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# THE EVOLUTION AND ONTOGENY OF NESTMATE RECOGNITION IN SOCIAL WASPS

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During the past decade, a substantial and rapidly expanding literature has documented that a diversity of hymenopterans have the ability to recognize their conspecific nestmates (22). As recognition research enters its second generation, investigators are turning their attention to elucidating the mechanisms of nestmate recognition and how the features of these mechanisms, as well as recognition ability itself, relate to an animal's sociobiology. Such studies are important not only because of their relevance to an understanding of the evolution and ecology of hymenopteran sociality, but also because of their potential application for control of economically important social insects.

In our review, we summarize the evidence for nestmate recognition ability in social wasps, and examine in detail the mechanism of female-female nestmate recognition using primitively eusocial wasps (*Polistes*) as a model. We also compare the *Polistes* mechanism with mechanisms proposed for other social Hymenoptera and with the major theoretical models of kin recognition developed for animals in general. This is followed by a discussion of the possible adaptiveness of both female-female nestmate recognition ability and the specific mechanisms underlying this ability. Finally, we explore the preadaptations

that may have led to the evolution of *Polistes*-like female-female nestmate recognition. We conclude our review with a brief discussion of future directions of recognition research in social insects.

## EVIDENCE OF NESTMATE RECOGNITION ABILITY IN SOCIAL WASPS

We define nestmate recognition broadly as the differential treatment of conspecifics according to their nest of origin. Nestmates of north temperate *Polistes* are, on average, closely related (40). In most laboratory tests of nestmate discrimination in social wasps, non-nestmates have been collected from sites >10 km apart or are from colonies of distinct, known lineages and thus are probably unrelated. Nestmate recognition in social wasps has been investigated in spring foundresses (colony-founding females), fall gynes (potential queens), workers, and males.

### *Spring Foundresses*

Although nestmate recognition in social wasps was discussed in several early papers (e.g. 46, 63), the first definitive experimental evidence of nestmate recognition ability in social wasps was provided by Noonan (44) in a field study of *Polistes fuscatus*. She reported that resident foundresses were significantly more tolerant of introduced nonresident sister foundresses than of introduced non-sister foundresses.

Ross & Gamboa (54) documented that foundresses of *P. metricus* recognize nestmate foundresses by utilizing individually borne recognition cues. They conducted laboratory observations of pairs of nestmate foundresses and pairs of presumably unrelated foundresses of *P. metricus*. Nestmates spent significantly more time paired (motionless, <5 cm apart), engaged in significantly fewer agonistic behaviors, and had significantly more highly tolerant behaviors than did unrelated foundresses. In addition, *P. metricus* foundresses preferentially associated with nestmates in constructing laboratory nests, although a limited sample size prevented statistical analysis of this preferential nesting association.

Bornais et al (4), in a laboratory study of *P. fuscatus*, recorded pairing of foundresses (nestmates and non-nestmates) in nestboxes prior to nesting and, later, the identities of foundresses associated with newly constructed nests. This study, which documented highly significant values for both preferential nestmate pairing and preferential nestmate nesting association using blind observations (i.e. the observer was unaware of a wasp's colony affiliation), provides strong evidence of nestmate recognition. Nestmate foundresses were not only more spatially tolerant of each other, they also preferentially cooperated with each other in constructing laboratory nests.

Pratte (52) reported that foundresses of *P. gallicus*, despite extensive prior cohabitation with nestmates, do not have the ability to preferentially associate with nestmates under laboratory conditions. However, in 3 of 10 independent nesting groups, the "nestmate" pairs were actually non-nestmates that had overwintered together. Thus, relatedness was confused with overwintering association. Post & Jeanne (49) found that *P. fuscatus* foundresses do not preferentially associate with unrelated cohibernators at laboratory nests, but do preferentially associate with former nestmates regardless of whether they overwintered with them. In Pratte's (52) study, the small nestbox volumes (6000 cm<sup>3</sup>) may have forced the association of foundresses that would not normally associate in much larger nestboxes such as those used in similar studies (e.g. 4, 49, 54).

### *Fall Gynes*

Allen et al (1) found that altering colony composition within groups of laboratory overwintering gynes (potential queens) of *P. exclamans* affects the number of clumps gynes form. Groups of gynes consisting only of nestmates formed significantly fewer clumps than did equal-sized groups of gynes consisting of both nestmates and non-nestmates.

Shellman & Gamboa (57) and Pfennig et al (47) conducted blind observations of triplets of *P. fuscatus* gynes, each triplet consisting of two nestmates and an unrelated gyne, each with extensive previous exposure to its natal nest and nestmates. Gynes spent significantly more time paired with nestmates than with non-nestmate gynes. Using a second, independent bioassay of recognition (tolerance value) based on behavioral interactions, Pfennig et al (47) found that nestmates had significantly higher tolerance values than did non-nestmate gynes. Similarly, *P. carolina* nestmate gynes that had been exposed only to their natal nest for 2 hr spent significantly more time paired and had significantly higher tolerance values than did non-nestmate gynes.

Gamboa et al (15) conducted blind observations of young *P. fuscatus* gynes 15 to 70 hr after their eclosion. Nestmates had significantly greater tolerance values and minutes paired than did non-nestmates, demonstrating that very young gynes with prior exposure to their natal nest and nestmates have the ability to recognize nestmates. This appears to be the youngest age at which nestmate recognition ability has been documented in a social insect.

Ryan et al (55) recorded pairing behavior and behavioral interactions in blind triplet observations of gynes of the bald-faced hornet (*Dolichovespula maculata*). Gynes with extensive prior exposure to their natal nest and nestmates spent significantly more time paired with nestmates than with non-nestmates.

### Workers

Pfennig et al (48) conducted blind observations of triplets of *P. fuscatus* workers. In those triplets in which the two nestmates of a triplet (but not the non-nestmate) had been exposed as brood and adults to common foundresses and common nest stimuli, nestmates had significantly greater tolerance values and minutes paired than did non-nestmates.

### Gynes-Males

Larch & Gamboa (36), in a blind study, recorded behavioral interactions including copulations within triplets of *P. fuscatus* males and gynes that had extensive prior exposure to their own nest and nestmates. They found no evidence that wasps of the opposite sex recognized each other as nestmates. Post & Jeanne (50), in a follow-up study, investigated the effect of relatedness on insemination frequencies in presumed virgin *P. fuscatus* gynes that had previously been exposed to male and female nestmates for several days. They found no difference in the proportions of inseminated females that were nestmates and non-nestmates of males.

