The Red and the Black: Habituation and the Dear-Enemy Phenomenon in Two Desert Pheidole Ants
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ORIGINAL ARTICLE

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The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants

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Abstract Many species of territorial animals are more aggressive toward strangers than neighbors, a pattern of aggression referred to as the 'dear-enemy phenomenon.' In many cases, the mechanism by which neighbors are discriminated from strangers and the function of neighbor-stranger discrimination remain controversial. We investigated the spatial patterns of inter-colony aggression within and between two *Pheidole* species of seed-harvesting ants in the Mojave Desert of California by quantifying aggression between colonies in standardized staged encounters. We also tested whether the level of fighting between workers of two colonies is affected by previous exposure to each other. We show that neighbors (i.e., colonies less that 2.6 m away) of either species are treated less aggressively than more distant colonies and that habituation may be a mechanism by which this discrimination is achieved. The variation in aggression among spatially distant colonies also suggests that additional genetic or environmental factors are involved in recognition. The function of the dear-enemy phenomenon in these ant species may be related to the greater risk to the resources of a colony presented by strange workers than workers from a neighboring colony.

Key words Aggression · Dear-enemy phenomenon · Habituation · Territoriality · Recognition systems · Formicidae · *Pheidole*

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Introduction

Territorial animals in a wide variety of taxa respond less aggressively to challenges by neighbors than strangers; this 'dear-enemy' phenomenon appears to be the typical pattern in resource defense social systems (Temeles 1994). A few well-documented examples of greater aggression toward neighbors than strangers also exist. The proximate causes and ultimate function of dear-enemy neighbor-stranger discrimination and its converse remain controversial (Peeke 1984; Getty 1987, 1989; Ydenberg et al. 1988, 1989; Temeles 1994; Owen and Perrill 1998).

Most studies of the dear-enemy phenomenon have focused upon terrestrial vertebrates, especially birds, that defend breeding territories or nesting sites (Temeles 1994). Notable among the few studies of neighbor-stranger discrimination among invertebrates are those that investigate this phenomenon in eusocial Hymenoptera, primarily ants. Ants are particularly suitable for investigating the dear-enemy phenomenon for three reasons. First, ant workers of most species react aggressively to conspecific non-colony members both near the nest and in neutral settings (Hölldobler and Wilson 1990). Second, the question of how colony members distinguish neighbors from strangers is embedded in a larger issue of how colony members discriminate themselves from non-colony members (Hölldobler and Carlin 1987; Carlin 1989; Jaisson 1991). Finally, most ants defend some form of territory, and the patterns of aggression within and between species can have major consequences for ant community structure (Davidson 1977; Hölldobler and Wilson 1990; Ryti and Case 1992). Thus ants may be a key group for understanding both the mechanisms and the functional basis of neighbor-stranger discrimination, and also for providing insight into how aggression influences community structure. Both the dear-enemy phenomenon and its converse have been documented in ants (Jutsum et al. 1979; Stuart 1987; Gordon 1989), and for at least for one pair of congeners, the dear-enemy phenomenon occurs between as well as within species (Heinze et al. 1996).

Pheidole tucsonica and *P. gilvescens* are two abundant, sympatric species of seed-harvesting ants in the Mojave Desert (Wheeler and Wheeler 1986). Colonies of both species defend foraging areas and are active at similar times, and nests are often overdispersed, suggesting that colonies may compete for food (Bernstein 1979; Bernstein and Gobbel 1979). Although the recognition systems of *Pheidole* have not been extensively investigated, ants of this genus can learn to discriminate different species of ants and modify defensive actions accordingly (Carlin and Johnston 1984; Feener 1986, 1987). We investigated the spatial patterns of inter-colony aggression within and between *P. tucsonica* and *P. gilvescens*, and we also tested whether the level of fighting between workers of two colonies is affected by previous exposure to each other. We used these data to ask how and why these two species of *Pheidole* treat conspecific and heterospecific neighbors differently from strangers.

