1   **Evidence for a selective link between cooperation and individual recognition**

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22   signals, paper wasp

23 **Abstract**

24

25   The ability to recognize and discriminate among others is a frequent assumption of models of
26   the evolution of cooperative behavior. At the same time, cooperative behavior has been
27   proposed as a selective agent favoring the evolution of individual recognition abilities. While
28   theory predicts that recognition and cooperation may co-evolve, data linking recognition abilities
29   and cooperative behavior with fitness or evidence of selection are elusive. Here, we provide
30   evidence of a fitness link between individual recognition and cooperation in the paper wasp
31   *Polistes fuscatus*. Nest founding females in northern populations frequently form cooperative
32   multiple foundress nests and possess highly variable facial patterns that mediate individual
33   recognition. We describe a dearth of cooperative nesting, low phenotypic diversity, and a lack of
34   individual recognition in southern populations. In a common garden experiment, northern co-
35   foundress associations successfully reared offspring while all cooperative southern groups
36   failed to rear any offspring, suggesting a fitness link between individual recognition and
37   successful cooperation. Consistent with a selective link between individual recognition and
38   cooperation, we find that rates of cooperative co-nesting correlate with identity-signaling color
39   pattern diversity across the species' range. Moreover, genomic evidence of recent positive
40   selection on cognition loci likely to mediate individual recognition is substantially stronger in
41   northern compared to southern *P. fuscatus* populations. Collectively, these data suggest that
42   individual recognition and cooperative nesting behavior have co-evolved in *P. fuscatus* because
43   recognition helps mediate conflict among co-nesting foundresses. This work provides evidence
44   of a specific cognitive phenotype under selection because of social interactions, supporting the
45   idea that social behavior can be a key driver of cognitive evolution.

Introduction

The relationship between cognitive abilities and social structure is of long-standing interest to biologists. The social intelligence hypothesis (or social brain hypothesis) posits that selection pressures associated with social relationships in complex societies are an evolutionary driver of cognitive complexity[1–3]. For highly social animals, the abilities to track relationships within the group, cooperate with others, and predict how other individuals will behave in certain situations are considered to be cognitively challenging tasks that may impact individual fitness. Support for this hypothesis comes from comparative studies showing that cognitive performance[4–6] and neuroanatomical proxies for cognition[1,7–9] covary with proxies for social complexity, such as group size or mating system. Recently, general cognitive performance has been linked to group size and fitness in Australian magpies[10]. Additional indirect evidence of selection on cognition imposed by social systems comes from studies of brain gene expression showing, for example, shared transcriptomic signatures of monogamy across divergent vertebrate clades[11]. However, the evidence for the social intelligence hypothesis has come into question because predicted patterns do not hold for some clades and the use of different proxies for cognition and social complexity yields conflicting results[12–17]. More importantly, because of the reliance on such proxies, it has been difficult to identify specific cognitive traits that are under selection to facilitate social interactions.

Models for the evolution of cooperation frequently invoke animal recognition abilities as key mechanisms facilitating the evolution of cooperative behaviors[18–21]. Whereas kin recognition facilitates cooperation between relatives[22], individual recognition has been identified as a building block of social cognition because it allows for cooperation between unrelated individuals[23]. Theory indicates that individual recognition enables cooperation because it allows for the identification of group members and reciprocity between individuals[18,19,24,25]. Indirect evidence of the fitness benefits of individual recognition for cooperative relationships comes from studies showing that territorial animals have higher reproductive success when they have familiar neighbors[26–28]. This result is presumably due to the decreased costs of conflict with territory neighbors when neighborhoods have stable compositions and established "dear enemy" relationships, in which they respect mutual territory boundaries and are less aggressive to each other than they are to strangers[29,30]. Whether individuals that do or do not recognize others vary in fitness outcomes in relation to cooperative behavior, however, has received less empirical attention. Overall, a major limitation to our understanding of the evolution of social cognition is direct evidence of a selective advantage of individual recognition in cooperative groups.

Here, we test the hypothesis that cooperative nesting selects for individual recognition in the northern paper wasp (*Polistes fuscatus*). This species provides an excellent study system for understanding the relationship between individual recognition and cooperation because both behaviors have been reported to vary across populations of this species[31,32]. Female *P. fuscatus* found nests in the spring, either as solitary foundresses or cooperatively with other foundresses. When females found nests cooperatively, they establish an aggression-based dominance hierarchy that determines the amounts of reproduction and work that each individual does[33–35]. Conflict among co-foundresses manifests in aggression between individuals and egg-eating[36]. Individual recognition has been hypothesized to function as a behavioral mechanism that maintains stable dominance hierarchies and minimizes conflict among co-foundresses[37]. The

90 evolution of individual recognition in *P. fuscatus* is associated with increased phenotypic
91 diversity due to the evolution of individually distinctive facial color patterns which function as
92 identity signals and facilitate recognition[38,39] as well as perceptual and cognitive mechanisms
93 related to recognition[40,41]. However, a selective link between cooperation and individual
94 recognition has yet to be demonstrated. Within-species variation in recognition and patterns of
95 cooperation[31,32] provides a powerful system to test for an evolutionary relationship between the
96 two traits. In this paper, we test the hypothesis that cooperation selects for individual recognition
97 using a combination of (1) common garden fitness assays of cooperative nesting behavior
98 between populations with and without recognition, (2) an analysis of geographic clines in identity
99 signaling and cooperation, and (3) population genomic analyses of the strength of selection on
100 cognition loci. These three distinct lines of evidence are all consistent with an evolutionary
101 scenario where cooperation among paper wasp co-foundresses has selected for individual
102 recognition, an evolutionarily novel cognitive ability in northern *P. fuscatus* populations.
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105 **Results**

106

107 **Northern and southern populations of *Polistes fuscatus* differ in color pattern diversity**
108 **and rates of cooperation**
109 Northern populations of *Polistes fuscatus* in New York and Michigan have highly variable color
110 patterns on their faces[38,39,42]; Fig. 1a), regularly form multi-foundress cooperative nests[43], and
111 have been shown experimentally to recognize individuals[42,44]. Here, we identified *P. fuscatus*
112 populations at the southern end of the species range in Louisiana and coastal Georgia that have
113 relatively invariant red faces and low levels of cooperative nesting (Fig. 1a, b). Using whole
114 genome resequencing, we confirmed that these wasps are *P. fuscatus*. Wasps from these
115 southern populations are closely related to those from northern populations, with low genetic
116 differentiation between populations (F_{ST} = 0.07), matching previous findings of long-distance
117 gene flow in *P. fuscatus*[45]. Further, wasps collected from across the range form a monophyletic
118 clade, with wasps from southern populations interspersed with more northern populations (Fig.
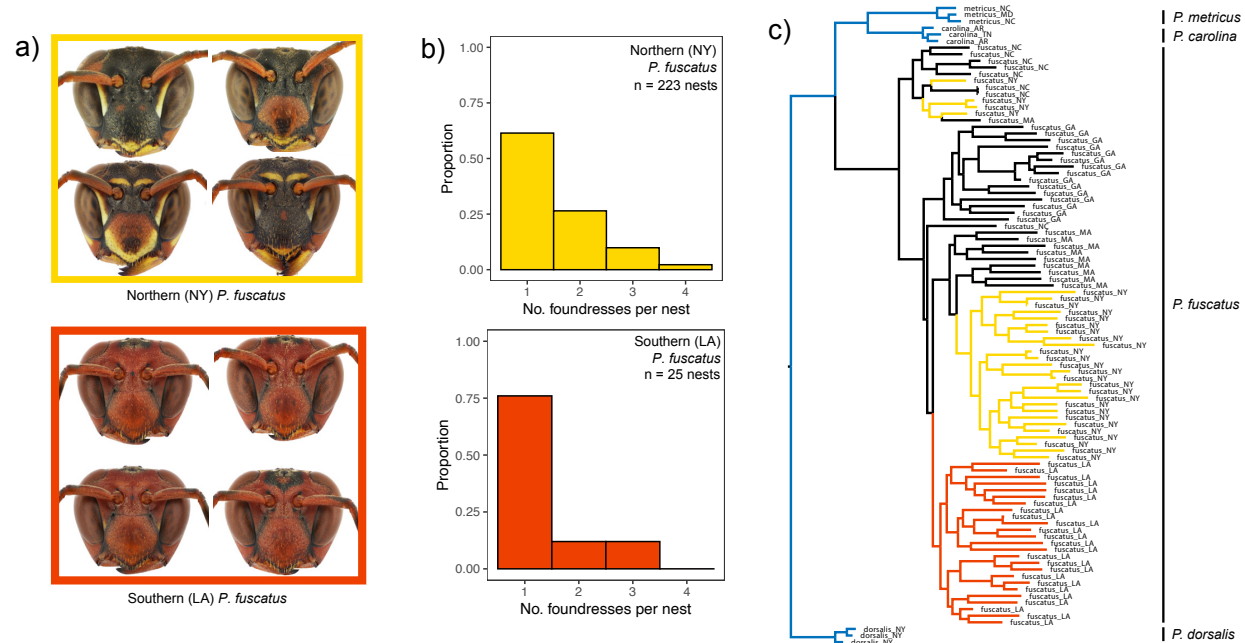119 1c and S1).
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Figure 1. Northern and southern populations differ in face color pattern diversity and cooperation rates. a) Photographs of the faces of wasps from New York (northern; top) and Louisiana (southern; bottom), representing the diversity of face color patterns observed in these two populations. b) Histograms showing the distribution of the number of foundresses per nest in New York and Louisiana populations, demonstrating greater cooperation in New York. c) A phylogeny generated from SNP data from whole genome sequencing of *Polistes fuscatus* from across the geographic range, confirming that samples from northern and southern populations cluster together as a monophyletic clade, indicating they belong to the same species. Three closely related species (*P. metricus*, *P. carolina*, and *P. dorsalis*) are included as outgroups. Species name and US state of origin are given for each DNA sample. Branches are colored to highlight samples from New York (yellow) and Louisiana (red), samples from North Carolina, Massachusetts, and Georgia are black, and outgroups are colored in blue. See Fig. 5 for example faces of *P. fuscatus* from other populations.

