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Know thine enemy: why some weaver ants do but others do not

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Recognition systems involve 3 components: an expression component, a perception component, and an action or response component. Disentangling the perception component from the action component can be difficult, as the absence of a discriminatory response may result from either a difference in perception or action. Social insects generally defend their colony against intruding conspecifics and provide a useful model for exploring recognition systems. However, whether differences in behavior at the colony or individual level result from the perception or action component of the recognition system is largely unknown. Furthermore, variation at the individual level has remained largely unexplored because research on social insects often focuses on the colony rather than on the individual. Using some novel behavioral bioassays, we here show that variation in the aggressive behavior of individual weaver ants (*Oecophylla smaragdina* L.) arises more from the identity of the recipient than of the intruder and, contrary to previous findings, that this often results from perceptual differences. We suggest that recognition in weaver ants may involve a template based on the individual's odor prior to intermingling with other odors rather than on a common odor. We also argue that a common odor might be more important for the survival of the colony than a shared template. Conversely, possessing a range of templates may provide a colony with additional fitness benefits. By focusing on the differences among individual workers within colonies, this study reveals complexities in nest mate recognition that might otherwise have gone unnoticed. *Key words:* colony odor, Formicidae, Hymenoptera, recognition systems, social insects. *[Behav Ecol 21:381–386 (2010)]*

Recognition systems involve 3 components: an expression component, consisting of a phenotypic cue borne by the target of the recognition process, a perception component, consisting of the template against which the cue borne by the target is assessed, together with the referent on which this template is based, and an action component, which is the response to the cue bearer (Tsutsui 2004). Disentangling the perception component from the action component can be difficult (Gamboa et al. 1991; Liebert and Starks 2004). Positive evidence that recognition has occurred is only obtained when it is accompanied by a differential behavioral response toward bearers of particular cues. The lack of any such differential response may result from either a recognition error or a lack of motivation to behave differently toward individuals bearing different phenotypic cues. A lack of recognition, therefore, cannot be inferred from the lack of such a differential behavioral response.

Among eusocial insects, it is generally acknowledged that the expression component consists of an odor that is particular to each colony (Wilson 1971; Hölldobler and Wilson 1990; Crozier and Pamilo 1996) and that cuticular hydrocarbons constitute a key component of this (Lahav et al. 1999; Thomas et al. 1999; Howard and Blomquist 2005; Dani 2006). Researchers have long been aware of intercolonial variation in the behavioral response toward conspecific intruders and have generally attributed this to differences in the breadth of the recognition template. It is argued that colonies with greater genetic diversity will possess a broader colony odor and a correspondingly broader recognition template (Breed and Bennett 1987), which in turn will make them more tolerant toward (action component) or less able to recognize (perception component) alien conspecifics. The U-present (undesirable present) model for phenotype matching, recently proposed by Guerrieri et al. (2009), provides a mechanism for understanding this. According to this model, undesirable components present in the intruder's, but not the recipient's, phenotype elicit an aggressive response. Thus, in the carpenter ant *Camponotus herculeanus*, workers responded aggressively only to intruders bearing a cuticular chemical component absent from their own profile (Guerrieri et al. 2009). A colony with greater genetic diversity will presumably possess a greater range of cuticular chemical components, and workers will therefore be less likely to encounter intruders possessing chemicals absent from their own profile.

Although this intercolonial variation has been the subject of considerable theoretical discussion and empirical research, intracolonial variation has received much less attention. Although it is evident from most behavioral bioassays that there is much individual variation within colonies in response to intruders (Roulston et al. 2003; Newey et al. 2008), this variation remains largely unexplored. One exception is the study by Crosland (1990) of *Rhytidoponera confusa* in which he explored variations in the behavior of individual workers toward nonnest mates. He identified a few individual ants that were highly aggressive in each colony, whereas others were relatively nonaggressive and attributed this to differences in the aggressor rather than the victim (Crosland 1990). However, he did not determine whether this difference in behavior could be attributed to a difference in the action or perception component of the recognition system. Individual variation in behavioral response has generally been discussed in the context of the division of labor within the colony. The tasks of foraging and defense, the more dangerous tasks within the colony, are often thought to be taken up by older workers