Methods

Study site and species

We conducted this study at the Sweeney Granite Mountains Desert Research Reserve in the Eastern Mojave Desert of San Bernardino County, California (34°48′ N, 115°39′ W). Our research was centered at Yucca Bajada Campground (1,200 m elevation), an area of typical Mojave bajada habitat dominated by the plants *Hymenoclea salsola*, *Salazaria mexicana*, *Yucca shidigera*, and *Larrea tridenta*. Some collecting was done at two other, ecologically similar sites at the Reserve (Allanson Center and Norris Camp). Further information on the Granite Mountains Reserve can be found in Luke and André (1999).

The two species in our study are the blackish *P. tucsonica* (synonym *P. xerophila tucsonica*) and the reddish *P. gilvescens* (keyed from Wheeler and Wheeler 1986; voucher specimens deposited in the Dickey Collection, University of California, Los Angeles). Both are small (minors 3–4 mm) seed-harvesting ants that forage along trunk trails and nest in the soil (Wheeler and Wheeler 1973, 1986; personal observation). Each species has dimorphic worker castes (majors and minors), but more than 95% of the workers on the soil surface were minors during our study. Colony densities were similar (mean±SE colonies per 100 m^2: *P. tucsonica* 3±0.0, *P. gilvescens* 4±1.0, *n*=3 plots). The two species were active at similar times of the day, and some colonies were as close as 0.5 m apart. Our experiments were conducted during three site visits in August and September 1998 and May 1999. Numbers of workers on the surface of actively foraging colonies were similar in both species during each of the visits (10–50 minor workers).

General methods

We collected ants by aspiration from the soil surface near nests. Multiple openings of the same species less than 20.0 cm distance were presumed to be the same colony. Ants were held in 25-ml collection vials until an encounter was staged.

To stage an encounter, we placed ten minor workers of each of the two test colonies in a 17-cm^2 neutral arena (a 100-ml beaker coated with fluon along the sides to prevent climbing). Initially, we videotaped the encounters, but we switched to direct visual scoring of behavior later in the study. Every 15 or 30 s (depending on the experiment), we estimated the number of dyadic fights between ants in an instantaneous scan sample. We classified any instance that an ant closed its mandibles upon the body of another as a fight, whether the interaction appeared mild or escalated (see Results for a description of fighting behavior). When odd numbers of ants participated in fights, we rounded the fight score to the next higher integer number (e.g., one fight involving three individuals was scored as two, but two fights of three individuals each was scored as three). Therefore, our scale ranged from zero (no fights) to ten (all ants involved in fights). Encounters were either observed for 5.0 or 15.0 min depending on the experiment. After an encounter, the beaker was cleaned with ethanol to remove odors and dried before reuse.

Post hoc examination of the data showed that the interval of sampling (15 or 30 s) and the duration of sampling (5.0 or 15.0 min) had no significant effect on the mean fight scores per encounter. Inter-observer reliability at scoring fights was tested both from a video record and direct observation and found to be very high. We examined the repeatability of fight scores by staging eight 'black-black' encounters (both colonies *P. tucsonica*) and eight 'mixed' encounters (one colony *P. tucsonica*, one colony *P. gilvescens*) and then retesting the same pairings on a subsequent day. Each colony was used in only one pairing. During an encounter, the number of fights was visually scored every 30 s for 15 min. Repeatability of mean fight scores between encounters was high (pooled *r*=0.77, one-tailed *P*=0.0001, *n*=16). The repeatability of the two combinations did not differ significantly (*Z*=0.34, *P*=0.7).

We initially tested the data for heterogeneity of effects among the three combinations (i.e., red-red, black-black, mixed). If none was detected, analyses were pooled across combinations. We also inspected the data for within-encounter time effects (trends for fight scores to increase or decrease with time) before averaging scores. Before statistical testing, the data were inspected for normality and transformed if needed. Probabilities are two-tailed unless otherwise stated.

