



How Does Individual Recognition Evolve? Comparing Responses to Identity Information in *Polistes* Species with and Without Individual Recognition

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Abstract

A wide range of complex social behaviors are facilitated by the recognition of individual conspecifics. Individual recognition requires sufficient phenotypic variation to provide identity information as well as receivers that process and respond to identity information. Understanding how a complex trait such as individual recognition evolves requires that we consider how each component has evolved. Previous comparative studies have examined phenotypic variability in senders and receiver learning abilities, although little work has compared receiver responses to identity information among related species with and without individual recognition. Here, we compare responses to identity information in two *Polistes* paper wasps: *P. fuscatus*, which visually recognizes individuals, and *P. metricus*, which does not normally show evidence of individual recognition. Although the species differ in individual recognition, the results of this study show that receiver responses to experimentally manipulated identity information are surprisingly similar in both species. Receivers direct less aggression toward identifiable individuals than unidentifiable individuals. Therefore, the responses necessary for individual recognition may pre-date its evolution in the *P. fuscatus* lineage. Additionally, our data demonstrate the apparent binary differences in a complex behavior between the two species, such as individual recognition, likely involve incremental differences along a number of axes.

Introduction

The ability to recognize and remember previous interactions with particular individuals is a key component of a wide range of complex social behaviors. Individual recognition is essential to the individuated relationships found in many vertebrate and some invertebrate societies (Bshary et al. 2002; Cheney & Seyfarth 2007; Dunbar & Shultz 2007; Gherardi et al. 2012) and has been theorized to influence cooperation (Crowley et al. 1996; Stevens et al. 2005; Brosnan et al. 2010), dominance hierarchies (Barnard & Burk 1979), and territorial acquisition and maintenance (Jaeger 1981; Stamps 1987).

Empirical research on the distribution of individual recognition among animals has largely focused on

two main areas. First, many studies have experimentally demonstrated the presence of recognition abilities across taxa and contexts (Beer 1969; Bee & Gerhardt 2002; Tibbetts 2002; Torriani et al. 2006; Carazo et al. 2008). Second, other studies have examined the extent of individual knowledge and memory (Godard 1991; Bergman et al. 2003; Gherardi & Atema 2005; Sheehan & Tibbetts 2008). The distribution of individual recognition across taxa is often described as being limited by species' cognitive abilities (Wilson 1975; Lehmann & Perrin 2002; Doorn et al. 2003; Stevens et al. 2005), although little research has in fact empirically examined which factors limit the distribution of individual recognition in different taxa.

To be functional, individual recognition requires that a species possess three characteristics (Sherman

et al. 1997): (1) variable phenotypes of senders that provide identity information, (2) receivers that can distinguish among individuals, and (3) receivers that respond differentially to individuals based on their identity and history of past interactions. Differences in individual recognition between species may arise from differences in any of these three characteristics: sender phenotypes, receiver processing, and/or receiver responses. Understanding which traits involved in recognition, if any, are shared with relatives that lack individual recognition is an important first step in elucidating the processes through which complex social behaviors utilizing individual recognition evolve.

Variation in sender phenotypes may be widespread, even in species that lack established individual recognition. A number of species lacking individual recognition possess traits that are variable among individuals but consistent within an individual (McCulloch et al. 1999; Cure et al. 2009; Dreier & D'Etorre 2009), suggesting that identity information may not limit the initial evolution of individual recognition in some species.

Receiver processing abilities are also unlikely to limit the evolution of individual recognition. Animals are generally adept at pattern recognition (e.g. Avargues-Weber et al. 2011). Honeybees are a prime example of this, as they can be trained to differentiate among human faces although there is no reason to believe that bees typically recognize individual humans or that bees have evolved specialized learning mechanisms for distinguishing among human faces (Dyer et al. 2005). Instead, bees likely learn human face images in the same way that they learn flower images. Operant conditioning studies have also shown that species that lack individual recognition are nevertheless able to distinguish among conspecifics when tasked with doing so and provided sufficient identity information (Loesche et al. 1991; Sheehan & Tibbetts 2011). Although both identity information and receiver processing may evolve to facilitate more efficient recognition, pre-existing variation in sender phenotypes and adequate receiver processing abilities may be widespread.

