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Weaver ants *Oecophylla smaragdina* encounter nasty neighbors rather than dear enemies

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Abstract. The evolution of territorial behavior requires that the benefits of territoriality outweigh the costs. The costs are primarily those of territorial defense against encroaching neighbors or against floaters seeking to establish their own territory. One way to reduce the cost of defense might be to restrict serious conflict to encounters with those posing the greatest threat. Studies of many animals have found that less aggression is shown toward neighbors than toward strangers, a phenomenon known as the "dear enemy" effect. However, the opposite can also be true, namely, that more aggression is shown toward neighbors than strangers: the "nasty neighbor" effect. This may be particularly true of group-living species that defend a resource-based territory. Here we show that (1) colonies of the weaver ant *Oecophylla smaragdina* were able to recognize a greater proportion of workers from neighboring colonies as non-colony members; and (2) when recognized as non-colony members, more aggression was exhibited toward neighbors than non-neighbors. We present for the first time evidence that differential levels of aggression involve both a perceptual and behavioral component. On the other hand, we found no evidence that weaver ant workers were better able to recognize workers from previously unknown colonies or responded more aggressively to them, even after a 10-day period of contact. This contrasts with other species in which rapid learning of the identity of new potential enemies has been demonstrated. We suggest that such a response is unnecessary for weaver ants, as encounters with intruders from non-neighboring colonies are probably rare and of little consequence. This study adds to the growing body of evidence that the nasty neighbor effect may be much more common than the dear enemy effect among group-living species.

Key words: aggression; dear enemy; nasty neighbor; Oecophylla smaragdina; *weaver ants.*

INTRODUCTION

The evolution of territorial behavior requires that the benefits of territoriality outweigh the costs. Benefits include access to a reliable pool of resources, such as food, nesting sites, potential mates, and refuge from predators. Costs are primarily those of territorial defense against encroaching neighbors or against floaters seeking to establish a territory. One way to reduce costs is to restrict serious conflict to encounters with those posing the greatest threat. Among territorial animals, the greatest threat often arises from floaters, who might seek to establish territory at the expense of existing territory holders. Neighbors already in possession of a territory pose less threat, because their status is generally known and they have less to gain from a conflict. The expression of less aggression toward a neighbor than a stranger is known as the "dear enemy" effect (Fisher 1954), and has been widely observed among individuals or breeding pairs defending a territory (reviewed in Temeles 1994). However, if there is intense competition for resources, the opposite effect may also occur (Temeles 1994): more aggression may be shown toward neighbors than toward strangers. This has been termed the "nasty neighbor" effect (Muller and Manser 2007).

Temeles' (1994) review of the dear enemy effect included only two group-living species, both ants. The dear enemy effect was evident in one (Jutsum et al. 1979) and the nasty neighbor effect in the other (Gordon 1989). In subsequent studies of group-living species, evidence for the dear enemy effect was found for the Green Woodhoopoe, *Phoeniculus purpureus* (Radford 2005), but most studies suggest that the dear enemy effect might occur less frequently than the nasty neighbor effect in a range of taxa including mammals (Herbinger 2004, Muller and Manser 2007), birds (Botero et al. 2007, Koetz et al. 2007), and social insects (Dunn and Messier 1999, Sanada-Morimura et al. 2003). This makes intuitive sense, as groups may compete more intensely than individuals for resources, and may fluctuate in size, increasing the demand for resources

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as they grow. Furthermore, an individual from a neighboring group may present a greater threat than a lone wandering individual from farther away, as the former is more likely to represent the vanguard of a potential invasion force, and can recruit reinforcements if necessary.

Social insects provide a useful model for exploring these issues. Many ant species control and defend large territories to provide sufficient resources for rearing large numbers of reproductive males and females. Furthermore, large colonies may be unable to relocate if their territory is threatened by conspecifics. There is evidence for the nasty neighbor effect in several ant species (Gordon 1989, Knaden and Wehner 2003, Thomas et al. 2005, Van Wilgenburg 2007) and in some termites (Dunn and Messier 1999). Some studies report evidence of the dear enemy effect, but there are often confounding factors. Low levels of aggression toward neighbors may occur because neighbors share common foraging materials (Jutsum et al. 1979), live in a homogeneous habitat (Heinze et al. 1996), or are closely related (Zinck et al. 2008). Observations of an apparent dear enemy effect need to be corroborated experimentally by determining whether aggression toward unknown intruders decreases after repeated exposure. This appears to be the case for *Pheidole tucsonica* and *P. gilvescens*, and Langen et al. (2000) hypothesize that this is because colonies occasionally relocate, and strangers may represent scouts searching for new nesting sites.

