

Kin recognition in eusocial wasps

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Received 22 Apr. 2004, revised version received 15 Sep. 2004, accepted 2 June 2004

Gamboa, G. J. 2004: Kin recognition in eusocial wasps. — *Ann. Zool. Fennici* 41: 789–808.

Greenberg's landmark publication (*Science* 206[1979]: 1095–1097) on kin recognition in sweat bees was followed closely by experimental studies of kin recognition in primitively eusocial paper wasps. These early studies of recognition in social wasps concentrated on documenting nestmate recognition ability, which then stimulated interest in the mechanism subserving recognition ability. For the major portion of my review, I summarize our current understanding of kin, brood, and nest recognition ability in social wasps and its underlying mechanism, relying primarily on paper wasps (*Polistes*) as a model system. In my discussion of the mechanism of recognition, I review our understanding of the perception, expression, and action components of recognition. I also provide a synopsis of the recent recognition studies of two species of *Polistes* and their congeneric, obligate social parasites. Finally, I discuss our understanding of the ecology of kin recognition in social wasps and then close my review by contemplating the future directions of kin recognition research.

Introduction

For some inexplicable reason, the serious study of kin recognition did not closely follow the publication of Hamilton's (1964a, 1964b) seminal theories on kin selection. It was 15 years later when the landmark publication by Greenberg (1979) first triggered intensive kin recognition research in both vertebrates and invertebrates. Greenberg (1979), in a classic study, documented that sweat bees recognized their relatives using odor cues that are at least partly genetically specified (reviewed in Holmes 2004).

The earliest experimental studies of kin recognition in social wasps were those of Noonan (1979) and Ross and Gamboa (1981) who examined nestmate recognition in the paper wasps, *Polistes fuscatus* and *P. metricus*, respectively. These early studies of kin recognition concen-

trated on documenting recognition ability, which then generated interest in the mechanism of recognition. Subsequently, the focus of most kin recognition studies of social wasps, including recent studies, has been the mechanism that underlies kin/nestmate recognition in wasps of the primitively eusocial genus, *Polistes*. There have been relatively few studies of kin/nestmate recognition in the highly eusocial wasps. Several studies of *Polistes* wasps have examined aspects of the ecology, evolution, or adaptiveness of kin recognition, which has provided an understanding of kin recognition in temperate *Polistes* that is as complete as that of any other taxon of animals.

In my review, I first summarize the evidence for recognition ability in social wasps and then, for the major portion of the article, discuss our current understanding of the mechanism that

suberves this ability. This is followed by a synopsis of the recent recognition studies of *P. dominulus* and *P. biglumis* in association with their obligate social parasites, *P. sulcifer* and *P. atrimandibularis*, respectively. I then discuss our understanding of the ecology of kin recognition and close by contemplating the future directions of kin recognition research in social wasps.

Kin recognition ability

Adult–adult recognition

Nestmate recognition, i.e., the differential treatment of conspecifics on the basis of colony origin, has been documented in at least seven of the approximately 200 species of *Polistes*. Although nestmate recognition in *Polistes* is probably widespread, it is not necessarily universal. All seven species of *Polistes* reported to exhibit nestmate recognition are temperate species. These species include *P. metricus*, *P. fuscatus*, *P. exclamans*, *P. carolina* and *P. annularis* (Gamboa 1996) as well as the more recently studied *P. biglumis* (Lorenzi *et al.* 1997) and *P. dominulus* (Starks *et al.* 1998). Since most species of *Polistes* are tropical (Reeve 1991), our knowledge of nestmate recognition in *Polistes* is limited to a minority subset of the genus.

Nestmate recognition has also been reported in the social wasps, *Vespula maculifrons* (Ross 1983), *Dolichovespula maculata* (Ryan *et al.* 1985), *Ropalidia marginata* (Venkataraman *et al.* 1988), *Belonogaster petiolata* (Keeping 1990), *Liostenogaster flavolineata*, *L. vechti*, *Parischnogaster jacobsoni* (Cervo *et al.* 1996, 2002), and *Vespa crabro* (Ruther *et al.* 1998, 2002). In all cases, with the exception of male–female recognition in a mating context (e.g., Ryan & Gamboa 1986), nestmates of social wasps have been more tolerant of each other than have non-nestmates.

To the best of my knowledge, the only species of social wasp that has been studied but not found to display nestmate recognition ability is *Parachartergus colobopterus*. Gastreich *et al.* (1990) conducted both laboratory and field recognition bioassays of *P. colobopterus* and found no evidence that females discriminated

nestmates from non-nestmates. Although negative results can be due to factors other than a lack of recognition ability (Gamboa *et al.* 1991a), it is not necessarily adaptive for all social species to manifest or possess kin recognition ability. In fact, kin recognition could be maladaptive in certain situations (Reeve 1989, Ratnieks & Reeve 1992, Keller 1997, Bull & Adams 2000).

Based primarily on studies of *P. fuscatus*, all classes of adult females including gynes, foundresses, and workers possess nestmate recognition ability (Gamboa 1996). In addition, males can recognize their male and female nestmates (Shellman-Reeve & Gamboa 1985, Ryan & Gamboa 1986), although there is presently no definitive evidence that *Polistes* females can recognize their brothers. However, it would be surprising if females lacked this ability since all classes of adults have the appropriate colony labels and perceptual systems for nestmate recognition.

Social wasps also have the ability to recognize some non-nestmate kin. In laboratory studies conducted with blind recognition assays, gynes of *P. fuscatus* treated non-nestmate aunts and nieces like nestmate sisters, i.e., highly tolerantly (Gamboa *et al.* 1987, Gamboa 1988). In blind field studies that involved switching colonies of known relatedness to determine how resident females treated returning non-nestmate kin, Bura and Gamboa (1994) found that the treatment of non-nestmate kin was highly variable. Most cousins and nieces (~50%–65%) were treated highly intolerantly, i.e., like unrelated non-nestmates. However, a minority of cousins and nieces were treated highly tolerantly, i.e., like nestmate sisters. Most aunts and non-nestmate sisters (~80%) were treated like nestmate sisters while a minority were treated like unrelated non-nestmates. Unlike the treatment of non-nestmate kin, resident females were uniformly tolerant and uniformly intolerant toward female nestmates and unrelated female non-nestmates, respectively.

I am unaware of any evidence that social wasps have the ability to discriminate among nestmates on the basis of relatedness. Queller *et al.* (1990) provided evidence that foundresses of *P. annularis* lack the ability to make intracolony discriminations on the basis of relatedness.

Using starch gel electrophoresis to determine relatedness, they reported that foundresses did not preferentially found field nests with more closely related nestmates. Their results are especially compelling since they found no evidence of discrimination among former nestmates in a context in which I believe such an ability would almost certainly have important fitness consequences for foundresses.

Brood recognition

Klahn and Gamboa (1983) switched pre-worker, brood-filled combs of *P. fuscatus* between colonies whose queens were former nestmates (sisters) and between colonies whose queens were unrelated. Foundresses destroyed the eggs and young larvae of unrelated colonies but accepted the brood of sister colonies. Although foundresses did recognize brood on the basis of relatedness, it was unknown whether the recognition cues were associated with the brood, comb, or both. Panek and Gamboa (2000) provided queens of *P. fuscatus* a binary choice of two larvae in a petri dish. Using blind behavioral observations, the authors reported that queens discriminated between their own and unrelated larvae, between the larva of a sister and an unrelated larva, but not between their own larva and that of their sister. Queens typically bit or ate unrelated larvae but not their own or sister larvae. Thus, queens clearly had the ability to recognize larvae on the basis of relatedness, and larvae obviously possessed individually borne recognition cues. However, the study by Panek and Gamboa (2000) did not reveal whether larvae produced or acquired their cues.

