Individual Recognition in Paper Wasps:
Correlated Evolution of Sender Phenotypes and Receiver Cognition

by

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Dedication

To my grandmother Pauline and my father Daniel who encouraged my love of nature and learning as a child

To my wife Tory who provided much needed perspective in the long road of the dissertation

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Abstract

Recognition systems allow animals to discriminate among social partners on the basis of species, group membership, kinship or individual identity. Despite the fact that recognition is central to theories of social evolution, relatively little work has examined the processes by which the traits involved in recognition evolve. Notably, recognition often involves highly diverse traits used for recognition and specialized cognitive abilities, though the evolutionary origins of these traits has been largely unexplored. I consider three questions regarding the evolution of individual recognition, using *Polistes* wasps as a model.

First, I examine the phenotypes used for recognition. Does selection favor individuals to broadcast their identity or is recognition akin to eavesdropping? Through a series of studies I show that the variable color patterns used by *P. fuscatus* to recognize conspecifics have arisen as the result of selection for distinctive easily recognizable identity signals. This work provides the first evidence that selection for recognition favors individuals to broadcast their identity. Selection for efficient recognition is likely to be a prominent mechanism maintaining polymorphism in social species.

Second, I examine the specificity of cognitive processes associated with recognition. Do wasps use general learning mechanism for recognition or is it a specialized process? I demonstrate that *P. fuscatus* wasps have face-recognition specific learning adaptations, suggesting that cognitive evolution may be highly specific. Additionally, I show that wasps have surprisingly robust social memories despite their small brain size.

Third, it is difficult to understand how sender and receiver phenotypes are elaborated in the absence of the other. I propose that the evolution novel recognition systems may be facilitated by pre-existing sender or receiver biases. I provide initial tests of the hypotheses, finding that sender bias is likely to be a widespread mechanism facilitating the evolution of novel recognition systems. Additionally, I provide experimental evidence for a receiver bias in *Polistes* wasps.

The work presented in this dissertation present a multi-faceted examination of the evolution of an important social trait – individual recognition. Importantly, the results of this dissertation demonstrate that individual recognition will be an important model for studies of phenotypic polymorphic and cognitive evolution.

Chapter 1: Introduction

Social interactions have major effects on animal fitness. Recognition systems, in particular, play an important role in mediating interactions among social partners. Indeed a wide body of literature has examined the evolutionary and ecological consequences of social recognition, with a particular focus the mechanisms underlying of kin and individual recognition (Beecher 1989; Frommen et al. 2007; Gamboa 2004; Sharp et al. 2005; Tang-Martinez 2001; Thom and Hurst 2004). Despite the importance of recognition systems in theoretical and empirical studies of social behavior, surprisingly little attention has been given to the evolution of recognition systems themselves (Tibbetts and Dale 2007).

One approach to understanding the evolution of recognition systems is to examine how selection has shaped the various components of recognition. For recognition to occur, one individual (the sender) must produce some information that is perceived and then acted upon by another individual (the receiver) (Sherman et al. 1997). Selection, then, is expected to influence both the phenotypes of senders and the cognitive abilities of receivers. When senders benefit from being recognized, selection is expected to favor the evolution of distinctive phenotypes that provide identity information (Johnstone 1997). Discriminating among senders is one of the major challenges facing receivers when recognizing social partners. Thus, selection is expected to favor the evolution of cognitive abilities allowing for efficient discrimination of conspecifics (Jouventin et al. 1999; Loesche et al. 1991; McKone et al. 2007).

Individual recognition, the most specific form of social recognition, provides an ideal system to investigate the evolution of recognition systems. There have been multiple independent origins of individual recognition across many taxa and social contexts (Tibbetts and Dale 2007). Additionally, the specificity of individual recognition has the potential to favor more extreme adaptations in both senders and receivers, allowing them to be more easily identified and studied.

In this dissertation I describe a series of studies examining the evolution of individual recognition, using *Polistes* paper wasps as a model. The Northern paper wasp, *P. fuscatus*, recognizes individuals using highly variable color patterns on the face and abdomen (Tibbetts 2002), though its close relatives lack phenotypic variation (Tibbetts 2004) making *Polistes* an ideal group for investigating the evolution of individual recognition. I first describe the function of individual recognition in *P. fuscatus* and then introduce the three sections of the dissertation focusing on adaptations in sender phenotypes, receiver cognition and the origins of novel recognition systems respectively.

Individual recognition in *Polistes fuscatus*

Why do wasps need to recognize each individually? Each spring, paper wasps emerge from diapause and initiate new colonies either alone or in cooperative multiple foundress groups. *P. fuscatus* has a flexible social system with some foundresses nesting singly and others multiply, where foundresses form a strict linear dominance hierarchy that determines relative contributions to work and egg-laying in the colony (West Eberhard 1969). This flexibility is associated with conflict among the multiple queens and appears to have favored the evolution of variable color patterns that may be used for signaling in multiple clades of *Polistes* (Tibbetts 2004). Thus, individual recognition is a tool for managing conflict among competing reproductives in a colony.

Sender adaptations: Are variable color patterns in *P. fuscatus* identity signals?

Identity signals are traits that have been selected to be distinctive in order to facilitate accurate and efficient recognition. For this to occur, individuals must benefit from distinctive phenotypes (Dale et al. 2001). If distinctiveness is favored, this is expected to give rise to increased phenotypic variation in signalers over evolutionary time (Dale 2006; Dale et al. 2001). I tested both of these predictions in a series of experimental and comparative studies with *P. fuscatus* and its relatives.

To test whether individuals benefit from identity advertisement, I experimentally altered the phenotypes of small groups of unrelated *P. fuscatus* foundresses so that one individual had a unique, distinctive phenotype (Chapter 2). Each wasp was painted so that they had an all-black face or a small yellow dot at the tip of their clypeus. The distinctive wasp was painted yellow or all-black in half of the groups respectively, with the three common wasps receiving the opposite color treatment. Each group was then placed in a small arena and allowed to interact for two hours. I videotaped the trials and later recorded the initiator and recipient of all aggressive acts.

Analysis of the distribution of aggression demonstrated that distinctive wasps received the least aggression in a disproportionate number of trials. In general, distinctive wasps received less aggression than wasps with a common appearance. Color treatment did not influence aggression, so distinctiveness rather than a particular phenotype was responsible for lower receipt of aggression. Given that receiving excess aggression is costly, these results demonstrate that individuals that advertise their identity with rare recognizable phenotypes benefit from identity signaling.

When distinctive phenotypes are beneficial they are expected to spread via a negative frequency-dependent process, with the benefits decreasing as a phenotype spreads and becomes less distinctive (Dale et al. 2001; Sheehan and Tibbetts 2009). At any time, however, new rare mutants may arise that would also be favored and spread. Over time the repeated spread of distinctive traits will give rise to multiple variable phenotypic components, such as color patches in different parts of a wasp's face (Dale 2006).

If selection favors the evolution of identity signaling, we expect species with individual recognition to be more variable than relatives lacking individual recognition. I examined two species, *P. dominulus* and *P. metricus*, for phenotypic variability and recognition abilities (Chapter 3). I measured the level of color polymorphism in *P. fuscatus*, *P. dominulus* and *P. metricus*, confirming that *P. fuscatus* color patterns are far more variable than the other species. Importantly, *P. fuscatus* show variation in multiple independent color patterns on their faces and abdomens whereas the other species only showed significant variation in one region. Next, I tested recognition abilities by pairing wasps with others they had and had not previously interacted with in a series of four encounters. If wasps recognize an individual, they are expected to show lower levels of aggression to familiar compared to unfamiliar wasps, as is seen in *P. fuscatus* (Sheehan and Tibbetts 2008). As predicted, the less variable species showed no evidence of individual recognition. This finding is consistent with the hypothesis that selection for identity signaling rather than other neutral processes is responsible for the evolution of elevated phenotypic polymorphism in *P. fuscatus*.

Receiver adaptations for individual recognition

The first challenge of recognizing individuals is to be able to reliably discriminate among them. Wasps are visual foragers with large eyes and well developed visual systems (Land 1997; Richter 2000) so there is no *a priori* reason to expect any specializations for visual learning of faces. Mockingbirds spontaneously recognize individual humans (Levey et al. 2009) and bees can be trained to distinguish among human faces (Dyer et al. 2005), demonstrating that specialization isn’t strictly necessary for face learning. However, primates also recognize individuals based on distinctive faces and do have cognitive specializations for learning conspecific faces (Pascalis and Kelly 2009), suggesting that specializations for learning conspecific faces may be adaptive. While it is possible to recognize individuals without specialized learning abilities, primates and wasps regularly interact with and recognize conspecifics so efficient face learning may be beneficial. If selection for individual recognition favors specialized face learning, then *P. fuscatus* should learn wasp faces differently than other image types while close relatives lacking IR should show deficits in face learning.

I tested visual learning abilities in *P. fuscatus* and *P. metricus*, a close relative lacking individual recongnition (Chapter 4). Using a negatively reinforced T-maze, we trained wasps on conspecific faces, abnormally configured jumbled faces, antenna-less faces, caterpillars (wasp prey), simple patterns and heterospecific faces. *P. fuscatus* learned conspecific faces more rapidly and accurately than the other image types. Jumbled faces were made from the same stimuli as normal faces, so poor performance on these stimuli demonstrates that faces *per se* are important for learning. Additionally, the mere removal of the antennae from the images led to significant deficits in performance. Simple, high contrast black and white patterns are predicted to be easy for hymenopteran compound eyes to discriminate (Lehrer and Campan 2004), yet *P. fuscatus* learned the complex face images more rapidly. In contrast to *P. fuscatus*, *P. metricus* failed to discriminate among conspecific faces. This pattern persisted when each species was trained to discriminate the heterospecific faces, with *P. fuscatus* performing well and *P. metricus* poorly on both species' face images.

Collectively the training data demonstrates an interesting case of convergent evolution of specialized face learning abilities between primates and wasps. Importantly, association between face learning and individual recognition in wasps provides evidence for cognitive adaptations for individual recognition.

In addition to discrimination, individual recognition also requires memory of previous interactions. Prior to founding new nests each spring, *P. fuscatus* wasps investigate possible nest sites and interact with multiple wasps over the course of many days (West Eberhard 1969). This presents a particular challenge as memories attenuate over time (Gherardi and Atema 2005) and are often replaced by memories of more recent experiences (Reinhard et al. 2006). I tested the robustness of *P. fuscatus* social memories to attenuation over 1 week and interference from interactions with 10 other wasps (Chapter 5). I paired two unfamiliar wasps together for one day, separated them for a week and later rejoined the pair. During the week of separation, each wasp was placed in a different communal cage with 10 other wasps. Upon rejoining, the wasps interacted more peacefully than they had when they first met a week earlier, suggesting recognition of their social partner. To ensure that reduced aggression levels were due to recognition and not a general decline in aggression, we paired each wasp with new unfamiliar wasps on the 6th and 8th day. On both days, wasps showed elevated levels of aggression, demonstrating that wasps remembered each other after a week of complex social interactions. Wasp social interactions are based on memories of past encounters rather than simple fighting rules. Given the small size of wasp brains (Gronenberg et al. 2008) this finding suggests that tracking individual social relationships may not be as cognitively demanding as is often assumed.

Evolutionary origin of novel recognition systems

As with any communication system, recognition requires coordination between senders and receivers (Bradbury and Vehrencamp 2011; Sherman et al. 1997). Within the context of an established recognition system, it is relatively straightforward to understand how selection may act on either sender phenotypes or receiver cognition and behavior. In the absence of recognition, however, is it less clear how selection might act on the components of a recognition system. How could selection act on sender phenotypes in the absence of receiver behavior? How can receiver behavior evolve in the absence of identifiable sender phenotypes?

In Chapter 6 I propose and provide initial tests of two hypotheses to explain the origin of novel recognition systems. The evolution of a recognition system may be facilitated by pre-existing biases in sender phenotypes or receiver behavior. The sender bias hypothesis proposes that the initial evolution of recognition is facilitated by existing variation in sender phenotypes that allows for identification. In effect, sender bias is a broader conception of the ritualization hypothesis for signal evolution, which posits that selection acts on existing behavioral variation during the initial process of signal evolution (Maynard-Smith and Harper 2003; Scott-Phillips et al. in press). Similarly, the receiver bias hypothesis proposes that the initial evolution of recognition is facilitated by pre-existing receiver behavior favorable to recognition. The exploitation of receiver biases by senders is a major explanation for the origin of sexually selected traits (Endler and Basolo 1998; Ryan and Rand 1993). Based on this previous work, we develop a hypothesis to explain the origin of novel recognition systems via biases in receiver behavior.

I tested the sender bias hypothesis by examining patterns of sender variation and receiver behavior across a wide range of animals. Our analysis finds broad support for the sender bias hypothesis, especially in taxa that use vocalizations for individual recognition. While support was widespread, our analysis showed that sender biases were not a universal explanation for the origin of novel individual recognition systems. Notably, *Polistes* wasp lineages with individual recognition are known to have lacked variable color patterns ancestrally (Tibbetts 2004), suggesting that receiver bias may play a role in the evolution of individual recognition in wasps and other lineages.

I experimentally tested the predictions of receiver bias in *P. metricus*, which lacks individual recognition and has uniform coloration (Sheehan and Tibbetts 2010). By painted small groups of *P. metricus* so that one wasp had a unique phenotype, I was able to test receiver responses under a circumstance mimicking the initial evolution of variable recognition traits. For selection to favor the evolution of recognition, receivers must respond to variations in behavior in a manner that favors senders to advertise their identity (i.e. senders must benefit from recognition, Sheehan and Tibbetts 2009). Receivers in *P. metricus* were able to discriminate among wasps based on the small experimental manipulation of color patterns. Importantly, receivers directed less aggression at unique wasps, regardless of their marking, suggesting that receiver behavior would facilitate the evolution of individual recognition in *P. metricus*.

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Chapter 2: Evolution of Identity Signals: Frequency-dependent benefits of distinctive phenotypes used for individual recognition

Abstract

Identifying broad-scale evolutionary processes that maintain phenotypic polymorphisms has been a major goal of modern evolutionary biology. There are numerous mechanisms, such as negative frequency-dependent selection, that may maintain polymorphisms, although it is unknown which mechanisms are prominent in nature. Traits used for individual recognition are strikingly variable and have evolved independently in numerous lineages, providing an excellent model to investigate which factors maintain ecologically relevant phenotypic polymorphisms. Theoretical models suggest that individuals may benefit by advertising their identities with distinctive, recognizable phenotypes. Here, we test the benefits of advertising one's identity with a distinctive phenotype. We manipulated the appearance of *Polistes fuscatus* paper wasp groups so that three individuals had the same appearance and one individual had a unique, easily recognizable appearance. We found that individuals with distinctive appearances received less aggression than individuals with nondistinctive appearances. Therefore, individuals benefit by advertising their identity with a

unique phenotype. Our results provide a potential mechanism through which negative frequency-dependent selection may maintain the polymorphic identity signals in *P. fuscatus*. Given that recognition is important for many social interactions, selection for distinctive identity signals may be an underappreciated and widespread mechanism underlying the evolution of phenotypic polymorphisms in social taxa.

Introduction

Phenotypic polymorphisms occur in a wide range of taxa from flowers (Gigord et al. 2001) to fish (Olendorf et al. 2006), although the adaptive value of many polymorphisms is often unclear. Given that selection and genetic drift typically reduce the amount of variation in a population, explaining these striking phenotypic polymorphisms has been a challenge for evolutionary biologists.

A number of explanations for the evolution of phenotypic polymorphisms have been proposed including local adaptation, mutation–selection balance, and negative frequency-dependent selection (Mitchell-Olds et al. 2007). In local adaptation, connected populations each adapt to separate ecological conditions so that individuals within a local population are relatively monomorphic (Hoekstra et al. 2006). Under the local adaptation hypothesis, phenotypic polymorphism within a population results from migration between populations with opposing selection regimes. Migrants with rare phenotypes generally have lower fitness so the polymorphism is a consequence of gene flow, not adaptation per se (Mitchell-Olds et al. 2007; Yeaman and Jarvis 2006). Polymorphisms may also arise via the accumulation of deleterious variants affecting phenotypes that have yet to be purged by selection. Although mutation–selection balance has been extensively studied from a theoretical perspective (Zhang and Hill 2005), few empirical studies have directly tested how much phenotypic variation arises from deleterious mutations. Unlike the local adaptation and mutation–selection balance hypotheses, the negative frequency-dependent selection hypothesis posits that rare phenotypes are favored by selection such that polymorphism within populations is adaptive. Although frequency-dependent selection has the potential to be a powerful evolutionary mechanism for the promotion and maintenance of polymorphisms, relatively few studies have documented frequency-dependent selection in natural populations. Documented examples have typically been narrow in scope (Fitzpatrick et al. 2007) or governed by unknown mechanisms (Nosil 2006; Olendorf et al. 2006). To date, there are few examples of widespread ecological and evolutionary processes that may favor polymorphisms.

One promising system for research into the evolution of phenotypic variation is individual recognition. The highly variable phenotypes used for individual recognition are among the most striking examples of phenotypic polymorphism in nature (Fig. 2.1 A). Individual recognition occurs when individuals are able to discriminate among multiple social partners based on unique phenotypic characters (Tibbetts and Dale 2007; Tibbetts et al. 2008). Individual recognition has evolved independently in a wide range of taxa, making it an excellent model for investigating the evolution of phenotypic polymorphism. Efficient navigation of complex social environments depends on individual recognition in a number of diverse species, including *Polistes* paper wasps (Sheehan and Tibbetts 2008; Tibbetts 2002), *Pachycondyla* ants (D'Ettorre and Heinze 2005), lobsters (Karavanich and Atema 1998), crayfish (Seebacher and Wilson 2007) as well as many vertebrates (Cheney and Seyfarth 1999; Grosenick et al. 2007; Hurst et al. 2001; Jaeger 1981; Jouventin et al. 1999; Paz-y-Mino et al. 2004). Species use individual recognition to discriminate among social partners in a number of different contexts such as parental care (Jouventin et al. 1999), the recognition of territorial neighbors (Jaeger 1981), and linear dominance hierarchies (Tibbetts 2002).

To date most of the research on individual recognition has focused on the presence or absence of recognition behavior in a given species, whereas relatively little research has focused on the individual being recognized. It is unknown whether individuals are selected to signal their identity with distinctive phenotypes (i.e., via an identity signal) or if observers cue into otherwise neutral phenotypic variation to recognize conspecifics (Tibbetts and Dale 2007). If being memorably different is advantageous, rare phenotypes are predicted to spread via negatively frequency-dependent selection such that individuals who look, sound, or smell unique will be favored (Dale et al. 2001). Even relatively minor benefits associated with distinctiveness can lead to the evolution of identity signals as long as the phenotypes used for recognition are not costly to produce or maintain (Dale et al. 2001).

Here, we experimentally test whether there are benefits associated with the distinctive, recognizable phenotypes used for individual recognition. Specifically, we test whether distinctiveness is beneficial within a linear dominance hierarchy. Within species with dominance hierarchies, individuals with unique, recognizable phenotypes are predicted to benefit by receiving less aggression than indistinguishable individuals (Barnard and Burk 1979; Dale et al. 2001). Both dominants and subordinates are predicted to benefit from distinctive phenotypes. When animals contest a resource (such as food or a position in a dominance hierarchy) both the winner and loser benefit by settling the contest without costly escalation (Maynard-Smith and Harper 2003). Although some species possess signals, such as badges of status, that allow contestants to assess relative agonistic ability, such signals are often poor predictors of fighting ability. Individual recognition, however, allows individuals to accurately assess social partners based on the outcomes of prior interactions. Typically, the first encounter between two competing individuals is quite aggressive, as individuals fight to establish their relative dominance ranks. When individuals can recognize each other, aggression typically declines in subsequent interactions because relative dominance ranks have already been established (Dreier et al. 2007; Sheehan and Tibbetts 2008). However, in species lacking individual recognition, aggression is not predicted to decline over subsequent encounters because the relative ranks of social partners are not clear unless individuals engage in new aggressive contests (Barnard and Burk 1979).

We experimentally tested the benefits of distinctive, easily recognizable phenotypes in the paper wasp, *Polistes fuscatus*, which uses variable facial patterns for individual recognition (Fig. 2.1 A , Sheehan and Tibbetts 2008; Tibbetts 2002). In this species, multiple queens often found nests together. The queens cooperate to rear offspring, but they also compete to form a linear dominance hierarchy (Reeve 1991; West Eberhard 1969). Individual recognition is thought to play an important role in mediating aggressive dominance interactions among wasp queens and aiding colony stability (Tibbetts 2002). We set up groups of four unrelated wasp queens: three wasps with a similar, common appearance and one with a distinctive, rare appearance (Fig. 2.1 B) and then compared the interactions of individuals with common and rare appearances.

We make a number of specific predictions about how distinctiveness will influence social interactions. First, distinctive individuals are expected to be more easily identifiable than nondistinctive individuals. Therefore, individuals with a unique phenotype are predicted to receive less aggression than individuals with a common phenotype. Second, individuals are predicted to have difficulty determining the relative ranks of individuals with common appearances, so the amount of aggression an individual initiates is expected to depend on the number of distinctive versus common individuals they interact with. As a result, wasps that interact with three nondistinctive individuals will initiate more aggression than wasps that interact with two nondistinctive and one distinctive individual.

Methods

In early spring 2007, behavioral interactions were observed among 18 groups of queens collected from distant locations separated by at least 1 km around Ann Arbor, Michigan. Each group contained four foundresses that had never previously encountered each other. This mimics natural foundress behavior in early spring. After *Polistes* foundresses emerge from diapause, they interact with many individuals before settling down to start a nest, either alone or with other foundresses that may or may not be related (Queller et al. 2000; Reeve 1991). Within each group, we painted three wasps to have similar appearances and one wasp to have a unique appearance. The experimental manipulation of markings created a situation in which only one individual (i.e., the unique wasp) was recognizable, allowing us to test the benefits of having a phenotype that allows for individual recognition. Unlike the quality signals found in *Polistes dominulus* (Tibbetts and Dale 2004; Tibbetts and Lindsay 2008; Zanette and Field 2009) and *Polistes satan* (Tannure-Nascimento et al. 2008), the variable patterns in *P. fuscatus* are not correlated with condition (Tibbetts and Curtis 2007) and do not convey information about their bearer's agonistic abilities. Nevertheless, to ensure that behavioral responses resulted from distinctiveness rather than a particular color pattern, the same color patterns were used for distinctive and nondistinctive wasps in different trials. In half the trials, the distinctive wasp had one yellow facial spot whereas in the other half of the trials; the common wasps had one yellow facial spot (Fig. 2.1 B). These color patterns mimic naturally occurring morphs of *P. fuscatus* (Tibbetts 2002). The initial experiment that found individual recognition in *P. fuscatus* did so by altering the color of small portions of the face, such as the tip of the clypeus (Tibbetts 2002), indicating that the wasps are able to distinguish between the treatments. Research on other social insects, such as honeybees, has shown that Hymenopteran visual systems are well developed and can easily distinguish among complex patterns (Stach et al. 2004). We chose the distinctive wasp randomly, so the neutral expectation is that the distinctive wasp will be just as likely to receive the most aggression from the other group members, as it is to receive the least aggression from the other group members.

