Developmental plasticity and the origin of novel communication systems: individual recognition in *Polistes* wasps

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Abstract

Although developmental plasticity facilitates the evolutionary origin of many traits, the role of plasticity in the origin of novel communication systems has received little attention. If plasticity mediates the origin of new communication systems, exposure to a novel environment will induce new traits that could function as signals or receiver responses. Here, we test whether plasticity facilitates the origin of individual recognition. We reared a species of paper wasp that naturally lacks individual recognition (*Polistes metricus*) with a relative that has facial patterns that signal individual identity (*Polistes fuscatus*). We found *P. metricus* reared with individual identity signals learned unique wasp faces significantly more accurately than *P. metricus* reared without individual identity signals. However, exposure to individual identity signals was not sufficient to induce individual recognition in social contexts. These results suggest that if variable facial patterns arose in *P. metricus*, wasps would immediately improve their ability learn variable facial patterns, thereby facilitating the origin of individual face recognition. Improved learning is an initial step toward individual recognition that would need to be refined by selection to produce an established signaling system. Developmental plasticity may be an underappreciated factor facilitating the evolutionary origin of novel recognition systems.

Introduction

The origin of novel traits is a key issue in evolutionary biology. Many novel traits are thought to arise either as byproducts or via developmental plasticity (West-Eberhard 1989; Moczek 2008; Moczek et al. 2011; Laland et al. 2015). The 'novelty as a byproduct' hypothesis proposes that novel features originated for reasons unrelated to their current function, then a new selective environment shaped and elaborated the traits. For example, feathers were originally involved in temperature regulation, water repellency, and communication before being coopted for flight (Prum 1999). The 'novelty through developmental plasticity' hypothesis proposes that a new environment induces novel phenotypes that are later genetically assimilated via selection (West-Eberhard 2003; Pigliucci et al. 2006). The classic example of developmental plasticity rapidly producing novel phenotypes is Waddington's work on *Drosophila* wing evolution. When raised at high temperatures, *Drosophila* express a new wing vein phenotype. The novel wing veins are initially induced by temperature stress, but rapidly became genetically assimilated under selection such that all flies expressed the new phenotype across environments (Waddington 1953). Both byproduct and plasticity hypotheses pertain to the evolutionary origin of traits rather than the mechanisms that currently influence trait development. The key difference between the byproduct and plasticity hypotheses is that the byproduct hypothesis focuses on traits that are expressed in the current environment, while the developmental plasticity hypothesis focuses on traits that are initially only expressed in novel environments.

Previous work on the evolutionary origin of communication has focused on the 'novelty as a byproduct' hypothesis (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). New communication systems can arise when traits that are neutral or functional in a different context become signals or influence receiver responses. From the signaler's perspective, preexisting traits can be modified to act as signals, though the traits may be constrained by their original function (West-Eberhard 1989). For example, nests originated to hold eggs, but, in some species, this initial function has been modified such that nests also function as condition dependent indicators of male quality (Barber et al. 2001). From the receiver's perspective, preexisting receiver responses, like sensory bias, can facilitate the origin of communication systems (Endler and Basolo 1998; Kokko et al. 2003; Borgia 2006). For example, females may have a preexisting preference for the color red as a byproduct of the sensory system. If females benefit by mating with redder mates, the initial preference for red may be refined and lead to an established sexually selected system.

Developmental plasticity could also contribute to the origin of novel communication systems, though this hypothesis has received little attention. If developmental plasticity facilitates the evolutionary origin of communication systems, we predict animals will respond to a new environment by developing novel traits that could function as signals or receiver responses. These traits are predicted to be absent in the current environment. As with the byproduct hypothesis, signals and receiver response induced by the novel environment need not be as sophisticated as traits in an established communication system. Instead, the novel environment exposes traits that are subsequently refined by selection.

Developmental plasticity can produce many different phenotypes, some of which will facilitate the origin of new signals and some of which will not. For example, the origin of quality signals may be facilitated by plasticity that causes a preference for extreme phenotypes but not by plasticity that increases social affiliation with common phenotypes. The specific type of developmental plasticity that will facilitate the origin of new signals depends on the information the signal conveys because signals that convey different information have different signaler phenotypes and receiver responses (Tibbetts et al. 2017). For example, quality signaling involves highly condition-dependent ornaments and receiver preferences for extreme phenotypes (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). As a result, the evolutionary origin of quality signals could be facilitated if a novel rearing environment induces the development of elaborate, condition-dependent traits or receiver preferences for particular phenotypes. In contrast, individual identity signaling requires signalers with highly variable, multi-modal phenotypes and receivers that can learn and remember these phenotypes (Tibbetts and Dale 2007). As a result, the evolutionary origin of individual identity signals could be facilitated if a novel environment causes signalers to develop highly variable phenotypes or improves receiver ability to learn and remember conspecifics.

