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How does communication evolve? Insights from geographic variation in facial signaling in *Polistes* paper wasps

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Communication systems require coordination between senders and receivers; therefore, understanding how novel signals arise is challenging. Intraspecific geographic variation in signaling provides an opportunity to investigate the factors that shape signal evolution. Facial signals in *Polistes* paper wasps provide an interesting case study for the causes and consequences of geographic variation in signaling systems. Two species of paper wasps, *Polistes dominula* and *Polistes fuscatus*, have been well studied for their facial patterns that signal quality and individual identity, respectively. Remarkably, whether or not facial patterns are used as signals at all appears to vary geographically in both species. The relative evidence for the roles of phenotypic plasticity versus genetic differentiation is discussed. Future research directions that leverage geographic variation in *Polistes* hold promise to substantially contribute to understanding the links between signals and behavior, as well as the evolution of cognition.

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Introduction

Communication is an interaction between a sender who produces a signal or cue and a receiver who perceives and responds. It is increasingly clear that both the signaling phenotypes of senders and the sensory and cognitive phenotypes of receivers can adaptively evolve to facilitate communication. How and why novel signaling systems emerge or what causes signaling systems to be lost is less clear. Given the importance of communication in animal ecology and evolution, identifying the factors that shape the gain and loss of signals is an important goal in behavioral and evolutionary ecological research. One promising route to understanding processes that shape the evolutionary process of signal gain and loss is to examine species with geographic variation in the presence and use of signals across their range [1–3]. Geographic variation in signaling within species has the potential to not only reveal ecological and social factors shaping signal evolution but also provide a means to leverage breeding and population genomic analyses to uncover the genetic basis of complex communication and cognition traits.

Polistes paper wasps show notable variation in color patterning within and between species [4–7], which has long been a headache for systematists working in the group [8–11]. In the past two decades, however, there has been a quickly developing body of literature documenting that many color pattern elements are socially and sexually selected signals [12–17]. Here, we focus our attention on signals of quality and identity that have been demonstrated in some populations of *Polistes dominula* and *Polistes fuscatus*, respectively. In both species, there is also evidence for the lack of signals in other populations [18–21]. In this piece, we (i) outline the leading hypotheses for why signaling is common in *Polistes* wasps, (ii) discuss signals and geographic variation in these two well-studied species, (iii) evaluate the evidence for different drivers of geographic variation, and (iv) discuss how future studies can leverage geographic variation in paper wasp signaling systems to answer novel questions about the ecological, developmental, genomic, and neurobiological basis of signal evolution.

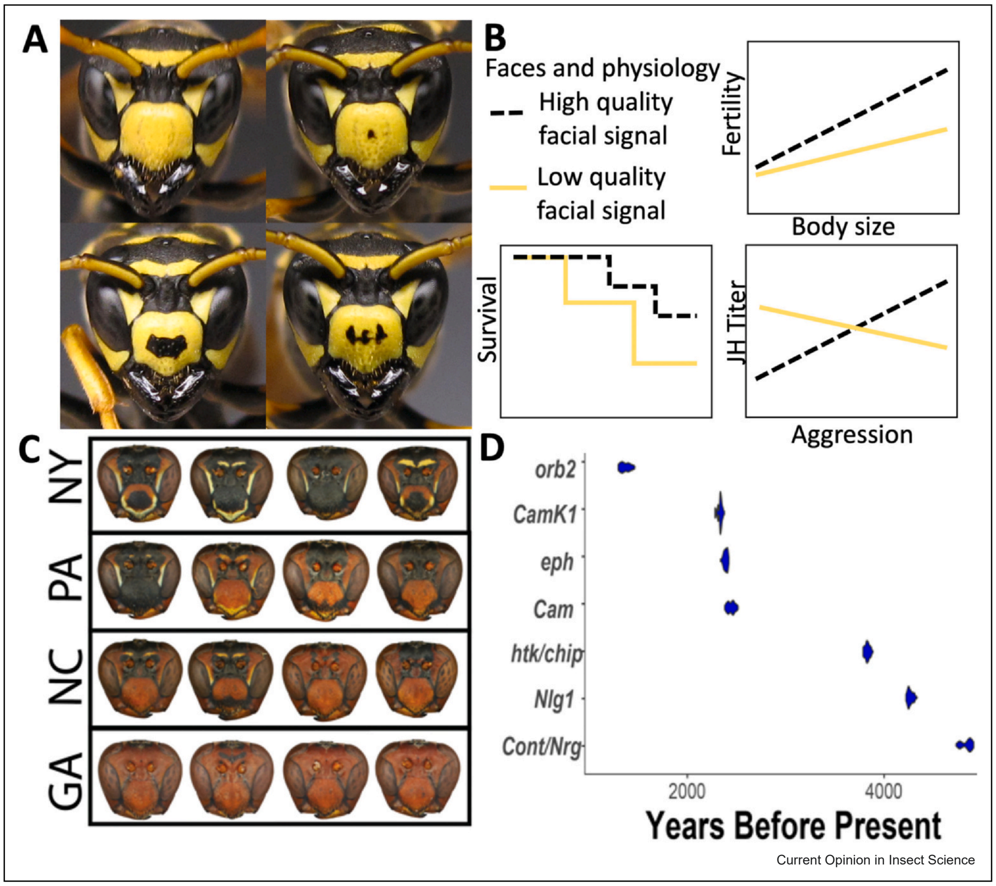
What is the function of social signaling color patterns in female paper wasps?

