Current Zoology, 2026, 72, 263–272
https://doi.org/10.1093/cz/zoaf041
Published: 22 July 2025
Original article

Nest-founding paper wasps aggregate in "social leks" and decrease aggression during partner selection

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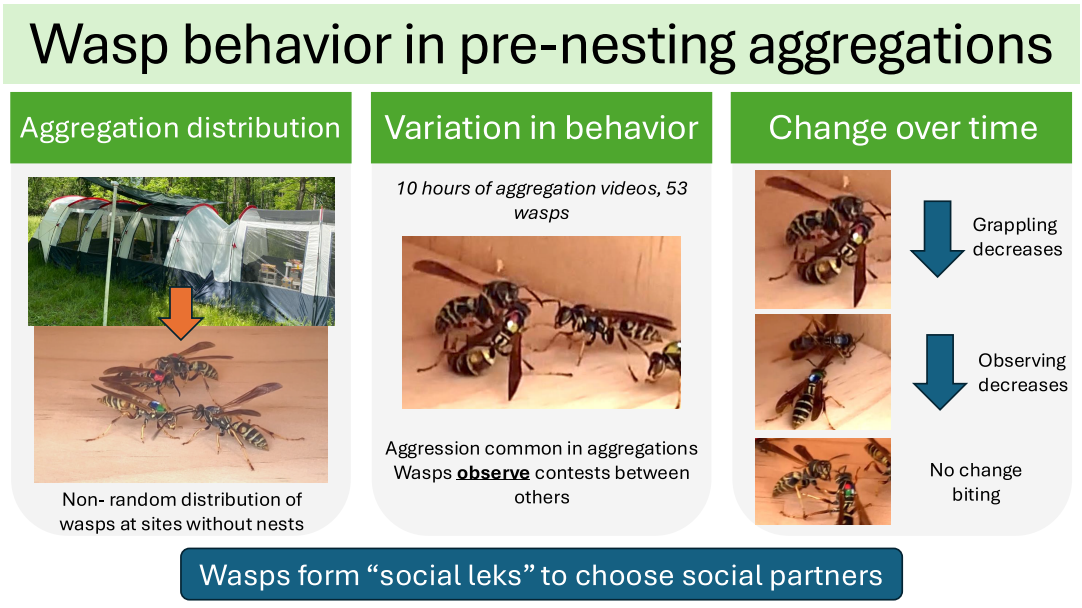
Handling editor: Zu-Shi Huang

Abstract

Many animals live in cooperative social groups. The success of social animals is thought to be influenced by both an animal's own characteristics and by the characteristics of its social partners. As a result, some social animals may devote substantial time and energy to assessing potential partners. Here, we study the process of social group formation in *Polistes fuscatus* paper wasps. Prior to founding nests, wasps engage in extended social partner sampling where they synchronously "shop" for co-foundresses. We quantify wasp behavior during partner sampling using day censuses and recording aggregations. We found that wasps preferentially aggregated at specific locations, without resources or nests, consistent with the formation of a "social lek." In aggregations, wasps engaged in a range of aggressive interactions. At the beginning of the shopping period, wasps engaged in more intensely aggressive behavior and they observe conspecifics fight. Later in the shopping season, wasps engaged in less aggressive behavior. Overall, *P. fuscatus* devote substantial time and energy to a period of partner selection prior to nest foundation that is suggestive of lekking.

Keywords cooperation, lek, partner choice, social behavior, social insect

Graphical abstract



Received: March 11, 2025. **Accepted:** July 9, 2025. **Corrected and Typeset:** December 23, 2025

Although much research examines reproductive partner selection, thus far little work examines the process of social partner selection, despite the important fitness impacts of social partners (Rosenthal 2017). Social partner choice, the process of individuals selecting conspecifics as group members or cooperators, is observed in a variety of taxa including insects (Cahan 2001; Helmkampf et al. 2016), fish (Croft et al. 2005; Snekser et al. 2006; Auld and Godin 2020), cetaceans (Gowans et al. 2007; Gerber et al. 2021), primates (Noë 1994; Schino and Aureli 2009; Martin et al. 2021), and rodents (Weidt et al. 2008; Smith et al. 2013; Linnenbrink and Von Merten 2017). Social partners may influence reproductive success by increasing nesting success (Heinze and Rueppell 2014), aiding mate attraction (Auld and Godin 2020; Gerber et al. 2021), and providing competitive alliances during competition with others (Noë 1994). Social partner choice may be of greatest importance to cooperative breeders as they must choose effective partners to help them raise their young (Arnold and Owens 1998; Wong and Balshine 2011; Lukas and Clutton-Brock 2012; Heinze et al. 2017).