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(Hölldobler and Wilson 2009). Thus, particular individuals are likely to demonstrate consistently a more aggressive response than others. This probably represents a difference in action rather than in perception, although the latter cannot be excluded if workers become more proficient at identifying intruders as they age. Furthermore, response thresholds can change with ecological conditions, as has been demonstrated, for example, among honeybees (Downs and Ratnieks 2000) and some ants (D'Ettorre et al. 2004). Although it is likely that behavior changes because individuals become more permissive in their response to conspecific intruders under certain conditions (action component), variation in their capacity to identify intruders (perception component) cannot be ruled out.

Using weaver ants (*Oecophylla smaragdina* L.), we explored in greater detail the variation between individuals within the same colony in their behavioral response toward conspecific intruders. *Oecophylla smaragdina* is a tropical arboreal ant found throughout south and southeast Asia and northern Australia (Azuma et al. 2006). Colonies can be very large, spanning several trees, and with up to 500 000 workers (Hölldobler and Wilson 1983). They are also aggressively territorial, with fierce battles often breaking out at colony boundaries (Hölldobler 1983). Furthermore, cuticular hydrocarbons clearly play a role in the ability of workers to identify intruders (Allan et al. 2002). However, recent evidence suggests that the aggressiveness of colonies, and of individuals within colonies, varies substantially (Newey et al. 2008). They therefore make an ideal subject for exploring these questions.

By employing a novel experimental design, we first sought to determine whether variation in the behavioral response to intruders could be attributed principally to the recipient or the intruder during one-to-one encounters. We then sought to determine whether variation in the behavior of the recipient was the result of a difference in the perception or action component of recognition. This could have important implications for understanding how recognition systems operate and particularly for the issue of template formation.

METHODS

Experiment 1

From November 2008 to March 2009, we collected medium sized nests from 10 *O. smaragdina* colonies in the grounds of James Cook University, Cairns, Queensland. Nests from 5 colonies were used as recipient nests, and nests from the other 5 colonies were used as intruder nests. We conducted 2 series of behavioral bioassays between workers from these colonies, Treatment 1 and Treatment 2. In both treatments, we placed a recipient worker in a small observation arena and allowed it to acclimate for 5 min. We then introduced an intruder into the arena. The antennae of the intruder were clipped to prevent an aggressive response toward the recipient: Without active antennae, a worker is unable to determine the status of another ant and tends to behave passively (Newey P, personal observation). We then observed the behavior of the recipient toward the intruder for a period of 5 min from the time that the former first made antennal contact with the latter. We recorded the frequency of the following behaviors of the recipient toward the intruder: antennation, grooming, trophallaxis, avoidance, recoil, aggressive posture, biting, and grappling (Table 1). If any observed behavior was maintained for a period of 5 s, it was scored as another instance of that behavior and so on for each subsequent period of 5 s. We assigned these behaviors a value from -2 to $+3$ (Table 1). Avoidance was given the same score as an aggressive stance, and recoil was given the same score as biting. We believe that this is justified, first, because it is more appropriate to regard aversive behavior as an alternative to aggressive behavior rather than as a less intense aggressive response and, second, because we feel that this more accurately reflects the energetic costs of these behaviors. However, we also repeated the analysis using a more conventional scoring system that interpreted aversive behavior as a lower level response on a continuum with more overt aggressive behavior (Table 1).

In Treatment 1 (Figure 1), 10 individual recipients were confronted consecutively with the same intruder. This was repeated 5 times (5 trials for each pair of recipient/intruder colonies), with a new intruder and 10 new recipients each time. This involved a total of 50 recipients and 5 intruders. In Treatment 2 (Figure 1), a single recipient was confronted consecutively with 10 different intruders. This was also repeated 5 times (5 trials for each pair of recipient/intruder colonies), involving 5 recipients and 50 intruders. If any intruder (Treatment 1) or recipient (Treatment 2) died before the full behavioral assay could be completed, the procedure was restarted with a new individual.

