SPECIAL ISSUE: MULTILAYER NETWORKS FOR ANIMAL SOCIALITY

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Special Issue: Multilayer Networks for Animal Sociality

Timing and behavioural situation of social interactions affect the relationship between sociality and fitness

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Sociality has important positive and negative fitness consequences, depending on the timing or behavioural situation of social interactions. In this study, we examined the impacts of social interactions on fitness in a population of paper wasps (*Polistes fuscatus*). We examined the effect of interaction timing by comparing the fitness consequences of interactions across different periods of the breeding season (social partner shopping, nest establishment and colony growth). We further studied how sociality in different behavioural situations (roosting and diurnal associations) impacted fitness. We found that wasps benefited from being highly social, i.e. interacting with many unique individuals, early in the breeding season. Quickly pruning social ties as the breeding season progressed was also beneficial. Furthermore, wasps benefited from strong social ties late in the season, when cooperation is important for maintaining a productive nest. Finally, we found that certain behavioural situations (roosting interactions) had a larger impact on fitness than other behavioural situations (diurnal associations). Our work suggests that considering both the timing and situation where social interactions occur may reveal important and variable fitness effects.

Sociality has important fitness consequences (Snyder-Mackler et al., 2020). Animals with strong and numerous social connections often have increased offspring survival (Cameron et al., 2009; Silk et al., 2010), mating success (Beck et al., 2021; Formica et al., 2012; Gerber et al., 2022) and higher survival rates (Campos et al., 2020; Silk et al., 2009). However, social contact is not beneficial in all species or at all times (Blumstein et al., 2018; Menz et al., 2020). For example, yellow-bellied marmot, *Marmota flaviventer*, adult females with more social connections have decreased winter survival, but yearling females receive survival benefits from sociality (Blumstein et al., 2018; Montero et al., 2020). Therefore, it is important to consider not only whether individuals are socially integrated but when they are socially integrated when examining the fitness consequences of social interactions (Thompson, 2019).

Much work examining how the timing of social interactions impacts fitness considers the effects of early life experiences on fitness outcomes. Social interactions early in life may promote the formation of important social relationships later in life; for example, early life social interactions are linked with future courtship success in brown headed-cowbirds, *Molothrus ater* (Kohn et al., 2013), and interactions early in life predict the strength of adult relationships in gorillas (*Gorilla beringei beringei*) (Rosenbaum et al., 2016). In hyaenas (*Crocuta crocuta*), dolphins (*Tursiops aduncus*) and geese (*Anser anser*), early sociality is positively linked with adult reproductive success (Holmes et al., 2024; Szipl et al., 2019; Turner et al., 2021). Specific social interactions in early life may impact fitness; for example the sociality of juvenile male dolphins is linked with more opportunities for social play and reproductive success as adults (Holmes et al., 2024). Although early life social experiences are important for fitness outcomes, adult sociality is also subjected to temporal changes, and much work considers how age (Albery et al., 2022; Almeling et al., 2017; Machanda & Rosati, 2020; Rathke & Fischer, 2021), food availability (Blersch et al., 2024; Gareta García et al., 2021) and season (Henzi et al., 2009; Patriquin et al., 2010; Philson et al., 2024; Prehn et al., 2019) may impact sociality and the associated fitness consequences. Adults may experience periods in which social contact has elevated fitness impacts, such as during breeding seasons (McDonald et al., 2020; Wey et al., 2013; Wyman et al., 2021).

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Animals interact in different types of social situations. Social interactions in each situation may provide different opportunities to strengthen social bonds, form dominance hierarchies or defeat rivals (Seyfarth, 1977; Tibbetts et al., 2022; Tiddi et al., 2012). Importantly, behaviours that are adaptive in one social situation may not be adaptive in others (Oliveira, 2009; Wyman et al., 2021). For example, before breeding, when competing for mates, aggressive interactions may provide access to mates, but outside competition for mates, aggression has net negative fitness consequences (Duckworth, 2006). There is growing appreciation that social interactions within one or more specific social situations may provide different opportunities to learn information and build relationships with conspecifics (Miller & Pinter-Wollman, 2023; Sharma et al., 2023). For example, work in griffon vultures, *Gyps fulvus*, suggests that interactions when roosting and feeding build strong social relationships, but interactions when flying are used for other purposes, such as gaining information about food (Sharma et al., 2023). Therefore, both when and how animals interact with conspecifics may impact fitness consequences in different ways.

