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Original Article

Geographic differences in individual recognition linked with social but not nonsocial cognition

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Cognition is a complex trait with multiple components that may vary independently or in concert. Thus far, we know little about how geographic differences in behavior are linked with different aspects of cognition. Behavioral differences could be linked with cognition in three ways: with multiple aspects of cognition, some but not other aspects of cognition, or no cognitive differences. Here, we compare cognitive performance in two populations of *Polistes fuscatus* wasps that differ in their capacity for individual face recognition. Individual recognition involves keeping track of multiple individual relationships and responding appropriately, so it is thought to increase social complexity. As a result, we predicted Michigan wasps that use individual recognition may have better cognitive performance than Pennsylvania wasps that are not able to individually recognize conspecifics. We find that Michigan wasps are more adept at individual face learning than Pennsylvania wasps. However, the populations perform similarly on other cognitive tasks, including color learning and memory, reversal learning, and odor learning and memory. Therefore, population differences in social behavior affect individual face learning, but are not linked with generalized differences in cognition. These findings suggest that socially complex societies may influence the evolution of social cognition specifically.

Keywords: associative learning; cognition; face recognition; geographic variation; long-term memory; social intelligence hypothesis.

Introduction

Cognition is the processes involved in learning, remembering, and using information. There are multiple aspects of cognition, including perception, learning, long-term memory, working memory, attention, and decision making (Dukas 2004; Shettleworth 2009). Cognitive processes play an important role in how animals interact with each other and their environment. For example, food-caching birds with better spatial learning and memory may have higher overwinter survival because they are better able to find and retrieve stored food (Welklin et al. 2024). There has been much interest in the evolution of cognition, particularly the selective pressures that shape cognition (Morand-Ferron et al. 2016; Pritchard et al. 2016) and whether these selective pressures lead to generalized differences in multiple aspects of cognition or specialized differences in one or a few aspects of cognition (Shaw and Schmelz 2017; Poirier et al. 2020).

Multiple selective pressures are thought to influence cognitive evolution (Dunbar 1998; Farris and Schulmeister 2010; Holekamp et al. 2015; DeCasien et al. 2017; Rosati 2017; Amodio et al. 2019), though most research has focused on ecological and social selective pressures. Some taxa live in ecologically complex environments where learning and remembering the location of nests or food is key to success. As a result, taxa with more ecologically complex behavior may have relatively larger brains or enhanced cognitive abilities compared to taxa with less ecologically complex behavior (ecological intelligence hypothesis; (Humphrey 1976; Milton 1981; Sol et al. 2005; MacLean et al. 2009; DeCasien et al. 2017). For example, frugivorous primates, who remember the location of specific fruit trees, score better on spatial memory assays than folivorous primates, who do not return to consistent foraging locations (Rosati et al. 2014). In other taxa, the challenge of learning individual identities and remembering individualized social relationships is thought to influence cognitive evolution (social intelligence hypothesis; (Jolly 1966; Chance and Mead 1988; Dunbar 1998, 2003; Seyfarth and Cheney 2015). Taxa that have socially complex groups, including individual recognition, large group sizes, fission-fusion dynamics, or dominance hierarchies, may outperform taxa with less complex social groups on cognitive assays (Bond et al. 2003; Sheehan and Tibbetts 2011). Detailed behavioral measures of cognition in a few species indicate that social cognition may be enhanced in species with more complex social behavior (Reader and Laland 2002).

Although it's clear that ecological and social selective pressures likely shape cognition, less is known about whether these selective pressures lead to generalized differences in multiple aspects of cognition or specialized differences in one or a few aspects of cognition (Fodor 1983; Cosmides and Tooby 1994). Under the specialization hypothesis, also termed "domain specific cognition," selective pressures influence a subset of similar cognitive abilities. For example, social benefits associated with the ability to learn and remember individual relationships with conspecifics (eg ability to direct aggressive and affiliative behavior appropriately) may influence social cognition, but not other aspects of cognition (Kanwisher 2000). Under the generalization hypothesis, also termed "domain general cognition," selective pressures influence a broader range of cognitive abilities (Fodor 1983). For

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example, social benefits associated with the ability to learn and remember individual relationship with conspecifics could influence social cognition, associative learning, cognitive flexibility, and performance on other cognitive tasks.