Variation in female color patterning has been shown to serve as signals of individual identity [22], badges of status [13,14], or correlate with fertility [16] across a diverse range of paper wasps. Before diving into intraspecific geographic variation in signaling, it bears asking the question — Why is signaling with color patterning so common among paper wasps? The fact that wasps as a group tend to have large eyes and reasonably acute vision [23] certainly plays a role in the predisposition to communicate via color patterning. Additionally, a cursory view of wasp diversity reveals that color patterns vary dramatically among species, indicating that color patterning is evolutionary labile [5,7,8], though formal phylogenetic analyses of color pattern diversification are greatly needed. Social systems of many paper wasp species may also favor the evolution of signals of identity or quality. In *Polistes* wasps, nests are initiated by one or a small group of foundresses [24], who are generally but not always close relatives [25–27]. Rates of cooperative nesting among groups of foundresses vary within and between species [28]. Comparative analyses indicate that wasps with flexible founding strategies, those species where mixed strategies of solitary versus cooperative nest founding commonly co-occur within populations, are associated with greater facial pattern variation [6]. Further, functional studies of facial signals in wasps suggest that both identity and quality signals are involved in mediating cooperation and conflict among nestmates and during defense of nests from potential usurpers [21,29]. Thus, the extent of cooperative nesting within a population is likely to be a major driver of color pattern signaling in paper wasps. Experimental tests of facial color patterns as social signals have only been conducted in a few species [12–14,30–33], though an assessment of color pattern variation across the genus suggests the possibility that many more species may have evolved signals — and that those signals may vary across populations [7].

Polistes dominula: badges of status that signal quality

Variation in the shape and number of black spots on the clypeus serves as a badge of status or kind of signal of quality in some populations of *P. dominula* (Figure 1a).

Figure 1



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Facial signals in *P. dominula* and *P. fuscatus*. **(a)** Facial pattern variation in *P. dominula* consists of variation in the extent and shape of black markings on the clypeus (the large yellow patch in the center of the face). The proportion of wasps with any black markings on the clypeus varies across populations. The wasps shown here were photographed in Michigan, USA. **(b)** Multiple correlations between badge of status signal expression and physiology have been reported in the invasive population in Michigan, USA. These include (clockwise) that wasps treated with juvenile hormone (JH) show higher increases in fertility if they have higher quality facial signals [71], that JH titers differed in response to aggressive encounters depending on a wasps facial signal [35], and that survival in response to physiological challenge was greater in wasps with high-quality facial signals [37]. The graphs here show schematic results. **(c)** The facial patterns in *P. fuscatus* signals individual identity. In northern populations, wasps tend to be more variable, while in the southernmost populations, wasps tend to have uniform coloration. Wasps in each row are from a different state, with the northernmost state at the top and southernmost at the bottom. Please note: A population from the central, mountainous regions of Pennsylvania is described as having low color pattern variation and lacking individual recognition and discussed in the text. The Pennsylvania wasps shown here are from a lower-elevation region near Philadelphia, suggesting that color patterns can vary over short distances. **(d)** Population genomic analyses indicate strong selective sweeps on multiple genes related to learning, memory, and visual systems in the past few thousand years, suggesting the possible recent evolution of individual recognition in this lineage.
(c) Photos are shown after Refs. [21] and **(d)** [49].