Here, we test whether developmental plasticity could play a role in the evolutionary origin of individual recognition. We specifically test whether rearing wasps with individual identity signals influences receiver capacity to learn unique individuals. Individual recognition is a type of communication where receivers discriminate a signaler from other individuals based on the signaler's unique characteristics, associate the unique characteristics with individual-specific information about the signaler, and recall the information during subsequent encounters (Cely and Tibbetts 2019). Effective individual recognition requires receivers that can learn the unique features of conspecifics and recall that information during subsequent interactions (Tibbetts and Dale 2007). Therefore, we test whether wasps given experience with individual identity signals are better able to learn other wasps than wasps given no experience with individual identity signals.

Polistes wasps provide a good model for studying the origin of individual recognition because there are multiple closely related *Polistes* that differ in their capacity for individual recognition. *Polistes fuscatus* have variable facial patterns that signal individual identity (Fig. 1, (Tibbetts 2002). Wasps learn the unique facial patterns of conspecifics during social interactions, then recall this information during subsequent encounters. Individual recognition is beneficial in *P. fuscatus* because it reduces conflict and stabilizes social interactions in groups of cooperating queens (Tibbetts 2004; Sheehan and Tibbetts 2009). In contrast, a closely related species, *Polistes metricus*, lack individual recognition (Sheehan and Tibbetts 2010). *P. metricus* lack the type of variable facial patterns required for visual individual recognition (Fig. 1) and are unable to learn unique faces during training or social interactions (Sheehan and Tibbetts 2010, 2011). There is likely no social benefit associated with individual recognition in *P. metricus* because queens typically found nests alone rather than cooperating with other queens (Tibbetts 2004).

We test if a novel rearing environment influences how well *P. metricus* learn and remember the unique facial patterns of other wasps. Specifically, we take a species that is normally unable to learn and remember individual wasps (*P. metricus*), and rear them with wasps that have variable signals of individual identity (*P. fuscatus*). We test whether rearing *P. metricus* with individual identity signals influences their ability to learn and remember unique individuals in two contexts:

during training and during social interactions. If exposure to individual identity signals induces receiver capacity for learning unique individuals during training, we predict *P. metricus* reared with *P. fuscatus* will learn *P. fuscatus* faces better than *P. metricus* reared with conspecifics. If exposure to individual identity signals induces individual recognition in social situations, we predict *P. metricus* reared with *P. fuscatus* will be capable of learning and remembering unique individuals during social interactions. Specifically, *P. metricus* reared with *P. fuscatus* will be less aggressive and have more non-aggressive contacts when interacting with familiar wasps than when interacting with unfamiliar wasps.

Methods

Wasp nests used in these experiments were collected from areas surrounding Ann Arbor, Michigan in late June, just prior to worker emergence. After collection, wasps and their nests were housed in the lab and given access to water, rock candy, and *ad lib Galleria mellonella* caterpillars. All wasps used in these experiments were workers that eclosed before males. Females that emerge after males are potential reproductives and were not used in these experiments.

Nests were checked daily for newly eclosed adults. At eclosion, wasps were uniquely marked and placed in one of three treatments. 1) Inexperienced with individual identity signals, housed with nestmates: *P. metricus* were marked, then returned to their natal nest to live with their nestmates. *P. metricus* naturally lack individual identity signals (Sheehan and Tibbetts 2010), so *P. metricus* that live with nestmates have social experience but no experience with identity signals. 2) Inexperienced with individual identity signals, housed with non-nestmates: *P. metricus* were marked and placed with 2 *P. metricus* from different nests in a new container with an orphaned nest. These *P. metricus* lack experience with individual identity signals just like treatment 1. Their adult social experience is similar to treatment 3 because they are housed with 2 non-nestmate adults on an orphaned nest. 3) Experienced with individual identity signals: *P. metricus* were marked and placed with 2 *P. fuscatus* in a new container with an orphaned nest. *P. fuscatus* have variable facial patterns that function as individual identity signals, so the experienced *P. metricus* were exposed to individual identity signals for their entire adult life. Wasps remained in their treatment for at least 5 days before being used in experiments.

Training

P. metricus were trained to differentiate between pairs of *P. fuscatus* face images using established methods (DesJardins and Tibbetts 2018). 18 *P. metricus* inexperienced with individual identity signals housed with nestmates (treatment 1), 18 *P. metricus* inexperienced with individual identity signals housed with non-nestmates (treatment 2), and 26 *P. metricus* experienced with individual identity signals (treatment 3). were trained to discriminate wasp face images. Face images used for training were photographs of *P. fuscatus* from Michigan, USA that showed the face and antenna. Wasps were trained on one of three unique pairs of face stimuli (Suppl Fig. 1). All images were printed at life size using a commercially available Sony Picture Station photo printer.

