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Original Article

Geographic variation in individual face learning based on plasticity rather than local genetic adaptation in *Polistes* wasps

Meagan Simons, Delbert A. Green II, and Elizabeth A. Tibbetts
Ecology and Evolutionary Biology, University of Michigan, 1105 North University Ave Biological Sciences Building Ann Arbor, MI 48109-1085, USA

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Signals and receiver responses often vary across a species' geographic range. Effective communication requires a match between signal and receiver response, so there is much interest in the developmental mechanisms that maintain this link. Two potential mechanisms are genetic covariance between signal and receiver response and plasticity where individuals adjust their phenotype based on their partner's phenotype. Here, we test how plasticity contributes to geographic variation in individual face recognition in *Polistes fuscatus* wasps. Previous work has shown that *P. fuscatus* from Michigan, USA (MI) have variable facial patterns used for individual recognition, while *P. fuscatus* from central Pennsylvania, USA (PA) lack variable facial patterns and are unable to learn individual conspecifics. We experimentally altered rearing environment, so wasps were either reared with their own population or in a common garden with wasps from both populations. Then, we tested the wasps' capacity to learn and remember individual conspecific faces. Consistent with previous work, MI wasps reared with MI wasps were adept at learning conspecific faces, while PA wasps reared with PA wasps were unable to learn conspecific faces. However, MI and PA wasps reared in a common garden developed similar, intermediate capacity for individual face learning. These results indicate that individual face learning in *Polistes* wasps is highly plastic and responsive to the social environment. Plasticity in receiver responses may be a common mechanism mediating geographic differences in non-sexual signaling systems and may play a role in maintaining links between signals and receiver responses in geographically variable communication systems.

Key words: **common garden, evolutionary divergence, face recognition, geographic variation, individual recognition, learning.**

INTRODUCTION

Understanding the developmental basis of phenotypic divergence among natural populations is a fundamental goal of evolutionary ecology (Kawecki and Ebert 2004; Pfennig et al. 2010). Divergence is particularly interesting in complex traits where selection on one individual depends on the phenotype of other individuals (e.g., mutualism, predator–prey relationships, cooperation, communication) (Moore et al. 1997; Herre et al. 1999). For example, during communication, selection on senders depends on receiver phenotypes and vice versa (Bradbury and Vehrencamp 1998; Nowicki and Searcy 2005). Effective communication depends on senders having variable phenotypes that convey information to receivers and receivers paying attention to these phenotypes and responding appropriately. Either component alone is ineffective (Scott-Phillips et al. 2012). As a result, divergence in either signals alone or responses alone could disrupt a communication system.

Two mechanisms may allow geographic variation in communication systems while still maintaining a match between signal and receiver response: genetic covariance between signal and receiver response and plasticity. In taxa with genetic covariance between signal and receiver response, selection on either trait leads to a change in the other trait. Genetic covariance between mating signals and mate preferences has been found in many sexual signaling systems (Bakker and Pomiankowski 1995). It arises because there is assortative mating between senders with ornaments and receivers that prefer the ornaments (Fowler-Finn and Rodríguez 2016). Plasticity can also maintain a link between signal and receiver response because plasticity allows individuals to rapidly adjust their phenotype based on their partner's phenotype (Tibbetts and Snell-Rood 2021). Plasticity can occur in signals, receiver responses, or both signals and responses. For example, many species learn mate preferences, so exposure to signals with a novel phenotype can rapidly alter receiver mate preferences (Irwin and Price 1999). Birds reared with a novel male phenotype exhibit receiver plasticity, as they sexually imprint on parental traits, then prefer the parental traits as

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Address correspondence to E.A. Tibbetts. E-mail: tibbetts@umich.edu.

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an adult (ten Cate and Bateson 1989; Witte et al. 2000). Signals are also highly plastic (Bradbury and Vehrencamp 1998; Nowicki and Searcy 2005). For example, sexual ornaments are highly condition-dependent and senders often alter adjust their signals based on biotic and abiotic factors like receiver behavior, local habitat characteristics, and the perceptual environment (Patricelli et al. 2002; Miller et al. 2022).