The findings of Panek and Gamboa (2000) indicated that queens of *P. fuscatus* lacked the ability to make intracolony discriminations among larvae on the basis of relatedness since queens failed to discriminate between their own larvae and those of their sisters. Strassmann *et al.* (2000), in a blind field study of *P. annularis*, a species known to possess nestmate recognition ability (Pfennig *et al.* 1983b), provided convincing evidence that foundresses do not discriminate among larvae on the basis of relatedness. By using videography of foundresses feeding larvae

and subsequent DNA microsatellite analyses to determine the maternity of larvae, Strassmann *et al.* (2000) found that foundresses of multiple-foundress associations did not preferentially feed their own larvae. Thus, the laboratory study of Panek and Gamboa (2000) and the field study of Strassmann *et al.* (2000) both failed to find evidence of intracolony brood recognition on the basis of relatedness. Later, in my discussion of the mechanism of recognition, I discuss a feature of the mechanism that appears to preclude intracolony recognition.

Comb recognition

Female *P. fuscatus* (Ferguson *et al.* 1987), *P. metricus* (Espelie *et al.* 1990b), *Dolichovespula maculata* (Ferguson *et al.* 1987), *P. dominulus* (Starks *et al.* 1998, Lorenzi & Caprio 2000, Starks 2003), and *P. biglumis* (Lorenzi & Caprio 2003) can discriminate their own comb or comb fragment from that of foreign colonies. Pfennig (1990) reported that *P. exclamans* workers can discriminate between a brood-filled fragment from their own comb and that from another colony although it's not clear whether workers recognized the comb, brood, or both. These studies indicate that the ability to recognize one's comb is common in social wasps. Comb recognition has typically been documented in those species that have been found to have nestmate recognition ability. Most nest recognition studies have been laboratory studies, but in a recent study, Starks (2003) found that spring foundresses of *P. dominulus* preferentially perched on fragments of their natal comb over fragments of unrelated colonies in a large field enclosure.

The mechanism of recognition

Perception component

Kin recognition consists of three components: perception, expression, and action. The perception component includes the development of a kin template, the sensory processing of recognition cues, and the algorithm for matching the template and encountered phenotype (Reeve

1989, Gamboa *et al.* 1991a). Most of the empirical studies dealing with the perception component in social wasps have investigated the role, timing, and form of learning in the ontogeny of recognition ability. For a discussion of the perception component in recognition, *see* Mateo (2004).

Early studies of *P. fuscatus* and *P. carolina* utilized blind observations to demonstrate that manipulating the experiences of young females immediately after eclosion disrupted the development of recognition ability. For example, wasps isolated at eclosion later failed to discriminate between nestmates and non-nestmates (Shellman & Gamboa 1982). However, exposure of newly eclosed females to their natal comb for at least one hour (but not extensive exposure to nestmates) was necessary and sufficient for the development of recognition ability. Furthermore, unrelated wasps that had been exposed to different fragments of the same unrelated comb (pseudonestmates) treated each other tolerantly, i.e., like nestmate sisters (Shellman & Gamboa 1982, Pfennig *et al.* 1983a, 1983b). These studies demonstrated that newly emerged wasps were learning recognition cues and that the cues were learned from the comb. Interestingly, exposing a wasp to its natal nest for more than four hours had no effect on its recognition ability indicating that learning was complete within four hours after emergence. Ross and Gamboa (1981) sequestered individual gynes of *P. metricus*, which had extensive previous exposure to their nest and nestmates, from their nest and nestmates for 99 days. They reported that despite this extensive isolation, gynes were still able to discriminate nestmates from non-nestmates, demonstrating that the memory of the learned recognition cue was very durable. Post and Jeanne (1982) found that laboratory overwintered foundresses of *P. fuscatus* preferentially associated with their former nestmates in founding a colony regardless of whether they had overwintered with them or with unrelated gynes. Starks (2003) documented that foundresses of *P. dominulus* recognized their natal nest after winter diapause. Both of these studies clearly show that the memory of recognition cues is long lasting.

Although females of *P. fuscatus* isolated from their natal nest and nestmates at emergence later

failed to discriminate nestmates from non-nestmates (Shellman & Gamboa 1982), it wasn't clear whether isolates failed to discriminate because they were deprived of the opportunity to learn recognition cues from the nest or because they were deprived of the opportunity to acquire cues from the nest, or both. To determine this, isolate nestmate and non-nestmate gynes of *P. fuscatus* were presented to experienced females, i.e., females with extensive previous exposure to their nest and nestmates. In blind observations, Gamboa *et al.* (1986b) documented that these experienced females discriminated between isolate nestmates and isolate non-nestmates. Thus, isolates clearly possessed recognition cues and their failure to develop recognition ability was because they had been deprived of the opportunity to learn cues from the nest. Furthermore, these results demonstrated that learning was restricted to the adult stage and that wasps did not learn their own cues (Gamboa 1996). Venkataraman *et al.* (1988) conducted blind triplet observations and reported that *Ropalidia marginata* also learns recognition cues. Wasps that had been exposed as adults to their nest and nestmates, but not wasps isolated at eclosion, later discriminated nestmates from non-nestmates.

The learning of recognition cues in *Polistes* resembles imprinting. Young adults learn recognition cues from the nest within a few hours after emergence and form durable memories of these cues (Ross & Gamboa 1981, Shellman & Gamboa 1982, Pfennig *et al.* 1983a, 1983b, Gamboa *et al.* 1986b). Since *Polistes* learn recognition cues from their natal comb, it is difficult to understand how wasps could develop the ability to make intracolony discriminations on the basis of relatedness. Presumably, such discrimination ability would require that wasps learn their own recognition cues (self-referent learning; reviewed in Göth & Hauber 2004) rather than the cues of the nest.

The ontogeny of recognition ability in *Polistes* appears to involve the development of intolerance to unfamiliar cues rather than the development of tolerance to familiar cues. For example, at eclosion female *P. fuscatus* are initially highly tolerant of all conspecifics but only later become intolerant of conspecifics with unfamiliar cues (Gamboa *et al.* 1986a, 1986b).

Polistes appear to treat conspecifics either tolerantly or intolerantly, and nothing in between. For example, females of *P. fuscatus* treat non-nestmate kin either tolerantly, like nestmates, or intolerantly, like unrelated non-nestmates (Gamboa *et al.* 1987, Gamboa 1988, Gamboa *et al.* 1991b, Bura & Gamboa 1994). Therefore, females do not exhibit a graded behavioral response to conspecifics that is proportional to relatedness. Similarly, Pfennig (1990) and Gamboa *et al.* (1991b) found that females of *P. exclamans* and *P. fuscatus* were not more tolerant of non-nestmates from nearby colonies (~6–100 m apart) than non-nestmates from distant colonies ($\geq 10\,000$ m apart). One would assume that nearby non-nestmates are more likely to share environmental and genetic cues than distant non-nestmates. The lack of graded behavioral responses is consistent with the cue similarity threshold property (Gamboa *et al.* 1986a, 1986b, Reeve 1989) in which a wasp matches the template of the learned cues with the cues of the encountered wasp. If there is a sufficient match (or minimum similarity) between the learned and perceived cue, the encountered wasp is treated tolerantly. Otherwise, the wasp is treated intolerantly. Therefore, tolerance of conspecifics does not increase continuously as a function of increasing similarity between the template and encountered cue. Unfortunately, we know little about the matching process that wasps use to compare their template with the encountered phenotype. We also know little about the requisite minimum similarity between the template and encountered cues that elicits tolerance or acceptance.