During training, wasps were placed in a 2.5 x 4 x 0.7 cm wood and plexiglass box with six identical faces glued to the inside walls. In half the bouts, the focal wasp was placed in a box with negative stimuli and received a mild electric shock from an electrified pad for two minutes. The electrified pad was made of anti-static conductive foam electrified by two copper wires connected to a Variac transformer. In the other half the bouts, the wasp was placed in a similarly sized box with neutral faces and the pad was not electrified for two minutes. Between each bout, the wasp was given a one minute break in a holding container. For example, a wasp trained to discriminate between face A and B would experience the following training. First, the wasp was placed with face A and received a shock for two minutes. The wasp was removed and given a 1 minute break. Then, the wasp was placed with face B and did not receive a shock for two minutes. The wasp was removed and given a 1 minute break. This process was repeated 5 times per wasp, so wasps saw face A and B 5 times each.

After training, the wasp was given a 45 minute break in a holding container with food and water. Then, learning was tested by measuring whether the wasp approached the neutral or negative stimuli over 10 trials. Testing occurred in a 3 x 10 x 0.7cm rectangle. One end of the rectangle had neutral stimuli and the other end of the rectangle had the negative stimuli. The entire floor of the rectangle was electrified except the 2.25cm closest to the neutral stimuli, the ‘safety zone’. Most of the rectangle was electrified because shock motivates wasps to move. The neutral stimuli was associated with safety to ensure learned preferences from the initial training were not extinguished during the 10 trial test. Receiving a shock while choosing a preferred stimuli can rapidly extinguish learned preferences.

The center of the rectangle had two removable, clear partitions that confined the wasp. At the beginning of each trial, the wasp was placed in the center of the rectangle between the clear partitions, the electric shock was turned on for five seconds, both partitions were removed simultaneously, and the wasp was free to walk through the rectangle. Wasps who learned typically turned toward the neutral stimuli while confined in the center of the rectangle. When the partitions were removed, the wasp quickly walked toward the neutral stimuli. A wasp was scored as making a choice when its head and thorax move beyond the partition placed 2.5cm from each end of the rectangle. After a wasp made a choice, it was removed from the rectangle and given a one minute break in a holding container. The placement of the neutral and negative stimuli (right or left side) was determined randomly and changed between trials. This ensures that wasps did not associate a particular direction with correct choices. The particular face images that were neutral vs. negative was also swapped across wasps.

Statistical analyses were performed in SPSS v. 24. We measure learning as the total number of correct choices. We tested whether wasps learned by comparing the number of correct choices vs. incorrect choices to the 50:50 random expectation with a binomial test. The binomial test provides an exact test of whether the distribution of two groups differs from the theoretically expected distribution. We tested whether rearing environment influenced how well *P. metricus* learned faces by comparing the number of correct choices in the three developmental environments with a mixed linear model. Adult housing group was included as a random effect in the model to address any potential similarity in learning within wasps housed in the same group. LSD posthoc tests were used for posthoc pairwise comparisons between the three treatments. A total of 62 wasps were trained from 31 nests (26 experienced with individual identity signals, 18 inexperienced with individual identity signals housed with nestmates, and 18 inexperienced with individual identity signals housed with non-nestmates).

Social individual recognition

We assessed the social recognition abilities of *P. metricus* reared with *P. fuscatus* by staging contests between pairs of wasps with and without a prior history of social interactions. This study used the same sample size and methods used previously to test individual recognition in a range of social insects, including *Polistes fuscatus* (Tibbetts 2004; D'Ettorre and Heinze 2005; Injaian and Tibbetts 2014; Souza et al. 2017) and to show that *Polistes metricus* naturally lack individual recognition (Sheehan and Tibbetts 2010).

In each trial, a *P. metricus* reared with *P. fuscatus* was paired with a *P. fuscatus* who was reared with 1 *P. fuscatus* and 1 *P. metricus*. *P. metricus* were paired with *P. fuscatus* to ensure their social partner had the type of variable facial patterns required for visual individual recognition. Paired wasps had not encountered each other prior to the trials.

All wasps used in the social individual recognition experiment were removed from their natal nest at eclosion and placed in the 'Experienced with individual identity signals group'. For this treatment group, one *P. metricus* was marked and placed with 2 *P. fuscatus* in a new container with an orphaned nest. 30 of the 78 *P. fuscatus* used in this experiment were from the interspecific groups created for the training experiment described above. The other *P. fuscatus* and all 26 of the *P. metricus* were from interspecific groups created only for the social recognition experiment.