Ryan & Gamboa (manuscript in preparation) modified the design of Larch & Gamboa (36) by using virgin *P. fuscatus* gynes that had never been exposed as adults to conspecific males (treatments). In blind behavioral observations, treatment nestmates had significantly higher tolerance values but significantly fewer copulations than non-nestmates. In control observations, which were identical to the treatments except that control gynes had been previously exposed to male nestmates for approximately two weeks, nestmates and non-nestmates did not differ significantly in copulation frequency or tolerance value. Moreover, control non-nestmates had significantly higher tolerance values than did treatment non-nestmates. These results indicate that previous exposure to male nestmates affects a male's or gyne's behavior toward non-nestmates of the opposite sex. Kukuk (33) reported that male sweat bees mark females with an antiaphrodisiac. Such behavior by male wasps might explain Larch & Gamboa's negative results (36).

Ross (53), in a laboratory study of mating preference in the eastern yellow-jacket (*Vespa maculifrons*), found that virgin queens preferentially mated with male nestmates when given an equal opportunity to mate with non-nestmate males. The experimental designs employed by Ross (53) and Ryan & Gamboa (manuscript in preparation), however, do not reveal whether males, females, or both males and females have the ability to recognize nestmates of the opposite sex. For example, preferential mating may be due to male choice, female choice, or both. The significance of nestmate mating preference in *V. maculifrons* and non-nestmate mating preference in *P. fuscatus* in a laboratory setting is unclear (R. E. Ryan, G. J. Gamboa, manuscript in preparation).

## Males

Ryan et al (56) recorded behavioral interactions and pairing in blind observations of triplets of male *P. fuscatus* and found no evidence that males recognize male nestmates. However, Shellman-Reeve & Gamboa (58), using procedures modified from Ryan et al (56), conducted two separate blind recognition studies and independently documented that male *P. fuscatus* pair significantly more often with male nestmates than with unrelated males. This is the only documentation of male "brother" recognition ability in social insects; however, the significance of this ability is unknown (58). There are several important factors, including habituation and age of males, (58) that may explain the disparity in the results of Ryan et al (56) and Shellman-Reeve & Gamboa (58).

## Brood

Klahn & Gamboa (32) switched preemergence, brood-filled combs of *P. fuscatus* between nestmate foundresses and between unrelated foundresses. Foundresses accepted nestmates' combs with little brood destruction but destroyed younger brood in the combs of unrelated foundresses and frequently deserted these combs. These results established that *P. fuscatus* foundresses can discriminate between related and unrelated brood, although it is unknown if the recognition cues reside in the comb and/or brood.

## Summary

Nestmate discrimination in social wasps has been documented among spring foundresses, fall gynes, workers, males, and nestmates of the opposite sex. In addition, foundresses of *P. fuscatus* can discriminate kin from non-kin brood. Without exception, nestmates/kin are more tolerant of each other than are non-nestmates/non-kin. Moreover, preferential tolerance of adult nestmates is apparently not due to differences in size between nestmates and non-nestmates (47, 58).

Nestmate discrimination has been documented in six temperate species of social wasps from three genera and two subfamilies. Thus, nestmate discrimination ability appears to be widespread in at least temperate social wasps. *P. gallicus* is the only species of social wasp in which nestmate recognition ability has been studied but not documented. Because of Pratte's (52) experimental protocol (see Spring Foundresses), the nestmate recognition ability of *P. gallicus* should be reinvestigated. In any event, the failure to document recognition ability does not necessarily establish the lack of such ability, but rather may simply reflect the insensitivity of a particular assay for detection of recognition ability.

Tolerance value, a recognition assay based on 10 common behavioral interactions ranked by their tendency to elicit a retreat away from the initiator of the interactions, appears to be highly sensitive in detecting recognition ability in

social wasps. Such an assay, which uses information from all common behavioral interactions between triplet members, is more likely to be sensitive to recognition ability than an assay based solely on a single or a few arbitrarily chosen behavior(s). Indeed, tolerance value is more sensitive to recognition ability than pairing in social wasps when triplet members are behaviorally active (15, 47, 48). In all cases, however, both estimates of spatial tolerance, tolerance value and pairing, exhibit parallel trends.

For the remainder of this article, we shall confine our discussion to the mechanism, adaptiveness, and evolution of female-female nestmate recognition since there is little evidence on these topics for other classes of adults. Future studies may reveal important similarities and differences, at both the proximate and ultimate level, in nestmate recognition involving different adult classes.

## MECHANISM OF NESTMATE RECOGNITION

Nestmate (kin) recognition consists of two distinct components, expression and perception: One animal expresses a recognition cue while a second animal perceives and decodes it (2, 59). Most recent studies of nestmate recognition in ants and bees have focused on the expression component (e.g. 5, 6, 18, 19, 42). In contrast, recent studies of nestmate recognition in social wasps have concentrated on the perception component (e.g. 47, 48, 57). In the following discussion, we consider the evidence for the expression and perception components of recognition in social wasps and then compare this with evidence from other social Hymenoptera. The evidence for the mechanism of nestmate recognition in social wasps is based, with few exceptions (e.g. 32, 48, 55) on laboratory studies of *Polistes* gynes.

### *Expression Component of Nestmate Recognition*

**PHYSICAL NATURE OF THE RECOGNITION CUE** Wasps learn recognition cues from the natal nest and/or brood; thus recognition cues cannot be visual, tactile, or auditory features of adult nestmates (47). Only chemical cues are likely to be shared by the nest (and/or brood) and adult nestmates. Pfennig et al (47) also documented that gynes can acquire recognition cues from a nest, a result that further points to odors (including contact chemicals) as recognition cues. Finally, when gynes have been reared under conditions of controlled (homogeneous) environmental odors and have been recently exposed to their natal nest and nestmates, they fail to discriminate between familiar nestmates and unfamiliar non-nestmates reared under the same conditions (15). Thus, all of the experimental laboratory evidence strongly implicates odors as nestmate recognition cues.