In contrast to the evolution of identity signatures and receiver processing, the evolution of receiver responses to identity information remains poorly understood. Receiver responses are likely to be the selective force driving the evolution of recognition behavior because they reflect the action component of recognition (Liebert & Starks 2004). Receivers respond to identity information in a variety of ways depending on the particular context (e.g. changes in aggression in territorial neighbors, the preferential

feeding and care of a parent's chicks) although responses can be classified into three broad categories based on their average effects on sender fitness—beneficial, neutral, and harmful. The effects of receiver responses on senders are critical for predicting the evolution of individual recognition, as different responses will have different consequences for the evolution of identity information (Beecher 1988). Where receiver responses to identity information are beneficial for senders, the evolution of identity signals is favored (Dale et al. 2001; Sheehan & Tibbetts 2009). In contrast, harmful receiver responses should favor concealment of individual identity (Johnstone 1997), which may prevent the evolution of individual recognition.

Species comparisons provide a powerful method for testing the factors that facilitate the evolution of individual recognition. In particular, do appropriate receiver responses pre-date established individual recognition or are responses the result of selection for individual recognition? Recognition requires the interaction of sender phenotypes and receiver behavior (Sherman et al. 1997). The initial evolution of recognition, then, would be facilitated by pre-existing variation in sender phenotypes or appropriate receiver behavior (Scott-Phillips et al. 2012). If two species differ in the occurrence of established individual recognition, but have similar responses to identity information, the differences in individual recognition behavior must be due to factors other than receiver responses. For example, there may not be sufficient naturally occurring variation to distinguish individuals. Comparing receiver responses to identity information among closely related species will shed light on the extent to which appropriate receiver responses may either pre-date or be the result of selection for individual recognition.

Here, we experimentally examine receiver responses to identity information in *Polistes metricus*, a paper wasp that lacks individual recognition (Sheehan & Tibbetts 2010). We compare our results with *P. metricus* to previously published results from a closely related wasp, *P. fuscatus* (Sheehan & Tibbetts 2009). *Polistes fuscatus* wasps possess strikingly variable color patterns on their face and abdomen that are used for individual recognition (Fig. 1a, Tibbetts 2002). Our previous work has demonstrated that the variable color patterns in *P. fuscatus* are identity signals that have evolved as a result of selection for recognizability (Sheehan & Tibbetts 2009, 2010). Nest founding queens benefit by receiving less aggression when they are easily identifiable (Sheehan & Tibbetts 2009). Additionally, *P. fuscatus* show evidence of specialized

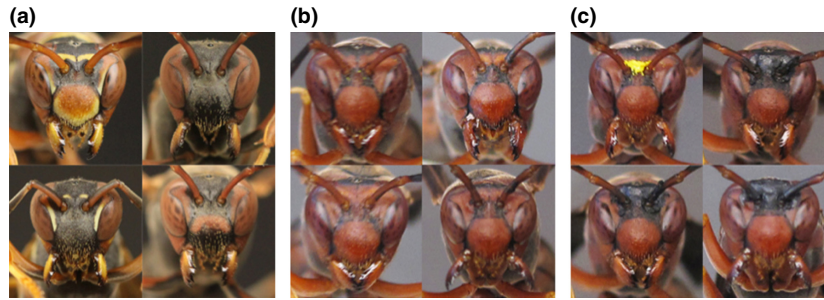


Fig. 1: (a) *Polistes fuscatus* wasps have distinctive, identity-signaling color patterns used for individual recognition (Tibbetts 2002; Sheehan & Tibbetts 2008). (b) *Polistes metricus* wasps lack variable color patterns and do not recognize individuals (Sheehan & Tibbetts 2010). (c) Example of the experimental manipulation of *Polistes metricus* wasps. Each experimental group contained four wasps collected at different sites. The appearances of all wasps in the group were altered with either yellow or black enamel paint. In each group, three individuals were given the same appearance (i.e. common phenotypes), while one was given a unique appearance (i.e. an identifiable phenotype). The color of the unique wasp was balanced across groups, so that the unique wasp was painted yellow in half the groups and black in half the groups.