Expression component of recognition

The expression component involves the nature and production (or acquisition) of the cues (labels) that identify kin (Gamboa 1996). For a discussion of the expression component in recognition, see Tsutsui (2004).

The nature of the recognition cue

Since *Polistes* learn their recognition cues from the natal comb, recognition cues cannot be

visual, tactile, or auditory features of adult nestmates. Only chemical cues could potentially be shared by the comb and nestmates. Pfennig *et al.* (1983b) found that females exposed to different fragments of the same unrelated comb shortly after emergence later treated each other as nestmates. These females, pseudonestmates, must have learned *and* acquired common cues from the nest fragments in order to later recognize each other. These acquired cues must have been odors. Finally, Gamboa *et al.* (1986b) reared colonies of *P. fuscatus* from egg through adult in the laboratory under identical environmental conditions, including identical food and nesting materials. Females from these laboratory colonies failed to discriminate nestmates from non-nestmates *if* they had been recently exposed to their common environmental odors. Again, these results point to odors, particularly environmental odors, as recognition cues.

Although the laboratory reared females of Gamboa *et al.* (1986b) initially failed to discriminate between nestmates and unrelated non-nestmates, after several days of isolation females did discriminate between nestmates and unrelated non-nestmates. These results indicated that the recognition odors must have had heritable components. The authors reasoned that the most likely explanation for their results was that the common environmental odors shared by laboratory colonies had decayed after several days of isolation thereby exposing the wasps' heritable odors (Gamboa *et al.* 1986b).

The laboratory study of Gamboa *et al.* (1986b) provides evidence that environmental odors from food and/or nesting materials can serve as components of the recognition odor in social wasps. Although environmental odors have considerable potential information value as recognition cues (Gamboa *et al.* 1986a), the evidence that recognition odors of social wasps have heritable or genetic components is much more extensive and conclusive than the evidence for environmental components of recognition odors. Nevertheless, environmental recognition odors may be important for species that live in chemically diverse environments (Gamboa *et al.* 1986a).

Although the laboratory study of Gamboa *et al.* (1986b) provided evidence for a herit-

able component of the recognition odor, it was possible that their results were due to maternal rather than genetic effects. However, several studies later documented recognition between non-nestmate kin that had different mothers (e.g., Gamboa 1988, Bura & Gamboa 1994), which clearly demonstrated that the recognition odor of *P. fuscatus* has a genetic component.

The ultimate origin of recognition odors (i.e., environmental or genetic) differs from the proximate source of recognition odors (i.e., endogenous or exogenous). For example, endogenous odors could be genetic or environmental (e.g., environmental odor sources such as food could affect the metabolic byproducts of wasps) and exogenous odors could be environmental or genetic (e.g., genetic odors might be deposited on the nest by the queen and then acquired from the nest). Gamboa *et al.* (1986b) conducted a reciprocal nest exposure study of *P. fuscatus* using blind observations and found that nestmate recognition could be mediated by endogenous odors, exogenous (acquired) odors, or both. Interestingly, wasps that learned both the endogenous and exogenous components of their nestmates' odor were not more tolerant of each other than wasps that had learned only one component of their nestmates' odor. Either exogenous or endogenous odors were sufficient to mediate a full recognition response, but the two components were not additive in their effect on tolerance (Gamboa *et al.* 1986b). These results provided additional support for the cue similarity threshold property (*see* Gamboa *et al.* 1986b, 1986a, Reeve 1989).

There appears to be some confusion as to whether recognition in paper wasps is mediated by endogenous odors, acquired odors, or both. For example, in a review of recognition, Sherman *et al.* (1997) state that paper wasps use odors acquired from the comb after eclosion to discriminate nestmates from non-nestmates. Although *Polistes can* acquire recognition odors from the comb, wasps possess a colony-specific odor independent of prior exposure to the comb after eclosion. The results of Gamboa (1986b), together with the results of Panek *et al.* (2001), demonstrate that *P. fuscatus* utilizes endogenous, colony-specific recognition odors in nestmate recognition. Presumably, the rec-

ognition odors acquired from one's natal comb are similar to those endogenous odors produced by individual wasps. The relative importance of endogenous and acquired odors in *Polistes* is unknown. Venkataraman *et al.* (1988) reported that female *Ropalidia marginata* lack endogenous odors and must acquire recognition odors from their natal nest. As discussed in considerable detail elsewhere (Gamboa 1996), the results of Venkataraman *et al.* (1988) may have been affected by their asymmetric exposures of triplet members. It would be extremely worthwhile to present isolate nestmates and non-nestmates of *R. marginata* to experienced females in the context of their nest to determine if isolates possess colony-specific odors independent of exposure to their natal comb.

Identification of the recognition odor

In two elegant and convincing studies, Singer and Espelie (1992, 1996) demonstrated that workers of *P. metricus* used cuticular hydrocarbons as nestmate recognition cues. Using blind triplet observations, the authors found that newly emerged wasps that had been exposed to their untreated nest, but not wasps exposed to a hexane-washed nest, later discriminated nestmates from non-nestmates. Newly emerged wasps that had been exposed to a washed nest in which the hydrocarbon extracts had been reapplied also later discriminated nestmates from non-nestmates. Singer and Espelie (1996) further reported that experienced females were more likely to accept newly emerged nestmates if they had been previously exposed to their natal nest with its hydrocarbons intact. This finding indicated that adult wasps had acquired colony odors, i.e., hydrocarbons, from their natal nest. In addition, as had been reported in *P. fuscatus*, Singer and Espelie (1996) provided evidence that *P. metricus* females do not learn their own odor and that learning is restricted to the adult stage. They also presented evidence that the ontogeny of recognition ability in *P. metricus*, as in *P. fuscatus*, involves the development of intolerance to unfamiliar odors rather than the development of tolerance to familiar odors.

In a study of nest recognition, Espelie *et*

al. (1990) reported that workers of *P. metricus* could discriminate between their own nest and a foreign nest when nests were untreated and when hexane-washed nests had their hydrocarbon extracts reapplied. However, workers did not manifest this ability when presented with nests that had their hydrocarbons extracted. In a similar study, Layton and Espelie (1995) found that workers of *P. metricus* previously exposed to fragments of their nests displayed different behaviors and nest affinities depending on whether the nests to which they have been exposed contained hydrocarbons (untreated and reapplied) or not. The results of these two studies showed that wasps utilize hydrocarbons for nest recognition and that the cues are learned from the nest shortly after eclosion.