West-Eberhard (63, 64) stated that *Polistes* colony residents identify non-

nestmates by their manner of approach to the nest and by their dominance behavior. She reported that resident wasps usually fly swiftly and directly to the nest while nonresidents approach the nest in a hesitating manner; heavily laden foragers returning to their own nest in a similar hesitating manner frequently evoke the same kind of "aggression" as that directed at non-nestmates. These observations did not differentiate between nestmate recognition and recognition of nonconspecific intruders such as parasites, or between aggression toward foragers and vigorous solicitation of foragers. Additional evidence is required to show that social wasps use anything other than odors as nestmate recognition cues. No colony or individual recognition cues other than chemical signals are known in ants and bees (22), although redundant, multimodal recognition cues are theoretically possible.

**PROXIMATE SOURCE OF NESTMATE RECOGNITION ODORS** Nestmate recognition may be mediated by individually produced (endogenous) and/or acquired (exogenous) recognition odors. Although Pfennig et al (47) documented that recognition odors can be acquired by young *Polistes* gynes, it was not then known whether nestmate recognition is mediated by only adult-acquired recognition odors. To investigate this, Gamboa et al (15) conducted a "reciprocal nest exposure study" entailing blind observations of control and treatment triplets of *P. fuscatus* gynes. Each control triplet consisted of two nestmates and an unrelated gyne, each of which had been exposed to its own natal nest and nestmates. In treatment triplets the two nestmates had been exposed to the nest and nestmates of the unrelated gyne in the triplet; conversely, the unrelated gyne had been exposed to the nest and nestmates of the two nestmates of the treatment triplet. Nestmates in treatment triplets should have been the most tolerant pair of wasps *if recognition odors were entirely acquired in the adult stage* since nestmates (but not non-nestmates) had the opportunity to learn, from different fragments of the same nest, a common odor that they both shared via acquisition. However, treatment nestmates should have been the least tolerant pair of wasps *if recognition odors were endogenous (or acquired prior to emergence)* since nestmates would have learned different odors than they expressed, but non-nestmates would have learned the same odor that non-nestmates expressed.

The results of the reciprocal nest exposure study were intermediate between the two predicted results and this, together with additional evidence (15), indicated that both endogenous (or brood acquired) odors and odors acquired as an adult mediate recognition in *P. fuscatus*. Interestingly, control nestmates, which learned both components of each others' odor, were not more tolerant than treatment gynes, which learned only the adult-acquired component of each others' odor. That is, even though tolerance values are sensitive to continuous differences in tolerance, endogenous and adult-acquired odors were not additive in their effects on tolerance.

**ULTIMATE ORIGIN OF NESTMATE RECOGNITION ODORS** The question of the ultimate origin (i.e. heritable or environmental) of recognition odors differs from, and cuts across, the question of the proximate source (i.e. endogenous or exogenous) of recognition odors (15). Although both endogenous and adult-acquired odors mediate nestmate recognition in *Polistes*, it was unknown if intercolony variation in recognition odors was independent of environmental factors (i.e. heritable) or dependent on variable environmental factors such as food or nesting materials (i.e. environmental). Therefore, Gamboa et al (15), in a blind study of *P. fuscatus*, investigated the nestmate recognition ability of gynes reared in a controlled (homogeneous) laboratory environment and compared these results with results of nestmate recognition studies of *P. fuscatus* gynes reared in an uncontrolled (heterogeneous) field environment. Non-nestmates reared in a controlled laboratory environment had significantly higher tolerance values than non-nestmates reared in uncontrolled field environments, indicating that the recognition odor has a significant environmental component. However, these laboratory gynes, which spent their entire life cycle from egg through adult in a controlled laboratory environment, later (after a period of isolation from the nest) preferentially paired with nestmates in follow-up surveys, demonstrating that the recognition odor also has a heritable component. Since laboratory non-nestmates, which shared environmental but not heritable recognition odors, initially treated each other as nestmates, environmental recognition odors must have at least temporarily overridden differences in heritable recognition odors. Interestingly, environmental and heritable recognition odors were not additive in their effects on tolerance.

Klahn & Gamboa (32) suggested that foundresses of *P. fuscatus* might utilize genetic cues to recognize related brood since foundresses discriminated between their sisters' brood-filled comb and the brood-filled comb of an unrelated foundress regardless of the proximity of the two sister colonies and the two unrelated colonies.

In three of the most extensively studied social insects, *Apis mellifera* (5, 28), *Lasioglossum zephyrum* (8, 19), and *P. fuscatus* (15), there is convincing evidence of both heritable and environmental components of recognition odor. Despite confirmation of environmental components of recognition odors in these and other social insects, their potential importance may be underestimated. This may be due in part to the erroneous assumption that recognition of genetic relatives implies recognition of a genetically based cue, an idea that is perhaps reinforced by the tendency of mathematical models of kin recognition to assume a strictly genetic basis for the recognition cue (11, 16, 17, 35). Natural selection should favor individuals that use any available information about kinship, regardless of the ultimate origin of the information.

In light of the possible importance of environmental recognition cues in *Polistes*, we have examined the potential information value of environmental

recognition odors by developing a model of *Polistes*-like nestmate discrimination based entirely on environmental recognition odors. Consider a set of interacting colonies that share a foraging area containing  $M$  types of chemically distinct nest construction materials. A fraction  $p_i$  of all spots in the foraging area contain the  $i$ th nesting material ( $1 \leq i \leq M$ ). The initial choice of a foraging spot is random with respect to nesting material; subsequently, all colony workers preferentially collect the same nest material, either by repeated visits to the same spot (which may be nearest to the colony) or by actively searching for this material at other spots. As in *Polistes*, individuals learn the odors of their nest after emergence; in particular, they learn and absorb into their epicuticle the odor of their nest's most abundant nest material ("principal odor").

When a colony worker encounters a conspecific intruder, it identifies the intruder by its cuticular principal odor. If the principal odor is different from that of the worker's own nest, the intruder is rejected; otherwise, it is accepted into the colony. Let us measure the "recognition error" for this recognition system after Getz (16) as  $\frac{1}{2}$ (probability that a nestmate will be rejected + probability that a non-nestmate will be accepted). The mean recognition error for our system is  $(\sum_{i=1}^M p_i^2)/2$ .

For a wide range of conceivable parameter values, this recognition system can generate moderate to small recognition errors. For example, if  $M=2$ , with  $p_1=p_2=0.50$ , the recognition error is 0.25. If  $M=3$ , with  $p_1=0.40$ ,  $p_2=0.30$ , and  $p_3=0.30$ , the recognition error drops to 0.17.