Populations differ in individual recognition behavior

Individual variation in color patterns of female *P. fuscatus* from New York and Michigan has previously been shown to mediate individual recognition[38,42]. Conversely, the lack of color pattern variation in other species of *Polistes* is associated with a lack of individual recognition[39]. Therefore, we reasoned that southern *P. fuscatus* populations lacking variable color patterning would also fail to show individual recognition. To test for individual recognition, we compared aggression between encounters of familiar and unfamiliar wasps from populations at the northern and southern portions of the range of *P. fuscatus*, following previous studies[32,39,44,46]. We compared the aggression between pairs of wasps that interacted for the first time (Day 0, 'unfamiliar') with their aggression when they met again two days later (Day 2, 'familiar'). We controlled for the possibility of a general decrease in aggression over time that was not specific to a particular individual by also measuring the aggression between pairs of unfamiliar wasps on

149   Day 1 and Day 3 of the experiment (n = 40 northern wasps, 42 southern wasps, 164 total trials).
150   To compare the behavior of wasps from these two populations in the same experiment and at
151   the same life stage, we collected foundress-destined female wasps ("gynes") in the fall from
152   northern and southern populations and overwintered them in the lab so they could emerge from
153   overwintering at the same time in a controlled environment.
154   Wasps from both populations interacted most aggressively on the first day (Day 0) of the
155   experiment (Fig. 2). There were significant differences in aggression between days for both
156   northern (χ^2 = 10.66, p = 0.014) and southern wasps (χ^2 = 21.78, p < 0.001). However, only
157   northern wasps showed evidence of individual recognition; northern wasps were significantly
158   less aggressive to familiar individuals they encountered on Day 2 compared with the first time
159   they encountered these individuals on Day 0 (t = 3.21, p = 0.010). However, they did not show
160   significantly less aggression to other unfamiliar individuals on Day 1 (t = 1.79, p = 0.288) or Day
161   3 (t = 2.11, p = 0.159) relative to their initial aggression on Day 0. In contrast, southern wasps
162   showed a general decrease in aggression after Day 0 regardless of whether the wasp they were
163   interacting with was familiar or unfamiliar. Compared with Day 0, southern wasps were
164   significantly less aggressive on Day 1 (t = 3.25, p = 0.009), Day 2 (t = 4.36, p < 0.001), and Day
165   3 (t = 3.45, p = 0.005). Overall, these data indicate that southern wasps use simpler decision
166   rules and show a generalized decrease in aggression with repeated social interactions, while
167   the decrease in aggression of northern wasps was specific to particular individuals they had
168   encountered previously.
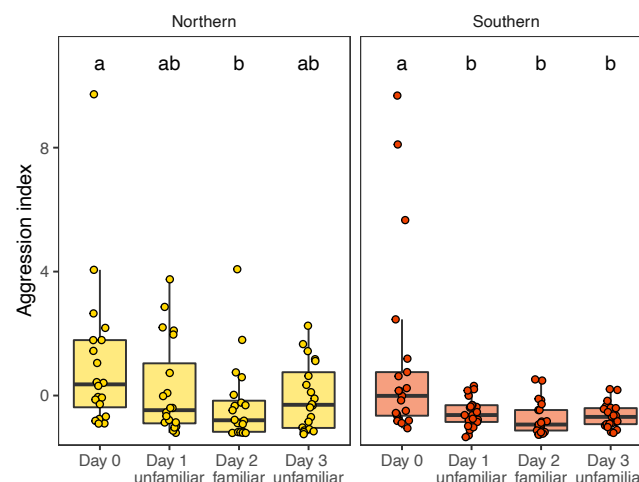169

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171   **Figure 2.** Results from experiments testing for individual recognition in northern and southern
172   populations. On Day 2, wasps interacted with the same individual they interacted with on Day 0,
173   while on Days 1 and 3, they interacted with individuals they had never encountered before.
174   Different letters indicate days that are significantly different from each other from post-hoc
175   comparisons within each population. Boxplots and individual data points show the aggression
176   index computed from a PCA of the total numbers and durations of aggressive behaviors
177   exhibited by both wasps during the trials.
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Recognition abilities are associated with differences in social organization between populations

The ability to recognize and discriminate among potential social partners is predicted to shape social networks and influence how animals interact with each other[47,48]. Therefore, we assessed whether recognition differences between northern and southern populations manifested in different social organizations and interactions. We established a lab common garden experiment in which the lab-overwintered foundresses were housed in groups of four individuals per enclosure. Each enclosure included four nesting huts, construction paper to provide nesting material, and *ad libitum* food and water. These groups were composed of three individuals from one nest of origin and another individual from a different nest. This design was chosen to reflect how cooperative nesting associations are often thought to occur, with co-foundresses often being former nestmates, but with unrelated foundresses sometimes joining nests[33,49]. We constructed social networks based on nocturnal associations of individuals before nests were established; paper wasps often "huddle" together in groups (or "cluster", *sensu* West-Eberhard, 1969) when they are not on a nest. Therefore, we recorded which individuals were huddling together each night.