Tibbetts and Dale first described the signal in an invasive population of paper wasps from Ithaca, New York [14]. In that population, females have a wide range of black patterns on their yellow clypeus ranging from no black marks to multiple small dots to large black splotches and even wavy bands of black across the clypeus. Larger females tend to have patterns that are more 'broken', meaning that they contain more variance in the amount of black within the central portion of the face, generally resulting in a pattern with increased perimeter relative to a simple circle or rectangle. In staged fights between wasps, individuals with more broken black patterns were more likely to win the encounter. Manipulations of signal content showed that individuals with signals that were made artificially stronger (i.e., appearing to 'bluff' about their strength) suffered more intense aggression when they lost the contest, leading to the conclusion that social costs work to maintain honesty in the system [14,34,35]. Subsequent work on *P. dominula* populations in North America has shown that the variation in facial patterns in *P. dominula* is (i) dependent on rearing condition [36], (ii) associated with other aspects of physiological quality (Figure 1b) [35,37], (iii) flexibly responded in relation to context and contest value [38], and (iv) associated with increased fitness in wild populations [39]. Collectively, these studies provide strong evidence for the role of black clypeal markings functioning as signals of quality in North American *P. dominula* populations.

The extent of black marking varies notably across *P. dominula* populations. In North American populations measured in New York and Michigan, upwards of 80% of wasps have at least some black markings on their clypeus, while in a population from Spain, the rate of wasps with black markings is only 20% of foundresses [19,40]. Work testing the role of clypeal patterning in Spain has found no evidence supporting signaling function across analyses of interactions in the field to direct replications of studies that demonstrate signaling function in North American populations [18,40,41]. Studies of Italian populations, where clypeal markings occur on roughly 40% of foundresses, have found mixed support for the effect of clypeal markings. Most work on Italian *P. dominula* has suggested that black markings do not function as badges of status in that population [42,43]. However, one study that presented dead wasps with their cuticular hydrocarbons removed to foundresses on their nests found that foundresses challenged the individuals signaling the highest quality less than those with moderate or low-quality signals, indicating that under that condition at least signals may have a role [29].

Polistes fuscatus: signals of individual identity

Female color pattern diversity in *P. fuscatus* was described by systematist J Bequeart to 'run riot and to defy any attempt at rational analysis' [8]. In other words, the amount of phenotypic variation is very high (Figure 1c). In a landmark study, Tibbetts demonstrated that wasps recognized individuals based on their facial patterning by manipulating color patterns of wild wasps in a population in Ithaca, New York [12]. Females that had their appearance altered received increased aggression, while those that were painted but whose appearances were not altered did not receive increased aggression. Subsequent work has shown that the wasps have robust social memories [44], use specialized cognitive mechanisms to discriminate among faces [45–47], and can even eavesdrop on third-party interactions using individual recognition [48]. There is experimental evidence that the diverse color patterns act as signals of individual identity, meaning that senders benefit by advertising their identity with distinct traits [22]. Furthermore, genomic selection analyses suggest that cognitive abilities related to recognition involving learning, memory, and visual processing have been among the strongest selective pressures in recent evolutionary history among northern *P. fuscatus* populations [49] (Figure 1d).