Thus far, most work on geographic variation in communication has focused on signals used during mate choice, finding evidence that both plasticity and genetic covariance link signals and receiver responses across species' geographic range. For example, geographic variation in bird song is often mediated by plasticity (Beecher et al. 1994; Slabbekoorn and Smith 2002a). Young birds learn songs from adult tutors, so young birds learn to sing the local song dialect (Slabbekoorn and Smith 2002b). Young birds also learn preferences from tutors, so they prefer mates with local song dialects (Slabbekoorn and Smith 2002a). The plasticity in signals and receiver preferences maintains a link between signal phenotype and receiver preference in each region. In contrast, male guppies have geographically variable color patterns that differ, in part, due to local genetic adaptation to high vs low predation environments (Endler 1992; Endler and Houde 1995; Kemp et al. 2018). Female mate preference is influenced, in part, by genetic correlation with male traits. The trait/preference genetic covariance is thought to play a role in the geographic match between male signals and female preferences (Fowler-Finn and Rodríguez 2016).

Less is known about the development of geographic variation in non-sexual signals and how developmental factors maintain links between signal and response. Studying diverse signal types is important because signals that convey different information differ in many ways. For example, in sexual signaling systems, assortative mating between senders with ornaments and receivers that prefer the ornaments is the key mechanism that leads to trait/preference genetic covariance (Fowler-Finn and Rodríguez 2016). Assortative mating does not occur in nonsexual signaling systems. As a result, theory suggests there will be no genetic covariance between signal and receiver response in non-sexual signals. In addition, signals that convey different information (e.g., kinship, quality, individual identity) have different developmental characteristics (Dale 2006; Bradbury and Vehrencamp 2011). For example, signals of mate quality have low and inconsistent heritability and are condition dependent (Tibbetts et al. 2017). In contrast, signals of individual identity are highly heritable and not condition-dependent (Tibbetts et al. 2017). As a result of the different developmental processes that influence signals that convey different information, the processes that underlie geographic variation may also differ across signal types.

Individual recognition is one type of communication system that often varies geographically, but we currently know little about the developmental basis of the geographic variation in individual recognition. Individual recognition is an essential aspect of social communication across many taxa (fish, birds, crustaceans, mammals, and insects), social contexts (cooperation, reciprocity, social monogamy, parental care, dominance hierarchies), and modalities (chemical, visual, auditory) (Tibbetts and Dale 2007). During individual recognition, receivers learn the unique phenotype of conspecifics, associate the phenotype with individual-specific information, and recall the phenotype-information link during subsequent interactions (Tibbetts and Dale 2007). The variable phenotypes used for individual recognition are called individual identity signals. Some individual identity signals vary geographically. For example, orangutan vocal calls used to individually identify neighbors (Spillmann et al. 2003) vary in their duration and pulse rate across populations (Delgado 2007). Similarly, parrot contact calls, dolphin signature whistles, and human facial features have different characteristics across populations (Wright 1996; Janik et al. 2006). Less is known about cases where receiver capacity for individual recognition differs across populations.

Polistes fuscatus provide a good model system to explore the development of geographic variation in individual recognition because individual identity signals and capacity for individual recognition varies across populations (Tibbetts, Ortiz, et al. 2021). In Michigan and New York, *P. fuscatus* have variable facial patterns that signal individual identity (Tibbetts 2002). Wasps are adept at learning and remembering individual conspecifics and use individual recognition during social interactions on and off nests (Tibbetts 2002; Sheehan and Tibbetts 2008; Tibbetts et al. 2020) and also learn to discriminate between individual conspecific faces during training (Tibbetts, Injaian, et al. 2018). In contrast, *P. fuscatus* from Rothrock, Pennsylvania, USA, lack individual identity signals, as they have less variable facial patterns than *P. fuscatus* from Michigan (Tibbetts, Ortiz, et al. 2021). Further, *P. fuscatus* from Pennsylvania are not capable of individual face recognition. Pennsylvania *P. fuscatus* do not learn and remember individual conspecifics during social interactions or during training (Tibbetts, Ortiz, et al. 2021).

