is itself favored by selection?

Does lack of discrimination pay off?

Whether lack of discrimination is adaptive depends on the inclusive fitness costs of accepting strangers, compared with the costs of aggression and of erroneously behaving aggressively to group members (Figure 2). In *F. paralugubris*, it seems that workers are prone to making mistakes in recognition, probably because the large number of queens in each family cluster increases genetic diversity within, and decreases differentiation between, the clusters [3]. Thus, aggression would sometimes mistakenly be directed against relatives. This is the risk against which the benefits of discrimination need to be weighed.

Indiscriminate acceptance is beneficial if the probability of encountering unrelated individuals is low. This is likely in *F. paralugubris*, because the population structure found by Holzer *et al.* [3] suggests that movement between the extended family clusters is limited. Of particular importance in this regard, Keller and colleagues previously found that the dispersal of queens in *F. paralugubris* is limited. This would help to guarantee that brood care by the young workers is directed towards relatives, even if the workers later disperse. Workers in *F. paralugubris* increase their inclusive fitness not by territorial aggression, but by rearing related queens and males that disperse and compete with queens and males from less related nests in other clusters over recruitment as a breeder [5]. Holzer *et al.* [3] found that especially males are prone to disperse and spread genes across the clusters. In other words, relatedness will be above zero in the brood-rearing context, which is most important for inclusive fitness, even where territorial aggression is lacking (Figure 1). The current study by Holzer *et al.* [3] confirms previous findings by Keller and colleagues that family structures are more obvious in queens and the brood than in old workers in another supercolonial *Formica* ant [6]. This suggests that young workers take care of related broods, even if they drift away from their relatives later in their lives. Whether similar patterns of genetic structure and behavior also occur in invasive supercolonies remains to be seen.

Is lack of discrimination more apparent than real?

It is also worth noting that acceptance of non-kin in the context of artificial aggression bioassays does not necessarily mean that they are always accepted in natural contexts more directly connected to inclusive fitness. Favoring individuals that are likely to be relatives is adaptive only in contexts where the inclusive fitness benefits of discrimination are large. If competition for breeding places occurs mainly by the recruitment of sexuals into the breeding population, workers should be most prone to discriminate in contexts more directly linked to their inclusive fitness, such as behavior towards queens and males, and brood care [7,8].

Thus, worker ants in *Formica* supercolonies might be able to direct the benefits of brood care mainly to the 'right' individuals as dictated by kin selection theory. The other

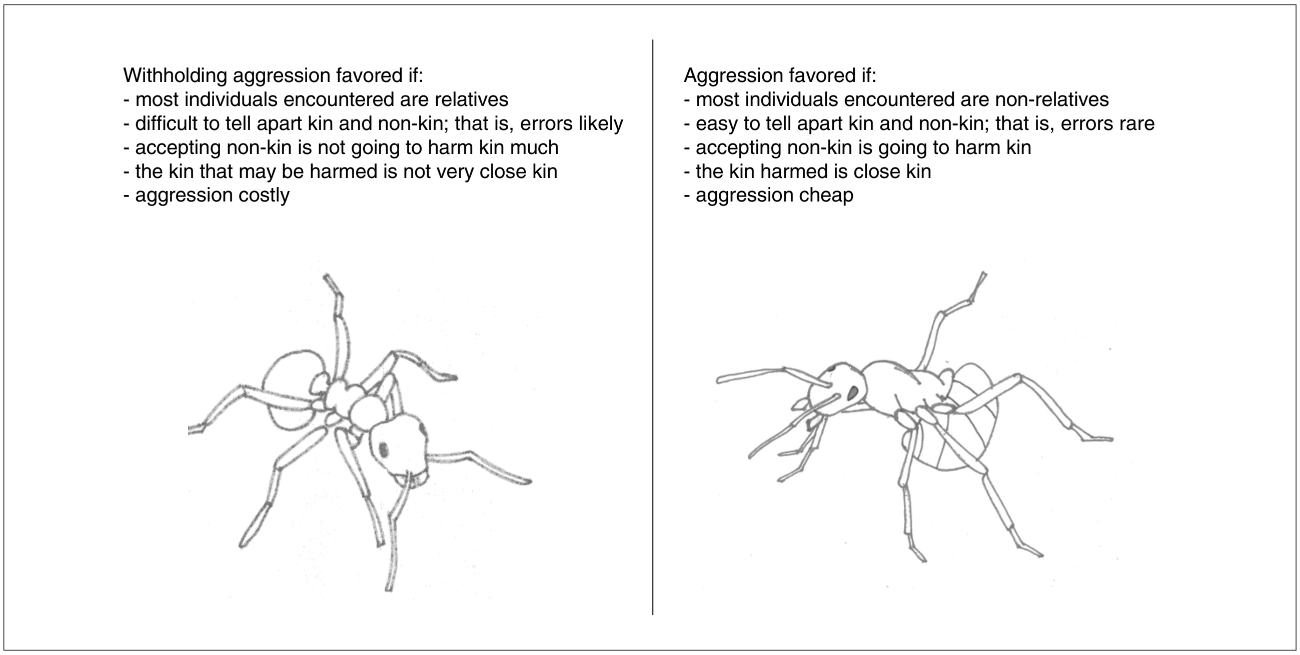

Figure 2
Factors that select for or against indiscriminate acceptance in social insects.

side of the non-aggression coin is whether it is harmful to the rearing of related reproductives to allow strangers into the territory. As long as this does not harm the production of reproductives in your own nest, the risk of aggression is perhaps not worth taking. This might be the case when resources are abundant and the benefits of territorial defense are subsequently small. Wood ants tend aphids, a resource that thrives when ants are abundant, so resource limitation may not be too severe in their case [3]. It will be very interesting to see whether the putative family clusters in wood ants also correspond to foraging areas and the flow of resources, and whether ants are more prone to discrimination at food sources, especially when resources are scarce. Study of nutrient flow within a supercolony of the Argentine ant has also shown that a seemingly uniform supercolony might actually consist of separate nest networks across which food resources are not shared [9]. Ideally, relatedness should be measured at the level of such functional units, in both native and invasive supercolonies.

Is there really a dilemma?

The problem of indiscriminate altruism demonstrates how complicated assessing the adaptive benefits of a behavioral strategy can be. In particular, we need to consider all the contexts in which a behavioral rule is applied. The ability to readily recognize and respond to environmental information is an important constraint on adaptation [10], and organisms are not always able to adjust their behavior to make an optimal response to a given situation. Instead, they might need to rely on rules that work on average. In the case of ant workers in a supercolony, the payoffs of behavioral rules need to be assessed across all the contexts in which they are used, over seasons, over the lifetime of the workers, but also over the lifetime of the supercolony.

There may be cases where workers in a supercolony seem to be in a dilemma. They are obeying the behavioral rules that made their family big and strong, but this has brought them to a situation where the rules no longer pay off. But this is only a dilemma for evolutionary theory if we assume that adaptation must always be perfect. The dilemma disappears if we consider the rules underlying the behavior. Even if the rules seem maladaptive in some cases, the evolutionary benefits may have already been reaped in another.

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