In our model, nest odor is analogous to a single genetic locus: It can exhibit multiple alternative states. We can describe this equivalence quantitatively by asking what number of alleles at a single genetic locus for a genetic cue recognition system will give rise to a recognition error equal to that generated by our environmental cue recognition system. For example, consider a version of Getz's (16) model of kin recognition: Individuals learn their own genetic labels (each allele produces a unique, identifiable label) and perceive the number of labels they have in common with other individuals. An individual is rejected by a worker if the number of shared labels falls below a criterion; otherwise it is accepted. The minimum recognition error for nestmate (full sib)-non-nestmate (unrelated individual) discrimination for a one locus genetic system, as a function of  $n$  equally frequent alleles, is equal to  $(4n^2 - 6n + 3)/2n^3$ . Thus, in our first example of the environmental cue model ( $M=2$ ), the recognition error is equal to that yielded by the genetic cue model if there are 6 alleles at the genetic locus. For our second example ( $M=3$ ), the environmental cue model is equal in efficiency to the genetic cue model if there are 10 alleles at the genetic locus.

Clearly then, environmental cues can theoretically be useful indicators of colony affiliation, even in our conservative model, and may provide kin recognition accuracy comparable to that provided by genetic cues. If assump-

tions of the model are relaxed (e.g. different foraging areas and consequent variation in the  $p_i$  vector for interacting colonies, or detectability of quantitative as well as qualitative differences in odors), then recognition efficiency can be even further enhanced. If other kinds of environmental odor variation (e.g. variation in larval and adult food odors) are added, recognition errors could be reduced dramatically, just as multiple genetic recognition loci permit more efficient recognition than a single locus (11, 16, 17, 35). Finally, we emphasize an advantage of environmental recognition odors over endogenous (but not exogenous) genetic recognition odors: The uniformity of recognition odors across colony members may greatly promote nestmate recognition efficiency (11). When environmental recognition odors are acquired by colony members from a common odor source (as in our model), or if these odors are readily transferred among individuals, there is likely to be less intracolony variation in recognition odors than when the odors are genetic and endogenous, especially if colonies contain multiple or multiply mated queens.

The decay of environmental odors in the absence of the odor source (e.g. the nest) could greatly diminish their utility unless individuals are regularly exposed to the odor source. However, environmental cues could mediate recognition even in recognition contexts involving prolonged absence from the odor source. M. Locke (personal communication) has suggested that insects may be especially prone to acquire environmental odors at or shortly after the time of eclosion, and that odors acquired during this time may become semi-permanently "locked" into the cuticle. After molting, the newly formed epicuticle changes from water permeable to highly hydrophobic as it becomes tanned with quinones and stabilized with lipids (39). It is possible that a number of environmental compounds could be trapped by the new epicuticle at this time. If these environmental odors diffuse through the epicuticle slowly, they could give rise to long-lasting odors in the same way that a scented candle produces a persistent odor.

If this "scented candle" model is even partly correct, some environmental odors could rival endogenous, genetic odors in permanence. Therefore, investigators should not assume that partial control of environmental odors, such as the isolation of field collected adults in a homogenous laboratory environment for a period of time, will result in a decay of (thus "control for") environmental odors. Even very young adults (and conceivably even brood) might already possess persistent environmental recognition odors that might be mistaken for genetic odors. Even if one documents genetic recognition odors by carefully controlling environmental odors, this does not establish that genetic odors are important (or more important than environmental odors) in field contexts. Social insects may be programmed to perceive odor differences without regard to ultimate origin, and field intercolony environmental odor variation may be greater than field intercolony genetic odor variation.

We do not argue that environmental recognition cues are necessarily more important than genetic recognition cues, but merely emphasize their potential role. The actual relative importance of genetic and environmental odors in and among species may depend upon the ecology of the species, the ages and castes of the interactants, and the context of recognition. For example, if interacting colonies of a species nest and feed in a relatively uniform chemical environment, as does the acacia ant *Pseudomyrmex ferruginea*, recognition odors might be primarily genetic in origin (42). For species living in relatively diverse chemical environments (such as *Polistes*), environmental recognition odors may have an important role. In *Polistes*, environmental odors might be important in mediating worker nestmate recognition and in promoting fall diapause associations of nestmate gynes, but genetic odors may be critical in sorting spring foundresses into nestmate associations if environmental odors decay or are altered during diapause.

When environmental odors have a major role in nestmate recognition, there are several implications: (a) Lacy & Sherman (35) argue that the high informational costs of having an adequate number of genetic recognition loci and alleles constrain the evolution of recognition mechanisms based on phenotype matching. To the extent that environmental information supplements genetic information about colony affiliation, the informational burden placed on the genetic cue system is relaxed, facilitating the evolution of nestmate recognition mechanisms such as phenotype matching. (b) Selection might favor behaviors (e.g. nonrandom foraging for nest materials as described in our environmental cue model) that maintain or increase the distinctiveness of colony odors.

### *Perception Component of Nestmate Recognition*

**EVIDENCE FOR LEARNING** Shellman & Gamboa (57) documented that gynes of *P. fuscatus* with extensive prior exposure to both their natal nest and nestmates (but not gynes isolated at emergence or gynes exposed only to female nestmates) recognized nestmates. Gynes of *P. fuscatus* and *P. carolina* with a limited (1 hr to 13.5 hr) prior exposure only to their natal nest (but not gynes of *P. carolina* isolated at emergence) also recognized nestmates (47). Ryan et al (55) found that the isolation of *Dolichovespula maculata* gynes from their natal nest at emergence altered nestmate discrimination. Pfennig et al (48) reported that nestmate preference among *P. fuscatus* workers occurred only if the unrelated triplet member was not exposed to the foundress and nest stimuli of the two nestmates of the triplet. Since these four reports demonstrate that manipulating the experiences of female wasps alters or disrupts nestmate discrimination, they suggest that learning is critical for the development of nestmate discrimination. However, the results of these studies are also consistent with the hypothesis that the manipulation of a wasp's experience alters its acquisition of recognition cues rather than its learning of recognition cues.

Pfennig et al (47) exposed unrelated gynes (pseudonestmates) to different fragments of the same foreign nest and to different fragments of different foreign nests (non-pseudonestmates). The investigators, using blind observations of triplets (two pseudonestmates and a non-pseudonestmate), found that pseudonestmates were significantly more tolerant of each other than were non-pseudonestmates. These results unequivocally establish that *P. fuscatus* gynes learn recognition cues, since unrelated pseudonestmates must have learned common recognition cues to later recognize each other.