face-specific mechanisms for processing identity information (Sheehan & Tibbetts 2011). *Polistes metricus* is closely related to *P. fuscatus* (Fig. 2, Pickett & Carpenter 2010; Buck et al. 2012), but lacks color pattern variation (Fig. 1b) and shows no evidence of individual recognition (Sheehan & Tibbetts 2010). Although *P. metricus* has difficulty differentiating between images of conspecifics, *P. metricus* can differentiate between images of *P. fuscatus* in an operant training paradigm (Sheehan & Tibbetts 2011). Therefore,

P. metricus are capable of distinguishing between wasps if there is sufficient identity information. Previous work has not tested whether *P. metricus* receivers respond to identity information during social interactions.

We test receiver responses to identity information in *P. metricus* by assessing how experimentally increasing identity information influences receiver behavior. Distinctive phenotypes allow individuals to discriminate among potential social partners and

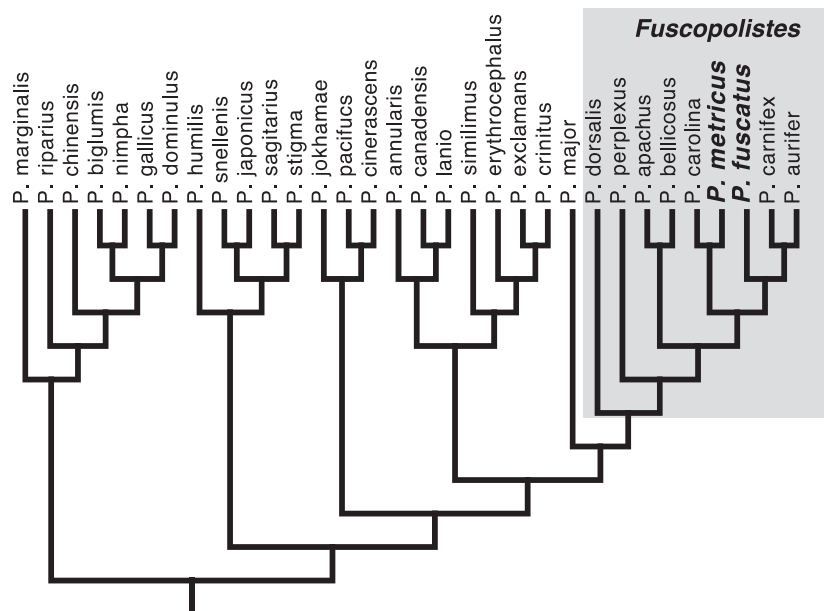


Fig. 2: Cladogram of *Polistes* highlighting the subgenus *Fuscopolistes*, which contains both *P. fuscatus* and *P. metricus*. The tree is drawn from data presented by Pickett & Carpenter (2010) based on a phylogeny of the Vespid wasps using both morphological and molecular characters. Please note that in this cladogram, branch lengths are not scaled for relative divergence as such a phylogeny is currently unavailable for the genus. However, recent attempts to delineate species within the *Fuscopolistes* subgenus in the eastern USA (where both *P. fuscatus* and *P. metricus* are found) using DNA barcodes found extremely low levels of divergence among species suggesting a relatively recent radiation within this group (Buck et al. 2012).

associate information with their identity, such as the outcome of a past interaction. Previous work in a closely related species with established individual recognition, *P. fuscatus*, has shown that distinctive, identifiable individuals receive less aggression than individuals with common, unrecognizable appearances even among groups of previously unfamiliar individuals (Sheehan & Tibbetts 2009). Indeed, lower aggression toward familiar individuals is the hallmark of individual recognition in paper wasps (Tibbetts 2002; Sheehan & Tibbetts 2008) suggesting that reduced aggression toward distinctive unfamiliar individuals is the result of learning individual identity during the course of the trials. Therefore, we experimentally increase identity information in *P. metricus* to test the following question: does identity information influence receiver behavior and if so, what is the likely fitness consequence of the response for senders?