Both the dear enemy and nasty neighbor effects have implications for recognition systems. The dear enemy effect indicates a capacity to differentiate between different types of other, as well as between self and other, and to modify behavior accordingly. This constitutes a shift in the response component of the recognition process. The nasty neighbor effect, on the other hand, is open to two interpretations. Failure to react aggressively to a stranger may mean that types of other can be differentiated, but that behavior is adjusted only when the unknown other becomes a greater threat, as signaled by increased contact. This constitutes a shift in the response component. Alternatively, failure to react aggressively may arise from recognition errors: unknown strangers are recognized as other only after a period of familiarization. This implies a shift in the perception component of recognition: all conspecifics recognized as other are responded to aggressively, but they are only recognized as other with experience. The methodology of previous studies, in which the nasty neighbor effect has been detected among ants, has not made it possible to differentiate between these possibilities. Only if this question is resolved can it be claimed with confidence that the nasty neighbor effect also involves the capacity to differentiate between different types of other (Gordon 1989).

We sought to shed light on these issues by exploring the response of weaver ant colonies (*Oecophylla smaragdina* Fab.) to intruders from neighboring and distant colonies. Weaver ants are a tropical arboreal species that develops large, multi-nest colonies, frequently occupying several trees, and foraging over a large area within the trees and on the ground. Where colonies meet, extensive battles can sometimes be observed (Hölldobler 1983). This suggests that the dear enemy effect might be absent in this species. However, colonies also exhibit some aggression toward individuals from distant colonies (Newey et al. 2008), and it has been unclear whether they respond differently to neighbors than to strangers. We observed the behavior of weaver ant workers toward intruders from both neighboring and distant colonies. We also sought to determine if and how the behavior of a colony changed after extended contact with a previously unknown colony. Our predictions for this species were that (1) the nasty neighbor effect would be present and (2) colonies would become more aggressive toward previously unknown colonies after a period of exposure. We also explored whether differential treatment of neighbors and strangers reflected a difference in behavior, perception, or both. In this way we hoped to increase our understanding of the mechanisms determining self/nonself recognition systems, particularly among species living in social groups.

Methods

Experiment 1: field nests

Throughout April and May 2008 we selected 10 colonies of weaver ants from the campus of James Cook University, Cairns, Queensland, to serve as recipient colonies (R_1 to R_{10}), collecting a small nest from each, as well as a nest from a neighboring colony (N_1 to N_{10}), the foraging area of which was seen to overlap that of the R colony, and from a more distant colony (D_1 to D_{10}) with which the R colony could have had no previous interaction. We estimate that each nest contained upward of 1000 major workers, with abundant brood (larvae and pupae). Each colony was used only once in the course of the study. Each group of three nests was taken to the laboratory, where a series of aggression bioassays were conducted between workers from R colonies and workers from N and D colonies over a period of two or three days.

The protocol for the behavioral bioassays was as follows. For each trial, five individuals were introduced from the R colony into a small observation area (a 250-mL specimen jar modified for this purpose). Individuals were selected haphazardly from the nest (held in a Ziploc plastic bag during the course of the trials), but callow individuals were avoided. A spot of water-based acrylic paint was applied to the rear of the head capsule of an individual from the N or D colony, which was then placed into a small tube adjacent to the test area. N and D workers were used alternately to eliminate any bias introduced by changes in levels of aggression over time. An opening between the tube and the test area was initially sealed. The recipient ants and intruder ant were given several minutes to acclimate, before the seal between the tube and the test area was removed and the intruder was permitted to enter the test area. The behavior of the recipient ants toward the intruder was recorded over a period of five minutes, timed from the moment of first contact between the recipients and intruder. When recording behavior, if any observed behavior was maintained for a period of five seconds, it was scored as another instance of that behavior, and so on for each subsequent period of five seconds. The first five recipient ants were left overnight in the test arena to increase the likelihood that they would identify the test arena as defensible territory. Twenty encounters were staged for each colony pair, with different recipient and intruder ants for each trial. On the rare occasions when the intruder seized and immobilized one of the recipient ants, the trial was repeated with different individuals.