During the contests, we scored the occurrence and intensity of aggressive interactions as well as displays of nonaggressive behavior. On the first day (day 0), we placed a *P. metricus* reared with *P. fuscatus* with an unfamiliar *P. fuscatus* in a small plexiglass container (8 × 8 cm). After filming, the wasps were housed together until the next day (day 1), at which point they were separated and returned to their initial 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 consequence of recognition and not a change in behavior or motivation over time, we paired the wasps with other unknown social partners on the day before and after (days 1 and 3). The first half hour of all interactions was videotaped for later analysis of behavior. 26 sets of trials were performed.

Start date was staggered across trials to ensure that differences in behavior across days were caused by experimental treatment rather than day-specific effects (e.g. any slight differences in temperature, humidity across days). For example, on a particular date, some focal wasps experienced the day 0 treatment, while others experienced the day 3 treatment.

Behavior in all videos was scored by a research assistant who was blind to experimental predictions and treatment. Cooperative and aggressive behaviors were ranked as follows: (0) nonaggressive bodily contact (partners within one body length of each other, but no darts, bites, grapples or mounts occurred); (1) dart (rapid body movement towards partner); (2) dart with open mandibles (rapid body movement towards partner with open mandibles); (3) bite (mandibles closing on body of partner); (4) grapple/mount (wrestling/bodily contact that forces partner to accept submissive positioning). For each trial, we summed the ranks of cooperative and aggressive behaviors. We then divided the sum by the number of total interactions per tape to calculate an aggression index (Dreier et al. 2007). The aggression index standardized behavior by taking into account the number and intensity of interactions of each pair, which allowed behavior to be compared across trials. The aggression index has been used to measure individual recognition behavior in multiple studies (Dreier et al. 2007; Sheehan and Tibbetts 2008; Sheehan and Tibbetts 2010; Injaian and Tibbetts 2015). If the wasps are able to recognize and remember social partners, they should be less aggressive and have more non-aggressive contacts when they interact with a known individual (day 2) than when they interact with an individual they encounter for the first time (days 0,1,3).

Statistical analyses were performed in SPSS v. 24. Aggression index and number of non-aggressive contacts were compared across trials using Friedman's ANOVA using asymptotic estimation for the exact test. Friedman's ANOVA is a non-parametric test that is similar to the parametric repeated measures ANOVA. It tests whether there are differences in behavior across days 0, 1, 2, or 3. Posthoc pairwise analyses were not performed because the overall ANOVA found no significant differences in behavior across days. The aggression index or number of nonaggressive contacts were the dependent variables. A non-parametric analysis was used because the dependent variables were an index and non-normally distributed count data. We also analyzed the data using general linear models, a parametric analyss, for comprehensiveness (Supplemental material). The results of the parametric analysis do not differ from the non-parametric analysis. 26 trials were performed, with 4 contests per trial. The trials involved 26 *P. metricus* from 14 nests and 78 *P. fuscatus* from 33 nests.

Results

Experience with individual identity signals significantly influenced *P. metricus* face learning (Fig. 2, $F_{2,59}=5.1$, p=0.0092). *P. metricus* experienced with individual identity signals learned to discriminate between unique face images significantly more accurately than inexperienced *P. metricus* (Fig. 2, experienced vs inexperienced housed with nestmates p=0.041, experienced vs inexperienced housed with non-nestmates p=0.003). There was no difference in face learning between inexperienced *P. metricus* housed with nestmates vs non-nestmates (p=036). Experienced *P. metricus* also learned to discriminate faces significantly more accurately than expected by chance (p=0.004). However, inexperienced *P. metricus* who had not previously encountered individual identity signals did not learn to discriminate facial patterns, as they chose the correct face no more often than expected by chance (inexperienced, housed with nestmates p=0.82, inexperienced, housed with non-nestmates p=0.41).

Experienced *P. metricus* were not able to learn and remember unique wasps during social interactions. Aggressive and nonaggressive behaviors were not influenced by a previous history of social interactions. First, there was no difference in aggression between any days of the social recognition experiment (Fig. 3, $\chi 2_3=2.6$, p=0.45), indicating that new social partners and wasps who interacted previously were similarly aggressive. When the aggression initiated by each wasp was analyzed separately (SFig. 2), there was still no evidence that aggression differed between any days of the social recognition experiment. Experienced *P. metricus* directed a similar amount of aggression toward familiar and unfamiliar *P. fuscatu*s ($\chi 2_3=5.8$, p=0.12). *P. fuscatus* directed a similar amount of aggression toward familiar and unfamiliar *P. metricus* ($\chi 2_3=1.57$, p=0.67). Second, the number of non-aggressive contacts did not change over time (Fig. 3, $\chi 2_3=3.3$, p=0.54). Overall, there was no evidence that aggression or non-aggressive interactions differed between pairs of familiar and unfamiliar wasps. Parametric statistical analysis yielded similar results (Supplemental material). Therefore, *P. metricus* reared with *P. fuscatus* did not remember other unique individuals during social interactions.