Using the frequencies of each type of behavior, we first measured the similarity between each pair of encounters in each trial using the Bray–Curtis Index (BCI):

$$\mathrm{BCI} = \frac{\sum \left| f_{i,j} - f_{i,k} \right|}{\sum \left(f_{i,j} + f_{i,k} \right)},$$

where $f_{i,j}$ is the frequency of the ith behavior in the jth encounter of the pair, $f_{i,k}$ is the frequency of the same behavior in the kth encounter, and $j \neq k$. Thus, for each individual intruder (Treatment 1) or recipient (Treatment 2) in each trial, there were 10 encounters, with 45 pairwise comparisons. We determined the mean similarity for each trial for each colony pair, in each treatment.

We also calculated a behavioral response index (RI):

Table 1
Observed behavior and associated score (*s*)

Behavior	Description	*s*
Trophallaxis	Recipient and intruder exchange fluids orally	−2 (−2)
Grooming	Recipient "licks" any part of intruder's body	−1 (−1)
Antennation	Recipient's antennae make contact with any part of intruder's body	0 (0)
Avoidance	Recipient abruptly changes direction on contact with intruder	1 (1)
Recoil	Recipient violently recoils from the intruder after contact	2 (2)
Aggressive posture	Recipient opens mandibles toward intruder	1 (3)
Bite	Recipient seizes some part of intruder's body with mandibles	2 (4)
Grapple	Recipient wraps body around intruder while biting	3 (5)

The alternative scoring system is shown in parenthesis.

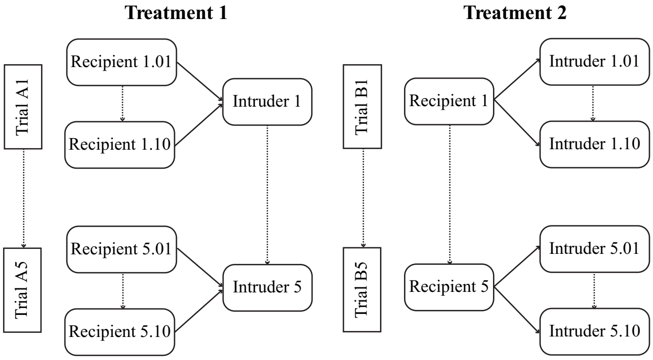

Figure 1
Design for Experiment 1, shown for a single pair of recipient/intruder colonies. This was repeated with 5 pairs of colonies.

$$\mathrm{RI} = \frac{\sum f_i s_i}{T} + 2,$$

where f_i is the frequency of a behavior, s_i is the score for that behavior, and T is the total number of observed interactions. We added “2” to the right-hand term to avoid negative values so that we could calculate the coefficient of variation (CV) for this variable in each trial. We determined the mean CV for each colony in each treatment.

In Treatment 1, individual intruders were subjected to repeated consecutive trials, so we tested for the possibility that this might have a systematic effect on the behavioral response by recipients using regression models with trial number (1–10) as the independent variable. In Treatment 2, individual recipients were subjected to repeated consecutive trials, so we also tested for the possibility that this might have a systematic effect on their response using the same procedure.

We used a repeated-measures analysis of variance (ANOVA) to compare the effects of Treatment 1 and Treatment 2 on both the BCI and the CV of RI. These variables were normally distributed and met the assumptions for this test. Analyses were performed using SPSS 16.0 for Windows.

Experiment 2

In March and April 2009, we collected a nest from each of 18 additional colonies in the grounds of James Cook University. Six of these were used as recipient colonies and 12 as intruder colonies. Individual encounters were staged as described above between 2 workers from each of the recipient colonies and 5 workers from each of 2 intruder colonies. Intruders from the 2 colonies were presented in random order to the recipients, and different intruders were used for each of the recipients. Thus, each recipient encountered 5 intruders from one colony and 5 from another (Figure 2). This was repeated for each of the 6 recipient colonies. We determined the mean behavioral RI for each series of encounters.