The different capacity for individual face recognition in Michigan and Pennsylvania could be due to local genetic adaptation, plasticity, or a combination of the two. The relative roles of plastic and genetic changes in geographically variable phenotypes can be tested by rearing populations with different phenotypes in a controlled environment. Here, we test how population of origin and rearing environment influence *P. fuscatus* individual face recognition by rearing wasps from Michigan (MI) and Pennsylvania (PA) with wasps from their own population or in a common garden with individuals from both populations. If populations remain distinct when reared in the common environment, it suggests that genetic differences strongly contribute to geographic variation in recognition. In contrast, if populations have similar phenotypes when reared in the same environment, it suggests that plasticity plays a large role in geographic differences in recognition. In some cases, both genetic adaptation and plasticity contribute to geographic variation (West-Eberhard 2003), so individuals reared in a common environment have phenotypes that are intermediate between their population of origin and rearing environment.

METHODS

Polistes fuscatus wasps were collected from the area surrounding Ann Arbor, Michigan (MI) (42°17′59″N, 83°39′46″W) and Rothrock State Forest, Pennsylvania (PA) (40°38′13″N, 78°4′29″W) in early-late June 2019 and 2020. In previous work, we used DNA barcoding to confirm that wasps collected in both populations are *P. fuscatus* (Tibbetts, Ortiz, et al. 2021). Wasps were collected at the foundress stage, where one or multiple foundresses had formed a nest, but workers had not emerged. When wasps were collected, they were individually marked on their wing tips using non-toxic modeling paint. All wasps were returned to the University of Michigan and placed in enclosures (4.5 in × 3.5 in × 9 in) in an environmental chamber under natural day/night cycles with ad lib sugar, water, caterpillars, and nest building materials. The chamber was kept at 80F during the day and 60F at night. Nests from Michigan and Pennsylvania were checked every 24 h for worker emergence. New

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workers were identified as wasps with no paint on their wings and were immediately placed in the treatment groups described below. Workers used in the experiment were collected from 20 nests from Pennsylvania and 19 nests from Michigan.

Treatment groups

When a newly emerged worker was found on a nest, she was removed and painted with an individually identifying color code. Then, wasps were placed into a new enclosure (4.5 in × 3.5 in × 3 in) of four newly emerged wasps with ad lib sugar and water. There were three treatment groups: 1) MI with MI (six groups, *n* = 22), 2) PA with PA (five groups, *n* = 18), 3) PA and MI together (common garden, 2 PA and 2 MI, 15 groups, *n* = 30 PA, 29 MI). These numbers reflect the final sample size of wasps tested during the learning phase of the experiment. Sample sizes differ slightly across treatment groups because a few wasps died before training. Wasps were reared in groups of 4 to allow cross-rearing of individuals from different populations without social conflict. There is substantial facial pattern variation both within and between *P. fuscatus* nests, so wasps reared with non-nestmates experience similar facial pattern variation as wasps reared with nestmates. MI wasps reared in groups of 4 developed similar face learning capacity as MI wasps reared on their natal nest (Pardo-Sanchez et al. 2022), indicating that the experimental setup produces biologically reasonable outcomes.

Wasps were housed with their treatment groups for 7–10 days. *Polistes* are considered behaviorally mature at 5 days old because they engage in a range of adult *Polistes* behavior, including cooperative and competitive interactions with conspecifics, egg laying, flying, hunting, and navigating (Reeve 1991; Giray et al. 2005; Shorter and Tibbetts 2009). Although some social experience is required for the development of individual face learning (Tibbetts et al. 2019), performance does not differ between wasps given 7 days social experience and those given 14 days social experience (Pardo-Sanchez and Tibbetts 2022).

Stimuli

Wasps from both populations were trained to discriminate between *P. fuscatus* face images using previously established methods (Tibbetts, Ortiz, et al. 2021). *P. fuscatus* faces from Michigan and Central Pennsylvania, USA were photographed and printed to be used as stimuli (Figure 1). All images were printed at life size (approximately 3.5 mm wide) using a commercially available Xerox Altalink C8035 that uses ink cartridges.