Lorenzi and Caprio (2000) examined nest recognition in post-worker colonies of *P. dominulus* and *P. nimphus*. When presented with a choice of their own nest and a nearby nest, females of both species preferentially rested on their own nest. As expected, females of *P. dominulus* did not discriminate between their own and nearby nests if the nests had been washed in hexane. Females of both species discriminated between their own and nearby nests after the hexane-washed nests had their hexane extracts reapplied. Surprisingly, female *P. nimphus* did discriminate between their own nest and a nearby nest after the nests had been washed in hexane. Lorenzi and Caprio (2000) suggested that insufficient washing of *P. nimphus* nests might explain why nests were discriminated after being washed with hexane. It is not clear whether the results of Lorenzi and Caprio (2000) reflect nest and/or brood recognition ability since the authors did not mention whether they had removed brood from combs prior to their tests of nest recognition.

Soleilhavoup *et al.* (2001) investigated the relative importance of nest hydrocarbons, hydrocarbons from immature brood, and their combinations on the probability of nest adoption in laboratory colonies of *P. dominulus*. The authors reported that artificial, plastic nests were likely to be adopted if the nests contained eggs transplanted from the original nest or contained a combination of transplanted eggs, transplanted larvae and pupae, and hydrocarbons from the original comb. Soleilhavoup *et al.* (2001) con-

cluded that nest hydrocarbons were not as important as a combination of factors, including the presence of brood, in nest adoption. They further concluded that nest recognition in *P. dominulus* is probably affected by a variety of complementary stimuli rather than solely by isolated stimuli such as nest hydrocarbons.

However, it is possible that the recognition assay utilized by Soleilhavoup *et al.* (2001), nest adoption, does not assess nest recognition ability. Nest adoption may be affected by the presence of brood, and wasps may perceive nests with brood as a more valuable resource than an empty nest. In fact, Starks (1998, 2001) has presented evidence that *P. dominulus* foundresses preferentially adopt colonies with more mature brood. Nests with brood could provide a food source for adoptees or provide adoptees a worker force. Both consumption of brood and adoption of unrelated workers are commonly observed in females that usurp colonies of other conspecific females (e.g., Klahn & Gamboa 1983).

Lorenzi *et al.* (1997) reported that female *P. biglumis* had the ability to discriminate dead nestmates from dead non-nestmates unless the dead wasps had been washed in pentane. However, when the pentane-washed dead wasps had their solvent extracts reapplied, females were able to discriminate between dead nestmates and non-nestmates. Similarly, Cervo *et al.* (2002) presented dead nestmates and dead non-nestmates to field colonies of *Liostenogaster flavolineata* and found that dead non-nestmates were treated more aggressively than dead nestmates. However, dead nestmates and non-nestmates were treated equally tolerantly if they had been washed in hexane. Dead, solvent-washed, non-nestmates treated with nestmate cuticular extracts were treated more tolerantly than dead, solvent-washed, non-nestmates treated with non-nestmate cuticular extracts.

Ruther *et al.* (2002) used blind behavioral observations to examine the responses of female *Vespa crabro* to (1) dead nestmates and non-nestmates, (2) dead nestmates that had extracts of heneicosane, tricosane, or (Z)-9-tricosene applied, and (3) dead nestmates that had all three compounds applied. The authors found that females were more aggressive to dead non-nestmates than dead nestmates and that dead nest-

mates with applied hydrocarbons received significantly more aggression than either untreated dead nestmates or dead nestmates that had their cuticular extracts reapplied. The results of Lorenzi *et al.* (1997), Cervo *et al.* (2002), and Ruther *et al.* (2002), like those of Singer and Espelie (1992, 1996), demonstrated that wasps were using cuticular hydrocarbons as recognition cues.

Pickett *et al.* (2000) added a novel compound (pentacosanoic acid methyl ester) to the nest material of *P. dominulus* and then exposed females to the manipulated nest. Subsequently, females preferentially associated with nestmates that had acquired the novel compound demonstrating that wasps can learn and acquire artificial chemicals as recognition cues and can distinguish between chemical profiles that differ by a single compound. The study by Pickett *et al.* (2000), together with the study by Gamboa *et al.* (1986b), also demonstrates the potential importance of environmental odors in kin recognition.

Concurrent with studies demonstrating that paper wasps were utilizing hydrocarbons as recognition cues were numerous studies that examined the cuticular hydrocarbon profiles of various species of social wasps. By using a gas chromatograph/mass spectrometer (GC/MS), researchers have identified the cuticular compounds and their relative amounts for a number of species of social wasps. These species include *Parachartergus aztecus* (Espelie & Hermann 1988), *P. metricus* (Espelie *et al.* 1990), *P. annularis* (Espelie & Hermann 1990), *Dolichovespula maculata* (Brown *et al.* 1991), *P. dominulus* (Bonavita-Cougourdan *et al.* 1991), *Vespula squamosa* (Butts *et al.* 1991), *Vespula maculifrons* (Butts *et al.* 1991), *Vespula germanica* (Brown *et al.* 1991), *P. biglumis* (Lorenzi 1992), *P. exclamans* (Singer *et al.* 1992), *P. fuscatus* (Espelie *et al.* 1994), *Vespa crabro* (Butts *et al.* 1995), and *Liostenogaster flavolineata* (Cervo *et al.* 2002).

In general, investigators have found that the cuticular hydrocarbon profiles of social wasps are both species specific and colony specific (Singer *et al.* 1998). Typically, interspecific differences in cuticular hydrocarbons involve differences in the types, proportions, and classes of compounds present. For example, Singer *et al.* (1998) compared the cuticular hydrocarbons

of six species of social wasps and found that they differed in the presence or absence of alkenes and methyl-branched alkanes as well as in the proportions of alkenes, n-alkanes, and methyl-branched alkanes. In contrast, members of different colonies of the same species tended to have the same cuticular compounds (but different relative amounts) and similar proportions of classes of compounds. For example, Espelie *et al.* (1994) identified 20 cuticular hydrocarbons in *P. fuscatus* and found that the vast majority of wasps shared the same compounds.

Espelie *et al.* (1994) postulated that those cuticular hydrocarbons that serve as recognition pheromones should (1) be colony specific, (2) be heritable, (3) not differ markedly between castes since the compounds proclaim colony identity, and (4) have a distinctive stereochemistry, which would make them easier for wasps to distinguish. Using ANOVA and stepwise discriminant-function analyses of the hydrocarbon profiles of 124 wasps from 23 *P. fuscatus* colonies (including 15 sister colonies), Espelie *et al.* (1994) found that the compounds most efficacious for assigning wasps to the correct colony and sister group primarily were several methyl-branched alkanes. These methyl-branched alkanes had a distinctive stereochemistry and did not differ significantly between foundresses and workers. Thus, Espelie *et al.* (1994) considered these methyl-branched hydrocarbons to be leading candidates for kin recognition pheromones in *P. fuscatus*.

In order to understand which cuticular compounds might serve as recognition cues, Gamboa *et al.* (1996) switched sister colonies of *P. fuscatus* in the field and recorded whether aunts accepted or rejected their nieces. The authors then analyzed the cuticular extracts of the females with a GC/MS. A stepwise discriminant function analysis (DFA) was conducted to predict the behavioral outcomes (accept or reject) on the basis of differences in cuticular hydrocarbon profiles. The stepwise DFA was highly significant. A 100% correct classification of nieces' acceptance or rejection was made on the basis of differences in 10 cuticular hydrocarbons. This was the first evidence of a linkage between differences in cuticular hydrocarbon profiles and behaviors typically observed in a recognition context.

