# Nestmate recognition in ants (Hymenoptera: Formicidae): a review

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**Abstract**

Nestmate recognition is the process by which individuals discriminate between nestmates and con- and hetero-specifics. Nestmate recognition is based on recognition cues, which include cuticular hydrocarbons (CHCs). Models of nestmate recognition predict that recognition decisions are based on the overlap of recognition cues. Colony recipients assess cue differences by comparing an individual's CHC profile to an internal template, which is based on the colony-specific cues. The behavioral response to this assessment depends on cue similarities or differences with the template. Ants show graded responses to cue differences. More recent models of nestmate recognition include adjustable thresholds that account for graded responses and intra-colony individual variation in behavioral responses towards non-nestmates. Ants display differing levels of aggression towards conspecifics under different contexts, which suggests that nestmate recognition is context-dependent. Here, we review models of decision rules and the role of CHCs in nestmate recognition. We discuss the role of ecological and social context in nestmate recognition, and explore future directions of research for the field.

**Key words:** Context-dependent, Formicidae, hydrocarbons, nestmate recognition, review.

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## Introduction

Nestmate recognition allows workers in social insect colonies to discriminate between nestmate and non-nestmate con- and hetero-specifics (FIELDE 1903, FOREL 1923). Colonies compete for resources with neighbors. Intra- and inter-specific competition among neighbors affects colony behavior and survival (RYTI & CASE 1988, GORDON 1991, YAMAGUCHI 1995, ROWLES & O'DOWD 2007). Nestmate recognition maintains colony cohesiveness and prevents the exploitation of colony resources by non-nestmates (CROZIER & PAMILO 1996).

Nestmate recognition consists of the expression, detection, and perception of recognition cues and the corresponding action based on cue differences (NEWEY & al. 2010). Ants express recognition cues on their cuticle, which are detected and perceived as nestmate cues or non-nestmate cues. Recognition cues are thought to be compared to a template which resides in the peripheral and central nervous system (LEONHARDT & al. 2007). A template is an internal representation of the recognition cues of nestmates (LACY & SHERMAN 1983). Individuals are recognized as nestmates when the recognition cues of a recipient are sufficiently close to the template used by the individual assessing the recipient (OBIN & VANDER MEER 1989, NUNES & al. 2008).

The action component of nestmate recognition is the behavioral response. It is the definitive signal that researchers use to determine whether recognition has occurred. However, social insects may be able to discriminate between nestmates and conspecifics without any response apparent to us (BREED 2003). In addition, evidence suggests that the action component is context-dependent (BUCZKOWSKI &

SILVERMAN 2005, BOS & al. 2010) and may not simply depend on differences in recognition cues.

Cuticular hydrocarbons (CHCs) are of particular importance in nestmate recognition in social insects because they very often contain the recognition cues used to distinguish nestmates from non-nestmates (SINGER & ESPELIE 1992, DAHBI & al. 1996, GAMBOA & al. 1996, SINGER & ESPELIE 1996, LORENZI & al. 1997, LIANG & SILVERMAN 2000, RUTHER & al. 2002, LORENZI & al. 2004, BUCZKOWSKI & SILVERMAN 2006, ROMANA DANI 2006, TORRES & al. 2007, VAN WILGENBURG & al. 2006, TANNURE-NASCIMENTO & al. 2007, VASQUEZ & SILVERMAN 2008, LALZAR & al. 2010, VAN WILGENBURG & al. 2010). Nestmates share similar CHC profiles due to genetic relatedness (PAGE & al. 1991, ESPELIE & al. 1994, DRESCHER & al. 2010, NEHRING & al. 2011) and hydrocarbon transfer through trophallaxis and grooming (SOROKER & al. 1994, SOROKER & al. 1995, DAHBI & al. 1999, SOROKER & HEFETZ 2000, LENOIR & al. 2001a, FOITZIK & al. 2007). Sharing of hydrocarbons among nestmates creates a colony-specific CHC profile (DAHBI & LENOIR 1998) that encodes multiple levels of recognition (reviewed by D'ETTORRE 2008).