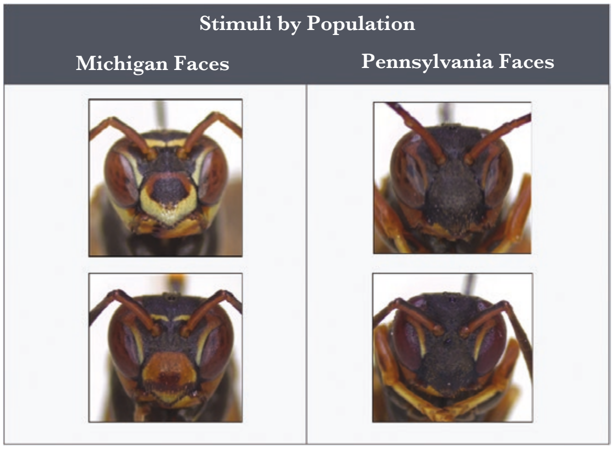

Figure 1
Examples of *P. fuscatus* face images from Michigan (left column) and Pennsylvania (right column).

Wasps raised in the treatment groups were trained to differentiate pairs of MI face stimuli. We used a standard set of face images for wasps from both populations to ensure that any differences in performance were due to receiver capacity rather than differences in stimuli characteristics. A total of six different MI wasp faces were used as training stimuli, but each individual was only trained and tested using a single pair of randomly chosen face images. The specific face that was neutral vs negative (see below) was swapped across trials to ensure that the specific face does not influence performance.

We confirmed that using a standard set of MI stimuli is appropriate in a second experiment where we compared how well *P. fuscatus* from PA and MI learn to discriminate faces of conspecifics from both PA and MI populations. Comparing learning of local and non-local signal phenotypes is important because some taxa learn local signals more accurately than non-local signals (Beecher et al. 1994; Slabbekoorn and Smith 2002a). If wasps learn *P. fuscatus* faces from all populations with similar accuracy, it indicates that using a standard set of wasp face images to train wasps from all treatment groups provides a comparable measure of individual face learning capacity. To collect these data, additional wasps from PA and MI were trained to differentiate pairs of PA face stimuli. Wasps used during this test were raised in groups of four individuals from their population and trained when they were 7–10 days old. Six different PA wasp faces were used as stimuli. *P. fuscatus* from PA have less variable facial patterns than *P. fuscatus* from MI (Tibbetts, Ortiz, et al. 2021). However, there is still some variation in PA wasp faces. For training, we chose six PA faces that differed to ensure wasps could differentiate the stimuli. Training and testing methods were identical to our common garden methods.

Individual face learning across populations

We trained and tested wasps' ability to discriminate between a neutral face stimulus and a negative face stimulus (Tibbetts, Ortiz, et al. 2021). Previous work has shown that the ability to learn and remember individual faces during training is linked with individual recognition capacity. Within and between species, wasps that are capable of individual recognition can learn and remember faces during training, while wasps that are not capable of individual recognition are unable to learn and remember faces (Sheehan and Tibbetts 2011; Tibbetts, Pandit, et al. 2018; Tibbetts et al. 2019). For example, *P. metricus*, socially isolated *P. fuscatus* from MI, and *P. fuscatus* from central PA are not capable of individual recognition in social situations and are unable to learn to discriminate faces during training (Sheehan and Tibbetts 2011; Tibbetts et al. 2019; Tibbetts, Ortiz, et al. 2021). In contrast, *P. fuscatus* from MI and NY are capable of individual recognition and readily learn to discriminate faces (Sheehan and Tibbetts 2011; Tibbetts, Pandit, et al. 2018).

We trained wasps by placing them in a 2.5 cm × 4 cm wooden box, with a plexiglass top. Along each wall of the box, we placed identical images of a conspecific face. The chamber and wasp were placed on an electrified pad that delivered either 0.4 volts of electric shock or no shock to the wasp as she was viewing the conspecific face. Previous work has shown that training and testing is not harmful, as wasps behave normally and survive for months after training (Laub 2023). The chambers were less than a centimeter

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high so that wasps could not escape the electrical current. In half the trials, wasps were exposed to an incorrect face (CS+) while receiving a mild electric shock for 2 min. In half the trials, wasps were exposed to a correct face (CS−) while receiving no electric shock. The wasp received a 1-min break in a separate container between each trial. The sequence of one CS+ and one CS− trials was repeated five times per wasp, so wasps experienced five CS+ and five CS− trials in total. After training, the wasp was given a 45-min break in a separate container with water.

After training, we measured learning accuracy with a 10-trial test. In each trial, the wasp was able to walk toward the correct (CS−) or incorrect (CS+) image. Between each trial, wasps rested for 1 min in a separate container. Performance was measured as the number of correct choices over 10 trials.