Social networks varied between enclosures of northern versus southern wasps. The mean huddle size per group was larger for southern wasps than northern wasps ($W = 20$, $p = 0.006$, Fig. 3a), and the within-group variance in huddle size was greater for southern wasps than northern wasps ($W = 16$, $p = 0.003$, Fig. 3b). These results suggest that southern wasps are more gregarious but form less stable associations than northern wasps. We tested this idea more directly by using these associations to construct social networks for each group. From these social networks, we computed what we define here as "edge evenness". Analogous to species evenness in ecology[50], edge evenness describes how evenly distributed relationships are across the network. Networks in which individuals interact at similar rates with all other individuals in the network have higher edge evenness than those in which some pairs or trios of individuals have stronger relationships than others. Social networks of southern wasps showed relatively even associations among individuals with little apparent sub-structure in the network (Fig. 3c, Fig. S3). In contrast, networks of northern wasps were characterized by stronger associations between pairs or trios of individuals to the exclusion of other individuals (Fig. 3c, Fig. S2). The edge evenness of southern wasps was greater than that of northern wasps ($W = 19$, $p = 0.003$, Fig. 3d). Overall, these data suggest that southern wasps are more gregarious but less discriminating about who they associate with.
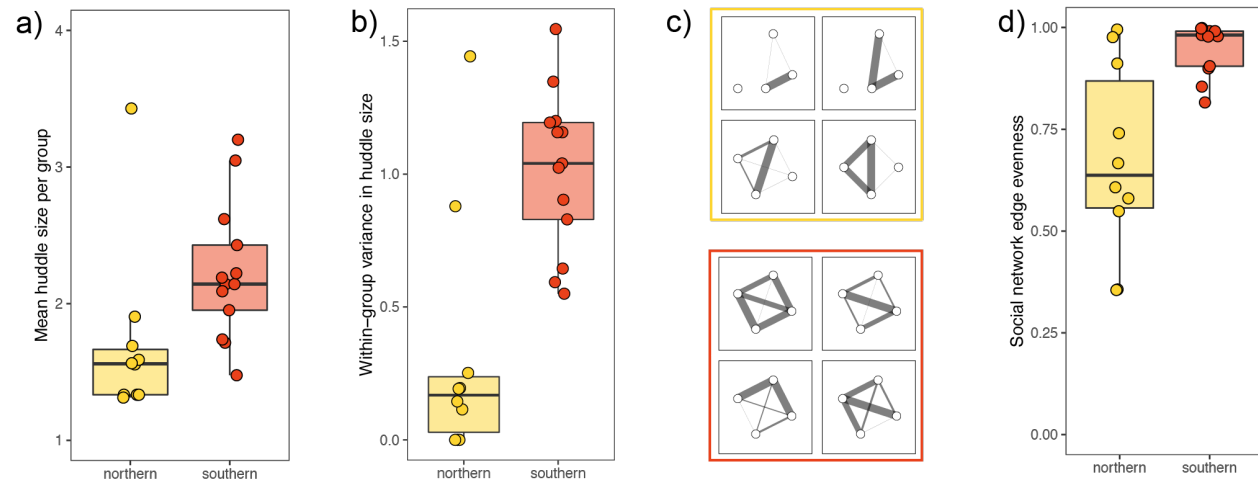
Figure 3. Pre-nesting associations of northern wasps are smaller, more stable, and less evenly distributed across the social network compared with those of southern wasps. a) Mean number of individuals per huddle (huddle size) per group prior to nest establishment. b) Within-group variance in huddle size across observation days. c) Representative social networks derived from pre-nesting association data for northern (top) and southern (bottom) wasps (networks for all groups can be found in supplemental figures S2 and S3). d) Edge evenness of social networks for northern and southern wasps. Higher values indicate connections are relatively evenly distributed among individuals in a network, while lower values indicate more skewed networks with stronger subgroups within the network.

Cooperative southern nests are unsuccessful and fail to rear brood

Individual recognition in *P. fuscatus* is hypothesized to be an important behavioral mechanism stabilizing dominance hierarchies and reducing conflict among co-foundresses[37]. Therefore, we monitored the groups of wasps in the lab common garden experiment to compare the nesting success of multi-foundress wasps from both populations. Wasps from both populations started nests in the lab at similar rates. Among the groups that initiated nests in the lab, southern groups showed less stable nesting associations and less evidence of successful cooperation. Nests began with small pedicels attached to the ceilings of the cardboard huts and then were built out several cells at a time. In total, 4 northern groups and 3 southern groups tended nests. The nests were established between 4 and 12 days after housing. Interestingly, both northern and southern nests had multiple foundresses, and the mean number of foundresses per nest was similar between populations (Fig. 4a). However, the number of foundresses observed on a nest was not stable through time, and foundress number varied more for some nests than others (Fig. 4b). Overall, there was a trend of greater variance in the number of foundresses per nest for southern nests than northern nests (Fig. 4c), suggesting southern foundress associations were less stable.

Strikingly, all the southern multi-foundress nests failed to develop; these nests were built to between 7 and 8 cells, and eggs were laid in these cells, but the eggs never developed into larvae and the nests were never expanded with additional cells. In fact, new eggs continued to be laid in cells throughout the two months of the experiment, clearly indicating previous eggs

246 were eaten or removed by foundresses on the nest (Fig. 4d). In contrast, all the northern multi-
247 foundress nests developed normally, with eggs developing into larvae and pupae (Fig. 4d).
248 Cells continued to be added to these nests, and the number of cells after two months ranged
249 from 17 to 31. Two northern nests had workers successfully emerge after two months. Overall,
250 the biomass of northern nests was much greater than that of southern nests at the end of two
251 months (Fig. 4d). Additionally, we know that the failure of southern multi-foundress nests to
252 develop in our lab was not due to some problem with housing conditions that were specific to
253 southern wasps, because two solitarily housed southern wasps built successful nests and
254 reared offspring to pupation as single foundresses under the same lab conditions at the same
255 time (Fig. 4d). This nesting experiment suggests that instability and conflict among southern co-
256 foundresses prevented nesting success, providing evidence that individual recognition in
257 northern populations is key to enabling stable dominance hierarchies and successful
258 cooperation among co-foundresses.
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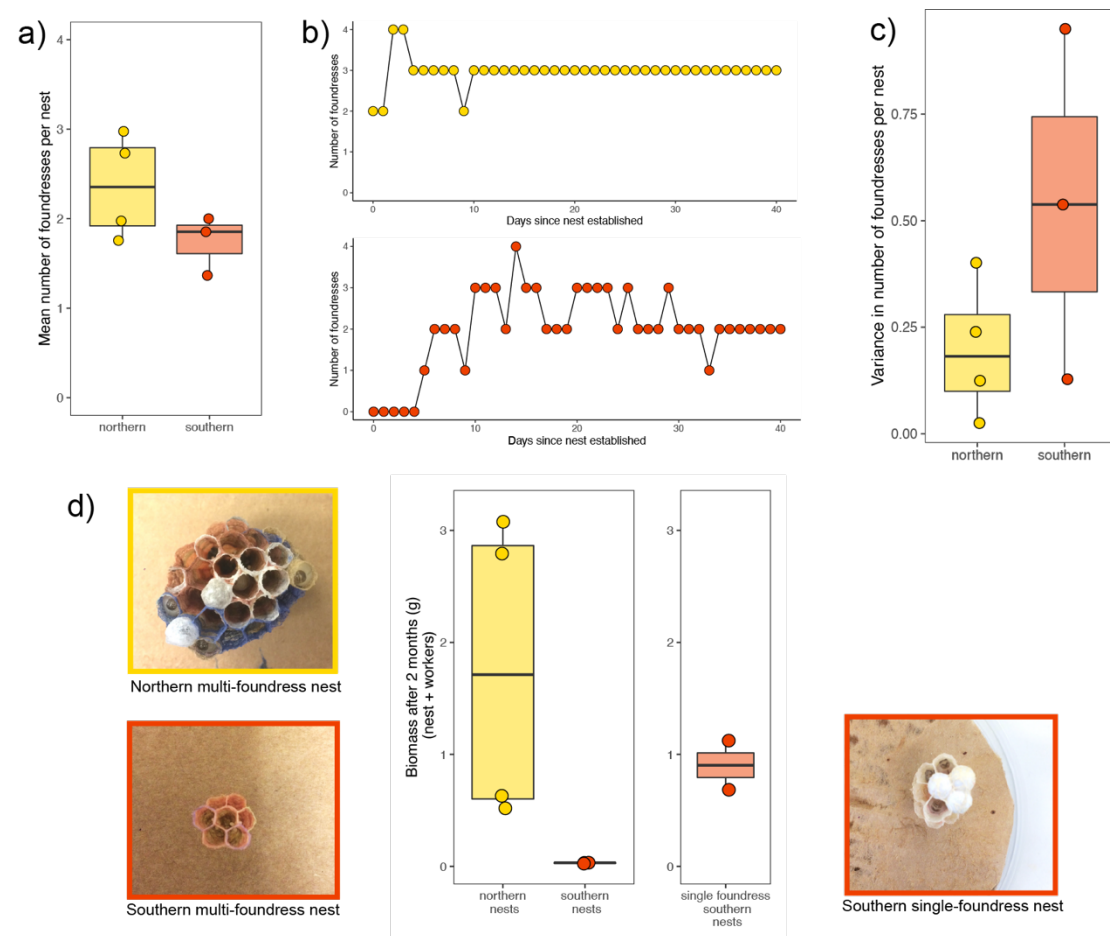260

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262 **Figure 4. Southern multi-foundress nests failed to rear offspring.** a) The mean number of
263 foundresses per nest. b) The number of foundresses observed on a nest each day, for two
264 example nests, displaying differences in the stability of foundress associations for different
265 nests. c) Variance in the number of foundresses per nest. d) Nest biomass after two months of