For each trial, we chose four wasps with similar weight (within 0.015 g) and general body coloration. To allow identification by the experimenters, each wasp was marked with two small red dots in slightly different locations on the top of the thorax. Given the position and coloring of the red dots the markings are unlikely to increase the distinctiveness of wasps, as wasps do not see red (Briscoe and Chittka 2001). Any additional variation provided by the markings would only dampen the effect of the experimental treatment. After allowing the paint to dry, wasps were placed in an 8 cm × 8 cm × 2 cm sized container and filmed for 2 h. The paint treatments remained on all of the wasps' faces throughout the trials. Each wasp participated in only one trial.

MJS watched the tapes without knowledge of the specific experimental treatment. The actor and the recipient were noted for each aggressive act. All aggressive acts including darts, lunges, bites, grapples, and mounts were recorded (West Eberhard 1969). Aggressive behaviors in social wasps are stereotyped, so researchers score these same suites of aggressive behaviors across studies (Reeve and Nonacs 1992; Strassmann et al. 2004; Tibbetts 2002; Weiner et al. 2009). To ensure that there was no subconscious observer bias; MJS trained an individual with no knowledge of the experimental treatment or expected outcomes to score behavioral data. The naive observer watched 12 5-min samples of video from various trials. There was nearly perfect agreement between the initial received aggression ranks found by MJS those found by the naïve observer (Cohen's Kappa with quadratic weighting, k= 0.87), demonstrating that the results are robust across observers (Landis and Koch 1977).

We analyzed the relative distribution of aggression using two complimentary methods. First we asked whether distinctive wasps engaged in a different number of aggressive interactions than nondistinctive wasps. Because the levels of aggression differed among trials (mean = 254.44 ± 50.01, range = 120–1049 aggressive acts), we standardized aggression scores within each trial. To calculate the score, we subtracted the mean number of aggressive acts received or initiated in a trial from the number received or initiated by the wasp of interest and divided this by the standard deviation in aggression scores of that trial. The standard aggression scores for distinctive wasps could then be compared to the population average (set to 0) with one sample t-tests (Sokal and Rohlf 1995). Second, we considered the relative distribution of aggression. Within each trial, wasps were ranked 1 (most aggression received) to 4 (least aggression received) to analyze the distribution of aggression across all the trials. Because the distinctive wasp was chosen randomly the null expectation is that they should receive the most aggression in one-fourth of the trials, second most in one-fourth of the trials, and so on. We conducted a Monte Carlo simulation of the multinomial sampling distribution for 50,000 iterations. This procedure samples the probability that a given distribution would occur compared to expected values and approximates a chi-square goodness-of-fit test with a sufficiently large number of iterations. Means are shown ± SEM and all tests described are two-tailed.

Results

Rare, easily recognizable phenotypes provided a benefit during social interactions, as the distinctive wasps received less aggression than the population average (mean aggressive acts received = 0.43 SD less than the population + 0.15 SE, one sample t-test, $t_{17} = -2.95$, $P = 0.0089$). The color treatment did not affect the amount of aggression that distinctive wasps received (two sample t-test, $t_{16} = 1.05$, $P = 0.31$). Therefore, aggression was influenced by whether a wasp was distinctive rather than the individual's particular color pattern. Because distinctive wasps were chosen randomly among four individuals, the null expectation is that they should receive the most aggression in one-fourth of the trials and the least in one-fourth. The distribution of aggression, however, was skewed. Distinctive wasps received the least aggression in a disproportionate number of trials (Fig 2.2. multinomial sampling distribution, N = 18, $P = 0.038$), providing additional evidence that individuals with distinctive phenotypes benefis by receiving less aggression

The amount of aggression initiated by an individual depended on the number of distinctive versus common individuals they interacted with. Distinctive wasps interacted with three unidentifiable individuals during each trial whereas common wasps interacted with two unidentifiable individuals and one distinctive individual. As a result, distinctive wasps were more aggressive than the population average (mean aggressive acts initiated = 0.38 SD more than the population ± 0.17 SE, one sample t-test, $t_{17} = 2.18$, $P = 0.044$). There was no relationship between the amount of aggression a wasp initiated and the wasp's color, i.e., yellow spot or all black (two sample t-test, $t_{14.7} = 0.42$, $P = 0.68$). When considering the distribution of aggression, distinctive wasps initiated the most aggression in a disproportionate number of trials (Fig 2.3. multinomial sampling distribution, N= 18, *P* = 0.033).

Discussion

Overall, our results provide experimental evidence that individuals benefit when they advertise their identities with rare, distinctive phenotypes. Wasps with distinctive, easily recognizable appearances received less aggression than wasps with common indistinguishable appearances. Given that receiving aggression is costly (Maynard-Smith and Harper 2003; Reeve 1991; West Eberhard 1969) these results indicate that distinctive phenotypes are beneficial. In addition, our results indicate that identity signaling likely provides a colony-level benefit in wasps. Wasps that interacted with indistinguishable social partners were more aggressive than individuals that interacted with distinctive individuals. Thus, identity signaling plays an important role in mediating the distribution of aggression in animal societies by allowing aggression to be targeted appropriately. Our experimental results demonstrate that there are benefits associated with having a rare phenotype as well as interacting with individuals that have rare phenotypes. Taken together, these results provide a mechanism through which selection may have driven the evolution of variable visual features in *P. fuscatus*: negatively frequency-dependent selection.

EVIDENCE FOR IDENTITY SIGNALS

Prior research on individual recognition has primarily focused on recognition behavior, with little research testing how selection acts on the phenotypes of individuals being recognized (Tibbetts and Dale 2007). Models for the evolution of identity signals critically predict that recognizable individuals will benefit by advertising their identities (Dale et al. 2001), and our results support the predictions of these models.

Traits that evolved to signal individual identity are expected to have a number of properties that distinguish them from traits that evolved to convey other types of information (Dale 2006). Specifically, identity signals are predicted to (1) be highly variable with multimodal frequency distributions, (2) show low to no correlations between traits, (3) be uncorrelated with fitness, (4) expressed independently of condition, and (5) show a high degree of genetic determination (Dale 2006). Any phenotype that fits this specific set of criteria is a plausible candidate for an identity signal.

Previous work indicates that *P. fuscatus* facial patterns fit the predictions of identity signaling models. (1) The facial patterns are highly variable (e.g., Fig. 2.1 A) with a multimodal frequency distribution and (2) no correlation among traits (Tibbetts 2002). (3) The color variation does not correlate with indicators of fitness. Tibbetts (2002) failed to find any relationship between facial patterns and aspects of quality in nest founding queens such as founding strategy, dominance rank, or weight. (4) The facial patterns are also expressed independent of condition. Experimental manipulation of larval nutrition had no effect on the development of *P. fuscatus* color patterns (Tibbetts and Curtis 2007). (5) Finally, facial patterns are more similar within a nest than between nests. This similarity occurs across both workers and gynes (future reproductives), although the different castes are reared in different conditions. Therefore, there is likely to be a heritable component to variation in facial patterns (M. J. Sheehan and E. A. Tibbetts, unpubl. data). Of course, other mechanisms, such as developmental stochasticity (Leimar 2005) can give rise to polymorphisms, so additional research will be important to assess the precise heritability of *P. fuscatus* color patterns. Overall, the tight fit between the theoretical predictions for identity signals and the characteristics of *P. fuscatus* facial patterns suggests that paper wasp facial patterns have likely evolved to signal individual identity.

Comparative work in *Polistes* provides further evidence that variable color patterns have evolved because distinctiveness is beneficial in certain paper wasp species. The kind of variable color patterns required to signal individual identity have evolved multiple times in *Polistes* species with complex social interactions and linear dominance hierarchies (Tibbetts 2004). Species with simpler social interactions, however, do not have variable visual markings. Instead, they have a uniform, species typical color pattern with low intraspecific variability. Given that the majority of *Polistes* species do not have variable coloration patterns (Tibbetts 2004), the conspicuous phenotypic polymorphisms used for identity signaling in

P. fuscatus are unlikely to be the result of neutral processes. Rather, selection for distinctive identity signals likely drives the evolution of elaborated, recognizable phenotypes.

Although our results demonstrate that individuals can benefit by advertising their identities, social interactions will not necessarily lead to the evolution of phenotypic polymorphism and identity signals. For example, the chemical profiles that *Pachycondyla* queens use for individual recognition (D'Ettorre and Heinze 2005; Dreier et al. 2007) are not more variable than chemical profiles in ant species lacking individual recognition (Dreier and D'Ettorre 2009). Therefore, observers can cue into variation that has not evolved specifically to signal identity. When being recognizable is neutral, variable features used for individual recognition may be lost. In some circumstances, selection may even favor individuals that conceal their identities (Johnstone 1997).

IDENTITY SIGNALING AND NEGATIVE FREQUENCY-DEPENDENT SELECTION

Most previous examples of negative frequency-dependent selection focus on systems with a limited number of morphs that are at an evolutionarily stable state. When multiple, evolutionarily stable foraging or mating strategies are maintained in a population via negative frequency-dependent selection, selection maintains the relative frequencies of the strategies at equilibrium (Maynard Smith

1982). In contrast to many other examples of negatively frequency-dependent selection, selection for identity signaling favors individuals with a unique appearance rather than a particular strategy. As a result, it is expected to produce a large array of polymorphic phenotypes. Unique traits are favored because they are useful for discriminating among conspecifics and thus are expected to spread in a population. As a trait increases in frequency, it will become less useful for discriminating among individuals at which point it is no longer expected to spread in the population. Unlike evolutionary stable strategies, new variants are expected to invade the population because they provide individuals with distinctive phenotypes. Over time, this dynamic is expected to produce populations with numerous polymorphic traits that are uncorrelated (Dale 2006; Dale et al. 2001), as observed in *P. fuscatus* (Tibbetts 2002). Therefore, selection for identity signaling differs from many other examples of negatively frequency-dependent selection because it favors extremely high variation, rather than maintaining a limited number of morphs at equilibrium.

BENEFITS: INDIVIDUAL OR GROUP?

Polistes fuscatus paper wasps live in complex social groups where the fitness of an individual is influenced by the productivity of their colony, so distinctive phenotypes may provide benefits for both the individual and the group (Korb and Heinze 2004). Our experiment was designed to test Dale et al.'s (2001) model, which posits that individuals with rare, recognizable phenotypes will benefit by receiving less aggression during social interactions; our results are consistent with this prediction. In most taxa, high levels of aggression are costly, as fighting increases the chance of injury (Jaeger 1981). In *Polistes*, intense fighting can lead to severe injury including the loss of limbs and wings or even death (West Eberhard 1969, M. J. Sheehan and E. A. Tibbetts, pers. obs), suggesting that reductions of aggression through identity signaling may increase individual fitness. Further, individuals that receive intense aggression often reduce other activities, including brood care, foraging, and social interactions. Previous research on individual recognition in *P. fuscatus* indicates that distinctiveness may reduce aggression in a range of contexts. Known individuals receive less aggression than unknown individuals on nests (Tibbetts 2002) and in the laboratory (Sheehan and Tibbetts 2008).

The results of this experiment suggest that there may also be colony-level benefits associated with identity signaling. Individuals that interacted with indistinguishable conspecifics initiated more aggression than those that interacted with more distinctive conspecifics. Further, interacting with distinctive conspecifics may increase colony stability, as distinctiveness allowed individuals to target their aggression appropriately. In natural colonies of *P. dominulus*, lower levels of aggression are associated with higher rates of resource sharing (Tibbetts and Reeve 2000). Whether increased cooperation is a cause of consequence of lower aggression levels is unknown, though at least one theoretical model predicts that individual recognition will increase cooperation (Crowley et al. 1996). Therefore, distinctive phenotypes are likely to be favored at both the individual and colony level in *P. fuscatus*.

Conclusion

Overall, selection for identity signals is likely to occur across a range of taxa and sensory modalities. Our results demonstrate that easily recognizable individuals with rare, distinctive phenotypes benefit by receiving less aggression from conspecifics than individuals with common, nondistinctive phenotypes. Highly polymorphic features facilitate recognition in a wide range of taxa from paper wasps to swallows (Medvin et al. 1993) to humans (Kanwisher and Yovel 2006). Further, recognition is an essential component of social interactions across a range of behavioral contexts (Mateo 2004; Sherman et al. 1997; Tibbetts and Dale 2007). Therefore, negative frequency-dependent selection favoring identity signaling is likely to be an underappreciated mechanism for the maintenance of phenotypic polymorphisms in many social taxa. Future research on identity signals is likely to uncover many more social situations in which the benefits of being unique have driven the evolution of phenotypic diversity.

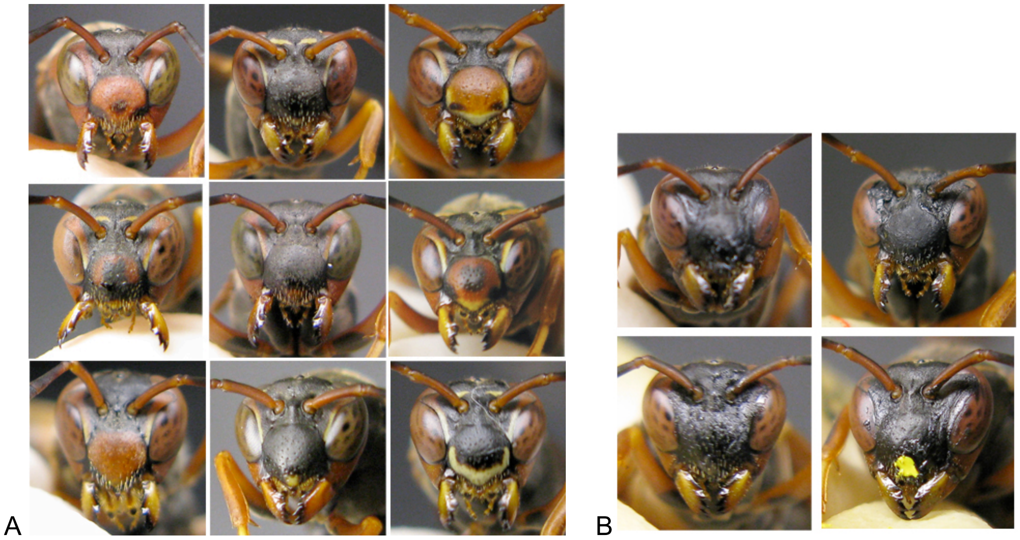

Figure 2.1. (A) *Polistes fuscatus* use highly variable facial markings for individual recognition. (B) Examples of wasps with experimentally altered facial patterns. The wasp in the lower right hand corner has a yellow dot on its clypeus. Ten trials contained three wasps with black clypeus tips: one wasp with a yellow clypeus tip whereas eight trials contained one wasp with a black clypeus tip: three wasps with yellow clypeus tips.

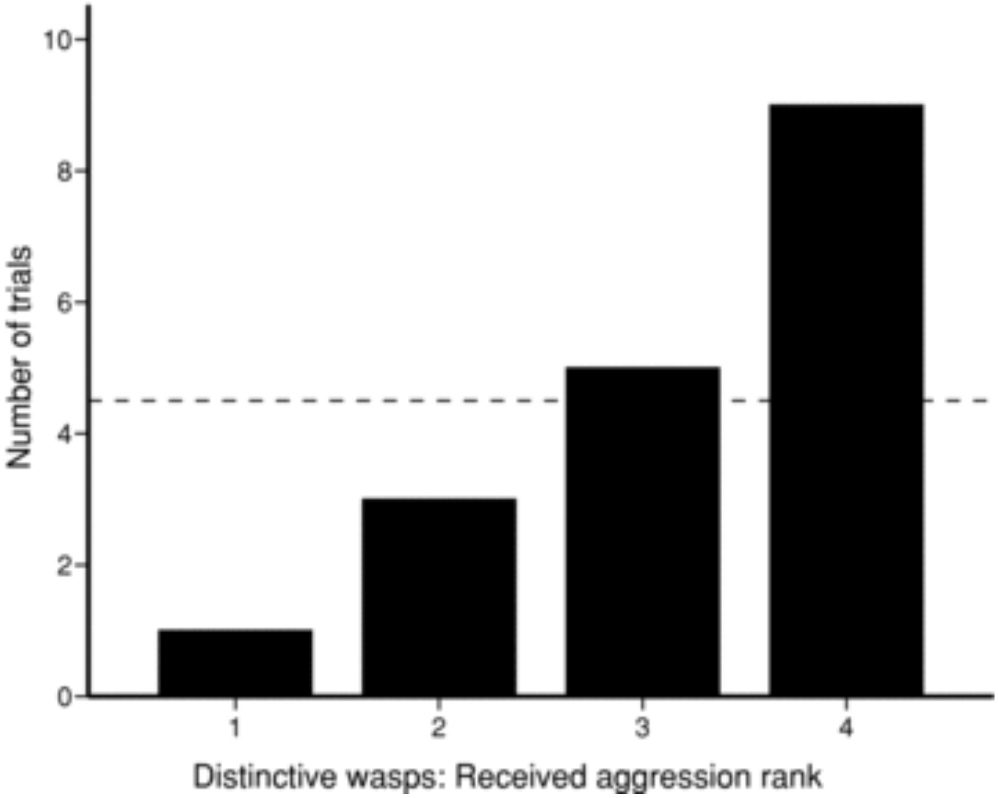

Figure 2.2. Wasps with distinctive phenotypes (i.e., the rare morph) benefit from advertising their identity. Distinctive wasps received the least aggression in a disproportionate number of trials (multinomial sampling distribution, *N*= 18, *P*= 0.038). In each trial, wasps were ranked based on the total number of aggressive acts they received from 1 (most) to 4 (least). The dotted line illustrates the null expectation if aggression had been distributed randomly. Only the ranks of distinctive wasps are shown.

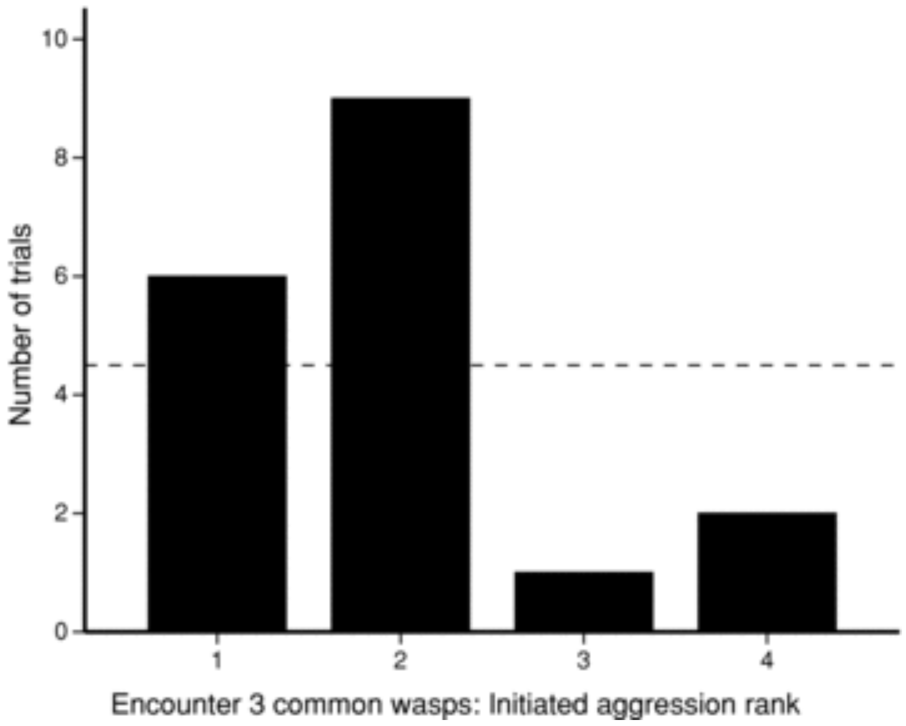

Figure 2.3. Wasps with distinctive phenotypes encountered three wasps with the same appearance, whereas common wasps encountered two wasps with the same appearance. Wasps that encountered three individuals with the same appearance were the most aggressive in a disproportionate number of trials (multinomial sampling distribution, N= 18, P= 0.033). The dotted line shows the null expectation if aggression had been initiated randomly with respect to the number of common versus distinctive individuals each wasp interacted with. Only the ranks of distinctive wasps are shown.

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Chapter 3: Selection for individual recognition and the evolution of polymorphic identity signals in *Polistes* paper wasps

Abstract

Individual recognition (IR) requires individuals to uniquely identify their social partners based on phenotypic variation. Because IR is so specific, distinctive phenotypes that stand out from the crowd facilitate efficient recognition. Over time, the benefits of unique appearances are predicted to produce a correlation between IR and phenotypic variation. Here, we test whether there is an association between elevated phenotypic polymorphism and IR in paper wasps. Previous work has shown that *Polistes fuscatus* use variable colour patterns for IR. We test whether two less variable wasp species, *Polistes dominulus* and *Polistes metricus*, are capable of IR. As predicted, neither species is capable of IR, suggesting that highly variable colour patterns are confined to *Polistes* species with IR. This association suggests that elevated phenotypic variation in taxa with IR may be the result of selection for identity signals rather than neutral processes. Given that IR is widespread among social taxa, selection for identity

signalling may be an underappreciated mechanism for the origin and maintenance of polymorphism.

Introduction

Phenotypic variation is essential for recognizing and differentiating between social partners. Recognition occurs when one individual, the receiver, discriminates between other individuals, the senders, using cues or signals produced by the senders (Mateo 2004; Sherman et al. 1997). There are many different types of recognition, including species, kin, nestmate and individual. Individual recognition (IR) is the most precise form of social recognition, because it requires receivers to uniquely identify each social partner (Beecher 1989; Tibbetts and Dale 2007).

Selection may act on the senders and/or the receivers during recognition system evolution. As a result, IR can evolve through two nonexclusive paths: (i) receiver cognition and perception may evolve so receivers can discriminate between individual conspecifics using neutral variation or (ii) the phenotypes of senders may evolve so that senders have distinctive, highly variable features that permit easy individual identification (Dale et al. 2001; Johnstone 1997).

To date, most of the research on recognition systems has documented the extent of recognition, whereas less is known about the evolution of recognition systems and how selection has acted on sender phenotypes (Tibbetts and Dale 2007). A method for testing whether recognition selects for the evolution of phenotypic variation is to assess the legacy of selection by comparing recognition abilities with the extent of phenotypic variation in a group of closely related species. If species with IR have more variable phenotypes than species lacking IR, the elevated phenotypic variation in taxa with IR may have evolved to facilitate accurate recognition. For example, swallow species with IR have more variable calls than species lacking IR, suggesting that selection has favoured call diversification in swallow species with IR (Beecher et al. 1986; Medvin and Beecher 1986; Medvin et al. 1993).