Individuals may evaluate the cooperative and competitive value of potential partners prior to establishing stable partnerships. Much theoretical work suggests that individuals may signal cooperative value to conspecifics to promote selection as a social partner, with some empirical work demonstrating that social partner assessment occurs via incremental cooperation (Noë and Hammerstein 1995; Barclay 2016; Leimar and Bshary 2024). For example, vampire bats test potential social partners via mutual grooming (a low-cost behavior) and strengthen alliances until they engage in higher cost behaviors, such as food sharing (Carter et al. 2020). Competitive ability and aggression often play an important role in social partner selection. Individuals with high competitive ability may be preferred as they may provide an advantage in winning contests against rivals. For example, male baboons prefer to form coalitions with males of high fighting ability (Noë, 1994). However, potential cooperators may also become within-group competitors, so in some species, individuals may prefer to cooperate with others that have lower fighting ability (Wong et al. 2016; Reed et al. 2019).

Much of the research on social partner choice has focused on nest-founding females in social insects. In a broad range of social insect taxa, potentially reproductive females can initiate nests in cooperative groups, including some termites (Atkinson and Adams 1997; Matsuura et al. 2002), halictine bees (Richards et al. 2003), ants (Cahan 2001; Heinze et al. 2017; Haney and Fewell 2018; Suarez and Goodisman 2021), wasps (Grinsted and Field 2017), and thrips (Morris et al. 2002). In some taxa, co-localization likely plays an important role in group formation. For example, in some ants and termites, foundresses are most likely to nest with individuals that land nearby after mating and are more likely to form cooperative associations in environments with high conspecific density (Tschinkel and Howard 1983). Individual characteristics may also influence foundress cooperation. For example, ant (*Lasius pallitarsis*) foundresses preferentially join nests of foundresses that are smaller than them, likely because larger foundresses have competitive advantages over smaller co-foundresses and can take over the majority of reproduction (Nonacs 1992). Genetic differences within populations may impact likelihood of foundress cooperation, for example co-founding *Pogonomyrmex californicus* queens have different gene regulation patterns compared with solitary queens (Helmkampf et al. 2016). In some taxa, it is difficult to assess the extent to which individuals make active choices about partnerships. For example, partner choice in *Solenopsis invicta* ants may be based on nest site selection rather than on the characteristics of partners (Tschinkel 1998). However, other species may compare specific partnerships rather than nest sites (Grinsted and Field 2017). A major challenge of studying the process of social partner selection is that it is often difficult to observe.

Polistes fuscatus (northern paper wasp) are an excellent model for studying the process of social group formation, as they engage in extended social partner sampling every spring when they synchronously "shop" for nest co-foundresses, where they evaluate many potential social partners and nests before settling onto stable nests (Roseler 1991). *Polistes fuscatus* nest founding queens may nest alone or join a nest with as many as 6 other co-foundresses. Solitary foundresses lay all the eggs in a nest. However, solitary nests are vulnerable to queen death and usurpation by rivals, incentivizing nest co-founding (Tibbetts and Reeve 2003). When multiple foundresses cooperate, the dominant individual lays the majority of the eggs and subordinates do most of the foraging (Jandt et al. 2014). Selecting specific cooperative co-foundresses may be beneficial, because cooperation may promote fitness and choosing specific partners may allow individuals to optimize their position in the nest dominance hierarchy. Nest-founding queens spend several weeks shopping for partners, a substantial time investment given that queens only have 1 summer to build nests and raise offspring. During the shopping period, foundresses interact with others in large aggregations during the day and roost with other foundresses at night. *Polistes fuscatus* use individual recognition to learn and remember dominance hierarchies and interactions between conspecifics, therefore wasps may learn about the individual characteristics of potential partners during the partner shopping period (Tibbetts 2002; Tibbetts et al. 2020). However, we do not understand what behaviors wasps engage in during aggregations where they may learn about potential partners (Jandt et al. 2014). Although foundress shopping has been observed previously, we lack information on how wasps aggregate, behave within aggregations, and how behaviors in aggregations change as the shopping period progresses (West-Eberhard 1967; Dapporto et al. 2004; Laub et al. 2024). Previous work suggests that wasp behavior is temperature dependent, but it is unclear how temperature may impact aggregation behavior in the early spring when temperatures may be more variable (Tibbetts and Reeve 2000).

In this study, we investigated how *P. fuscatus* assess social partners in shopping aggregations. We investigated the size, number, and distribution of shopping aggregations and the behavior of wasps within them. We address 3 specific questions: (1) Where do wasps aggregate? (2) Does aggregation size change with time and temperature? (3) What behaviors are used to assess conspecifics during the shopping period? (4) How do specific behaviors within aggregations change with time and temperature?

Materials and methods

Animal care statement

Wasps were handled with care throughout the duration of experiment and provided food and water ad libitum. Wasps were monitored daily to ensure that temperatures within the wasp tent did

not pose a danger to the wasps. As wasps are invertebrates, permits from IUACUC were not required. At the end of the study, wasps were removed from the vespiary to participate in other research projects and allowed to live out their natural lifespans.

Wasp collection

We collected 115 female *P. fuscatus* on 3 May 2023 and 4 May 2023 from 2 parks east of Minneapolis, MN, located 26 miles from each other. Wasps were collected with nets and vials and housed at 21 °C on a 15:9 h light cycle and provided with sugar cubes and water ad libitum. After 3 days, the wasps were transported by car to the University of Michigan. Wasps were kept in an environmental chamber on a 15:9 h light cycle with 23 °C daytime and 13 °C nighttime temperatures. We labeled wasps with unique identifying color combinations using Testors™ model train paint so that they could be individually identified once the behavioral observations began. Wasps were weighed with a microscale accurate to 0.001 g to collect body mass data.

