



# Personality and body mass impact social group formation and function in paper wasps



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Many animals devote substantial time, energy and resources to assessing nonmating social partners. However, relatively little is known about how individual characteristics influence the process and outcome of social partner choice. Social partner choice is an important aspect of *Polistes fuscatus* wasp lives, as nest-founding queens form and dissolve many short-term social relationships before settling down in stable cooperative groups. Here, we asked how personality and body size influence social partner assessment, the specific partners chosen, behaviour within social groups and group offspring production. We evaluated social and nonsocial personality traits (exploration, affiliation, aggression, investigation) and body mass in 75 individually marked queens, then released them in a large naturalistic enclosure where we recorded social partner assessment, nest founding behaviour and behaviour on nests. At the end of the season, we collected nests as a measure of group reproductive output. Exploratory personality had a stronger effect on social behaviour than other personality measures. More exploratory wasps sampled more social partners, joined nests later and spent fewer days as members of stable nests. Less exploratory wasps were more likely to become dominant on nests and were more aggressive after partnerships were established. Larger wasps sampled more potential nest sites, suggesting that sampling induces energetic costs that larger individuals are better able to bear. Among dominant and solitary-nesting wasps, more affiliative wasps built larger nests and more aggressive wasps built smaller nests. We did not find that wasps selected partners based on any measured trait. Overall, our work demonstrates that personality traits play an important role in how social partners are assessed, how social groups are formed, behaviour within established social groups and the success of social groups. Our study also suggests that personality mediates a trade-off between time spent sampling partners and social bond stability.

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Social group formation, the process by which individuals choose social partners, has important implications for the evolution of cooperation (Brask et al., 2019). Theoretical models predict that preferential assortment of mutually beneficial partners can accelerate the evolution of cooperative phenotypes (Aktipis, 2011). However, individuals differ in which traits make them a good social partner and which partner traits are beneficial to them (Barclay, 2016; Barta, 2016). Thus, the individual traits of animals might shape both partner choice and the process used for assessing potential social partners (Jennions & Petrie, 1997; Reinhold & Schielzeth, 2015). Partner assessment is also likely subjected to

time and opportunity trade-offs. For example, individuals that wait to make choices may have a smaller market of available partners (Castellano & Cermelli, 2011; Chittka et al., 2009; Sullivan, 1994). Despite the growing appreciation of how individual traits shape behaviour within social groups, little work has examined how the traits of individuals influence both the process and the outcome of social group formation (Gartland et al., 2022; Laskowski et al., 2022).

Thus far, most research on partner choice has focused on mate choice rather than choice of cooperative social partners. There are strong similarities between mate and social partner choice, as both involve ‘choosiness’, influence reproductive success and are subject to trade-offs (Edward, 2015; Hammerstein & Noë, 2016; Neelon et al., 2019; Noë & Hammerstein, 1994; Weidt et al., 2008). The reproductive fitness consequences of social partner choice may be particularly important for cooperative breeders, so social partner choice dynamics may resemble mate choice in these systems

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(Bourke & Heinze, 1994; Doutrelant & Covas, 2007; Hatchwell et al., 1999; Shaffer et al., 2016; Sturrock et al., 2022). There are also important differences between mating and partner choice, as mating dynamics like Fisherian runaway selection and sensory biases are unlikely to influence social partner choice (Fuller et al., 2005; Pomiankowski & Iwasa, 1998). As a result, further work investigating how individual traits mediate social partner assessment, fitness consequences of partner choices and opportunity trade-offs is needed to understand the evolution of cooperative behaviour.

Body mass may have important impacts on group formation and assessment because of its relationship with energetics, competitive ability and dominance. Sampling partners is energetically costly; therefore, larger or better conditioned individuals may assess more social partners (Byers et al., 2005; Dougherty, 2023; Vitousek et al., 2007). Furthermore, body mass may impact how likely individuals are to join a group. Dominance contests are costly, with the greatest conflict when individuals have similar competitive ability (Tibbetts et al., 2022). Therefore, individuals may attempt to join groups with others that differ from them in size to reduce intragroup conflict (Buston, 2003; Wong et al., 2016). Body size could also influence whether individuals are welcomed into a group. Individuals with large body size and high competitive ability may be preferred as partners if these traits also increase other group level benefits (e.g. nest defence, foraging). For example, larger individuals provide greater advantages during intergroup conflict in ants (*Formica rufa*) (Batchelor et al., 2012). However, if larger individuals are more likely to monopolize group resources, such as food or reproductive opportunities, they may be less preferred as partners. Although body mass plays an important role in social groups, little work has empirically examined how body mass impacts both the process and the outcome of partner choice and group formation.

Personality, defined as consistent differences in behaviour among individuals, may be important in social group formation because personality shapes activity patterns, roles and task partitioning within social groups (Chapman et al., 2011; Jandt, Bengston, et al., 2014; Loftus et al., 2021; Pinter-Wollman, 2012; Reznikova, 2021; Webster et al., 2011). Much work has focused on understanding the impact of personality traits, such as exploration (propensity to enter new environments) and activity (movement within familiar environments), on behaviour of individuals within groups (Bell et al., 2009; Laskowski et al., 2022). Personality may influence partner assessment because personality traits can contribute to speed–accuracy trade-offs (Castellano & Cermelli, 2011; Hui & Pinter-Wollman, 2014; Luttbeg, 2002; Sih & Del Giudice, 2012). Recent work on mate choice suggests that exploration and activity may increase sampling of social partners, with highly exploratory individuals sampling more potential mates than less exploratory individuals (Bierbach et al., 2015; David & Cézilly, 2011; Roth et al., 2022). Thus far, we know little about the impact of personality traits on social partner assessment and group formation.

In addition to nonsocial personality traits, social personality traits, such as aggression and affiliation, may also impact social group formation and social bonds (Gartland et al., 2022; Tkaczynski et al., 2020). Social personality traits may influence the process of choosing partners by influencing conspecific tolerance or changing the type of information used to assess partners. Furthermore, socially central individuals may benefit from priority access to social information and social contacts (McFarland et al., 2017; Sade et al., 1988; Wooddell et al., 2020). For example, highly sociable fish (guppies, *Poecilia reticulata*) are more likely than less social fish to use social information when choosing mates (White et al., 2017). Recent work also finds that individuals often assort by social personality traits, with individuals engaging in more prosocial

behaviours assorting together (Ebenau et al., 2019; Massen & Koski, 2014). Most work examines the impact of social traits on how individuals assort within large groups, like flocks, rather than on group formation (Ebenau et al., 2019), despite the important consequences of these choices. Personality may impact group and individual behaviour and success after social groups are formed. Increased variation in personalities among group members may enhance group success through differentiation of social roles and tasks (Bergmüller & Taborsky, 2010; Loftus et al., 2021). For example, in cichlids (*Neolamprologus pulcher*), more active individuals engage in more territory defence than less active fish (Le Vin et al., 2011). Furthermore, social personality traits may impact group fitness. For example, the sociability of female marmosets (*Callithrix jacchus*) predicts the reproductive output of bonded pairs (Masilkova et al., 2022) and the composition of aggressive personalities in ant groups affects their ability to compete with heterospecifics (Neumann & Pinter-Wollman, 2019).