Alternatively, selection may act on receiver cognition and perception alone, rather than the phenotypic variation in senders. For example, *Pachycondyla* spp. ants use distinctive chemical signatures for IR (D'Ettorre and Heinze 2005; Dreier et al. 2007), although their chemical profiles are not more diverse than species that lack IR (Dreier and D'Ettorre 2009). Thus, IR may select for receivers that can differentiate between individuals based on otherwise neutral phenotypic variation. Selection for efficient IR systems can affect both sender and receiver phenotypes. Examining the associations between recognition abilities and phenotypic polymorphism can differentiate between these two processes.

Polistes paper wasps provide a good model for testing whether there is an association between the specificity of recognition and the extent of phenotypic variation within a species. The amount of phenotypic variation is dramatic across paper wasps(Enteman 1904; Tibbetts 2004). Some species such as *Polistes fuscatus* have extremely variable colour patterns, whereas other species such as

Polistes dominulus and *Polistes metricus* have less variable colour patterns (Fig. 3.1). Less is known about *Polistes* recognition behaviour. In at least one species, *P. fuscatus*, the variable colour patterns are used for visual IR (Fig. 3.1, top row) (Sheehan and Tibbetts 2008; Tibbetts 2002), but *P. fuscatus* is the only wasp species where IR has been tested. Wasp species that appear to be less variable may be able to recognize individuals through two means. First, receiver perception may have evolved such that receivers can discriminate between individuals based on apparently minor colour variation. Second, wasps may use other sensory modalities, such as variable chemical signatures, to recognize individuals. As a result, it is important to test whether wasp species that lack variable visual features also lack IR abilities.

Here, we test the relationship between IR and phenotypic variation in three species of paper wasps (*P. fuscatus*, *P. dominulus* and *P. metricus*). First, we quantify the levels of intraspecific colour pattern polymorphism in the species. Then, we experimentally test their ability to individually recognize conspecifics by comparing the response to familiar and unfamiliar individuals. If selection for IR in *Polistes* promotes and maintains highly variable colour patterns (Tibbetts, 2004), then species with low marking variability, such as *P. dominulus* and *P. metricus*, are not predicted to individually recognize conspecifics.

Methods

Colour pattern analysis

We describe the relative variation in colour patterns between species by assessing the distribution of colours on five different regions of the face (Fig. 3.2). Adobe Photoshop CS3 was used to measure the fraction of pixels in each of the five areas that were black, yellow or brown. These colour categories provide good estimates of the colour variability in *P. dominulus* and *P. metricus*. *Polistes fuscatus* have a wider range of brown colours, so any colour that was not black or yellow was classified as brown. This categorization underestimates the variability of *P. fuscatus*, so it provides a conservative method of scoring colouration with respect to our hypothesis. We collected wasps from nests at a number of sites in Michigan throughout the year. For colour analysis, 20 additional individuals from each species, all from different nests, were randomly chosen, freeze-killed and stored in a freezer at −20 °C to ensure that colour patterns did not fade. All wasps were measured by a student with no knowledge of the specific experimental predictions.

Behavioural assessment of recognition abilities

We assessed the recognition abilities of *P. dominulus* and *P. metricus* by scoring the intensity of aggressive interactions between foundresses with and without prior social experiences with each other. Wasps of both species were collected near Ann Arbor, MI, in the early spring of 2008. We used 26 focal *P. dominulus* and 28 focal *P. metricus* foundresses in our trials. Immediately before the experiment, all individuals were housed individually and kept in social isolation. Previously, the *P. dominulus* foundresses had participated in choice experiments similar to those described elsewhere (Tibbetts 2008; Tibbetts and Lindsay 2008), in which they interacted with model wasps. We previously used methods similar to those described in the following paragraph to demonstrate that *P. fuscatus* can recognize individuals (Sheehan & Tibbetts, 2008), so we did not test this species again.

Our experimental design measured the abilities of both *P. dominulus* and *P. metricus* to remember individual social partners regardless of sensory modality. To ensure that foundresses had not encountered each other previously, all interactions were staged between foundresses collected from sites at least 2 km apart. In the first trial (day 0), two foundresses were introduced to each other in a small, sterile container and their interactions were filmed. After filming, they were housed together until the next day (day 1) at which point they were separated and returned to their initial solitary housing. One day later, the same two wasps were filmed interacting again (day 2). To ensure that any changes in aggression between days 0 and 2 were a result of IR and not of decreases in motivation over time, we paired the wasps with other unfamiliar social partners on the day before and after (days 1 and 3). On day 1, wasps were housed individually for approximately 5 h between separation from their initial partner and meeting a new partner. If the wasps are able to recognize and remember social partners, they should be least aggressive when they interact with a known individual (day 2). Species capable of IR behave differently towards individuals with whom they share a history of prior interactions (D'Ettorre and Heinze 2005; Dreier and D'Ettorre 2009; Dreier et al. 2007; Karavanich and Atema 1998;

Sheehan and Tibbetts 2008; Tibbetts et al. 2008). In this case, species with IR are predicted to be less aggressive towards the individual they have previously encountered (day 2) than towards individuals they are encountering for the first time (days 0, 1 and 3).

All of the behavioural trials lasted 2 h. Trials were videotaped and the first half hour of each trial was scored by an observer who was blind to the identity of wasps and the day the trial took place. Wasps engage in a range of aggressive and affiliative behaviours. Behaviours were rated on a scale of 0–4 with higher scores, indicating more intense aggression: (0) nonaggressive physical contact, (1) darts, (2) darting while snapping mandibles, (3) bites and (4) mounting or grappling. To compare the levels of aggression between trials, we calculated three measures: an intensity index, the number of nonaggressive interactions and an overall aggression index. The intensity index measured how intense aggressive interactions were and was calculated by summing the scores of aggressive interactions and dividing by the number of aggressive acts. The number of nonaggressive interactions was calculated by tallying the number of discreet nonaggressive interactions that took place. The overall aggression index took into account both aggressive and affiliative acts. The aggression index was calculated using the same method as the intensity index with the addition of the number of nonaggressive interactions in the denominator (Dreier *et al*., 2007; Sheehan & Tibbetts, 2008). The indices and number of nonaggressive contacts were compared between days using Friedman’s anova and multiple comparisons (Sokal and Rohlf 1995). *Post hoc* power tests were carried out using G*Power.

Results

Intraspecific colour pattern variation

Polistes fuscatus have far more variable colour patterns than either *P. dominulus* or *P. metricus*, and the differences in variation across species are obvious after examining a few pictures of each species (Fig. 3.1). The greater variability in the colour patterns of *P. fuscatus* arises from a combination of two factors. First, *P. fuscatus* have large amounts of variation in each area of the face (Fig. 3.3), whereas the variation in *P. dominulus* and *P. metricus* is limited to small areas of the face (clypeus in *P. dominulus* and antennal region in *P. metricus*). Second, there are more potential variants for each face region in *P. fuscatus* than *P. metricus* or *P. dominulus*. For example, the clypeus in *P. fuscatus* can contain a huge range of yellow, black and brown colour patterns (Fig. 3.1, top row). In contrast, the variation in *P. dominulus* is largely restricted to the size and shape of black clypeal spots, which previous research has shown acts as a signal of fighting ability (Tibbetts & Dale, 2004). Variation in *P. metricus* is restricted to the brown vs. black pigment in the eyebrow and frons areas. The variation in *P. metricus* is likely to be less visually apparent than the variation in *P. fuscatus* and *P. dominulus*, as the differences in colouration are quite subtle, and this area is typically obscured by the antennae during social interactions.

Behavioural recognition experiments

Polistes dominulus

There is no evidence of IR in *P. dominulus.* Aggressive encounters between wasps with prior histories of social interactions were just as intense as encounters between wasps that had not previously met (Fig. 3.4 A. Friedman's anova, $F_{(3,\, n = 26)}$ = 1.51, P = 0.68; *post hoc* power analysis, Power = 0.95). Additionally, the number of nonaggressive contacts did not differ between trials (Fig. 3.4 B. Friedman's anova, $F_{(3,\, n = 26)}$ = 3.79, P = 0.29; *post hoc* power analysis, Power = 1.00). Finally, the overall aggression index, which accounts for both aggressive and nonaggressive interactions, did not differ between trials (Fig. 3.4 C. Friedman's anova, $F_{(3,\, n = 26)}$ = 5.67, P = 0.13; *post hoc* power analysis, Power = 0.91).

Polistes metricus

There is no evidence of IR in *P. metricus*. The intensity of aggression declined after the first encounter in *P. metricus* (Fig. 3.5 A. Friedman's anova, $F_{(3,\, n = 28)}$ = 18.06, P < 0.0001; *post hoc* power analysis, Power = 0.95). However, there were no differences in the intensity of aggression after the first encounter. Aggressive intensity was similar among pairs of individuals with and without prior social histories (Fig. 3.5 A). There were also a similar number of nonaggressive contacts across all trials (Fig. 3.5 B. Friedman's anova, $F_{(3,\, n = 28)}$ = 1.72, P = 0.63; *post hoc* power analysis, Power = 1.00). The overall aggression index, which incorporates both aggressive and nonaggressive interactions, was highest during the initial trial and lower in subsequent trials (Fig. 3.5 C. Friedman's anova, $F_{(3,\, n = 28)}$ = 13.76, P = 0.003; *post hoc* power analysis, Power = 0.95). Although aggression indices declined between a pair's first (day 0) and second (day 2) encounters [Nonparametric Tukey's HSD (Honestly significant difference), $P < 0.05$], there was no difference in aggression between the unfamiliar pairs on days 1 and 3 and the familiar pair on day 2 (Nonparametric Tukey's HSD, $P > 0.2$). In sum, there was no difference in the intensity of aggressive or nonaggressive interactions between wasp pairs that had interacted previously vs. pairs that lacked a prior history of social interactions.

Discussion

Paper wasp species differ markedly in their relative levels of intraspecific colour pattern variation. As predicted, the extent of colour variation is associated with recognition abilities in the three species tested. *Polistes fuscatus* are far more variable than *P. metricus* or *P. dominulus* and have robust long-term memories of individual conspecifics (Sheehan & Tibbetts, 2008). In contrast, *P. dominulus* and *P. metricus* have little variation in colour patterns. In both species, aggressive and affiliative behaviours did not vary with social history, indicating that neither species recognizes individual social partners.

The pattern of aggression across trials was slightly different in *P. metricus* than *P. dominulus*. *Polistes metricus* were more aggressive during their first encounter with a conspecific than during subsequent social encounters, whereas *P. dominulus* were similarly aggressive across all social encounters. The pattern of aggression in *P. metricus* is not evidence of IR, as aggression did not vary with individual social experience. Further, other species that lack IR show similar patterns of declining aggression over subsequent encounters (Dreier & D'Ettorre, 2009). Instead, the pattern of aggression may reflect differences in the social behaviour of the species. For example, *P. metricus* are less likely to form co-operative foundresses associations than *P. dominulus* or *P. fuscatus* and have extremely high rates of nest usurpation (Gamboa 1978; Gamboa et al. 2004). As a result, *P. metricus* may have a stronger initial aggressive response to conspecifics than *P. dominulus* or *P. fuscatus*.

The results of this study support a key prediction of the hypothesis that selection for efficient IR promotes and maintains phenotypic polymorphism. Selection for efficient social recognition has been hypothesized to favour the evolution of variable, distinctive phenotypes, thus promoting and maintaining polymorphism within populations (Dale 2006; Dale et al. 2001; Sheehan and Tibbetts 2009). Over time, we expect selection for identity signalling to produce numerous phenotypes, such as those seen in *P. fuscatus* (Fig. 3.1, top row). In contrast, individuals in species lacking IR are not under selection to advertise their identity with unique phenotypes. Therefore, species without IR are predicted to have less variable phenotypes than those with IR, as we found in *Polistes*. A similar relationship between variation and recognition has been found in a few other species, suggesting that evolution can adaptively shape sender phenotypes to facilitate accurate recognition [e.g. comparative studies call variation in swallows (Beecher et al. 1986; Medvin et al. 1993) and penguins (Jouventin and Aubin 2002; Jouventin et al. 1999)].

An alternative hypothesis for the relationship between IR and phenotypic variation is that pre-existing variation is required to allow the evolution of IR. That is, pre-existing variation may be co-opted to allow IR rather than IR selecting for phenotypic variation. If pre-existing variation has been co-opted for recognition in the wasps, variation is predicted to be more strongly associated with a species' evolutionary history than its social behaviour. In fact, variable colour patterns in the *Polistes* are significantly associated with a species' social behaviour rather than its evolutionary history, suggesting that the benefits of social recognition have selected for phenotypic variation in certain taxa (Tibbetts, 2004). For example, *P. metricus* and *P. fuscatus* are sister species, yet foundresses of each species have different social behaviour and different patterns of phenotypic variation. Further, recent behavioural work has illustrated the mechanism that could drive the evolution of phenotypic variation. Wasps with unique phenotypes receive less aggression during dominance contests than individuals with a common appearance, indicating that phenotypic variation provides benefits by facilitating recognition (Sheehan & Tibbetts, 2009). Although inferring the direction of evolutionary change can be difficult, current evidence suggests that IR selects for phenotypic variation rather than standing variation being co-opted for recognition behaviour in paper wasps. Future behavioural analysis on additional *Polistes* species with and without phenotypic variation will be important to confirm this pattern.

Data on chemical communication also suggest that IR has selected for variation rather than *vice versa*. In *Polistes*, variable cuticular hydrocarbon profiles have been found in all species examined to date (Gamboa 2004). Both *P. dominulus* and *P. metricus* pay attention to the variation and use hydrocarbons to communicate nest membership (Cini et al. 2009; Singer and Espelie 1996) and individual fertility (Izzo et al. 2010). However, the results of this study demonstrate that neither *P. dominulus* nor *P. metricus* recognize individuals based on their variable hydrocarbon profiles. Therefore, pre-existing variation is not sufficient to allow the evolution of IR. Perhaps, the evolution of IR using chemical information is difficult in *Polistes*, because cuticular hydrocarbons already convey information about nestmate identity and fertility. Evolving a novel signal in a different modality may be easier than modifying chemical information to convey multiple, different kinds of information. Examining whether the presence of a pre-existing communication system constrains the evolution of other types of recognition within the same sensory modality presents an exciting possibility for future research. Overall, most evidence suggests that IR has been selected for variable visual features in *P. fuscatus.*

Mechanisms other than identity signalling may also maintain colour polymorphism in a population, including apostatic selection, mate choice for heterozygosity and alternative behavioural strategies. However, these alternatives are unlikely to explain the pattern of polymorphism in *P. fuscatus*. Apostatic selection favours phenotypic variation that is visually apparent to predators (Bond and Kamil 2002). However, variation in *P. fuscatus* is primarily confined to the face (Tibbetts, 2002), which is useful during face-to-face social interactions but is not noticeable from a distance. Therefore, it is unlikely that variation in paper wasps has evolved to avoid detection by predators. Polymorphic colour patterns can also evolve via sexual selection when mates are chosen for novelty or mate heterozygosity (Eakley and Houde 2004; Farr 1977). This hypothesis predicts that the sex under strong sexual selection will be polymorphic. However, facial pattern polymorphism in *Polistes* is confined to females, even though males are lekking and experience strong sexual selection (Beani and Turillazzi 1988; Matthessears and Alcock 1986; Polak 1993; Post and Jeanne 1983). Finally, phenotypic polymorphism is often associated with alternative social or mating strategies (Sinervo et al. 2001; Svensson et al. 2005). However, the colour pattern variation in *P. fuscatus* is not related to behavioural strategies such as founding strategy, dominance or social caste (Tibbetts, 2002). Therefore, although numerous mechanisms can maintain phenotypic polymorphism, most of these mechanisms are unlikely to be relevant to the variation in *Polistes* colour patterns. Instead, this study and other published work suggest that selection for identity signals is likely to have driven the evolution of the highly variable colour patterns in the paper wasps (Sheehan & Tibbetts, 2009).

Identity vs. quality signalling

The results of this study confirm that *P. fuscatus* and *P. dominulus* rely on different communication systems. *Polistes fuscatus* use IR (Tibbetts, 2002; Sheehan & Tibbetts, 2008), whereas *P. dominulus* are incapable of IR, relying instead on a visual signal of quality (Tibbetts and Dale 2004; Tibbetts and

Lindsay 2008; Tibbetts et al. 2010). Despite the differences in communication behaviour, these species have very similar social systems. Both species display complex, flexible founding strategies, where queens may initiate a nest either alone or in co-operative groups. When multiple queens co-operate, they form a linear dominance hierarchy that influences work, reproduction and aggression (Gamboa et al. 2004; Roseler et al. 1991). Foundress associations remain flexible for weeks, so foundresses of both species engage in aggressive contests with numerous familiar and unfamiliar individuals (Reeve 1991; West Eberhard 1969; Zanette and Field 2009).

Given the similar social systems of *P. dominulus* and *P. fuscatus*, what accounts for the differences in the species' signalling systems? One possibility is that their social systems differ in subtle ways that have influenced signal evolution. Signals of fighting ability are expected to evolve when individuals compete with many unfamiliar rivals (Tibbetts and Safran 2009), while identity signals are more important in smaller, stable groups (Tibbetts & Dale, 2007). Empirical data indicate that the quality signals in *P. dominulus* may be used primarily during interactions with non-nestmates (i.e. during early spring dominance contests before nesting groups are established or during attempted nest usurpation) (Tibbetts and Shorter 2009; Zanette and Field 2009). Identity signals in *P. fuscatus* are important during dominance interactions within established nests (Tibbetts, 2002). Therefore, identity and quality signals may reflect solutions to different types of social problems faced by *Polistes* wasps – non-nestmate interactions during colony foundation vs. linear dominance hierarchies among queens. Although communication researchers sometimes considers signal evolution to be a deterministic process, with a set of social conditions leading to a certain type of signalling system, historical contingency may also play an important role in signal evolution.

Conclusions

IR requires receivers to distinguish between many individual social partners on the basis of unique cues (Tibbetts et al. 2008). Recognition systems may evolve via two paths: (i) receivers may be favoured to pay attention to pre-existing phenotypic variation and (ii) senders may be favoured to advertise their identities with variable phenotypes. Distinguishing between these two non–mutually exclusive alternatives is challenging, although studies examining the relationship between phenotypic variation and recognition behaviour can provide insight into the dynamics of recognition system evolution. The results of this study demonstrate that two *Polistes* species without variable phenotypes lack IR, supporting the hypothesis that sender phenotypes have evolved to facilitate accurate recognition. Together with other published results (Tibbetts, 2004; Sheehan & Tibbetts, 2009), the current study provides evidence that the variable colour patterns in *P. fuscatus* have evolved via selection for easily recognizable identity signals rather than neutral processes.

Figure 3.1. Portraits showing the colour pattern variation within each of the three species in this study. *Polistes fuscatus* (top row) have variable colouration in numerous regions of the face. Note that there is also a wide range of colour including numerous shades of brown. *Polistes dominulus* (middle row) has species-typical yellow markings on its face that show low levels of variability, although the black mark in the middle of the clypeus (the badge of status) is variable. *Polistes metricus* has some invariant colour regions (clypeus and inner eyes), but the species-typical markings on the frons and eyebrow show some variability in the extent of brown colouration.

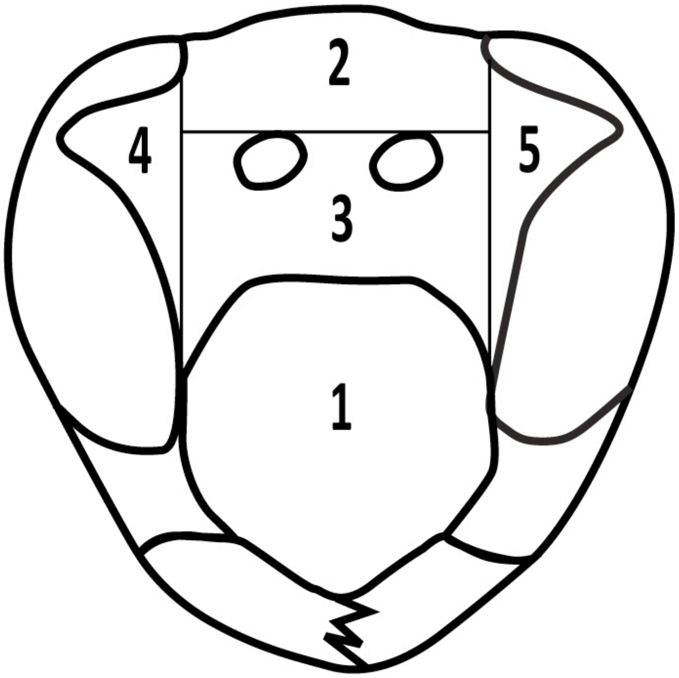

Figure 3.2. Schematic of the regions of the wasp face considered in this study. (1) the clypeus, (2) the upper frons or ‘eyebrow’, (3) the frons, (4) the right inner eye and (5) the left inner eye. For the frons (region 3), the antennal sockets were not included in the total area.

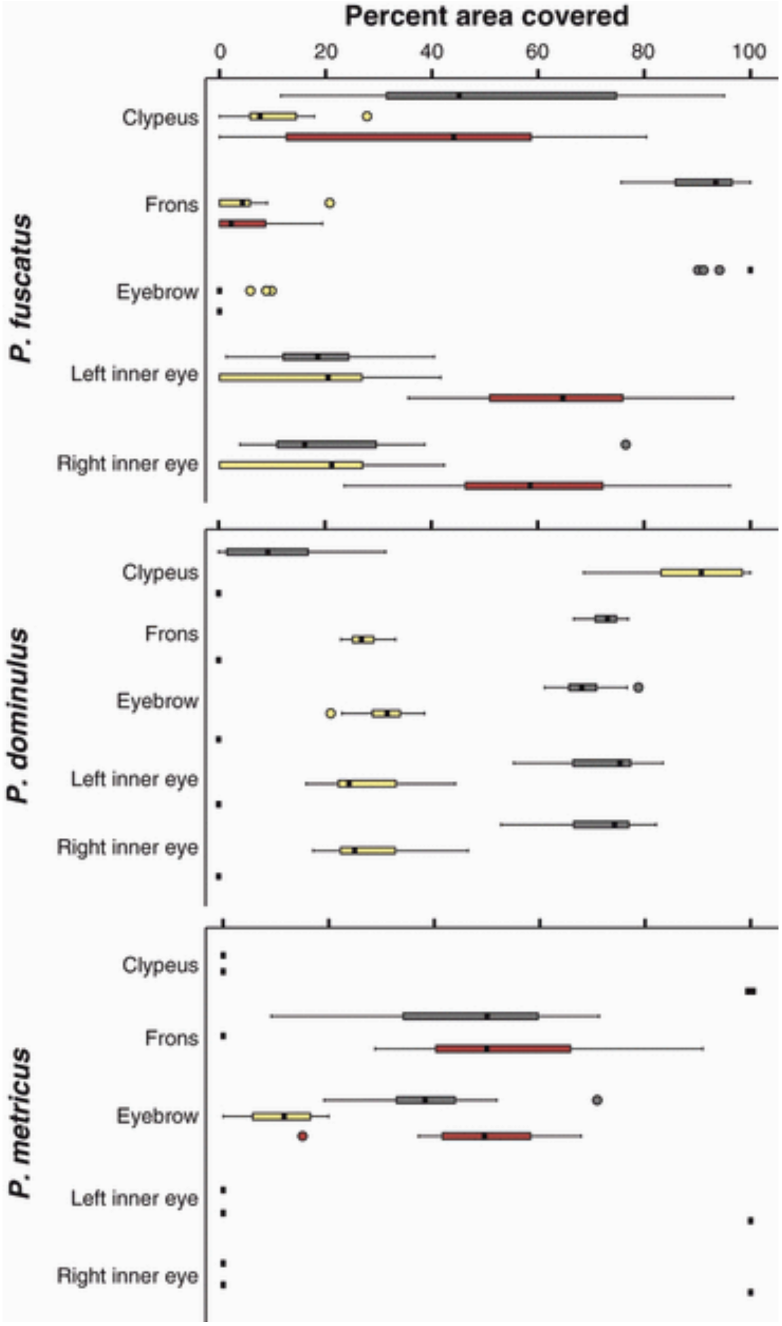

Figure 3.3. *Polistes fuscatus* is by far the most variable of the three species. For each region, the percentage covered by each of the three colours is shown by the box plots. Black is at the top, yellow is in the middle and brown is at the bottom. Note that *P. fuscatus* shows variability in all of the regions and that the clypeus shows a wide of colouration patterns.