We recorded the frequency with which recipients antennated the intruder (however briefly), the frequency with which a recipient and the intruder engaged in trophallaxis, and the frequency with which one or more recipients groomed the intruder. Antennation was interpreted as exploratory behavior. Both trophallaxis and grooming were interpreted as acceptance of the intruder as a colony mate. We also recorded the frequency with which one or more recipients visibly avoided the intruder. While avoidance is sometimes interpreted as a low level aggressive response (Roulston et al. 2003), we believe it is more appropriately interpreted as an alternative strategy: in some circumstances it may be more cost effective to avoid an intruder than to engage in dangerous conflict. We also recorded the following overtly aggressive behaviors: threatening posture (mandibles open toward the intruder, with or without raised gaster), pursuit, biting (some part of the intruder's body held in the mandibles of one or more recipient), and grappling (one or more recipient ant with its body curled around the intruder while biting; once this occurs the position is held until both ants are dead). These were graded in intensity as follows: (1) threatening posture, (2) pursuit, (3) biting, and (4) grappling. An index of aggression (A) was calculated:

$$A = \frac{\sum f_i i}{T}$$

where i is the intensity of response, f_i is the frequency of that response, and T is the total number of interactions observed. We calculated the mean and maximum aggression score for each colony pair. We also determined the proportion of individuals that elicited either an aggressive or aversive response as a measure of the extent to which intruders were correctly identified as alien conspecifics. We recalculated the mean aggression score, using only these individuals, to determine whether the level of aggression expressed toward those correctly identified as aliens differed between intruder types. In this way we sought to determine whether differences in aggression could be attributed to differences in perception or differences in behavior. We calculated the mean proportion of avoidance behavior for each colony pair to determine if different strategies were adopted toward intruders from familiar and unfamiliar colonies. Finally, we calculated the mean proportion of grooming and trophallaxis, as an indication of the extent to which intruders were accepted as colony mates.

We demonstrated recently (Newey et al. 2008) that weaver ants respond more aggressively to intruders from other colonies as the spectral distance, measured using near-infrared spectroscopy (NIRS), increases. Functional groups in molecules have characteristic vibration frequencies in the near-infrared region of the electromagnetic spectrum (approximately 800–2500 nm; Scarff et al. 2006), and NIRS uses radiation at these wavelengths to generate absorption spectra for scanned samples. The chemical bonds forming the basis of most NIRS information are X–H bonds, including C-H, O-H, N-H, and S-H (Foley et al. 1998, Scarff et al. 2006), which are primary constituents of the organic compounds found on the insect cuticle. NIRS spectra therefore provide a broad picture of the chemical "signature" of the insect cuticle.

We therefore determined the mean spectral distance between colonies to control for any confounding effect on the level of aggression between colonies. Spectra of 20 individuals from each colony were obtained using a Bruker Optics Multi Purpose Analyzer (Bruker Optics, Ettingen, Germany), following the protocol of Newey et al. (2009). We identified seven key peaks, located at the following wave number per centimeter, respectively: 8668.63 ± 20.58, 7026.61 ± 23.17, 5791.41 ± 3.48, 5647.50 ± 12.76, 5228.38 ± 10.78, 4615.53 ± 19.45, and 4212.68 ± 25.69 wave number/cm (mean ± SE). The location, intensity, and width (at 50% intensity) of each peak were recorded for each individual, resulting in 21 parameters. We used principal components analysis to reduce the spectral data to six orthogonal factors, and calculated the mean value of each factor to locate the centroid of each colony in six-dimensional Euclidean space. We then calculated the Euclidean distance between these centroids as an estimate of the spectral distance between colonies.

Experiment 2: manipulated nests

Between August 2008 and February 2009, we collected nests from 10 additional colonies in the university grounds and surrounding suburbs. Each nest was divided into two approximately equal sections, an "a" section and a "b" section, designated Ra_1 to Ra_{10} and Rb_1 to Rb_{10}, respectively. At the same time we collected nests from 10 other colonies that were distant from each of the first colonies. These were similarly divided into two sections, designated Ia_1 to Ia_{10} and Ib_1 to Ib_{10}. Nest sections were maintained in clear plastic boxes (food containers, 18 × 12 × 7 cm) inside a shadehouse with unregulated temperature and humidity and provided with mealworms (*Tenebrio* spp. larvae)