Gamboa *et al.* (1996) reported that two of the three compounds postulated by Espelie *et al.* (1994) to be prime candidates for recognition pheromones were ranked highly in their discriminant function analysis. However, several other compounds that were ranked highly in the discriminant function analysis were not compounds postulated to be likely recognition pheromones by Espelie *et al.* (1994). In addition to demonstrating a linkage between behavior and differences in cuticular hydrocarbons, Gamboa *et al.* (1996) provided evidence that recognition in *P. fuscatus* involved many compounds rather than a few and that recognition was not based on the presence or absence of a compound.

Dani *et al.* (2001) applied various hydrocarbons known to be part of the cuticular profile of *P. dominulus* to live workers. These treated workers were then introduced to their own colony in the laboratory. The application of linear alkanes to introduced workers did not elicit aggression from nestmates. However, the application of methyl-branched alkanes and methyl-branched alkenes did elicit aggression from nestmates. This is the first study to provide direct evidence that methyl-branched alkanes and alkenes can serve as recognition cues in social wasps.

The timing of the expression of the colony odor

A number of investigators have reported that newly eclosed social insects can be successfully transferred between conspecific colonies (e.g., Litte 1976, Breed *et al.* 1988, Morel *et al.* 1988, Jeanne *et al.* 1992, Venkataraman & Gadagkar 1993, Lorenzi *et al.* 1999). One explanation for why newly eclosed non-nestmates are treated tolerantly by resident females is that young adults lack a colony odor and thus are not recognized as foreign conspecifics. Panek *et al.* (2001) examined this hypothesis by isolating *P. fuscatus* wasps at eclosion for various periods of time to determine the age at which wasps were first recognized as nestmates and non-nestmates by experienced conspecifics. In blind observations, Panek *et al.* (2001) reported that mature resident females did not discriminate between nestmates and non-nestmates that were 1, 24,

or 48 h old. However, resident females did discriminate between nestmates and non-nestmates that were 72 h old, which indicated that a wasp's colony signature developed between 2 and 3 days of age. Panek *et al.* (2001) also found that the cuticular hydrocarbons of young wasps (24 h old) had changed significantly in older wasps (72 h old) in colony specificity, abundance, and relative abundance. More specifically, 10 of 13 identified hydrocarbons were found in significantly greater abundance in 72 h-old wasps than in 24 h-old wasps and 6 of the hydrocarbons changed significantly in relative abundance between the two age classes. These results indicate that wasps begin producing an endogenous, recognizable colony odor at about three days of age.

The source of cuticular hydrocarbons

A number of investigators have reported that queens of paper wasps stroke the comb with the venter of their abdomen. Cervo and Turillazzi (1989) reported that when *P. gallicus* combs were switched between queens, queens stroked the foreign comb with their gaster, possibly releasing a secretion onto the comb. Dani *et al.* (1992) documented abdominal stroking in *P. dominulus* and hypothesized that a glandular secretion was being applied to the comb. Lorenzi and Cervo (1992) and Cervo and Lorenzi (1996) reported that *P. biglumis* queens of both switched and naturally usurped colonies exhibited significantly higher frequencies of abdominal stroking than control queens. They hypothesized that stroking may function to apply the usurper's odor to the comb, and that the usurper's acceptance by subsequently emerging workers may depend on the odor similarity between the comb and the usurper.

Van Hooser *et al.* (2002) approximated intraspecific usurpation in *P. fuscatus* by switching field nestboxes containing combs between unrelated queens and then they compared the behavior of these alien queens with the behavior of matched, control queens in the field. In blind observations, the authors found that alien queens spent significantly more time stroking the comb than control queens. Furthermore, the tolerance of alien queens by subsequently emerging workers was significantly, positively correlated with

the length of time alien queens had been on the nest prior to worker emergence. These results were consistent with the hypothesis that abdominal stroking functions to apply the queen's recognition pheromone to the nest. Van Hooser *et al.* (2002) also observed stroking in workers, although workers stroked much less than queens. Interestingly, Van Hooser *et al.* (2002) reported that in high resolution video sequences of abdomen stroking, the point of contact between the abdomen and the comb was at or near the opening to the sting chamber. A large exocrine gland that opens into the sting chamber, the Dufour's gland, has been hypothesized to be a source of kin recognition pheromones in *Polistes*.

Dani *et al.* (1996b) analyzed the cuticular hydrocarbons and Dufour's gland contents of multiple-foundress colonies of *P. dominulus*. The authors found that the cuticle contained the same hydrocarbons as did the Dufour's gland. However, linear alkanes were more abundant in the cuticle than in the Dufour's gland while dimethyl-alkanes were more abundant in the Dufour's gland. Dani *et al.* (1996b) also reported that the cuticular hydrocarbons and Dufour's gland contents were very similar in individuals as well as among colony members. In a behavioral study, Dani *et al.* (1996a) presented dead, Dufourecitimized, hexane-washed females that had been treated with Dufour's gland extracts to laboratory colonies of *P. dominulus*. If the donors of the Dufour's gland extracts were nestmates of the colony responding to the introduced dead wasps, the dead wasps were accepted. However, if the donors of the Dufour's gland extracts were non-nestmates of the colony responding to the introduced dead wasp, the dead wasps were attacked. Dani *et al.* (1996a) concluded that the secretions of the Dufour's gland, like epicuticular lipids, are involved in nestmate recognition.

Although considerable evidence does suggest that the Dufour's gland is a source of nest/nestmate recognition pheromones, it may not be the only source of these pheromones. Dani *et al.* (2003) recently reported that the main compounds found in the sternal gland secretions (sampled by contact SPME on the van der Vecht glands and intersegmental membrane) were the same long chain hydrocarbons found on the cuticle and in the Dufour's gland.

Other recognition functions of cuticular hydrocarbons

In an early morphological and behavioral study, Downing and Jeanne (1983) collected colonies of *P. fuscatus* at various phases of the colony cycle and dissected several exocrine glands, including the Dufour's gland. Downing and Jeanne (1983) reported that the Dufour's gland was most active in those females that were involved in aggressive interactions and postulated that the gland might be involved in dominance interactions, including differential oophagy. In a later study, Downing (1991) provided evidence that the Dufour's gland was the source of the cues by which queens of *P. fuscatus* could distinguish their own eggs from those of subordinates. It is not clear whether this egg recognition ability is an example of individual recognition, dominance recognition, or kin recognition.

Sledge *et al.* (2001a) examined the relationship between ovarian activity and the proportions of cuticular hydrocarbons in queens, subordinate foundresses, and workers of *P. dominulus*. The authors reported that queens and subordinates were similar in their proportions of cuticular hydrocarbons immediately after nest foundation, but at the time of worker emergence, they had diverged in their chemical profiles. The authors found that the amounts of several hydrocarbons (alkanes) characterized queens, subordinates, and workers. Interestingly, when the authors removed the queen from a colony, the replacement queen developed a cuticular signature that was characteristic of the original queen. The authors suggested that cuticular hydrocarbons are used as cues of ovarian activity in *P. dominulus*. Although Sledge *et al.* (2001a) have provided compelling evidence that queens, subordinates, and workers have different chemical profiles, there is presently no evidence that females utilize these chemical differences for recognition of social status, ovarian activity, or any other function.