There is growing interest in understanding how fitness may be impacted by social interactions across multiple situations (Hasenjager et al., 2021; Silk et al., 2018). Recent work proposes using multilayer networks to link social interactions across behavioural situations (Finn et al., 2019). This approach may uncover individuals of social importance that are not detected when considering social interactions in multiple behavioural situations separately. For example, work in *Ropalidia marginata* paper wasps found that wasps who ascend to queenship in a colony are the most central in a multilayered network, but they are not the most central individuals in each social network of the separate behavioural situations, or when the situations are summed up in an aggregate network (Sharma et al., 2022). Thus, the ability to predict fitness consequences of social behaviour may require not only examining social interactions in more than one behavioural situation but also integrating them in a multilayered framework. Still, many studies combine different types of social interactions in an aggregate network, which adds up all interactions into one network. Therefore, we aim to compare how integrating different social situations in a multilayer network differs from combining them as an aggregate network in identifying fitness consequences of social interactions.

Paper wasps (*Polistes fuscatus*) are an excellent system to examine how both the timing and situation of social interactions impact fitness consequences. Throughout the adult life of nest-founding individuals, the objective of social interactions changes. At the beginning of the spring, nest-founding wasps engage in a behaviour called ‘shopping’ when they cluster at nesting and non-nesting locations and use social interactions to sample potential social partners to establish a nest (Laub et al., 2025). Wasps then establish nests alone or with the social partners they select. At the end of spring, wasps enter a phase of colony growth during which they engage in cooperative brood care (Reeve, 1991; Turillazzi & West-Eberhard, 1996). In the colony growth period, wasps typically interact with nestmates, however, the stability of the social relationships and nest membership is variable, and little is known about how wasps may continue to interact away from nests or with non-nestmates. Solitary foundresses may attempt to gain social partners or may have weak social relationships throughout the season that never become stable partnerships. Additionally, wasps engage in different types of interactions throughout their nesting cycle (Jandt et al., 2014). Wasps interact at roosts overnight, where they huddle with each other. Furthermore, they engage in active associations during the day, including affiliative interactions on and off nests (Jandt et al., 2014; Reeve, 1991; Röseler, 1991; Tibbetts & Reeve, 2000; Turillazzi & West-Eberhard, 1996). As ectotherms, wasps do not move from a roost at night. Thus, interactions during roosting might provide different information than active interactions during the day, when the wasps move around. Wasps gain fitness benefits through successfully founding, joining or usurping ownership of a nest, as wasps that do not have a nest are unable to produce offspring (Liebert et al., 2005; Nonacs & Reeve, 1995; Starks, 1998).

In this study, we ask how both the timing of interactions throughout a breeding season and the type of interactions (roosting or diurnal associations) (Fig. 1) impact fitness in a population of paper wasps. We predicted that social interactions early in the breeding season would have a positive relationship with fitness because wasps benefit from more social information and a larger market of potential nestmates to choose from. We further predicted that, as the breeding season progresses, the number of social interactions would have a stronger relationship with fitness than the number of unique individuals a wasp encounters because wasps benefit from forming stable social relationships when they are cooperating on building and maintaining a nest. We used multilayer network analysis to determine whether our ability to predict the fitness consequences of sociality throughout the breeding season changed when considering each social situation separately (i.e. aggregated in a single network or integrated in a multilayer network). We predicted that active diurnal associations would have a greater effect on fitness than passive roosting interactions because wasps can engage in more informative cooperative behaviours when associating during the day. We further predicted that, if active diurnal interactions and passive roosting interactions relate to fitness consequences in opposite directions (e.g. the relationship with active interactions is positive and the relationship with passive interactions is negative), then aggregating these interactions, or linking them in a multilayer network, would mask the relationship between social interactions and fitness. However, if active diurnal interactions and passive roosting interactions relate to fitness in a similar manner, then we expected that their aggregation, or integration in a multilayer network, would strengthen the relationships with fitness consequences found when examining interactions in each situation separately.