266   development, with photographs of example nests for each population. Also shown are nest
267   biomass for southern single-foundress nests, which displayed normal development under the
268   same conditions.
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271   Identity signal diversity is associated with geographic variation in cooperation rates
272   Comparisons of recognition and nesting behavior between the northern and southern
273   populations of *P. fuscatus* provide empirical support for the hypothesis that mediation of conflict
274   and cooperation among co-nesting foundresses has been a selective agent favoring individual
275   recognition in this species. If cooperative nesting has been a selective agent favoring the
276   evolution of individual recognition in *P. fuscatus*, then identity signals that facilitate recognition
277   should co-vary with rates of cooperative nesting across the species range, with regions with
278   higher rates of cooperative nesting also showing greater color pattern diversity.
279   We collected female *P. fuscatus* across the East Coast of North America, spanning
280   much of its latitudinal geographic range, and measured color pattern diversity (Fig. 5a). We
281   chose to focus on the latitudinal gradient because of previous work suggesting cooperation
282   rates in the north are higher for this species[31]. To quantify color pattern variation, we
283   photographed faces and used a novel multi-step methodology for extracting homologous color
284   patterns from images. We first normalized the lighting in the photos and aligned face images
285   using homologous landmarks. We then segmented the images by color, by forcing each pixel to
286   the nearest of three colors: yellow, red, or black (example images in Fig. S6). Finally, we
287   subjected these color-segmented face images to a PCA and used a statistically significant set of
288   24 components to characterize variation among faces (Fig. S7, Table S2). We only sampled
289   one wasp per nest to reduce the possibility that individuals in the sample were close relatives
290   who might bias samples to being more homogeneous since color patterning is highly heritable in
291   this species[51]. We computed the pairwise Euclidean distance between faces in PCA space for
292   each site and took the mean of these distances as our measure of face diversity for a site.
293   There was a strong positive relationship between latitude and face diversity in a site (R^2 = 0.74,
294    $F_{1,16}$ = 46.1, p < 0.001; Fig. 5b). The relative lack of facial diversity was especially pronounced in
295   the southernmost populations from Louisiana and coastal Georgia, which occur below 32°
296   latitude (Fig. 5b). Compared with these southernmost populations, face diversity was about 1.6
297   times higher at around 35° latitude in South and North Carolina, with diversity increasing further
298   in more northern populations (Fig. 5b).
299   We observed nesting behavior in southern wasp populations and added these data to
300   previously published datasets of nesting behavior in *P. fuscatus*[31,43]. There is a positive
301   relationship between the number of foundresses per nest and latitude (z = 6.81, p < 0.001, *n* =
302   2,021 nests, Fig. 5c), consistent with the findings of earlier studies[31]. At the southern end of the
303   range, the majority of foundresses nest solitarily, whereas at the northern end of the range,
304   most foundresses are part of cooperative groups (e.g. 56% solitary in Louisiana, 60%
305   cooperative in New York). Additionally, the occasional cooperative nests that were observed in
306   the southern portion of the range never had more than 3 foundresses. At northern latitudes,
307   large nesting associations of 4 or 5 foundresses occur with some regularity, and groups of 6 or
308   7 foundresses are observed as well (Fig. 5c). Results from these two clinal datasets are

309 consistent with the hypothesis that cooperation selects for individual recognition by favoring
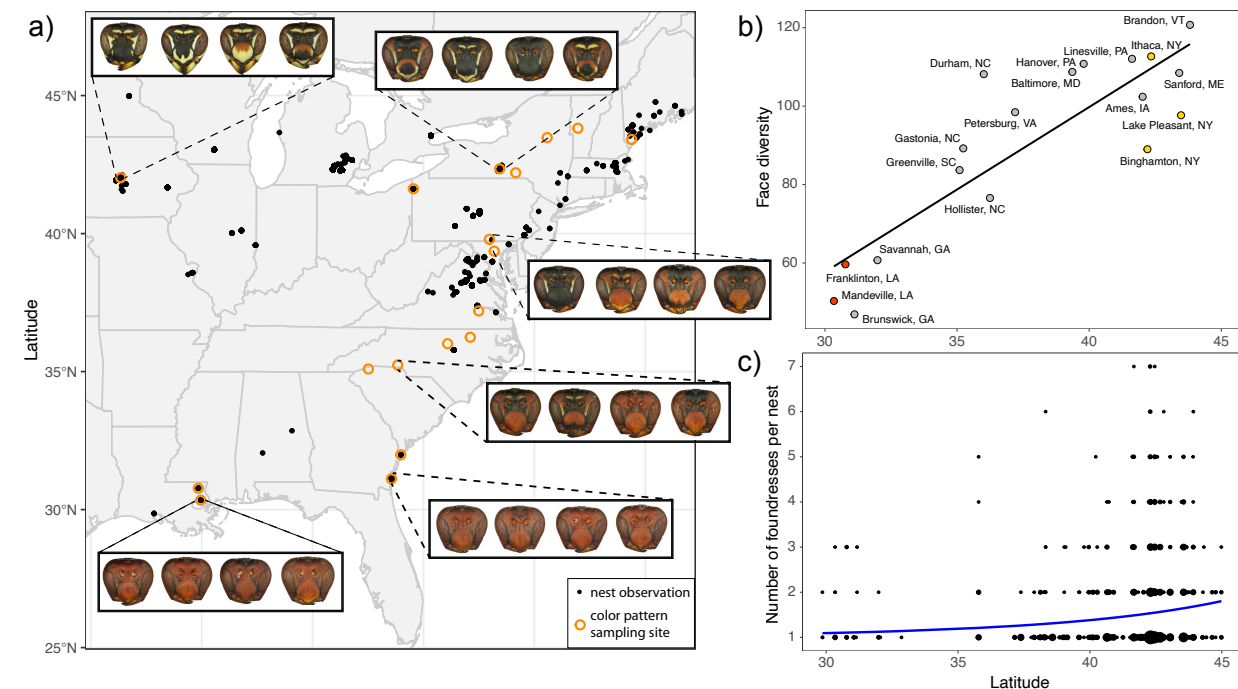310 individuals who signal their identity.

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**Figure 5. Color pattern diversity and cooperative nesting rates both increase with
latitude.** a) Map of sampling locations for color pattern diversity and cooperation rates of *P.
fuscatus* wasps. Black points represent nest observations taken from the WASPnest dataset[31,43]
as well as new observations reported in this paper. Orange open circles mark sites where we
collected and photographed wasps to measure color pattern variation. Also shown are
photographs of representative individuals from several sites to demonstrate the color pattern
variation across the range. b) The relationship between face diversity and latitude across the
range of sampling sites fit with a linear regression line. Face diversity was measured as the
mean distance between faces within a population in PCA scores computed from color
segmented images. Points representing sites in Louisiana are colored red, and those
representing sites in New York are colored yellow. c) The relationship between the number of
foundresses per nest and latitude fit with a zero-truncated Poisson regression line. The sizes of
points are scaled according to the number of observations

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Genomic evidence of selection on cognition associated with individual recognition
Previous population genomics studies of northern *P. fuscatus* populations identified multiple
strong recent selective sweeps in genomic regions related to learning, memory, and visual
processing[52]. Evidence of selection on learning, memory, and visual processing was
substantially weaker in two closely related species, *P. metricus* and *P. dorsalis*, which lack
individual recognition, suggesting that the patterns of selection in northern *P. fuscatus*
populations may be associated with individual recognition. If the signatures of selection on these
loci are the result of an evolutionary advantage of individual recognition in the more cooperative