Paper wasps provide an excellent system to evaluate how traits of individuals influence social group formation and subsequent cooperative behaviour. Paper wasp (*Polistes fuscatus*) nest-founding queens engage in an extended period of social partner assessment called ‘shopping’ at the beginning of the spring. During this period, they sample many potential social partners and possible nests before settling on stable nests to cooperatively rear offspring with their partners. Paper wasp nest-founding queens may roost overnight on one nest for a few nights before leaving to join a different association, with a high degree of variation in the number of potential partners and nest sites sampled (Roseler, 1991; E. C. Laub, personal observation). *Polistes fuscatus* form social groups of up to five queens or can build a nest alone. Members of the same nest will collectively build nests from regurgitated wood pulp, process food, provision larvae and defend the nest from nest usurpation (Roseler, 1991). If queens form a group, they compete for rank to form a linear dominance hierarchy (Roseler, 1991). The dominant queen lays most of the eggs on a nest and subordinate wasps perform more foraging leaving the nest to collect nectar, prey and wood pulp (Reeve et al., 2000). There is high variability in both nest behaviour and group stability, with variation in foraging rates and duration of stable nest membership by queens (Reeve, 1991). Previous work in a closely related species (*Polistes metricus*) demonstrates that nest-founding queen resistance to predator intrusion may predict colony predator response. Thus far, no work has demonstrated that personality is associated with task specialization or intra-nest behavioural differences in paper wasps (Giray et al., 2005; Wright et al., 2017). Prior work in *P. fuscatus* (Jomaa et al., 2023) found that wasps have repeatable social and nonsocial personality traits. However, how personality traits influence partner assessment behaviour, the specific partners chosen and behaviour once social groups are formed is unknown.

Here, we investigate how individual characteristics influence social partner assessment, the specific partners chosen, behaviour within social groups and group success. We specifically tested how body mass and nonsocial and social personality traits influence (1) the process that wasps use to assess social partners, including the number of potential partners assessed, the number of potential nesting sites assessed and the number of days to choose a partner, (2) partner assessment interactions, including the number of unique individuals assessed (degree) and global connectedness among assessed partners (betweenness), (3) behaviour within social groups, including the number of days in a stable cooperative group, aggression and cooperative behaviours like food sharing between cofounding wasps and (4) group reproductive success (the number of offspring produced, measured as final nest size). By studying how individual traits impact social group formation and

success, we will improve our understanding of what maintains behavioural variation in social animals.

## METHODS

We examined the impact of paper wasp body mass and personality on how wasps assess social partners prior to nest foundation, the specific partners chosen, behaviour within social groups and group success at the end of the season.

### *Wasp Collection*

We collected nest-founding queens during 7–11 May 2021 from parks surrounding Minneapolis, Minnesota, U.S.A. using nets and collection vials prior to founding a nest, or in the earliest stages of nest foundation. After collection, we housed wasps individually in round deli cups (10.2 cm in diameter, 5 cm in height) with sugar and water provided *ad libitum* and kept them at 22 °C on a 14:10 h light:dark cycle, with lights on at 0700 hours, until they were transported to the University of Michigan by car. Upon return to the University of Michigan on 12 May 2021, we housed wasps on a 15:9 h light:dark cycle, with lights on at 0600 hours, and at 24 °C during the day and 16 °C at night. Wasps were weighed on a scale accurate to 0.002 g and individually marked with Testors™ model paint. Wasps were painted with a unique colour pattern (1–4 different colours used) on their wings and thorax to enable individual identification after release.

### *Behavioural Assays*

To measure paper wasp personality, we conducted two behavioural assays, one to quantify nonsocial behaviours and one to quantify social behaviours. Both assays provide repeatable information about personality (Jomaa et al., 2023; Appendix, Table A1). To quantify nonsocial behaviour, we evaluated exploration within a 10-chambered maze (Supplementary Fig. S1). We placed wasps head-first through a small hole into the centre chamber and allowed them to freely explore the maze for 10 min. Exploration was scored as the number of chambers entered during this time. To quantify social behaviours, we recorded aggressive, affiliative, and investigative responses to a neutrally positioned dummy wasp during 10 min (Supplementary Fig. S1). Aggression was scored as the number of times the focal wasp bit, darted, darted with open flared mandibles or mounted the dummy, then log-transformed to normalize data. Affiliation was scored as the number of seconds the wasp spent engaged in nonaggressive body contact with the dummy. Investigation behaviour was scored as the number of times the wasp antennated the dummy. Each wasp participated in four trials for each of the two assays, and the final personality scores for each individual was the average across all trials. All trials were completed within 1 week, with no repeats of the same assay on the same day. All trials were videorecorded and later scored by observers naïve to experimental predictions.

### *Release in Vespiary*

After individual marking, weighing and behavioural testing, we released 75 wasps on the night of 30 May 2021 into a large naturalistic enclosure (vespiary) to evaluate their partner assessment behaviour, partner choices and group outcomes. The vespiary is a screened hoop house (7.32 × 5.5 m and 2.7 m height) located in an open field at the Matthaei Botanical Gardens (Supplementary Fig. S2). It contains 40 individually marked nestboxes (10.2 × 7.6 cm and 15.24 cm height) and four food stations placed at the corners of the vespiary supplied with sugar, water and

caterpillars (combination of waxworms, silkworms and cabbage loopers) *ad libitum*. In addition to the supplied food items, natural flowers provided additional nectar sources. The vespiary provides a highly naturalistic experience for wasps founding nests as they have the opportunity to fly between potential nest sites, navigate a complex environment, forage for food and avoid predators (such as spiders).