Learning is also thought to mediate the development of nestmate discrimination ability in many species of ants and bees (22). Convincing evidence for learning is provided by Breed (5) for honey bees and Buckle & Greenberg (8) for sweat bees.

**TIMING AND FORM OF LEARNING** Since experimental manipulations altering adult experiences affect nestmate recognition (47, 48, 55, 57), the learning of recognition cues in wasps appears to occur in the adult stage. Pseudonestmates of the nest fragment study (47) must have learned recognition cues as adults, since only as adults were pseudonestmates exposed to the common cues that later mediated recognition. Although this latter result documents that the learning of recognition cues does occur in the adult stage, it does not establish that learning is restricted to the adult stage.

Gamboa et al (15) have recently provided evidence that the learning of recognition cues in *P. fuscatus* is restricted to the adult stage. Gynes of *P. fuscatus* were isolated at emergence into individual cups for 1.7–71.8 hr, and then introduced into boxes containing either experienced resident (*R*) nestmates (controls) or experienced resident (*R*) non-nestmates (treatments). Experienced *R* females (females with extensive exposure to their natal nest and nestmates) were significantly more tolerant of introduced (*I*) nestmates than of introduced (*I*) non-nestmates in blind, matched control and treatment introductions. Furthermore, there was no significant correlation between the age of an *I* gyne and its tolerance by *R* females. Since these results document that young *I* gynes possess recognition odors<sup>1</sup>, the failure of gynes to exhibit nestmate recognition after isolation from their natal nest (15, 57) must be due to the disruption of the adult learning, not the adult acquisition, of recognition cues. These results, therefore, eliminate the possibility that learning of recognition cues occurs in the larval or pupal stage; otherwise, young gynes isolated at emergence should be able to recognize their nestmates.

<sup>1</sup>Sweat bees (3) and *Mischocyttarus* wasps (38) less than 2 days old appear to lack recognition odors. However, honey bees, like *Polistes* wasps, possess recognition odors within 48 hr after emergence (6).

Unlike *R* females, young *I* gynes showed no evidence of recognition ability (15); this result was consistent with previous isolation treatments (i.e. 47, 57). Interestingly, these previously isolated gynes treated all *R* females as nestmates, regardless of whether the gynes were related to the *R* females. This latter result, as well as additional evidence (15), suggests that the ontogeny of nestmate recognition ability in *Polistes* involves the development of intolerance to unfamiliar recognition odors rather than the development of tolerance to familiar recognition odors (15). The development of intolerance to unfamiliar recognition odors may be common to other social insects besides wasps. Honey bee workers, deprived of their memory through narcosis, treat all queens tolerantly regardless of whether the workers are related to the queens (5).

Social bees, like social wasps, also can learn recognition cues as adults. Previously narcotized honey bee workers can learn new queen-recognition odors as adults (5). Young mixed colony sweat bees (i.e. bees reared as adults with both sisters and unrelated bees), which admit non-nestmate sisters of their unrelated nestmates, must have learned recognition odors as adults since only in the adult stage were they exposed to unrelated nestmates. Since odd bees (i.e. bees reared as adults with only unrelated bees) apparently fail to recognize their non-nestmate sisters, they do not appear to learn recognition cues as larvae and/or pupae (8).

Female *Polistes* appear to learn recognition odors within several hours after they emerge from the natal nest. Gynes of *P. fuscatus*, exposed only to their natal nest for 1 hr, and gynes of *P. carolina*, exposed only to their natal nest for 2 hr, later recognized nestmates (47). Since gynes previously exposed only to their natal nest for 1 hr exhibited significantly weaker nestmate discrimination than did gynes with more extensive prior exposure to their natal nest and nestmates, the learning of recognition odors appears to continue after the first hour following emergence. However, increasing a gyne's exposure to its natal nest beyond 4.16 hr did not affect the strength of nestmate discrimination, suggesting that learning may be complete at 4.16 hr after emergence (47). By comparison, previously narcotized honey bee workers also appear to learn queen recognition cues within 3–5 hr (5).

The learning of recognition cues in *Polistes* results in durable memories of recognition cues. Gynes of *P. fuscatus* isolated for up to 46 days (47) and foundresses of *P. metricus* isolated as long as 99 days (54) later recognize nestmates. It is not known, however, if the memory of the learned recognition cue is permanent. Kukuk et al (34) reported that guard sweat bees (*Lasioglossum zephyrum*) isolated for 12 days rejected nearly all nestmates, suggesting a loss of memory in guard bees. However, factors other than memory loss can also explain this change in guard bee behavior (8).

The learning of recognition cues in *Polistes* resembles imprinting since

young adults learn recognition cues rapidly after emergence and retain the memory of these cues for extensive periods of time. However, it is presently unknown if learning is reversible or restricted to a specific time interval. Although it is generally assumed that the development of nestmate discrimination in ants and bees involves imprinting (22), there is little experimental evidence to support this assumption. In a study of species recognition, Jaisson (26) and Jaisson & Fresneau (27) presented evidence that imprinting is involved in the discrimination of conspecific from nonconspecific cocoons by the ant *Formica polyctena*.

**LOCATION OF THE LEARNED RECOGNITION CUE** Wasps learn recognition odors from the nest (and/or its contents) and not from nestmates and probably not from themselves. Exposure to the natal nest is necessary (57) and sufficient (47) for the development of nestmate discrimination ability in *Polistes* gynes. Gynes exposed only to their natal nest as adults and gynes exposed to both their natal nest and nestmates as adults later recognize nestmates, but gynes with extensive prior exposure (up to 115 days) to only adult nestmates and gynes isolated from their natal nest at emergence later fail to recognize their nestmates.

Additional evidence strongly implies that *Polistes* wasps do not learn recognition cues directly from themselves. Gynes isolated at emergence clearly possess recognition cues (15) and thus have the opportunity to learn their own cues, but they later fail to recognize nestmates or even exhibit a hint of nestmate preference (15, 47, 57). Although one cannot exclude the possibility that wasps learn their own odors indirectly (i.e. by learning odors that they apply to a nest), unrelated pseudonestmates of the foreign fragment study would not have recognized each other had they learned only their own odors (47).