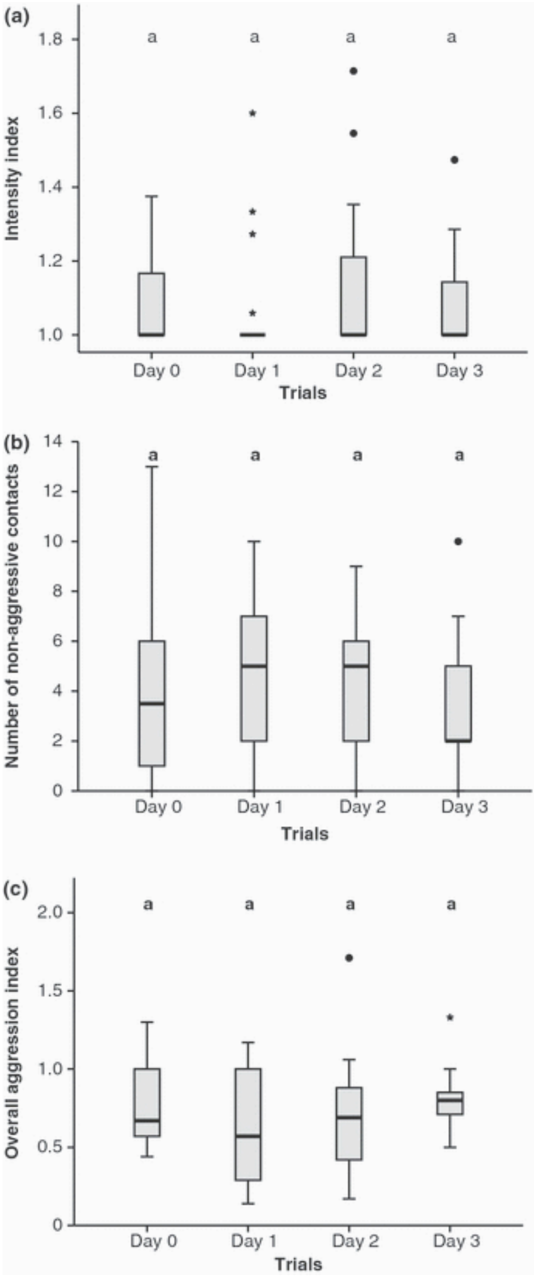

Figure 3.4. *Polistes dominulus* show no evidence of individual recognition. Individuals with whom they have interacted previously (day 2) receive similar amounts of aggression as individuals they have never encountered (days 0, 1 and 3). The overall aggression indices (a), the number of nonaggressive contacts (b) and the intensity of aggressive acts (c) towards individual they have interacted with previously as individuals they have never encountered before does not differ. Days that are significantly different (Nonparametric Tukey's HSD, $P < 0.05$) are designated with different letters. Box plots show medians and quartiles.

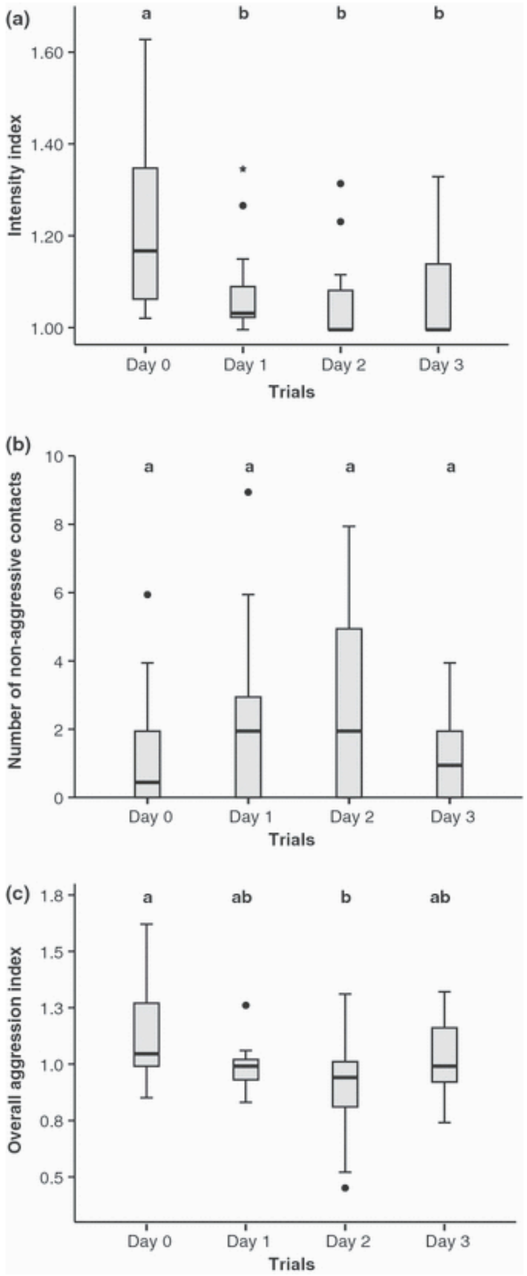

Figure 3.5. Levels of aggression among *Polistes metricus* decline over time and do not show evidence of individual recognition. Interactions are the most aggressive during the first encounter and are less aggressive in subsequent encounters. When wasps re-encounter their social partner from days 0 to 2, they are less aggressive (a, c). However, they are similarly less aggressive to other new social partners on days 1 and 3, suggesting that motivation for aggression declines over time. Additionally, there are no differences in affiliative behaviours across trials (b). Days that are significantly different (Nonparametric Tukey's HSD, $P < 0.05$) are designated with different letters. Box plots show medians and quartiles.

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Chapter 4: Specialized face learning is associated with individual recognition in paper wasps

We demonstrate that the evolution of facial recognition in wasps is associated with specialized face-learning abilities. *Polistes fuscatus* can differentiate among normal wasp face images more rapidly and accurately than nonface images or manipulated faces. A close relative lacking facial recognition, *Polistes metricus*, however, lacks specialized face learning. Similar specializations for face learning are found in primates and other mammals, although *P. fuscatus* represents an independent evolution of specialization. Convergence toward face specialization in distant taxa as well as divergence among closely related taxa with different recognition behavior suggests that specialized cognition is surprisingly labile and may be adaptively shaped by species-specific selective pressures such as face recognition.

The cognitive mechanisms underlying learning abilities are surprisingly similar across taxa as diverse as mammals, birds, insects, and mollusks (Papini

2002). Although the mechanisms that underlie learning are broadly generalized across animals, there is increasing evidence that learning abilities are adaptively shaped by species' ecology and can be highly specialized (Shettleworth 2010). One of the most striking examples of specialized cognition is specialized face learning found in some mammals, including humans (Kendrick et al. 1996; McKone et al. 2007; Pascalis and Bachevalier 1998). Individual face recognition is an important aspect of human social interactions, and our brains process the images of normal conspecific faces differently than any other images (Yovel and Kanwisher 2004). Further, individual recognition is a type of complex social behavior that could favor specialized cognition (Tibbetts and Dale 2007) because it requires flexible learning and memory and has the potential to dramatically increase cognitive demands. However, the claim that face specialization is an adaptation to facilitate individual recognition has been contentious, in part because it is unclear whether face learning is based on conserved mechanisms or has evolved independently in multiple mammalian lineages (Leopold and Rhodes 2010; Pascalis and Kelly 2009). If face specialization is an adaptation to facilitate face recognition, we predict that specialization will be associated with the evolution of facial individual recognition across distant taxa.

Paper wasps are a good system for examining the evolution of face specialization because closely related wasp species differ in their ability to individually recognize conspecific faces. The paper wasp, *Polistes fuscatus*, has variable facial features that are used to recognize individual conspecifics (Sheehan and Tibbetts 2008; Tibbetts 2002). Visual recognition is possible in

Polistes wasps because they have acute vision (Land 1997) and live in well-lit nests. *P. fuscatus* nests are often initiated by groups of cooperating queens, in which relative reproduction is determined by a strict linear dominance hierarchy (Reeve 1991; Reeve et al. 2000); individual recognition stabilizes social interactions and reduces aggression within these cooperative groups (Sheehan and Tibbetts 2009). Some wasp species, such as *Polistes metricus*, typically nest alone (Hughes et al. 1993) and therefore lack competition among queens. Solitary nest founding is associated with a lack of facial pattern variability (Tibbetts 2004), and experiments have shown that *P. metricus* does not recognize conspecifics as individuals (Sheehan and Tibbetts 2010).

We tested the adaptive evolution of specalized face learning by comparing face specialization in *P. fuscatus* and *P. metricus*. We predicted that *P. fuscatus* will learn normal face images faster and more accurately than nonface images or manipulated faces (Fig. 4.1), whereas *P. metricus* will not. Comparing learning of normal and manipulated face images (Fig. 4.1) provides a particularly good test of face specialization because manipulated faces are composed of the same colors and patterns as those of normal faces (table 4.1), but alteration may prevent the perceptual system from identifying the stimuli as faces. We tested learning by training wasps to discriminate between two images using a negatively reinforced T-maze (Fig. 4.5; Supplemental materials and methods). The floor of the entire maze was electrified, except for a “safety zone” in one arm of the maze, which was consistently associated with one image in a pair. The position of the safety zone switched across trials in a predetermined pseudo-random order. Wasps were placed in an antechamber, allowed to acclimate, and then released into the electrified maze for 2 min. A wasp “chose” when it entered a chamber in one of the arms of the maze. Each wasp was a healthy wild-caught adult female naïve to the training paradigm and was tested only once. We trained 12 wasps for 40 consecutive trials on each image type (Fig. 4.1). We compared the speed of acquisition using generalized estimating equations (GEEs) and total number of correct choices between image treatments using 2-by-2 χ^2 tests.

We found that individual recognition is associated with specialization for conspecific face learning in paper wasps. *P. fuscatus* distinguished pairs of normal faces more rapidly and accurately than nonface and manipulated face images (GEE, full model: Wald $\chi^2 = 32.06$, df = 4, $P < 0.0001$, $n = 2400$ trials) (Fig. 4.2, A and B). These results are surprising because Hymenopteran visual systems are predicted to distinguish between high-contrast patterns more readily than complex images of natural scenes, such as faces and caterpillars (Lehrer and Campan 2005). Nevertheless, *P. fuscatus* that were trained to discriminate faces learned faster (for trials 1 to 30: GEE, Wald $\chi^2 = 5.61$, $P = 0.018$, $n = 720$ trials) and made more correct choices than did wasps trained to discriminate simple patterns ($\chi^2 = 9.1$, $P = 0.0026$, $n = 960$ trials) (Fig. 4.3 A). A greater familiarity with faces than patterns cannot explain the result because paper wasps are generalist visual predators of caterpillars (Land and Fernald 1992) yet learn to discriminate between pairs of caterpillars more slowly (GEE, Wald $\chi^2 = 25.45$, $P < 0.0001$, $n = 960$ trials) and with fewer correct choices than between pairs of faces ($\chi^2 = 45.02$, $P < 0.0001$, $n = 960$ trials) (Fig. 4.3 A). The most striking evidence for specialized face learning in *P. fuscatus* is that they have trouble learning faces without antennae. Wasps learn pairs of antenna-less faces more slowly and less accurately than normal faces (lower rate of acquisition GEE, Wald $\chi^2 = 13.98$, $P < 0.0001$, $n = 960$ trials; and fewer correct choices $\chi^2 = 18.85$, $P < 0.0001$, $n = 960$ trials). Therefore, antennae are an essential cue for effective face recognition. In a separate image manipulation, we rearranged the components of the wasp face and found that facial configuration also influences learning. Wasps trained to discriminate pairs of rearranged faces had lower rates of acquisition (GEE, Wald $\chi^2 = 20.18$, $P < 0.0001$, $n = 960$ trials) and made fewer correct choices ($\chi^2 = 18.28$, $P < 0.\ 0001$, $n = 960$ trials) (Fig. 4.3 A) than did wasps trained to discriminate pairs of normal faces. Taken together, these data suggest that *P. fuscatus* do not use general pattern- or shape-discrimination abilities to recognize conspecific faces. Instead, faces appear to be treated as unique visual inputs.

We next examined how face specialization co-varies with individual face recognition by testing learning in *P. metricus*, which lacks individual recognition (Sheehan and Tibbetts 2010). *P. metricus* showed no evidence of specialized face learning. In fact, wasps trained to discriminate pairs of face images performed no better than chance ($\chi^2 = 0.2$, $P = 0.65$, $n = 480$ trials) (Fig. 4.3 B). In contrast to *P. fuscatus*, *P. metricus* had higher rates of acquisition when trained to discriminate patterns and caterpillars than conspecific faces (GEE full model: Wald $\chi^2 = 8.48$, df = 2, $P = 0.014$, $n = 1440$ trials; patterns: Wald $\chi^2 = 8.27$, $P = 0.004$, $n = 960$ trials; caterpillars: Wald $\chi^2 = 4.02$, $P = 0.045$, $n = 960$

trials) (Fig. 4.2 C). Additionally, *P. metricus* choose the correct pattern and caterpillar images more often than the correct conspecific face image (pattern: $\chi^2 = 10.47$, $P = 0.0012$, $n = 960$ trials, caterpillar: $\chi^2 = 7.37$, $P = 0.0066$, $n = 960$ trials) (Fig. 4.3 B).

To ensure that the difference in face-learning abilities between the two species is caused by cognitive differences rather than the particular face stimuli used, we trained each species to discriminate heterospecific face images. *P. fuscatus* learned the face stimuli of both species more rapidly and made more correct choices than did *P. metricus* (rate of aquistion GEE full model: Wald $\chi^2 = 39.43$, df = 2, $P < 0.0001$, $n = 1920$ trials; *P. fuscatus* faces: Wald $\chi^2 = 32.38$, $P < 0.0001$, $n = 960$ trials; *P. metricus* faces: Wald $\chi^2 = 7.11$, $P = 0.008$, $n = 960$ trials; number correct choices, *P. fuscatus* faces: $\chi^2 = 42.52$, $P < 0.0001$, $n = 960$ trials; *P. metricus* faces: $\chi^2 = 10.05$, $P = 0.0015$, $n = 960$ trials) (Fig. 4.4, A and B). Although *P. metricus* learned face images poorly, they were able to discriminate between pairs of *P. fuscatus* faces; wasps performed better than chance in the last 10 trials (65.8%; $\chi^2 = 5.54$, $P = 0.019$, $n = 120$ trials) (Fig. 4.4 A). We further analyzed whether *P. metricus* treat faces as unique visual inputs by examining how antennae removal influenced face learning. Unlike *P. fuscatus*, digital removal of the antennae from images did not reduce the number of correct choices ($\chi^2 = 3.33$, $P = 0.068$, $n = 960$ trials) (Fig. 4.4 C) or rates of learning (GEE, Wald $\chi^2 = 2.23$, $P = 0.14$, $n = 960$ trials), providing further evidence that faces are not special for *P. metricus*. Differences in face learning between the two species cannot be attributed to general differences in visual learning because both species learned to discriminate between pairs of artificial patterns and caterpillars at the same rate and with the same accuracy (rate of acquisition GEE full model: Wald $\chi^2 = 2.66$, df = 2, $P = 0.27$, $n = 1440$ trials; number correct choices patterns: $\chi^2 = 3.47$, $P = 0.063$, $n = 960$; caterpillars: $\chi^2 = 1.52$, $P = 0.22$, $n = 960$ trials) (Fig. 4.4 D). Therefore, *P. fuscatus* and *P. metricus* differed only in their ability to learn normal face stimuli. Differences in visual acuity between the two species cannot account for the results because morphological measurements of facet diameter demonstrate that *P. metricus* is likely to have more acute vision than that of *P. fuscatus* (Table 4.2 and Fig. 4.6). Instead, specialized face learning is an evolutionarily labile trait that tracks individual recognition.

Overall, our data suggest that selection for efficient individual recognition has led to the adaptive evolution of specialized face learning in the paper wasp *P. fuscatus*. Specialized face learning provides a remarkable example of convergent evolution between wasps and mammals. Although mammals and wasps have dramatically different eyes and neural structures (Farris 2005; Land and Fernald 1992), specializations for recognizing conspecific faces have arisen independently in both groups. Although specialized face learning in mammals and wasps are phenomenologically similar, they are likely to have different mechanistic bases. Face learning in primates and sheep is highly specialized, involving multiple brain regions and face-specific neurons (Kendrick and Baldwin 1987; McKone et al. 2007). Examining whether similar neural signatures of cognitive specialization are found in the “miniature” brain of an insect (Chittka and Niven 2009) provides an interesting avenue for future comparisons. The evolutionary flexibility of specialized face learning is striking and suggests that specialized cognition may be a widespread adaptation to facilitate complex behavioral tasks, such as individual recognition.

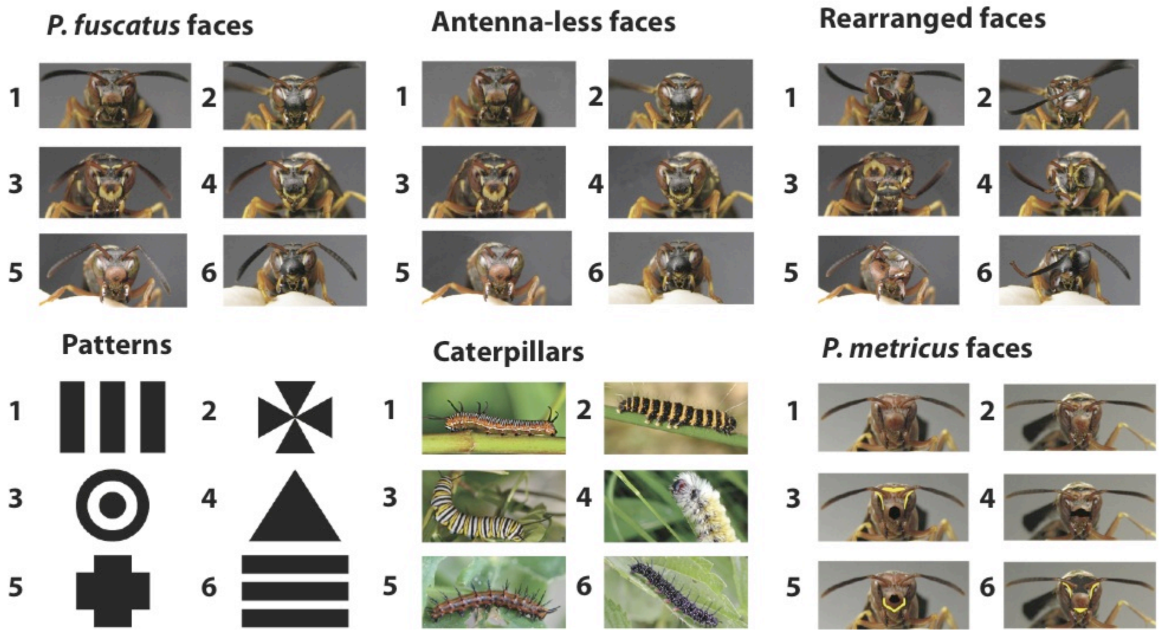

Figure 4.1 Images used for training wasps. Wasps were trained to discriminate between pairs of images. Pairs are shown in the same row except for *P. metricus* face images. For *P. metricus* face images, the unmanipulated faces in the top row were paired with the manipulated images of the other face (for example, top left paired with middle left and bottom left). Image statistics for all images are provided in table S1.

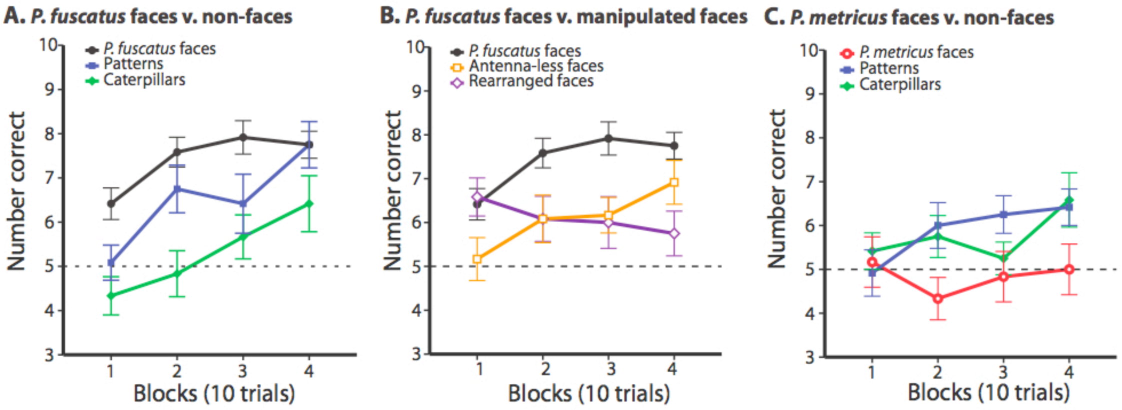

Figure 4.2. *P. fuscatus* learned to discriminate between pairs of conspecific face images faster than (**A**) other images such as patterns and caterpillars and (**B**) manipulated face images. (**C**) *P. metricus* learned to discriminate between pairs of patterns and caterpillars faster than conspecific face images. Line graphs show the mean number of correct choices (±SEM) per 10 trial blocks. Chance performance is 5 correct choices per 10 trial blocks; *n* = 12 wasps for each treatment.