There are three possible outcomes that might emerge from our experiment. First, identity information may have no influence on *P. metricus* receiver behavior, suggesting that variation in receiver responses may contribute to differences in recognition between the two species. Second, *P. metricus* receivers may respond to identity information in a way that harms senders, such as increasing the rate of aggression toward identifiable individuals, suggesting that *P. metricus* receiver behavior could favor the lack of identity information in senders and hinder the evolution of individual recognition. Third, *P. metricus* receivers might respond to identity information by reducing aggression toward recognizable individuals with whom they have interacted. Such a response would be expected to favor the evolution of identity signals (Dale et al. 2001; Sheehan & Tibbetts 2009), potentially facilitating the evolution of individual recognition under the appropriate contexts. Additionally, this outcome would suggest that *P. metricus* receivers were likely associating social information with identifying phenotypes.

Methods

Polistes metricus is a common paper wasp found throughout the eastern United States that is closely related to *P. fuscatus* (Fig. 2, Pickett & Carpenter 2010). As with all temperate paper wasps, *P. metricus* colonies are initiated each spring by foundresses that have recently emerged from diapause. We used foundresses collected from human structures in three locations during April and May of 2007: Ann Arbor, Michigan (43°16'N, 83°44'W), Columbus, Ohio (39°59'N, 82°59'W) and Knoxville, Tennessee (35°58'

N, 83°56'W). All nests were collected in the early founding phase when nests were small and had eggs or early instar larvae. They were brought into the laboratory, housed individually and provided *ad libitum* access to sugar cubes and water.

Using 80 foundresses, we created 20 different groups of four, unfamiliar weight-matched individuals collected from locations at least 1 km apart to reduce the possibility individuals had not previously interacted as wasps tend to be highly philopatric and dispersal distances of greater than 300 m have not been observed (Klahn 1979; Hirose & Yamasaki 1984; Makino et al. 1987). 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 an increase in identity information that could be used for discrimination or recognition. For all foundresses in each trial, we painted the region just above the antenna with either black or yellow paint (Fig. 1c). Previous studies have shown that, while *P. metricus* color patterns are largely invariant, there is slight variation in this region of the face (Sheehan & Tibbetts 2010). This region, then, is a plausible candidate for the location that a proto-identity signal may evolve in this lineage. Our paint treatments provided variation in this region that is roughly similar to that seen in *P. fuscatus* in the same region (Fig. 1a), although beyond what is naturally found in *P. metricus* populations (Fig. 1b). The distribution of color patterns was balanced across trials such that the identifiable wasp was yellow in half the trials and black in half the trials. Identifiable 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 the perception of identity information as they are small and on the backs. Additionally, data from other hymenopterans suggest that *Polistes* wasps are unlikely to see red (Briscoe & Chittka 2001). All groups contained sized-matched foundresses (mean foundresses size: 0.177 ± 0.003 g, range of mean foundress sizes across trials: 0.143–0.222 g, mean coefficient of variation of foundress size: 0.04 ± 0.007). There were not consistent differences in size between foundresses based on their color treatment ($F_{1,74} = 1.98$, $p = 0.16$, $n = 76$) or whether or not they received an identifiable marking ($F_{1,74} = 0.16$, $p = 0.69$, $n = 76$). Trials were conducted from June 12 to 13, 2007.

After the paint treatments dried, the wasps were placed in a small container ($8 \times 8 \times 2$ cm) and their interactions were filmed for 2 h. During the early nest founding period, foundresses typically compete with numerous rivals over dominance rank in areas without nests or resources (Roeseler 1991; MJS and EAT personal observations). Our experimental setup mimics this situation, so foundresses readily engage in aggressive competition in the trials. 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 (West Eberhard 1969; Reeve & Nonacs 1992; Strassmann et al. 2004). 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 trials.