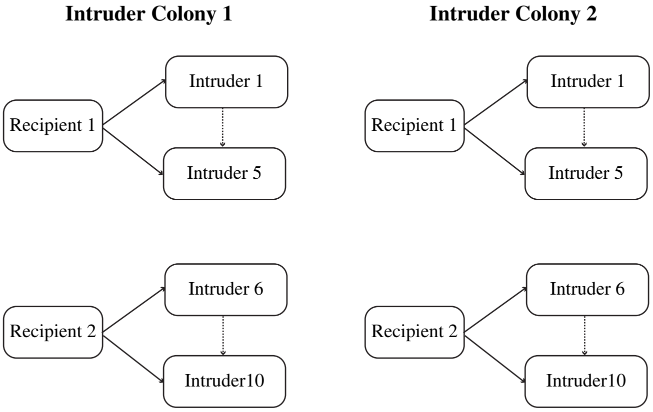

Figure 2
Design for Experiment 2, shown for a single recipient colony with 2 intruder colonies. This was repeated with 6 recipient colonies.

To determine whether one recipient worker from a colony was consistently more aggressive than the other, we conducted a 2-way ANOVA for each recipient colony with RI as the response variable and recipient and intruder colony as fixed effects. Because sample sizes were small, we used a permutation method, testing for an interaction by permuting the residuals, after accounting for main effects, following Anderson and Ter Braak (2003). If the behavior of recipient A was consistently more aggressive than that of recipient B toward intruders from both colonies, this could indicate either that 1) A was simply more aggressive than B or 2) A was better able to identify the potential threat represented by intruders. If, on the other hand, there was a significant interaction between the behavioral responses of the 2 workers to intruders from the different colonies, for example, A responded aggressively to intruders from the first colony but not the second, whereas B responded aggressively to intruders from the second colony but not the first, this would indicate a difference in the perceptual component of the recognition system: A perceives the first colony as a threat but not the second, whereas the opposite is true for B.

RESULTS

Experiment 1

There was no significant linear or quadratic relationship between trial number and RI for either Treatment 1 (linear: $F_{1,248} = 0.625$, $R^2 = 0.013$, $P = 0.433$; quadratic: $F_{2,247} = 0.422$, $R^2 = 0.017$, $P = 0.658$) or Treatment 2 (linear: $F_{1,248} = 0.009$, $R^2 = 0.000$, $P = 0.926$; quadratic: $F_{2,247} = 0.508$, $R^2 = 0.004$, $P = 0.603$). So, we conclude that repeated use of the same intruder or recipient in several consecutive encounters did not have any systematic effect on the behavioral response of recipients.

Overall, the behavioral response of a single recipient toward several intruders was significantly more consistent than that of several recipients toward the same intruder, as measured using the BCI (Figure 3; $F_{1,20} = 36.862$, partial $\eta^2 = 0.662$, $P < 0.001$). There was a significant difference between colonies tested ($F_{4,20} = 4.082$, partial $\eta^2 = 0.449$, $P = 0.014$) and a significant interaction between treatment and colony ($F_{4,20} = 3.682$, partial $\eta^2 = 0.424$, $P = 0.021$). The interaction was

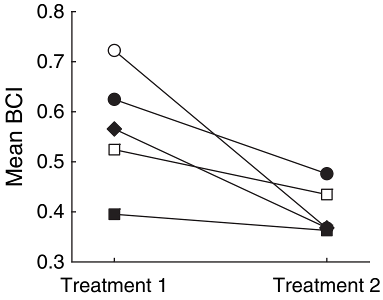

Figure 3
The mean BCI for each colony for one intruder facing several recipients (Treatment 1) and one recipient facing several intruders (Treatment 2).