Aggression and distance between colonies

To assay general patterns of aggression between colonies of each of the three combinations, we staged encounters using a wide range of between-colony distances (median distance 32 m, up to 4 km, and only 12% of pairings under 6 m), reusing most colonies repeatedly (*n*=91 encounters among 53 colonies). Encounters were scored at 15-s intervals for 5.0 min; each encounter was scored blind with respect to the distance between colonies. We tested for associations between (ln-transformed) distance and mean fight score using Mantel tests (Sokal and Rohlf 1995); *P*-values were calculated from Monte Carlo simulations of 10,000 runs.

Neighbor-stranger discrimination experiment

To test more sensitively whether inter-colony aggression differs between neighboring and distant colonies, we selected 36 tester colonies:12 black colonies for black-black pairings, 6 black and 6 red colonies for mixed pairings, and 12 red colonies for red-red pairings. Each tester colony was paired with two other colonies: a near colony (less than 6.0 m distance) and a distant colony (greater than 20.0 m distance). For conspecific combinations (black-black or red-red), the minimum distance between near colonies was limited to those with nest openings more than 1.0 m apart to reduce the possibility that we had collected from the same, polydomous colony. All colonies (test as well as the near and distant colonies) were used only once.

We placed ten ants from a tester colony and ten ants from its matched near or distant colony in a neutral arena. We counted the number of fights every 15 s for 5.0 min. The order of near and distant encounters was alternated; when we scored an encounter, we were generally aware of the type of pairing (near or distant) but were blind to the near-pairing distance.

The distant colonies had probably never encountered the test colonies, as we never observed colonies foraging more than 10 m from their nest openings. Our categorization of under 6.0 m distance as near, however, may not have always corresponded with a biologically meaningful distance for these ants, i.e., their encountered neighborhood. To detect the true neighborhood distance, we compared the mean number of fights of tester colonies when matched with a near versus a distant colony using all matched pairings. We then systematically reanalyzed the data after eliminating the tester colony with the most distant near-distance encounter, the tester colonies with the two most distant near-distance encounters, etc. We inspected the data for significant changes in the magnitude of differences between near and distant colony encounters as we increasingly restricted the near-distance encounters to shorter and shorter distances.

Habituation experiment

To test whether aggression between colonies declines with short-term exposure to each other's workers, ants were collected from 24 black colonies and 8 red colonies to form eight conspecific (black-black) colony pairs and eight heterospecific (mixed) pairs. We staged one encounter with each pair immediately after collection. We also placed 12–15 minor workers from a test colony in each of two 25-ml vials. In one vial, we placed a smaller vial (2 ml volume) containing five ants of the other colony to which the test colony was paired. One end of the smaller vial had a 5-mm-diameter opening covered with a thin netting that permitted air flow between the vials, and which potentially allowed both sets of ants to contact one another without biting. Ants on both sides of the divider investigated it actively. In a second vial, we placed an identical small vial that contained no ants. Two vials were prepared in the same fashion for the other colony of the pair. Thus there were two vials of ants (one for each colony) that contained smaller empty vials and two vials of ants (one for each colony) that contained a smaller vial of ants of the other colony. A small moist cotton ball was placed in each vial, and the vials were left in a cool, dark place for 10–14 h.

After this waiting period, we staged two encounters. In 'no-exposure' encounters, ten ants from each of the two vials that contained empty small vials were placed in a neutral arena. We scored the number of fights every 30 s for 15.0 min. In 'exposure' encounters, we placed ten ants from each of the other two vials (i.e., those with small vials containing ants from the other colony) in a neutral arena and observed them in the same way. The order of testing was alternated with each trial; because of the field conditions, encounters were not scored blind. We then compared the mean number of fights per contest between no-exposure and exposure encounters of each colony pair.