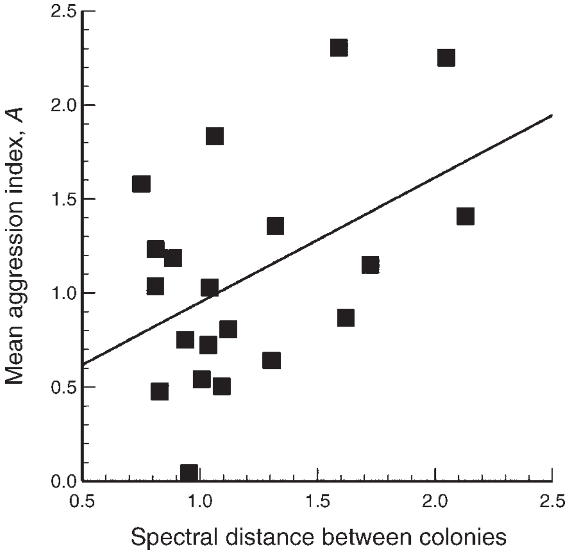

FIG. 1. The mean aggression index A plotted against the spectral distance between colonies of weaver ants (*Oecophylla smaragdina*), James Cook University, Cairns, Queensland, Australia.

and dilute honey as required. We conducted an initial behavioral bioassay, as previously described, between each Ra_i/Ia_i and Rb_i/Ib_i pair shortly after collection (t_1). Ra_i and Ia_i nests (treatment) were then connected by clear polyvinyl tubing to a shared third plastic box that was divided in two by a double layer of 1.6-mm aluminum mesh. Workers were able to contact each other through the mesh, and were even able to seize legs and antennae across the mesh, but were unable to gain access to the other side. These were now considered to be neighbors. Rb_i and Ib_i nests continued to be maintained separately as a control. After 9 or 10 days (t_2) the behavioral bioassays were repeated between each Ra_i/Ia_i and Rb_i/Ib_i pair to determine whether prolonged contact with previously unfamiliar conspecifics resulted in behavioral changes. We again calculated for each colony pair: the mean and maximum aggression score, the proportion of individuals that elicited either an aggressive or aversive response, and the mean proportion of grooming and trophallaxis.

Statistical analysis

Prior to statistical analysis, proportional data were transformed using the arcsine-square-root transformation, although untransformed values are reported in the results. All variables were normally distributed and we used regression and ANOVA models to analyze the results using S-PLUS 8.0 for Windows (S-PLUS 2007). We report the mean ± 95% confidence intervals in the results.

RESULTS

Experiment 1: field nests

A simple linear regression of aggression against spectral distance revealed, as expected, that the mean level of aggression increased as the spectral distance between colonies increased ($F_{1,18} = 4.967$, $R^2 = 0.216$, $P = 0.039$; Fig. 1). A one-way ANOVA with intruder type (N or D) as the predictor variable and spectral distance as a covariate showed that colonies were, on average, twice as aggressive toward N colonies than toward D colonies ($F_{1,8} = 17.299$, $P = 0.003$; Table 1). Aggression toward neighboring colonies ranged from 0.73 for colony R_9 to 2.30 for colony R_7, and aggression toward distant colonies ranged from 0.04 for colony R_6 to 1.14 for colony R_2. In each case, except colony R_9, less aggression was shown toward the distant colony than the neighboring colony. Colony R_9 exhibited similar low levels of aggression toward both intruder types (N, 0.73; D, 0.75). Aggression toward N colonies remained higher even when only those correctly identified as alien conspecifics were included in calculating the aggression index ($F_{1,8} = 14.792$, $P = 0.005$; Table 1). The maximum level of aggression was also higher between R and N colonies than between R and D colonies ($F_{1,9} = 5.442$, $P = 0.045$; Table 1). The proportion of intruders correctly identified as alien conspecifics by R colonies was significantly greater when intruders were from N colonies than when they were from D colonies ($F_{1,9} = 17.314$, $P = 0.002$; Table 1).

The mean proportion of avoidance behavior did not differ between intruder types ($F_{1,9} = 0.052$, $P = 0.825$; Table 1). The mean proportion of grooming and trophallaxis was significantly greater in R–D encounters than in R–N encounters ($F_{1,9} = 13.218$, $P = 0.005$; Table 1).