CHC profiles differ among species (MARTIN & al. 2008a, VAN WILGENBURG & al. 2011), colonies (LAVINE & al. 1990, DAHBI & al. 1996, MARTIN & al. 2008b), reproductive castes (MONNIN & PEETERS 1999), and task groups (WAGNER & al. 1998, MARTIN & DRIJFHOUT 2009a). In addition, CHC profiles change over time (LENOIR & al. 2001a, VAN ZWEDEN & al. 2009, DRESCHER & al. 2010), with diet (LE MOLI & MORI 1990, LIANG & al. 2001, ICHI-

NOSE & LENOIR 2009), age (CUVILLIER-HOT & al. 2001), and environmental conditions (WAGNER & al. 2001, BUCZKOWSKI & SILVERMAN 2006).

Several models have been proposed to explain nestmate recognition. The earlier models proposed that nestmate recognition is based on shared alleles at specific odor loci (CROZIER & DIX 1979, GETZ 1981, GETZ 1982). However, recognition cues are assessed at the phenotypic level and not the genetic level. Conspecifics contain the same CHCs but in colony-specific quantities (reviewed by LENOIR & al. 2001b). Consequently, CHC profiles overlap among colonies. Cue distribution models propose that ants base nestmate recognition decisions on the extent of overlap in recognition cues (reviewed by VAN ZWEDEN & D'ETTORRE 2010). Individuals make a decision to reject or accept based on cue similarities and / or differences. However, such binary recognition may be unlikely. Individuals show variation and graded responses to non-nestmates (NEWEY & al. 2010). More recent models suggest a graded response to nestmate recognition with dynamic thresholds for aggression that may be context-dependent (REEVE 1989, VAN ZWEDEN & D'ETTORRE 2010, NEWEY 2011).

In this review, we examine the basis for nestmate recognition in ants. We discuss current models of decision rules for nestmate recognition. We review the role of hydrocarbons as recognition cues, and we focus on nestmate recognition as a context-dependent process. We investigate the role ecological context plays in nestmate recognition for *Pogonomyrmex barbatus*. Finally, we explore future directions for research in the field.

## Nestmate recognition models

Earlier models of nestmate recognition assumed workers discriminated among kin and non-kin through the assessment of colony-specific alleles (CROZIER & DIX 1979, GETZ 1981, GETZ 1982). Of course, genes are not directly assessed by ants, and there are no clear examples of genetically encoded templates (ALEXANDER 1990, PFENNIG & SHERMAN 1995). In addition, relatedness of the individuals within colonies varies with queen number, extent of polyandry, and colony size (BOOMSMA & al. 1999, PEDERSEN & BOOMSMA 1999, MURAKAMI & al. 2000, DIEHL & al. 2001, KELLNER & al. 2007). In certain ant species, colonies are comprised of genetically unrelated individuals, as in slave-making ant colonies (TALBOT & KENNEDY 1940, BUSCHINGER 2009) or parabiotic ant colonies (ORIVEL & al. 1997). Nestmate recognition appears to function even when nestmates are not related making it apparent that nestmate recognition is distinct from kin recognition.

It became clear through observations of mixed colonies and mixed species studies (MORLEY 1944, KING & SALLEE 1957, SANWALD 1968, ALLOWAY 1980, CARLIN & HÖLLDOBLER 1983, CARLIN & HÖLLDOBLER 1986, CARLIN & al. 1987) that ants incorporate unrelated con- and hetero-specifics into their colonies. This implied a transfer of recognition cues among naturally or artificially mixed nestmates, which was similarly proposed by the Gestalt model (CROZIER & DIX 1979). ERRARD & VIENNE (1994) showed that mixed species groups of *Manica rubida* and *Formica selysi* gradually acquired hydrocarbons from their heterospecific nestmates. Furthermore, CHC analysis of the slave-maker ant suggested that *Polyergus rufescens* adjusted the proportions of some common CHCs

to match that of their *Formica rufibarbis* or *F. cunicularia* slaves (BONAVITA-COUGOURDAN & al. 1997). SOROKER & al. (1994) provided definitive evidence for the Gestalt model by showing that radioactively labeled hydrocarbons are transferred to the post pharyngeal gland (PPG) and cuticle of nestmates through trophallaxis, grooming, and contact. The authors suggested that the PPG is the site for the colony odor in ants.