Steinmetz *et al.* (2003) recently investigated the origin and composition of the trail pheromone of *Vespula vulgaris* and found that an artificial trail made from an extract of cuticular lipids was as biologically active as a naturally laid trail. Furthermore, chemical analyses revealed

that natural trail extracts and cuticular extracts were very similar. Interestingly, Steinmetz *et al.* (2003) found that trail pheromones of nestmates and non-nestmates were equally effective in eliciting trail following behavior. Thus, the trail pheromones did not appear to be colony specific. However, it could be that the trail pheromones of *V. vulgaris* are colony specific, and that in the context of trail following, acceptance thresholds are more permissive resulting in wasps not manifesting a discrimination between their own trail and that of another conspecific colony. If trail pheromones and cuticular hydrocarbons are not colony-specific in *V. vulgaris*, one would assume that *V. vulgaris* lacks the colony-specific odors required for nestmate recognition.

Finally, it has been suggested that cuticular hydrocarbons may be used to communicate age and sex. Layton *et al.* (1994), for example, presented evidence that the cuticular hydrocarbon profiles of queens, workers, and males of *P. metricus* are both distinctive and colony specific.

Recognition by *Polistes* invaded by obligate social parasites

The literature on recognition in *Polistes* obligate social parasitism is extensive, and a thorough consideration of the literature would be more appropriate for a review of social parasitism. My limited discussion will focus on the recent literature that examines the two best understood systems, *P. dominulus* and its obligate parasite, *P. sulcifer*, and *P. biglumis* and its obligate parasite, *P. atrimandibularis*. The ability of social parasites to gain access to a colony and then dupe workers into caring for their offspring is a first-class mystery.

P. dominulus and its social parasite *P. sulcifer*

Turillazzi *et al.* (1990) reported that *P. sulcifer* queens either kill or evict queens of their host, *P. dominulus*, and then begin stroking the nest with their abdomen. The parasitic queen also licks the bodies of host females and initiates frequent trophallactic interactions with them (Turillazzi

et al. 2000). Later in the colony cycle, emerging adults (*P. dominulus* and *P. sulcifer*) tolerate each other, the parasitic queen, and the mixed brood.

In order to understand the mechanism by which *P. sulcifer* queens successfully parasitize *P. dominulus*, Turillazzi *et al.* (2000) used non-destructive microextraction procedures to examine the cuticular hydrocarbons of parasites, host females, and nests before usurpation and at various intervals after usurpation. The authors found that the parasite's odor began to change within 90 min after usurpation and that the chemical profiles of the parasitic queen and host females were very similar within 3 days after usurpation. The parasitic queen's odor was also more similar to the nest odor after usurpation than before. Interestingly, the parasitic queen deposited a compound (9,15-dimethyl C₂₉) on the nest after usurpation that was unique to the parasite. Turillazzi *et al.* (2000) also found that the chemical profiles of host larvae were more similar to those of the parasite than to host adults. Within two months after usurpation, parasitic larvae displayed a hydrocarbon profile almost identical to *P. dominulus* larvae from unparasitized nests. The parasitic larvae lacked 9,15-dimethyl C₂₉ although the compound reappeared in the parasitic pupae and parasitic reproductives that emerged later. Turillazzi *et al.* (2000) postulated that, after removing the host queen, the parasitic queen utilized chemical disguise to enter the nest. Furthermore, they hypothesized that the parasitic queen manipulated the odor of the nest, which changed the recognition template formed by subsequently emerging workers thereby inducing them to accept the parasitic queen and her brood.

Sledge *et al.* (2001b) collected parasitized field colonies of *P. dominulus* and placed them in individual laboratory nestboxes. The authors removed parasites (*P. sulcifer*) and host females (*P. dominulus*) from nestboxes and presented them to their own colony or other colonies. Using blind observations, Sledge *et al.* (2001b) found that host females were significantly less aggressive toward parasites from their own nest than other nests. Similarly, host females were significantly less aggressive toward conspecific nestmates than conspecific non-nestmates. Sledge *et al.* (2001b) conducted similar experiments using

hexane-washed, dead wasps to which cuticular extracts had been applied (lures). Host females were significantly more aggressive toward lures with parasite extracts from other nests than lures with parasite extracts from their own nest. The same results were found when host females were presented with lures containing extracts of non-nestmate conspecifics and nestmate conspecifics, respectively. Host females were, in addition, significantly more aggressive toward pieces of cotton treated with foreign parasite extracts than cotton treated with resident parasite extracts.

Sledge *et al.* (2001b) also conducted a principal components analysis and a stepwise discriminant function analysis of the cuticular profiles of parasitic and host females. By three days after usurpation, all but one parasitic female was correctly assigned to her colony. By 14 days, all parasitic females were assigned correctly. Furthermore, the matching of the parasite's odor with the host's odor after usurpation was due to changes in the parasite's cuticular profile. Sledge *et al.* (2001b) concluded that their study provided the first compelling evidence that parasites adopt the colony-specific odors of their hosts.

Polistes biglumis* and its social parasite *P. atrimandibularis

Unlike *P. sulcifer*, the parasitic queen of *P. atrimandibularis* unobtrusively enters a host colony by adopting a submissive posture and enduring attacks from the host queen (Cervo *et al.* 1990). The host queen and the parasitic queen co-habit the nest for most of the colony cycle although the parasitic queen typically remains on the nest after the host queen leaves (Bagnères *et al.* 1996).

Bagnères *et al.* (1996), in a revealing chemical study, reported that queens of *P. biglumis* and *P. atrimandibularis* had distinct cuticular profiles before usurpation. The parasitic queen had a number of unsaturated hydrocarbons (alkenes) while the host queen had only saturated hydrocarbons (alkanes). Soon after invasion, however, the alkenes disappeared from the cuticle of the parasite and some of the alkanes characteristic of *P. biglumis* began to appear on the parasitic queen. Later in the colony cycle, when the

workers and reproductives of *P. biglumis* began to eclose, the chemical profiles of the host and parasitic queens were indistinguishable.

Bagnères *et al.* (1996) found that the reproductive offspring of *P. atrimandibularis*, which are produced late in the colony cycle, had a chemical profile that was intermediate between that of the host and parasitic queen. The offspring of the host queen, however, retained their characteristic saturated hydrocarbon profile. Host workers took care of the emerging parasitic reproductives despite the fact that the reproductives had a different chemical profile from them. At the end of the colony cycle, the parasitic queen displayed her preinvasion chemical profile that was rich in alkenes. The authors provided two possible explanations for their findings. The first involved a hormonal process in which the parasitic queen had the ability to control her metabolic pathway producing hydrocarbons so that she could reproduce the chemical profile of the host queen. Alternatively, the parasitic queen may have stopped producing hydrocarbons, which was accompanied by a degradation of her chemical signature followed by the absorption of the host colony's hydrocarbons.

Lorenzi and Bagnères (2002) conducted a chemical study of *P. biglumis* and *P. atrimandibularis* to determine if parasitic queens might use an "odorless strategy", in addition to chemical mimicry, to gain access to host colonies. They found that the quantity of hydrocarbons in host females did not change over the colony cycle, but that the quantity of hydrocarbons in parasitic females increased throughout the summer. Female offspring of the parasitic queen (gynes), which emerged near the end of the colony cycle, had very low quantities of cuticular hydrocarbons.