TABLE 1. Summary of behavior (mean ± 95% CI) shown by recipient colonies of weaver ants (*Oecophylla smaragdina*) toward intruders from neighboring (N) and distant (D) conspecific weaver ant colonies, James Cook University, Cairns, Queensland, Australia.

Behavior	N	D
Mean aggression index		
Including all individuals	1.45 ± 0.33	0.72 ± 0.24
Including only individuals correctly identified as alien conspecifics	1.70 ± 0.33	1.10 ± 0.24
Maximum aggression index	3.49 ± 0.25	2.94 ± 0.50
Proportion correctly identified as alien conspecifics†	0.85 ± 0.08	0.64 ± 0.15
Proportion of avoidance†	0.02 ± 0.02	0.03 ± 0.02
Proportion of grooming and trophallaxis†	0.02 ± 0.02	0.14 ± 0.12

† Untransformed data.

Experiment 2: manipulated nests

Being in contact with the intruder nest for a period of 9–10 days had no effect on the behavior of the ants in the recipient nest, compared to the control. Using a repeated-measures ANOVA model we detected a nonsignificant trend for aggression to increase over time ($F_{1,18} = 4.041$, $P = 0.059$), but there was no significant interaction between time and treatment ($F_{1,18} = 1.147$, $P = 0.298$). Thus, if aggression increased, it increased in a similar fashion for recipient nests that were connected to the intruder colony and those that were not. The maximum aggression score did not increase over time ($F_{1,18} = 0.036$, $P = 0.852$), and there was no interaction between time and treatment ($F_{1,18} = 0.546$, $P = 0.469$). The proportion of intruders identified correctly also remained unchanged (time, $F_{1,18} = 1.648$, $P = 0.059$; interaction, $F_{1,18} = 0.321$, $P = 0.578$). The proportion of grooming and trophallaxis increased significantly from t_1 to t_2 ($F_{1,18} = 4.536$, $P = 0.047$), but with no interaction between time and treatment ($F_{1,18} = 1.109$, $P = 0.306$).

Discussion

Our results revealed that workers from colonies of weaver ants were more aggressive toward intruders originating from neighboring colonies than toward intruders from more distant colonies. Both the mean level of aggression and the maximum level of aggression were greater toward neighbors than strangers. This strongly suggests that the nasty neighbor effect occurs in this species rather than the dear enemy effect. This adds to the growing number of group-living organisms in which this is the case. Our argument is further strengthened by the fact that colonies remained more aggressive toward neighboring colonies than distant colonies even when the spectral distance between colonies was taken into account. This eliminated a potentially confounding factor, given that the chemical (Suarez et al. 2002, Kaib et al. 2004, D'Ettorre et al. 2006, Foitzik et al. 2007) or spectral (Newey et al. 2008) distance between colonies is known to affect the level of aggression between them. The context in which encounters occur can also influence acceptance thresholds (Liebert and Starks 2004), and it is possible that the test arena may not have been regarded by the ants as defensible territory. Nevertheless, the context remained constant for all ants and we believe that our comparisons are valid.

Colonies were both more aggressive toward individuals, and aggressive toward a higher proportion of individuals, from neighboring colonies than from distant colonies. This suggests that there is both a behavioral and a perceptual component to this effect. The behavioral component is evident from the fact that among individuals correctly identified as alien conspecifics, the aggressive response was greater toward intruders from neighboring colonies. The perceptual component is indicated by the fact that a smaller proportion of workers from distant colonies than from neighboring colonies elicited any aggressive or aversive response. While we cannot completely rule out the possibility that recipients made a behavioral decision to treat some workers from a colony aggressively and some nonaggressively, it seems more likely that the difference was the result of misidentification. There was no evidence that intruders from distant colonies were avoided rather than engaged in conflict, as might have been expected if they were recognized as alien conspecifics. Furthermore, workers from recipient colonies were more likely to engage in grooming or trophallaxis with workers from unfamiliar than from familiar colonies. We therefore conclude that intruders from distant colonies were more likely to be misidentified as colony mates than workers from neighboring colonies; in addition, when intruders were correctly identified as alien conspecifics, they were greeted with a more aggressive response when they originated from a neighboring colony than when they originated from a more distant colony. It seems clear from this that experience plays an important role in both the ability of weaver ants to differentiate between self and other, and in determining the level of aggression directed toward those identified as other.