Discussion

Our results indicate that plasticity may play a role in the evolutionary origin of individual recognition. Learning and remembering the unique features of conspecifics is the cornerstone of individual recognition (Tibbetts and Dale 2007). *P. metricus* typically lack individual recognition and are unable to learn the unique faces of other wasps during training (Sheehan and Tibbetts 2011) or social interactions (Sheehan and Tibbetts 2010). However, capacity for learning other wasps is induced when *P. metricus* are reared with wasps that have variable facial patterns that signal individual identity (this study). Therefore, the ability to learn the unique features of other wasps is developmentally plastic and can be induced by experience with individual identity signals. Learning unique facial patterns is an initial step toward individual recognition that would need to be refined and shaped by selection to produce an established social signaling system.

Although exposure to wasps with facial patterns that signal individual identity induced *P. metricus* face learning, exposure alone was not sufficient to produce individual recognition in social contexts. *P. metricus* do not naturally learn and remember individual conspecifics during social interactions (Sheehan and Tibbetts 2010). After experience with individual identity signals, *P. metricus* were still unable to learn and remember familiar individuals during social interactions (this study). Instead, wasps treated known and unknown individuals similarly. Learning and remembering individuals during social interactions is cognitively challenging (Seyfarth and Cheney 2015), so it is not entirely surprising that exposure to wasps with variable facial patterns is not sufficient to induce social individual recognition in *P. metricus*.

If experienced *P. metricus* can be trained to discriminate between unique wasp faces, why don't experienced *P. metricus* discriminate between individual wasps during social interactions? One possibility is that learning and remembering unique individuals in social contexts is more cognitively challenging than learning unique wasp face images during training, so experienced *P. metricus* lack the cognitive capacity for social individual recognition. Alternatively, experienced *P. metricus* may have the capacity to learn and remember individuals, but lack the motivation or attention to learn individuals. Wasps are motivated to learn faces during training because individuals that make incorrect choices receive an electric shock. There may be no similar reinforcement for learning other wasps during social interactions. Some of our previous work suggests *P. metricus* may pay attention to conspecific color patterns during social interactions (Sheehan et al. 2013). When *P. metricus* are placed in groups of conspecifics with experimentally increased facial variation, they treat individuals with unique faces differently than individuals with a common appearance. The slight difference in aggression toward unique individuals in a new environment could be another example of plastic behavioral response that provides a small, initial step toward individual recognition when the environment changes. However, *P. metricus* do not learn and remember unique individuals during social interactions (this study, (Sheehan and Tibbetts 2010), suggesting that individual recognition requires receiver adaptations beyond a general capacity to perceive and learn stimuli. Future research will be valuable to explore the receiver adaptations that facilitate social individual recognition in taxa with established signaling systems like *P. fuscatus*.

Plasticity in receiver response may resolve a major challenge associated with the origin of signals: the interdependence of signaler and receiver (Maynard Smith and Harper 2003; Searcy and Nowicki 2005). Effective communication depends on signalers having variable phenotypes that convey information to receivers and receivers attending to these phenotypes and respond appropriately. Either component alone is not effective, so the origin of new communication systems presents a causality dilemma (Scott-Phillips et al. 2012). The origin of new signaling systems is easier to understand if receiver behavior changes as soon as new signaler phenotypes arise. Consistent with this hypothesis, we found that receiver responses are flexible such that rearing wasps with individual identity signals immediately alters receiver capacity to learn and remember unique individuals. These results suggest that if variable facial patterns arise in *P. metricus*, wasps would immediately improve their ability learn variable facial patterns, thereby facilitating the origin of individual face recognition.

While little previous work has examined plasticity in individual recognition, much more is known about plasticity in quality signaling systems (Jennions and Petrie 1997; Rodríguez et al. 2013). Receiver responses to sexually selected ornaments are often influenced by the developmental environment (Bailey and Zuk 2008; Cornwallis and Uller 2010). For example, when female spiders are reared with males that have brown coloration, the females prefer to mate with brown males as adults (Hebets 2003). Signaler phenotypes also change in response to the developmental environment (Griffith and Sheldon 2001; Cotton et al. 2004). For example, juvenile male crickets exposed to conspecific songs during development are more likely to use song to attract females than juvenile crickets who are not exposed to conspecific songs during development (Bailey et al. 2010). Such plasticity in signaler phenotypes and receiver responses could play an important role in the origin of novel sexual signaling systems. For example, if female preference for male traits is induced by rearing with individuals that have a particular phenotype, the origin of a new ornament would immediately alter female preferences, thereby facilitating the origin of new sexual signaling system.