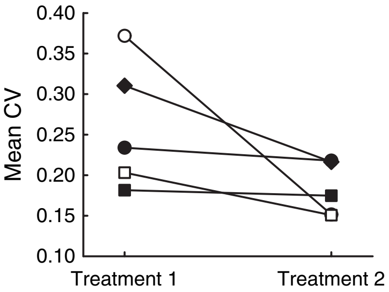

Figure 4
The mean CV of the RI for each colony for one intruder facing several recipients (Treatment 1) and one recipient facing several intruders (Treatment 2).

driven by colonies differing significantly with regard to the effect of Treatment 1 ($F_{4,20} = 6.564$, partial $\eta^2 = 0.568$, $P = 0.002$) but not Treatment 2 ($F_{4,20} = 1.186$, partial $\eta^2 = 0.192$, $P = 0.347$). Thus, colonies varied in the extent to which the same intruder elicited a different behavioral response from different recipients but not in the extent to which the same recipient responded differently to different intruders.

The CV of the behavioral RI revealed a similar pattern. It was also significantly lower in Treatment 2 than in Treatment 1 (Figure 4; $F_{1,20} = 12.604$, partial $\eta^2 = 0.387$, $P = 0.002$). Using the alternative scoring system for behavior (Table 1) did not qualitatively change this result ($F_{1,20} = 11.177$, partial $\eta^2 = 0.318$, $P = 0.003$). Again there was a significant difference between colonies ($F_{4,20} = 4.682$, partial $\eta^2 = 0.484$, $P = 0.008$) and a significant interaction between treatment and colony ($F_{4,20} = 3.310$, partial $\eta^2 = 0.385$, $P = 0.038$). The interaction was again driven by colonies differing significantly with regard to the effect of Treatment 1 ($F_{4,20} = 6.489$, partial $\eta^2 = 0.565$, $P = 0.002$) but not Treatment 2 ($F_{4,20} = 1.100$, partial $\eta^2 = 0.180$, $P = 0.384$).

Experiment 2

We detected a significant interaction in 3 of the 6 colonies tested (Figure 5): colony 1 ($F_{1,16} = 74.495$, $P = 0.008$), colony 5 ($F_{1,16} = 4.838$, $P = 0.042$), and colony 6 ($F_{1,16} = 10.231$, $P = 0.007$). This strongly suggests that in these colonies individual workers perceive intruders differently rather than just responding differently to them. In colony 1, the RI of the first recipient was higher toward intruders from the first colony than that of the second recipient ($F_{1,8} = 6.488$, $P = 0.040$), but their behavioral response toward intruders from the second colony did not differ significantly ($F_{1,8} = 2.700$, $P = 0.166$). In colony 5, there was no significant difference in the behavioral response to intruders from the first colony ($F_{1,8} = 1.366$, $P = 0.271$), but the RI of the first recipient toward the second intruder colony was lower than that of the second recipient ($F_{1,8} = 6.160$, $P = 0.047$). In colony 6, the behavioral response of the first recipient was similar toward both intruders ($F_{1,8} = 14.098$, $P = 0.022$), whereas that of the second recipient varied significantly between intruder colonies ($F_{1,8} = 1.378$, $P = 0.301$).

In 2 colonies, the RI of one recipient was significantly higher than that of the other (colony 4: $F_{1,16} = 41.746$, $P < 0.001$; colony 6: $F_{1,16} = 50.593$, $P < 0.001$), suggesting that some individuals consistently had a stronger response toward intruders than others.

Finally, in colony 2, the RI of both recipients toward intruders from both colonies was similar, whereas in colony 3, the RI of both recipients to intruders from the first colony was greater than their RI to intruders from the second colony (first recipient: $F_{1,16} = 11.341$, $P = 0.032$; second recipient: $F_{1,16} = 8.402$, $P = 0.031$).