Results

General patterns of aggression

Aggression and distance between colonies

We examined the distribution of fight scores for all colony pairs tested in the study (Fig. 1). We split these data between far colonies (colonies ≥6.0 m distance, workers probably encountered each other rarely if ever) and near colonies (colonies <6.0 m distance, workers probably encountered each other frequently). There was a discontinuity in the distributions of mean fight scores near 0.5; we classified those below this score as 'non-aggressive', and scores of 0.5 and above as 'aggressive.'

Among the three combinations of encounters (black-black, red-red, and mixed), there were significant differences in the relative proportion of far pairings that were aggressive (Fig. 1; $\chi^2_2=11.6$, $P=0.002$). The two conspecific combinations (black-black, red-red) did not differ ($\chi^2_1=0.6$, $P=0.5$), but there were relatively more far, conspecific pairings that were non-aggressive than far, heterospecific (mixed) pairings ($\chi^2_1=10.9$, $P=0.0009$). Among aggressive, far pairings of the three combinations, there were no significant differences in the variance of fight scores (variance ratio test Ps>0.45 for all three pairwise comparisons), nor did the mean fight scores differ (ANOVA $F_{2,97}=1.0$, $P=0.4$). The results were qualitatively the same for the near pairings, and were also similar when we restricted the data to only one pairing per colony (thus eliminating all but one pairing for any colony that was tested against multiple colonies).

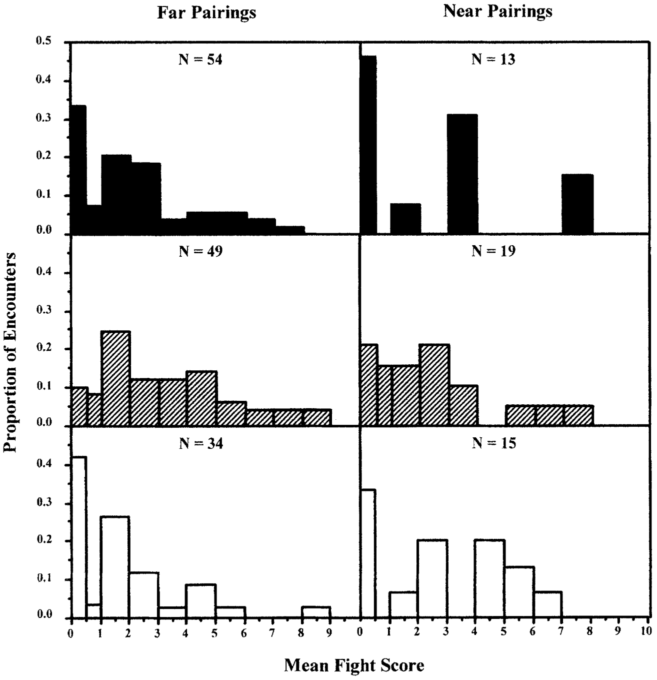

Fig. 1 Distribution of mean fight scores of black-black (*solid bars*), mixed (*hatched bars*), and red-red (*open bars*) combinations for far (colony distances ≥6.0 m) and near (distances <6.0 m) pairings. Each mean fight score was calculated from the first 5.0 min of an encounter. All unique pairings are included; some colonies were paired against multiple colonies, but no pairings of the same two colonies was included more than once

We also examined how fight scores varied with (ln-transformed) distance. We performed the analyses twice: (1) including pairings of colonies from different locations (i.e., 4 km apart), and (2) restricting pairings to those in which the two colonies were collected at the same location (i.e., colonies <115 m apart). When all data were included, the mean level of fighting changed significantly with distance for red-red pairings and mixed pairings but not for black-black pairings (Table 1). When the data were restricted to pairings within a site, fighting levels appeared to covary significantly with distance only for mixed pairings (Table 1).