Early experience in the nest affects the ability to discriminate between nestmates and non-nestmates (GAMBOA & al. 1986, LORENZI & al. 1999, ERRARD & al. 2008), which suggests a learning period for template acquisition (however see LE MOLI & MORI 1985). Callow workers are generally less aggressive to non-nestmates than their adult counterparts (JAISSON 1991) and can be placed with unrelated callows to form mixed colonies (ERRARD 1984), which suggests template learning occurs early in development. Additionally, colony CHC profiles change over time (DRESCHER & al. 2010), so adult workers must constantly update their profile and template (LE MOLI & MORI 1989, ERRARD & HEFETZ 1997, LENOIR & al. 2001a). Since the PPG is located close to the brain and contains the mixture of nestmate hydrocarbons, it is considered an important organ for template formation and learning in nestmate recognition (LEONHARDT & al. 2007).

Individuals within species generally share the same hydrocarbon molecules in their profiles; therefore, conspecifics often exhibit overlapping cues (GETZ 1981, LACY & SHERMAN 1983, GETZ 1991, COUVILLON & al. 2009). Cue distribution models of nestmate recognition propose that the amount of overlap between the recipient's cues and the actor's template determines whether an individual is accepted into the colony (LACY & SHERMAN 1983). The probability of acceptance and rejection errors depends on the position of the acceptance threshold, the boundary at which workers will no longer accept individuals as nestmates (Fig. 1).

The "desirable-present" (D-present) and the "undesirable-absent" (U-absent) models (SHERMAN & al. 1997) predict different positions for the acceptance threshold, based on the types of cues ants assess during dyadic encounters. Under the D-present model, workers accept individuals with desirable cues. Desirable cues are present in all nestmates and some non-nestmates, therefore, workers will accept some non-nestmates in error. Under the U-absent model, workers reject individuals with undesirable cues. Undesirable cues are present in all non-nestmates and some nestmates. Workers reject nestmates whose recognition profiles are too far from the colony mean.

REEVE (1989) found that an acceptance threshold that maximizes fitness must consider the fitness consequences of making recognition errors. REEVE (1989) proposed a context-dependent, plastic acceptance threshold that minimizes acceptance and rejection errors. Acceptance thresholds may change according to environmental conditions or resource availability. For example, in the honeybee, *Apis mellifera*, non-nestmates are found in neighboring hives when nectar flow is abundant, but in times of low food supply when loss of resources to the colony entails a high fitness cost, non-nestmates are readily identified and killed (RIBBANDS 1954).

VAN ZWEDEN & D'ETTORRE (2010) build on the D-present and U-absent models by proposing the "undesirable-present" (U-present) model to explain nestmate recognition
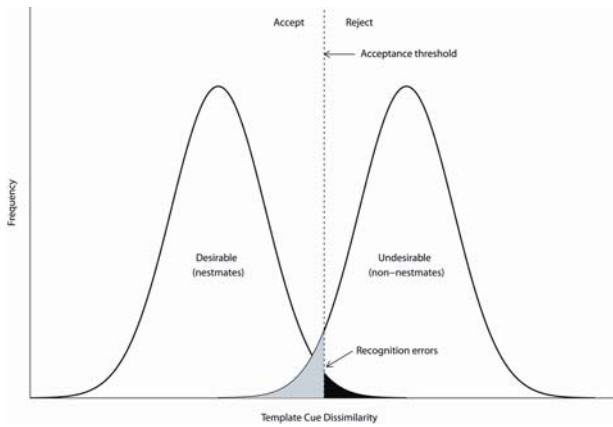
Fig. 1: Acceptance threshold for nestmate recognition in recognition cue dissimilarity models. The dashed line represents the acceptance threshold for which ants either accept or reject individuals. The shaded areas represent recognition errors. The shaded area in grey represents acceptance errors, and the shaded area in black represents rejection errors. Adapted from SHERMAN & al. (1997). Printed with permission from Wiley-Blackwell: Behavioral ecology: an evolutionary approach, copyright 1997.

and its underlying neural mechanism. The authors suggest individuals respond to the presence of undesirable cues. Implicit to the model is that individuals are habituated to their colony odor, and therefore only respond to unfamiliar recognition profiles. Their model follows the rule "if olfactory receptor neurons are not spiking and/or the pattern of activation in the antennal lobes is not altered, the encountered individual is accepted as a nestmate." The model assumes that nestmate recognition occurs at the level of the antennae and antennal lobes. It predicts graded responses to increasingly dissimilar CHC profiles and a context-dependent threshold. Graded responses follow a non-linear relationship between cue dissimilarity and rejection response where low dissimilarity between individuals produces a mild rejection response followed by an increase in aggression with increasing profile dissimilarities until it reaches the leveling off stage.