In interspecific comparisons, Lorenzi and Bagnères (2002) found that early season parasitic queens had significantly lower quantities of hydrocarbons than host queens, but by the end of the season, the parasitic queens actually had a greater amount than did the host queens. The authors postulated that *P. atrimandibularis* queens enhanced their acceptance into host colonies by having a hydrocarbon-deficient profile. They further hypothesized that a hydrocarbon-deficient profile might facilitate their entry into

other host nests. After establishing themselves on a host nest, queens of *P. atrimandibularis* often rob larvae and pupae from other colonies of *P. biglumis* and then feed these brood to their own larvae (Lorenzi & Bagnères 2002).

In order to compare the recognition behaviors of parasitized and non-parasitized workers of *P. biglumis*, Lorenzi (2003) presented live, cooled females to field colonies of *P. biglumis*. Using blind behavioral observations, Lorenzi (2003) reported that workers from non-parasitized colonies discriminated conspecific nestmates from conspecific non-nestmates. Furthermore, workers were equally aggressive to conspecific non-nestmates, parasitic queens (*P. atrimandibularis*), and gynes of *P. atrimandibularis*. *P. biglumis* workers from parasitized colonies also discriminated conspecific nestmates from conspecific non-nestmates as well as their own parasitic queen from a foreign parasitic queen. Workers from parasitized colonies were equally tolerant of nestmate parasitic queens and conspecific nestmates and equally intolerant of foreign parasitic queens and conspecific non-nestmates.

When comparing the behavior of workers from parasitized and non-parasitized colonies, Lorenzi (2003) found that workers of parasitized colonies were significantly more tolerant of non-nestmate conspecifics than were workers of non-parasitized colonies. Surprisingly, workers of parasitized colonies were significantly more aggressive toward nestmate conspecifics than were workers of non-parasitized colonies. Furthermore, significantly more recognition errors were made by workers from parasitized colonies than workers from non-parasitized colonies. Both acceptance errors and rejection errors were more frequent in parasitized colonies.

Lorenzi (2003) concluded that the differences in tolerance exhibited by parasitized and non-parasitized workers of *P. biglumis* could not have been caused by differences in their acceptance thresholds. A more permissive acceptance threshold in parasitized *P. biglumis* workers would result in greater tolerance of both conspecific non-nestmates and conspecific nestmates. In addition, parasitized workers should exhibit fewer rejection errors but more acceptance errors. Lorenzi (2003) suggested that host workers of parasitized colonies might have had their

learning of recognition odors impaired leading to a decrease in their recognition efficiency.

The ecology of kin recognition

This section includes discussions of certain aspects of the action component, i.e., the behavioral response of an individual that has assessed the similarity between its own template and the encountered phenotype (Reeve 1989, Gamboa *et al.* 1991a). It is obvious, however, that the behavioral responses of wasps in various kin recognition studies have been discussed throughout this review. For a discussion of the action component, see Liebert and Starks (2004).

Adaptiveness of recognition ability

There have been a number of hypothesized advantages for nestmate recognition ability in social wasps. These include: (1) preventing usurpation by non-nestmate conspecifics (e.g., Gamboa 1996), (2) avoiding colonies of close relatives as usurpation targets (Gamboa *et al.* 1986a), (3) preferentially associating with former nestmates in founding multiple-foundress colonies (Gamboa *et al.* 1986a), presumably to enhance the kin components of associated foundresses, (4) excluding non-nestmates from sharing colony resources such as nectar (Gamboa *et al.* 1992), (5) minimizing inbreeding (e.g., Ryan & Gamboa 1986), and (6) preventing brood cannibalism by non-nestmates (see Kasuya *et al.* 1980).

One of the most important ecological pressures favoring nestmate recognition in some North American species of *Polistes* is, almost certainly, intraspecific usurpation. These pressures can be intense. For example, in a high wasp density habitat, Gamboa (1978) reported that single-foundress colonies of *P. metricus* had as many as eight different queens (i.e., usurpers) before the first workers emerged from the colony. Similarly, Michigan field colonies of *P. fuscatus* had, on average, one usurpation attempt per day throughout most of the pre-worker phase of the colony cycle (Gamboa *et al.* 1992). Since *P. fuscatus* usurpers are typically unrelated to

the colonies they usurp (Klahn 1988), usurpers might use their kin recognition abilities to avoid usurping colonies of close relatives. However, Gamboa *et al.* (1992) and others have reported that most usurpers are unmarked, indicating that they have migrated from other sites. Thus, it's not clear whether usurpers avoid usurping closely related colonies by dispersing, by recognizing and avoiding closely related colonies, or both.

A number of studies have reported that cofoundresses of temperate *Polistes* are usually former nestmates (e.g., West Eberhard 1969, Klahn 1979, Strassmann 1983). Bornais *et al.* (1983) documented that foundresses of *P. fuscatus* preferentially built laboratory nests with former nestmates when given an equal opportunity to found nests with unrelated non-nestmates. These results suggest that *P. fuscatus* foundresses might utilize their nestmate recognition ability to associate with former nestmates in the field. However, temperate and tropical species of *Polistes* tend to be philopatric (Reeve 1991), and thus spring associations of former nestmates may be due to philopatry. Nonetheless, I have recorded foundress associations in *P. fuscatus* consisting of colony-marked nestmates that have dispersed a considerable distance from their natal nest site. These observations and the results of Bornais *et al.* (1983) suggest that both nestmate recognition ability and philopatry likely facilitate the association of former nestmates as cofoundresses.

The potential use of nestmate recognition ability for mate choice has received little attention in social wasps. Ryan and Gamboa (1986) conducted blind laboratory observations of *P. fuscatus* and reported that males copulated significantly less often with nestmate gynes than non-nestmate gynes. Although these results are suggestive, the authors did not examine whether the copulations resulted in sperm transfer or fertilization. Ross (1983) reported that virgin queens of *Vespula maculifrons* preferentially mated with nestmate males in the laboratory. The opposite results for *P. fuscatus* and *V. maculifrons* are difficult to explain. It is especially difficult to understand why *V. maculifrons* would exhibit mating preferences that are consistent with inbreeding.

The evidence that non-parasitic species of *Polistes* rob resources or cannibalize brood of other colonies is scanty. Kasuya *et al.* (1980) reported intercolonial cannibalism of brood in the Japanese paper wasp, *P. chinensis*. I am unaware of any other reports of intercolonial resource or brood theft in temperate *Polistes*. Since several temperate species of *Polistes* have been observed extensively, including thousands of hours of videography (personal data for *P. fuscatus*), I believe it is likely that brood and resource theft would have been reported if they were common occurrences.

Effect of context on recognition

In blind laboratory studies of *P. fuscatus*, Gamboa *et al.* (1991b) reported that resident females were significantly more intolerant of unrelated non-nestmates when they were encountered on the nest than off the nest. This modulation of tolerance in different contexts is almost certainly adaptive since the negative fitness consequences of encountering an unrelated wasp on one's nest is presumably greater than encountering an unrelated wasp away from the nest. As discussed by Gamboa (1996), there may be little or no advantage for displaying aggression toward non-nestmates encountered away from the nest such as in the context of foraging.