Six red and nine black colonies were used in five or more contests with different opponents (conspecific and heterospecific pairings combined). All of these colonies

Table 1 Results of Mantel tests of the association between the distances of colony pairs and their mean fight scores. *All pairs* include pairings between colonies from different locations (maximum between colony distances 4 km), whereas *Same location only* is restricted to colonies at the same location (under 115 m distance)

Combination	*Z*	*n*	*P*
All pairs			
Black-black	218.5	35	0.80
Red-red	112.9	25	0.045
Mixed	249.3	31	0.048
Combined	580.7	91	0.11
Same location only			
Black-black	168.7	28	0.27
Red-red	62.8	23	0.40
Mixed	155.9	27	0.052
Combined	387.4	78	0.052

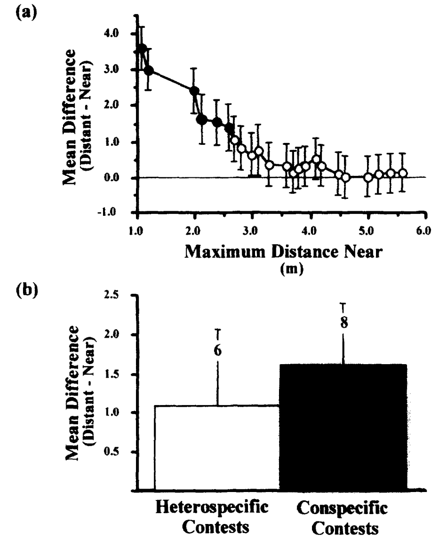

Fig. 2 a The mean difference (and SE) in fighting level between distant and near colony pairs, pooled for all combinations, at different maximum distances of near pairs. *Filled points* represent statistically significant ($P<0.05$) differences between pairings based on paired *t*-tests. **b** The mean difference between near and distant pairs at the maximum near distance for which there is a significant difference between them (2.6 m). Conspecific contests are comprised of black-black and red-red pairings, heterospecific contests include a colony of each species. The number of paired comparisons is indicated along the SE bar

were aggressive toward a majority of the opponents with which they were paired, but 83% of the red colonies and 78% of the black colonies were non-aggressive toward at least one far (greater than 6.0 m) pairing. Some of the pairings that were non-aggressive were at the maximum distances between colonies.

Behavior during encounters

During low-intensity fighting in all three combinations, ants approached one another with raised, open mandibles and then either locked mandibles or retreated. One ant might grab another's leg or antenna and hold on for a short period, then release. Few interactions lasted more than one sample interval (i.e., 15 or 30 s). During intermediate levels of fighting, some individuals grabbed others with the mandibles and carried the victims aloft for more than one sample interval. During high-intensity fighting, individual fights lasted many sample intervals and additional ants would typically join the nuclear pair of contestants. Fighting 'balls' or 'chains' containing multiple ants developed and persisted. Ants curved their abdomens toward their opponents, appearing to sting. In the most escalated contests, all ants eventually aggregated into one large fighting mass. In one instance, we let an escalated black-black encounter continue after the end of a sample period. The ants were still fighting at the same level 5 h later.

Heterospecific encounters appeared qualitatively different from conspecific encounters. Black ants, which appeared to be slightly larger than red ants, dominated the other species. We frequently observed black ants run up to red ants, climb over them, bite the victims near the head, then release them. This even occurred in combinations for which escalated fighting was rare. The reciprocal was not observed (red performing this behavior toward black) nor was it noticed in conspecific encounters. During escalated fights, red ants sometimes appeared to 'feign death;' they became immobile, with the body flexed and the legs and antennae curled inward. A few seconds after release from the opponent, the red ant would right itself and resume its activities. We never observed black ants performing this 'death-feigning' behavior. However, although red ants generally appeared subordinate to blacks, in some mixed pairings, red ants initiated fighting and were at least as aggressive as the other species.