Initial work in this species focused on populations in Ithaca, New York, and Ann Arbor, Michigan, which are at a similar latitude, and both have populations with variable faces used for individual recognition. In the past few years, however, two groups have independently described other populations in central Pennsylvania [20] and southern Louisiana [21] that have much lower color pattern variation and have been experimentally shown to lack individual recognition. In both cases, experimental tests showed that the populations with low phenotypic variation lack recognition across any modality. Work in the central Pennsylvania population has shown that they also have difficulty telling apart faces in an operant training paradigm, in which wasps from Michigan and New York tend to do well [20]. However, Michigan wasps were nevertheless able to differentiate among faces of wasps from Pennsylvania, suggesting that there is not a total lack of identity information. A recent study that reared wasps from Michigan and Pennsylvania in a common garden design found that facial discrimination abilities in Pennsylvania wasps improved when they were reared with wasps from Michigan, which tend to show higher facial pattern variability indicating that at least some of the population differences are due to socially driven plasticity in development of cognitive abilities [50]. Work comparing wasps between New York and Louisiana examined how recognition abilities related to social structure, finding that New York wasps formed closer associations between a subset of individuals, while the wasps from Louisiana were less discerning among potential social partners [21]. Thus, populations with low identity signal diversity show evidence of different cognitive or behavioral responses to facial patterns in the context of social interactions. There is a broad latitudinal cline in color pattern diversity, with more northern populations tending to show increased phenotypic diversity [21], suggesting that co-variation between color pattern diversity and cognitive abilities may be widespread in this species.

Assessing evidence for drivers of geographic variation

Climate as a potential driver of plasticity and adaptation

Temperature and humidity influence the evolution and development of color patterning across a range of insect species, with many groups showing increased melanism at colder temperatures. As a result, geographic variation in rearing environments could be a driver of differences in signaling across populations. Two studies examining color patterning in *Polistes* found that wasps are darker at both higher altitudes and in colder climates [51,52]. Consistent with this broader pattern, *P. dominula* populations from colder climates also show more melanization on their clypeus (i.e., more individuals tend to have black spots, and the black tends to be larger) [19]. Moreover, a rearing study of Spanish wasp pupae under controlled environmental conditions demonstrated a strong effect of temperature on the expression of clypeal color patterns [53]. Cooler temperatures lead to a dramatic increase in the amount and 'brokenness' of black patterns, though it did not lead to a relationship between color patterning and body size or other measures of quality as has been observed in North American populations. Similarly, an experimental manipulation of humidity and rearing temperature in *P. fuscatus* pupae revealed that lower humidity is associated with overall light coloration, roughly matching patterns of very light coloration found among paper wasps in the desert Southwest [54]. Phenotypic plasticity to climatic conditions alone, however, is unlikely to be able to explain the patterns of geographic variation in either species as substantial variation in coloration exists within and among nests that experience the same climate conditions. Anecdotally, rearing of *P. fuscatus* nests from disparate populations side-by-side in the same lab produces offspring with population of origin typical color patterns (MJS, personal observation). However, these observations do not preclude the possibility that color pattern variation among populations is related to environmental adaptation across species' ranges that happens to also influence patterns of signal variation. The increase in black markings that serve as signals of quality and identity in the two species could have been initially facilitated by greater melanization as populations inhabited colder climates. Patterns of local adaptation to climate have not received substantial attention to date in paper wasps, though climate-driven adaptation is likely an important factor impacting geographic variation across species [55].