METHODS

Wasp Collection and Maintenance

We collected nest-founding wasps (reproductive foundresses) emerging from hibernation in the spring, prior to founding a nest or in the earliest stages of nest foundation, from 7 May 2021 to 11 May 2021 from parks surrounding Minneapolis, Minnesota, U.S.A. using nets and collection vials. At the time of wasp collection, there were no workers because workers hatch from eggs that are laid later in the summer. After collection, we housed wasps individually in 2 × 4 inch (5.1 ×10.2 cm) round deli cups with sugar and water ad libitum and kept them at 22.2 °C with a 10:14 h light:dark cycle 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 at 25 °C day temperature and 15.5 °C night temperature with an LD 11:13 h cycle to match natural temperature and light cycles in Ann Arbor, MI in May. Wasps were weighed on a scale accurate to 0.002 g and uniquely marked with Testors model paint using one to four different colours on their wings and thorax to enable individual identification.

To observe wasp behaviour during the breeding season in a naturalistic environment, on the night of 30 May 2021, we released 75 wasps into a large outdoor enclosure (vespiary). The vespiary is a 7.3 × 5.4 × 2.74 m screened hoop house located in an open field

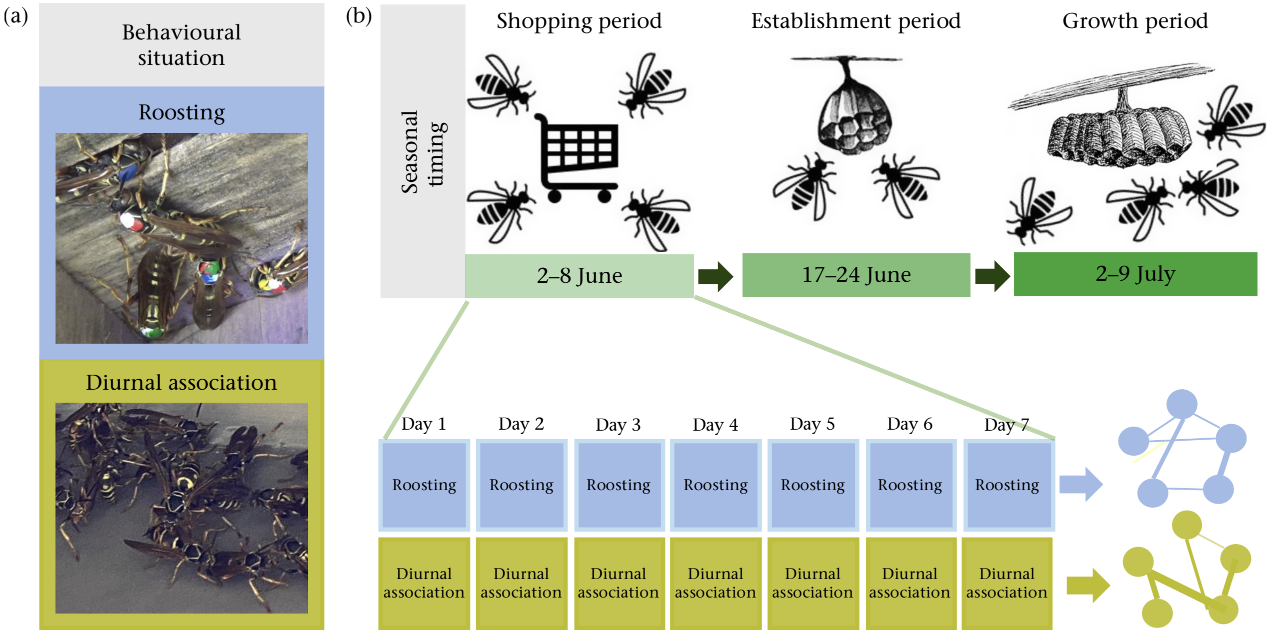

Figure 1. Behavioural situation and time period of social interactions over the breeding season. (a) Behavioural situations included roosting at night and diurnal associations. Photo credit: Emily C. Laub. (b) Seasonal time periods included shopping, colony establishment and colony growth (date ranges for each period are listed in the green boxes). During each of the three time periods, we sampled both roosting and diurnal associations on 7 days to form a single social network for each situation in each period, as shown for the first period.

at the Matthaei Botanical Gardens. It contains 40 individually marked nestboxes (10.2 × 7.6 × 15.2 cm) 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 must fly among potential nest sites, navigate a complex environment, forage for food and avoid predators (such as spiders).

