

Myrmecological News	13	131-132	Vienna, April 2010
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Focus

What brings peace to the world of ants (Hymenoptera: Formicidae)?

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Myrmecol. News 13: 131-132 (online 22 March 2010)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)
Received 1 November 2009; revision received 12 January 2010; accepted 12 January 2010

Are all ants aggressive?

Ants are generally believed to be aggressive animals whose population is structured into many mutually hostile colonies by fierce aggression toward aliens (e.g., LEVINGS & TRANIELLO 1981). Therefore, unicoloniality – in which a population seemingly becomes a single, spatially large-scale, polydomous-polygynous colony in which intraspecific aggression is absent, as often seen in invasive species such as the Argentine ant and some indigenous species – had been regarded as an exceptional phenomenon. Some researchers even consider that unicoloniality of invasive ants is a maladaptive trait caused by anthropogenic events such as a genetic bottleneck upon introduction to a new geographic range (TSUTSUI & al. 2000). Recently, however, a growing body of evidence has suggested that the absence of intraspecific aggression may be more common than previously thought. Some studies have indicated that important preadaptations for ant unicoloniality, a paradox in kin selection theory, may be involved in these phenomena (STEINER & al. 2007, HELANTERÄ & al. 2009).

Aggression as a kin-selected behavior

What do ants protect by aggression? Hostility toward aliens must be a strategy against resource exploitation. In ants such exploitation can be divided into two categories: (1) ecological exploitation, such as predation and plundering food competitively by conspecific aliens; and (2) genetic exploitation, the consumption of colonial resources stored in the nest, such as the workforce, by reproduction of the intruder. (Intraspecific dulosis may be an intermediate case between the two.) Occupation by ants of an absolute territory – an area always occupied more or less exclusively by a colony by means of aggression – is rare. In many species aggression is spatio-temporally restricted, and possibly the most generally observable aggression occurs when a worker meets a conspecific alien near the nest entrance. There is no example of an ant that is nonaggressive toward a conspecific alien entering the nest yet aggressive toward an alien encountered far from the nest. This suggests that genetic exploitation is a more general threat to ant colonies than is ecological exploitation, and aggression could be a counterstrategy against such a threat. In other words, the primary adaptive significance of the repulsion between con-

specific ant colonies may be the maintenance of intracolony relatedness: Aggression is a kin-selected trait. Then why do some ants not show such aggression?

Nonaggression despite sensing the "difference"

The colony-discrimination mechanism is important in any consideration of the loss of aggression. Colony discrimination has three components: (1) intraspecific differences in labels; (2) sensory mechanisms that allow detection of the differences in labels; and (3) rules of behavioral response to the sensed information (REEVE 1989). The bottleneck and frequency-dependent selection hypotheses (GIRAUD & al. 2002) proposed for invasive ants assume that the proximate mechanism for nonaggression lies only in the loss of label variability. However, recent studies suggested that the rules of behavioral response can be another key factor in the nonaggression found in some ants, because some ants refrain from aggression even when they seem to detect a difference in labels (reviewed in the appendix of STEINER & al. 2007).

The following are three examples of indigenous ant species in which workers do not show aggression toward alien workers. In all three cases, workers are considered to "recognize" nestmates and non-nestmates, as indicated by their nonaggressive but differential responses. *Pachycondyla luteipes* is a polygynous and polydomous species in which workers are totally sterile. Workers are easily integrated into other nests when experimentally introduced, whereas the majority of introduced alien queens are killed by workers (KIKUCHI & al. 2007). *Formica paralugubris* also forms a polygynous and polydomous supercolony. Recent studies using molecular markers, however, revealed a significant population subdivision into moderately genetically related nest-groups within a large supercolony despite the absence of aggression in the local population. Limited migration of reproductive queens but more or less freely moving workers and males could account for this phenomenon (HOLZER & al. 2009). *Lasius austriacus* also lacks intraspecific aggression. Remarkably, this ant even has typical multicolonial societies composed of single-nest and single-queen colonies. A study using DNA markers suggested that despite the absence of aggression, high intracolony relatedness is maintained, but natural exchange of workers also occurs (on average ca. 10% workers are aliens; STEINER & al. 2007).

These examples suggest a pattern in which the sterile or reproductively less able worker caste is allowed to move more freely than the reproductive queen caste, which supports the hypothesis that ant hostility is a kin-selected trait. HOLZER & al. (2009) contend that ant unicoloniality may be a situation in which overt interference competition through mutual ecological exploitation has completely disappeared and cryptic genetic exploitation within a supercolony may prevail instead.

Conditions for the evolutionary loss of aggression

Many myrmecologists seem to consider that environmental saturation and the resultant increased intraspecific competition are the most likely factors causing loss of intraspecific aggression, because ants without intraspecific aggression usually reach a high density (for review, see HELANTERÄ & al. 2009). However, there are two problems with this idea. First, the causation might be the reverse. It is possible that the absence of intraspecific aggression has led to the high density, as shown experimentally in the Argentine ant (HOLWAY & al. 1998), rather than that intraspecific aggression is too costly when densities are high. I contend that disturbances, rather than competition, can give rise to preadaptations leading to unicoloniality (TSUJI & TSUJI 1996, NAKAMARU & al. 2007), as I discuss elsewhere (TSUJI in press). Second, the absence of aggression seems to challenge classical evolutionary game theory. The situation may fit the Hawk-Dove game. An aggressive colony can be regarded as a Hawk and a nonaggressive one as a Dove. The high cost of a Hawk-Hawk interaction in comparison with a Dove-Dove interaction was revealed by an elegant experiment by HOLWAY & al. (1998). Although payoffs of players in the asymmetrical Hawk-Dove interaction have rarely been estimated, one can easily infer that a Hawk should defeat a Dove. In this situation, classical game theory (MAYNARD SMITH 1982) predicts that even with the high cost of the Hawk-Hawk interaction, the evolutionarily stable strategy (ESS) is a mix of Hawk and Dove or pure Hawk depending on the payoff matrix. Being a non-aggressive Dove never becomes an ESS. However, the loss of intraspecific aggression in ants seems to be a case in which the Dove strategy has been fixed.

There are two possible situations that may explain this apparent paradox. First, it may not be a true Hawk-Dove game in terms of the payoff matrix. For example, a non-aggressive colony may immediately counter-attack when attacked by an aggressive colony, and consequently the payoff would not differ between the two players. Such a conditional nonaggressive strategy is called Retaliator (KILLINGBACK & DOEBELI 1996). Second, there might be a spatial structure that often dramatically changes the predictions from those of classical game theory (DOEBELI & HAUERT 2005). A spatially explicit model (lattice model) predicts that Dove or Retaliator can operationally be an ESS when interactions occur only locally (KILLINGBACK & DOEBELI 1996). This is because when dispersal is limited, Dove encounters Dove more frequently than expected in a well-mixed population with unlimited dispersal.

In conclusion, future empirical studies should focus on the dispersal distance to better understand the loss of aggression in some species of ants. Long-distance dispersal may be linked to strong intraspecific aggression, and limited dispersal with nonaggression. Reproduction of ant nests by budding (fission) and a locally restricted nuptial flight can lead to limited dispersal. Precise modeling with unambiguously defined strategies and empirical estimation of the payoff matrix are also needed. Payoffs should be

quantified in terms of inclusive fitness of individuals that determine the colony's behavior and as a function of both the genetic architecture and the ecological framework.

Acknowledgements

I thank T. Kikuchi, N. Nakamaru, and S. Dobata for discussion, and three anonymous referees for criticism.

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