### *Tracking and Monitoring Nest Foundation*

We measured partner assessment and nest-founding behaviour daily, during early morning censuses from 1 June to 22 July 2021 (51 days). Censuses were performed early in the morning because overnight roosting behaviour provides crucial information about partner assessment. We recorded three types of information. First, we attempted to locate each wasp based on their unique colour markings. We visually inspected all nestboxes, corners of the vespiary and food stations. Wasps typically roost in multiple locations before choosing a final nesting site. Second, we recorded co-roosting behaviour, with all wasps roosting within 15.24 cm of each other considered to be roosting together. Co-roosting provides information about partner assessment because wasps change whom they roost with overnight prior to forming stable cooperative associations. Wasp social groups were considered stable when the wasps spent three consecutive nights together, because wasps rarely move to other nests after three consecutive nights. Third, we recorded evidence of nest building. In analysis of roosting site assessment, we only included wasps that had been observed on at least 5 days ( $N = 52$  wasps). Wasps that were observed fewer than five times disappeared early in the season due to presumed escape from the vespiary or death. Within this subset of 52 wasps, wasps were observed an average ( $\pm$  SD) of  $27 \pm 14$  times. Thirty-two wasps chose nests within our census period, with eight wasps nesting alone, eight joining small groups and 16 joining large groups. Wasps who were on nests, in groups with other wasps or at potential nesting sites were easier to find than wasps that hide alone in the tall grass. As a result, we may have obtained fewer observations of solitary wasps that were not on nests. This sampling bias is unlikely to influence our results because we analysed visits to nest sites and partners, both of which are straightforward to accurately quantify. We defined ‘site choice day’ as the third consecutive time a wasp was observed on a nest site overnight, as wasps rarely defect from nests after three consecutive overnights at a nesting site. For wasps that chose partners, ‘partner choice day’ was the third consecutive night a wasp was observed with a social partner. The number of days a wasp spent as a member of a stable nest was counted as the time between her partner choice day and the last time she was observed on her nest. For wasps that never chose partners, partner choice day was the same as site choice day, the third consecutive day on a nest.

### *On-nest Behaviour and Group Success*

Once wasps had established nests, we videorecorded on-nest behaviour using SONY™ Handycams. Eleven established nests were recorded between 29 June 2021 and 28 July 2021. Videos were recorded between 1145 and 1500 hours weekly, with a few videos recorded on consecutive days. Video duration was 31–140 min, with most videos being 90–120 min long. Nests were recorded between one and five times, with most nests recorded three or four times. Videos were recorded to capture nests with their greatest number of members and at different stages in nest development, adding some variation in the timing of videos as nests were founded at different times. We aimed to collect 2 h of video during each session, but lighting and weather conditions reduced the amount of

useable footage; thus, we accounted for the number of minutes wasps were present in videos to account for this variation. Temperature and weather conditions were obtained from [timeanddate.com](https://timeanddate.com) (weather station: Ann Arbor Municipal Airport). We assessed offspring development (presence of eggs, presence and developmental stage of larvae, presence of capped cells that contained pupae) on the day of each video recording.

Observers with no knowledge of the wasps' personality or weight scored the behaviours on the videos. Behaviours scored included aggressive interactions (bite, dart with open mandibles, mount, grapple, attempted mount), cooperative interactions (trophallaxis (liquid food sharing), passing food, passing nest material) and activation interactions (dart) (Sumana & Starks, 2004; West-Eberhard, 1969). Dominance rank of cooperating queens was assessed based on mounting behaviour. During a mount, the dominant wasp positions herself above the subordinate and drums her antennae on the subordinate, while the subordinate lowers her antennae and remains stationary. Dominant wasps regularly mount subordinates, monopolize the centre of the nest and spend more time on nests. Subordinates never mount dominants (Jandt, Tibbetts, et al., 2014).

We evaluated success of social groups by collecting nests at the end of the summer (15 August 2021) and counting the number of nest cells (Supplementary Fig. S3). Each cell generates one offspring, so nest size provides a good measure of offspring production. Nests typically dissolve in late summer, with foundresses disappearing and workers dispersing. Four of 15 nests dissolved before collection, with foundresses dying or abandoning them before the end of the summer.

## Data Analysis

### Quantifying social position using social network analysis

To understand how personality influenced assessment of and interactions with potential partners, we constructed social networks of roosting associations. Only individuals that were observed at least five times (with or without partners) were included in the network analysis to reduce the effect of sampling bias on network structure ( $N = 52$ ). An interaction between two wasps was recorded if two wasps roosted overnight at the same location. To evaluate the relationship between personality and the social centrality of an individual in the co-roosting network, we computed two commonly used network centrality measures: degree, which is the number of unique individuals a focal animal encountered; betweenness, which is the number of shortest paths that connects the focal animal with all other individuals in the social network. Biologically this means that individuals with high betweenness roost with more individuals that do not themselves roost with each other. To determine whether the relationship we observed between personality and network measures was statistically significant, we used a randomization procedure because network position is not independent from other individuals' positions (Hobson et al., 2021; Wyman et al., 2021). We first used general linear models (GLM) with degree or betweenness as the dependent variable and exploration, affiliation, investigation, aggression and body mass as fixed effects. We then ran 1000 permutations in which node (individual) identities (IDs), along with their attributes, were shuffled without replacement while preserving the observed network structure to create a reference model in which individual attributes and network position were decoupled. We calculated the estimates of the relationship between the individual attributes and network centrality measures for each permutation with general linear models to create a distribution of reference estimates. We calculated a two-tailed  $P$  value as the proportion of trials in which the

observed estimate was greater than 97.5% or less than 2.5% of the distribution of the reference correlation coefficients.

We further examined whether individuals with similar personalities preferentially assorted with one another (i.e. if highly active individuals assorted with other highly active individuals), or whether individuals disassorted (i.e. highly active individuals preferentially interacted with nonactive individuals). We calculated the assortativity of the social network based on exploration, affiliation, investigation, aggression and body mass. We then compared the observed assortativity with the assortativity of the 1000 simulated networks described above to determine whether observed assortativity or disassortativity was greater or smaller than expected by chance (Hobson et al., 2021). All data were analysed in R version 3.6.3 (R Core Team, 2023). Social network analysis was conducted with the 'igraph' R package version 1.5.1 (Csárdi et al., 2023).

### Relating nest-founding behaviour and on-nest behaviour with personality

We used general linear models (GLMs) to evaluate whether nest assessment was related to body mass and/or personality. We ran separate models for each of four dependent variables describing nest assessment: number of roosting locations sampled; days to join a stable group; days to choose a nest; days present on a stable nest. We analysed the number of roosting locations and the number of days stable on a nest with a Poisson distribution. We analysed days to join a stable group and days to choose a nest with a negative binomial distribution. All models included the continuous fixed effects of exploration, affiliation, investigation, aggression and body mass. Only individuals that were observed at least 5 days were included in the analysis of assessment behaviours, and only individuals that chose a nest were included in analyses of days to choose nest site, days to choose partners and the number of stable days on a nest. GLMs were analysed with the 'lme4' R package (Bates et al., 2015) and the 'MASS' R package (Venables & Ripley, 2002). Analysis of deviance was performed using the 'Anova()' function in the 'car' R package (Fox & Weisberg, 2019).