Release into vespiary

Wasps were released into an outdoor vespiary in the Matthaei Botanical Gardens the night of 22 May 2023. The vespiary is a tube tent created by sewing 2 tents together and cutting a partition to make 1 large enclosure, measuring 11 m long, 3.6 m wide, and 2 m tall (Supplementary Fig. S1). Each tent was divided into sections with partial walls connected by opened doors. All doors were open, and wasps were observed flying between all sections of the connected tents. Wasps were provided with 30 uniquely painted nest boxes measuring 15 × 15 × 15 cm. The nest boxes were stacked on top of cinder block towers that were 41 × 20 × 60 cm. We secured the nest boxes to the blocks with bungee cords. We provided wasps with sugar, water, and wood, for nest building, ad libitum at 4 food stations (Fig. 1). The vespiary was in partial shade, and shade cloths were installed over the tent when outside temperatures were over 32 °C to prevent wasps from overheating.

Scan sampling of aggregation location

To determine where wasps were aggregating within the vespiary, behavior of shopping wasps was assessed with scan samples conducted on 23–26 May and 31 May between 11 AM and 2 PM, when wasps are most active. Sampling was not conducted on 27 May–30 May 2023 due to a federal holiday. Two to 3 researchers conducted 6 cycles of scanning per day, with each cycle separated by 5 to 15 min. During a scan sampling cycle, the observers checked all areas of the tent and recorded the location and social proximity of each wasp (alone, or with conspecifics). An aggregation was defined as a group of 3 or more wasps within 15 cm of each other (the length of a nest box) that were not gathering food at a food station.

Behavior and size of shopping aggregations

To evaluate the size of shopping aggregations and behavior of wasps within shopping aggregations, we recorded videos of wasp aggregations. Videos were recorded with Sony HDR-CX405 and Canon Vixia HF R700 cameras. Videos were taken from 5/23/23 through 5/31/23 and were recorded between 11:30 AM and 2:30 PM to capture wasp behavior during the period of greatest activity. There was some variation in video start and end times each day due to lighting conditions and weather as glare and cloudy weather altered the amount of usable footage. We recorded 10 h of footage with 58 wasps represented from 10 aggregation sites, with aggregations recorded in nest boxes and walls of the tent. We used videos to estimate the size of shopping aggregations. To estimate the size of shopping aggregations, we counted the total number of wasps within 15 cm distance (the maximum distance within a nest box) of each other at approximately 10-min intervals for each video. The behavior in the videos was scored by students who were naïve to the experimental predictions. Students recorded aggressive behaviors initiated by a haphazard subset of wasps in each video. Aggressive behaviors recorded include darting, biting, grappling, mounting, and boxing (West-Eberhard 1967; Sumana and Starks 2004):

Darting—a wasp lunging at another without making contact.
Biting—a wasp opening and closing its mandibles on another.
Grappling—2 wasps wrestling with each other and may include biting and stinging.
Boxing—a wasp batting at another with its front legs. This behavior frequently transitions to grappling.
Mounting—1 wasp dominating another by positioning itself on top of the other while drumming its antennae on the other wasps' head or thorax.

We also recorded when wasps observed fights between other wasps, defined as when a wasp faces 2 wasps that are engaged in any of the previously listed aggressive behaviors and moves their head and antennae to follow the interactions of the other wasps. Previous work has shown that wasps can learn about each other's fighting ability by watching aggressive contests (Tibbetts et al. 2020). Finally, we recorded 1 cooperative behavior, trophallaxis—the exchange of liquid food among wasps via regurgitation.

Statistical analysis

Spatial distribution of aggregations

Data were analyzed in R version 4.3.1 with package Lme4 version 1.1-34, Car version 3.1-2, and igraph version 1.5.1 (Bates et al. 2015; Fox and Weisberg 2019; Csárdi et al. 2024). To evaluate the spatial distribution of aggregations, we counted the number of scans in which an aggregation (3 or more wasps) was observed at locations in the vespiary where wasps were observed (36 total scans from 6 days of scan sampling, with 6 scans conducted each day). To determine if wasps aggregated at certain locations more frequently than others, we compared if the number of aggregations observed at each location differed from chance expectation using a Fisher's Exact test calculating *P* values by Monte Carlo simulation with 2,000 replicates. To determine which locations had an overrepresentation of number of aggregations observed compared with chance expectation, we compared standardized residuals from a Chi square, with a cutoff of >2.