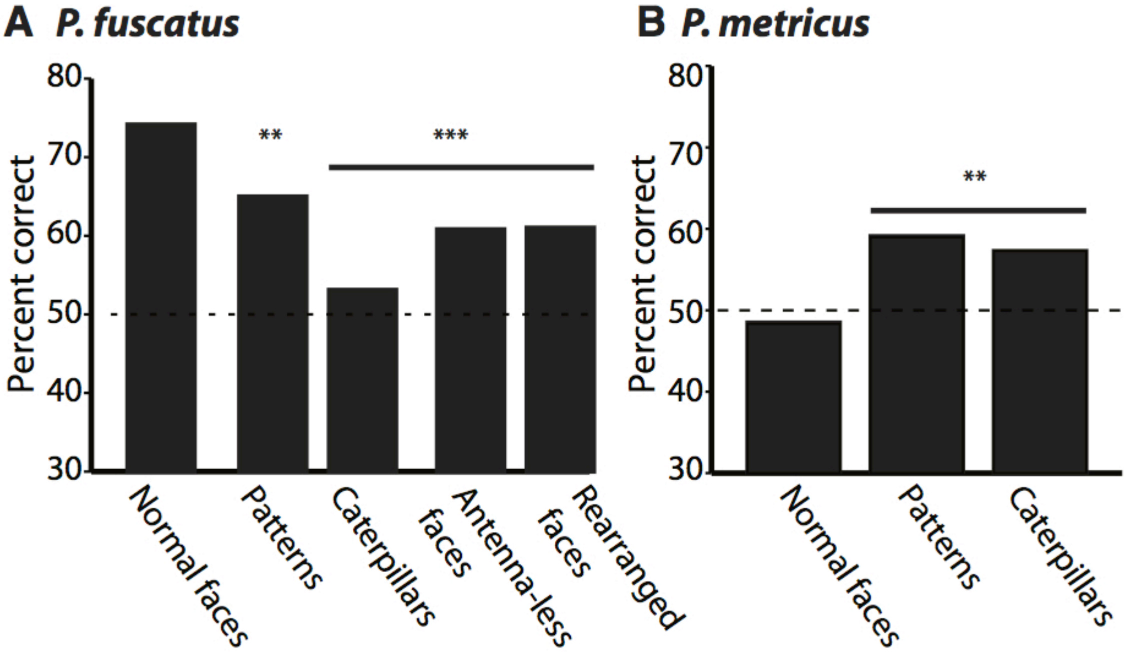

Figure 4.3. (**A**) *P. fuscatus* made more correct choices when trained to discriminate between pairs of conspecific face images than nonface or manipulated face images. (**B**) *P. metricus* made fewer correct choices when trained to discriminate between pairs of conspecific face images than nonface images. Bars show the sum of correct choices across all wasps in a treatment as a percent of 480 trials. Random choice is 50%; *n* = 12 wasps for each treatment. Asterisks denote the statistical significance level for comparisons to normal conspecific faces: **$P < 0.001$; ***$P < 0.0001$.

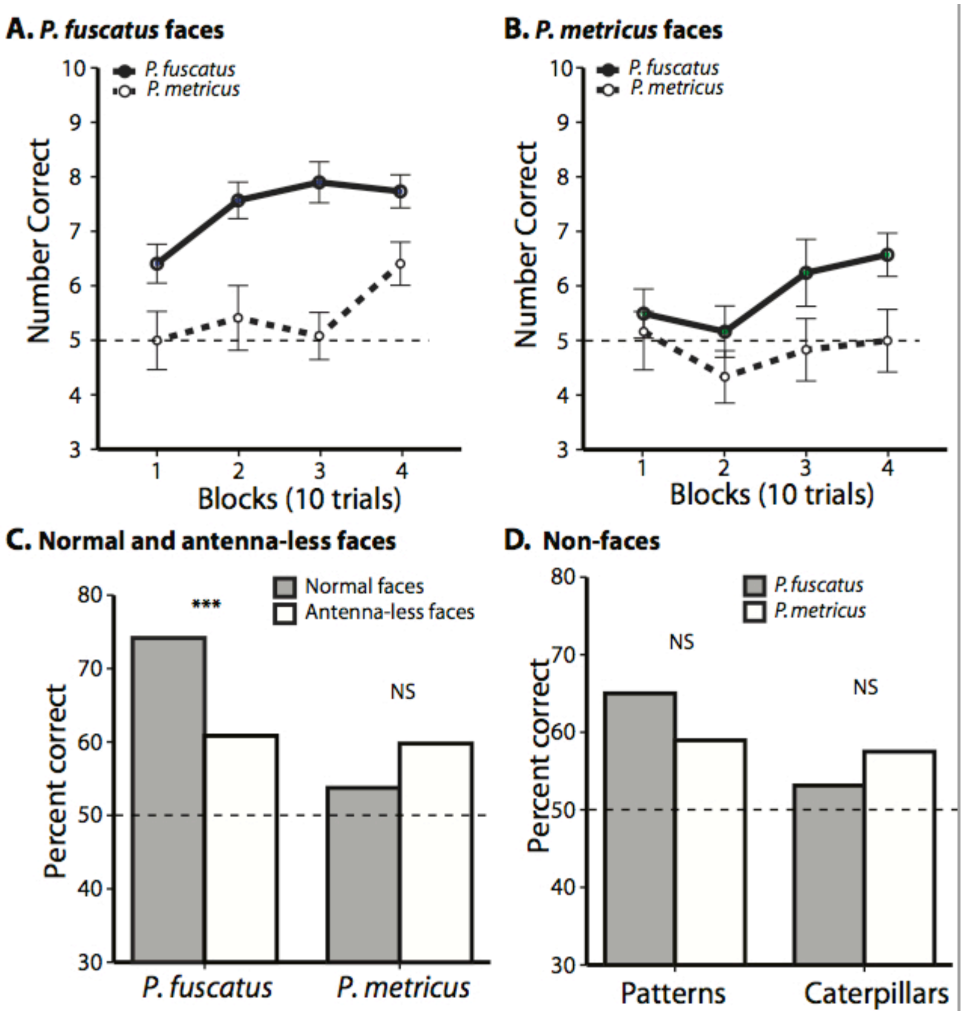

Figure 4.4. *P. fuscatus* learned to discriminate between wasp face images faster than did *P. metricus* when trained to discriminate both (**A**) *P. fuscatus* and (**B**) *P. metricus* face images. Line graphs show the mean number of correct choices (±SEM) per 10 trial blocks. Chance performance is 5 correct choices per 10 trial blocks. (**C**) Removal of the antenna from faces decreases learning performance in *P. fuscatus* but not in *P. metricus*. (**D**) The two species make a similar percent of correct choices when learning nonface images. Bars show the sum of correct choices across all wasps in a treatment as a percent of 480 trials; *n* = 12 wasps for each treatment. Asterisks denote the statistical significance: NS, *P* > 0.05; ****P* < 0.0001.

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Materials and Methods

Maze Construction

Maze walls were white foam board that was glued to a clear acrylic ceiling (Optix brand by Plaskolite, www.plaskolite.com, Fig 4.5). The walls were 7mm high, which is shallow enough to prevent wasps from flying inside the maze. This ensured that wasps received a small electric shock at all times, unless they were in the 'safety zone'.

The floor of the maze was a small piece of anti-static conductive foam (Abramson et al. 2004). The foam is impregnated with graphite, so it carries a small electrical current. To create an electrified surface, two parallel copper wires were run through opposite ends of the foam. Anti-static foam provides a consistent, low-level electric charge, so it is ideal for negative reinforcement training. Voltage was regulated using a variac transformer and regularly checked using a digital multimeter. Voltage was set so that wasps received approximately 4 volts of electricity, which elicits a response but does not inhibit movement. A 'safety zone' was created by placing a separate, non-electrified piece of foam next to the electrified piece so that they made a seamless floor.

Stimulus Creation

All images used in training are shown in Fig 4.1 of the main text. We tested wasps on different three pairs of stimuli for a total of six stimuli per image set (Fig 4.1). Normal facial images of *P. fuscatus* were photographs of wasps from Michigan, USA that showed the face and antenna. Antennae-less faces were created by digitally covering the portion of the antennae external to the face with the same color as the background of the image. Rearranged face stimuli were created by digitally manipulating these same images using Adobe Photoshop CS3. For each face, facial features (e.g. clypeus, mandible, antennal, eye, etc) were traced and copied onto separate layers. The facial features were then re-arranged and placed in abnormal configurations, while maintaining the overall shape of the face. Face images of *P. metricus* were photographs of wasps from Michigan, USA that showed the face and antennae. Natural face variation is limited in *P. metricus*, so variation was added to some images using Adobe Photoshop CS3. Images were altered to add variation that commonly occurs in the *Polistes*: yellow inner eye stripe, black clypeus spots, yellow stripes above the antenna, etc. *P. metricus* did not show any preference for normal or modified faces. During the first block of ten trials, when any bias should be strongest, *P. metricus* chose normal and modified faces at the same rate (Normal faces = 53.3%, N=12 wasps, χ^2 = 0.25, P = 0.60). Because *P. metricus* failed to learn normal conspecific face images we did not train them to discriminate manipulated conspecific faces. Pictures were all taken using a Cannon Powershot G10 at the highest resolution using the macro setting. All pictures were cropped and re-sized so that they were 7 mm high and 14 mm wide with a 300 DPI resolution (approximating the size of a wasp).

The simple black and white patterns were created using Adobe Illustrator CS3. Patterns were created based on previously published patterns used to train honeybees (Benard and Giurfa 2004). All patterns were sized to be 7 mm high.

To create the caterpillar stimuli, we searched the internet for high resolution images of caterpillars available under creative commons. We chose pictures with similar backgrounds (i.e. green vegetation). As with other pictures, caterpillar images sized to be 7 mm high and 14 mm wide with a 300 DPI resolution. All images were printed using a commercially available Sony Picture Station photo printer.

Stimuli were placed both inside and outside the side chambers of the maze (Fig 4.5). This design ensured that wasps could view the stimuli at close range before making a decision. For all trials, the maze was well lit using a full-spectrum incandescent light bulb, ensuring that the stimuli were easily visible.

Image Analysis

When discriminating among complex images, Hymenopteran vision is particularly sensitive to the level of contrast in the images (Lehrer and Campan 2004; Lehrer and Campan 2005), with higher contrast images being easier to discriminate. We examined the amount of contrast in the stimuli used in our study by calculating the high spatial frequency (>5 deg) power for each image, following methods by Rajimehr et al (Rajimehr et al. 2011). To do so, we processed the images in MATLAB by extracting the high spatial frequency power spectrum with a bandpass filter. To compare images, we standardized the high spatial frequency by the total power in the image. Normalized high spatial frequency values for the images are presented in Table 4.1. Overall differences in color could also influence learning if some image sets were more diverse in color than others. Therefore, we also calculated the overall RGB values with Photoshop CS3 (Table 4.1). Finally, we report the complexity of the images as measured with JPEG file sizes (Table 4.1). Simpler images compress to smaller file sizes, with increasing file size indicating increasing image complexity (Wu et al. 2008).

The image analysis confirms that the *P. fuscatus* face images used for training do not differ substantially from other natural images such as caterpillars or from the manipulated versions of the faces. Additionally, patterns are the simplest images with the highest contrast. Further, *P. metricus* faces tend to have less contrast (as measured by high spatial frequency) than the other natural images, which may help explain the relatively poor performance of both species when trained to discriminate between *P. metricus* face images.

Training Process

All wasps used in this experiment had no prior experience in the maze. Each wasp received 40 successive 2-minute trials. In each trial, a wasp was placed by hand into the antechamber. Wasps were left in the antechamber for approximately 10 seconds. During this time, wasps did not receive any electric shock. Once wasps were acclimated to the chamber, the electricity was turned on and a sliding door was opened. After release, wasps were given two minutes in the maze to choose between chambers associated with two images. A wasp ‘chose’ when it fully entered one of the chambers. Even though choices occurred prior to two minutes, wasps were left in the electrified maze until the end of the 2-

minute period. In rare cases (31 out of 5840 trials) wasps had not chosen by the end of the 2 minute trial, so we continued the trial until the wasp had chosen (typically within 30 seconds), at which point the wasp was removed. Wasps could choose between two chambers, one of which was a ‘safety zone’ that did not provide electric shock. The ‘safety zone’ was positioned on the right or left side of the maze in a predetermined pseudo-random order. One of the images was consistently associated with the ‘safety zone’ while the other image was consistently associated with the electrified chamber. At the end of a trial, a wasp was manually removed from the maze and placed in a small container with sugar and water while the maze was set-up for the next trial.

Some individuals showed a strong, consistent bias toward one size of the maze, a common issue in animal training. For each wasp, the ‘safety zone’ was on the right and left sides of the maze in an equal number of trials (i.e. 20 out of 40 trials). Individuals that choose the same side of the maze in more than 30 trials were excluded from data analysis. If a wasp was excluded, a new wasp was trained on the same images to maintain a sample size of 12 individuals per image set. In total, 8 of 80 *P. fuscatus* and 6 of 66 *P. metricus* were excluded for a directional bias. The ratio of included:excluded individuals does not differ between the species ($\chi^2 = 0.01$, $P = 0.92$). Individuals that have a directional choice bias are commonly excluded from training experiments (Cassia et al. 2004; Giurfa et al. 1999; Kendrick et al. 1996). Additionally our exclusion rates of 10% and 9.1% respectively for *P. fuscatus* and *P. metricus* are low compared to other published values that include values as high as 26% and 41% ((Cassia et al. 2004; Giurfa et al. 1999; Kendrick et al. 1996). We confirmed that directional choice bias was consistent within individuals by training a sample of biased individuals on a simple choice task (yellow versus blue rectangles), finding that 4/5 biased individuals retained their bias in the color choice task.

Visual Acuity in *Polistes*

Discriminating between facial patterns requires reasonably acute vision. In comparison to insects generally, all *Polistes* wasps have relatively acute vision, as is expected for large visual predators. The extent to which visual acuity varies among *Polistes* wasps is unknown. We tested whether differences in visual acuity could account for some of the differences in visual learning by estimating the relative acuity of *P. fuscatus* and *P. metricus* wasps. Increased acuity can be achieved by larger facet diameter (Land 1997), in the forward looking 'acute zone' or fovea. Among close relatives, differences in facet diameter correlate with differences in acuity (Rutowski et al. 2009). We measured the size of facets by making a replica of the right eye, flattening the replica, and photographing it with a dissecting microscope (Greiner 2006). First, we fully mapped the sizes of all eye facets for one specimen of each species (Fig. 4.6). The maps show strong similarity in eye structures between the two species, though *P. metricus* has the largest facets. We note here that both species' eyes maps are very similar to the eye map of *P. occidentalis* (Greiner 2006), a more distantly related paper wasp, suggesting that eye structure is likely conserved within *Polistes*. We further investigated relative acuity in each species by estimating the largest facet diameter from the acute zone for three specimens of each species. To do so, we measured the length of 10 sets of 5 consecutive facets from the eye maps in each direction (i.e. the x, y and z-axis). To estimate the largest facet diameter, we average the 3 largest measurements from each direction. The results show that *P. metricus* tend to have slightly larger facets (Table 4.2), concurring with the eye maps. Therefore, the poor performance of *P. metricus* on face images cannot be attributed to differences in visual acuity between the two species.

Statistical Analysis

We analyzed the data to assess rates of learning and overall performance. Rates of learning were assessed using a binomial logistic regression, which takes into account the changes in the number of correct choices across trials (Hartz et al. 2001). We modeled the change in responses (correct or incorrect) as a function of the trial (1-40) and the interaction of the trial and image type. A significant interaction between trial and image type demonstrates that rates of learning differed between the image types. When comparing species, we added the interaction of trial, image and species to the model. Overall performance accuracy was compared between groups using 2x2 chi-square tests.

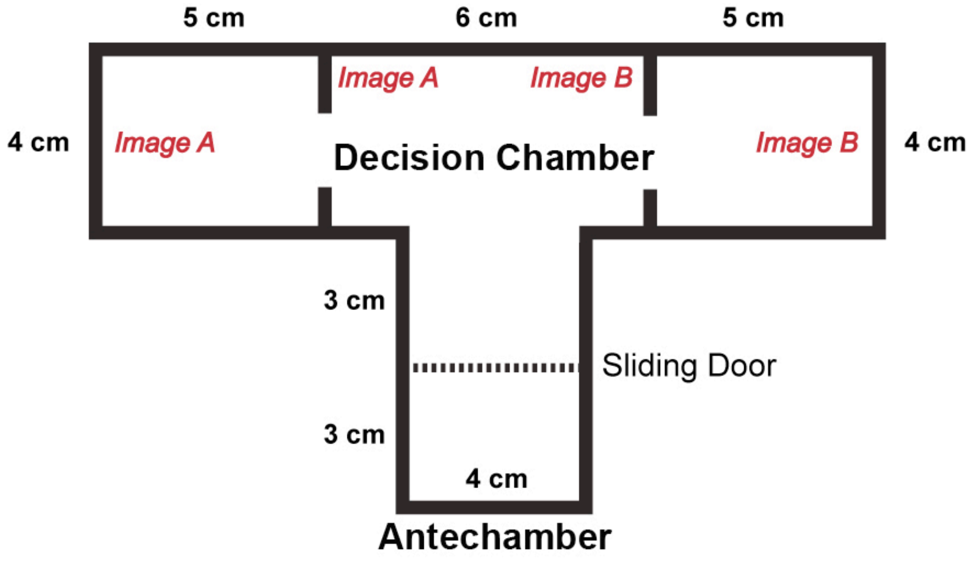

Figure 4.5.
Diagram of the T-shaped maze used to train wasps.

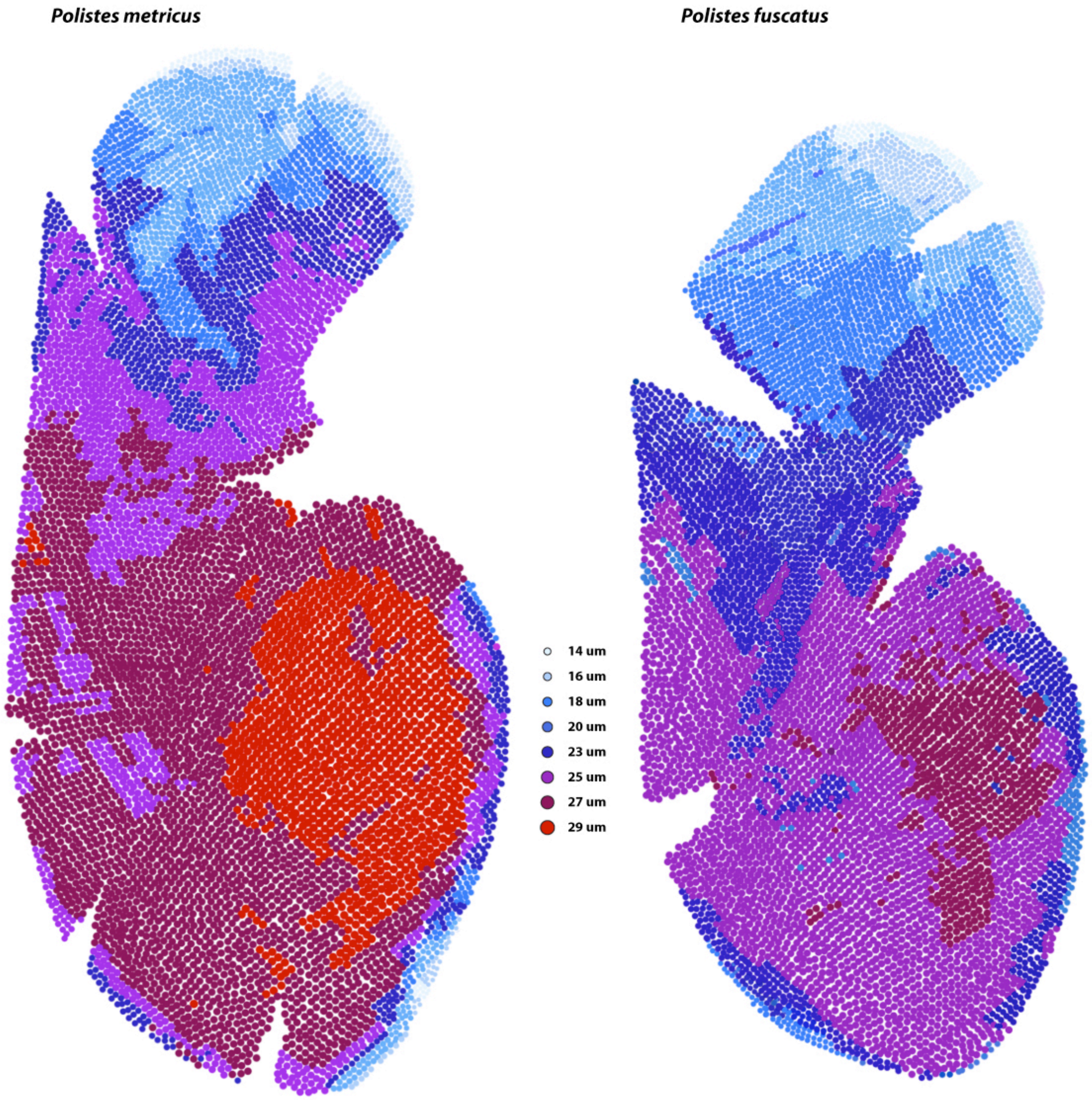

Figure. 4.6

Distribution of facet sizes for *P. metricus* and *P. fuscatus* eyes. The eye-maps represent a flattened mirror image of the right eye of an individual wasp. The lower right-hand portion of each eye, where the facet sizes are largest, is the forward-looking acute zone (i.e. fovea) for each species. Both eyes are shown at the same scale.

Table 4.1.
Image statistics

	Position in Fig 1 in main text	HSF Index	Overall RGB	JPEG size (kb)
Patterns	Top left	22.07		17.2
	Top right	21.32		18.8
	Mid left	22.30		22.3
	Mid right	16.54		16.7
	Bottom left	19.05		15.4
	Bottom right	16.61		18.3
Caterpillars	Top left	12.15	102.44	40.1
	Top right	6.30	120.12	34.3
	Mid left	10.47	96.30	36.1
	Mid right	6.02	97.94	38.5
	Bottom left	13.54	131.10	38.8
	Bottom right	9.80	121.98	38.4
P. fuscatus faces	Top left	6.01	89.71	31.4
	Top right	5.06	87.83	31.9
	Mid left	13.33	82.14	32.8
	Mid right	16.26	89.85	35.7
	Bottom left	9.88	109.13	35.3
	Bottom right	9.34	115.19	32.9
P. metricus faces	Top left	6.30	103.80	28.9
	Top right	5.98	97.41	29.1
	Mid left	7.99	102.90	29.9
	Mid right	7.53	97.24	29.3
	Bottom left	7.22	103.53	29.8
	Bottom right	6.00	96.00	29.2
Antenna-less *P. fuscatus* faces	Top left	5.71	93.81	30.9
	Top right	4.88	90.62	31.0
	Mid left	13.25	82.95	32.1
	Mid right	16.17	91.47	35.4
	Bottom left	9.53	109.14	33.9
	Bottom right	8.89	118.04	31.3
Re-arranged *P. fuscatus* faces	Top left	5.14	89.32	31.3
	Top right	8.94	89.24	34.5
	Mid left	4.55	80.94	32.8
	Mid right	7.22	88.38	35.1
	Bottom left	9.95	109.30	34.0
	Bottom right	10.10	114.86	32.8

The HSF index provides a measure of the proportion of the power spectrum for each image that is high spatial frequency. High values indicate more contrast in the image.