Aggression in paired near versus distant colonies

Using all the paired comparisons, there was no significant difference in fighting scores between paired near and distant encounters (paired t_{35}=0.2, P=0.8). However, we did detect a significant difference between near and distant encounters when the maximum difference between near colonies was 2.6 m (Fig. 2a ; paired t_{13}=2.3, P=0.04). There was no significant difference among the three combinations in the magnitude of this difference at the 2.6-m cutoff for inclusion (repeated-measures ANOVA: combination $F_{2,11}$=0.6, P=0.5; combination× distance $F_{2,11}$=2.2, P=0.16). At cutoffs of less than 2.6 m, results were qualitatively the same but the significance of the difference between near and far encounters was greater (e.g., restricting near pairs to a maximum of 2.0 m distance: paired t_7=3.8, P=0.007).

One potential artifact of our experimental design was that some of the nearest conspecific pairings may have been comprised of ants collected at two different openings of the same polydomous colony, despite our precaution in

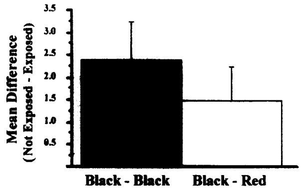

Fig. 3 Mean difference (and SE) in fighting level between not-exposed and exposed treatments for the eight conspecific and eight heterospecific colony pairs

limiting such pairings to colonies with openings separated by more than 1 m. If true, the difference in fight scores between the near and far encounters of the two conspecific combinations should have been greater than the heterospecific combination. There was no significant difference between heterospecific and conspecific encounters at the critical 2.6 m distance, however (Fig. 2b; repeated-measures ANOVA: combination $F_{1,12}$=0.4, P=0.5; combination×distance $F_{1,12}$=0.2, P=0.7), nor did they differ at shorter near-pair distances.

Reduction of inter-colony aggression by habituation

The mean level of fighting was significantly lower between colonies in the exposure treatments than the no-exposure treatments (Fig. 3; repeated-measures ANOVA using ln-transformed data: $F_{1,14}$=14.1, P=0.002). The magnitude of this difference did not vary significantly between the two combinations tested (combination $F_{1,14}$=0.6, P=0.5; combination×treatment $F_{1,14}$=0.9, P=0.4).

Discussion

Our study provides three principle results. (1) In a neutral arena, *P. tucsonica* and *P. gilvescens* workers from two different colonies of the same species or mixed species are nearly always aggressive, but a minority of colony pairings are not. Some of the colony pairings that are not aggressive are too distant for their workers to have met previous to the encounter, and these same colonies are aggressive when paired with other colonies. Mixed-species pairings are more frequently aggressive than conspecific pairings. (2) Workers from colonies less than 2.6 m apart are less aggressive toward their conspecific and heterospecific neighbors than toward workers of either species from more distant colonies. (3) Fighting is subsequently reduced between workers of two conspecific or heterospecific colonies when the workers are exposed to members of the other colony for a short period while prevented from fighting.

Results 2 and 3 indicate that the dear-enemy phenomenon occurs both within and between these ant species, and this phenomenon may be mediated by simple recognition learning. Workers from one colony habituate to workers from neighboring colonies that they regularly encounter. Result 1 suggests that colonies which are spatially distant sometimes share matching recognition cues. These cues may be genetically and environmentally influenced for intraspecific recognition but are probably produced environmentally for heterospecific recognition.

Colony recognition and the dear-enemy phenomenon in ants

Ants recognize colony members primarily by olfactory cues, including genetic and environmentally influenced odors (Hölldobler and Carlin 1987; Carlin 1989; Hölldobler and Wilson 1990; Jaisson 1991). Three mechanisms associated with recognition systems may result in the dear-enemy phenomenon in ants and other animals.