We used generalized linear mixed effects models (GLMMs) with a negative binomial distribution to evaluate wasp behaviour on nests. We ran separate models for each of three dependent variables: trophallaxis; darting; aggression. All models included the fixed effects of exploration, affiliation, investigation, aggression, body mass, temperature, number of wasps on the nest, day of video collection, log-transformed minutes present in the video and presence of big larvae (yes/no). Nest ID with nested individual ID was included as a random effect to account for any nonindependence of individuals from the same nest and multiple observations of the same individual.

We evaluated the relationship between dominance status of individuals in multifoundress nests and individual traits through generalized estimating equations (GEE), with dominance status (categorical: dominant or nondominant) as the dependent variable and exploration, affiliation, investigation and body mass as independent variables. Nest ID was included as a cluster variable to account for the nonindependence of relationships within the same nest. Aggression was not included as an independent variable due to collinearity with exploration.

We used general linear mixed effects models (GLMMs) with a Poisson distribution to analyse the impact of individual traits on group offspring production. The dependent variable was final cell count. Fixed effects were exploration, affiliation, investigation, aggression, body mass and group size, with nest ID included as a random effect to account for potential nonindependence of values. We ran a second general linear model (GLM) with a Poisson distribution to examine the impact of traits of individuals who were

responsible for the majority of reproduction (i.e. dominant and solitary nesting wasps). The dependent variable was final cell count, and the independent variables were exploration, affiliation, investigation, aggression, body mass and group size. Data were analysed in R with packages 'lme4' version 1.1-21 (Bates et al., 2015), 'geepack' version 1.3.9 (Højsgaard et al., 2006) and 'car' version 3.1-2 (Fox & Weisberg, 2019).

### Ethical Note

Wasps are invertebrates and therefore require no special institutional permissions for research. All work was conducted in accordance with ASAB/ABS guidelines. Wasps were collected with permission from the Minnesota Department of Natural Resources (Special Permit Number: 202138). Wasps were transported gently from Minnesota to Ann Arbor, Michigan with care taken to minimize stress. Wasps were allowed to live outside in natural conditions and provided with sufficient resources to thrive. Care was taken during personality trials to reduce stress to wasps by transporting them and placing them in trial arenas gently. Wasps were given ample time to rest in between personality trials to minimize stress.

## RESULTS

### Impact of Personality on Nest-founding Behaviour

Nest-founding behaviour was best predicted by personality and body mass, with exploration and affiliation linked with several nest-founding behaviours. Wasps that were more exploratory took more days to choose a nest site, took more days to choose a partner and spent fewer days as part of a stable group. Wasps that were more affiliative sampled fewer roosting sites. Number of roosting sites sampled was significantly negatively correlated with affiliation (GLM:  $\chi^2_1 = 10.12$ ,  $P = 0.0015$ ; Fig. 1a) but significantly positively correlated with body mass ( $\chi^2_1 = 5.76$ ,  $P = 0.016$ , Fig. 1b). Number of roosting sites sampled was not correlated with exploration (GLM:  $\chi^2 = 2.49$ ,  $P = 0.114$ ), investigation ( $\chi^2 = 0.87$ ,  $P = 0.35$ ) or aggression ( $\chi^2 = 0.066$ ,  $P = 0.53$ ). The number of days to choose a nest site was significantly positively correlated with exploration (GLM:  $\chi^2_1 = 9.28$ ,  $P = 0.0023$ ; Fig. 2a) but was not correlated with affiliation ( $\chi^2_1 = 0.95$ ,  $P = 0.33$ ), investigation

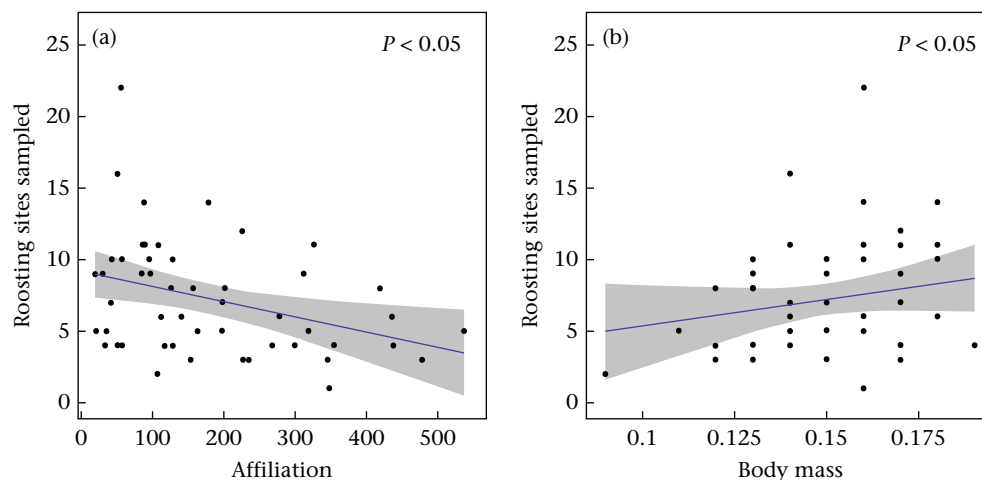
( $\chi^2_1 = 0.00$ ,  $P = 0.99$ ), aggression ( $\chi^2 = 1.48$ ,  $P = 0.223$ ) or body mass ( $\chi^2_1 = 0.03$ ,  $P = 0.873$ ). The day to choose nest partners was significantly positively correlated with exploration (GLM:  $\chi^2_1 = 4.84$ ,  $P = 0.028$ ; Fig. 2b) but was not correlated with affiliation ( $\chi^2_1 = 0.80$ ,  $P = 0.37$ ), aggression ( $\chi^2_1 = 1.49$ ,  $P = 0.223$ ), investigation ( $\chi^2_1 = 0.06$ ,  $P = 0.811$ ) or body mass ( $\chi^2_1 = 0.75$ ,  $P = 0.385$ ).