P. metricus naturally lack individual recognition because it provides little social benefit. Experimental and comparative work in *P. fuscatus* indicates that individual recognition is beneficial for *P. fuscatus* nest-founding queens because it reduces aggression and minimizes and cost of conflict in groups of cooperating queens (Tibbetts 2004; Sheehan and Tibbetts 2009). *P. metricus* typically found nests alone, so there is no need for individual recognition to manage social relationships among foundresses. While *P. metricus* do interact as workers, previous work indicates that individual recognition does not seem to play an important role in worker-worker interactions on queenright nests (Tibbetts et al. 2018).

One challenge of studying the origin of communication systems is that ancestral states are no longer available. *P. metricus* were used for this study because they lack individual recognition and are unlikely to have an evolutionary history of individual recognition. *P. fuscatus* are the only species with individual recognition in the *Polistes*. Further, although *P. metricus* and *P. fuscatus* are closely related, they are not sister taxa (Santos et al. 2015; Sheehan et al. 2015). Additional work on the plasticity of recognition in additional species will be useful to understand the scope of plasticity across the genus.

Overall, the results of this study indicate that receiver behavior is flexible and rapidly changes in response to novel signaler phenotypes. We found that exposure to individual identity signals immediately alters receiver behavior by improving *P. metricus*' ability to learn and remember wasp facial patterns. However, experience alone was not sufficient to induce social individual recognition, suggesting that plasticity is an initial step that would need to be refined by selection to produce a stable signaling system. Reconstructing the evolutionary origin of complex traits like communication systems is notoriously difficult. Our results suggest developmental plasticity may be an underappreciated factor facilitating the evolutionary origin of recognition systems. However, additional work across different types of signals and taxa will be useful to test the role of plasticity in the origin of novel communication systems.

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Figures

Fig. 1, Portraits illustrating facial variation in a) *P. fuscatus* and b) *P. metricus*