Social Interactions

To understand how the timing of social interactions impacts fitness, we examined the social interactions of wasps during the three periods of the breeding season. Wasps were given 2 days to habituate in the vespiary, which is enough time as wasps quickly learn to navigate the vespiary (Laub et al., 2024). The breeding season periods included social partner shopping, colony establishment and colony growth (Fig. 1). Time periods were classified by observing nest and larvae development. The ‘shopping’ period starts immediately post-hibernation and may continue for several weeks while nests are still small (fewer than 10 cells with small eggs) (2 June 2021–8 June 2021). Wasps engage in shopping behaviour both in nestboxes (with and without established nests) and in non-nest site locations as detailed in Laub et al. (2025). We classified the ‘establishment’ period as the time when most nests had at least 10 cells with eggs and some small larvae (17 June 2021–24 June 2021). The ‘growth’ period is when nests have large larvae (visible dark head capsule) and capped cells (2 July 2021–9 July 2021). Although nests continue to expand until mid-August, we only studied social interactions from the growth period until early July because that is when workers begin to emerge. Observing interactions after workers emerge would conflate interactions among co-foundresses and interactions with workers. Within each period we sampled interactions on a daily basis, as detailed below.

To understand how the behavioural situation of social interactions impacts fitness, we examined social affiliation in two different behavioural situations (roosting and diurnal associations) (Fig. 1a). Wasps huddle together, usually touching or in close contact, when they roost overnight. To evaluate which wasps interacted with one another while roosting, we conducted dawn censuses, before it was warm enough for wasps to fly. Wasps that were found in the same roost were considered as ‘interacting while roosting’. Once wasps leave their roosts, they will actively interact in aggressive and affiliative (cooperative) interactions. We recorded interactions of wasps that were within one body length of each other and not engaged in aggressive interactions as ‘diurnal associations’. To evaluate wasp diurnal associations, we conducted scan samples. Data were collected by observers trained to identify wasp behaviour. A cycle of scan sampling (20 min) consisted of an observer walking in a circuit through the vespiary and recording wasp behaviours. Wasps were observed in nestboxes, on the walls of the vespiary and at food stations. Wasps were recorded as roosting together if they were within one body length of each other or sharing a nestbox. Six scan sample cycles were conducted daily during the hottest part of the day, between 1100 and 1400 hours, when wasps are most active. Only four scans were conducted on 4 June 2021.

To understand how sociality impacts fitness, we created social networks of wasp interactions for both behavioural situations across each time period (Fig. 1b). We combined into one network all the interactions we observed over the 7 days in each period, for each social situation (Fig. 1b). Therefore, each node in the network represents a wasp observed in one of the two situations, connected by undirected edges that are weighted by the number of interactions within each situation.

To examine how roosting and diurnal interactions may impact fitness in synergistic or opposing ways, we created aggregate and multilayer networks of wasp interactions. Aggregate networks were constructed by combining roosting and diurnal interactions (summing edge weights for each dyad) in each period into one social network. For example, if individuals A and B interacted once while roosting (edge weight of 1 during roosting) and associated twice during the day (edge weight of 2 in the diurnal association network), then in the aggregate network, they would be connected with an edge weight of 3. In a multilayer network, we represented each social situation (roosting or diurnal associations) as a layer with interlayer edges (of weight 0) linking the same individual (node) across layers. Thus, we had four networks for each time period (one for roosting, one for diurnal associations, an aggregate network and a multilayer network), totalling 12 social networks overall.

To measure how many unique individuals each wasp interacted with, we computed the ‘degree’ and ‘strength’ of each node in the network. Degree is the number of unique individuals a wasp interacted with. Strength is the total number of interactions each individual participated in. Aggregate degree and strength are the degree and strength of each node in the aggregate network. Multilayer versatility quantifies node centrality by adding the number of unique edges in all the layers of the multilayer network. For example, if individual A interacts with four individuals during roosting, then associates with one of the same individuals during the day (diurnal associations), the versatility of individual A would be 5, its aggregate degree would be 4, its degree in roosting would be 4 and its degree in diurnal associations would be 1 (Supplementary Fig. S1). To compare across networks with different numbers of individuals and different numbers of interactions in each time period, we normalized degree and strength. Degree was normalized by dividing the degree of each individual by the number of individuals in the network minus one, which is the standard procedure for normalizing degree and is implemented using the function ‘degree()’ in the ‘igraph’ R package (Csárdi et al., 2006). Versatility was normalized by dividing the versatility of each individual by the sum of the number of nodes in the roosting network and the number of nodes in diurnal association network minus two (because there were two layers).