### Social Position and Personality

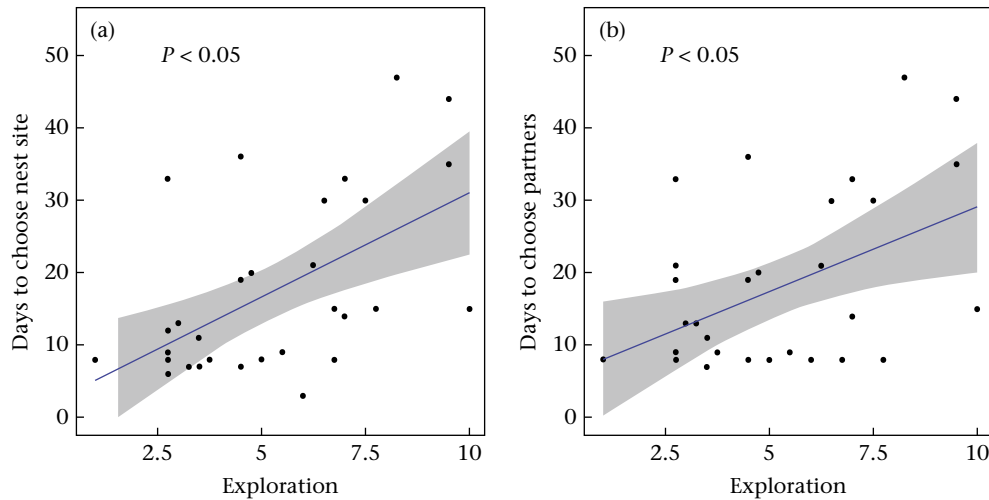
The social centrality of wasps while assessing partners was significantly linked with personality but not with body mass. Wasps that were more exploratory roosted with more potential partners and had more roosting associations with wasps that themselves did not roost together, as shown by a positive relationship between exploration and degree and exploration and betweenness. However, wasps did not assort by personality or by body mass. Degree (number of individuals sampled during roosting) was significantly linked with exploration (GLM, permutation analysis:  $\beta = 0.083$ ,  $P_{\text{adj}} = 0.022$ ; Fig. 3), with more exploratory wasps sampling more partners. We did not detect a statistically significant relationship between degree and affiliation (GLM, permutation analysis:  $\beta = -5.92e-05$ ,  $P_{\text{adj}} = 0.852$ ), aggression ( $\beta = 0.069$ ,  $P_{\text{adj}} = 0.662$ ), investigation ( $\beta = 0.054$ ,  $P_{\text{adj}} = 0.098$ ) or body mass ( $\beta = 5.46$ ,  $P_{\text{adj}} = 0.114$ ). Betweenness, a measure of global centrality within the social network of wasps, was not linked with personality or body mass. Betweenness was not significantly linked with exploration (GLM, permutation analysis:  $\beta = 3.41$ ,  $P_{\text{adj}} = 0.052$ ), investigation ( $\beta = 1.59$ ,  $P_{\text{adj}} = 0.31$ ), affiliation ( $\beta = -0.02$ ,  $P_{\text{adj}} = 0.512$ ), aggression ( $\beta = 2.76$ ,  $P_{\text{adj}} = 0.74$ ) or body mass ( $\beta = 142$ ,  $P_{\text{adj}} = 0.434$ ). Wasps did not significantly assort by exploration (permutation analysis: assortativity =  $-0.059$ ,  $P = 0.4$ ), affiliation ( $-0.0234$ ,  $P = 0.892$ ), investigation ( $-0.0132$ ,  $P = 0.722$ ), aggression ( $0.0257$ ,  $P = 0.192$ ) or body mass ( $0.001$ ,  $P = 0.52$ ).

### On-nest Behaviour and Nest Size

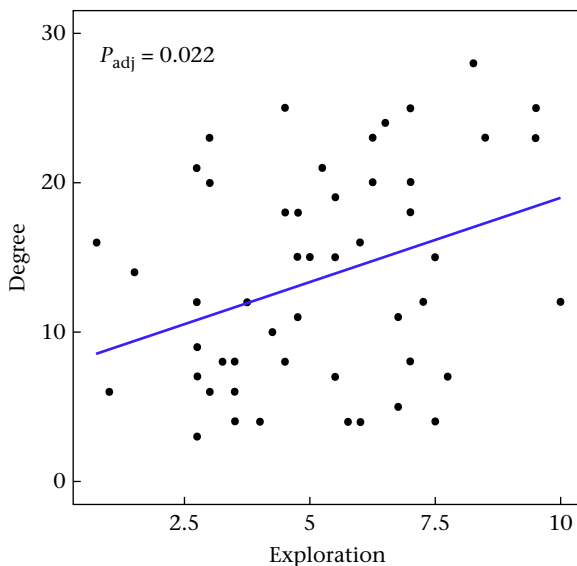
After social groups formed, we assessed how multiple on-nest behaviours and nest size were influenced by personality and body mass. The number of days a wasp spent as a member of a stable group was significantly negatively correlated with exploration (GLM:  $\chi^2_1 = 27.50$ ,  $P < 0.001$ ; Fig. 4a) and aggression



**Figure 1.** Relationship between the number of roosting sites sampled and (a) affiliation and (b) body mass. Blue line indicates linear regression of relationship and shading indicates standard error.



**Figure 2.** Relationship between exploration and (a) the number of days to choose nest sites and (b) the number of days to choose social partners. Blue line indicates linear regression of relationship and shading indicates standard error.



**Figure 3.** Relationship between exploration and social centrality when assessing partners, where higher degree indicates a greater number of unique social partners sampled during roosting. Blue line indicates linear regression of relationship.

( $\chi^2_1 = 28.42$ ,  $P < 0.001$ ; Fig. 4b) but was not correlated with affiliation ( $\chi^2_1 = 3.56$ ,  $P = 0.059$ ) or body mass ( $\chi^2_1 = 2.84$ ,  $P = 0.092$ ).

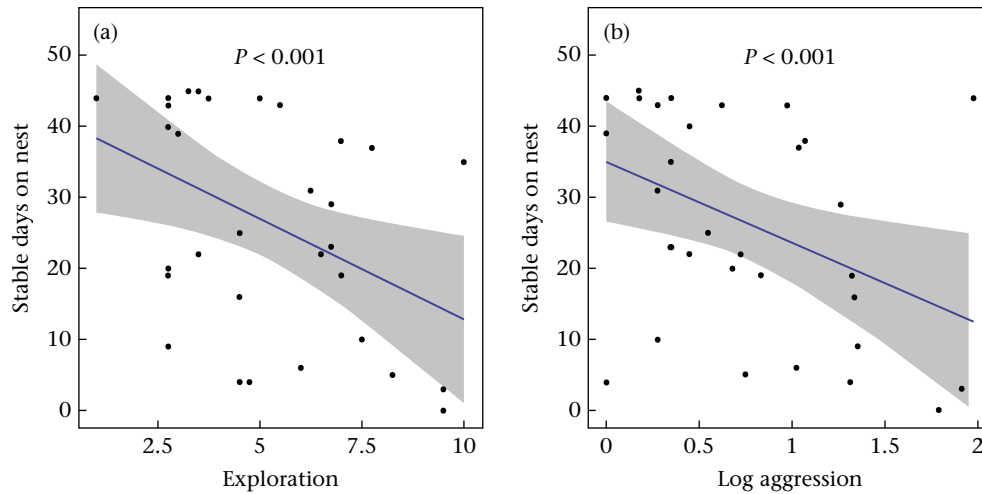
Wasps that were less exploratory initiated more aggressive behaviour than wasps that were more exploratory (Fig. 5a), and wasps that were less aggressive initiated more darting (Fig. 5b), an activation behaviour that promotes off-nest foraging and on-nest tasks. However, trophallaxis was not linked with personality or body mass (Appendix, Table A1). On-nest aggression was negatively correlated with exploration (GLMM:  $\chi^2_1 = 7.96$ ,  $P = 0.004$ ; Fig. 5a, Table 1) but not with affiliation ( $\chi^2_1 = 1.19$ ,  $P = 0.275$ ; Table 1), investigation ( $\chi^2_1 = 1.19$ ,  $P = 0.556$ ; Table 1), aggression ( $\chi^2_1 = 0.001$ ,  $P = 0.977$ ; Table 1) or body mass ( $\chi^2_1 = 2.14$ ,  $P = 0.142$ ; Table 1). On-nest aggression was significantly linked with the number of wasps on a nest (GLMM:  $\chi^2_1 = 4.02$ ,  $P = 0.045$ ; Table 1) but not with any other environmental factor (temperature:

$\chi^2_1 = 0.29$ ,  $P = 0.594$ ; day of video recording:  $\chi^2_1 = 2.72$ ,  $P = 0.099$ ; minutes present on nest:  $\chi^2_1 = 3.27$ ,  $P = 0.0706$ ; presence of big larvae:  $\chi^2_1 = 0.05$ ,  $P = 0.821$ ). The variance of nest ID was 1.905 with a standard deviation of 1.38, and the variance of individual ID nested within nest ID was  $<0.0001$  with a standard deviation of  $<0.0001$ .

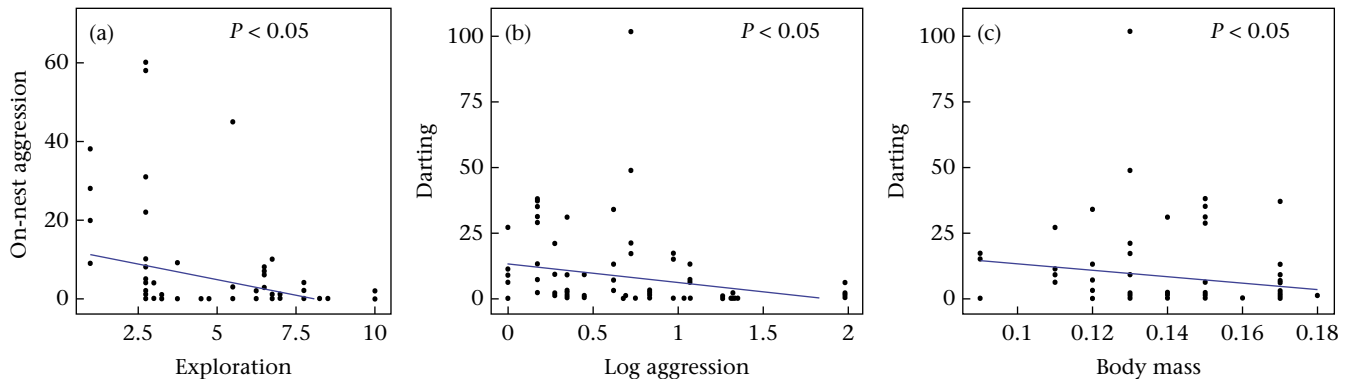
Interestingly, we found that darting was negatively correlated with personality aggressiveness (GLMM:  $\chi^2_1 = 10.29$ ,  $P = 0.0013$ ; Fig. 5b, Table 2) and body mass ( $\chi^2_1 = 8.44$ ,  $P = 0.0037$ ; Fig. 5c, Table 2) but was not correlated with exploration ( $\chi^2_1 = 1.41$ ,  $P = 0.2352$ ; Table 2), affiliation ( $\chi^2_1 = 0.01$ ,  $P = 0.9233$ ; Table 2) or investigation ( $\chi^2_1 = 1.76$ ,  $P = 0.1844$ ; Table 2). We found that darting was significantly correlated with all environmental variables (GLMM: temperature:  $\chi^2_1 = 7.02$ ,  $P = 0.0081$ ; number of wasps on nest:  $\chi^2_1 = 4.36$ ,  $P = 0.0367$ ; day of video recording:  $\chi^2_1 = 28.77$ ,  $P < 0.001$ ; minutes present on nest:  $\chi^2_1 = 8.43$ ,  $P = 0.0037$ ; presence of big larvae:  $\chi^2_1 = 27.19$ ,  $P < 0.001$ ; Table 2). The variance of nest ID was  $<0.0001$  with a standard deviation of  $<0.0001$ , and the variance of individual ID nested within nest ID was 0.267 with a standard deviation of 0.516.

Surprisingly, wasps that were less exploratory were more likely to become dominant on nests. Dominance rank was significantly negatively linked with exploration (GEE: Wald  $\chi^2 = 4.27$ ,  $P = 0.039$ ; Fig. 6a). Dominant wasps were less exploratory than subordinate wasps. However, dominance rank was not linked with body mass (GEE: Wald  $\chi^2 = 0.37$ ,  $P = 0.542$ ), affiliation (Wald  $\chi^2 = 0.04$ ,  $P = 0.834$ ) or investigation (Wald  $\chi^2 = 0.36$ ,  $P = 0.546$ ).

At the end of the season, we collected nests to estimate offspring production, as each nest cell produces one offspring. Nest size was not linked with any of the individual traits evaluated when all wasps on the nest were included in the analysis. Final cell count was not significantly linked with exploration (GLMM:  $\chi^2_1 = 0.04$ ,  $P = 0.845$ ), affiliation ( $\chi^2_1 = 0.55$ ,  $P = 0.456$ ), investigation ( $\chi^2_1 = 0.36$ ,  $P = 0.546$ ), aggression ( $\chi^2_1 = 0.61$ ,  $P = 0.433$ ) or body mass ( $\chi^2_1 = 0.87$ ,  $P = 0.35$ ). However, nest size was significantly positively linked to group size (GLMM:  $\chi^2_1 = 7.67$ ,  $P = 0.0056$ ), with larger groups producing larger nests. However, when comparing only the traits of wasps who were dominant or solitary foundresses, nest size was positively correlated with affiliation (GLM:  $\chi^2_1 = 39.6$ ,  $P < 0.001$ ; Fig. 6b). Nest size was negatively correlated with



**Figure 4.** Relationship between the number of stable days on a nest and (a) exploration and (b) log aggression. Blue line indicates linear regression of relationship and shading indicates standard error.