The formation of the template for nestmate recognition occurs at either the level of the antennae and antennal lobes (first-order brain centers) or the lateral horn and mushroom bodies (higher-order brain centers). Previous research concluded that nestmate recognition requires long-term memory to establish a neural template, which suggests that higher-order brain centers are involved (ERRARD 1994, FOUBERT & NOWBAHARI 2008). However, recent work supports the possibility that nestmate recognition occurs in the first-order brain centers of the antennae and antennal lobes (OZAKI & al. 2005, STROEYMEYT & al. 2010). OZAKI & al. (2005) found a chemosensory sensillum on the antennae of *Camponotus japonicus* that only responds when presented with non-nestmate CHC profiles which suggests that ants are anosmic to their colony odor. However, BRANDSTAETTER & al. (2011) report conflicting results. The authors investigated the neuronal correlates of colony odors and found that *Camponotus floridanus* is not anosmic to nestmate odors. It is still unclear whether the template for nestmate recognition occurs at the level of the peripheral or central nervous system.
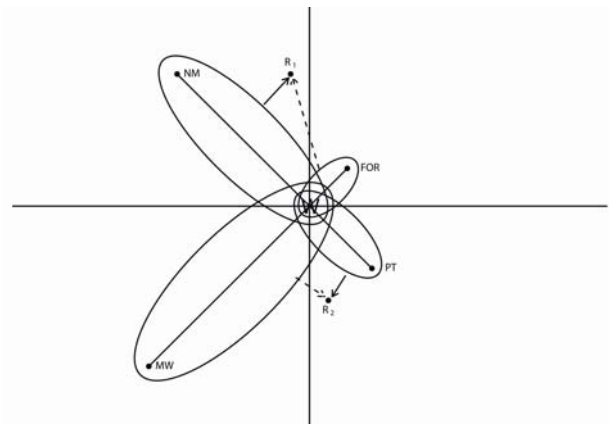


Fig. 2: Diagram based off the model proposed by NEWEY (2011) using the findings from *Pogonomyrmex barbatus* task groups. Each line is a vector originating at the origin Ω (0, 0) and ending at an endpoint, e.g., • (2, 2). Each endpoint represents a specific *P. barbatus* task group: FOR – forager, PT – patroller, NM – nest maintenance, and MW – midden worker. The origin Ω represents the colony template. Each end point • represents the average distance in chemical space of a task group from the colony template. Ellipses around the vectors represent the space in which ants will accept individuals into the colony. NM and MW have significantly larger ellipses than FOR and PT. •R$_1$ and •R$_2$ represent non-nestmates. The distance in chemical space of non-nestmates from the acceptance thresholds of *P. barbatus* task groups is represented by solid and dashed arrows. The further away the non-nestmate is from the perimeter of the ellipse, the more aggression it receives. Printed with permission from Elsevier: Journal of Theoretical Biology, NEWEY (2011), copyright 2011.

A recent model proposed by NEWEY (2011) addresses the role of individual variation in recognition behavior within colonies. Not all individuals in a colony have the same CHC profiles (WAGNER & al. 1998, KAIB & al. 2000, FERREIRA-CALIMAN & al. 2010) or react in the same manner to non-nestmates (NOWBAHARI & al. 1999). NEWEY & al. (2010) showed that in the weaver ant, *Oecophylla smaragdina*, individuals in a colony vary in aggressive response to non-nestmates. Their model proposes that ants use both their own odor and a colony template to discriminate between nestmates and non-nestmates. Nestmates whose individual profile is close to the colony profile will be less tolerant of non-nestmates than an individual whose profile is further away. The beauty of the model is that it predicts quantifiable and testable acceptance thresholds in social insect recognition systems.

Our work (S.J. Sturgis & D.M. Gordon, unpubl.) offers evidence to support Newey's model. We examined the chemical distances of individuals from their colony-specific CHC profile among *Pogonomyrmex barbatus* task groups. Task groups that were closer in chemical space to their colony-specific CHC profile displayed significantly more aggression towards non-nestmates than those that were further away (Fig. 2). The more aggressive task groups were those most likely to encounter non-nestmate conspecifics in the field. This finding reveals that ecological contexts may play a significant role in nestmate recognition.