To measure how many social interactions a wasp participated in, we computed the ‘strength’ of each node. Aggregate strength was the strength of each node in the aggregate network. Multilayer strength is equivalent to aggregate strength because interactions were summed across layers. Because strength measures number of interactions, its normalization needs to account for the total number of interactions observed. Therefore, to normalize strength, we divided the strength of each individual by the sum of strengths of all individuals in each network.

Only individuals that were observed in the vespiary over a span of at least 5 days in either the dawn census or daytime scan sampling (with or without partners) over the course of the entire season were included in the analyses. Because wasps died or escaped from the vespiary throughout the breeding season, and because not all wasps always engaged in all types of social interactions, the number of individuals in each network ranged from 34 to 62. Wasps that were observed in the vespiary but did not interact with other wasps were given 0 scores for degree and strength and were not included in the normalization procedure. Four wasps were observed but did not interact during the day or night with any other individual throughout the study. Social networks were constructed and analysed using the R package igraph version 2.1.2 (Csárdi et al., 2026).

Fitness Estimates

To determine how social position impacts fitness, we evaluated the fitness of wasps using two different measures: likelihood to nest (yes/no) and ultimate nest size. Whether a wasp nests or not is crucial for fitness because nesting gives wasps an opportunity to lay eggs, inherit a nest or receive indirect fitness benefits through nesting with sisters (Nonacs & Reeve, 1995). A foundress was considered to be nesting if she roosted at the same nest for more than three consecutive nights. The day a wasp was determined to choose a nest was the third day of consecutive roosting because, after three nights, wasps rarely defect from a chosen nest (Laub et al., 2024). Foundresses that founded, joined or usurped a nest were all considered to be nesting. Foundresses typically maintain stable membership of nests for 14–50 days.

We quantified nest size by counting the number of nest cells built by the end of the season (15 August 2021). Nest size is an informative fitness estimate because each nest cell generates only one offspring. Paper wasp reproduction is determined by a dominance hierarchy, with the dominant individual receiving the vast majority of reproduction on a nest (Reeve & Keller, 2001). Therefore, we included only dominant wasps and those that ultimately nested alone (no consistent nestmate for three or more consecutive nights) in our analysis of how interactions affect nest size (Reeve & Keller, 2001; Tibbetts & Reeve, 2000).

Dominance

To determine which wasp was the dominant individual on each nest, we videorecorded on-nest behaviour using Sony Handicams, once nests were established. We recorded the behaviour of wasps on 11 established nests once a week between 29 June 2021 and 28 July 2021. Nests were recorded one to six times, with most nests recorded three or four times ($N = 10$ nests total). A few videos were recorded on consecutive days. We spread recording throughout June and July to capture behaviour of wasps during the different stages of nest and larvae development and to capture interactions before wasps died or abandoned nests later in the season. Thus, there was some variation in when different nests were videorecorded because nests were founded at different times (Supplementary Table S8). Video duration was 31–140 min, with most videos being 90–120 min long, and all videos were recorded between 1130 and 1500 hours to capture the peak of wasp activity. We aimed to collect 2 h of video during each recording session, but lighting and weather conditions reduced the amount of useable footage.

To determine dominance hierarchies, observers scored the behaviours in the videos. The dominant wasp on each nest was the wasp that engaged in the most mounting behaviours, monopolized the centre of the nest and spent the most time on the nest. 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 and subordinates never mount dominants (Jandt et al., 2014).