Starks *et al.* (1998) examined the effect of context on recognition in a laboratory study of *P. dominulus*. Using blind observations, the authors observed behavioral interactions between dyads of nestmates, dyads of non-nestmates, and triads of two nestmates and a non-nestmate. The aggression between neighbor non-nestmates and non-neighbor non-nestmates was also compared. Starks *et al.* (1998) found that non-nestmate dyads were not significantly more aggressive than nestmate dyads, but in triads, non-nestmate interactions were significantly more aggressive than those of nestmates. When these recognition trials were repeated with a fragment of the nest present, significantly more aggression was observed in non-nestmates than nestmates in both dyads and triads. Starks *et al.* (1998) also found that in triads, but not in dyads, significantly more aggression was directed at

neighbor non-nestmates than non-neighbor non-nestmates. These results demonstrated that context was modulating the recognition response to conspecifics in *P. dominulus*. More specifically, the presence of a nestmate or a familiar nest fragment, which indicated the proximity of a colony, affected tolerance in a way that is consistent with the fitness interests of the wasps. Starks *et al.* (1998) concluded that his results indicate that context causes adaptive shifts in the acceptance threshold and thus supports the optimal acceptance threshold model developed by Reeve (1989).

Ruther *et al.* (2002) reported that workers of *Vespa crabro* leaving the nest on foraging flights were much more aggressive to all classes of dead wasps than workers returning to the nest. In an explanation similar to that of Starks *et al.* (1998), Ruther *et al.* (2002) stated that the motivation to defend the nest may be higher in departing workers due to their temporal closeness of contact with the chemical and physical clues of the nest.

Caste-specific acceptance thresholds

Gamboa *et al.* (1991b) investigated whether tolerance of conspecifics (nestmates and unrelated non-nestmates) changed adaptively over the colony cycle in field colonies of *P. fuscatus*. The authors had assumed that females would be the most aggressive toward non-nestmates early in the colony cycle when conspecific usurpation pressures are severe (e.g., see Gamboa *et al.* 1992). When the tolerance of wasps was examined with blind behavioral assays, females did the opposite of what had been predicted: females were the most aggressive toward both nestmates and non-nestmates late in the colony cycle.

Gamboa *et al.* (1991b) reported that when compared with variances early in the colony cycle, the variances in tolerance toward nestmates and non-nestmates were significantly higher and lower, respectively, in late season females. These results suggested that the acceptance threshold of late season females (gynes) was more restrictive than that of early season females (workers). Subsequently, Fishwild and Gamboa (1992) conducted a blind field study of *P. fuscatus* to determine if there was a division of labor

between queens and workers in colony defense against conspecific intruders. They reported that queens were significantly more involved in colony defense than workers. In addition, queens were significantly less tolerant than workers of both returning nestmates and unrelated intruders. These results and others indicated that queens and gynes had a more restrictive acceptance threshold than workers.

Gamboa *et al.* (1991b) reasoned that the negative fitness consequences of accepting an unrelated intruder into the colony are more negative for queens than for workers. Usurpers kill or evict resident queens but allow resident workers to remain on the nest. Workers of usurped colonies also have a higher probability of becoming a replacement queen than workers of a colony headed by the original queen (Klahn 1988). Thus, the more restrictive acceptance threshold of queens and the less restrictive acceptance threshold of workers appear to be consistent with their fitness interests.

The unexpected finding that colonies of *P. fuscatus* are not more aggressive early in the colony cycle may be due, in part, to the mechanism that subserves tolerance. An extremely restrictive acceptance threshold early in the colony cycle would indeed reduce the chances of accepting non-nestmates, but it would also increase the chances of rejecting nestmates. Since the presence of nestmates early in the colony cycle is known to greatly reduce the probability of successful usurpation (Gamboa 1978, Klahn 1988), the optimal setting of the acceptance threshold is likely constrained by the probabilities of accepting non-nestmates *and* rejecting nestmates. Gamboa *et al.* (1991b) also reported that nectar sharing was extensive among late season nestmates and that nectar consumption at this time likely affected winter survivorship, a time of very high mortality. Sharing nectar with non-nestmates may have severe negative fitness consequences, and thus gynes may be especially aggressive toward conspecific intruders late in the season. In summary, the fitness interests of queens and workers, as well as the mechanism (cue similarity threshold property) that underlies tolerance of conspecifics, appear to explain the empirical results of Gamboa *et al.* (1991b) and Fishwild and Gamboa (1992).

Future directions

Despite the fact that the mechanism of recognition has received considerable scrutiny, we know relatively little about certain aspects of the perception component. For example, we don't know if wasps can update their learning of recognition odors. One would assume that colony odors change over the colony cycle, either because sources of environmental odors (e.g., nectar, prey, or nesting materials) change or because genetic odors change. Genetic odors might change if many colony members contribute to the comb odor and different adults are on the comb in different phases of the colony cycle. We also don't know if wasps can learn multiple colony odors, perhaps by forming multiple templates or an expanded template that encompasses more than one colony's odor. Such knowledge might help us understand the recognition system of parasitized wasps (e.g., *P. biglumis*) that recognize both conspecific and parasitic nestmates. We also know virtually nothing about the template-phenotype matching process that results in tolerance/acceptance of conspecifics.

As I discussed briefly earlier, kin recognition has been examined in only a small percentage of social wasps and these have been mostly temperate, primitively eusocial species. Thus, there is a great need to study kin/nestmate recognition in tropical and advanced eusocial species. Our understanding of the mechanism underlying kin recognition in social wasps is based largely on studies of two species of *Polistes*, *P. fuscatus* and *P. metricus*. Although present evidence indicates that the mechanism underlying recognition is the same in various species, an insufficient number of species have been examined to conclude that the mechanism reported for *Polistes* is shared by all social wasps. It would be particularly worthwhile to study the mechanism underlying recognition in *Ropalidia marginata* and in stenogastrine wasps to determine if they conform to the *Polistes* model. Such studies should utilize the same rigorous methodologies (i.e., blind behavioral assays and large numbers of colonies to prevent pseudoreplication) that have been used to decipher the recognition mechanism of *Polistes* wasps. Recognition studies of non-*Polistes* wasps, besides being of intrinsic

interest, may shed light on the adaptiveness and evolutionary origins of kin recognition in wasps.

Finally, I believe that the study of the ecology of recognition will prove to be the most rewarding and challenging area of future research. Our understanding of the adaptiveness of kin recognition, the ecological pressures favoring recognition ability, the adaptive modulation of tolerance in different contexts, and the evolution of kin recognition is rudimentary. It would be profitable to examine nest, brood, and conspecific neighbor recognition in solitary wasps to determine if the ancestors of social wasps had the precursors for evolving nestmate recognition. It may be that the solitary ancestors of social wasps already possessed the perception and expression components of recognition. Indeed, Pfennig and Reeve (1989, 1993) reported that the solitary cicada killer wasp can use genetically specified odors to recognize its nest soil and conspecific neighbors. Many of the questions that address the ecology of kin recognition will require the study of recognition in natural contexts, possibly supplemented with laboratory studies. Surprisingly few kin recognition studies of wasps, particularly recent studies, have been field studies. Perhaps it is time to return to the field to learn why social wasps have the ability to recognize their relatives and how such a remarkable ability evolved.

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