We analyzed whether the levels of aggression initiated and received differed between identifiable and indistinguishable wasps. Aggression was markedly elevated in the initial part of the trial in *P. metricus* (Fig. S1, 1st h – 280.21 ± 74.60 aggressive acts, 2nd h – 176.32 ± 41.91 ; $N = 19$ trials, paired *t*-test, $t_{18} = 2.9$, $p = 0.0095$), so we measured the effect of distinctiveness during the first and second half of the trials separately. To account for differences in overall levels of aggression across trials ($\bar{x} = 261$ aggressive acts, 25th percentile = 157.5 aggressive acts, 75th percentile = 531.5 aggressive acts), we calculated a standardized score for each wasp. To do so, we subtracted the mean number of aggressive acts initiated or received in a trial from the number of aggressive acts initiated or received by the focal wasp. This score was divided by the standard deviation of aggression within a given trial. With this technique, the standard aggression scores of distinctive wasps could be compared to the overall trial averages (set to zero) with one sample *t*-tests (Sokal & Rohlf 1995). Positive standardized scores indicate that the wasp received more aggression than others in her trial, while negative standardized scores indicate that the wasp received less aggression than others in her trial. We conducted the same analyses of the data from our previous experiment with *P. fuscatus* (Sheehan & Tibbetts 2009). The earlier experiment followed the same procedures, except that we painted clypei either black or yellow in *P. fuscatus*. Standard scores are reported as the mean number of standard deviations that identifiable wasp aggression (given or received) differed from the trial average. In addition, we report the standard error around the mean standard score. Variation reported around means is reported as standard error throughout. All tests described are two-tailed.

Results

During the 1st h of the *P. metricus* trials, when aggression was most intense (see Fig. S1, Methods), identifiable wasps received less aggression than non-identifiable wasps (Fig. 3, mean aggressive acts received = 0.33 SD less than the trial average ± 0.15 SE, $N = 19$, $t_{18} = -2.14$, $p < 0.05$). Identifiable wasps were equally aggressive as the other wasps (mean aggressive acts initiated = 0.013 SD less than the trial average ± 0.17 SE, $N = 19$, $t_{18} = -0.08$, $p = 0.94$), so the lower levels of aggression received are not a by-product of the identifiable wasps being less aggressive. The color a wasp was painted did not affect the amount of aggression it received during this period (black = 0.03 SD more than the trial average ± 0.14 SE, $N = 39$, $t_{38} = 0.23$, $p = 0.82$; yellow = 0.03 SD less than the trial average ± 0.14 SE, $N = 37$, $t_{36} = -0.24$, $p = 0.81$). Additionally, the aggression received by the identifiable foundress was not influenced by the mean mass of foundresses in her trial (linear regression: $F_{1,17} = 0.20$, $r^2 = -0.05$, $p = 0.66$, $n = 19$ identifiable wasps) or the standardized mass of the identifiable foundress relative to those in her trial (linear regression: $F_{1,17} = 1.24$, $r^2 = 0.013$, $p = 0.28$, $n = 19$ identifiable wasps).

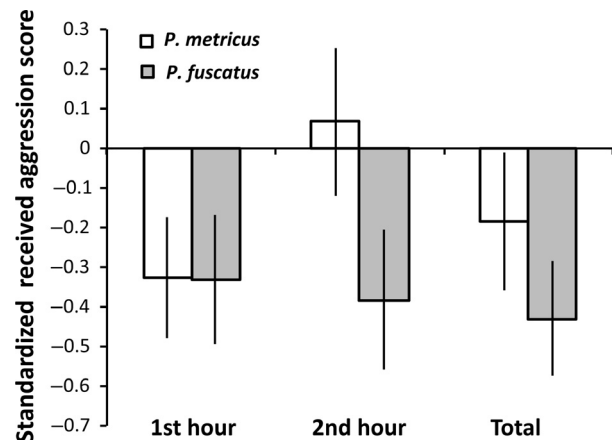


Fig. 3: Mean standardized aggression scores (\pm SEM) for the wasps with distinctive, identifiable phenotypes. Individuals with phenotypes experimentally manipulated to provide identity information receive less aggression than the average individual within the trial. Standardized aggression scores show how much aggression an individual received as the number of standard deviations from the mean of the trial in which they participated. Negative values indicate that identifiable individuals received less aggression than the trial mean. Reduced aggression toward identifiable individuals is only detectable in the 1st h of the trials in *Polistes metricus*, although the effect is consistent in *Polistes fuscatus*. See text for statistics.