A good way to test the extent to which cognition evolves in a specialized versus generalized way is to compare multiple aspects of cognition in populations that differ in social behavior or ecology. Thus far, most research on population differences in cognition has focused on testing a small number of cognitive abilities in groups that vary ecologically. Population differences in cognition have been found across different geographic locations (Pravosudov and Clayton 2002; Roth et al. 2010), elevations (Croston et al. 2017), urban gradients (Audet et al. 2016), and habitat types (Huntingford and Wright 1992). For example, black-capped chickadees (*Poecile atricapilla*) from Alaska and Colorado differ in spatial memory ability, likely due to differences in the benefits of seed caching in areas with different winter harshness, but it is currently unknown whether the populations differ in other cognitive domains (Pravosudov and Clayton 2002). Predation also influences cognition, as fish from areas with higher predation are better at spatial learning than those from areas with lower predation, perhaps because improves spatial learning helps the fish rapidly navigate to safe areas (Girvan and Braithwaite 1998; Burns and Rodd 2008; Lucon-Xiccato and Bisazza 2017). It is unclear whether other aspects of cognition differ in fish populations with different predation risk (Lucon-Xiccato and Bisazza 2017). Though there is strong evidence that ecology impacts cognitive performance, we lack analysis of multiple aspects of cognition that test whether population differences in behavior lead to specialized or generalized cognitive differences.

While it's clear that intraspecific variation in ecology can influence cognition, less is known about how intraspecific variation in social behavior is linked with cognition. One notable exception is Ashton and colleagues' (2018a) work on Australian magpies. Using a battery of cognitive tests that assess inhibitory control, associative learning, reversal learning, and spatial memory, they found that magpies that live in larger groups had better cognitive performance and higher fitness than magpies that live in smaller groups (Ashton et al. 2018a). Their results suggest that sociality may shape cognitive development and evolution in a generalized way. However, in long-lived birds like magpies, it is difficult to identify the directionality of the relationships between cognition, group size, and fitness. Further, other factors, such as nutritional differences between groups, may drive the relationships between cognition, group size, and fitness (Ashton et al. 2018b; Wascher et al. 2018). Population differences in social behavior provide exciting potential model systems for intraspecific analyses of how social behavior influences cognition. For example, many taxa have geographic differences in social organization, social structure, or mating system (Travis et al. 1995; Schradin 2013; Kappeler 2019), all of which could influence cognition in either a specialized or generalized way. Previous work on population differences in social behavior has focused on culture and social learning (Whiten and van Schaik 2007), while less work has tested how population differences impact social and nonsocial cognition.

Here, we take advantage of geographic variation in *Polistes fuscatus* social behavior to test how social behavior influences cognitive performance. Previous work has shown that *P. fuscatus* from Michigan, USA rely on individual face recognition to manage their social relationships using unique facial patterns (Tibbetts 2002). Wasps live in complex social groups with linear hierarchies established through aggressive encounters and social eavesdropping both on and off the nest (Tibbetts et al. 2020). Individual recognition helps wasps manage social relationships and minimize the costs of conflict (Tibbetts 2002; Sheehan and Tibbetts 2009). However, *P. fuscatus* from Pennsylvania, USA are not capable of individual face recognition (Tibbetts et al. 2021a). Wasps from Pennsylvania treat known and unknown individuals similarly. The geographic difference in individual recognition is interesting because individual recognition is argued to increase social complexity (Seyfarth and Cheney 2015). For example, Bergman and Beehner (2015) propose that the number of differentiated social relationships provides a good measure of social complexity. Individuals with superior cognitive capacity are thought to be better able to keep track of multiple individual relationships and respond appropriately during social interactions. Given the proposed links between individually differentiated social relationships and social complexity, wasps from populations with individual face recognition may have enhanced cognition compared to wasps from populations that lack individual face recognition.

In this study, we compare cognitive performance in populations of *P. fuscatus* with and without individual recognition. We test whether there are cognitive differences between populations and whether these differences occur in multiple cognitive abilities or are restricted to a subset of cognitive abilities. Testing performance across multiple cognitive tasks is crucial for understanding the evolution of cognitive structure (Shaw and Schmelz 2017). We tested wasps from both Michigan and Pennsylvania to discriminate conspecific faces, colors, and odors. We also tested their ability to reverse a learned color association as a measure of behavioral flexibility. Finally, we tested their memory for odor stimuli one week after initial testing.