335   northern populations, these same loci are predicted to show weaker or no evidence of selection
336   in southern populations due to the absence of individual recognition. Therefore, we repeated
337   this analysis using southern populations to directly compare evidence of recent selective
338   sweeps between northern and southern populations. Selective sweeps were identified using
339   SweepFinder2[53], which uses deviations in the local site frequency spectrum to generate a
340   composite likelihood ratio (CLR) of a selective sweep in that genomic region. Larger CLR values
341   provide evidence of stronger selection, more recent selection, selection on newer mutations, or
342   some combination of these phenomena[52].
343   Both northern and southern populations show evidence of recent strong positive
344   selection, with some selective sweeps shared across populations and other selective sweeps
345   that are unique to only one population (Fig. 6a, S8). We assessed patterns of selection on loci
346   that likely contribute to cognitive abilities underlying individual recognition using two
347   approaches. First, we compared scaled CLR values between northern and southern populations
348   for loci annotated with gene ontology (GO) terms related to learning, memory, and visual
349   processing, directly replicating the previously published analysis of northern *P. fuscatus*
350   populations[52]. Scaled CLR values for these annotated "visual cognition genes" were elevated in
351   both populations, but there was a significant interaction between population and gene type
352   (gene type: χ^2 = 82.43, $p < 0.001$; population: χ^2 = 268.73, $p < 0.001$; gene type × population: χ^2
353   = 28.50, $p < 0.001$), indicating that selection on visual cognition genes is stronger in northern
354   populations than southern populations (Fig. 6b). Second, we compared scaled CLR values
355   between northern and southern populations for genes that are differentially expressed during
356   social interactions in northern *P. fuscatus*[54]. Experimental evidence for differential regulation in
357   response to social interactions suggests these genes could play a role in recognition behavior in
358   this species. Again, we find evidence of stronger selection on socially regulated genes in
359   northern compared to southern populations (gene type: χ^2 = 206.56, $p < 0.001$; population: χ^2 =
360   78.85, $p < 0.001$; gene type × population: χ^2 = 78.69, $p < 0.001$; Fig. 6c). Rather than comparing
361   the relative evidence of selection across all genes, we can also ask whether genes in these two
362   datasets are overrepresented among the most strongly selected genes. We find greater
363   enrichment of strongly selected genes in northern compared to southern populations for both
364   GO term and socially regulated gene sets (Table S3). Together, these data show that,
365   compared with southern populations, selection in the north has been stronger on genes that are
366   likely involved in the perceptual and cognitive abilities of wasps to recognize individuals and
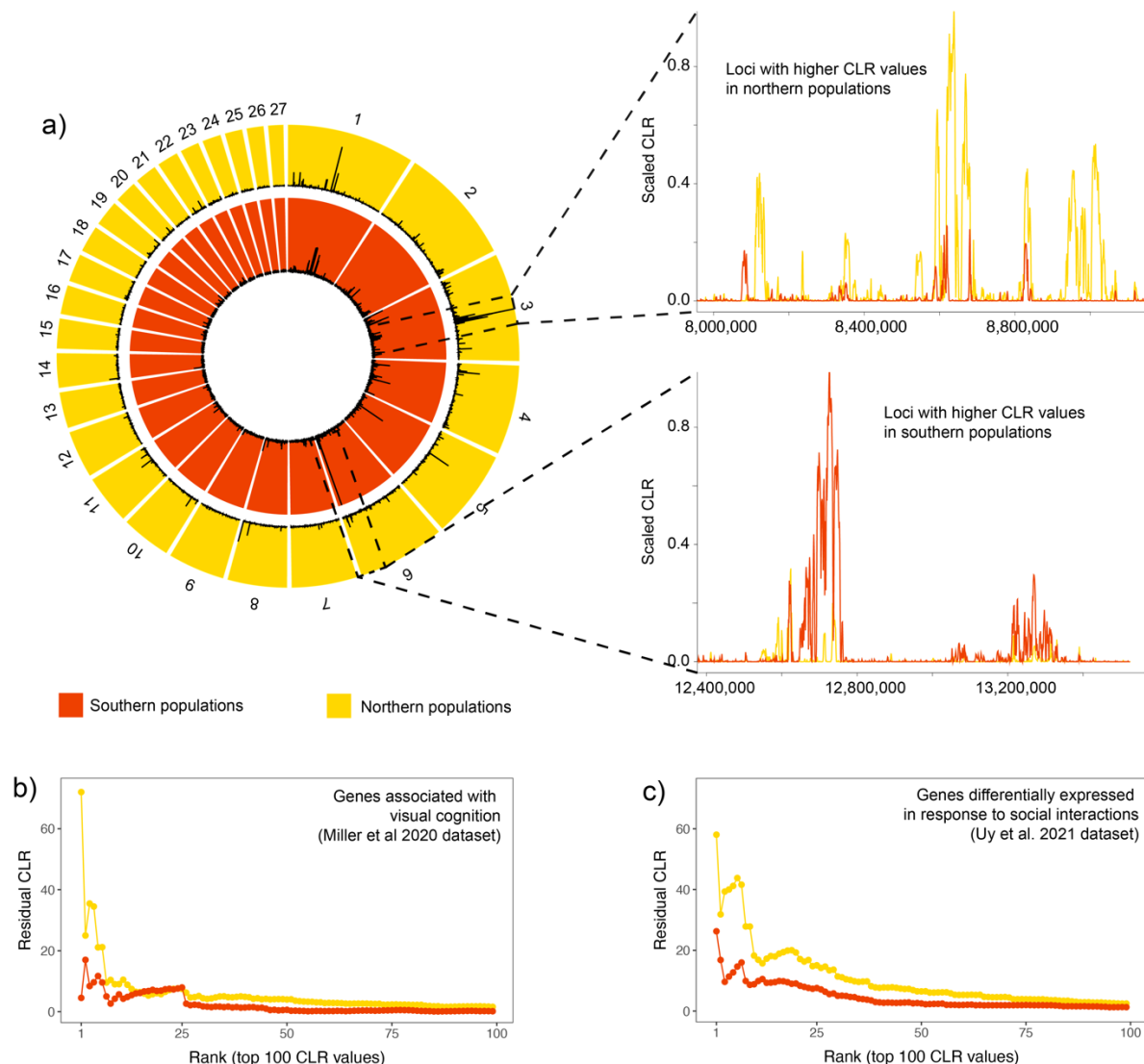367   mediate social interactions.

Figure 6: Stronger and more recent selection on candidate cognition loci in northern populations. a) Comparison of scaled composite likelihood ratio (CLR) values between northern (outer) and southern (inner) populations for the largest 27 scaffolds in the *P. fuscatus* genome. CLR values have been smoothed over 10,000 bp windows. Examples of regions where CLR values are greater in the north (top) and south (bottom) are shown. b & c) Residual CLR values for the top 100 CLR values of putative social cognition genes from datasets of a) genes with gene ontology (GO) terms related to learning, memory, and visual processing and b) genes that are differentially expressed in response to social interactions in northern populations. Both data sets show that northern populations have elevated signatures of selection on putative social cognition genes.

Discussion

Despite longstanding interest in the evolutionary relationship between social organization and recognition, direct evidence that recognition abilities are under selection for social interactions

385   has been missing. This limitation is due, in part, to the fact that within-species variation in
386   recognition abilities has rarely been documented. Using within-species variation in cooperation
387   and individual recognition in the northern paper wasp (*Polistes fuscatus*), we provide three
388   distinct lines of evidence that together provide strong support for the hypothesis that
389   cooperation selects for individual recognition. First, in a common garden lab nesting experiment,
390   southern wasps lacking individual recognition (Figs 1-2) were more gregarious but had less
391   stable social networks. Southern multi-foundress nests failed to successfully rear offspring,
392   providing evidence of a direct fitness consequence of the absence of individual recognition in
393   cooperative groups (Figs 3-4). Second, across the range of this species, color pattern diversity
394   co-varies with rates of cooperation such that identity signals used for individual recognition are
395   most apparent in the more cooperative northern populations (Fig 5). This pattern is consistent
396   with expectations of selection favoring signalers who signal their identity to facilitate recognition
397   in cooperative populations[38,55–57]. Third, genomic analyses reveal stronger signatures of
398   selection in northern populations, compared with southern populations, on genes related to
399   visual cognition and social experience (Fig 6). This pattern is consistent with expectations of
400   selection favoring improved perceptual and cognitive abilities to recognize individuals in more
401   cooperative populations[23,58,59].
402