Table 4.2.
Maximum Eye Facet Diameter (um)

Polistes fuscatus	28.36 ± 0.83 SEM
F1	29.02
F2	29.34
F3	26.72
Polistes metricus	30.10 ± 0.66 SEM
M1	31.23
M2	28.95
M3	30.12

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Chapter 5: Robust long-term social memories in paper wasps

Abstract

Remembering individual identity is necessary for the complex, individually-differentiated social relationships found in many vertebrates, including humans. Despite the complexity of social insect colonies, individual social insects are generally thought to have simple, undifferentiated relationships. Here we show that *Polistes fuscatus* paper wasps, which individually recognize conspecifics, remember the identity of social partners for at least a week, even if they interact with ten other wasps. Therefore, social interactions among paper wasps are based on robust memories of past interactions with particular individuals rather than simple rules. Considering the small size of wasp brains, these results suggest that at least some aspects of social cognition may not be as cognitively demanding as is generally assumed.

The complex, individually-differentiated social relationships common in social vertebrates rely on individual recognition. Remembering the individual identity of social partners reduces aggression, promotes cooperation, and stabilizes long-term social relationships (Crowley et al. 1996; Tibbetts and Dale 2007). Given the importance of social knowledge, it is not surprising that the cognitive challenge of remembering the identities, ranks and relationships among many individuals is thought to have driven the evolution of social intelligence in many taxa, including primates and humans (Dunbar and Shultz 2007).

Large colony social insects are on the other end of the social complexity spectrum, as they are thought to lack individually-differentiated relationships. Instead, colony-level social complexity is thought to emerge from the interactions among numerous, cognitively simple individuals following basic decision rules (Anderson and McShea 2001). Recently, individual recognition has been shown in *P. fuscatus* paper wasps, which use variable visual features (Fig. 5.1) for individual recognition (Tibbetts 2002), and in *Pachycondyla* spp. ants, which have distinctive hydrocarbon profiles (Dreier et al. 2007). These studies suggest that previous ideas about social relationships among insects may be overly simplistic.

Individual recognition is typically considered a relatively complex form of recognition because it requires flexible learning and memory. Individuals must learn the unique features of conspecifics, then recall that information during subsequent social interactions. However, prior research indicates that social insects have relatively limited memories; new learning experiences quickly degrade previous memories. For example, honeybees can remember two foraging locations, each associated with a scent, but fail to complete the same task if a third location is tested simultaneously (Reinhard et al. 2006). Considering the size and complexity of social insect colonies, individual recognition can only produce complex, individually-differentiated social relationships if social memories are sufficiently robust.

We have assessed the extent of social memory in *P. fuscatus* by testing whether memories of past interactions with a particular conspecific are robust to attenuation over the course of a week and to interference from subsequent social interactions with ten other individuals. The strength of memories is predicted to vary with the relative cost and benefits of the memories and may also be influenced by cognitive constraints (Dukas 1999). For paper wasps, robust memories of prior social interactions would be especially useful given the complex social interactions among nest founding queens. *P. fuscatus* can found nests alone or in groups. When multiple queens cooperate to found a nest, they have intense battles to establish relative dominance ranks. Queens assess multiple nest sites and battle with many potential partners before starting a nest (Reeve 1991), so remembering prior social interactions with particular individuals would allow individuals to avoid additional, costly escalated dominance contests. Previous work has demonstrated that *P. fuscatus* are more aggressive to individuals with unfamiliar appearances (Tibbetts 2002). Therefore, if wasps have robust social memories, they should be less aggressive towards individuals they have interacted with previously than individuals they have not previously encountered.

Memory was tested by measuring aggression among 50 unrelated wasp queens in four different encounters over eight days (Dreier et al. 2007; Supplemental methods). Initially, wasps encountered a new social partner from a distant collection location (Day 0). Then, we separated the pair, returning each wasp to different communal cages containing ten other wasps. One week later

(Day 7), the same wasps interacted again. To ensure that any decreases in aggression on Day 7 resulted from memory of their partner rather than a general decrease in motivation over time, focal wasps interacted with new social partners on Days 6 and 8. If the wasps have robust memories, aggression levels between wasps with prior social histories (Day 7) should be lower than between two wasps that encounter each other for the first time (Days 0, 6 and 8).

Our results demonstrate that previous social partners remembered each other's identities after one week apart even though they interacted with ten other wasps during the intervening time. Aggression indices differed significantly among the days of the experiment (Fig. 5.2 A; Friedman's ANOVA, (3, $n = 50$) = 48.10, $p < 0.0001$). Importantly, on Day 7, when wasps were paired with the same individuals from Day 0, the aggression index was lower than all other days (Non-parametric Tukey's HSD, $p < 0.05$). One important reason for the lower aggression indices was that wasps with prior interaction histories (Day 7) engaged in more non-aggressive social behaviors (Fig. 5.2 B; Friedman's ANOVA, (3, $n = 50$) = 21.42, $p < 0.0001$). Aggression did not differ between Days 0 and 8, indicating that wasps remained motivated to fight. Therefore, the lowered aggression on Day 7 was due to individual memory rather than a general reduction in focal wasp aggression over time.

P. fuscatus wasps therefore remember the individual identity of social partners after one week of interactions with ten other wasps. This is by far the most robust social memory demonstrated in an insect (Dreier et al. 2007). Social interactions in *P. fuscatus* are not based on simple rule-driven decisions, but on a robust memory of past interaction histories with particular individuals. Robust social memories are a necessary component of the complex relationships hypothesized to be responsible for evolutionary increases in brain sizes among many vertebrates (Dunbar and Shultz 2007). So it is interesting that even small-brained invertebrates (Gronenberg et al. 2008) can form cognition-based social relationships. Perhaps basic components of social cognition may not be as demanding as is assumed by the current formulation of the social intelligence hypothesis. Future research that addresses exactly which aspects, if any, of social relationships are especially cognitively demanding will be important to understanding the role of social complexity in encephalization.

Figure 5.1. Examples of variable facial patterns used for individual recognition in *Polistes fuscatus*.

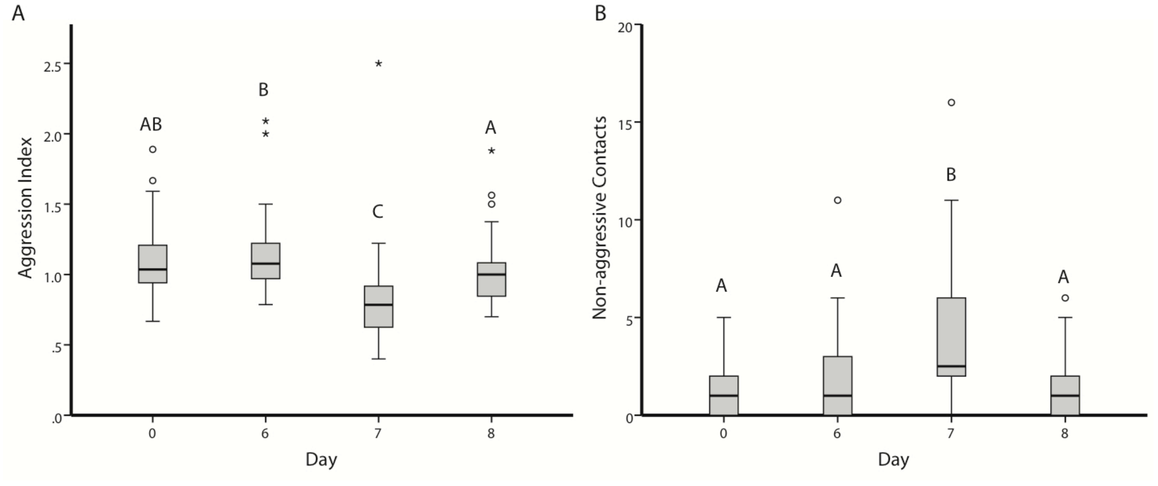

Figure 5.2. Long-term social memory in a paper wasp. Wasps were (A) less aggressive and (B) engaged in more non-aggressive interactions with known individuals than with unknown individuals. (A) Aggression indices (Friedman's ANOVA, (3, $n = 50$) = 48.10, $p < 0.0001$) and (B) the number of non-aggressive physical contacts (Friedman's ANOVA, (3, $n = 50$) = 21.42, $p < 0.0001$) for the four days of dyadic encounters between foundresses. The aggression index weights interactions based on the intensity of aggression with lower scores indicating less intense aggression (non-aggressive physical contacts (0 pts) to grappling (4 pts)). On Days 0, 6 and 8 wasps interacted with a new social partner for the first time. On Day 7, wasps re-encountered the same partner from Day 0. Different letters indicate significant differences between days (Non-parametric Tukey's HSD, $p < 0.05$). Box plots show the median and 25th and 75th percentiles.

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Supplemental Methods

In early spring 2007, emerging *P. fuscatus* were collected in and around Ann Arbor, Michigan. After emerging from diapause, wasps do not immediately begin nest construction, but rather spend up to a few weeks assessing potential nest sites. During this time, they also engage in aggressive dominance contests with multiple other foundresses (West Eberhard 1969), possibly assessing potential co-foundresses. Prior to this experiment, wasps were housed with approximately 10 other wasps from the same collection location (mean + SE. = 10.38 + 0.50, range = 9-13, mode = 10, n = 8 cages) for one week. All collection locations were separated by at least 1 km, and most by more than 20km to ensure wasps from different collection locations had not previously interacted. In total, the aggressive interactions of 50 focal wasp queens were followed over the entire length of the experiment. On the first trial (Day 0), focal wasps were introduced to a new wasp that was collected from a distant location, with whom they had not previously interacted. The first two hours of their encounter were filmed and then the pair of wasps were housed together for one day. After one day together, the wasps were separated and returned to their initial housing situations. On the sixth day after the separation (Day 6), focal wasps were paired with a new and different social partner and their interactions were filmed for two hours. After the two-hour trial, the wasps were returned to their initial housing situation. Similar procedures were used on Days 7 and 8. On Day 7, the focal wasp was re-paired with the same wasp from Day 0. On Day 8, the focal wasp was paired with another new social partner.

Videotapes of the behavioral interactions were watched double blind to the identity of wasp and the day of the trial. While wasps do engage in a number of non-aggressive interactions, these generally occur after prolonged interactions on a next. In our trials, the only clearly measurable interactions were proximity and aggression. To compare aggression between trials, we calculated an aggression index that takes into account the intensity of each aggressive interaction for the first half hour, when interactions were most intense (Dreier et al. 2007). The aggression index was calculated by assigning each behavior a score and dividing the summed aggression score by the total number of interactions. We recorded each instance of the following behaviors (score): bodily contacts that did not result in aggressive behaviors (0), darts (1), dart with open mandibles (2), bites (3), mounts (4) and grapples (4). While the wasps are extremely visual, contacts were assigned conservatively, only when one of the wasps actually made sustained physical contact. If wasps were simply passing by each other (i.e. no sustained interaction) no contact was scored. We compared the aggression indices among the rounds using Friedman ANOVA and multiple comparisons.

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Chapter 6: A role for sender and receiver biases in evolutionary origins of recognition systems

Abstract

Recognition requires coordination between a sender, who produces a phenotype containing identity information, and a receiver, who responds to information from the sender. Understanding the origin of novel recognition systems poses a problem: How can selection act on senders in the absence of receiver behavior? How can selection act on receivers without the necessary sender phenotypes? Here, we propose that the origin of recognition systems may be facilitated by pre-existing biases in sender phenotypes or receiver behavior. We outline the two hypotheses and their predictions and provide preliminary tests of the hypotheses using individual recognition as a model. First, we test the sender bias hypothesis with published data on recognition behavior and phenotypic variability. Recognition phenotypes are often individually variable in species that do not use the phenotypes for recognition, supporting the sender bias hypothesis for the evolution of individual recognition. Second, we experimentally confirm the predictions of the receiver bias hypothesis in *Polistes* paper wasps by testing receiver responses to individually distinctive phenotypes in a species that is known to lack individual recognition. The results indicate that

receiver bias may be involved in the evolution of individual recognition in *Polistes* wasps. Overall, sender biases may be a widespread mechanism facilitating the evolution of individual recognition and receiver bias may be applicable to a wider set of communication behaviors than typically considered.

Introduction

Social interactions depend on the recognition of social partners based on species, kinship, group membership or individual identity. Recognition occurs through three steps – production, perception and action (Sherman et al. 1997) and involves both the individual being recognized (i.e. the 'sender') and the individual doing the recognizing (i.e. the 'receiver'). Thus, for a recognition system to function, senders must produce sufficiently recognizable phenotypes (Tsutsui 2004) and receivers must be able to differentiate among senders and respond to them appropriately (Liebert and Starks 2004; Mateo 2004). As recognition has important effects on animal social behavior and fitness, selection is expected to act on both senders and receivers to facilitate efficient recognition. Sender phenotypes will be selected to reliably and effectively convey relevant information to receivers. Receiver physiology and cognition will be selected to facilitate perception and processing of the traits used for recognition. Indeed, studies from a variety of organisms have shown that selection acts on both sender phenotypes (Jouventin and Aubin 2002; Medvin et al. 1993; Pollard and Blumstein 2011; Sheehan and Tibbetts 2009) and receiver psychology (Loesche et al. 1991; Sheehan and Tibbetts 2011) to promote efficient recognition.

While it is straightforward to understand how selection can fine-tune an existing recognition system, it is less clear how recognition systems initially emerge. Recognition requires coordination between senders and receivers, so it is difficult to understand how such a relationship originates. In the absence of appropriate receiver responses, how do recognizable phenotypes evolve? Without the phenotypes needed for recognition, how do receiver responses evolve?

Here, we use individual recognition as a model for exploring the evolutionary origin of recognition systems. Though we focus on individual recognition, the concepts are applicable to other recognition systems. Individual recognition provides a particularly good model for studying the origin of recognition systems because there have been many independent evolutions of individual recognition across a wide range of animal lineages, in a variety of social contexts and sensory modalities (Tibbetts and Dale 2007). Individual recognition is the most specific and complex form of recognition because it requires unique recognition phenotypes (Beecher 1989) and flexible learning and memory (Thom and Hurst 2004; Tibbetts and Dale 2007). When recognizing an individual, receivers learn the unique characteristics of senders and then recall these characteristics during subsequent social interactions. In the presence of the appropriate receiver behavior, selection is expected to favor the evolution of distinctive sender phenotypes that signal individual identity (Dale et al. 2001; Sheehan and Tibbetts 2009). When sender phenotypes are sufficiently variable to allow identification, selection for individual recognition is expected to favor receivers that discriminate among, remember and respond to individuals appropriately based on their unique phenotypes. With communication in place, senders and receivers are expected to undergo correlated evolution producing sender phenotypes and receiver psychology are well suited to each other (Bradbury and Vehrencamp 2011; Guilford and Dawkins 1991; Johnstone 1997b). How the initial evolution of individual recognition occurs is unclear and the subject of this paper.

Hypotheses

Recognition may originate via two different pathways: sender bias or receiver bias. First, pre-existing variation in sender phenotypes provides a route to the initial evolution of recognition. The ‘sender bias’ hypothesis proposes that there is variation in sender phenotypes that predates appropriate receiver responses. Second, recognition may evolve if receivers are able to respond differentially to individuals based on the identity information in their phenotypes. The ‘receiver bias’ hypothesis proposes that appropriate receiver responses predate variation in sender phenotypes. Initially, sender variation and receiver responses are likely to be more rudimentary than those found in established recognition systems. For example, less variation in sender phenotypes is required for sender bias than is expected in established identity signals. Similarly, receiver responses required for receiver bias may be quite simple and more akin to discrimination than recognition. Receivers need only respond to differences in sender phenotype when differences occur. If there are sufficient benefits associated with recognition, selection will fine-tune both sender phenotypes and receiver responses to facilitate efficient recognition.

Though few previous studies have examined the origin of recognition, both sender and receiver biases are plausible hypotheses. First, there are many evolutionary and developmental processes unrelated to recognition that are known to maintain phenotypic variation in populations (Leimar 2005; Mitchell-Olds et al. 2007), suggesting that sender bias is a possible route for the initial evolution of individual recognition. Second, previous models examining the evolution of individual recognition have implicitly assumed that receiver biases exists (Barnard and Burk 1979; Dale et al. 2001), though receiver bias has not been experimentally tested. Although previous studies have not examined receiver bias in the context of recognition systems, numerous studies have examined receiver or sensory biases in the evolution of signals related to mate choice (Endler and Basolo 1998; Ryan 1998; ten Cate and Rowe 2007). More recently, receiver bias arguments have been used to explain a wider range of signals including floral displays and warning coloration (Jansson and Enquist 2003; Naug and Arathi 2007; Sherratt 2002). Typically, receiver bias hypotheses posit that receivers have a pre-existing preference for a particular trait, which is then exploited by senders during the initial process of signal evolution. In the case of individual recognition, receiver bias would merely require that receivers are able to discriminate among individuals and act on the observed differences. Animals are adept at distinguishing among stimuli and frequently treat social partners differentially, so a bias in receiver behavior that facilitates the evolution of recognition systems appears plausible. Our main objective in this paper is to outline the potential role of sender and receiver biases in the evolution of recognition systems and provide initial tests of each hypothesis.

The sender and receiver bias hypotheses make distinct and testable predictions. The sender bias hypothesis critically predicts that variation in sender phenotypes predates the origin of individual recognition. As a result, ancestral state reconstructions of recognition behavior and phenotypic variation will show that variation in sender phenotypes originated prior to recognition behavior. In contrast, the receiver bias hypothesis predicts that variation in receiver behavior predates the origin of variation. Therefore, receivers will respond differentially to senders when sufficient phenotypic variation is provided. Receiver bias for individual recognition requires that 1) receivers perceive and respond to phenotypic variation and 2) the response provides some benefit to the sender. If receiver responses were on average harmful to senders, then selection would favor senders that obscure rather than advertise their identity (Johnstone 1997a), effectively precluding the evolution of individual recognition. The specific response from receivers, however, may vary across contexts. Across contexts, the receiver response will only facilitate the evolution of individual recognition if it provides a selective benefit to the sender.

Here we use a literature review and an experiment to explore how sender and/or receiver bias contribute to the evolution of individual recognition. First, we review existing literature to assess whether there is general support for the sender bias hypothesis by testing whether the type of phenotypic variation used for individual recognition is associated with receiver recognition behavior. The sender bias hypothesis predicts that the type of variation used for individual recognition will commonly exist in the absence of receiver recognition behavior. The origin and/or maintenance of individualized variation in lineages without recognition behavior supports the sender bias hypothesis because it suggests that forces unrelated to recognition maintain the variation (Fig. 6.1). In contrast, if variation only co-occurs with recognition behavior, sender bias is unlikely. The rejection of the sender bias hypothesis would, by default, provide a weak suggestion that receiver bias facilitated the evolution of individual recognition. Receiver bias cannot be adequately tested with a review of the current literature, so we perform a separate experiment to directly test receiver bias. The receiver bias hypothesis predicts that species that lack sender variation and established individual recognition will detect and respond to differences in sender phenotype when such differences appear. We tested receiver bias in *Polistes metricus*, a species of paper wasp that lacks individual recognition and the type of phenotypic variation used for individual recognition. Variation in visual appearance was experimentally added to some *P. metricus* to test how receivers respond to the variation.

Test of the Sender Bias Hypothesis

Methods

The goal of this literature review is to assess whether patterns of sender phenotypic variation and receiver behavior within multiple different groups and contexts are consistent with the sender bias hypotheses. To do this, we surveyed the literature to find examples of clades that show variation in presence of individual recognition among species or populations. Definitive tests of the sender bias hypothesis require extensive information on the individual recognition abilities and phenotypic variation in recognition traits within a clade with a well-supported phylogeny. At present, such information does not exist so we use existing information to provide a preliminary test of the hypothesis. Together, information on sender phenotypic variability and receiver behavior allow us to assess whether the evolution of individual recognition in each case is likely to have been facilitated by sender bias (Fig 1). If sender bias has facilitated the evolution of individual recognition, we expect to find that species that lack individual recognition nevertheless have individually identifiable phenotypes. In contrast, if species that lack individual recognition also lack variation in sender phenotypes, then we can conclude that biases in sender phenotypes are unlikely to have driven the evolution of individual recognition.

We searched for articles published prior to November 2011 using the Web of Science and GoogleScholar databases. We located articles using a variety of search terms related to individual recognition including individual recognition, mate recognition, mother recognition, offspring recognition, pup recognition, chick recognition, vocal recognition, odor recognition, etc. In addition to searching the databases using these terms, we also looked for additional articles in the reference lists of relevant papers found during our search.

We included individual recognition studies that fit the following criteria. First, the study must experimentally demonstrate that animals individually recognize social partners. We required that studies demonstrate recognition (or lack thereof) using ecologically relevant tasks, rather than test the ability to discriminate among individuals in an operant training paradigm (Thom and Hurst 2004). Second, the study must identify the specific phenotype used for recognition and assess its intraspecific variability. These criteria exclude studies where authors suggest that a species uses individual recognition based on the level of phenotypic variability (Jahelkova et al. 2008; Koren and Geffen 2011; Lawson et al. 2000) without experimental tests of recognition behavior (Tibbetts et al. 2008). In addition, the second criteria excluded many studies using olfactory recognition, as few studies have identified the specific compounds used for recognition or quantified inter-individual variation (Thom and Hurst 2004).

There are multiple definitions of individual recognition in the literature that primarily differ in the number of individuals receivers must differentiate among and the extent to which receivers are required to react differently to individuals from the same social category (Gherardi and Tiedemann 2004; Steiger and Muller 2008; Thom and Hurst 2004; Tibbetts and Dale 2007; Tibbetts et al. 2008; Van Dyk and Evans 2007). For this analysis, species were considered to have individual recognition if they responded to animals or a stimuli based on the unique features of the other individual in an ecologically relevant context (Tibbetts et al. 2008). The essential requirement, then, was that receivers attend to the unique phenotypes of senders and change their behavior accordingly.

Under this definition a parent with a single chick would only be considered to recognize its chick by individual recognition if it attended to the particular features of the chick (e.g. an individually unique call) as opposed to indirect cues such as the chick's spatial location. Similarly we would consider a parent with multiple chicks that recognized them based on their unique calls to individually recognize its chicks, even if there is no difference in the way it responds to one chick versus another. Thus we consider recognition to be individualized when the means by which animals use to respond to their social partners is based on prior experience with individually unique phenotypes, regardless of the specificity of the response (Tibbetts et al. 2008).

We used the following criteria to score species as individually identifiable. Individually recognizable phenotypes must be relatively consistent within an individual and variable among individuals

(Beecher 1989; Dale 2006). Attempts to quantify the amount of identity information in phenotypes have focused primarily on vocal and chemical signals, which tend to show some variation within and between individuals. Typically researchers conclude that such phenotypes are individually distinctive if individuals differ significantly from one another in ANOVA analyses (Beecher 1989) or if there is above chance less of correct classification in discriminate function analyses (Cure et al. 2009; D'Ettorre and Heinze 2005; Koren and Geffen 2011). In some studies, traits that show weak, but reliable, differences among individuals are not considered to have individual signatures. However, sender bias requires only that traits show some statistical association with individual identity, so we consider traits to be individually distinctive in one study where the authors had concluded they were not distinctive (Torriani et al. 2006). Assessing the identifiably of color patterns, which tend not to vary considerably within an individual over short periods of time, is more problematic. Technically any color pattern variation between individuals is likely to be unique, though in practice minor variants are likely to be undetectable by animal's perceptual systems. Dale (2006) suggests that color patterns used for individual recognition should have multiple variable components each showing elevated levels of polymorphism. Therefore, we used these criteria to assess whether or not color patterns for each species or population were individually identifiable.