**Figure 5.** Relationship between (a) on-nest aggression and exploration, (b) darting and log aggression and (c) darting and body mass. Blue line indicates linear regression of relationship.

aggression (GLM:  $\chi^2_1 = 10.7$ ,  $P = 0.0011$ ; Fig. 6c) and body mass ( $\chi^2_1 = 3.9$ ,  $P = 0.048$ ). Group size was also significantly positively linked with offspring production (GLM:  $\chi^2_1 = 21.8$ ,  $P < 0.001$ ).

## DISCUSSION

We examined the impact of individual characteristics on behaviour during social group formation and within stable groups of nest-founding paper wasps. Assessment behaviour, nest foundation and behaviour within social groups were all linked with personality and body mass. Individuals that were more exploratory assessed more individuals as potential partners (Fig. 3), joined groups later (Fig. 2b) and were less likely to become dominant on nests (Fig. 6b). Individuals that had less exploratory personalities were more aggressive once nests formed (Fig. 5a). However, we did not find that wasps assessed specific social partners based on any measured trait, as wasps did not assort by personality or body mass when assessing partners. Among wasps that were solitary queens or dominant queens within multiqueen associations, affiliation was positively linked with group offspring production (Fig. 6b) and aggression was negatively linked with group offspring production (Fig. 6c). However, across all nesting wasps, group success was not linked with personality.

One of our most interesting findings was that personality and body mass influenced social partner assessment. More exploratory

wasps sampled more partners and chose partners later, while less exploratory wasps sampled fewer social partners and chose faster (Figs. 2 and 3). Less exploratory wasps may sample fewer partners because they may be better able to form cooperative bonds early on and therefore may not need as much partner sampling to find a compatible social partner (Berghänel et al., 2011; Martin et al., 2021). Our data do not directly test why wasps that sample more partners choose partners later. However, one possibility is that increased sampling may make wasps more selective, as increased partner availability often increases choosiness (Henshaw, 2018; Jennions & Petrie, 1997; Willis et al., 2011). Body mass was positively linked to the number of roosting sites sampled, perhaps because sampling more potential roosts may come with energetic costs that larger individuals are better able to bear. Interestingly, wasps that were more affiliative sampled fewer roosting sites, potentially because they were more tolerant of other wasps at roosting sites, reducing their need to sample different roosts. Work in other species has similarly found that more sociable individuals disperse less (Cote, Fogarty, et al., 2010). Further work is needed to understand the mechanisms by which personality influences the market of available social partners or the ease of forming partnerships (Weir et al., 2011).

Although highly exploratory wasps assessed more potential partners, these wasps did not make more successful social choices. Exploratory wasps were less likely to achieve high dominance rank

**Table 1**  
Analysis of relationship between on-nest aggression, personality, body mass and environmental conditions

Fixed effect	Estimate	SE	Z	P
<b>Exploration</b>	<b>-0.358</b>	<b>0.127</b>	<b>-2.82</b>	<b>0.005</b>
Affiliation	0.002	0.002	1.09	0.276
Investigation	0.094	0.159	0.59	0.556
Aggression	0.014	0.517	0.03	0.978
Body mass	-18.81	12.835	-1.47	0.143
Temperature	0.022	0.042	0.53	0.595
<b>Number of wasps on nest</b>	<b>0.959</b>	<b>0.478</b>	<b>2.00</b>	<b>0.045</b>
Video day	0.047	0.029	1.65	0.099
Log minutes on nest	1.125	0.622	1.81	0.071
Big larvae	-0.215	0.951	-0.23	0.821

Significant relationships in bold.

**Table 2**  
Analysis of relationship between darting, personality, body mass and environmental conditions

Fixed effect	Estimate	SE	Z	P
Exploration	-0.098	0.083	-1.19	0.235
Affiliation	-0.0001	0.001	-0.10	0.923
Investigation	-0.133	0.100	-1.33	0.184
<b>Aggression</b>	<b>-1.148</b>	<b>0.036</b>	<b>-3.21</b>	<b>0.001</b>
<b>Body mass</b>	<b>-0.219</b>	<b>7.536</b>	<b>-2.91</b>	<b>0.004</b>
<b>Temperature</b>	<b>0.064</b>	<b>0.024</b>	<b>2.65</b>	<b>0.008</b>
<b>Number of wasps on nest</b>	<b>0.493</b>	<b>0.235</b>	<b>2.09</b>	<b>0.037</b>
<b>Video day</b>	<b>0.075</b>	<b>0.139</b>	<b>5.36</b>	<b>&lt;0.001</b>
<b>Log minutes on nest</b>	<b>1.615</b>	<b>0.561</b>	<b>2.90</b>	<b>0.004</b>
<b>Big larvae</b>	<b>1.725</b>	<b>0.331</b>	<b>5.22</b>	<b>&lt;0.001</b>

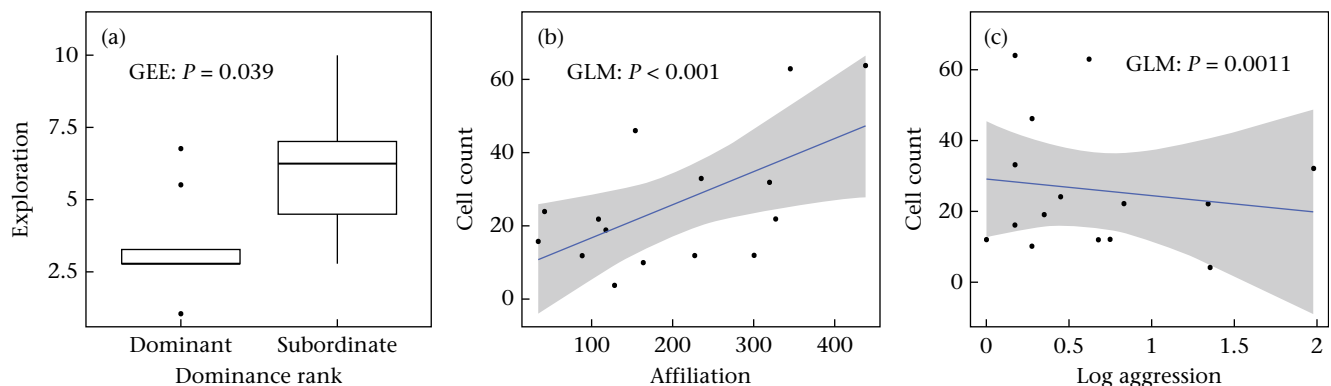
Significant relationships in bold.

on nests and did not have nests that were more successful. These results suggest that assessing more social partners does not directly translate to more successful partnerships. Assessing and remembering many individuals is cognitively taxing, and it is possible that there is a limit to the number of individuals that wasps can recall and compare (Dunbar, 2020; Jenkins et al., 2018; Sheehan & Tibbetts, 2011). There may also be a trade-off between time spent gathering information about social partners and time spent forming stable social relationships, as highly exploratory wasps spent fewer days as members of a stable nest but sampled more social partners and chose nests later (Fig. 4). Work in other taxa found a similar relationship between personality and bonds within social networks (Díaz López, 2020; Snijders et al., 2014). For example, highly exploratory birds (great tits, *Parus major*) have more

numerous but weaker ties to other birds within the social network (Aplin et al., 2013).