Relating Fitness Consequences to Social Position

To evaluate whether the likelihood to join a nest, through founding, joining or usurping an existing nest, was related to social position during the shopping period, we used five generalized linear models (GLMs) with a binomial distribution ($N = 58$ wasps, 32 joined nests, 26 without nests). We focused this analysis only on the first period of the breeding season (the shopping period) because wasps engage in extensive partner sampling during this period and have not formed stable nests yet. Therefore, variation in interactions during this period may alter the social information that wasps use to make nesting decisions. The response variable was whether or not a wasp nested (yes/no). Five models were used to avoid collinearity between the network measures (see Results). The first model had normalized roosting degree and normalized association degree as explanatory variables. The second model had normalized roosting strength and normalized association strength as explanatory variables. The third model had normalized aggregate degree as an explanatory variable. The fourth model had normalized aggregate strength as an explanatory variable. The fifth model had normalized versatility as an explanatory variable. Body mass, the wasp weight as measured upon arrival at the laboratory after collection in the field (see above), was included as an explanatory variable in all models. We used a Bonferroni correction to set a significance threshold of $P = 0.01$ to account for an increase in type I errors from multiple testing (number of tests = 5).

To evaluate whether nest size was related to social network position of dominant and solitary wasps across behavioural situations in each different seasonal time period, we ran five different generalized linear models (GLMs) with a Poisson distribution for each time period (shopping: $N = 15$ wasps; establishment: $N = 15$ wasps; growth: $N = 14$ wasps; mean ± SD nest size = 26 ± 18 cells, range 4–64 cells; 5 models per time period, 15 total models). We could not include all three time periods in a single statistical model because three of the main effects (body mass, nest size, maximum group size) were measured only once during the entire study. To avoid collinearity between network measures within a behavioural situation, separate models were run with each network measure (degree or strength) as an explanatory variable. The first model for each period had normalized roosting degree and normalized association degree as explanatory variables. The second model had normalized roosting strength and normalized association strength as explanatory variables. The third model had normalized aggregate degree as an explanatory variable. The fourth model had normalized aggregate strength as an explanatory variable. The fifth model had normalized versatility as an explanatory variable. All models included maximum stable group size, nest choice day and body mass as explanatory variables. To account for the different number of foundresses of established nests, which may influence nest size (Tibbetts & Reeve, 2003), we included 'maximum stable group size' in our statistical models (6 nests with one foundress, 4 nests with two foundresses, 5 nests with 3 foundresses). We defined maximum stable group size as the largest number of co-foundresses observed on the nest during dawn census for ≥3 days. Solitary foundresses received a value of 1 for their maximum stable group size. Wasps who start nests earlier may have a longer period of nest growth, so we included nest choice day as an explanatory variable in our models. To evaluate collinearity between explanatory variables, we evaluated the variance inflation factors (VIFs) in all models and the fit of models (see Results, Supplementary Material). To account for type I errors due to multiple testing, we used a Bonferroni correction to adjust the statistical significance threshold to $P = 0.01$ (number of tests = 5). We analysed the data in R version 4.4.2 with packages 'lme4' version 1.1–21 (Bates et al., 2015), 'performance' version 0.12.4 (Lüdecke et al., 2021) and 'car' version 3.1-2 (Fox & Weisberg, 2019). We used packages 'ggeffects' version 2.3.1 (Lüdecke, 2018) and 'ggplot2' version 3.5.1 (Wickham, 2016) to visualize the fit of models.

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). All wasps were handled carefully during transportation and marking to minimize stress. Wasps were provided sufficient resources to thrive outside in seminatural conditions and lived a natural life span in the vespiary.

RESULTS

Social Position and Likelihood to Join or Establish a Nest

We did not find that wasps' social position in multilayer or aggregate networks during the shopping period predicted whether they would or would not join nests. We did not find that examining interactions in each social situation during the shopping period separately was predictive of nest joining. Whether or not wasps would join nests was not predicted by normalized degree while roosting or during diurnal associations (GLM: roosting: $\chi^2_1 = 0.0002$, $P = 0.996$; diurnal associations: $\chi^2_1 = 0.73$, $P = 0.39$; Table 1) or by body mass (GLM: $\chi^2_1 = 2.71$, $P = 0.099$; Table 1). Nest joining was not predicted by normalized strength while roosting (GLM: $\chi^2_1 = 0.046$, $P = 0.829$; Table 1) or during diurnal associations (GLM: $\chi^2_1 = 5.44$, $P = 0.019$; Table 1) or by body mass (GLM: $\chi^2_1 = 3.77$, $P = 0.052$; Table 1); note that we adjusted the P value to 0.01 to account for multiple testing. Pooling interactions in an aggregate network, or integrating them in a multilayer network, did not predict nest joining better than considering social position in each behavioural situation separately. Nest joining was not significantly related to normalized degree (GLM: $\chi^2_1 = 1.03$, $P = 0.309$; Table 1) or normalized strength (GLM: $\chi^2_1 = 5.78$, $P = 0.016$; Table 1) in the aggregate network. Finally, nest joining was not predicted by versatility in the multilayer network (GLM: $\chi^2_1 = 0.64$, $P = 0.421$; Table 1), nor was it linked with body mass in any model (Table 1).