## Hydrocarbons as recognition cues

Hydrocarbons are the most abundant chemical compounds found on ant cuticles, and they are found in the glands, crop, stomach, and hemolymph of ants (ATTYGALLE & MORGAN 1984). Hydrocarbons are synthesized in the fat bodies and oenocytes located within the epidermal layer through the elongation and conversion of fatty acids (BLOMQUIST 2010). Hydrocarbons on insect cuticles generally range in size from 21 to > 40 carbons in chain length, and consist of the hydrocarbon structural classes of *n*-alkanes, mono-, di-, and tri-alkenes, and methyl-branched hydrocarbons (reviewed by MARTIN & DRIJFHOUT 2009b). It is likely that CHCs precede eusociality in evolutionary history, since they function in many insects to prevent desiccation and cuticle abrasion, promote water balance, and act as a barrier to microorganisms (reviewed by HOWARD & BLOMQUIST 2005).

Because of the number of hydrocarbon structural classes and the variations in chemical structure within each class (reviewed by MARTIN & DRIJFHOUT 2009b), hydrocarbons permit a complex nestmate recognition system. Ant hydrocarbons are comprised of several variations of *n*-alkanes, methyl-branched alkanes, and *n*-alkenes (SCHAL & al. 1998, TISSOT & al. 2001, LENOIR & al. 2001b). *n*-Alkanes are saturated hydrocarbons that are believed to be the major components involved in water-loss prevention. WAGNER & al. (1998) found a higher abundance of *n*-alkanes on *Pogonomyrmex barbatus* foragers, which spend long periods outside the nest, than on nest maintenance workers, which mostly stay inside the nest. *n*-Alkanes have high melting temperatures, which suggests they may function to prevent dessication (GIBBS 1998, GIBBS & al. 2003).

Methyl alkanes are saturated hydrocarbons with functional methyl groups attached, while *n*-alkenes are unsaturated hydrocarbons that have ≥ one, but no more than three, double bonds along its carbon chain. Methyl alkanes and *n*-alkenes have lower melting temperatures than alkanes of the same chain length, and are typically not as effective as *n*-alkanes in waterproofing (reviewed by GIBBS 1998). Both methyl alkanes and *n*-alkenes are considered to be primary candidates for species and nestmate recognition cues (LUCAS & al. 2005, MARTIN & al. 2008a, MARTIN & al. 2008b). However, more than one hydrocarbon structural class may be needed to illicit stronger behavioral responses to non-nestmates, as in *Linepithema humile* and *Aphaenogaster cockerelli* (see GREENE & GORDON 2007a) or *Formica japonica* (see AKINO & al. 2004).

Many studies implicate CHCs as correlates of nestmate recognition behavior or as direct causes of aggression among individuals (HOWARD & BLOMQUIST 2005). Dyadic encounters between individuals from different colonies of the polydomous ant, *Cataglyphis iberica*, were highly aggressive and correlated with the quantitative differences between colonies in the major CHCs (DAHBI & al. 1996). WAGNER & al. (2000) found that *Pogonomyrmex barbatus* ants were able to distinguish nestmates from non-nestmates based on CHCs alone. The authors presented ants with glass blocks coated with whole lipid and purified HC extracts from nestmate and non-nestmates and measured the proportion of aggression to each stimulus. Blocks bearing extracts from non-nestmates elicited higher levels of aggression than blocks from nestmates. Both whole lipid and CHC extracts elicited similar levels of aggression. LUCAS & al. (2005) found that only the CHC fraction and the methyl subfraction elicited behavioral responses in the *Pachycondyla villosa* species complex. The two latter studies show a direct relationship between CHCs and nestmate recognition behavior. Other studies manipulated the CHC profiles of workers, rather than using immobile objects, and led to similar results (LIANG & al. 2001, TORRES & al. 2007, MARTIN & al. 2008c).