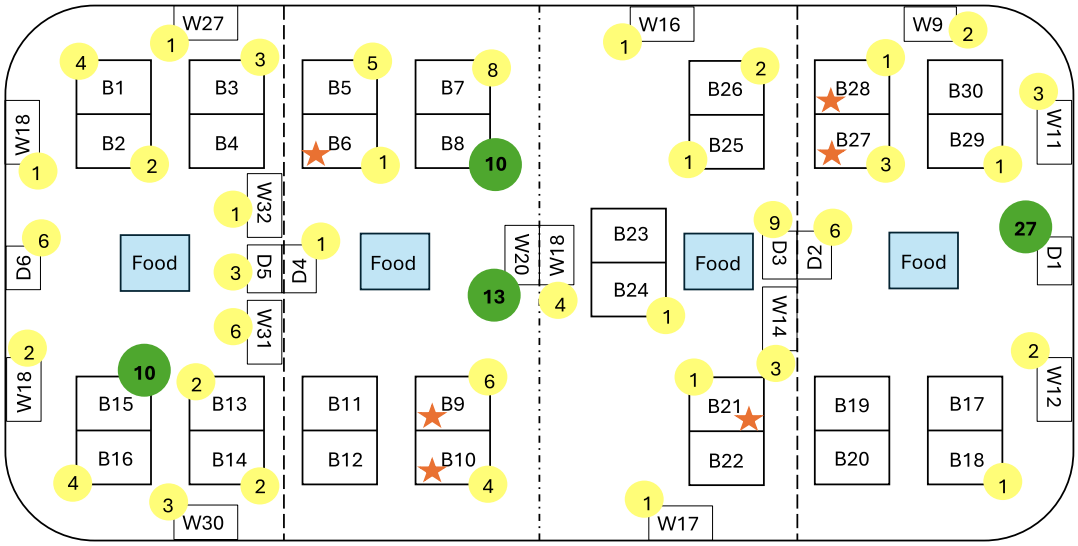


Figure 1 Vespiary layout and locations of aggregations. Sides of the tent are indicated with a solid line, opened partition walls are indicated with a dashed line, wall connecting the 2 tents indicated with the dot-dash line. Nest boxes are represented by squares with B and a number in them, locations of aggregations on the walls of the vespiary are represented by W and a number. The number of aggregations at each location is shown in circles. Yellow circles are locations where the number of aggregations did not differ from chance and green circles with bolded text are locations where aggregations occurred significantly more than expected by chance. Locations where wasps built nests are indicated with orange stars. Wasps aggregated in nest boxes B8, and B15, and the apexes of walls at D1 and W20 significantly more than expected by chance (Standard residual > 2, $P < 0.001$).

Change in aggregation size

To evaluate how aggregation size changed over time and temperature, we used a General Linear Mixed Model (GLMMs) with a Poisson distribution. Aggregation size was determined from counting the number of wasps observed at approximately 10-min intervals in aggregation videos recorded in nest boxes and walls of the tent. The dependent variable was number of wasps present in the aggregation. The independent variables were integer day of video collection (last date of video collection—–first date of video collection +1) and temperature. To account for autocorrelation, video ID was included as a random effect. Number of wasps in the tent was included as a random effect as some wasps left the tent over the course of the experiment. Temperature was recorded from readings collected at a weather station located at (removed to maintain anonymity) accessed from website timeanddate.com.

Change in behavior in aggregations

To investigate change in behavior within shopping aggregations over time and temperatures, we used 4 Generalized Linear Mixed Models (GLMMs) with a negative binomial distribution. Dependent variables included the number of observed darts, biting, observing, or grappling and boxing. Observations of grappling and boxing were combined as they are similar behaviors, with boxing often transitioning to grappling as an interaction continues. Independent variables included integer day of video collection (date of video collection—first date of video collection +1), temperature, and body weight. Body mass was included in models as many studies suggest that body mass may be linked with aggressive behavior. Individual ID was included as a random effect to account for repeated measured of the same individual.

Data availability

Data and code are publicly available at the corresponding author's Github profile (https://github.com/EmilyLaub/Social-Lek).

Results

Spatial distribution and size of aggregations

Wasps joined aggregations at specific locations on walls and in nest boxes in the tent. 64 total locations in the tent were observed with wasps, with 44 locations with aggregations observed, and 178 aggregations observed in total. Aggregations of shopping wasps were non-randomly distributed in the vespiary, with wasps aggregating at specific sites to sample partners (Fisher's Exact test: $P = 0.0004$, Fig. 1). Wasps were most likely to aggregate in 2 specific nest boxes (B8 and B15, Fig. 1) and at the apex of 2 different walls (D1 and W20, Fig. 1) of the vespiary (standardized residual, Chi square > 2, Fig. 1). There were 6 nests found during this study, located at sites B6, B9, B21, B28, B10, and B27 (see Fig. 1). None of the locations where aggregations occurred more often than expected by chance occurred at nesting sites.

Aggregation size changes across temperature and time

Wasps were more likely to join aggregations when the temperature was warm, but aggregations did not change size over the season. Aggregation size was positively linked with temperature (GLMER: $X^2 = 6.91$, $df = 1$, $P = 0.008$, Fig. 2), but it did not change over time (GLMER: $X^2 = 0.31$, $df = 1$, $P = 0.57$).