Cognitive performance across Michigan populations with individual recognition and Pennsylvania populations without individual recognition could differ in three ways. (1) Social differences in *P. fuscatus* populations could be linked with differences in social cognition alone, consistent with cognitive structure evolving in a specialized way. Under the specialization hypothesis, we predict that Michigan wasps will learn conspecific faces more accurately than Pennsylvania wasps, but the populations will not differ in other tests. (2) Social differences in *P. fuscatus* populations could be linked with broader differences in multiple aspects of cognitive performance across populations, consistent with cognitive structure evolving in a more generalized way. Under the generalization hypothesis, we predict that Michigan wasps will perform better than Pennsylvania wasps on multiple tasks. (3) Social differences across *P. fuscatus* populations could be inconsistently linked with cognitive performance, consistent with compensation (Åbjörnsson et al. 1997; Hartman and Abrahams 2000). Compensation could occur if Pennsylvania wasps compensate for their reduced individual face learning by excelling at other tasks. For example, Michigan wasps could learn faces more accurately than Pennsylvania wasps, while Pennsylvania wasps could learn odors more accurately than Michigan wasps.

Methods

Wasp rearing

We collected *Polistes fuscatus* foundresses from southeast Michigan, USA and Rothrock State Forest in State College, Pennsylvania, USA. We reared wasps with their nests in the lab with ad lib food, and water. We tracked each nest for newly

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emerged workers daily. All wasps used in this experiment eclosed in the lab. Upon emergence from pupation, new workers were individually marked on their wings with nontoxic model train paint (Testors Enamel Paint, USA; Product Number 9179). In 2022, we tested 45 Michigan wasps from 25 nests and 42 Pennsylvania wasps from 16 nests. In 2023, we tested 23 Michigan wasps from 15 nests and 25 Pennsylvania wasps from 13 nests. Each wasp was trained and tested on one cognitive task of the three tasks tested. Wasps averaged 24.4 ± 17.2 days old when tested (mean age plus/minus standard deviation). Wasps are considered mature at 5 days old because they exhibit a full range of adult behaviors (Reeve 1991; Giray et al. 2005; Shorter and Tibbetts 2008) so all wasps were tested after they were at least five days old.

Stimuli

Wasps were trained to discriminate one of three different types of stimuli: *P. fuscatus* face images, colors, and nonvolatile cuticular hydrocarbon odors. Wasps were trained and tested using the same methods used in previous studies (DesJardins and Tibbetts 2018; Tibbetts et al. 2019; Weise et al. 2022). Each wasp was trained and tested on one pair of stimuli. One stimulus in each pair was associated with shock (negative stimulus) and the other stimulus in each pair was associated with no shock (neutral stimulus). The specific stimuli associated with shock versus no shock was balanced across wasps to ensure that specific stimuli did not influence results. The training and testing method is explained in more detail under "Training and Testing."

Face images were photographs of unfamiliar *P. fuscatus* wasps printed at life size (approx. 3.5 mm wide) using a commercially available Xerox Altalink C8035 that uses ink cartridges. Four wasp faces with naturally variable facial patterns were used.

We used dotriacontane (Sigma Aldrich, USA; Product Number D223107-5G) and octacosane (Sigma Aldrich, USA; Product Number O504-25G) alkane odors for odor learning and memory assays. These odors are nonvolatile components of cuticular hydrocarbons (Sharma et al. 2015). Odors were prepared as described by Weise et al (2022). Briefly, the odors were dissolved in pentanes, applied to saturating tape, and left for 24 hours to allow the pentanes to evaporate. Once the odors were ready for testing, they were applied to glass mazes. *P. fuscatus* wasps naturally learn and use hydrocarbon odors to distinguish between nestmates and non-nestmates, communicate dominance rank, or health status (Sumner and Cini 2021).

We used the colors yellow and blue for the reversal learning assay (DesJardins and Tibbetts 2018), two colors that wasps can readily differentiate (Briscoe and Chittka 2001). Color stimuli were printed using a commercially available Xerox Altalink C8035 that uses ink cartridges.