Other cuticular chemicals besides CHCs may also mediate nestmate recognition behavior. KATZAV-GOZANSKY & al. (2004, 2008) showed that exposure to nest volatiles in *Camponotus fellah* decreases aggression towards nonnestmates. Environmental odors, likely volatile, have been shown to play a role in nestmate recognition in bees (GILLEY & al. 2006, SCHMITT & al. 2007), wasps (STEINMETZ & SCHMOLZ 2005), and ants (ERRARD & al. 2008). However, environmental odors may consist of hydrocarbons. It is well-established that ant nests contain colony-specific CHCs (GRASSO & al. 2005, LENOIR & al. 2009, STURGIS & al. 2011). In addition, hydrocarbons may display more volatility then originally thought. CHCs analyzed by structural class show consistent melting and boiling temperatures, however mixtures of different structural classes can drastically decrease the melting and boiling points of hydrocarbons (reviewed by GIBBS 1998). BRANDSTAETTER & al. (2008) showed that *Camponotus floridanus* are able to recognize non-nestmates from a distance of 1 cm, which suggests that CHCs have some volatility.

Several methods have been employed to determine the recognition cues responsible for nestmate recognition. The use of synthetic hydrocarbons allows investigators to control the quantity and quality of hydrocarbons used to manipulate an ant's cuticle, but such synthesis is difficult. Statistical analysis, such as principle component analysis and discriminant analysis is often used to group ants according to their CHC profiles. However, hydrocarbons in the same structural class tend to be collinear, leading to violations in the model assumptions (MARTIN & DRIJFHOUT 2009c). In addition, large samples of workers are needed to perform multivariate analysis without reducing the dimensionality of the data set. VAN ZWEDEN & al. (2009) introduced diagnostic power to address questions about which HC components are crucial. Diagnostic power assesses the contribution of individual CHCs in distinguishing between colonies. CHCs with high diagnostic power are significant predictors of colony of origin.

It is important to note that statistical methods may only narrow the list of potential candidates for recognition cues, but bioassays using natural or synthetic hydrocarbons are needed to determine which compounds are used in nestmate recognition.

## Context-dependent nestmate recognition in ants

Measurements of aggression are often used as a proxy for nestmate recognition. However, lack of aggression does not always signify lack of nestmate recognition (BREED 2003). BJOERKMAN-CHISWELL & al. (2008) found an absence of aggression towards non-nestmates in the invasive Argentine ant, *Linepithema humile*, among nests ranging over hundreds of kilometers but found that non-nestmates had greater antennation frequencies than nestmates suggesting that nestmate recognition occurred. Indeed, BUCZKOWSKI

& SILVERMAN (2005) showed that aggression in *L. humile* varies with the number of ants, location of encounters, as well as other social and ecological contexts.

It was originally thought that nestmate recognition in social insects involved a binary recognition of group membership where an individual either accepts or rejects another individual based on recognition cues (ARNOLD & al. 1996, LENOIR & al. 1999). Today, it is accepted that nestmate recognition in social insects is more nuanced than previously thought, and the action component of nestmate recognition may be context-dependent (TANNER & ADLER 2009).

In the wood ant, *Formica polyctena*, aggression varies with season and temperature (MABELIS 1979). In the spring, war ensues between neighboring colonies with overlapping foraging trails. Aggression among colonies is highest during the spring when nests become active and tapers off in the summer. The number of ant casualties in war during the spring is positively correlated with temperature. In the fall, neighboring *F. polyctena* colonies share foraging trails without aggression. A related species, *Formica exsecta*, also shows seasonal variation in nestmate recognition behavior with aggression among workers of different nests being highest in spring (KATZERKE & al. 2006). In addition, aggression varies with season in the invasive ant *Paratrechina flavipes* (see ICHINOSE 1991).

Certain ant species mark their territories with colony-specific chemical cues (GRASSO & al. 2005, LENOIR & al. 2009, STURGIS & al. 2011), and these cues provide a social context in which ants will fight to defend their territory. The leaf cutter ant, *Atta laevigata,* holds a fighting advantage on trails marked with colony-specific cues and is reluctant to fight on unmarked land (WHITEHOUSE & JAFFE 1995). WENSELEERS & al. (2002) showed a similar result in the desert ant, *Cataglyphis niger*, in which disputes are settled through non-escalating fights where the territory owner generally wins. Ants may even perceive chemical cues differently depending on the context in which they are presented. BOS & al. (2010) showed that *Camponotus aethiops* were able to associate non-nestmate CHC profiles with food and still remain aggressive towards non-nestmates carrying the same CHC profiles.