Therefore, the presence of experimentally added identity information *per se* rather than a particular color or size of the foundress was responsible for the reduction in aggression.

In the 2nd h of the trials, when aggression levels were significantly lower (see Fig. S1, Methods), there was no discernable effect of identity information on the distribution of aggression among wasps (Fig. 3, mean aggressive acts received = 0.067 SD more than the trial average \pm 0.19 SE, $N = 19$, $t_{18} = 0.36$, $p = 0.73$). Consistent with the reduced effect of identity information in the 2nd h, the benefit of identity information is obscured if the entire 2-h trial is analyzed (Fig. 3, mean aggressive acts received = 0.18 SD less than the trial average \pm 0.17 SE, $N = 19$, $t_{18} = -1.06$, $p = 0.3$).

The responses to identity information at the beginning of the *P. metricus* trials mirror those observed in the same experiment performed with *P. fuscatus* (Fig. 3, mean aggressive acts received = 0.33 SD less than the trial average \pm 0.16 SE, $N = 18$, $t_{17} = -2.02$, $p = 0.06$). Unlike, in *P. metricus*, however, levels of aggression did not decline over time in *P. fuscatus* (1st h = 116.11 + 10.31 aggressive acts; 2nd h = 138.33 + 44.45 aggressive acts; $N = 18$, $t_{18} = -0.51$, $p = 0.61$) and the response to identity information was increasingly detectable in the 2nd h (mean aggressive acts received = 0.38 SD less than the trial average \pm 0.18 SE, $N = 18$, $t_{17} = 2.15$, $p < 0.05$) or when analyzing both hours together (mean aggressive acts received = 0.43 SD less than the trial average \pm 0.15 SE, $N = 18$, $t_{17} = -2.95$, $p = 0.009$).

Discussion

When provided with sufficient identity information, *P. metricus* receivers discriminate between individuals. Foundresses direct less aggression toward identifiable individuals than unidentifiable individuals in the course of staged social interactions. This pattern of behavior is similar to what we previously reported using the same experimental paradigm in *P. fuscatus* (Sheehan & Tibbetts 2009), a close relative that recognizes individuals using variable color patterns (Tibbetts 2002). There were also some differences in behavior toward identifiable individuals across species. Specifically, a significant difference in aggression toward identifiable and indistinguishable individuals was only detectable in the 1st h of the trials in *P. metricus*, which coincided with a period of elevated aggression within the groups (Fig. S1). An examination of patterns of aggression across the trials shows that identifiable wasps tend to receive less aggression

than indistinguishable wasps during the peak of aggression at the outset of the trial (Fig. S1). Levels of aggression decline in both groups of wasps, although levels of aggression toward identifiable individuals bottom out more rapidly than in indistinguishable individuals (Fig. S1). In *P. fuscatus*, identifiable individuals received less aggression than indistinguishable individuals over all time periods with no observed decline in aggression. This suggests that the effect of identity information on receiver behavior, while detectable, is weaker in *P. metricus* compared to *P. fuscatus* and most apparent when during periods of intense aggression. The overall reduction in aggression in *P. metricus* that is absent in *P. fuscatus* also suggests that aggressive interactions may differ between the two species because of factors not directly related to individual recognition. The decline in aggression within the *P. metricus* trials reported here is similar to the large decline in aggression previously reported in a series of briefer interactions among *P. metricus* over the course of 4 d (Sheehan & Tibbetts 2010). Nevertheless, both species show similar responses to identity information, despite differing in recognition behavior. Therefore, key components of receiver responses to identifiable individuals are shared between the two species, suggesting that similar receiver responses likely existed in their recent common ancestor, prior to the evolution of individual recognition in the *P. fuscatus* lineage.