403   **Evolution of recognition abilities**
404   The adaptive value of recognition and discrimination is often conceptualized as the
405   shifting of optimal thresholds for "accepting" or "rejecting" individuals[60–62]. There are many
406   examples of plastic shifts in acceptance thresholds showing that animals often adjust decision
407   rules in an adaptive way[e.g.,63–66], but less work has documented evolutionary changes in the
408   decision rules that determine acceptance thresholds[67]. The results of our behavioral
409   experiments suggest that southern *P. fuscatus* foundresses universally reject or accept
410   conspecific foundresses depending on the context. Wasps from these populations are
411   characterized by a lack of individual recognition, a generalized decrease in aggression to
412   conspecifics through time, and gregarious, indiscriminate huddling behavior in pre-nesting
413   associations. Similar patterns of aggression to southern *P. fuscatus* were seen in the closely
414   related (and also rarely cooperatively nesting) *P. metricus* using the same trial design[39]. Thus,
415   decision rules of southern *P. fuscatus* likely represent the ancestral state for this species.
416   Therefore, the evolution of individual recognition in *P. fuscatus* is associated with increasing the
417   specificity of acceptance and rejection decision rules depending on specific individuals rather
418   than behavioral context, as evidence of discriminating behavior was observed in all behavioral
419   experiments. The result that individual recognition in wasps evolved from an ancestral state of
420   context-dependent universal acceptance provides an important example of how the decision
421   rules guiding acceptance thresholds may be targets of selection during the evolution of
422   recognition systems.
423   Our results have multiple implications for how social complexity relates to the cognitive
424   demands of social life[68–70]. First, our results add to a growing literature demonstrating that group
425   size and social complexity are not the same[9,70–72]. Initial expectations might be that individual
426   recognition should be associated with larger social groups in general. This pattern is observed
427   in the finding that the number of foundresses per nest and signal identity information covary
428   latitudinally in *P. fuscatus* (Fig. 1b; Fig. 5c). However, southern wasps actually formed larger

429   huddles, on average, but these huddles were less stable. Social network analysis revealed that
430   northern wasps had stronger relationships among sub-sets of individuals to the exclusion of
431   others, while southern wasps had relatively evenly distributed relationships across the network.
432   This result is consistent with the idea that individual recognition allows for relational social
433   complexity within groups[48,71] and highlights that group size alone may be a poor proxy for social
434   complexity in many contexts. Second, our work provides insights into which features of social
435   relationships may drive increased cognitive complexity. Social interactions can involve
436   cooperation and/or conflict, and both have been hypothesized to be cognitively
437   demanding[17,69,73–76]. The common garden nesting experiments suggest that conflict among co-
438   nesting foundresses is a main driver of selection for individual recognition. The southern wasps
439   failed to rear offspring because of oophagy, a sign of conflict among the foundresses. These
440   data argue for a role of recognition in facilitating cooperation by managing conflict.
441   Results from the common garden experiments shed light on the behavioral mechanisms
442   favoring recognition but are only one means to test for evidence of selection linking cooperation
443   and individual recognition. The results of our geographic sampling of color pattern and
444   cooperation are consistent with expectations of selection favoring individuals who signal their
445   identity to facilitate recognition in cooperative populations[38,55–57]. The extensive variation in color
446   patterns within and between populations of *P. fuscatus* has long been a source of consternation
447   and puzzlement for students of paper wasps[77,78]. Geographic variation in color patterning is
448   commonly reported in insects and other animals and is frequently linked to selection imposed by
449   the abiotic environment, predation, or sexual selection[e.g.,79–84]. Our data suggest social selection
450   among female foundresses is the driver of color pattern variation in *P. fuscatus*. These data add
451   to a growing body of research showing that identity information in signals often correlates with
452   measures of social complexity, suggesting social environments can impose selection on signals
453   to make individuals more recognizable[85–90].
454
455   **Evidence for recent evolution of individual recognition in *P. fuscatus***
456   Individual recognition appears to be evolutionarily derived and unique to *P. fuscatus*
457   among closely related species[39,91]. Further, population genomic analyses have revealed multiple
458   selective sweeps within the last few thousand years that are enriched for genes likely involved
459   in individual recognition, such as genes related to visual processing, cognition, learning, and
460   memory[52]. Many of these selective sweeps occurred since the last glacial maximum when the
461   Laurentide Ice Sheet covered much of the current northern range of *P. fuscatus*[92]. Together with
462   our results demonstrating individual recognition and identity signals are absent in southern
463   populations (Figs 2 and 5), these studies suggest a hypothesis in which ancestral populations
464   lacking identity signals with low rates of cooperation recently evolved individual recognition as
465   an adaptation to enable successful cooperation as the species expanded northward following
466   the last glacial retreat. The ecological factors that favor cooperation at northern latitudes are
467   currently unknown, but cooperative nesting decreases the probability of nest failure before
468   workers emerge[34], and shorter summers in northern climates might reduce the probability that
469   solitary foundresses can make multiple nesting attempts and still succeed. It will be important to
470   test this hypothesis in the future.
471
472   **Why do southern populations lack individual recognition?**

473   Given the low population genetic structure at the continental scale of *P. fuscatus*[45],
474 population differences in color patterning and selection on social cognition suggest multiple
475 possibilities for why we do not observe individual recognition or color pattern diversity in
476 southern populations. First, it may be the case that alleles related to individual recognition arose
477 recently in northern populations and have yet to reach southern populations. Evidence for this
478 scenario comes from a previous analysis of selection in this species that demonstrated that
479 many selective sweeps involved recent *de novo* mutations[52]. However, the lack of population
480 structure suggests that the recent evolution of individual recognition is unlikely to fully explain
481 the geographic pattern of coloration and recognition abilities, as we would expect recognition-
482 associated alleles to quickly spread if they were beneficial in all populations. Indeed, migration
483 of alleles under strong selection in northern populations into southern populations may explain
484 some, though not all, of the shared signatures of selection found here. Another possibility is that
485 individual recognition is costly in *P. fuscatus*, meaning it is only favorable when rates of
486 cooperation are sufficiently high to make the benefits of recognition outweigh these costs. In
487 particular, the cognitive abilities related to recognition are assumed to be costly in terms of
488 growth and maintenance of the requisite neural tissues[93–95]. Low rates of cooperation in
489 southern populations may then remove the potential benefits of the cognitive mechanisms
490 related to individual recognition, so the alleles for these traits are selected against. Lack of
491 recognition behavior would then also remove benefits of signaling identity via distinctive color
492 patterns. A similar model may explain the lack of individual recognition described in a *P.*
493 *fuscatus* population in mountainous regions of central Pennsylvania with relatively low rates of
494 cooperation and relatively low color pattern diversity[32]. However, models of identity signal
495 evolution suggest that increased signal diversity may be favored even under very small fitness
496 benefits provided the costs of distinctiveness are very small or non-existent[56]. Thus, the
497 absence of color pattern diversity in the southern populations suggests that there may be
498 selection either against particular color pattern variants involved in identity signaling or selection
499 favoring the red facial color pattern that is common throughout the Gulf coast region. Future
500 comparative analyses of clinal variation in alleles associated with cognition and color patterning
501 will be useful to help discriminating among the hypotheses raised by the present dataset.
502

503 **Conclusions**
504 Social structure and cognitive abilities vary widely among animals. The extent to which they are
505 linked has been an ongoing subject of debate, often involving proxies of both social behavior
506 and cognition. Using three distinct types of studies examining common garden fitness assays,
507 geographic patterns of behavior and signal diversity, and population genomic analyses of
508 selection on cognition loci, we provide cohesive evidence that cooperation favors the evolution
509 of individual recognition. Individual recognition is a bedrock of many complex social behaviors.
510 Our study demonstrates that understanding the factors that shape the evolution of specific
511 cognitive abilities rather than just brain size or other proxies of general cognition can provide
512 clear evidence for a link between social behavior and cognitive evolution.
513

514

515 **Methods**
516

Individual recognition experiment

Experiments were performed on lab overwintered *P. fuscatus* gynes that were collected in the fall of 2019, from Northern (NY and ME) and southern (LA) populations. Individuals were overwintered in plastic deli cups along with their nestmates, and provided water and sugar, as well as crumpled construction paper in which to hide. They were overwintered for approximately three months at 4°C for northern wasps and 10°C for southern wasps, to account for natural differences in winter temperatures between these populations. Following overwintering, wasps were weighed, paint-marked on their thorax (Testors enamel paint), and housed individually in deli cups for 5-6 days before the start of the experiment at a temperature of approximately 23°C with 12:12 light–dark cycle.