Training and testing

Across all stimulus types, we trained and tested the ability of wasps to discriminate between a neutral stimulus and a negative stimulus using established methods (Fig. S2) (Tibbetts et al. 2018a). Wasps were trained and tested using negative reinforcement. Experimenters placed wasps in 2.5 × 4 × 0.7 cm boxes with stimuli lining the walls. In half of the training trials, the wasp was placed in a box while receiving a mild shock (~0.4 volts) for two minutes while viewing the incorrect stimuli (CS+). This non-lethal shock was delivered via an electrified pad made of anti-static conductive foam electrified by two copper wires connected to a Variac transformer. 0.4V is the minimum level of shock that causes a response in wasps (personal experience, Roussel et al. 2009). In the other half of trials, the wasp was placed in a box while receiving no shock and viewing the correct stimuli (CS) for two minutes. After each trial, wasps received a one-minute break in a dark container with access to water. Wasps were placed in each box five times for a total of ten trials. At the conclusion of the training, wasps received a 45-min break in a dark container with access to water.

We measured learning accuracy with a ten-trial test. In each trial, a wasp was placed in a 3 × 10 × 0.7 cm rectangular box. The correct stimulus (CS) was on one side of the box and the incorrect stimulus (CS+) was on the other. The floor was not electrified. At the start of each trial, the rectangle was divided by two partitions. One partition had the correct stimulus (CS) on it and the other had the incorrect stimulus (CS+). The partitions were removed simultaneously after the wasp had been in the antechamber for a few seconds. Upon removing the doors, the wasp moved to one side of the rectangle. A wasp was scored as making a choice when its head and thorax moved beyond a small partition placed 2.5 cm from each end of the rectangle. Once the wasp made a decision, she was removed and given a one-minute break in a separate container with access to water. The location of the correct stimulus varied in a pseudo-random order to avoid any side biases. This ensures that wasps did not associate a particular direction with correct choices. The ten trial test provides a good way to measure learning accuracy, as wasps who learn typically approach the correct stimuli rapidly. There is no reinforcement during the test and previous work has shown that wasps tested on individual face learning without any initial training perform at chance level during the ten trial test (Weise et al. 2022).

Individual face learning

Wasps were trained and tested as they differentiated two different unfamiliar *P. fuscatus* wasp face images using the methods described above. Previous work has shown that the ability to learn and remember individual faces during training is linked to social recognition capacity. Within and between species, wasps that are capable of individual recognition during social interactions learn and remember faces during training, while wasps that are not capable of individual recognition during social interactions are unable to learn and remember faces (Sheehan and Tibbetts 2011; Tibbetts et al. 2018b, 2019). For example, *Polistes metricus* wasps and *P. fuscatus* from Michigan that were socially isolated since emergence from pupation 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, 2021a). In contrast, *P. fuscatus* from Michigan and New York are capable of individual recognition and readily learn to discriminate faces (Sheehan and Tibbetts 2011; Tibbetts et al. 2018b).

Our previous work also shows that wasps do not learn conspecific faces in the same way they learn other complex visual stimuli (Tibbetts et al. 2021b; Pardo-Sanchez and Tibbetts 2022). In previous work, we trained wasps to discriminate between wasp face images that were experimentally altered so the outer parts of the face (antennae, background, legs) were identical and the central part of the face had natural levels of variation. If wasps process faces as typical, complex stimuli, they would be equally able to discriminate whole faces and central faces because the two types of stimuli contain the same amount of variation. Instead, Michigan wasps excelled at identifying whole conspecific faces but were completely unable to discriminate the central part of the face. These results show that wasps process conspecific faces using specialized recognition mechanisms that are not used for

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Table 1. Results of posthoc analysis of the mixed effects model comparing performance of Michigan and Pennsylvania wasps for each type of test. Populations differed in individual face learning, but not other learning and memory tests. These tests were corrected for multiple comparisons using the Bonferroni correction thus using a p-value of 0.01. Bold values represent significant differences.

Treatment	Michigan Sample Size	Pennsylvania Sample Size	Estimate	Standard Error	Z Ratio	P Value
Individual Face Learning	18	16	0.91	0.23	3.96	**0.0004**
Initial Color Learning	19	16	0.18	0.25	0.70	1.00
Color Memory	15	14	0.090	0.26	0.35	1.00
Color Reversal	15	13	-0.49	0.27	-1.84	0.39
Odor Learning	32	33	0.28	0.17	1.68	0.557
Odor Memory	16	14	0.16	0.24	0.67	1.00

processing non-face stimuli (Tibbetts et al. 2021b; Pardo-Sanchez and Tibbetts 2022).