Individual recognition requires receivers to learn and associate information about individuals with their identity phenotypes (Tibbetts & Dale 2007; Gherardi et al. 2012). Our data are consistent with learning as a mechanism that leads to reduced aggression toward identifiable wasps in *P. metricus*. If the responses to our treatment depended on innate preferences or responses, then the color an individual was painted should have a strong influence on how others interacted with them. In contrast, the results of our experiment were not influenced by the particular color an individual was painted (i.e. yellow or black) but rather if they displayed the rare marking within the group. The fact that outcomes are context-dependent is consistent with *P. metricus* receivers learning to associate information with identifying paint marks and reducing aggression toward individuals with whom they have previously interacted. Additional evidence of learning comes from the observation that at the outset of the trials, levels of aggression directed toward identifiable and indistinguishable individuals are similar but begin to diverge after a few minutes, with identifiable individuals receiving less aggression (Fig. S1).

Familiarity commonly reduces aggression among a wide range of animals (Jaeger 1981; Godard 1991; Gherardi et al. 2012) and in *Polistes* wasps in particular (Tibbetts 2002; Sheehan & Tibbetts 2008). When the relative status between two individuals is unknown, animals commonly engage in aggressive interactions to determine relative status, which may range from brief encounters to escalated bouts (Arnott & Elwood 2009). Memories of prior interactions allow individuals to assess their relative status and dominance without the need for aggression, leading to reduced aggression and ritualized dominance and subordination displays (Barnard & Burk 1979; Van Rhijn & Vodegel 1980; Tibbetts & Dale 2007; Carazo et al. 2008). As a result, learning can lead to reduced aggression for identifiable individuals because the outcomes of past interactions can be associated with a particular individual. When individuals are indistinguishable, past interactions with multiple individuals (who may differ in relative dominance status) cannot be differentiated.

Associative learning is required for identity information to reduce aggression. It is not surprising that *P. metricus* are able to associate visual identity information with social interactions. Even in the absence of a history of selection for individual recognition, receiver learning abilities in many species are likely sufficient to mediate discrimination based on identity information. For example, foraging in social insects such as bees and wasps is mediated by associative learning as well as more complex non-elemental forms of learning (Lehrer & Campan 2004; Avargues-Weber et al. 2011; Dyer 2012). Selection for individual recognition may favor the evolution of more specialized learning mechanisms as has been shown in *P. fuscatus* (Sheehan & Tibbetts 2011), although learning and discrimination abilities used in other tasks such as foraging are likely to facilitate discrimination of individuals in our experiment.

The similar receiver responses in *P. metricus* and *P. fuscatus* suggest that the lack of identity information in *P. metricus* senders is a key factor limiting the potential expression of individual recognition in *P. metricus*. On longer evolutionary timescales, however, we do not expect that the lack of identity information presents a significant constraint to the evolution of individual recognition in *P. metricus*. Color pattern evolution is highly labile in *Polistes*, and identity-signaling traits are not costly to produce or maintain (Tibbetts 2004; Tibbetts & Curtis 2007). Therefore, under the appropriate circumstances, existing receiver responses in *P. metricus* should favor the evolution of increased identity information in senders.

If the benefits of identity information in *P. metricus* are sufficient to select for identity signals, why does *P. metricus* lack variable color patterns? It is likely that identity signals have not evolved in *P. metricus* because there are few social interactions among *P. metricus* foundresses in natural populations, as *P. metricus* overwhelmingly initiate solitary nests (Starr 1976; Bohm & Stockhammer 1977; Hughes et al. 1993; Singer & Espelie 1996). Interactions among competing co-foundresses are thought to be particularly important for the evolution of social signaling in *Polistes* (Tibbetts 2004). Cooperating foundresses form a dominance hierarchy in many species that determines relative rates of reproduction and work, with the most dominant foundress monopolizing egg laying (Reeve 1991). Within foundress associations, then, there is the potential for individually differentiated interactions where foundresses invest differently in cooperative and aggressive acts depending on their interaction partners and their relative places in the hierarchy (West Eberhard 1969). Indeed, *P. fuscatus*, which has highly variable identity signals, frequently founds nests in large foundress associations and forms a strict dominance hierarchy among foundresses (West Eberhard 1969; Reeve et al. 2000).