In our study of weaver ants, we were unable to detect any significant change in the behavior of workers in nests that were forced to spend time as neighbors, compared to workers in control nests that remained apart. Carlin and Johnston (1984) were among the first to observe that ant colonies, in this case, *Pheidole dentata*, were better able to identify potential heterospecific enemies after repeated exposure. Within the context of conspecific encounters, in contrast with our results, Sanada-Morimura et al.'s (2003) study of *Pristomyrmex punctatus* (previously *P. pungens*) found that colonies exhibited increased hostility toward new neighbors within a day of first contact. However, unlike weaver ants, *P. punctatus* colonies relocate approximately once every two weeks during the warmer months, so workers are likely to encounter new neighbors quite frequently (Sanada-Morimura et al. 2003). New neighbors represent either a rival whose territory is to be taken, or a rival threatening to take over the colony's territory. In these circumstances, neighbors and strangers are ephemeral phenomena, and a capacity to continually reevaluate the threat is essential.

Knaden and Wehner (2003) also found, in contrast to our study, that the aggression shown toward intruders by *Cataglyphis fortis* workers was greater if there had been a prior encounter only 18 hours earlier. However, these ants form only small colonies of ~50 workers, and are spaced sufficiently widely apart that encounters with workers from other colonies are rare (Knaden and Wehner 2003). In this context, there are no real neighbors, only strangers.

For most weaver ant colonies, neighbors are an ever-present and fairly stable reality. While the boundaries of colonies fluctuate, and colonies expand and contract seasonally (Lokkers 1990), entire colonies do not relocate, and the identity of neighbors remains fairly constant over time. New neighbors are therefore likely to be encountered only rarely, and only repeated encounters over an extended period of time are likely to result in a modified response. The 9 or 10 days during which our experimental nests lived as neighbors may not have been long enough to generate any behavioral change. Colonies in the field may have spent years as neighbors, perhaps from shortly after their establishment.

It is also possible that individual weaver ants are unable to learn the identity of a new potential enemy after an older enemy has been identified: the template for "enemy" may become fixed after an encounter with an alien conspecific. This does not preclude the possibility that aggression might increase after repeated or prolonged exposure to the known enemy, or that more individuals would recognize neighbors than non-neighbors as enemies, both of which are consistent with the results of our first experiment. However, it could mean that workers identify as an enemy the first non-colonymate that they encounter, which is much more likely to be a neighbor than a non-neighbor, and do not have the capacity to add other conspecifics to their list of enemies. In this case, only subsequent workers would be able to learn the identity of a new enemy, a system that would work quite effectively if neighbors changed only rarely.

It is clear that weaver ants learn at some stage in colony development that neighbors represent a serious threat. Non-neighbors are frequently not identified as nonself, and even if they are recognized, they are treated less aggressively than neighbors. The ability to recognize new potential threats may exist, but if colonies, once established, are fairly stable, there may be little benefit in being able to recognize and respond aggressively to non-neighboring alien conspecifics if they represent only the occasional stray worker. Enough workers do respond aggressively to suggest that few strays would ultimately survive. However, even if they did survive, they represent little threat to the colony: they are simply additional "free" workers in which the colony has made no investment. The only real threat would arise from neighboring colonies that can invade in large numbers and steal valuable territory and resources.

Among group-living species that frequently relocate in search of resources, the ability to quickly identify any new potential enemies in the neighborhood may be essential for the survival of the group. Many tropical rain forest ants that nest in leaf litter move nests frequently (McGlynn 2006), and always run the risk of encountering new conspecific competitors. So too do the vast colonies of army ants that move through various old and new world tropical communities (Hölldobler and Wilson 1990). In contrast, colonies of other ants, such as those of weaver ants and meat ants, remain in place for years and even decades (for example, *Iridomyrmex purpureus*; Greenslade 1975). Comparative studies of the ability to learn the identity of new neighbors, among related or sympatric species with different strategies, would be informative.

There is increasing evidence, from a wide range of taxa, that the nasty neighbor effect may be a general phenomenon among group-living animals that defend a territory and compete for limited resources. Here we have presented evidence that the differential treatment by social insects of neighbors compared to strangers results from both a difference in perception and a difference in behavior. Strangers from previously unknown colonies are less likely to be recognized aliens; but even when they are, they are responded to with less aggression than neighbors. With weaver ants the challenge remains to determine the extent to which, and mechanism by which, the identity of new enemies can be learned.

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