Separately for each population, we ranked individuals by weight to create three weight classes of similarly sized individuals. We then paired individuals together such that they always encountered other individuals from different nests but from the same weight class. These criteria resulted in 40 northern and 42 southern wasps for the experiment. On Day 0 of the experiment, pairs of wasps were placed together in plastic petri dishes and their interactions were filmed for 45 mins. Immediately following this trial, the pair was housed together a new deli cup overnight to give the individuals additional time to become familiar with each other. Between 9 and 10 AM the next morning (Day 1) these paired wasps were then put into solitary housing where they remained for the rest of the experiment. On Day 1 and 3 of the experiment, wasps were paired and filmed interacting as described above but with new individuals they had never encountered before. On Day 2 of the experiment, they were paired again with the same individual they interacted with on Day 0. We additionally controlled for potential day effects by starting the experiment for half of the wasps on one day and the other half on the subsequent day. All interaction trials occurred during the afternoon (13:00-18:00) at temperatures ranging from 25 to 26°C.

We scored aggressive behaviors for the first 15 minutes of each trial using BORIS[96]. Our ethogram was developed based on a combination of established ethograms for *Polistes*[35], and our own preliminary observations of the aggressive behaviors that are common in this type of experiment. We scored the following as point behaviors (instantaneous behaviors that are counted for each occurrence): dart, a rapid forward movement towards another individual; snap, open mandibles towards another individual; bite, mandibles closing on another individual; kick, rapid leg extension that appeared to push off or push away another individual. We scored the following as state behaviors (behaviors that have durations) and denoted the start and stop times: approach, orienting and moving towards another wasp to engage in an interaction; chase, one wasp pursuing another wasp who appears to be avoiding the interaction; antennation, probing another individual with antennae; grapple, wrestling-type behaviors with both individuals engaged with biting and kicking. Each behavior was coded to one of the two subjects. Observers were blind to treatments and experiment day when scoring behaviors.

For each trial (*n* = 164), we summed the total numbers of point behaviors, and summed the durations of all state behaviors. We included all behaviors associated with aggressive physical interactions (approach, bite, dart, dodge, kick, snap, antennation, chase, and grapple) in a principal components analysis (centered and scaled) using the 'prcomp' function in R. We took the first principal component, which explained 33% of the variation, as an aggression index (see Table S1 for factor loadings). For statistical models, the aggression index was log-

561 transformed to better meet assumptions of parametric tests. Separately for each population, we
562 fit linear mixed effects models of the aggression index using the *lme4* package[97], with
563 experiment day as a fixed effect and cohort as a random effect. Tukey adjusted post-hoc
564 comparisons among experiment days were performed using the *emmeans* package[98].
565

566 **Common garden lab nesting experiment**
567 Lab overwintered wasps from the recognition trials were individually marked and housed in
568 groups of four individuals: three individuals from one nest of origin and another individual from a
569 different nest. Groups of wasps were housed in enclosures consisting of two 36.8 cm × 22.2 cm
570 × 24.8 plastic Kritter Keepers (Lee's Aquarium & Pet Products) stacked on top of each other,
571 with ventilation holes drilled into the sides and top. Four 10 cm x 10 cm cardboard nesting "huts"
572 were attached to the top of the enclosure to provide each wasp the option to either nest alone or
573 co-found a nest with other individuals. Each enclosure was provided with ample crumpled
574 cardboard paper to provide nesting material, as well as a sugar cube, honey, water, and, once
575 nests were established, an *ad libitum* variety of larval insects (waxworms (*Galleria mellonella*),
576 hornworms (*Manduca sexta*), and mealworms (*Tenebrio molitor*); Rainbow Mealworms). Wasps
577 were kept in a temperature-controlled room under conditions meant to mimic warm summertime
578 environments to stimulate nesting (14:10 light-dark cycle, 25-28°C daytime temperature, 21-
579 25°C nighttime temperature, 20-40% humidity).
580 Before the lights came on each morning, we recorded the location of each individual
581 relative to other individuals in the group as either: alone – greater than one body length from
582 any other individual; in proximity – within one body length of another individual; or huddled –
583 touching or close enough to be capable of touching another individual. Once a nest was
584 established in an enclosure, we also recorded which individuals were on or next to the nest
585 overnight for the duration of the experiment. Individuals often leave the nest to forage or acquire
586 nesting materials during the day but return and remain on the nest at night[31,35]. Therefore,
587 nighttime surveys provide a reliable measure of which individuals are associated with the nest.
588 During these surveys we also visually inspected nests, counted cells, and recorded the most
589 advanced larval stage observed in a nest. In total, 8 groups started nests, but one nest was
590 quickly abandoned after only one day and is not included in nest descriptive statistics. We
591 measured nest development by weighing all nests two months after housing.
592 We analyzed pre-nesting associations for the first two weeks of the experiment because
593 all nests were established by two weeks into the experiment. For groups that did not build a
594 nest, we used the full two weeks of data. For groups that built a nest, we only used data from
595 before the nest was established. Similarly, 4 individuals from 4 different groups died during the
596 experiment, so for these groups we also only used data from before one individual in the group
597 died. Note, conclusions did not change when restricting the data of all groups to observations
598 that occurred before any nests or deaths (first 4 days of the experiment). To compute
599 descriptive statistics of the number of individuals per huddle (huddle size), we first computed the
600 mean huddle size per group-per day, and then used these numbers to compute grand mean
601 and variance for each group. We statistically compared the mean and variance in huddle size
602 using Wilcoxon rank sum tests. Because of the small sample size of numbers of nests, we only
603 report descriptive statistics of foundress associations and nest development.
604

605 **Social network analysis**
606 We used the pre-nesting huddle data (above) to construct social networks for each group.
607 Connections between individuals ("edges") were weighted depending on whether individuals
608 were huddled together (weight = 2) or simply in proximity (weight = 1). From these social
609 networks, we computed what we define here as "edge evenness", which is analogous to the
610 species evenness metric in ecology, derived from the Shannon diversity index[50]. Edge
611 evenness (J') was computed as

612
$$J' = \frac{H'}{\ln(S)}$$

613
614 where S is the number of possible edges in the network, in our case 6 for a 4-individual network,
615 and H' is the Shannon diversity index

616

617
$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$

618
619 where p_i is the proportion of weight of the ith edge in the network relative to the sum of all
620 weights in the network. Edge evenness describes how evenly distributed edge weights are
621 across the network. Networks in which individuals interact at the same rates with all other
622 individuals in the network have an edge evenness of 1, while lower values indicate skewed
623 networks in which some pairs or trios of individuals have stronger relationships than others. We
624 statistically compared edge evenness between populations using Wilcoxon rank sum tests.
625
626 **Photography and color pattern measurement**
627 Individuals were captured using nets, freeze-killed, and stored in a -20°C freezer for
628 preservation. To photograph faces, we first removed the head and the antennae to allow full
629 view of the color pattern. We photographed faces under standardized lighting conditions in the
630 lab in a photographic tent using a Canon 6D camera and Canon 100mm macro lens. We
631 confirmed that *P. fuscatus* faces do not reflect light in the ultraviolet range (Fig. S4), therefore
632 standard camera equipment captures the full range of color variation in this species. Specimens
633 were illuminated with bright, diffuse light to minimize shadows and glare by positioning three
634 lights (compact fluorescent) facing away from the specimen to reflect off the walls of the
635 photographic tent and surrounding the specimen with a cylinder of translucent plastic. To control
636 for potential slight differences in lighting across days, we also photographed three spectrally flat
637 gray standards (90%, 27%, and 3% reflectance: Color-aid gray set) under identical conditions
638 during each photography session[99].
639 Although there is some minor variation in brightness and hue within colors, it is clear that
640 the meaningful variation among individuals occurs in patterns of black, red/brown, and yellow
641 (Fig. 1, 5, S6). These three colors are present in most populations of this species and are also
642 the primary colors observed across species of *Polistes*. Therefore, our goal in this analysis was
643 not to measure color *per se*, but to objectively quantify color pattern and compare patterns in
644 homologous regions across individuals. To do so, we first used the MICA toolbox[99] to normalize
645 the light levels across photographs using the gray standards photographed during each session.