As in *Polistes*, the nest is also involved in the development of nestmate discrimination in gynes of the bald-faced hornet, *D. maculata* (55). Treatment gynes isolated at emergence and treatment gynes exposed only to adult nestmates had significantly higher variances in tolerance values than gynes (controls) exposed to both their natal nest and nestmates. The isolation of a *D. maculata* gyne from its nest at emergence, unlike isolation of *Polistes*, did not prevent it from later recognizing nestmates. However, in the laboratory there appears to be a pronounced difference in the preemergence behavior of young *Polistes* and *Dolichovespula* gynes. Unlike young *Polistes* gynes, laboratory gynes of *D. maculata* spent variable periods of up to 3 hr sitting in their cells after removing their pupal cap; thus some treatment gynes may have had the opportunity to learn recognition odors from the nest. This may explain the greater variances in tolerance observed in treatment groups as well as the hornets' apparent ability to recognize nestmates despite their isolation from the nest at emergence (55).

Although sweat bees and honey bees learn recognition cues of their nestmates, it is not clear whether they learn these cues directly from nestmates and/or indirectly from nestmates via the nest (i.e. the soil or comb). The results of odd sweat bee and honey bee narcosis experiments suggest (but do not establish) that sweat bees and honey bees can learn recognition cues directly from their nestmates (5, 8). It would be interesting to know if sweat bees exposed as adults only to their natal nest (but not to nestmates) could later recognize their nestmates. The failure of odd bees to later recognize their sisters suggests that sweat bees do not learn their own recognition cues (8). Although this conclusion has been questioned (17), there is presently no published evidence that social insects learn recognition cues directly or indirectly from themselves. However, honey bees may learn their own odors as recognition cues (M. D. Breed, W. M. Getz, personal communication).

**CUE SIMILARITY THRESHOLD** The evidence that heritable and environmental odors and endogenous and adult-acquired (exogenous) odors are not additive in their effects on tolerance is more consistent with a "cue similarity threshold" model of recognition than with a model that postulates tolerance increasing continuously with increasing similarity between the learned and perceived cue. A wasp likely matches the template of the odor learned previously from the natal nest with the odor of an encountered wasp; if the match between the learned template and perceived odor is greater than a minimum threshold similarity, the wasp treats the encountered wasp, in terms of mean tolerance, as a nestmate; otherwise, it treats the wasp as a non-nestmate (15). Such a threshold phenomenon has not been investigated in ants and bees, although its existence does not appear to be inconsistent with available evidence. For example, in sweat bees the positive linear relationship between the degree of relatedness and the proportion of passes (19) may be the result of binary decisions of guard bees to either consistently accept or consistently reject a given bee, with increasing proportions of more highly related bees falling above the acceptance threshold.

**THEORETICAL MECHANISMS OF KIN RECOGNITION** Four different (though not necessarily mutually exclusive) proximate mechanisms have been proposed for the ontogeny of kin (nestmate) recognition in animals (reviewed in 23, 59): (a) Spatial proximity, (b) recognition alleles, (c) prior association, and (d) phenotypic matching. Here, we briefly examine which mechanism best describes the ontogeny of nestmate recognition in *Polistes*.

1. Recognition based on spatial cues differs from the other three mechanisms in that it does not involve individually or group-borne cues; locations rather than conspecifics themselves are recognized (59). Obviously, this mechanism does not explain the *Polistes* data since it has been demonstrated unequivocally

in the laboratory that individually borne cues mediate nestmate recognition. However, spatial cues (e.g. cues mediating philopatry) may reinforce individually borne cues in promoting nestmate association among spring foundresses (30).

2. Recognition mediated by recognition alleles, unlike the other three mechanisms, does not entail learning. Instead, recognition alleles are postulated to code for a phenotypic marker, for the ability to recognize the marker in other conspecifics, and for the tendency to aid individuals that display the marker (23, 59). We exclude this mechanism as a possible explanation for *Polistes* recognition because *Polistes* must learn recognition cues; individuals that are removed from their nest at eclosion display no innate recognition of nestmates.

3. Recognition based on prior association requires individuals to have had prior exposure to one another for recognition to occur (23). This mechanism, by itself, is insufficient to explain the evidence for *Polistes* since prior exposure to adult nestmates is neither a necessary nor a sufficient condition for nestmate recognition to occur in social wasps.

4. In phenotype matching, individuals form a template by learning their own phenotype or that of their nestmates. Individuals recognize nestmates by matching the nestmate's phenotype to the previously learned template (23). This mechanism is consistent with our *Polistes* data if we consider the natal nest (rather than one's own phenotype or the phenotype of nestmates) as the locus from which the template is formed. In phenotype matching, it is not necessary that phenotypic attributes be heritable, only that they be reliable predictors of relatedness (59).

## ADAPTIVENESS OF NESTMATE RECOGNITION

A complete understanding of nestmate recognition in social wasps requires a consideration of the selection pressures that have favored recognition ability and shaped the underlying mechanism. An obvious first step in the evolutionary analysis of nestmate discrimination is the description of natural social contexts in which recognition ability may be beneficial. For *Polistes*, it is convenient to group these adaptive recognition contexts into two categories: "search" contexts and "guard" contexts. In search contexts the discriminating individual chooses which individuals or colonies to usurp, rob, or join. In guard contexts the discriminating individual decides whether to admit or accept approaching individuals.

Evidence exists for at least two search contexts in *Polistes*. (a) Searches for usurpation targets: Usurpation (nest takeover) is common among foundresses of temperate *Polistes*, and there is evidence that usurpers are not closely related to foundresses of the usurped colony (13, 31, 32). Although usurpers may minimize usurpation of relatives by long-distance dispersal, it is possible that

they also use colony-borne cues to guide their choice of a target colony. By preferentially targeting unrelated individuals or colonies, usurping females may avoid losses in the kin component of their inclusive fitness. (*b*) Searches for colonies to join: Females seeking to join (and subsequently aid) other colonies or individuals may preferentially join relatives, thereby increasing the kin component of their inclusive fitness. This context is almost certainly implicated in the formation of sister foundress associations in the spring (4, 30) and may be implicated in the formation of sister diapause associations in the fall, if by joining a diapause aggregation, a gyne somehow enhances the kin component of her inclusive fitness. Other search contexts may arise when workers from recently failed colonies seek to join new colonies (25) or when workers partition their work among several neighboring colonies, a possibility raised by the occurrence of "satellite" nests (62) and between-nest drifting by workers (29).