Queen presence has been shown to affect the levels of aggression in several ant species (STARKS & al. 1998, VANDER MEER & ALONSO 2002, VANDER MEER & al. 2008, VASQUEZ & SILVERMAN 2008). CARLIN & HÖLLDOBLER (1983, 1986) found that workers from queenright colonies in several *Camponotus* species were more aggressive to non-nestmates than workers from queenless colonies. These results led the authors to conclude that nestmate recognition in *Camponotus* is mediated by queen discriminators. We propose that queen presence may simply be a social context in which ants display higher levels of aggression.

LAHAV & al. (1998) tested the hypothesis that queen discriminators mediate nestmate recognition in *Cataglyphis niger*. They found that queens produce significantly lower amounts of hydrocarbons than workers, which would make it difficult for the queen's recognition cues to be transferred to all members of the colony. The authors also showed that the flow of hydrocarbon transfer was predominately from worker to queen and not queen to worker, which led the authors to reject the queen discriminator hypothesis for *C. niger*.

BOULAY & al. (2003) also rejected the queen discriminator hypothesis in *Camponotus fellah*, but the authors found that queenless workers often merged with other non-nestmate queenless workers. The authors concluded that queens influence worker behavior by reducing social motivation and decreasing tolerance of alien conspecifics. In addition, VIENNE & al. (1998) demonstrated that queen presence in three Myrmicinae species has a nonspecific affect on colony-level social behavior. Their results suggest that colony behavior in general, not simply aggression, changes in the context of queen presence or absence.

Aggression varies with the presence of nestmates and the ratio of nestmates to non-nestmates (GORDON & al. 1993). ROULSTON & al. (2003) and SORRELLS & al. (2011) have shown aggression to differ depending on the number of ants involved in bioassays. Aggression also varies with time and rearing conditions. CHC profiles change over time (PROVOST & al. 1993, LAHAV & al. 2001, LENOIR & al. 2001a, ICHINOSE & LENOIR 2009), and colonies that were aggressive towards each other at one time point may not be as aggressive at another due to a convergence of CHC profiles (ICHINOSE 1991) or fluctuating environments (BUCZKOWSKI & SILVERMAN 2005). Laboratory-reared colonies often display less aggression towards conspecifics than their field-reared counterparts (OBIN 1986).

Aggression can also be task-dependent. Worker aggression toward conspecifics varies in colonies (NEWEY & al. 2010). In the red harvester ant, *Pogonomyrmex barbatus*, ants that work outside the nest showed significantly higher aggression towards non-nestmate conspecifics than did ants that work inside the nest (S.J. Sturgis & D.M. Gordon, unpubl.). *Pogonomyrmex barbatus* workers switch tasks, moving from working inside the nest to outside. Inside workers will eventually become exterior workers, and their levels of aggression will change accordingly. The only time *P. barbatus* workers are likely to encounter non-nestmates are when they are performing tasks outside the nest. Therefore, in this system, higher levels of aggression in exterior workers is ecologically relevant.

The response component of nestmate recognition has been shown to be context-dependent and may vary with time (PROVOST & al. 1993), age of workers (NOWBAHARI & LENOIR 1989), queen presence (VIENNE & al. 1998), worker numbers (SORRELLS & al. 2011), worker size (NOWBAHARI & al. 1999), etc. Ants must assess the cost and benefits of fighting. In situations in which workers have an advantage, such as territory or worker number, aggression may be more likely. The decision for aggression must also be associated with ecological factors. Ant species vary largely in ecology and behavior. Therefore, the context in which they display aggression will likely vary and may be highly species-specific. A more complete understanding of the ecology and social structure of ant species are needed before a more general pattern of nestmate recognition can be presented.

Aggression is very obvious, but other less obvious behaviors may be as important in nestmate recognition, especially depending on the context in which ants are tested. It is unclear whether the detection and perception component of nestmate recognition is context-dependent. BRANDSTAETTER & al. (2011) found that upon repeated stimulation with the same colony odor, spatial activity patterns were as variable as activity patterns elicited by different col-

ony odors. This result underscores the complexity of nest-mate recognition and olfaction in general. However, combining ecologically relevant bioassays with neurophysiological studies may be the key to understanding the process of and the likely response to recognition cues.