Changes in behavior in aggregations

We observed many different behaviors within aggregations of shopping wasps, with the majority of behaviors being aggressive (Fig. 3). There were 303 total behaviors recorded from 54 wasps

observed in videos. Biting was the most recorded behavior (178, 59%) followed by darting (59, 19%). There were many instances of wasps observing fights between other wasps (37, 12%) (Fig. 3). More intensely aggressive behavior was also recorded, but at lower frequencies than other interactions. Grappling and boxing were observed 27 times (9%) and mounting was observed once. Trophallaxis, a cooperative behavior, was only observed once. The most aggressive behaviors, grappling and boxing, decreased over the course of the shopping period (GLMER: $X^2 = 10.48$, $df = 1$, $P = 0.003$, Fig. 4A) as did observing behavior (GLMER: $X^2 = 9.65$, $df = 1$, $P = 0.002$, Fig. 4B) and darting (GLMER: $X^2 = 4.95$, $df = 1$, $P = 0.006$, Fig. 4C). However, biting did not change over the shopping period (GLMER: $X^2 = 3.51$, $df = 1$, $P = 0.06$, Fig. 4D). The frequency of some behaviors within aggregations increased with temperature. Observing was positively linked with temperature (GLMER: $X^2 = 11.49$, $df = 1$, $P < 0.001$, Fig. 5A) as was darting (GLMER: $X^2 = 16.05$, $df = 1$, $P < 0.001$, Fig. 5B). In contrast, grapple-boxing (GLMER: $X^2 = 3.75$, $df = 1$, $P = 0.053$, Fig. 5C) and biting (GLMER: $X^2 = 0.79$, $df = 1$, $P = 0.37$, Fig. 5D) did not statistically significantly relate to temperature. Grapple-boxing was negatively linked with body-mass (GLMER: $X^2 = 4.2$, $df = 1$, $P = 0.0404$, Table 1), but we did not find a statistically significant relationship between body mass and any other of the behaviors that we measured (Table 1).

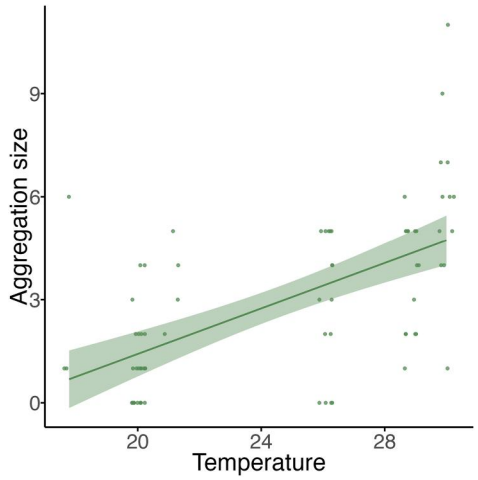


Figure 2 Relationship between number of wasps in each aggregation and temperature. Aggregation size is positively linked with temperature. Each point is an observed video recorded aggregation and points are slightly jittered along the *x* axis to improve visibility. Solid line shows linear regression and the shaded area is standard error.

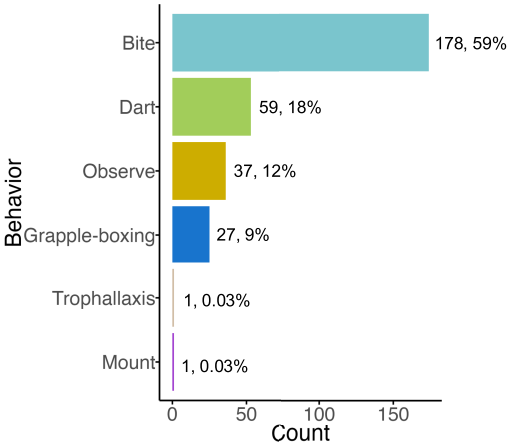


Figure 3 Behavior counts and percentages from 10 h of videos taken of aggregations between 23 May 2024 and 31 May 2024 with 54 wasps represented.

Discussion

Our study suggests that paper wasps form social leks to assess social partners. We found that foundresses aggregated at specific locations that were preferred over other locations. Notably, most aggregations and the only significantly over-represented aggregation locations occurred at sites without resources (food or nests). Aggregation locations did allowed assessment of multiple potential partners (Fig. 1). Aggregation size was affected by temperature, with larger aggregations occurring at high temperatures (Fig. 2). Wasps exhibited diverse behaviors in aggregations, with the majority of these behaviors being aggressive (Fig. 3). Notably, wasps were often seen observing the contests of others, suggesting that aggregations may be used to assess conspecifics via social eavesdropping (Tibbetts et al. 2020).