Color learning and reversal

Color reversal training involved training a wasp to discriminate two colors, then reversing the association the next day. Initially, we trained wasps to associate shock with one color and tested their learning via the ten trial test (e.g. blue associated with safety during training, initial color training). Twenty-four hours later, we performed the ten trial test again without any additional training to assess the wasp's memory of the initial training (color memory). Wasps were not trained prior to the memory test because the purpose of the memory test was to ensure the wasp remembered the association that was learned the previous day. Immediately after the color memory test, wasps underwent a new round of training where the previously negatively reinforced color was now the neutral stimulus, and the previously neutral stimulus was negatively reinforced. The initial training involved five rounds of electric shock training whereas the reversal involved two rounds. We used two rounds of shock for the reversal learning because our preliminary experiments indicated two rounds was sufficient for most, but not all individuals to reverse the initial association. Reversal learning measures how willing the wasp is to let go of previously trained association when the associations is suddenly changed.

Only wasps that scored 6/10 or higher on their initial color test were used in the reversal analyses. Wasps that scored 5/10 or lower likely did not learn the initial color, so we followed the common convention by excluding them from reversal analyses (Cantwell et al. 2022). Four wasps were excluded (2 from Michigan, and 2 from Pennsylvania) from color memory and color reversal analyses (Table S1). Including the 4 wasps does not influence the overall results (Table S1 & S2). Model results with all wasps included can be found in the supplementary materials (Fig. S1).

Odor learning and memory

Odor learning and memory tests were performed using the same methods as used for other training and testing. We used glass mazes for odor testing to prevent odor residuals from previous trials. Odor memory tests were conducted 7 to 8 days after the initial odor learning to measure their long-term memory. The odor memory tests were ten trial tests performed without additional training to ensure that the responses were based on what the wasp learned a week before.

Only wasps that scored 6 or higher on their initial odor test were used for odor memory analyses. As with the color learning, we believe that wasps scoring 5 or below likely did not learn the initial odors. Three Michigan wasps and six Pennsylvania wasps were excluded from the odor memory test. The odor memory analysis has a smaller sample size than other tests because some wasps were lost, and others died between the initial test and the memory test (n = 16) (Table S1). Including the 9 wasps does not influence the overall results (Table S1 & S2). Model results with all wasps included can be found in the supplementary materials (Fig. S1).

Statistical analysis

We analyzed the data in R v. 4.1.2 (Team 2021). We compared learning across the two populations on the three different tests using a generalized linear mixed effects model using a binomial distribution from the *lme4* R package (Bates et al. 2015). The dependent variable was the trial choice (incorrect (0) or correct (1)). The independent variables were the population (categorical: Michigan, Pennsylvania), test type (categorical: faces, initial colors, color memory, color reversal, initial odors, odor memory), and the interaction between population type and test type. We also included wasp age (continuous) as a fixed effect. We included year, trial number (1 to 10) and wasp ID nested into nest ID as random effects.

We then compared fixed effects using a Type II Wald Chi-square test to create an Analysis of Deviance table using the Anova function in the *car* package (Fox and Weisberg 2019). We used the emmeans function from the *emmeans* package for post-hoc analyses to compare test performance between populations on each test type using a Bonferroni correction for multiple comparisons since the interaction between population and test type was significant (Lenth 2021). Finally, we used binomial tests from the *stats* package to determine if the number of correct choices in each group differed from the 50:50 random expectation (Team 2021). Binomial tests provide p-values with no test statistics.

Results

Wasps from Michigan and Pennsylvania differ in their ability to learn conspecific faces, but not in their performance on other cognitive tasks (Table 1, Fig. 1). The overall statistical model shows that there is a significant population by test type interaction (X^2 = 16.9, df = 5, *P* = 0.0048), indicating that the relationship between population and performance differs across cognitive tasks. There are also differences in performance in the main effects of population (X^2 = 6.75, df = 1, *P* = 0.0093) and test type (X^2 = 13.42, df = 5, *P* = 0.020). Age of wasps at training (X^2 = 0.15, df = 1, *P* = 0.70) did not affect test scores.