First, environmentally influenced recognition cues, such as scents derived from the diet or domicile, are likely to be more similar between neighbors than the population at large simply because their environment is more likely to be similar. The dear-enemy phenomenon may result from a recognition mistake that occurs when neighbors are difficult to discriminate from colony members due to an environmentally induced similarity, and are therefore treated less aggressively. In ants, reduced aggression between colonies due to shared environmentally produced odors has been shown experimentally (Jutsum et al. 1979; Crosland 1989), and observed in the field (Heinze et al. 1996).

Second, the dear-enemy phenomenon could be a consequence of colony recognition cues if these are genetically based, and recognition alleles do not lead to unique labeling of all colonies within a population (i.e., some colonies share the same recognition genotype by chance). If aggression by a colony impedes the establishment of new territories near it, then pioneers with genotypes that match the resident colony may be more likely to become established simply because they are less likely to elicit aggression (Grosberg and Quinn 1986; Sherman et al. 1997). In this case, the dear-enemy phenomenon is the result of a selection process that leads to greater similarity in recognition features within neighborhoods. For several ant species, aggression is reduced toward those colonies that share genotypes, and neighboring colonies tend to be related (Jutsum et al. 1979; Stuart 1987; Beye et al. 1998; Suarez et al. 1999).

A third way for the dear-enemy phenomenon to be a consequence of a colony recognition system is via a simple form of recognition learning called habituation. Habituation is a common and rapid form of learning in animals that results in a reduced responsiveness toward a specific, repeatedly perceived stimulus such as a persistent odor. It does not, however, affect the responses to similar, but discriminable stimuli (Peeke 1984; Owen and Perrill 1998; Shettleworth 1998). Worker ants may habituate to cues provided by repeatedly encountered members of another colony (their neighbors), and therefore show less aggression toward them than ants with novel cues (strangers).

In our study, serendipitous recognition cue matching was probably the cause of the idiosyncratic patterns of aggression between distant colony pairs, and plausibly may account for some instances of dear-enemy neighbor-stranger discrimination. However, our results indicate that the dear-enemy phenomenon may be primarily a consequence of habituation. In our habituation experiment, an alternative explanation, that the reduced aggression in exposure treatments was due to convergence upon common environmentally influenced recognition cues, is unlikely, since the control no-exposure ants were kept under similar conditions. This experiment indicated that habituation associated with exposure to one set of workers from an unfamiliar colony generalized to other members of the same colony. A weakness of our experimental design, however, was not having an additional exposure treatment composed of ants from a different colony in the small vials. This would have permitted testing the specificity of the habituation effect, i.e., whether ants only show decreased aggression toward the specific colony to which they have been exposed.

How habituation translates from the individual to the colony level is unclear. The distance over which the dear enemy phenomenon in *Pheidole* is detectable at our field site (under 3 m) appears concordant with the foraging ranges of the ants and thus habituation may occur because workers regularly encounter the foraging trails of their neighbors. However, we do not yet know whether individual ants interact with members of a neighboring colony as frequently in the field as they were forced to do in our habituation experiment. Even if individuals do interact with neighbors infrequently, the identity of neighbors may be learned and communicated among colony members (Passera et al. 1996; Brown and Gordon 1997).

Function of the dear-enemy phenomenon in *Pheidole*

The three recognition-based hypotheses presented above suggest that the dear-enemy phenomenon could occur in the absence of any adaptive benefit. Alternative to these are several functional hypotheses that propose adaptive explanations for the widespread dear-enemy phenomenon and the less commonly reported instances of the converse (greater aggression toward neighbors than strangers). From the perspective of the functional hypotheses, the recognition-based explanations for the dear-enemy phenomenon described above provide proximate discrimination mechanisms that can be used for strategic modification of aggression depending on the opponent.

For example, treating kin less aggressively than unrelated individuals may often be worthwhile, so if related colonies cluster near each other then the dear-enemy phenomenon may result. However, kin selection is an unlikely functional explanation for the dear-enemy phenomenon in the two species of *Pheidole* that we studied. The probable mating system of these ants (dispersal of alate reproductives in nuptial flights; Hölldobler and Wilson 1990) makes it unlikely that neighbors are relatives, and heterospecific dear enemies are clearly not related.