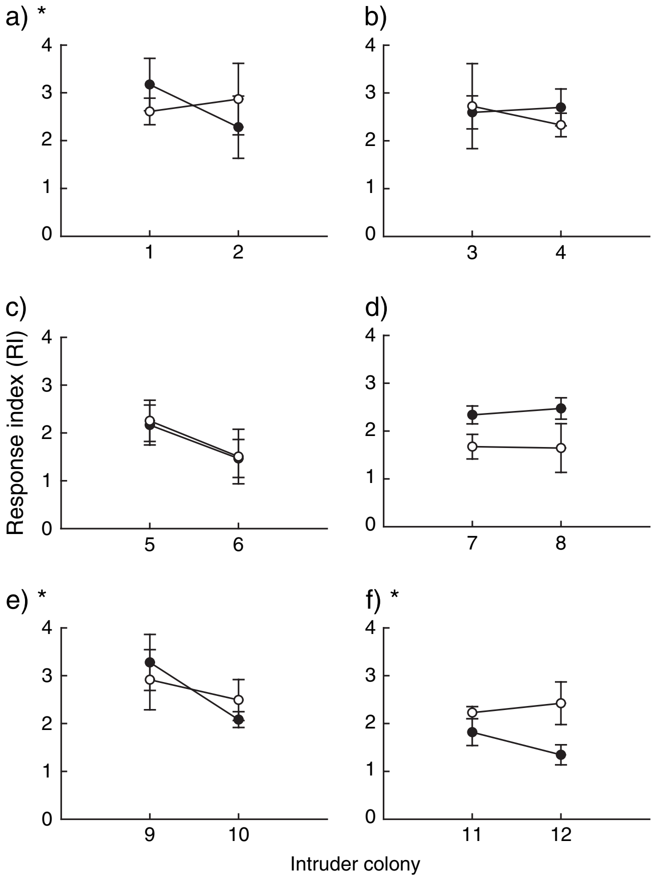

Figure 5
The mean RI of recipients facing intruders from 2 different colonies. Parts (a–f) show the results for recipient colonies 1–6, respectively. Open circles and filled circles represent the 2 individuals from each recipient colony, and asterisk indicates a significant interaction between the responses of the 2 recipients to intruders from different colonies. The error bars represent the 95% confidence intervals around the mean.

The results using the alternative scoring system for behavior (Table 1) were similar to these except that the interaction term was no longer significant for recipient colony 5 ($F_{1,16} = 2.290$, $P = 0.147$). Thus, it is unlikely that our results are simply an artifact of the method used to assess behavior.

DISCUSSION

The results of the first experiment demonstrate that there is greater variation in the behavioral response of recipients to a common intruder than in that of a single recipient to several intruders. This suggests that the behavioral response of the recipient toward an intruder is determined more by characteristics of the recipient than of the intruder. This is consistent with Mintzer's (1982) finding at the colony level in the acacia ant *Pseudomyrmex ferruginea*: Variation in aggression was greater when colonies were considered as recipients in aggressive encounters than when they were considered as intruders. At the level of the individual, our finding also supports that of Crosland (1990) but provides even stronger evidence as we used the same recipient with several intruders on the one hand and the same intruder with several recipients on the other. This could suggest that some *O. smaragdina* workers play a more aggressive role in the defense of the colony than others, in accordance with the division of labor within the colony, as Crosland concluded with respect to *R. confusa* (Crosland 1990).

However, our second experiment does not support this conclusion. Although a recipient's behavioral response is consistent toward intruders from any given colony, it is not always consistent toward intruders from different colonies. Although some recipients appear to be consistently more aggressive than others, regardless of the colony of origin of the intruder, the significant interaction term in some colonies indicates that an individual worker from a recipient colony can be aggressive toward intruders from one colony but not toward intruders from another colony whereas the reaction of another worker from the same recipient colony may be the opposite of this. Hölldobler (1983) attributed the role of colony defense primarily to older weaver ant workers. However, if age alone were the determining factor, we might expect to see an individual behaving consistently toward intruders, whatever their colony of origin. Nor do we believe that the differences in aggressive response can be attributed solely to differences between the acceptance thresholds of workers (cf., D'Ettorre et al. 2004). One worker with the same template as another, but with a higher acceptance threshold, will tend to respond less aggressively to an intruder from a given colony, but it is difficult to see how that same worker would respond more aggressively toward an intruder from another colony when its colony mate with a lower acceptance threshold responded less aggressively (Figure 5a,e). Our results suggest, rather, that different individuals undertake the defense of the colony, depending on the colony of origin of the intruder. This provides the first evidence that the variation in behavioral response arises from a difference in perception rather than just a difference in behavior: Conspecific intruders from different colonies are recognized as such and responded to aggressively by different workers within the recipient colony.