To further understand the population by test type interaction, we compared performance of the two populations for each type of test. The populations differed in their face learning performance, with Michigan wasps learning faces more accurately than Pennsylvania wasps (Z ratio: 3.96; *P* = 0.0004). There were

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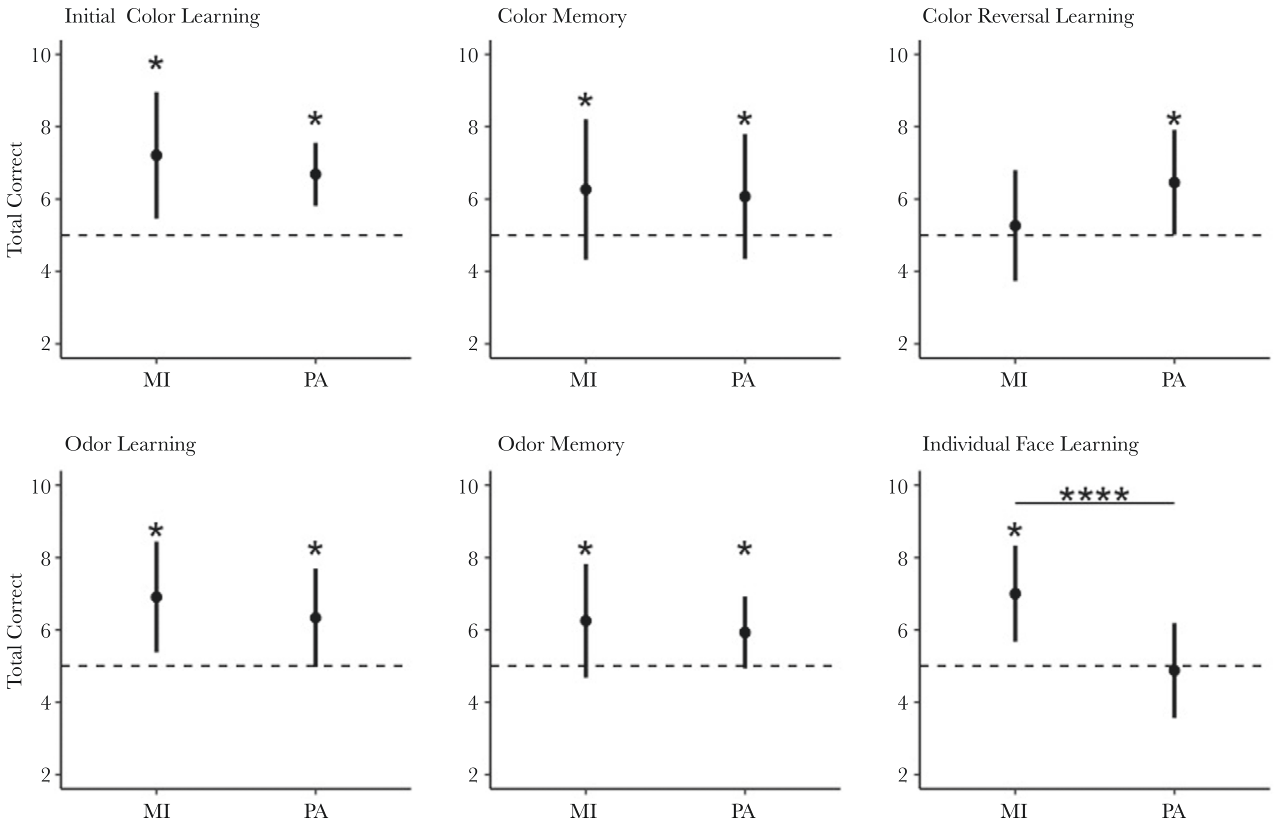

Fig. 1. Michigan (individual recognition) and Pennsylvania (no individual recognition) *Polistes fuscatus* choice accuracy across six different tests. Michigan and Pennsylvania populations differ in face learning, but not any of the other five tests (Table 1). Mean and standard deviation plots shown with dashed lines showing 50:50 random expectation. * directly above lines denote that that group learned, as they chose correctly more often than expected by chance ($P < 0.05$) (Table 2). **** between two groups denote a significant difference between groups via post-hoc testing (alpha value = 0.01) (Table 1).

Table 2. Results of binomial tests for Michigan and Pennsylvania wasps for each test type. Both populations scored above chance on some tests and not others. Results from binomial tests which provide p-values and no test statistics. Bold values indicate that wasps chose the correct stimuli significantly more often than expected by chance.