Table 1

Output of statistical models examining the relationship between the likelihood to nest and social network position in diurnal associations, roosting interactions, an aggregate network and a multilayer network during the shopping period (first period of the breeding season)

Network measure	Fixed effect	Estimate	SE	χ^2_1	P	VIF
Degree	Degree roosting	-0.018	4.359	<0.001	0.99	1.16
	Degree association	2.265	2.671	0.733	0.391	1.16
	Body mass	-23.813	14.921	2.713	0.099	1.13
Strength	Strength roosting	-6.254	29.03	0.046	0.829	1.37
	Strength association	71.022	32.96	5.44	0.019	1.37
	Body mass	-29.029	15.62	3.775	0.052	1.17
Aggregate degree	Aggregate degree	2.404	2.405	1.032	0.309	1.06
	Body mass	-25.082	14.85	3.05	0.08	1.06
Aggregate strength	Aggregate strength	70.814	32.56	5.78	0.016	1.17
	Body mass	-30.791	15.54	4.36	0.036	1.17
Versatility	Versatility	3.089	3.89	0.647	0.421	1.13
	Body mass	-24.30	14.89	2.844	0.091	1.13

Statistical significance was set at $P = 0.01$ after Bonferroni correction for multiple testing.

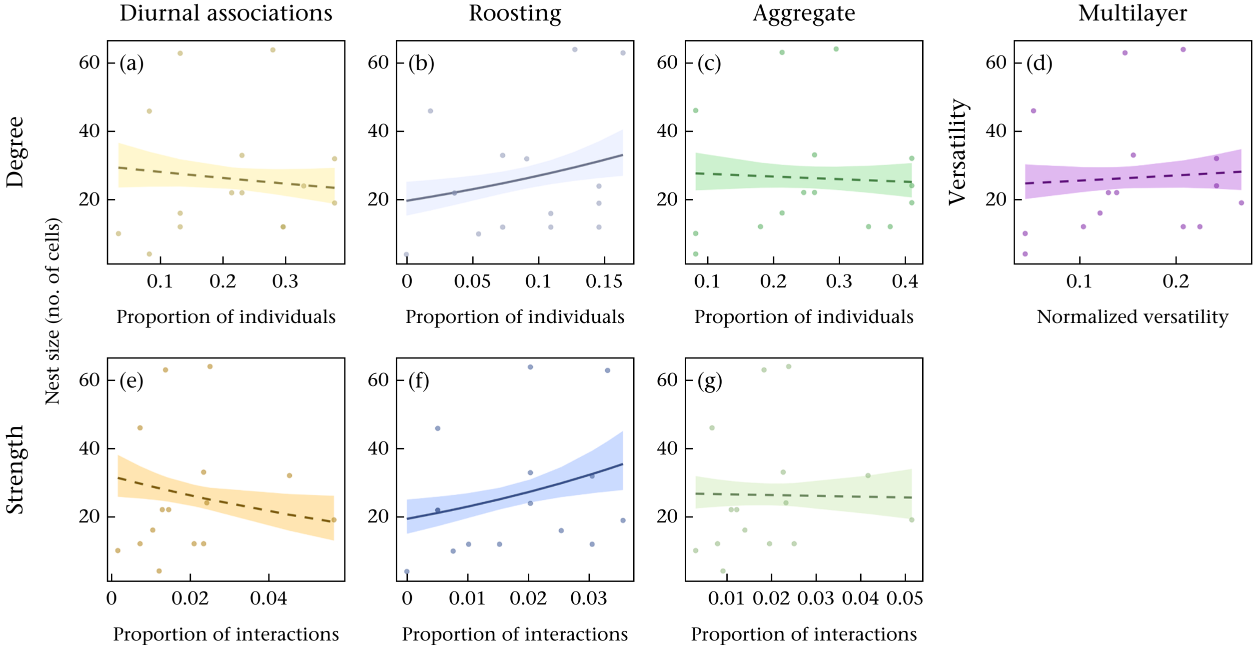

Figure 2. Relationship between final nest size (number of cells) and social position of nest foundresses (dominant or solitary wasps) during the ‘shopping’ period. The proportion of unique individuals a wasp interacted with (normalized degree) (a) in diurnal associations, (b) when roosting, (c) when both behavioural situations were aggregated into one network and (d) when both behavioural situations were integrated in a multilayer network. The proportion of social interactions (normalized strength) (e) in diurnal associations, (f) when roosting and (g) when both behavioural situations were aggregated into one network. Each point is a wasp; lines are the statistical model fit to the data; solid lines indicate significant relationships; dotted lines indicate insignificant relationships; shading shows the standard error. There is no plot for multilayer strength because it is the same as the aggregate strength.

Social Position by Time Period and Nest Size