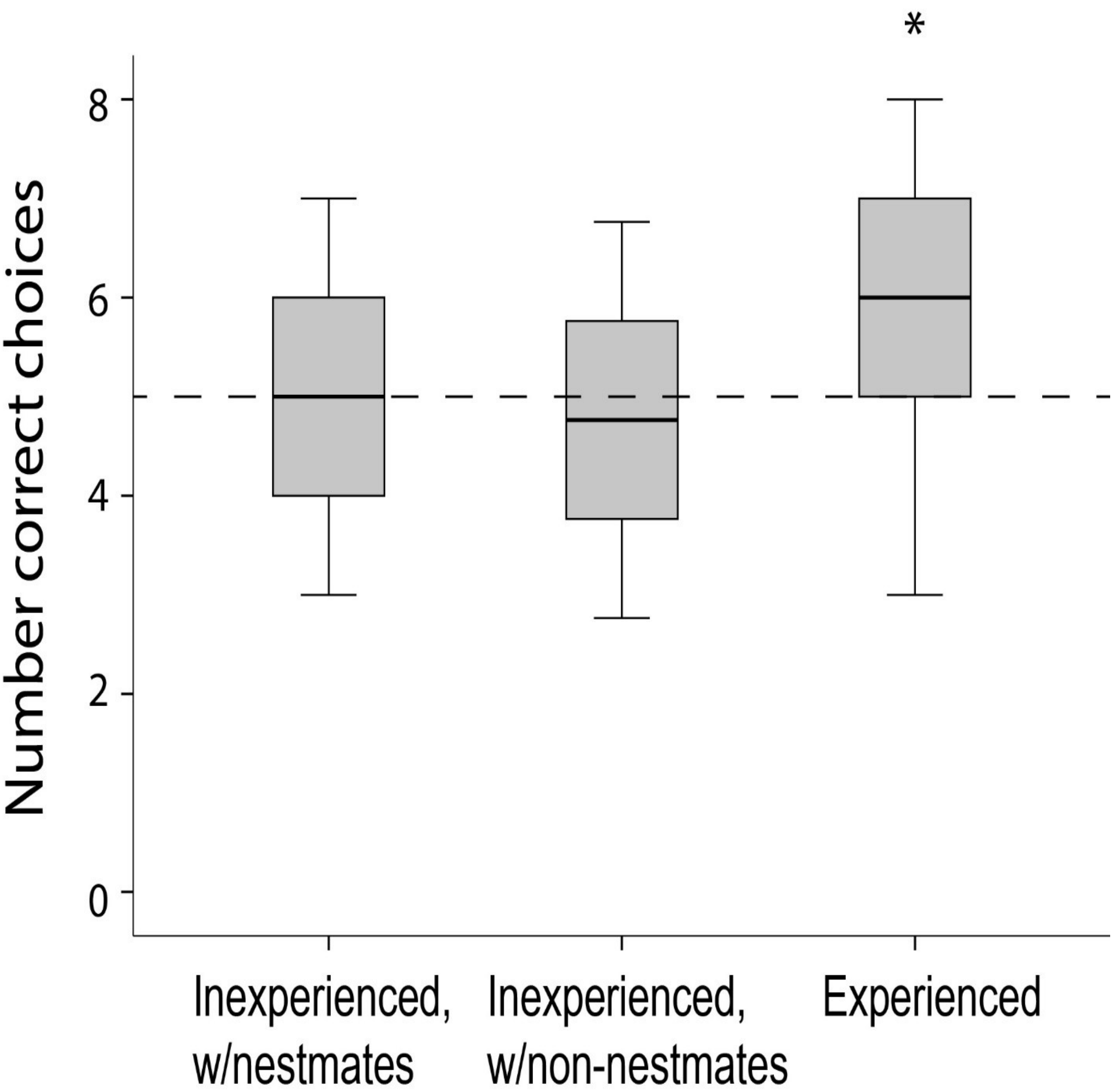
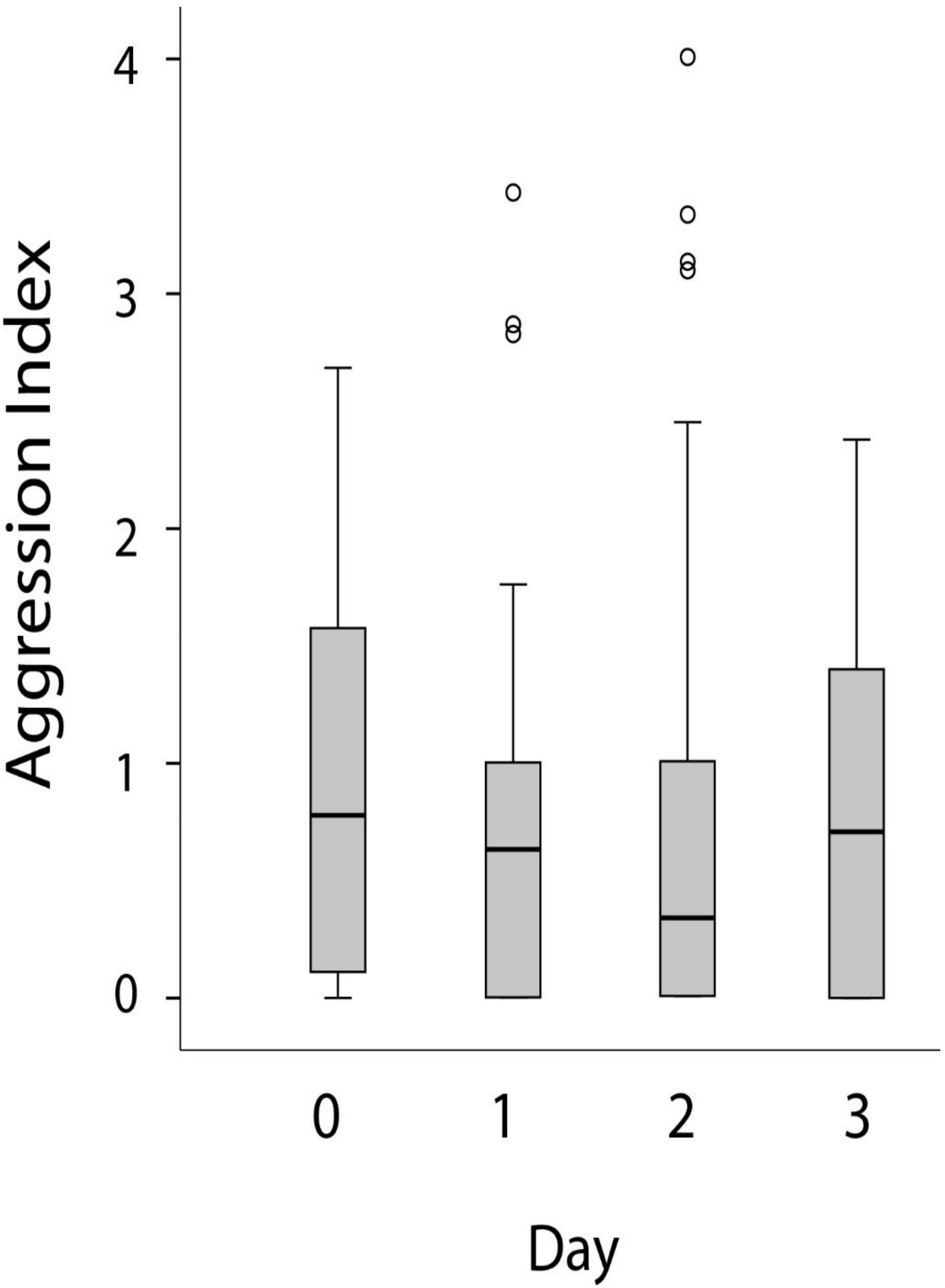