Treatment	Michigan *P*-Value	Pennsylvania *P*-Value
Individual Face Learning	**<0.0001**	0.81
Initial Color Learning	**<0.0001**	**<0.0001**
Color Memory	**0.0024**	**0.014**
Color Reversal	0.57	**0.001**
Odor Learning	**<0.0001**	**<0.0001**
Odor Memory	**0.0020**	**0.034**

no differences in performance on any of the other tests (all P values > 0.39; results in Table 1).

We also assessed which stimuli were learned in each population by splitting the data by test type and population and performing a binomial test within each group. These analyses show that both Michigan and Pennsylvania wasps performed above chance levels on initial color learning, color memory, initial odor learning, and odor memory ($P < 0.05$ for all). Michigan wasps did not score above chance levels on color reversal learning ($P = 0.57$) whereas Pennsylvania wasps did ($P = 0.001$). Consistent with the population differences in face learning, Pennsylvania wasps did not score above chance levels on faces ($P = 0.81$) whereas Michigan wasps chose the correct face more often than expected by chance ($P < 0.001$).

Discussion

The results of this study indicate that geographic differences in social complexity influence cognition via specialized rather than generalized changes in cognition. Wasp populations that differ in their capacity for individual recognition also differ in individual face learning performance, but not in their performance on other cognitive tests. The population differences in individual face learning are consistent with previous work. *P. fuscatus* wasps from Michigan are adept at individual face recognition and also excel at individual face learning, while *P. fuscatus* wasps from Pennsylvania are unable to individually recognize conspecifics and also are unable to learn to differentiate between conspecific faces during training (Tibbetts et al. 2021a). However, no previous work has compared the performance of Michigan and

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Pennsylvania wasps in other cognitive domains. We found that Michigan and Pennsylvania wasps do not differ in their performance of any other learning and memory tasks, including color learning, color memory, color reversal, odor learning, and odor memory.

It is somewhat surprising that populations differed in their capacity for individual face learning but not other tasks because similar methods were used for training and testing wasps on individual face learning, initial color learning, and odor learning. The only difference between the three associative learning tasks was the stimuli learned: faces, colors, or odor. All training involved negative reinforcement associative learning in a similar apparatus. All tests measured the number of correct choices out of ten in a non-reinforced binary choice paradigm. Despite the methodological similarities between tests, populations differed only in their capacity for individual face learning, consistent with cognitive performance evolving in a highly specialized manner.

There has been long-standing debate over whether cognition evolves in a generalized or specialized way. Hypotheses like the social and ecological intelligence hypotheses were originally proposed as explanations for generalized differences in cognition and/or brain size between species (Jolly 1966; Humphrey 1976; Milton 1981; Chance and Mead 1988). Social or ecological complexity was hypothesized to select for larger brains and/or increased general cognitive sophistication. However, more recent work suggests that the benefits of sophisticated cognitive abilities often produce specialized differences in cognition (Amici et al. 2012; Shaw and Schmelz 2017). For example, this study found that population differences in social complexity were linked with specialized differences in social cognition. Similarly, cleaner fish are known for their sophisticated social behavior, but do not show generalized intelligence when tested on a variety of cognitive tasks (Aellen et al. 2022). Therefore, benefits associated with cognitive performance do not necessarily produce generalized changes in cognition. At the same time, it's clear that generalized cognitive differences exist both within and between species. Some taxa excel at a broad range of cognitive tasks, while others do not (Deaner et al. 2006; Reader et al. 2011). Similarly, some individuals show broadly enhanced cognitive abilities compared to other individuals (Esther and Josep 2012). As a result, we still have much to learn about the evolution of specialized versus generalized cognitive structure.

Our evidence of cognitive specialization for face learning in wasps is broadly consistent with previous work on face specialization in both wasps and humans. While humans show remarkable capacity for general intelligence, they also have highly specialized face recognition abilities mediated via neural mechanisms that are not used for other types of learning and memory (Yin 1969; Tanaka and Farah 1993). For example, humans have a dedicated brain region, the fusiform face area, primarily involved in facial recognition (Kanwisher 2000; McGugin et al. 2020; White and Burton 2022; Parker et al. 2023). Humans also identify faces using specialized, holistic mechanisms rather than generalized, featural mechanisms (Tanaka and Farah 1993; Burke and Sulikowski 2013). *P. fuscatus* also process conspecific faces using specialized, holistic mechanisms that are not used for learning and remembering non-face stimuli, indicating a similar pattern of selection for recognizing faces (Tibbetts et al. 2021b; Pardo-Sanchez and Tibbetts 2022). There is some evidence that *P. fuscatus* may also process faces in a specific brain region, the anterior optic tubercle, which increases in volume with social experience (Jernigan et al. 2024). Current work suggests there may be a tight link between form and function for highly specialized cognitive functions, though additional work on the neural mechanisms of face and non-face learning will be important.