Testing occurred in a wooden chamber that was 9.5 cm × 3 cm long, with plexiglass on top. One end of the rectangle displayed the correct stimulus (CS−) while the other end of the rectangle displayed the incorrect stimulus (CS+). The entire chamber was electrified except for the 2.25 cm section closest to the correct stimulus to ensure that the learned associations from the training were not extinguished during testing. The rectangle was divided by two clear partitions. Wasps were placed in between the two partitions at the beginning of each testing trial. Then, the partitions were removed simultaneously to allow the wasp to walk to either side. We considered a wasp to have made a choice when their head and thorax crossed into one of the formerly partitioned areas. The 2.25 cm closest to the correct stimulus was a non-shocking "safety zone" and the rest of the rectangle was electrified. Scoring was done before wasps reached the "safety" zone in order to ensure that their choices were based in the learned stimuli, and not localized reactions to the presence or absence of a shock. After the wasp made a choice, she was removed from the chamber and placed into a dark container for 1 min. This was repeated 10 times. The correct and incorrect choices were randomly placed on either the left or right side of the pad each time to ensure wasps made choices based on stimuli rather than location.

Statistical analysis

Statistical analyses were performed in SPSS v.28 (data in supplementary material). We tested how rearing environment and population of origin influenced individual face learning using a mixed linear model. The dependent variable was number of correct choices (out of 10). The independent variables were rearing environment (categorical: with their own population or a common garden with both populations), population of origin (categorical: Michigan or Pennsylvania), and the two-way interaction between rearing environment and population. Specific rearing group was included as a random effect in the model. Wasps were collected from 39 total nests (19 MI and 20 PA. As wasps were collected and behaviorally tested over two field seasons (2019 and 2020). Year and nest ID were initially included as random effects. However, they did not explain any variation, so were not included in the final models. Because there was a significant interaction, we subsequently split the data to compare learning within groups. We ran separate mixed linear models within only wasps from PA and only wasps from MI to test how the number of correct choices differed across rearing environments. In a second analysis, we tested how individual face learning was influenced by population of origin (categorical, Michigan or Pennsylvania), stimuli type (categorical, Michigan face pictures or Pennsylvania face pictures), and the two-way interaction between population of origin and stimuli type. Nest of origin was included as a random effect in the model. This analysis included 22 MI wasps trained to MI faces, 13 MI wasps trained to PA faces, 13 PA wasps trained to PA faces, 14 PA wasps trained to MI faces. Wasps were from 36 nests. We used binomial tests to assess how performance in each treatment group and stimuli differed from the 50:50 random expectation. The binomial test provides an exact test of whether the number of correct vs incorrect choices differs from the 50:50 random expectation. Binomial tests provide *P*-values with no test statistics.

RESULTS

Individual face learning was influenced by the two-way interaction between population of origin and rearing environment (Est = −2.8, SE = 0.55, $F_{1,47} = 24.7$, $P < 0.001$), population of origin alone (Est = 2.9, SE = 0.47, $F_{1,47} = 31.8$, $P < 0.001$), but not rearing environment alone (Est 1.2, SE = 0.42, $F_{1,24} = 0.29$, $P = 0.59$). The significant interaction indicates that being raised in a group with wasps from both populations has different effects on individual face learning in wasps from MI and PA.

We followed up on the interaction by splitting the data by population and comparing how learning differed in PA and MI wasps reared with their own population vs reared in the common garden. The results show that rearing in a common garden had opposite effects on individual face learning in the two populations (Figure 2). Wasps from PA had higher individual face learning when reared in the common garden than when reared with individuals from their own population ($F_{1,12} = 8.5$, $P = 0.013$). In contrast, wasps from MI had lower individual face learning when reared in the common garden than when reared with individuals from their own population ($F_{1,17} = 15.8$, $P < 0.001$). Notably, MI and PA wasps had similar face learning accuracy when reared in the common garden ($F_{1,43} = 0.47$, $P = 0.49$). Binomial tests show that MI wasps reared with MI wasps ($P < 0.001$), MI wasps raised in the common garden ($P < 0.001$), and PA wasps raised in the common garden ($P < 0.001$) learned to discriminate between the faces, as they chose the correct face significantly more often than chance. However, PA wasps raised with PA wasps did not learn to discriminate between wasp faces ($P = 0.94$).