Fig. 2 Mean ± SE correct choices in *P. metricus* trained to discriminate pairs faces. Wasps were: 1) Inexperienced with individual identity signals, housed with nestmates (trmt 1), Inexperienced with individual identity signals, housed with non-nestmates (trmt 2), or Experienced with individual identity signals (trmt 3). * indicates wasps learned to discriminate face images, as they chose the correct image more often than expected by chance. Dotted line shows the 50:50 random expectation. The box reflects the first quartile, median, and third quartile. The whiskers denote minimum and maximum values.

(a)



(b)

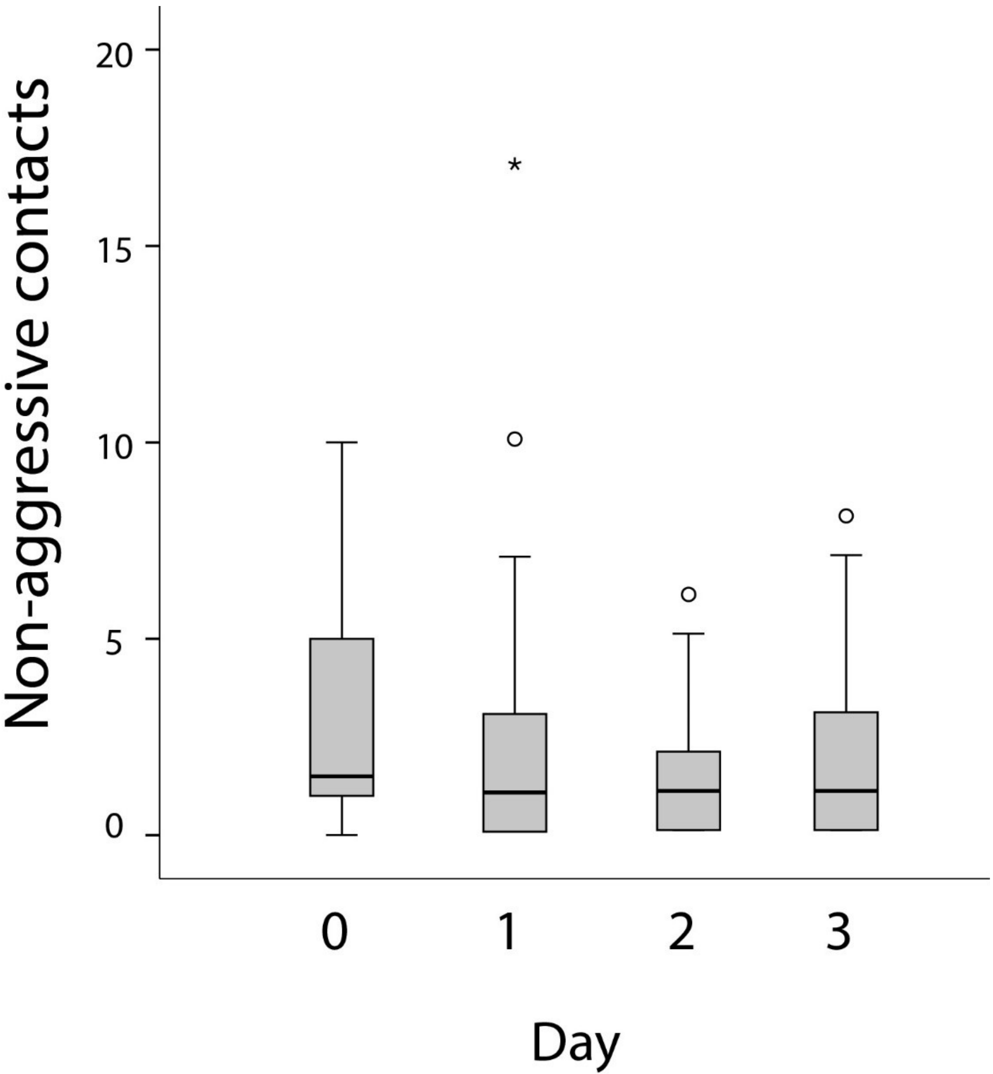


Figure 3. Mean ± SE (a) aggression index and (b) nonaggressive contacts per day. On days 0, 1 and 3, focal wasps interacted with individuals that they had not previously encountered. On day 2, wasps interacted with a previously encountered partner. There are no differences in behavior across days. The box reflects the first quartile, median, and third quartile. The whiskers denote minimum and maximum values. Outliers are represented by circles (<1.5× interquartile range) and asterisks (>3× interquartile range).