Pennsylvania wasps did not outperform Michigan wasps on any cognitive task, indicating that Pennsylvania wasps do not compensate for their lack of visual individual recognition by excelling in other ways. Some taxa compensate for reduced performance in one sensory modality by improved performance in a different modality (Åbjörnsson et al. 1997; Hartman and Abrahams 2000; Yoshizawa 2015). For example, blind cave fish often have better chemosensory and vibratory perception than typical fish (Yoshizawa 2015). As a result, one might predict that *P. fuscatus* with reduced visual individual recognition may be more adept at perceiving and responding to odor signals, especially given that *Polistes* species rely on chemical recognition in many contexts (Sumner and Cini 2021). However, previous work has shown that Pennsylvania wasps are unable to recognize individual conspecifics using odors (Tibbetts et al. 2021a). Furthermore, the results of this study indicate that Pennsylvania wasps are no better than Michigan wasps at learning and remembering hydrocarbon odors (Fig. 1). Cognitive compensation has been less well studied than sensory compensation, though it's possible that individuals or populations that perform poorly on one type of cognitive task may compensate by excelling at other tasks (Audet et al. 2016). However, we found no evidence of sensory or cognitive compensation across paper wasp populations.

One of the challenges of studying cognitive structure is that it can be difficult to design tests that measure different aspects of cognition. Test design and performance are influenced by non-cognitive factors that may vary across taxa, including motivation, neophobia, persistence, motor control, and perceptual biases (Shaw and Schmelz 2017). Further, it is often difficult to design tests that assess multiple different cognitive domains. For example, typical cognitive test batteries for birds and mice lack tasks that require inference or are in the social domain (Thornton and Lukas 2012; Shaw and Schmelz 2017). In this study, we used very similar methods across tests that all involved negative reinforcement association. Nevertheless, we were able to test wasps on both social and nonsocial cognition as well as cognitive flexibility via a novel reversal task. Future work that increases the diversity of cognitive tasks will be important to broaden our understanding of cognitive structure in wasps (Simons and Tibbetts 2019).

Much of what we know about insect cognition comes from studies performed in honeybees and bumblebees. As a result, a range of cognitive assays exist to measure learning, behavioral flexibility, and innovation in social and nonsocial contexts (Carcaud et al. 2009; Chandra et al. 2010; Raine and Chittka 2012; Avarguès-Weber and Giurfa 2013; Chittka 2017; Schultheiss et al. 2017; Chittka and Rossi 2022). Much less is known about other invertebrates, though diverse invertebrates have potential to be important models for understanding cognitive evolution (Tarsitano and Jackson 1997; Mery et al. 2007; Amodio et al. 2019; Young et al. 2024). The small brain size and ease of experimental manipulations make invertebrates exciting systems to explore cognitive evolution. Increasing both the diversity of cognitive tests and the diversity of taxa being studied will provide more robust information about cognitive evolution (Simons and Tibbetts 2019).

Overall, this study demonstrates that the geographic variation in *P. fuscatus* individual recognition ability is linked to differences in individual face learning but not differences in performance in other cognitive tests. By using similar methods across

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cognitive tests, we demonstrate that the cognitive differences between populations are specific to social stimuli. These results highlight that social complexity may influence the evolution of relevant social cognition traits, but not other aspects of cognition.

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

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Author Contributions

Juanita Pardo Sanchez (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Funding acquisition [equal], Investigation [lead], Methodology [lead], Project administration [lead], Visualization [lead], Writing - original draft [equal], Writing - review & editing [equal]), So Eun Moon (Conceptualization [supporting], Writing - review & editing [supporting]), and Elizabeth Tibbetts (Conceptualization [equal], Formal analysis [supporting], Funding acquisition [equal], Resources [equal], Supervision [equal], Writing - original draft [equal], Writing - review & editing [equal])

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Conflict of interests

The authors have no competing or financial interests to disclose.

Data Availability

Analyses reported in this article can be reproduced using the data provided by Pardo-Sanchez et al. (2025).

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