Differential selection due to variation in cooperative behavior

Geographic variation in nesting behavior is also likely to be an important driver of geographic variation in signaling within as well as among species. If differences in patterns of cooperative behavior are a driver (data from both *P. dominula* and *P. fuscatus* are consistent with this idea), then differences in the presence of signaling across populations could be driven by three different processes. (i) On one hand, it could be that without sufficiently strong selection maintaining a signal within a population, signals may be lost due to drift or mutational decay. Colloquially, we might call this the 'use it or lose it hypothesis,' where traits that are not under sufficiently strong selection to be maintained are lost [56,57]. (ii) An alternative is that selection *against* signals may exist in populations that lack them. This might arise because signaling systems are costly, such that without the social benefits of signaling, signal production by senders or receiver investment in processing or responses is selected against. This differs from the first hypothesis in that it specifically posits that individuals could benefit from investing less in signals under some social conditions, as opposed to simply having less benefit when facial patterns are not used as signals. This hypothesis requires that signals are costly in terms of production or processing, such that individuals could potentially benefit from reduced costs if signaling is avoided under conditions where it is not beneficial. (iii) Selection against signaling (which inherently requires phenotypic diversity) can also be viewed as selection for uniformity. For example, selection to look distinct from another species or to have a more uniform appearance due to the benefits of aposematic coloration could be drivers of uniformity that might suppress signals in some populations where the ecological benefits of signal production are reduced [58]. In contrast to the second hypothesis, selection for uniformity does not posit that signals are lost due to costs of signaling but rather that individuals receive benefits from conforming to a population average. One example of this is observed in geographic variation in aposematism, where populations of multiple species of butterflies and bumblebees have been reported to converge on a shared appearance with a geographic region [59,60]. In the case of *P. fuscatus* and *P. dominula*, the less variable populations also tend to resemble closely related species with overlapping ranges.

Population structure and historical biogeography

The present-day distribution of genotypes and traits that we observe is the result of a mixture of local adaptation and historical biogeographic processes. One hypothesis to explain the geographic variation among 'populations' of any given species is that these different populations may actually represent more distinct lineages than has been traditionally appreciated. Thus, population differences in signaling could be expected to accumulate as lineages become more reproductively isolated. Both *P. dominula* and *P. fuscatus* are notable for having especially broad distributions within their native ranges, even compared to other closely related species of *Polistes* wasps. Various subspecies classifications have been historically proposed and debated for both species, indicative of potential substructure, local adaptation, and even some level of reproductive isolation. In the case of *P. fuscatus*, recent population genomic analyses of wasp populations along the eastern coast of the United States have revealed the existence of at least two genetically distinct but geographically overlapping subpopulations [61]. For both species, revisions of their respective subgenera and analyses of DNA barcode phylogenies have indicated the presence of multiple divergent lineages in many recognized species, including both species discussed in depth here [9,10]. While facial signaling has not been described in species closely related to *P. fuscatus*, other members of the *P. dominula* clade, for example, *P. gallicus* [33], also have black markings on their faces, and research shows that black clypeal markings function as signals of quality.

Historical biogeographic considerations are especially relevant in discussions of geographic variation in signals in paper wasps. In both northern temperate species that have been the focus of discussion here, population expansion northward from historical refugia during the last glacial maximum is likely to explain at least some of the observed patterns of diversity. For example, both New York and Michigan, where much of the work demonstrating evidence for signaling in both species has occurred, were under a mile or more of ice 10 thousand years ago [62]. The presence of native, let alone invasive, wasp species in these geographic regions is relatively recent on a geological scale. Recent expansions out of refugia have two potential implications for signal evolution. First, as populations expanded northward from refugia, previously isolated lineages may have come into contact. If populations differed in appearance, mixing could potentially lead to increased phenotypic diversity associated with signals. Second, range expansions are associated with trait evolution [63,64]. Expansion requires dispersal into new habitats, which may select for novel behavioral traits.

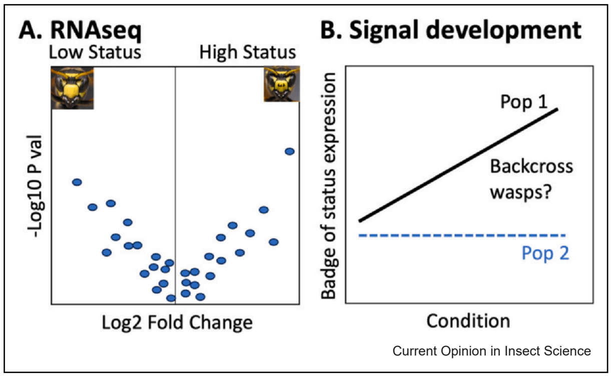
Geographic variation and prospects for understanding the production and neurobiology of animal signaling systems

While there are many interesting questions to pursue regarding the evolution, ecology, development, and neurobiology of animal signals using paper wasps as a model, three areas of inquiry will be especially enriched by leveraging the geographic variation found in the facial signaling in *Polistes* wasps.