Personality significantly impacted dominance rank and behaviour on nests, with individuals that were less exploratory achieving higher dominance rank and engaging in more aggressive behaviour on nests than individuals that were more exploratory during the partner assessment phase. It was initially surprising that wasps that were less exploratory and aggressive during the early spring went on to be more aggressive on nests. Often, aggression is positively correlated across contexts (Cain et al., 2011; Duckworth, 2006). However, wasps that attain high dominance rank typically initiate more aggression than subordinate wasps on nests (Jandt, Tibbetts, et al., 2014). Therefore, wasps that initially demonstrate lower exploration during personality assays may become more aggressive once they achieve dominant or nest founder status. These results differ from work in birds (David et al., 2011), fish (Colléter & Brown, 2011) and mammals (Kohn et al., 2016), which showed positive relationships between exploratory and aggressive personality traits and dominance rank. In wasps, 'first arriver' effects might influence hierarchy position. Wasps that arrive first at nest sites are more likely to attain high dominance rank, although other factors including direct contest outcomes, nest usurpation and cueing also impact rank acquisition (Jandt, Tibbetts, et al., 2014; Seppä et al., 2002; Zanette & Field, 2009). Therefore, less exploratory wasps may become dominant, in part, because they choose nest sites earlier than wasps that are more exploratory. Surprisingly, we found that personality had a greater impact on dominance rank than body size, one of the most common measures for estimating resource holding potential (Tibbetts et al., 2022). Although body size impacts contest success in many taxa, including paper wasps, our work suggests that behavioural phenotypes may play a more important role in rank acquisition (Jonart et al., 2007; Tibbetts & Shorter, 2009). Our results suggest that when competitors ultimately form cooperative relationships, multiple interacting factors likely influence dominance rank and on-nest behaviour (Holekamp & Smale, 1991; Taylor et al., 2021; Tibbetts et al., 2022).

Why might highly exploratory and aggressive wasps persist in the population given that they are less likely to be dominant, spend fewer days as members of stable nests and build smaller nests? Although we found no benefit associated with high exploratory or aggressive personalities, exploration might be more beneficial in environments with greater nest site heterogeneity (Kurvers et al., 2010). In our present experiment, we provided wasps with many nest sites of equal quality. In nature, nest site quality is likely more variable and optimal nest sites are likely to be limited. Exploratory individuals are often better dispersers, an advantage when



**Figure 6.** Relationship between (a) dominance and personality and (b, c) personality of dominant wasps and offspring production (nest cells). In (a), boxes show middle quartiles, whiskers show upper and lower quartile, dots show outliers (outside  $1.5\times$  the interquartile range). In (b, c), blue line indicates linear regression, shading indicates standard error.



territories are more widely distributed (Cote, Clobert, et al., 2010; Dingemanse et al., 2003; Krackow, 2003; Zhao et al., 2016). Further work is needed to disentangle how personality traits may impact the acquisition of optimal social and physical territories across multiple contexts and in a heterogenous environment.

Excitingly, we found that affiliative dominant and solitary wasps built larger nests, while aggressive wasps built smaller nests. Work in other taxa has shown that sociability is associated with increased fitness, although these results are mixed (Cote et al., 2008; Gartland et al., 2022; Nuñez et al., 2015; Yang et al., 2017). Wasps face substantial pressure to form cooperative groups to repel rival wasp usurpation (Starks, 1998). Affiliative personalities may be advantageous if they mitigate social stress or facilitate the formation of cooperative bonds against outgroup take-over (Bruitntjes et al., 2015; Martin et al., 2021; Massen & Koski, 2014; Radford, 2008). Interestingly, the relationship between personality and nest size was only found when considering dominant and solitary nesters. Further work is needed to understand how social environments may favour or disfavour personalities of specific individuals within social groups.

We found that personality had important impacts on how individuals sampled potential social partners, the timing of joining social groups and aggressive behaviour within groups. Notably, different personality characteristics influenced partner assessment and duration of stable partnerships. Much previous work on partner choice has focused on mating partnerships (Bierbach et al., 2015; Collins et al., 2019; Munson et al., 2020). Our work expands the concept of partner choice beyond a mating context, illustrating that animals use sophisticated and highly variable assessment to choose social partners.

#### Author Contributions

**Emily C. Laub:** Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – Original draft. **Noa Pinter-Wollman:** Formal analysis, Funding acquisition, Supervision, Validation, Writing – Review & editing. **Elizabeth A. Tibbetts:** Investigation, Project administration, Funding acquisition, Supervision, Validation, Resources, Writing – Review & editing.

#### Data Availability

Data are available on the corresponding author's GitHub (<https://github.com/EmilyLaub/Personality-and-Social-Group-formation-Paper-wasps>).

#### Declaration of Interest

None of the authors have any conflicts of interest.

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#### Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.03.020>.

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## Appendix

**Table A1**  
Repeatability of personality traits

Behavioural test/Personality trait	R		95% CI		P	
	Simple	Adjusted	Simple	Adjusted	Simple	Adjusted
<b>Maze</b>						
Exploration	0.497	0.513	[0.343, 0.596]	[0.357, 0.613]	<0.001	<0.001
<b>Dummy conspecific</b>						
Affiliation	0.344	0.377	[0.22, 0.465]	[0.253, 0.493]	<0.001	<0.001
Aggression	0.141	0.159	[0.031, 0.249]	[0.037, 0.277]	0.003	0.001
Investigation	0.425	0.464	[0.277, 0.54]	[0.336, 0.592]	<0.001	<0.001

CI: confidence interval. All personality traits were significantly repeatable.

**Table A2**

Model output for on-nest trophallaxis behaviour (GLMM)

Fixed effect	Estimate	SE	Z	P
Exploration	0.047	0.093	0.50	0.615
Affiliation	0.002	0.002	0.83	0.408
Investigation	-0.151	0.143	-1.05	0.291
Aggression	0.305	0.404	0.75	0.451
Body mass	4.310	2.904	1.48	0.138
Temperature	0.031	0.034	0.91	0.363
Number of wasps on nest	-0.121	0.424	-0.29	0.775
Video day	0.001	0.023	0.06	0.953
Log minutes on nest	0.857	0.524	1.64	0.102
Big larvae	-0.186	0.548	-0.34	0.734

No measured individual traits were predictive of trophallaxis behaviour on nests.