These findings are consistent with a model in which workers use different templates for assessing intruders and in which the common colony odor is not the referent for this template. One possible alternative for this referent is the individual's own odor prior to any mixing that later occurs via trophallaxis and grooming. Both genetic variation (Stuart 1988; Lahav et al. 2001; Dronnet et al. 2006; Foitzik et al. 2007) and differences in microclimate and diet (Liang and Silverman 2000; Richard et al. 2004; Buczkowski et al. 2005; Buczkowski and Silverman 2006; Richard et al. 2007) during rearing might contribute to this individual variation in odor. According to this model, different workers confronted with the same alien intruder will respond differently as the distance between each worker's template and the odor of the intruder will vary. The chemical distance between an individual recipient's current odor and that of the intruder is unlikely to be correlated with this behavioral response, as the original odor of the recipient no longer exists except as a template. Nevertheless, there is likely to be a correlation between mean colony distances and mean colony responses as the colony gestalt odor is effectively the mean of the individual odors that form the referent for the individual templates. This is consistent with observed results (Suarez et al. 2002; Newey et al. 2008).

Although we did not detect a significant interaction in all colonies, this does not invalidate our interpretation. Some individuals within any colony are always likely to have a similar template. If individual variation in odor has a genetic basis, this is more likely to occur in colonies with lower genetic variation. Because odor is shared to some extent, the current odor of individuals within the colony does not necessarily reflect the genetic diversity within the colony. However, if individuals use their original odor as a template, we predict that an interaction such as that described in the second experiment above will be more likely to occur in colonies with high genetic diversity than in colonies with low genetic diversity. Although *O. Smaragdina* is predominantly monogynous within our study population, queens are known to mate with 1 to 5 males (Schlüns et al. 2008); so this kind of variation almost certainly occurs within this population. The interaction detected in the first experiment, in which colonies varied in the extent to which the same intruder elicited a different behavioral response from different recipients but not in the extent to which the same recipient behaved differently toward different intruders, is also consistent with this model. The greater variation among recipients in some colonies is not mirrored by a greater variation among intruders in some colonies, as might be expected if it had its basis in existing differences in the odors of individuals. Thus, whatever causes the variability between the behavioral responses of different recipients is not detectable among the intruders. It is most likely masked by the sharing of odor cues throughout the colony. If the proposed model is correct, those colonies with the greatest behavioral variability between recipients will also have the greatest genetic variability.

Having a range of templates rather than a single template may result in some fitness benefits for the colony. Starks et al. (1998) found that greater genetic diversity resulted in a higher number of recognition errors in polygynous colonies of *Pseudomyrmex pallidus* compared with monogynous colonies. However, this may not always be the case. A colony with low genetic diversity, in which all workers share a common template, may consistently misidentify intruders from another colony if that colony has a similar odor, whereas in a colony with a variety of templates, some workers may identify the intruder and raise the alarm. In this case, selection may favor a variety of templates rather than a shared template, although it may still favor a shared colony odor if mistaking a colony mate for an intruder is more costly than mistaking an intruder for a colony mate. In the case of *O. smaragdina*, the first type of error could result in "civil war" and the collapse of the colony, whereas the second type of error might result only in the occasional adoption of an alien worker, who represents a "free" worker in which the colony has invested no resources.

By focusing on the differences among individual workers within colonies, this study reveals complexities in nest mate recognition that might otherwise have gone unnoticed. This individuality may itself contribute to the fitness of the colony. The evolution of polyandry (multiple queen mating) among social insects has been hypothesized to arise (among other things) from the benefits gained by having a genetically diverse workforce capable of performing the range of tasks necessary for the functioning of the colony and from the benefits gained in having greater resistance to pathogens (Crozier and Pamilo 1996). Rather than regarding the failure to recognize an intruder from a particular colony as an "error," this variability in the capacity of individual workers to recognize intruders from different colonies may represent another factor favoring selection for greater intracolonial genetic diversity.

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