Signal development — linking color patterning and behavior

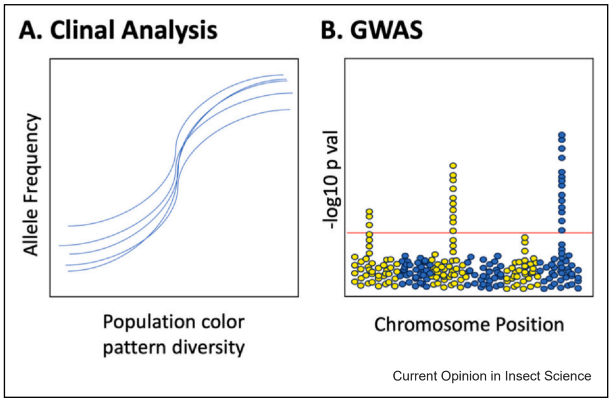
The black clypeal markings in *P. dominula* work as a signal because there is a relationship between color pattern development during the pupal stage and aggressive behavior in adults (typically measured months later). This suggests that developmental pathways that determine signal production are connected with the physiological mechanisms that influence neural development and behavior. One possibility is that individual behaviors are shaped by the signals that individuals possess, such that individuals develop adult behavioral traits in accordance with their signals and the social environment [65]. Such a system would be more likely to be susceptible to cheating and would not explain the relationship between signals and developmental rearing conditions [36]. More likely, signal development co-varies with neural development such that it influences patterns of adult behavior. This could arise if a shared development mechanism, such as variation in a hormone titer, influenced both signal and neural development. The badges of status are especially convenient ‘tools’ for assessing what kind of behavior an individual has developmentally ‘assessed’ is appropriate. In other words, wasps that develop to signal high-quality facial patches also develop other aspects of their physiology and nervous system consistent with increased aggression. Developmental studies identifying factors, such as hormones or nutrition, that manipulate signal development — and whether the same factors influence behavior — will help reveal how facial signals and behavior become linked across life history in populations. Presumably, signal production and behavior are influenced by the same factors over early development. Thus, identifying how condition is related to signals and behavior within and between populations has the potential to uncover which genomic modules correlate with behavioral variation and resource holding potential. One useful tool for this research with nonmodel organisms is RNA-seq, which allows straightforward assessment of differences in neurogenomic profiles or the metabolic states of other tissues (Figure 2a). How such relationships between signals and neurogenomic states change across adult development, in relationship to social histories and nest cycle, will also be vital for understanding how behavior-signal relationships are maintained across life. Critically, variation across populations in the relationship between clypeal patterning and adult behavior means that it will be possible to identify gene expression modules that are specific to populations in which patterns relate to condition and correlate with adult behavior (Figure 2b). Developmental factors influencing dominance behavior in North American *P. dominula* should also influence facial patterns, while the same link is not expected for Spanish populations that lack facial patterns. The year-long colony cycle of *Polistes* wasps makes breeding experiments lengthy, but conceivably researchers could generate crosses between Spanish and North American populations (or other populations with or without signals) to map the genetic basis of badges of status and the linkage between signals and behavior. It is important to emphasize that such an

Figure 2



Future directions leveraging geographic variation in *P. dominula* signals. **(a)** Research is needed to understand the developmental mechanisms that link signal and behavior. One possible approach is to examine how late-stage pupae, which express signals but have not yet had social interactions, differ in terms of neurogenomic signatures (or other measures of neural circuitry or receptor expression) depending on their signal. Similar analyses examining the neural differences between low- and high-status individuals across different life stages will reveal fixed versus flexible patterns of signal–gene expression correlations. Comparisons across populations with and without evidence of badge of status use will also help reveal genes and neural circuits that may be important to determining signal–behavior relationships. The schematic example shown here shows a volcano plot showing differential baseline gene expression between high- and low-status signaling individuals. **(b)** Current data suggest that condition-dependent expression of signals is present in some but not all populations of *P. dominula*. Breeding experiments between populations with and without badges of status have the potential to reveal the genetic architecture of signal expression as well as potentially identify genes that mediate condition-dependent expression.