646   We then converted these normalized and linearized images using a CIE XYZ cone catch model
647   that was specific to our camera and photography illuminant (Fig. S5) using the chart-based
648   cone-catch model procedure in the MICA toolbox. We exported these images as .jpg files and
649   adjusted the maximum pixel value to 0.4 out of 1 to make the image appear bright on the screen
650   but without any pixel values being oversaturated.
651   We then used the R packages *patternize*[100] and *recolorize*[101] to align images, map color
652   patterns, and analyze variation. First, we added 8 landmarks to each face image and then used
653   the 'alignLan' function in *patternize* to align all of the images by these landmarks and mask
654   areas of the image that fell outside of the main regions of interest, encompassing the clypeus,
655   inner eye region, and frons (see Fig. S6). Then, we used *recolorize* to classify pixels in these
656   masked images to three color clusters: black, red, and yellow. To do so, we first obtained a
657   color palette by running an initial color segmentation step on a subset of 30 images that
658   appeared representative of these three colors using the 'histogram' method with 6 bins per color
659   channel using the 'recolorize' function and then implementing the 'recluster' function using a
660   similarity cutoff of 15%. These parameters were chosen based on trial and error to create color
661   segmented images that appeared similar to the color patterns in the original images. We
662   clustered the colors by similarity to three color clusters and took the weighted average of these
663   three clusters which resulted in a color palette corresponding to the black, red/brown, and
664   yellow present in the images. We created a separate color palette for the southernmost
665   populations (Louisiana and Georgia) using a different set of 30 images from these populations
666   because these wasps tend to have darker reds than those in more northerly populations.
667   Finally, we classified the pixels of all images to the nearest of these three colors in the palettes
668   using the 'imposeColors' function in *recolorize*.
669   To quantify variation among individuals, we converted the images back to rasters
670   consisting of a stack of three binary rasters corresponding to pixel assignments for each of the
671   three colors. Because we were interested in pattern variation, we treated the slightly different
672   black and red colors of the northern and southern wasps as equivalent. We then analyzed
673   variation using *patternize* and computed a principal components analysis of these rasters which
674   yielded 269 components corresponding to the 269 images in the data set. We reduced this
675   dataset to 24 statistically significant components (Fig. S7, Table S2), which were determined
676   using permutation parallel analysis in the *jackstraw* package[102]. We then computed pairwise
677   Euclidian distances between points in this multi-dimensional PCA space and quantified within-
678   site face diversity as the mean pairwise distance between points collected from the same site.
679

680 **Cooperative nesting data**
681   We obtained data on the number of foundresses per nest across the latitudinal range of
682   this species using a combination of existing datasets compiled in WASPnest[31,43] and our own
683   observations of nesting behavior. For the WASPnest dataset, we restricted the dataset to
684   observations where the number of foundresses was directly reported. We also excluded
685   observations where the exact number of foundresses were unclear, for example if a paper
686   simply stated that nests were "multi-foundress" without providing the number. We supplemented
687   this dataset with our own observations of foundress associations across the range, including in
688   some key populations at the southern end of the range. We observed nests early in the season
689   before workers emerged. We also observed nests early in the morning or on cool and rainy

690   days when all individuals associated with a nest tend to be on the nest. In total, this dataset
691   consisted of 2,021 nest observations. We statistically analyzed the relationship between the
692   number of foundresses per nest and latitude using a zero-truncated Poisson regression using
693   the *VGAM* package[103].
694

695   **Genomic analyses**
696   To confirm that northern and southern *P. fuscatus* were the same species, we collected and
697   sequenced the genomes of unrelated female *P. fuscatus* from five populations: New York (*n* =
698   30), Massachusetts (*n* = 10), North Carolina (*n* = 8), Georgia (*n* = 15), and Louisiana (*n* = 25).
699   As an outgroup, we included three individuals each from three closely related species (*P.
700   carolina, P. dorsalis,* and *P. metricus*) with sympatric ranges. Sample information is provided in
701   Table S4.
702   Paired-end 150-bp Nextera libraries were sequenced on the Illumina HiSeq 2000. All
703   samples were aligned to the *P. fuscatus* reference genome[52] using the Burrow-Wheeler Aligner
704   (v.0.7.13)[104]. Variants were identified using GATK (v3.8)[105] and hard filtered to remove low
705   confidence variants, following the methods described in[45].
706   To examine the relationship between samples, we constructed a phylogenetic tree with
707   SNPhylo (v20160204)[106], a program designed to rapidly build phylogenetic trees from large SNP
708   datasets. To reduce the size of the dataset, variants were first filtered with VCFtools[107] to retain
709   only a single, informative, high-quality, biallelic SNP every 1,000 bp using the options: --max-
710   alleles 2 --mac 0.1 --max-missing-count 10 --min-meanDP 3 --max-meanDP 1200 --minQ 20 --
711   thin 1000. SNPhylo was run with 500 rounds of bootstrapping. We further explored relatedness
712   between samples by conducting a PCA of genetic variants using Tassel5[108]. Lastly, we
713   calculated genetic differentiation between the most distant populations, New York and
714   Louisiana, using Weir-Cockerham FST, implemented in VCFtools.
715

716   **Recent selection in northern versus southern wasps**
717   Using the 40 re-sequenced *P. fuscatus* genomes from Georgia and Louisiana, we looked for
718   evidence of selective sweeps in southern wasps with SweepFinder2[53]. SweepFinder2 uses
719   deviations in the local site frequency spectrum to infer selective sweeps, generating a
720   composite likelihood ratio (CLR) value for each window. CLR values are larger when selection is
721   stronger, more recent, and/or acting on new mutations rather than standing genetic variation [52].
722   We compared CLR values for the southern population to CLR values that were generated for a
723   prior study of northern populations[52]. Northern CLR values were calculated from the same 40
724   wasps from New York and Massachusetts described above. We included two sampling sites in
725   each analysis to avoid detecting selective sweeps caused by local adaptation. CLR values
726   between northern and southern wasps were scaled by the maximum CLR value in each dataset,
727   generating scaled CLR. Values were compared in 1000 bp windows across the genome and
728   plots were constructed with BioCircos[109]. For each gene in the genome, as well as the region +/-
729   5000 bp upstream/downstream of that gene, we calculated a maximum scaled CLR value.
730   Genes in the *P. fuscatus* genome had been previously classified as potential targets of
731   selection for cognitive evolution if annotated with one of the following Gene Ontology (GO)
732   terms: cognition (GO:0050890), mushroom body development (GO:0016319), visual behavior
733   (GO:0007632), learning or memory (GO:0007611), and eye development (GO:0001654). Out of

734   11,935 genes, 1,088 genes were considered potentially related to the perceptual and cognitive

735   mechanisms of individual recognition (hereafter: 'visual cognition genes'). We also categorized

736   genes based on whether or not they showed evidence of differential expression in response to

737   social experience based on data published in[54]. For both data sets, to statistically compare

738   scaled CLR values between populations and gene categories, we log transformed scaled CLR

739   values to improve linearity and fit linear mixed effects models using the *lme4* package, with

740   population (northern or southern), gene type (GO term dataset: visual cognition gene or other;

741   differential expression dataset: yes or no), and their interaction as fixed effects, and gene

742   identity as a random effect. We evaluated the significance of fixed effects and their interaction

743   using type III ANOVAs using the *car* package, and we report Wald chi-square test statistics. We

744   visualized population-specific elevation of CLR values for candidate social cognition loci by

745   computing the residual CLR value per locus. To do this, we generated expected CLR values by

746   randomly selecting 100 sets of n non-candidate loci, where n is the number of candidate loci for

747   a dataset, i.e., $n = 1,088$ genes based on visual cognition GO terms, $n = 733$ genes for socially

748   regulated genes. We then ranked each set by decreasing CLR value and took the mean CLR

749   value at each rank across the 100 sets to estimate expected CLR values for n random loci[110].

750   We also ranked the observed CLR values for candidate loci and took the difference between the

751   observed CLR value and expected CLR value for each rank as the residual CLR. These

752   residuals thus control for potential population differences in CLR values across the genome and

753   allow visualization of potential differences in the elevation of CLR values for candidate loci.

754

Data accessibility

New sequence data for samples from Louisiana and Georgia have been deposited to the NCBI sequence read archive in project PRJNA761367. Samples from other populations are available in project PRJNA482994. All other data will be made publicly available on Dryad upon publication.

Author contributions

JPT and MJS conceived of and designed the project; JPT and CMJ designed and performed the individual recognition experiment; JPT performed other behavioral experiments; JPT, CMJ, SV, RS, AWL, TJP, FMKU, and AW collected data; SMVB and HIW developed code for color pattern analysis; JPT analyzed non-genomic data; SEM and MJS analyzed genomic data; MJS secured funding; JPT, SEM, and MJS wrote the first draft of the paper; and all authors reviewed and edited the paper.

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