One of the most interesting aspects of this study was finding that wasps assess potential partners by aggregating at specific locations (Fig. 1). Sites where aggregations were over-represented compared with chance did not contain nests, suggesting that wasps are not aggregating only to compete for nest ownership. This nonrandom spatial assortment accompanied by aggression and contest observation behavior (Fig. 3) suggests that wasps could be forming "social leks". In conventional mating leks, males aggregate to display to observing females at sites without resources (Bradbury 1981). Physical competition is observed during lekking in many species, including fruit flies (various *Drosophila* species) (Shelly 2018), topi antelopes (*Damaliscus lunatus*) (Bro-Jørgensen 2002), and fallow deer (*Cervus dama*) (Apollonio et al. 1989). Wasp aggregations are similar in that wasps compete at locations with no resources in the presence of observers, suggesting that aggregations facilitate the evaluation and selection of partners rather than occurring only due to resource conflict. Although the definition of leks remains controversial, most studies agree that clustering of displaying individuals without resource guarding is an important characteristic of leks (Booth-Binczik et al. 2004; DuVal 2013; Isvaran and Ponkshe 2013). Male Polistine wasps form leks for mate attraction, where they defend lekking sites and engage in aggressive contests, suggesting that lekking behavior plays an important role in partner selection across contexts in wasps (Beani and Turillazzi 1988; Izzo and Tibbetts 2012; Beani et al. 2014; Cappa et al. 2015). Lekking behavior in wasps may be prevalent enough to be a target for manipulation by parasites (Hughes et al. 2004; Beani 2006; Beani et al. 2018). More work is needed to understand how social aggregation locations are chosen and whether participation in aggregations facilitates social partner choice.

In aggregations, moderately aggressive behaviors (biting and darting) were observed much more frequently than all other behaviors (Fig. 3). Biting was observed nearly 3× as often as the next most frequent behavior and was observed more than all other behaviors combined. Biting is an aggressive behavior,

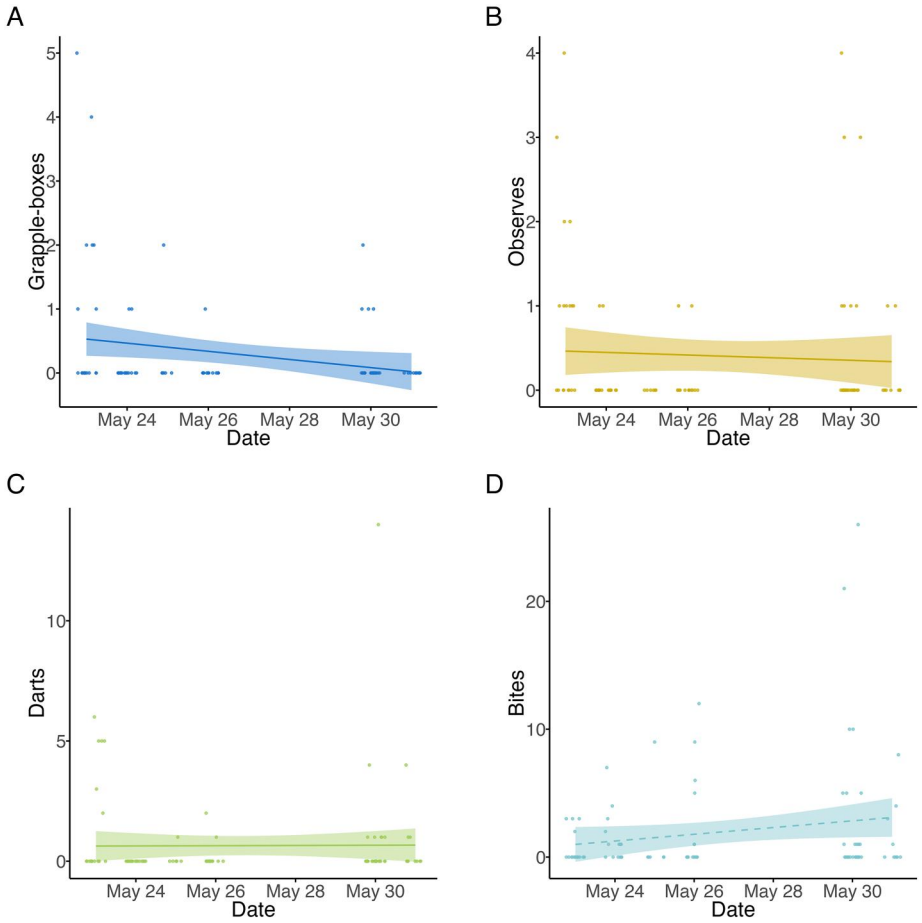


Figure 4 Change in behaviors over time. (A) Grapple-boxing, (B) observing, and (C) darting decreased as the season progressed. (D) Biting did not change as the season progressed. Each point is a wasp observed in videos of aggregations and points are slightly jittered along the *x* axis. Solid lines indicate a statistically significant linear relationship, dashed lines show a statistically insignificant linear relationship, and the shaded area shows standard error.

but it rarely results in substantial damage to the recipient. Biting could be used to assess another wasp's fighting investment without fully engaging in a contest, as fights that escalate to grappling can prove fatal (Jandt et al. 2014). Darting behavior was the second most observed behavior. On an established nest, darts are used by foundresses and workers to stimulate activity on nests (Sumana and Starks 2004). Like bites, they may be used as an assessment behavior to determine how the targeted individual will react. In a partner shopping context, darts may serve as a bluff charging behavior, as observed in many species, including chimpanzees (*Pan troglodytes*) (Aureli and De Waal 1997), Cross River gorillas (*Gorilla gorilla diehli*) (Wittiger and Sunderland-Groves 2007), and brown bears (*Ursus arctos*) (Swenson et al. 1999). Although only observed once, it is notable that trophallaxis, a cooperative behavior, was observed before the foundation of stable nests, in contrast to work examining behavior in hibernation aggregations in other wasp species (González et al. 2002). It is possible that trophallaxis is more prevalent when wasps are actively sampling social partners as a mechanism to gain future nest access or avoid aggression. However much more work is needed to understand what role trophallaxis may play in partner assessment and choice.