### Ecological context and nestmate recognition in *Pogonomyrmex barbatus*

The context in which nestmate recognition is tested matters. Ecological context plays a considerable role in nest-mate recognition. Ants may be more likely to display aggression when they are competing for resources. For example, in *Pogonomyrmex barbatus*, young colonies, which are competing for foraging space, are more persistent in returning to areas with overlapping foraging trails than older colonies (GORDON 1992, GORDON & KULIG 1996). Older colonies are more established and can therefore switch to other foraging trails whereas a young colony has less available foraging space. The cost of avoiding potential conflicts with neighbors differs between young and older colonies.

Individuals likely assess the cost and benefits of aggression. *Pogonomyrmex barbatus* foragers are slightly more responsive to neighbors, in which they compete for foraging territory, than non-neighbors (GORDON 1989a). Some may argue that workers learn neighbor CHC profiles through frequent encounters and may need more time to recognize non-neighbor conspecifics. However, *P. barbatus* patrollers are just as aggressive to non-neighbors as neighbors (S.J. Sturgis & D.M. Gordon, unpubl.). Since most foragers were patrollers before they were foragers (GORDON 1989b), this suggests that foragers weigh the cost and benefits of fighting. An unfamiliar individual from a non-neighboring colony may be less of a threat than an individual from a neighboring colony, especially considering neighbors may be able to recruit more individuals to a particular location.

In *P. barbatus*, the ants that fight are the patrollers. Patrollers are responsible for influencing foraging direction (GORDON 2002, GREENE & GORDON 2007b). Colonies avoid overlapping foraging trails with neighbors (ADLER & GORDON 2003). Foragers and interior workers are far less aggressive than patrollers (S.J. Sturgis & D.M. Gordon, unpubl.) which suggests that aggression in *P. barbatus* is primarily task dependent. Interior workers rarely, if ever, encounter non-nestmate conspecifics since they never leave the nest mound. It is likely more beneficial for foragers to forage than fight with individuals from neighboring colonies. Patrollers refrain from sending foragers in the direction in which they encountered neighbors (GORDON 1991, GORDON & KULIG 1996), which allows foragers to avoid fights.

Identifying the ants that are more likely to be aggressive may help explain individual variation in nestmate recognition behavior. It should also help guide nestmate recognition assays. For example, *P. barbatus* interior workers display very low levels of aggression to conspecifics, therefore, measuring other behavioral responses such as antennation frequency or avoidance may be a more accurate measure of nestmate recognition. CHC profiles also help explain individual variation in aggression. *P. barbatus* workers that are more likely to encounter non-nestmates are also closer in chemical space to their colony-specific odor (S.J. Sturgis & D.M. Gordon, unpubl.). This means that ants

that leave the nest mound smell more alike which should make it easier to identify nestmates and non-nestmates.

Placing nestmate recognition in the proper ecological context will help gain a better understanding of why and when ants fight. Models of nestmate recognition attempt to draw general conclusions for all social insects without thoroughly incorporating species-specific ecologies. Not all ants are alike, and therefore, the factors that influence nestmate recognition are likely to differ. More recent models of nestmate recognition recognize that acceptance thresholds are plastic and nestmate recognition is context-dependent. A thorough understanding of the ecology of ant species will likely reveal the important factors involved in nest-mate recognition.

### Future directions

Many advances have been made in our understanding of nestmate recognition. Even so, important questions remain unanswered. Nestmate recognition appears to be context-dependent in ants. In order to gain a better understanding of nestmate recognition, ecological and social factors must be linked with behavioral responses. How do these factors affect one another, and how do they differ among species? Is there a general pattern of nestmate recognition across ant taxa when ecological context is considered?

CHCs are the primary recognition cues; however, volatiles appear to play some role in nestmate recognition. Which hydrocarbon structural classes are the principal recognition cues in ants? What is the role of nest volatiles and other cuticular compounds? Synthetic hydrocarbons offer a means to identify the specific recognition cues responsible for nestmate recognition in ants. However, there are few commercially available hydrocarbons. Building a synthetic library of hydrocarbons to be used in bioassays may reveal surprising similarities in the recognition cues across ant taxa.

NEWEY (2011) proposed a promising model for nestmate recognition. By examining individual differences in chemical profiles, we may be able to predict behavioral responses of ants in dyadic encounters. Neurobiology offers a molecular perspective on nestmate recognition and promising insights into social insect olfaction. It has the potential to reveal the underlying mechanisms involved in nest-mate recognition. Further research on the behavior, ecology, chemistry, and neurophysiology of nestmate recognition will clarify how social insects manage the complex task of differentiating "us" from "them".

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