Robust tests of the sender bias hypothesis require phylogenetically controlled analyses. We attempted to control for the effects of phylogeny in our study by examining patterns of sender variation and receiver behavior within the multiple different groups of closely related species (Martins 2000). Given the state of available data, the clade-level groupings are necessarily variable in their scope. In a few instances we compared data from multiple populations of the same species or from congeners, but more often available data from multiple species was most logically grouped at broader taxonomic levels. For example, most of the passerine birds for which data is available come from various different families within that clade. However, a number of species of swallows have been well studied, so we considered them as a separate case even though they are passerines. In addition to phylogeny, we also grouped data based on the trait used for recognition (e.g. offspring vocalization versus adult vocalization) as traits used in different contexts are likely to be under differential selection pressures.

In the processes of conducting the literature search, it became clear that there are a number of publication biases regarding individual recognition. First, there is a well-known bias where negative results often go unpublished (Jennions and MØLler 2002; Moller and Jennions 2001), so it is not surprising that we identified relatively few taxa that are known to lack individual recognition. Second, much of the research documenting the degree of individual variation in recognition phenotypes has focused on vocalizations of birds and mammals, with less work on other taxa and signaling modalities. The overall goal of the literature review is to test whether sender bias is a plausible hypothesis for the evolution of individual recognition and the publication biases will not influence this conclusion. However, conclusions about the relative prevalence of sender bias as a facilitator of the evolution of individual recognition will require more even sampling of taxa and sensory modalities and recognition contexts.

Results and discussion

The results of the literature review are summarized in Table 1. The pattern of variation in sender phenotype and receiver behavior provides evidence for the sender bias hypothesis and also suggests that receiver bias may play a role the evolution of individual recognition. In 12 of 14 cases, the patterns are consistent with the sender bias hypothesis because species shown to lack individual recognition have individually identifiable phenotypes. In 2 of the 14 cases, the patterns do not support sender bias, as individually identifiable phenotypes are limited to species with individual recognition. Instead, these cases suggest that receiver bias may play a role in the evolution of individual recognition.

Patterns of sender phenotypic variation and receiver behavior in the literature are consistent with sender biases in most but not all cases examined. The limited data set begs a cautious interpretation of the patterns at this time, though it appears reasonable to conclude that sender bias is likely to be a common route for the evolution of individual recognition. This finding is particularly interesting given the emphasis on receiver biases in the broader literature on animal signaling (Endler and Basolo 1998; Fuller et al. 2005; Jansson and Enquist 2003; Ryan 1998; ten Cate and Rowe 2007). In models of receiver or sensory bias, signals are typically construed as adaptations on the part of senders to manipulate the behavior of receivers (Bradbury and Vehrencamp 2000; Guilford and Dawkins 1991; Krebs and Dawkins 1984). Under this view, senders are responsible for the initial changes that lead to the evolution of a signaling system. Counter to this view, verbal and mathematical models have claimed that biases in sender traits may be a common route for the evolution of communication (Maynard-Smith and Harper 2003; Scott-Phillips et al. in press; Zahavi 1980). Here, we use a literature review to show that individual recognition may commonly evolve by receivers adapting to utilize pre-existing variation in sender phenotype. Thus, the initial evolution of individual recognition may frequently result from receivers eavesdropping on identity information inadvertently broadcast by senders.

The literature review suggests that sender biases may be a particularly important route for the evolution of acoustic individual recognition. Acoustically based individual recognition has been reported in a wide range of taxa, perhaps because acoustic communication is well suited for a wide range of environmental conditions. The prevalence of acoustic individual recognition may also be due, in part, to the complex process of acoustic signal production. Acoustic signals are produced by multiple morphological components (Taylor and Reby 2010), so even small differences among individuals in each trait used to produce sounds may lead to detectable and consistent individual differences in sound production. The morphological basis of acoustic signal production means that individual differences in signal production will be widespread unless the signals are under selection to be highly uniform. Of course, individual variation in acoustic signals is not merely the result of random processes, as there is clear evidence that selection for increased recognizability favors more individually distinctive vocalizations (Pollard and Blumstein 2011). Rather, the evolution of acoustic individual recognition is likely facilitated by sender bias because of the inherent individual signature common in the production of acoustic signals.

In comparison to acoustic signals, which are easy to quantify and measure, many fewer studies have systematically documented the inter-individual variation of recognition phenotypes in other modalities. From the very limited evidence available in the literature, sender biases seem like a potentially important factor in the evolution of scent-based individual recognition. For example, individual recognition in ants appears to have evolved through a sender bias (Table 6.1). The mechanisms underlying odor production may be one reason why scent based individual recognition may commonly evolve via sender bias. Odors are frequently produced by processes that are expected to show a high degree of variation among individuals in a population. In vertebrates, variation at MHC loci, which is maintained by balancing selection from pathogens, also results in distinctive odors among individuals as a result of differences in bacterial communities supported by different MHC types (Brown and Eklund 1994). Analogous immunologically-based differences in chemical phenotypes are used in arthropod kin recognition (Giron and Strand 2004). Odor differences can also result from differences in diet, metabolism or physiological states among individuals (Schellinck et al. 1992). Reasonably stable differences in diet or physiological state among individuals are expected to produce unique odor signatures. These differences may be sufficient to allow individual identification in many cases, which can then facilitate the evolution of scent-based individual recognition.

Unlike acoustically and chemically mediated individual recognition, the argument for sender biases as an important factor in the evolution of visually-based individual recognition is less clear-cut. Both of the examples of visual individual recognition in the literature review are inconsistent with sender bias (Table 6.1). Why might the color variation in wasp faces and weaver eggs have evolved through receiver rather than sender bias? One possibility is that many color patterns may show less inherent inter-individual variation than other traits, such as acoustic and chemical phenotypes. For example, ancestral color patterns of wasp faces and weaver eggs were relatively simplistic. The ancestral color pattern for eggs is thought to be a solid white color lacking any other patterning (Kilner 2006). Similarly, the ancestral paper wasp is thought to have lacked variable patterning (Tibbetts 2004). Processes other than recognition can select for variable visual phenotypes, including apostatic selection and crypsis (Bond and Kamil 1998). Additionally, visual recognition in some species is mediated by individually distinctive performances of displays (Brandt and Allen 2004). Displays, like acoustic and chemical communication, are likely to have more inherent individual differences as a consequence of morphological differences among individuals. As a result, some species without individual recognition likely have the kind of inter-individual variation in color patterns or displays that are consistent with sender bias. Therefore, the apparent lack of support for sender bias in visually mediated individual recognition may also be the result of biases in the literature.

Importantly, the comparative analysis suggests that a sender bias is not the only route for the evolution of individual recognition. The lack of variable sender phenotypes in species or populations lacking individual recognition suggests that receiver bias may facilitate the evolution of individual recognition. However, experimental evidence that receiver behavior conducive to the evolution of individual recognition exists in these taxa is needed (see below).

Receiver Bias Experiment

Methods

Receiver behavior may facilitate the evolution of individual recognition if it meets three criteria. First, receivers must be able to distinguish among senders based on relatively minor variation in phenotypes. This is important because the initial mutations that give rise to identifiable variants would likely have minor effects on phenotypes. Second, receivers must respond to differences in individual appearance when they appear. Third, the responses must, on average, benefit senders that are identifiable. While recognition may evolve in the absence of benefits to senders – receivers can eavesdrop on unavoidable recognition cues produced by senders – the evolution of individual recognition via receiver bias can only work is senders benefit from recognition. If senders do not benefit by being identifiable, selection would act against the evolution of identity signaling phenotypes (Johnstone 1997a). Without selection to favor the elaboration of identity signaling phenotypes, recognition will not evolve in the absence of sender biases.

Paper wasps provide a good system to experimentally test receiver biases because variation in sender phenotypes and recognition behavior is not consistent with the sender bias hypothesis (Table 6.1). We assessed whether or not receiver behavior may play a role in the origin of individual recognition by altering the phenotypes of groups of *P. metricus* foundresses, which lack individual recognition and do not have variable color patterning (Sheehan and Tibbetts 2010). In doing so, we tested the three criteria for receiver bias, as differential responses to individuals with unique phenotypes are only possible if

(1) receivers distinguish individuals based on minor phenotypic variants and (2) receivers respond to those differences. Finally, we assessed if (3) senders benefit from the differential receiver response.

Polistes metricus is a common paper wasp found throughout the eastern United States. As with all temperate paper wasps, *P. metricus* colonies are initiated each spring by foundresses that have recently emerged from diapause (Reeve 1991). We used foundresses collected from human structures in three locations, Ann Arbor, Michigan, Columbus, Ohio and Knoxville, Tennessee. They were brought into the lab, housed individually, and provided *ad libitum* sugar and water.

We created 20 groups of four, unfamiliar weight-matched foundresses collected from locations at least 1km apart to ensure individuals had not previously interacted. All groups contained foundresses from at least two different collection regions. We experimentally altered the appearance of each wasp so there were three foundresses with a similar appearance and one foundress with a unique appearance in each group. This treatment is meant to mimic a situation where a rare mutation arises causing individuals to have a slightly different appearance that could be used for discrimination or recognition. The appearance of each foundress was altered by painting the region just above the antenna black or yellow (Fig 6.2). The distribution of color patterns was balanced across trials such that the distinctive wasp was yellow in half the trials and black in half the trials. Distinctive wasps were chosen randomly from among the four possible individuals. To allow individual identification by the experimenters, each wasp was given two small dots of red paint on the top of their thorax in a unique pattern. The red dots are unlikely to increase distinctiveness of the wasps, as wasps do not see red (Briscoe and Chittka 2001). After the paint treatments dried, the wasps were placed in a small container (8cm x 8cm x 2cm) and their interactions were filmed for 2hr. The tapes were scored for aggressive acts such as darts, lunges, bites, grapples and mounts – all of which are stereotyped behaviors commonly used to assess wasp aggression (Reeve and Nonacs 1992; Strassmann et al. 2004; West Eberhard 1969). Straub scored the videotapes blind to the treatments, experimental design, and predictions of the experiment. One tape was damaged and unable to be viewed, so the sample size was reduced to 19 from 20.

We analyzed the distribution of aggression in two ways. First, we compared the amount of aggression directed at unique and common wasps by receivers. The three wasps with common paint treatments each experienced two other common wasps as well as the unique wasp. In contrast, the unique wasp only experienced common wasps, so we did not include the aggressive acts performed by the unique wasp in the analysis. Second, we examined whether unique wasps received or directed aggression at others more or less often than common wasps.

The overall level of aggression differed among trials (mean aggressive acts = 456.58 ± 115.74), so we calculated standardized aggression scores based on the distribution of aggression within a trial (Sokal and Rohlf 1995). To examine the behavior of receivers towards each individual in the trial, we constructed a mixed model with treatment (unique v. common marking) and color (yellow v. black) and a treatment-by-color interaction as fixed factors. We included the collection region (Michigan, Ohio, Tennessee), trial, and receiver identity as random factors. To examine the aggregate patterns of aggression, we used the same model with the removal of the receiver identity as a random factor. A disproportionate amount of the total aggressive occurred soon after the trials began (the first 30 minutes accounted for 37% of the aggression), so we focused our analyses on the initial 30 minutes of the trials when aggression was most intense, as has been done in other studies (Dreier et al. 2007; Sheehan and Tibbetts 2008). This approach provided us the greatest power to detect differences in receiver behavior. Statistical tests were run in SPSS v19. Mean standard scores are shown $\pm$ SE and all tests described are two tailed.

Results and Discussion

The presence of an individual with a unique appearance influenced receiver behavior. The receivers directed significantly less aggression towards wasps with the unique paint treatment compared to common wasps (Fig. 6.2 A, $F_{1,112} = 4.89$, $P = 0.029$). There were no significant effects of the color of the marking ($F_{1,112} = 0.07$, $P = 0.79$) or the interactions between the color and uniqueness of the markings ($F_{1,65.1} = 0.001$, $P = 0.98$) on receiver behavior.

On the whole, wasps with the unique marking received less aggression than wasps with common markings (Fig. 6.2 B, $F_{1,70.5} = 4.09$, $P = 0.047$). There were no significant effects of the color of the marking ($F_{1,71.7} < 0.001$, $P = 0.99$) or the interactions between the color and uniqueness of the markings ($F_{1,72.0} < 0.001$, $P = 0.99$) on the total aggression received by wasps. Thus, the distribution of aggression was influenced by the uniqueness of the markings *per se* rather than the particular colors used. Additionally, wasps with unique and common markings initiated similar amounts of aggression (Fig. 6.2 C, $F_{1,70.0} = 0.003$, $P = 0.96$), so the lower aggression received by the unique wasps was not a byproduct of the unique wasps' own behavior. There were no significant effects of the color of the marking ($F_{1,70.4} = 0.28$, $P = 0.60$) or the interactions between the color and uniqueness of the markings ($F_{1,70.4} = 0.01$, $P = 0.93$) on the aggression initiated by wasps. Thus, the lower aggression received by the unique individuals is a result of changes in receiver behavior rather than other factors, such as the color of the paint treatment or aggressiveness of the unique wasp.

Together, the patterns of aggression provide experimental evidence for a receiver bias that could favor the evolution of individual recognition in *Polistes* wasps. *P. metricus* receiver behavior meets the three criteria for the evolution of individual recognition. First, receivers are capable of discriminating among senders based on relatively minor phenotypic differences. This is important since identity signals would likely originate with relatively phenotypic minor variation. In light of previous operant conditioning experiments demonstrating that *P. metricus* can learn to distinguish among images of variable wasp faces, their ability to discriminate minor variation in facial patterns is not surprising (Sheehan and Tibbetts 2011). Indeed, the ability to discriminate among individuals, in the absence of individual recognition, is likely to be common, since animals are often adept at discriminating among patterns. For example, barn swallows, which do not individually recognize their chicks, are nonetheless capable of discriminating among chick calls in operant tasks (Loesche et al. 1991). Second, discrimination among individuals led to a change in receiver behavior, as wasps directed less aggression to the unique individuals. The reduced aggression toward unique individuals also fulfilled the third criterion, as senders benefit by receiving less aggression for advertising their identity. While the evolution of individual recognition does not require that receiver behavior is beneficial for senders, elaborated identity signaling phenotypes will only evolve when senders benefit from recognition (Dale et al. 2001; Johnstone 1997a; Sheehan and Tibbetts 2009). Thus, the receiver behavior found in *P. metricus* would be expected to facilitate the evolution of identity signals and individual recognition. Provided that the distinctive phenotypes are not costly to produce, a relatively minor benefit from recognition will favor the elaboration of identity signaling phenotypes in senders (Dale et al. 2001), allowing for the evolution of highly specialized sender and receiver adaptations for individual recognition (e.g. paper wasps (Sheehan and Tibbetts 2009; Sheehan and Tibbetts 2011), cliff swallows (Loesche et al. 1991; Medvin et al. 1993)).

If the benefits of distinctiveness in *P. metricus* are sufficient to facilitate the evolution of identity signals, why does *P. metricus* lack variable color patterns and individual recognition? It is likely that identity signals have not evolved in *P. metricus* because *P. metricus* foundresses do not experience the relevant social circumstances in the wild. Interactions among foundresses are thought to be the primary selective pressure favoring the evolution of social signaling in *Polistes* (Tibbetts 2004), as social recognition is thought to minimize the costs of conflict among foundress. Foundresses of some species often nest in groups where they compete for status before forming a strict linear dominance hierarchy that determines relative rates of reproduction and work (Reeve 1991). *P. metricus* foundresses usually nest alone and rarely nest in groups of more than two wasps, so sophisticated recognition systems are unnecessary (Gamboa 1978; Hughes et al. 1993). In contrast, *P. fuscatus* have highly variable identity signals and frequently nests in large foundress associations (Klahn 1979; Tibbetts 2002; West Eberhard 1969). While foundresses in all wasp species eventually have extensive social interactions with their workers, foundress-worker interactions are unlikely to favor individual recognition. Instead, foundress-worker social interactions across *Polistes* are mediated through cuticular hydrocarbons that communicate queen fertility and status (Izzo et al. 2010; Monnin 2006). Overall, our results suggest that unique, identifiable phenotypes could be beneficial during foundress competition in *P. metricu*s, but their nesting habits provide little opportunity for selection to act in the wild.

Our results suggest that a bias in receiver behavior may be an explanation for the evolution of novel communication systems in a wider range of signal forms than is typically considered. Traditionally, receiver biases have been invoked to explain the evolution of female preference for exaggerated male traits (Endler and Basolo 1998; Fuller et al. 2005; Pryke and Andersson 2002; Ryan 1998). More recently, the same framework has been applied to the evolution of a wide variety of other types of signals including floral displays (Naug and Arathi 2007) and conspicuous warning colors (Halpin et al. 2008). In all of these cases, receivers have a pre-existing preference (or aversion) to certain stimuli, which are co-opted by senders during signal evolution (Endler and Basolo 1998). Here we present experimental evidence for a bias in receiver responses. These responses provide favorable conditions for the evolution of identity signals and individual recognition. Unlike the other examples or receiver biases, we are not arguing that receivers have a preference for a particular feature, but rather that receivers are capable of discriminating among individuals based on their distinctive phenotypes. Consistent with the theory of receiver biases for other types of signals (Endler and Basolo 1998), latent abilities for discrimination are likely to be a by-product of other aspects of animals' behavioral repertoire such as foraging and predator detection, which often require well-developed pattern discrimination abilities. Since all recognition systems depend on discrimination, it is likely that biases in receiver behavior may help explain the evolution of other recognition at other levels of specificity such as kin or species. While receiver discrimination abilities have obvious connections to behaviors not used in social recognition, the origin of receiver responses to individuals is less straightforward.

General Discussion

Individual recognition is associated with highly distinctive phenotypes and fine-tuned cognitive abilities in a number of taxa including swallows (Beecher et al. 1986; Medvin et al. 1993), penguins (Jouventin and Aubin 2002; Jouventin et al. 1999), humans (Kanwisher and Yovel 2006) and paper wasps (Sheehan and Tibbetts 2009; Sheehan and Tibbetts 2011). Once individual recognition is firmly in place, it is easy to understand how selection can favor increasing distinctiveness or finer discrimination abilities. Understanding how the process begins is less straightforward. Through a combination of literature review and experiments we have provided evidence for the role of sender and receiver biases in facilitating the evolution individual recognition. While the currently available data is not definitive, the patterns of phenotypic variation and receiver behavior suggest that sender biases may be a widespread contributor to the evolution of individual recognition. Given the emphasis on receiver biases in the much of the literature on signal evolution (Endler and Basolo 1998; Fuller et al. 2005; ten Cate and Rowe 2007), the apparent prevalence of sender biases in the evolution individual recognition is surprising (though see (Scott-Phillips et al. in press). Our experimental results, however, demonstrate that biases in receiver behavior explain the origin of individual recognition in *Polistes* wasps. Thus, biases in receiver behavior are a viable hypothesis for explaining the evolution of individual recognition. Though receiver biases appear uncommon in our survey of the literature, it is premature to draw any conclusions about the relative prevalence of sender or receiver biases in the evolution of individual recognition from existing data.

Regardless of whether individual recognition initially evolved via a sender or receiver bias, we expect similar evolutionary outcomes. In both cases, the pre-existing bias allows for selection to act on the other trait. As selection causes the ‘lagging’ trait to catch up, both traits may be elaborated in a correlated manner. There is growing evidence that selection for efficient recognition favors the evolution of distinctive identity signaling phenotypes (Pollard and Blumstein 2011; Sheehan and Tibbetts 2009; Sheehan and Tibbetts 2010). Identity signaling traits are expected to show a number of characteristics including: (1) composed of multiple traits, (2) each trait has a multi-modal distribution, (3) the traits are uncorrelated, (4) the traits are not associated with individual quality, and (5) the individual variations in the traits are stable (Beecher 1989; Dale 2006; Dale et al. 2001). Traits used for individual recognition in a number of species appear to fit these predictions including paper wasps *Polistes fuscatus* (Tibbetts 2002; Tibbetts and Curtis 2007), ruffs *Philomachus pugnax* (Dale et al. 2001), red-billed queleas *Quelea quelea* (Dale et al. 2001) and mice *Mus musculus domesticus* (Hurst et al. 2001; Hurst et al. 2008). While traits that have evolved as identity signals are expected to show a particular suite of characteristics, the precursors to identity signals need only to have some degree of variation that allows for improved individual identification. Provided that senders benefit from being recognized, selection for distinctive, identifiable phenotypes is expected to favor the evolution of identity signals (Dale et al. 2001; Johnstone 1997a).

Just as selection appears to favor the evolution of identity signals in senders, there is evidence for the evolution of receiver psychology in the context of individual recognition. Experiments in a diverse range of taxa and in different sensory modalities have demonstrated that receivers are particularly adept at recognizing individuals of their own species, often through specialized cognitive mechanisms. In humans, faces and voices are processed using specific brain regions and specialized cells (Kanwisher and Yovel 2006; Perrodin et al. 2011; Petkov et al. 2008). The paper wasp *Polistes fuscatus* shows cognitive specializations for learning conspecific faces, though its close relative that lacks individual, *P. metricus,* does not (Sheehan and Tibbetts 2011). Adaptations for acoustic recognition have also been found in swallows (Loesche et al. 1992; Loesche et al. 1991). Given that animals are capable of discriminating among and recognizing a wide range of patterns, it is somewhat surprising that such elaborate cognitive abilities associated individual recognition are present in primates, birds and wasps. Cognitive specializations for recognition have been tested in very few species to date, so the prevalence of cognitive specializations for individual recognition is unclear. Nevertheless, the existing work indicates that selection may shape cognitive processing in receivers to facilitate individual recognition. The exact nature of receiver behavioral evolution is expected to vary depending on the context of individual recognition and the specific history of a lineage. For example, territory holders in many species are often less aggressive to individually recognized territorial neighbors, such that the appropriate receiver behavior is to alter the levels of aggression depending on whether or not a particular they recognize a particular individual. If the ancestor prior to the evolution of individual recognition aggressively defended territories against everyone, selection for individual recognition in this context would be expected to favor receiver to reduce aggression to individuals that they recognize. Conversely, if the ancestor were passive to all individuals, selection for individual recognition would favor increased aggression to individuals that are not recognized. The nature of selection on receiver behavior will vary across taxa and contexts, though in call cases selection should favor receivers to respond to individuals differently depending on their past experiences with that particular individual.