The dear-enemy phenomenon may also result from a difference in the amount of information available to contestants about the condition and motivation of their opponent in contests between neighbors relative to contests between strangers. Escalated fighting between strangers may function toward acquiring this information, or may simply result from more frequent mistakes estimating their relative condition and motivation (Ydenberg et al. 1988, 1989; Getty 1989). The information asymmetry hypothesis appears more directly applicable to contests between individual opponents, however, than to patterns of aggression between ant colonies.

Finally, the dear-enemy phenomenon may be an adaptive consequence of the economics of territory defense. Temeles (1994) argued that in multiple-purpose territories (e.g., combined feeding and mating territories), strangers are a greater threat to a territory holder than a neighbor, and hence elicit a more aggressive response to intrusion. Strangers may lack a territory and hence present a risk in terms of usurpation of both mates and territory, whereas neighbors have known, established territories and may only usurp mates. Temeles (1994) further argued that when animals defend territories that are exclusively for feeding, the intrusion of neighbors presents a greater risk of loss of territory space than the intrusion of strangers, and therefore neighbors should be treated more aggressively than strangers. When the density of colonies is high, as it is for each of the *Pheidole* species in our study, the ergonomic cost of indiscriminate aggression towards non-colony mates is potentially quite high (e.g., Holway et al. 1998).

For two other ant species, the observed patterns of neighbor-stranger discrimination are hypothesized to be due to the economics of territory defense. *Pogonomyrmex barbatus* ants actively defend a feeding territory, rarely relocate their colony away from this territory, and are more aggressive toward workers of neighboring colonies than strangers. This pattern of aggression has been explained in terms of the relative risk of losing food: strangers are likely to be lost foragers rather than nest prospectors and are unlikely to recruit colony mates, but neighboring intruders can potentially recruit significant numbers of competitors and usurp part of the territory (Gordon 1989, 1992a, 1992b).

Leptothorax nylanderi forages a limited distance from the nest entrance. This ant frequently moves nests as colony size changes, and competition for nests is high. Strangers are treated more aggressively than neighbors, apparently because strangers are more likely to be nest prospecting than foraging and hence threater to usurp the domicile of a colony (Heinze et al 1996).

The two species of *Pheidole* we studied appear to have a pattern of territoriality similar to the related desert seed-harvester *Pheidole militicida*. Colonies of this species use more ephemeral trunk trails and have less defined territory boundaries than larger desert seed-harvesting ants like *P. barbatus* (Hölldobler and Möglich 1980; Hölldobler and Wilson 1990). For desert seed-harvesting *Pheidole*, the chance encounter with foraging neighbors may represent little competition, and warrant little aggression, unless the encounter occurs near a currently exploited food patch or the nest. If so, that neighbors show relatively little aggression in a neutral arena is not surprising.

But why, then, do strangers fight? In other species of desert seed-harvesting *Pheidole*, colonies are known to move to new locations frequently for various reasons, including invasion by *Neivamyrmex* army ants. Occasionally, colonies move more than 4 m (Droual and Topoff 1981; Droual 1983, 1984). During our study, we observed one instance of a *P. tucsonica* colony abandoning its home and moving a few meters to another site. As in *L. nylanderi*, strange *Pheidole* workers may be scouts from a colony looking for a new home. Therefore, strangers may warrant a more aggressive response from colony members than established neighbors because strangers are a greater threat than neighbors to annex part of the territory or usurp the nest.

Thus, the dear-enemy phenomenon in *P. tucsonica* and *P. gilvescens* appears explicable in terms of the relative threat to defended resources posed by neighbors versus strangers, neighbors being discriminated from strangers by habituation learning, and possibly other mechanisms. To fully evaluate this hypothesis requires more detailed data on the natural history of these ants.

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