The above search contexts can give rise to guard contexts, i.e. colony residents decide whether to accept or reject visiting conspecifics. Colony residents clearly would benefit in one or both components of inclusive fitness from an ability to discriminate between potential usurpers and nestmates (or willing helpers from other colonies). In sum, there appear to be numerous social contexts that possibly favor nestmate recognition ability.

An evolutionary understanding of nestmate recognition can be deepened by considering the possible selective advantages of specific design features of the recognition mechanism. We provide some tentative answers to five questions that can be raised about the adaptive significance of the design of the *Polistes* recognition mechanism.

1. Why is nestmate recognition based on phenotype matching? Sherman & Holmes (59) argue that phenotype matching mechanisms are most likely to evolve when (*a*) individuals often encounter unfamiliar relatives and (*b*) spatial cues are inadequate predictors of kinship. They point out that the first condition is likely in social insects with large colonies, since individuals might regularly encounter nestmates (both on and off the nest) with whom they have had no prior contact. This condition appears to hold for *Polistes*, especially when colonies become large during the period of gyne production. The second condition is less obviously found in *Polistes*. For example, since most overwintered gynes are strongly philopatric (30), it would seem that tolerance based simply on spatial proximity might be the most parsimonious mechanism ensuring association of sister foundresses. However, the latter mechanism is probably inadequate by itself, since unrelated foundresses occasionally infiltrate philopatric kin groups (31, 32) and the cost of cooperatively nesting with a non-nestmate may be large, especially from the viewpoint of a subordinate cofoundress. A phenotypic matching mechanism allows detection of unrelated interlopers.

2. Why does learning occur rapidly and early in adult life? Learning occurs rapidly perhaps because adults may become involved in critical recognition (e.g. guard) contexts soon after eclosion (13, 14). Learning of recognition odors is restricted to the adult stage perhaps because of the cost of evolving a larval or pupal nervous system capable of storing memories of recognition odors and preserving these memories through metamorphosis. In addition, colony recognition odors learned as brood might become obsolete; recognition errors may be reduced if the learning and utilization of recognition odors occur more closely in time.

3. Why do wasps learn recognition odors from the nest? The nest may have an advantage over other possible sources of template formation (e.g. self or nestmates) for phenotype matching. The nest, which is likely to contain an assortment of both genetic and environmental recognition odors, may provide a more complete record of colony-appropriate odors than would the subset of nestmates to which an individual might be exposed during the relatively brief postemergence period of recognition-cue learning. Consequently, an individual learning odors from the nest might be able to recognize a greater proportion of all nestmates than would an individual learning odors from a restricted sample of nestmates. The nest is also a more permanent or stable locus for learning recognition odors. Young wasps will always encounter their natal nest upon emergence, but may encounter no nestmates during the first few hours after emergence when recognition cues are learned, especially if they are among the first adults (e.g. workers) to emerge from the natal nest.

The learning of recognition odors from the nest rather than from self or nestmates, however, may prevent wasps from discriminating full from half sibs. The normal cohabitation of full and half sibs in *Polistes* is suggested by evidence of multiple paternity (40).

4. Why do young adults learn intolerance for non-nestmates rather than learn tolerance for nestmates? Learned intolerance for non-nestmates is probably more adaptive since young adults are likely to encounter nestmates before non-nestmates. An initial aggressiveness toward nestmates before learning tolerance for them might seriously disrupt the colony.

5. Why does there appear to be a "cue similarity threshold"? Although the threshold phenomenon may be a nonadaptive byproduct of unalterable constraints on sensory or effector systems, it may also reflect an optimal behavioral strategy. Suppose a guarding wasp is confronted with an intruder whose odors (when compared to the template) indicate that the probability that it is a nestmate is  $S$  and the probability that it is a non-nestmate is  $1 - S$ . If the guard admits the intruder (i.e. fails to make it retreat), the guard's inclusive fitness changes by  $X$  if the intruder is a nestmate and by  $Y$  if the intruder is a non-nestmate. The guard can choose any level  $t$  of mean tolerance toward the intruder, each level having a different probability  $p(t)$  of eliciting a retreat. The

guard's problem is to choose the  $t$  that maximizes the expected inclusive fitness increment  $[XS + Y(1-S)][1 - p(t)]$ . When  $X$  is positive and  $Y$  is negative, the optimal policy for the guard is to choose the level of highest tolerance (that least likely to produce a retreat) if  $S > -Y/(X - Y)$  and the level of least tolerance otherwise; in other words, the guard should implement an "all or none" acceptance threshold (Reeve, manuscript in preparation).

## PREADAPTATIONS FOR THE EVOLUTION OF NESTMATE RECOGNITION

Given the appropriate ecological pressures and preadaptations, recognition ability might be expected to evolve regardless of the level of sociality. Some form of intraspecific discrimination may have been present in solitary ancestors of modern social wasps. Indeed, there is evidence of such discriminatory ability (neighbor recognition) among female *Sphecius speciosus*, an aggregate nesting, solitary wasp whose mode of living is probably similar to that of an ancestor of eusocial wasps (H. K. Reeve, D. W. Pfennig, manuscript in preparation).

Since nestmate recognition in social wasps is mediated by olfaction, a primitive preadaptation for nestmate recognition in wasps may have been the ability to learn to discriminate between objects (e. g. food and nesting materials) on the basis of odor differences (12). From this basic preadaptation, which probably evolved in an ancestor of insects (43), we envision at least three subsequent preadaptations that may have led to *Polistes*-like female-female nestmate recognition: (a) parent-brood recognition (41), (b) mate recognition (10, 22, 60), and (c) nest recognition (10, 22, 34). The ecological contexts that may have led to these three adaptations are described in Figure 1. Below we outline the evidence for each preadaptation. Presumably, the same cues and/or perception systems that mediate brood, mate, and nest recognition could have been adopted to mediate nestmate recognition in adult females.

The possibility that parent-brood recognition served as a basis for female-female nestmate recognition is difficult to evaluate because of lack of definitive evidence of parent-brood recognition mediated by brood-borne odors in the Hymenoptera. Although it has been documented that *P. fuscatus* foundresses can discriminate between their sister's brood and the brood of an unrelated foundress in experimental nest switches, it is not known if the presumed odor cues reside in the brood or in the nest (32). Although *Polistes* queens of multiple foundress associations eat newly laid eggs of cofoundresses (64), it is not known if this recognition of eggs is mediated by odor. Even if adults of other hymenopteran species can recognize their broods by brood-borne odors (7, 37, 45), such behavior may be an outgrowth, rather than a precursor, of highly developed, adult female-female nestmate recognition ability.