In contrast to the interactions within foundress associations, the interactions between queens and workers are not thought to favor visual signaling, as there is less reproductive conflict between queens and their daughters (i.e. workers) (Reeve 1991; Tibbetts & Sheehan 2013). There is less evidence of individually differentiated interactions among workers within paper wasp colonies, although behavioral profiles among workers in temperate species tend to differ based on their age (Strassmann & Meyer 1983; Miyano 1986; Hughes & Strassmann 1988). Additionally, the recognition of queen vs. worker status is communicated using blends of cuticular hydrocarbons that convey information about reproductive state (Monnin 2006). Further, whereas all species of paper wasps have interactions between queens and workers, only those species with foundress associations have variable color patterning associated with visual signaling (Tibbetts 2004). While receiver responses could facilitate the evolution of identity information in *P. metricus*, there is little opportunity for selection to act given the rarity of interactions among foundresses, which helps explain why *P. metricus* lack identity signals and individual recognition.

The results of this experiment present the possibility that pre-existing receiver behavior could facilitate the evolution of individual recognition. Pre-existing receiver responses have been suggested to favor the

evolution of a range of sexually selected traits (Endler & Basolo 1998; Jansson & Enquist 2005; Kolm et al. 2012), but the role of receiver responses in the evolution of recognition systems has received less attention. Typically, biases in receiver responses manifest as pre-existing preferences for particular trait forms [i.e. longer sword tails (Morris et al. 2007), red coloration in sticklebacks (Smith et al. 2004), longer tail plumage in widowbirds (Pryke & Andersson 2002)]. However, pre-existing receiver behaviors facilitating individual recognition would involve differential responses to unique individuals rather than preferences for particular phenotypes. Receiver responses favorable to identity signaling are likely to be important in the evolution of individual recognition in many taxa. Whether such responses existed prior to selection for recognition or are a result of such selection is an unexplored question. Our data are consistent with pre-existing receiver behavior in *Polistes*, although tests of additional species within the *P. fuscatus-metricus* clade are needed to adequately test such a hypothesis (Fig. 2). Vespid wasps present an excellent opportunity to explore the role of receiver biases as there have been multiple independent evolutions of visual signaling across the group (e.g. individual recognition in *Liosteno-gaster*, Baracchi et al. 2012).

At a broader scale, the role of pre-existing receiver behavior in the origin of individual recognition is currently unclear. In many species that lack individual recognition, receivers do not respond to available identity information (McCulloch et al. 1999; Schibler & Manser 2007; Cure et al. 2009), suggesting that receiver responses do not favor individual recognition in those species. However, it is also possible that the sender phenotypes tested in these experiments appear individually distinctive when analyzed by researchers, but are not actually perceived as individually distinctive by the animals (Tibbetts et al. 2008). Therefore, researchers must consider the perceptual abilities of receivers, as well as the amount of identity information potentially available to receivers when testing the role of receiver responses in the evolution of individual recognition. Receivers may be more likely to respond to variation when such variation is easier to discern.

Individual recognition requires a number of cognitive steps, including distinguishing among individuals, learning individual identity, associating identity with individual specific information and later recalling that information (Tibbetts & Dale 2007; Gherardi et al. 2012). Although individual recognition appears cognitively complex, relatively little work has examined how cognition differs between closely related species

with and without individual recognition, although identifying such differences is crucial to understanding the evolution of complex cognition and behavior (Chittka et al. 2012). In the case of paper wasps, individual recognition is associated with differences in cognitive processing, social memory and color pattern variability (Sheehan & Tibbetts 2008, 2010, 2011). The present study, however, suggests that previously described differences in individual recognition abilities are a matter of degree rather than kind. The basic cognitive building blocks of individual recognition behavior—receiver discrimination and response—are present and expressed in a species that lacks individual recognition when provided with sufficient identity information. In the case of paper wasps, at least, receiver cognition and behavior does not appear to limit the initial evolution of individual recognition.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Figure. S1: Patterns of aggression over time.