We tested whether the specific face stimuli used during training influenced individual face learning performance in a second set of experiments where wasps from both populations were trained to differentiate wasp face images from both populations. Individual face learning was influenced by the wasps' population of origin (Est = 2.1, SE = 0.53, $F_{1,18} = 54.2$, $P < 0.001$). However, individual face learning did not differ between wasps trained to differentiate Michigan faces and those trained to differentiate Pennsylvania faces (Est = −0.66, SE = 0.48, $F_{28} = 0.57$, $P = 0.46$). Further, individual face learning was not influenced by the interaction between the population of origin and type of face stimulus (Est = 0.81, SE = 0.68, $F_{1,28} = 1.4$, $P = 0.24$) (Figure 3). The lack of a significant interaction between population of origin and face stimuli is important because it shows wasps from MI and PA have equal capacity to learn PA and MI faces. We also split the data by population and found that PA wasps performed similarly on MI and PA faces ($F_{1,26} = 2.6$, $P = 0.12$), as they were unable to learn faces from either population. MI wasps learned MI and PA faces with similar accuracy ($F_{33} = 0.43$, $P = 0.62$).

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DISCUSSION

Our results show that differences in individual face learning between MI and PA populations of *P. fuscatus* are driven by plasticity. Wasps from MI are typically more adept at individual face learning than wasps from PA (Figure 2, Tibbetts, Ortiz, et al. 2021). However, when MI and PA wasps are reared in a common garden, they show similar individual face learning (Figure 2). Notably, rearing in a common garden has opposite effects on face learning of MI and PA wasps. Wasps from MI learn faces less accurately when reared in a common garden, while wasps from PA learn faces more accurately when reared in a common garden. These results are particularly notable because they indicate that wasps from PA may have unexpressed potential for individual face recognition. Overall, individual face learning is highly plastic and responsive to the social environment.

Two factors could cause the difference in face learning when wasps are reared in the common garden: exposure to variable facial patterns and social behavior. First, increased exposure to variable conspecific facial patterns may improve individual face learning. Having unique, easily identifiable facial patterns is beneficial among MI *P. fuscatus* (Sheehan and Tibbetts 2009), but not among PA *P. fuscatus* (Weise et al. in review), leading to greater facial pattern variation in MI than PA (Tibbetts, Ortiz, et al. 2021). Many wasps from PA have entirely black faces with no yellow or brown facial markings. This phenotype does occur in MI, but is relatively rare. As a result, wasps reared in the MI treatment group experience the highest facial pattern variation and are also the most adept at individual face learning. Wasps reared in the common garden treatment group experience intermediate facial pattern variation and also show intermediate individual face learning. Wasps reared in the PA treatment group experience the lowest facial pattern variation and have the lowest individual face learning. Previous work in other systems has shown that animals improve their ability to perceive and learn stimuli when they encounter stimuli more frequently ("perceptual learning") (Watanabe et al. 2001). As a result, exposure to stimuli, like variable facial patterns, may often increase an animal's ability to learn and remember that stimuli (Seitz and Watanabe 2005). Across many contexts, increased variability makes initial learning more challenging, but eventually leads to more general and robust performance (Raviv et al. 2022). Previous work in paper wasps has also shown that exposure to variable facial patterns facilitates the development of individual face learning in both MI populations of *P. fuscatus* (Pardo-Sanchez et al. 2022) and congeners *P. dominula* and *P. metricus* (Tibbetts, Pandit, and Nondorf 2018; Tibbetts et al. 2019). Therefore, exposure to variable facial patterns may play a key role in the different capacity for individual face learning across treatment groups. Future work where facial pattern variation is experimentally altered in both populations would be useful to test how exposure to variable facial patterns alone influences population differences in behavior.