Wasps engage in fewer bouts of intensely aggressive behaviors (grappling and boxing) as the shopping season progresses (Fig. 5). Although grappling is thought to be energetically costly and dangerous, winning a grapple is a good way to establish high dominance rank. Early costly aggression may serve to establish rank but also to signal contest ability to observing wasps. It may be beneficial to invest in costly aggression early in the season because early contest wins could deter future aggression, as prior work shows that wasps are less aggressive to wasps they observe winning contests (Tibbetts et al. 2020, 2022). It is plausible that after early investment in costly signaling, a dominant wasp can maintain status through less intensely aggressive behaviors, such as biting which does not decrease over the shopping period. Many species use specific behaviors to reinforce the lower rank of subordinates, including mantis shrimp (*Gonodactylus bredini*) (Dingle and Caldwell 1969), caribou (*Rangifer tara*) (Barrette and Vandal 1986), and guineafowl (*Acryllium vulturinum*) (Dehnen et al. 2022).

We found that wasps observed their conspecifics at social aggregates frequently. Wasps typically observe aggressive behavior, like grapples. While observing fights, wasps move so that their head and antennae are directed toward an interaction, and will even fly over, once fights begin, to watch (Laub, personal observation). Observing may be used to evaluate both the viability of a wasp as a nesting partner and to gain information about relative fighting ability, as previous work shows that wasps adjust their investment in fights from observing the performance