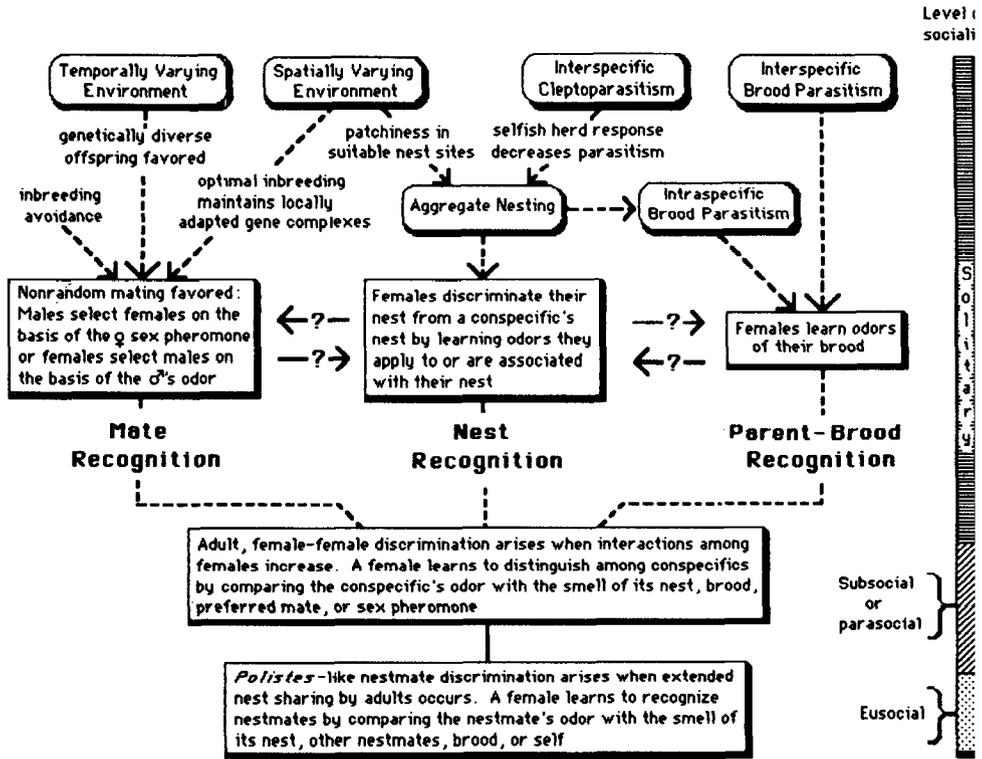


Figure 1 Ecological contexts (elliptical boxes) and evolutionary responses (rectangular boxes) that may have engendered the critical preadaptation(s) (boldface) for *Polistes*-like female-female nestmate discrimination. The solid arrows with question marks indicate that one preadaptation may have led to another before increased interactions among females occurred. At that point, one or more of the preadaptations shown here may have facilitated adult female-female recognition.

The mate recognition hypothesis is consistent with laboratory evidence that certain parasitoid wasps (65) and sweat bees (20, 60) use olfactory signals to mediate mate preference, as well as with evidence that pheromones mediating both mate and female-female recognition in sweat bees have a genetic component (20, 60). Nevertheless, it is presently unknown whether the same pheromone and/or perceptual system mediates both mate and female-female recognition. Although female sex pheromones are found in several social wasps including *P. fuscatus* (51), their role in female-female nestmate recognition or in recognition of nestmates of the opposite sex is unknown.

The nest recognition hypothesis is consistent with limited evidence that the learning of cues applied to (or associated with) a nest may be common in solitary wasps and bees (22, 61). Female cicada killers (*Sphex speciosus*) can discriminate between soil collected from the nest entrances of nearby and

more distant conspecifics (Reeve & Pfennig, manuscript in preparation). There is also evidence that such phylogenetically diverse aculeates as ants (21, 24), sweat bees (34), and honey bees (9) can recognize their natal nests by using odor cues. Perhaps the most suggestive evidence for the nest recognition hypothesis is that *Polistes* females learn nestmate recognition cues from the nest (and/or its contents) and not from nestmates; this possibly reflects an ancestral tendency to learn recognition cues from the nest. However, since females may learn nestmate recognition cues from the brood rather than the nest itself (47), this evidence is also consistent with the parent-brood recognition hypothesis.

In sum, the ecological pressures and preadaptations leading to female-female nestmate recognition remain unclear. A better understanding of the evolution of nestmate recognition in social wasps awaits additional investigation of adult-brood recognition, recognition among adult conspecifics, and mate recognition among nestmates—and the mechanisms underlying these abilities—in phylogenetically related solitary and social wasps.

## FUTURE DIRECTIONS

Although there has been a virtual explosion of new information about nestmate recognition in social insects during the past seven years, many issues in recognition remain either unresolved or unexplored. A major immediate goal is to explore the possibility of a unified mechanism of kin (and/or nestmate) recognition for social insects. Already, the rudiments of a general mechanism are apparent; young adult insects rapidly learn nestmate recognition odors. Both the perception and expression components of nestmate recognition should be rigorously investigated in male and female ants, social wasps, social bees, and termites. More specifically, investigations of the role, timing, and form of learning and the location and nature of the learned recognition cue are critical for comparing and contrasting the mechanisms of kin recognition in different social insects. A consideration of the possible dissimilarities in the recognition mechanisms of different social insects may lead to a better understanding of the ecological and evolutionary factors shaping insect recognition mechanisms.

The bulk of published recognition research in insects has been based on laboratory studies. Consequently, little is known about recognition in natural contexts. Obviously, the extrapolation of laboratory results to field contexts must be made with caution. Despite the difficulties inherent in conducting rigorous field studies of recognition, such studies are essential for a complete understanding of nestmate (kin) recognition.

Finally, we stress the importance of rigorous, quantitative studies in the investigation of insect recognition. In particular, it is critical that behavioral assays of recognition be both quantitative and blind. Behavioral observations, which serve as assays of recognition in most studies of insect nestmate (kin)

recognition, are especially susceptible to observer bias. Only through blind observations in well-controlled studies will investigators be able to make significant progress in understanding nestmate recognition in insects.

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