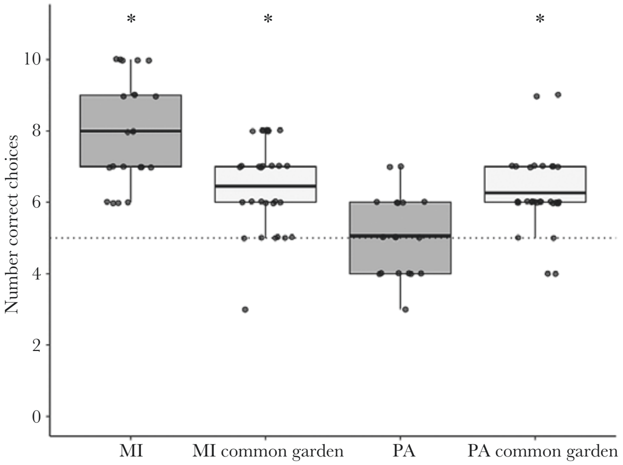

Figure 2
Individual face learning scores (out of 10) of MI wasps reared with MI wasps, MI wasps reared in a common garden with both MI and PA wasps, PA wasps reared with PA wasps, and PA wasps reared in a common garden with both MI and PA wasps. When reared with their own population, MI wasps are more adept at individual face learning than PA wasps. However, MI and PA wasps have similar individual face learning when reared in a common garden. Boxplots represent first quartile, mean, and third quartile. The dashed line reflects the 50:50 random expectation. * indicate wasps chose the correct face significantly more often than expected by chance.

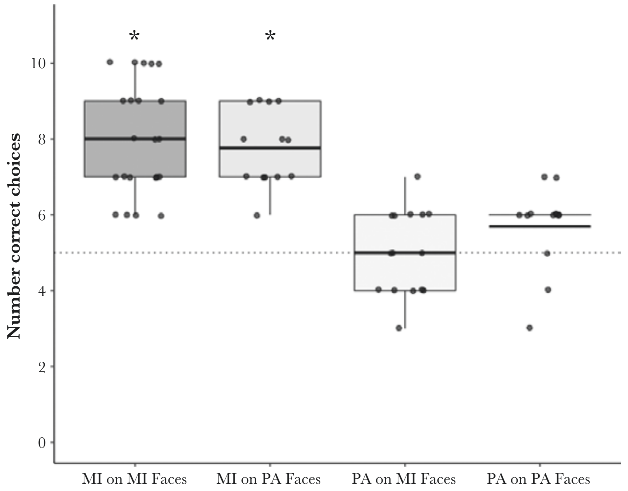

Figure 3
Individual face learning scores (out of 10) in wasps from MI and PA trained to discriminate conspecific face images from MI and PA populations. Face learning was influenced by the wasps' population of origin, but not whether the wasps were trained to differentiate MI or PA face stimuli Box shows lower quartile, mean, and upper quartile. The dashed line reflects the 50:50 random expectation. * indicate wasps chose the correct face significantly more often than expected by chance.

A second mechanism by which the rearing environment could influence individual face learning is through differences in social behavior between treatment groups. Previous work has shown that MI *P. fuscatus* use individual recognition to mediate social interactions both on and off nests (Tibbetts 2002; Sheehan and Tibbetts 2008; Tibbetts et al. 2020), while PA *P. fuscatus* do not (Tibbetts, Ortiz, et al. 2021). As a result, there may be subtle differences in aggressive and affiliative behavior between treatment groups. For example, wasps reared in groups with more MI wasps may receive greater benefits from directing aggressive and affiliative behavior toward individuals with particular color patterns (Sheehan and Tibbetts 2009), while wasps in groups with more PA wasps may not. Much research has shown that lack of social experience has lasting adverse effects on physical and behavioral development (Cacioppo et al. 2015), including the ability to assess, discriminate, and respond to social signals (Arnold and Taborsky 2010; Bailey and Moore 2018;

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Westwick and Rittschof 2021). For example, female crickets that were socially isolated during development were less choosy about mates compared to females reared with conspecifics (Judge, 2010). Mice reared in isolation use different patterns of ultrasonic vocalizations during male–male contests than mice with typical social experience (Keesom et al. 2017). More subtle differences in the social environment may not always have strong developmental effects. For example, socially isolated bumblebees develop differently than bees reared on their natal colony, while bees reared in small groups developed similarly to colony bees (Wang et al. 2022). Differences in social interactions during development could influence wasps' capacity for individual face learning. In general, future work that quantifies differences in social behavior between wasps from different populations will be useful to assess the role that social interactions play in the capacity for individual face learning.