Although individual recognition is thought to play a central role in many aspects of social evolution (Axelrod and Dion 1988; Crowley et al. 1996; Stevens and Hauser 2004), very few studies have examined how this highly specific recognition system has originated (Tibbetts and Dale 2007). In this paper, we provided a framework for future research examining the origin of individual recognition. Future research will ultimately need to combine analyses of phenotypic variability with experimental studies of receiver behavior in a robust phylogenetic framework. An important first step in understanding the evolution of individual recognition will be to identify more instances where closely related species differ in whether or not they individually recognize social partners, as variation in the trait will facilitate comparative analyses (Table 6.1).

This paper has focused on individual recognition though the general findings are likely to apply to other, less specific recognition systems. All recognition systems require variation in sender phenotypes as well as appropriate receiver discrimination abilities and responses (Sherman et al. 1997). The *de novo* evolution of any recognition system would likely be facilitated by sender or receiver biases. Previous work has not used the term sender bias, though it is a central theme in research on the evolution of kin recognition phenotypes. Numerous theoretical studies have pointed out that the variation required for kin recognition is unlikely to be maintained solely by selective pressures from recognition itself (Crozier 1986; Grosberg 1988; Rousset and Roze 2007). Indeed, many kin recognition systems are mediated by genes involved in immune responses to pathogens, so variation is maintained due to frequency-dependent selection and heterozygote advantages imposed by pathogens (Bernatchez and Landry 2003). Sender biases may play an important role in class-recognition as many natural categories of individuals (e.g. male - female, juvenile - adult, territorial - sneaker morphs) differ phenotypically, which could provide the basis for signals of class membership (Dale 2006; Roulin 2004).

Whereas sender biases may play a role in the evolution of a range of recognition systems, the scope of receiver bias may be more limited. Receiver bias provides a route for the evolution of recognition systems in the absence of variation in sender phenotypes. Thus, for receiver to be effective selection for recognition must be sufficient to maintain variation in recognition phenotypes. Selection for recognition appears to be sufficient to maintain variation in phenotypes used for individual recognition (Lahti 2005; Sheehan and Tibbetts 2010). However, Current theory suggests that may not be the case for other recognition systems such as kin recognition (Crozier 1986; Grosberg 1988; Rousset and Roze 2007). In models of kin recognition, individuals with a kin phenotype receive benefits, which favors common recognition alleles as those individuals have more beneficial interactions. Provided that senders on average benefit by being properly classified by receivers and suffer costs when incorrectly classified (as occurs in individual recognition), selection should favor the evolution of phenotypes that allow for proper classification whether that be at the individual, kin, group or species level. Thus, when senders benefit from proper identification, receiver bias may play a role in origin of novel evolution of recognition systems.

Conclusion

Recognition systems have been the focus of a great deal of research in biology and psychology because of their importance for understanding social evolution (Tang-Martinez 2001; Tibbetts and Dale 2007) Previous research has shown that selection for individual recognition can produce highly polymorphic and individualistic phenotypes (Pollard and Blumstein 2011; Sheehan and Tibbetts 2009) as well as highly specialized cognitive abilities (Sheehan and Tibbetts 2011; Zhu et al. 2010). Here we outlined the evolutionary routes through which recognition cues and cognition might originate via sender and receiver biases. As with the evolution of other signaling systems, receiver biases appear to play a role in the evolution of individual recognition. In contrast to the emphasis on receiver bias in the literature, we find evidence that sender biases may be particularly important in facilitating the evolution of recognition systems.

Table 6.1

		Individually Identifiable	Recognition	Citations
Vocal recognition				
Penguins (Offspring recognition)				
Gentoo	*Pygoscelis papua*	Y	Y	(Jouventin and Aubin 2002)
King	*Aptenodytes patagonicus*	Y	Y	(Jouventin et al. 1999)
Adelie	*Pygoscelis adeliae*	Y	Y	(Jouventin and Aubin 2002)
Macaroni	*Eudyptes chrysolophus*	Y	Y	(Searby et al. 2004)
Fiordland	*Eudyptes pachyrhynchus*	Y	N	(Studholme 1994)
Shearwaters (Mate recognition)				
Mediteranean Cory's	*Calonectris diomeda*	Y	Y	(Cure et al. 2009)
Yelkouan shearwater	*Puffinus yelkouan*	Y	N	(Cure et al. 2009)
Gulls (Offspring recognition)				
Kittiwakes	*Rissa tridactyla*	Y	N	(Storey et al. 1992)
Herring gulls	*Larus argentatus*	Y	N	(Knudsen and Evans 1986; Storey et al. 1992)
Gulls (Parental recognition)				
Herring gull	*Larus argentatus*	Y	Y	(Knudsen and Evans 1986)
Laughing gulls	*Larus atricilla*	Y	Y	(Beer 1969)
Black-headed gulls	*Chroicocephalus ridibundus*	Y	Y	(Charrier et al. 2001)
Kittiwakes	*Rissa tridactyla*	Y	N	(Storey et al. 1992)
Swallows (Offspring recognition)				
Cliff swallow	*Hirundo pyrrhonota*	Y	Y	(Stoddard and Beecher 1983)
Bank swallow	*Riparia riparia*	Y	Y	(Beecher et al. 1981a; Beecher et al. 1981b)
Tree swallow	*Tachycineta bicolor*	Y	N	(Leonard et al. 1997)
Barn swallow	*Hirundo rustica*	Y	N	(Medvin and Beecher 1986)
Passerines - excluding swallows (Offspring recognition)				
Pinyon Jay	*Gymnorhinus cyanocephalus*	Y	Y	(McArthur 1982)
Florida Scrub Jays	*Aphelocoma coerulescens*	Y	Y	(Barg and Mumme 1994)

Black-redstart	*Phoenicurus ochruros*	Y	Y	(Draganoiu et al. 2006)
White-throated sparrows	*Zonotrichia albicollis*	Y	Y	(Kopachena and Falls 1991)
Red-winged black birds	*Agelaius phoeniceus*	Y	N	(Edwards et al. 1999)
Western blue birds	*Sialia mexicana*	Y	N	(Leonard et al. 1995; Monk et al. 1997)
Passerines - excluding swallows (Parental/helper recognition)				
Long tailed tits	*Aegithalos caudatus*	Y	Y	(Sharp et al. 2005)
Red-winged balckbirds	*Agelaius phoeniceus*	Y	N	(Edwards et al. 1999)
Seals (Offspring recognition)				
Grey seal (Sable Island, Nova Scotia)	*Halichoerus grypus*	Y	Y	(McCulloch and Boness 2000)
Northern elephant seal	*Mirounga angustirostris*	Y	Y	(Petrinovich 1974)
Harbour seal	*Phoco vitulina*	Y	Y	(Renouf 1985)
Northern fur seals	*Callorhinus ursinus*	Y	Y	(Insley 2001)
Grey seal (Island of May, Scotland)	*Halichoerus grypus*	Y	N	(McCulloch et al. 1999)
Hawaiian monk seal	*Monachus schauinslandi*	Y	N	(Job et al. 1995)
Mongooses (Offspring recognition)				
Banded Mongoose	*Mungos mungo*	Y	Y	(Muller and Manser 2008)
Meerkat	*Suricata suricatta*	Y	N[a]	Manser per. comm.
Ungulates (Offspring recognition				
goats	*Capra hircus*	Y	Y	(Briefer and McElligott 2011)
Sheep	*Ovis aries*	Y	Y	(Searby et al. 2004)
Reindeer	*Rangifer tarandus*	Y	Y	(Espmark 1971; Espmark 1975)
Fallow deer	*Dama dama*	Y	N	(Torriani et al. 2006)
Bats (Parental recognition)				
Mexican free-tailed bats	*Tadarida brasiliensis*	Y	Y	(Balcombe and McCracken 1992)
Greater sac-winged bat	*Saccopteryx bilineata*	Y	N	(Knornschild and Von Helversen 2008)

Chemical Recognition

Ants (Co-foundress recognition)

Hairy panther ant	*Pachycondyla villosa*	Y	Y	(D'Ettorre and Heinze 2005)
	Pachycondyla inversa	Y	Y	(Dreier et al. 2007)
Black garden ant	*Lasius niger*	Y	N	(Dreier and D'Ettorre 2009)
Visual Recognition				
Village weavers *Ploceus cucllatus* (Egg recognition)[b]				
Gabon		Y	Y	(Lahti 2005; Lahti 2006)
South Africa		Y	Y	(Lahti 2005; Lahti 2006)
Mauritius (introduced)		N	Y/N	(Lahti 2005; Lahti 2006)
Hispaniola (introduced)		N	Y/N	(Lahti 2005; Lahti 2006)
Polistes paper wasps (Co-foundress recognition)				
Northern paper wasp	*P. fuscatus*	Y	Y	(Sheehan and Tibbetts 2008; Tibbetts 2002)
European paper wasp	*P. dominulus*	N	N	(Sheehan and Tibbetts 2010)
Common paper wasp	*P. metricus*	N	N	(Sheehan and Tibbetts 2010)

Notes:

a. Individual recognition of pup begging calls has not been explicitly tested in meerkats. However, experimental playbacks of begging calls recorded from pups outside of a group elicit feeding by helpers suggesting that meerkats do not recognize pups as individuals based on their begging calls (Madden et al. 2009).

b. In their native range, village weaver nests are parasitized by the diederick cuckoo and have evolved highly distinctive egg markings to counter cuckoo parasitism. Populations introduced to Hispaniola and Mauritius lack cuckoo nest parasites and have evolved less distinctive egg coloration within the past 200 years. Abilities for egg rejection behavior, however, have been maintained though are less accurate as a result of greater variation within and less variation between egg clutches.

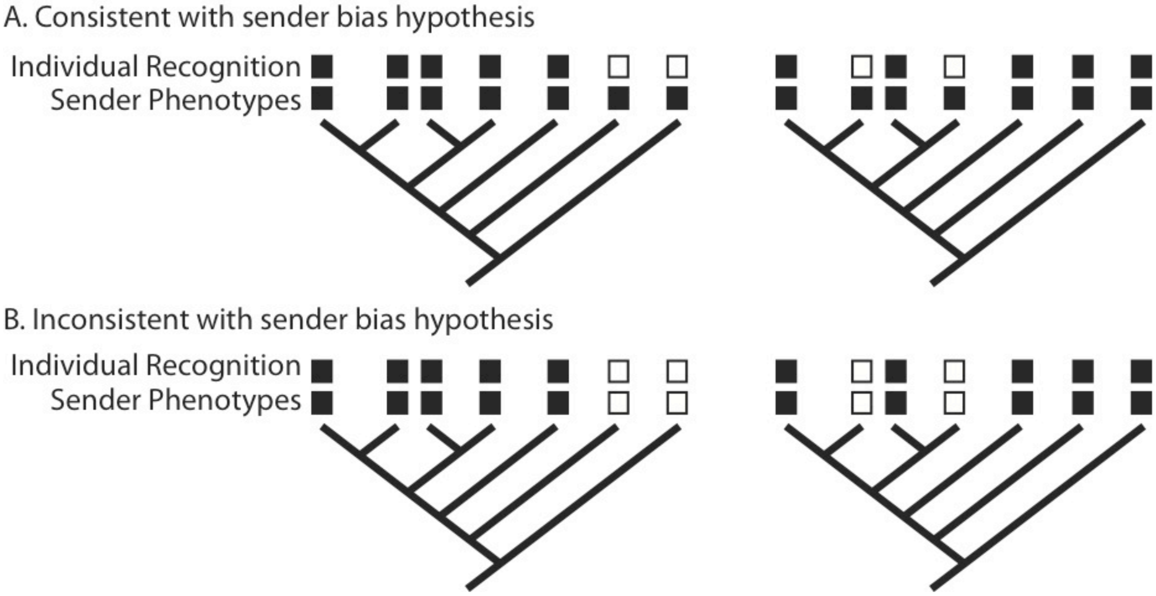

Figure 6.1
A schematic representation of the expected patterns of individual recognition and sender phenotypic variability under the sender and receiver bias hypotheses. Black boxes indicate that a trait is present. White boxes indicate that a trait is absent. For sender bias, taxa lacking individual recognition are expected to possess individually variable phenotypes. If taxa lacking individual recognition lack individually variable phenotypes, there is no support for receiver bias. The patterns are expected to be the same for each hypothesis, whether the lack of individual recognition is ancestral (left) or derived (right).

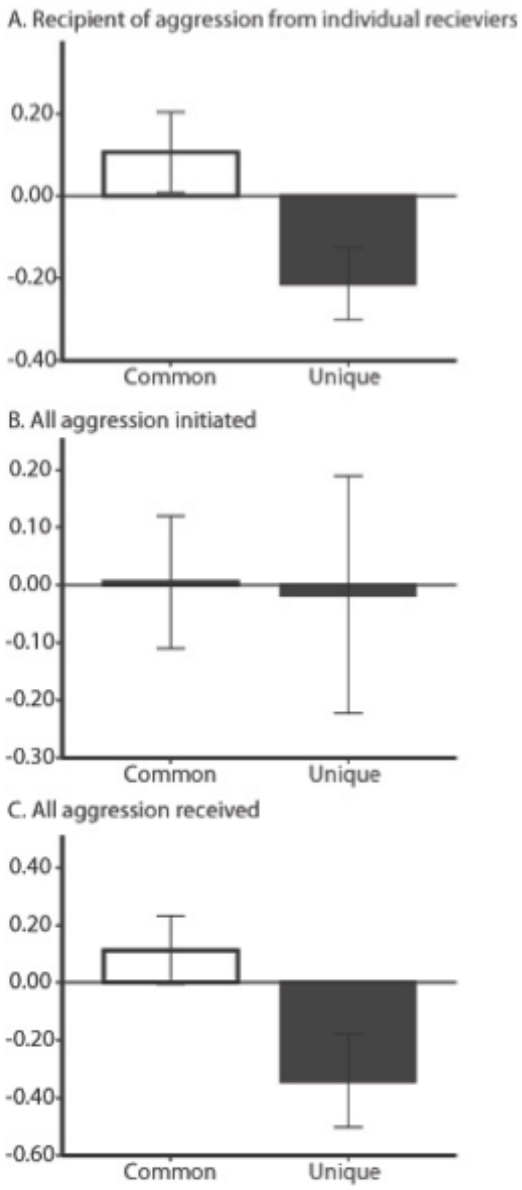

Figure 6. 2

Standardized aggression scores for wasps with common (white bars) and unique (black bars) appearances + SE. (A) The average aggression directed at distinctive and common wasps by individual receivers. This analysis specifically considers the effect of distinctive markings on the behavior of the average receiver. (B) The average aggression initiated by wasps of each treatment in the first half hour of interactions. (C) The average aggression received by wasps of each treatment in the first half hour of interactions. The mean standard scores differ in magnitude across the analyses because each analysis used an independently derived set of scores.

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Chapter 7: Conclusions

This dissertation has examined the evolution of individual recognition from the perspectives of both senders (Chapters 2-3) and receivers (Chapters 4-5) as well as the processes facilitating the origin of novel recognition systems (Chapter 6). In doing so, this work provides a foundation for thinking about the evolution of individual recognition and recognition systems more broadly. Additionally, this work has provided key insights in four areas.

First, understanding the mechanisms that maintain polymorphism in populations is a central goal of modern evolutionary biology. Recognition systems, which require variable phenotypes, are ideal study systems for investigating the evolution of ecological important polymorphisms. Our work provides the first evidence that selection favors the evolution of distinctive identity signaling phenotypes (Sheehan and Tibbetts 2009; Sheehan and Tibbetts 2010). Thus, selection that favors recognition is likely to be a common force maintaining polymorphism in populations.

Second, animal cognition is thought to play a central role in many areas of research in evolutionary biology such as mate choice (ten Cate and Rowe 2007) and predator-prey co-evolution (Bond and Kamil 2002), though the processes of cognitive evolution themselves are poorly understood (Bitterman 2000;

Shettleworth 2000). Recognition decisions are important for animals not only when they interact with social partners, but also when then search for mates or prey. Therefore, understanding the evolution of cognitive abilities associated with recognition systems may provide important insights. Our work on face recognition in paper wasps suggests selection for improved recognition abilities has favored the evolution of specialized face-processing abilities in paper wasps (Sheehan and Tibbetts 2011), analogous to those found in mammals (Pascalis and Kelly 2009). The striking patterns of convergent evolution across wasps and mammals and divergent evolution between closely related wasps, is consistent with the hypothesis that specialized cognition is the result of adaptive evolution. This means selection for cognitive abilities use for one task may have little influence cognitive abilities related to other tasks. Thus, counter to common wisdom, animal may best be viewed as a suite of independent abilities.

Third, the individual recognition is thought to dramatically increase the cognitive demands of social life. The presence of many individually-differentiated relationships have been a major selective force favoring the evolution of encephalization in primates and other vertebrates (Dunbar and Shultz 2007; Perez-Barberia et al. 2007; Shultz and Dunbar 2007). More recently, work on the cognitive abilities of insects has begun to challenge some of the long-held beliefs regarding brain size and cognitive abilities (Chittka and Niven 2009). In fitting with this trend, our work on social memories in *P. fuscatus* demonstrates that even insects with ‘mini-brains’ such as wasps are capable of maintaining individual social memories for relatively long periods of time in complex social environments (Sheehan and Tibbetts 2008). Interestingly, *P. fuscatus* does not have a larger brain than other paper wasps (Gronenberg et al. 2008), suggesting that the cognitive aspects of individual recognition may not be particularly costly in paper wasps.

Finally, the origin of recognition systems, like any communication systems, poses a chicken and egg problem. Recognition requires both variable phenotypes in senders and appropriate responses in receivers to function (Sherman et al. 1997). Understanding the origin of recognition systems is therefore predicated on identifying which came first – sender variation or receiver behavior. Our results demonstrate that pre-existing variation in sender phenotypes are likely to be a widespread facilitator for the evolution of novel recognition systems (Chapter 6). Verbal and mathematical models have predicted that the ritualization of pre-existing sender behavior into formal signals should be common (Maynard-Smith and Harper 2003; Scott-Phillips et al. in press), and our survey of the literature finds broad, though not universal, empirical support for this hypothesis. We also demonstrate that the evolution of recognition systems may be facilitated by appropriate receiver responses through experiments in *P. metricus*, which lack individual recognition (Chapter 6). Our results demonstrate that the receiver bias hypothesis for the origin of novel signals can also be extended to the origin of novel recognition systems.

Future directions

In addition to providing new insights into many areas of research in evolutionary biology, the work described in this dissertation suggests a number of avenues for future research on regarding identity signals and specialized cognition.

Genetic basis of individual variation in identity signals

A growing body of evidence suggests that the highly variable phenotypes used for individual recognition are the result of selection for distinctive, identity signaling phenotypes in a range of taxa (Logan et al. 2008; Medvin et al. 1993; Pollard and Blumstein 2011; Sheehan and Tibbetts 2009; Sheehan and Tibbetts 2010). While it is clear that selection for identity signaling promotes polymorphism, the mechanism underlying the polymorphism are unknown in any taxa. Generally, there are three basic mechanisms that can generate increased polymorphism: (1) negative frequency-dependent selection of genetically determined morphs, (2) increased phenotypic plasticity and (3) increased developmental stochasticity (Leimar 2005). Given that comparative studies have shown that identity signaling traits respond to selection, there must be a genetic basis to identity signaling. While any of the three mechanisms could function to provide increased polymorphism, the nature of the underlying genetics of identity signaling has important ramifications for the maintenance of genetic diversity. Whereas, selection for increased plasticity and developmental stochasticity would reduce genetic polymorphism (while increasing phenotypic polymorphism) negative-frequency dependent selection would increase genetic variation.

Dale (2006) has argued that identity signals should have strong genetic determination as that would enforce honest identity advertisement. Indeed, there is evidence from the calls of swallow nestlings (Medvin et al. 1992) and the urinary scents of mice (Cheetham et al. 2007) that there is a genetic basis for variation in identity signals. Additionally, there is evidence from paper wasps that identity signals are not condition dependent (Tibbetts and Curtis 2007), suggesting that the variation could have a genetic basis. At the moment, evidence for negative-frequency dependent selection maintaining genetic variation as a result of selection for identity signaling is lacking.

Interestingly, negative-frequency dependent selection for identity signaling is expected to differ from patterns of negative-frequency dependent selection on other traits. This occurs because in most instances negative-frequency dependent selection favors tight linkage between genes involved in traits under selection (Van Doorn and Dieckmann 2006). Empirical studies of self-recognition loci in plants are consistent with these predictions are loci show suppressed rates of recombination (Kamau and Charlesworth 2005). Additionally, the genetic basis of multiple male morphs in many species is controlled by a single mendelian locus (Lank et al. 1995; Sinervo et al. 2001), which is also consistent with the theoretical predictions. Unlike self recognition alleles or competing morphs, where a particular combinations of traits experience higher fitness, traits involved in identity signaling are expected to be phenotypically uncorrelated with each other, providing a greater number of possible phenotypic combinations and increased discriminatory power (Dale 2000; Dale et al. 2001). Thus, selection should favor the loci controlling variation at various identity signaling traits to be unlinked. Therefore, in contrast to traditional predictions of limited polymorphism maintenance under multilocus negative-frequency dependent selection (Van Doorn and Dieckmann 2006), identity signaling is expected to maintain polymorphism at multiple unlinked loci. Tests of this prediction will require information on the genetic correlations among traits that compose identity signals.

Comparative studies of specialized face learning

For a wide range of animals, faces provide a wealth of social information (Leopold and Rhodes 2010). Since animals typically orient towards each other during social interactions, faces provide an ideal canvass for conveying information regarding identity or aspects of quality to conspecifics. In primates, face learning is highly specialized, domain specific cognitive task (Pascalis and Kelly 2009). Decades of research have revealed a number of properties of specializations for face learning in primates, particularly that (1) processing occurs in a dedicated regions of the brain (Kanwisher and Yovel 2006), (2) the face template develops through a process of perceptual narrowing (Pascalis et al. 2002) and (3) that face learning abilities are heritable and genetically uncorrelated with other cognitive traits (Wilmer et al. 2010; Zhu et al. 2010). Whether these findings reflect general features of specialized learning or are specific to primates is unknown. Our recent demonstration of specialized face learning abilities in wasps (Sheehan and Tibbetts 2011) opens up exciting possibilities for comparative work between wasps and primates.

An additional avenue for future research on face learning in wasps will be to compare face-learning abilities among *Polistes* with independently evolved facial signals. Variable color patterning that could be used for signaling has evolved multiple independent times within *Polistes* (Tibbetts 2004). In addition to individual recognition in *P. fuscatus* (Sheehan and Tibbetts 2008; Tibbetts 2002), quality signals have been experimentally confirmed in *P. dominulus* (Tibbetts and Dale 2004; Tibbetts and Lindsay 2008) and *P. exclamans* (Tibbetts and Sheehan 2011). All three species (*P. dominulus, P. exclamans* and *P. fuscatus*) are distant relatives from distinct subclades within the genus (Pickett and Carpenter 2010). Whether species with quality signals will also show specializations for face learning is unknown. If *P. dominulus* and *P. exclamans* have independently evolved specialized face learning abilities, it will open up numerous research opportunities to study the repeatability of cognitive evolution, using face learning in *Polistes* as a model.

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