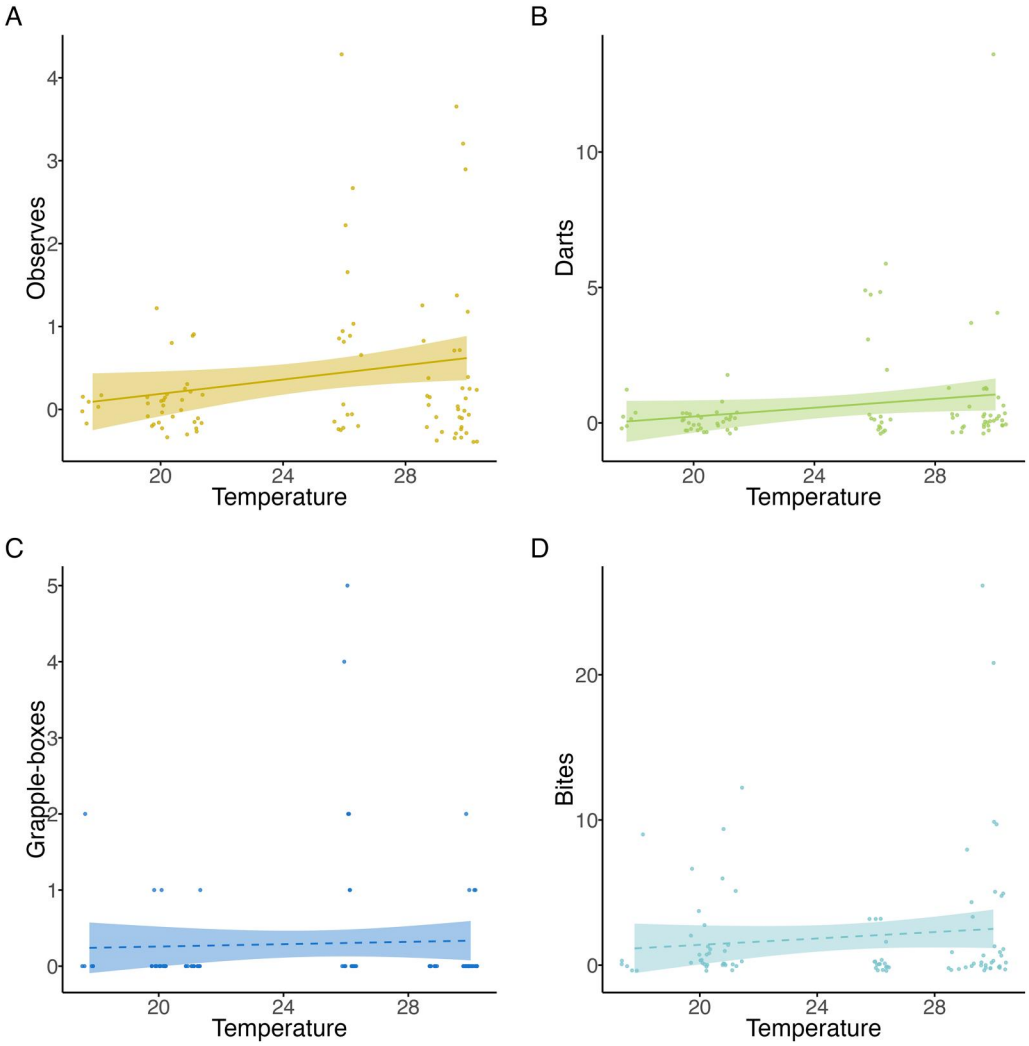


Figure 5 Relationship between behaviors in aggregation and temperature. (A) Observing and (B) darting increase with temperature. (C) Grapple-boxing and (D) biting do not increase with temperature. Each point is a wasp observed in videos of aggregations and points are slightly jittered along the *x* axis. Solid lines indicate linear regression and the shaded area shows standard error. Dashed lines indicate non-significant relationships.

Table 1 Output of statistical models examining the relationship between behavior in shopping aggregations and time, temperature, and body mass.

Behavior	Fixed effect	Estimate	Chi-squared	*P* value
Grapple-boxing	**Date**	**−0.36**	**10.48**	**0.003**
	Temperature	0.167	3.75	0.052
	Body mass	**−33.04**	**4.19**	**0.041**
Observes	**Date**	**−0.26**	**9.649**	**0.002**
	Temperature	**0.29**	**11.72**	**0.0006**
	Body mass	−0.52	0.002	0.96
Bites	Date	0.21	3.51	0.06
	Temperature	−0.039	1.15	0.28
	Body mass	−11.47	1.15	0.28
Darts	**Date**	**−0.27**	**7.46**	**0.006**
	Temperature	**0.38**	**17.32**	**<0.001**
	Body mass	1.34	0.004	0.95

Bolded text indicates significant effects in the model.

of others (Tibbetts et al. 2020). The frequency of contest observation also decreased over time. Wasps are most likely to observe grappling and boxing (Laub, personal observation), so the decline in observation over time may reflect the decrease in intense aggression. Once wasps identify the most aggressive and dominant wasps during early interactions, the importance of observing may decline. Contest observation shapes future social interactions in many species including swordtail fish (*Xiphophorus helleri*) (Earley and Dugatkin 2002) and chickadees (*Poecile atricapillus*) (Toth et al. 2012); however, thus far little work has shown that contest observation impacts selection of social partners. Further work is needed to understand how contest observation may impact specific choice in partners and dominance hierarchies on future nests.

Temperature had an important impact on wasp partner shopping, with wasps forming larger aggregations (Fig. 2) and engaging in more observation and darting behaviors (Fig. 5) in warmer temperatures. Wasps are ectotherms and are thus more active in warm temperatures. Because wasps are more active at warmer temperatures, the number of active wasps available to join an aggregation at any time is larger in warm temperatures, which leads to larger average aggregation sizes. Other studies have shown that wasps are more aggressive at warmer temperatures (Tibbetts and Reeve 2000), and many other ectothermic species display higher aggression and activity in warmer temperatures, including leopard lizards (*Gambelia wislizenii*) (Crowley and Pietruszka 1983), and cichlid fish (*Neolamprologus pulcher*) (Jones et al. 2024). Interestingly, we do not find that the most aggressive behaviors measured in our study (grappling and biting) are linked with temperature (Fig. 5). It is possible that the changing social environment has a greater impact than temperature on how wasps engage in aggressive behavior during partner shopping. Other studies on wasps that find a relationship between aggressive behavior and temperature have examined aggression on established nests (Tibbetts and Reeve 2000).

Overall, *P. fuscatus* exhibit rich and varied partner assessment behavior prior to nest foundation. Social partner choice is common in diverse taxa and is thought to have crucial impacts on social success. However, empirical work on partner choice has lagged behind theory due, in part, to the challenges of observing the process of partner choice in most taxa. Social insects have the potential to be valuable model systems for studying how different behaviors may predict partnerships and how individuals choose partners.

Acknowledgments

This data was collected with assistance from An Na Vi, Alba Mihalik, Fiona Corcoran, and Mason Collard. Wasps were collected with assistance from Zachary Leytus and Oscar Cardoner Sebio.

Authors' contributions

E.C.L. collected data, analyzed data, and substantially revised the manuscript. M.C.E. collected data, conducted preliminary analysis, and wrote early drafts of the manuscript. E.R.B. collected data. N.P.-W. provided key insights on data analysis and revised the manuscript. E.A.T. designed the experiment and revised the manuscript. E.C.L. and M.C.E contributed equally to this work.

Funding

This work was supported by the U.S. National Science Foundation (NSF IOS-2134910 to E.A.T.; NSF-IOS 2134911 to N.P.-W.; NSF GRFP DGE 1841052 to E.C.L.).

Conflict of interest

The authors declare they have no conflict of interest.

Ethics statement

Wasps were collected with permission from the Minnesota DNR (Permit number: 202360). Care of wasps did not require special approval. No researchers have conflicts of interest.

Supplementary material

Supplementary material can be found at https://academic.oup.com/cz.

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