We were initially surprised find strong plasticity in individual face learning because previous work has shown that individual face learning involves specific adaptations by both receivers and senders. In MI *P. fuscatus*, receivers have adaptations that facilitate accurate signal discrimination, learning and memory (Sheehan and Tibbetts 2011; Sheehan et al. 2014; Tibbetts et al. 2019). These include sensory adaptations that facilitate signal perception, including larger eye facets (Sheehan et al. 2014). MI *P. fuscatus* also use specialized cognitive mechanisms to identify conspecifics that are thought to facilitate rapid and accurate face recognition (Tibbetts, Pardo-Sanchez, et al. 2021). Future work will be important to assess how rearing environment influences the broad range of sensory, cognitive, and social adaptations involved in individual recognition. Thus far, our results suggest that plasticity may play a key role in the development of behaviors involved in individual recognition.

This study did not directly test how rearing environment influences the development of variable facial patterns that signal individual identity. Facial patterns develop during the pupal period and we altered the wasps' environment after pupation. Further, previous work has shown that the variable facial patterns that signal individual identity in *P. fuscatus* are highly heritable (Sheehan et al. 2017). Therefore, geographic differences in individual identity signals are likely due to local genetic adaptation rather than plastic responses to the environment. PA wasps may have less variable facial patterns than MI wasps because there may be less of a benefit associated with having unique, easily recognized color patterns in PA. MI nest-founding queens with unique facial patterns benefit because they are more easily recognized than wasps with a common appearance (Sheehan and Tibbetts 2009). However, PA *P. fuscatus* are known to be less cooperative than MI *P. fuscatus* (PA mean 1.2 foundresses per nest, MI mean 2.0 foundresses per nest). Reduced cooperation may reduce or eliminate the benefits associated with having unique facial patterns. As a result, the PA population may have lost or never gained individual identity signals.

A second result from this study is that *P. fuscatus* are equally adept at learning to discriminate the faces of conspecifics from their own population and from a different population. Some previous work has shown that recognition within a population is more effective than recognition between populations. For example, human face recognition improves with experience, so individuals are typically better at differentiating faces from their own population than faces from a different population (Tanaka et al. 2004). Similarly, many birds respond more strongly to songs with the local dialect than to songs from a distant dialect (Baker et al. 1981; Slabbekoorn and Smith 2002b). In contrast, MI and PA *P. fuscatus* learned to discriminate MI and PA facial features with consistent accuracy within their respective populations (Figure 3). One explanation is that there are relatively minor differences in PA and MI facial patterns. Wasps from PA have less variable facial patterns than wasps from MI, but many of the same facial types occur in both populations.

Overall, this study is the first to examine the developmental mechanisms that underlie geographic variation in individual recognition. Much previous work has explored geographic variation in sexual signals and preference, finding that there is typically a strong link between signals and receiver responses even when both traits vary geographically (Fowler-Finn and Rodríguez 2016). The link between sexual signals and receiver responses is maintained by both plasticity and genetic covariance between signal and receiver response (Greenfield and Rodriguez 2004). Theory predicts no genetic covariance between signal and receiver response in non-sexual signaling systems like individual recognition. Consistent with this theoretical expectation, we find that plasticity mediates the geographic differences *in P. fuscatus* individual recognition between MI and PA populations. Developmental plasticity in receiver responses allows individuals to rapidly adjust their phenotype based on their partner's phenotype (Agrawal 2001; Tibbetts and Snell-Rood 2021). Therefore, plasticity in receiver responses may be a common mechanism mediating geographic differences in non-sexual signaling systems and may often play a role in maintaining links between signals and receiver responses.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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AUTHOR CONTRIBUTIONS

Meagan Simons (Conceptualization [Supporting], Data curation [Equal], Formal analysis [Equal], Investigation [Equal], Methodology [Equal], Visualization [Lead], Writing – original draft [Equal]), Delbert (Andre) Green (Project administration [Supporting], Supervision [Equal], Writing – review & editing [Equal]), and Elizabeth Tibbetts (Conceptualization [Lead], Formal analysis [Equal], Funding acquisition [Lead], Methodology [Equal], Project administration [Equal], Writing – review & editing [Lead])

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Simons, Green, and Tibbetts (2024) and in the supplemental material.

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