Figure 3



Future directions leveraging geographic variation in individual recognition in *P. fuscatus*. **(a)** Clinal variation in color patterning and likely cognitive abilities related to recognition open up a possibility of conducting clinal analyses to identify loci within the genome that undergo more abrupt shifts than expected coincident with shifts in color pattern diversity of cognitive abilities across populations. In the schematic example shown here, multiple alleles are shown, which show a sharp increase in frequency in relation to color patterning. The fact that multiple alleles show a similar pattern suggests that they may be involved in local adaptation to signaling. **(b)** By measuring cognitive abilities in wild wasps, especially in populations where transitions between recognition and lack of recognition occur, it is conceivable to map the genetic basis of cognitive traits. Here, a Manhattan plot shows a schematic representation of a genome-wide association study (GWAS) with three loci reaching a genome-wide significant threshold (red line). Wasps have relatively large effective population sizes and high recombination rates, making fine-scale mapping of traits measured in wild populations possible. The major challenge will be measuring variation in cognition accurately in hundreds of unrelated individuals.

approach is unlikely to identify the genetic basis of facial processing but rather may reveal how dominance and aggressive behaviors are linked with signal production.

Genetic basis of cognitive evolution — leveraging clinal variation in recognition abilities

The clinal variation observed in color pattern variation in *P. fuscatus* (Figure 1c) strongly suggests that a latitudinal cline in cognitive abilities may also exist across populations. The most southern populations of *P. fuscatus* have essentially invariant color patterns and do not recognize individuals [21]. The cognitive abilities of these wasps to discriminate among faces have not yet been tested but will be important to determine in the near future. There are differences in face learning between *P. fuscatus* and its close relative *P. metricus*, indicating some genetic basis for learning and remembering faces [45]. It is highly plausible that the southernmost populations of *P. fuscatus* also lack many of the cognitive adaptations for individual recognition. Indeed, the evidence for selection on learning and memory genes related to recognition is much stronger in northern populations compared to southern populations. Getting at the genetic basis of complex cognitive abilities, like facial recognition, is a daunting challenge. However, the clinal variation in *P. fuscatus* may present a unique opportunity to conduct population genomic analyses in populations with intermediate levels of recognition abilities to identify genes related to cognitive abilities using clinal analyses and admixture mapping approaches (Figure 3) [66,67]. By measuring cognitive phenotypes across populations, it will also be possible to identify the genomic and cognitive architecture of recognition. For example, if populations vary in different aspects of recognition behaviors, it will allow researchers to identify phenotypic and genomic correlations between cognitive abilities related to social behavior.

Neurobiology of face processing

A recent preprint has provided the first insights into how paper wasp brains might process facial information [68]. While previous neuroanatomical studies have suggested possible modifications of mushroom bodies and visual processing glomeruli in association with face processing [69,70], these new neural data identify specific neural populations that encode facial patterns. Assuming that facial recognition has arisen through some degree of change to neural circuits, the populations lacking facial recognition abilities may also have differences at the level of individual neural responses. The possibility of conducting not only studies examining differences in neurobiological encoding of face processing across different species but also how neural circuits may differ across species will be particularly valuable for teasing apart how neural systems evolve. For example, the extent to which different neural traits may co-vary within and between populations will provide new insights into how evolutionary processes give rise to novel cognitive abilities.

Conclusion

Polistes wasps hold tremendous potential as a model clade to understand variation in the co-evolution of signal production and perception/processing, as well as the biogeographical features that contribute to variation in these traits across populations. Further, facial signaling has likely evolved multiple times across this clade [7] but remains to be broadly tested in other species. This provides additional opportunity to test these features repeatedly across multiple populations and multiple species to identify shared and species-specific factors driving facial signal evolution across ecological, developmental, and genomic dimensions.

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Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare not competing interests. Also, AI was not used in the preparation of this manuscript.

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