We found that different network measures were more predictive of fitness outcomes across different time periods and that pooling behaviours provided different information compared to examining interactions in each social situation separately. During the shopping period, we found that considering behavioural situations separately predicted nest size. Nest size was positively linked with normalized degree (GLM: $\chi^2_1 = 7.15$, $P = 0.007$; Fig. 2b, Table 2) and normalized strength (GLM: $\chi^2_1 = 7.20$, $P = 0.007$; Fig. 2f, Table 2) during roosting. However, for diurnal associations, nest size was not significantly related to normalized degree (GLM: $\chi^2_1 = 1.4$, $P = 0.23$; Fig. 2a, Table 2) or the number of social interactions (normalized strength) (GLM: $\chi^2_1 = 4.73$, $P = 0.029$; Fig. 2e, Table 2). Pooling interactions from both situations in an aggregate network and integrating interactions across situations

Table 2
Output of statistical models examining the relationship between nest size and social network position in diurnal associations, roosting, aggregate network and multilayer network during the ‘shopping’ period (first period of the breeding season)

Network measure	Fixed effects	Estimate	SE	χ^2_1	P	VIF
Degree	Diurnal degree	-0.654	0.553	1.40	0.236	1.17
	Roosting degree	**3.178**	**1.187**	**7.16**	**0.007**	**1.16**
	Body mass	-3.711	2.814	1.75	0.186	1.07
	Maximum stable group size	**0.323**	**0.073**	**20.63**	**<0.001**	**1.22**
	Nest choice day	-0.007	0.005	1.83	0.176	1.16
Strength	Diurnal strength	-9.719	4.481	4.74	0.029	1.26
	Roosting strength	**16.974**	**6.239**	**7.20**	**0.007**	**1.36**
	Body mass	-3.446	2.747	1.58	0.21	1.04
	Maximum stable group size	**0.315**	**0.073**	**19.49**	**<0.001**	**1.23**
	Nest choice day	-0.008	0.005	2.26	0.132	1.15
Aggregate degree	Aggregate degree	-0.291	0.489	0.35	0.551	1.21
	Body mass	-4.459	2.875	2.41	0.121	1.14
	Maximum stable group size	**0.386**	**0.074**	**29.26**	**<0.001**	**1.49**
	Nest choice day	-0.006	0.005	1.43	0.231	1.38
Aggregate strength	Aggregate strength	-0.896	4.059	0.05	0.825	1.09
	Body mass	-4.985	2.789	3.18	0.075	1.07
	Maximum stable group size	**0.378**	**0.073**	**27.88**	**<0.001**	**1.47**
	Nest choice day	-0.007	0.005	1.66	0.20	1.35
Multilayer versatility	Versatility	0.581	0.771	0.57	0.451	1.16
	Body mass	-5.34	2.83	3.54	0.059	1.10
	Maximum stable group size	**0.357**	**0.074**	**24.79**	**<0.001**	**1.48**
	Nest choice day	-0.007	0.005	1.93	0.165	1.36

Bold values indicate significant relationships with a threshold of $P = 0.01$.

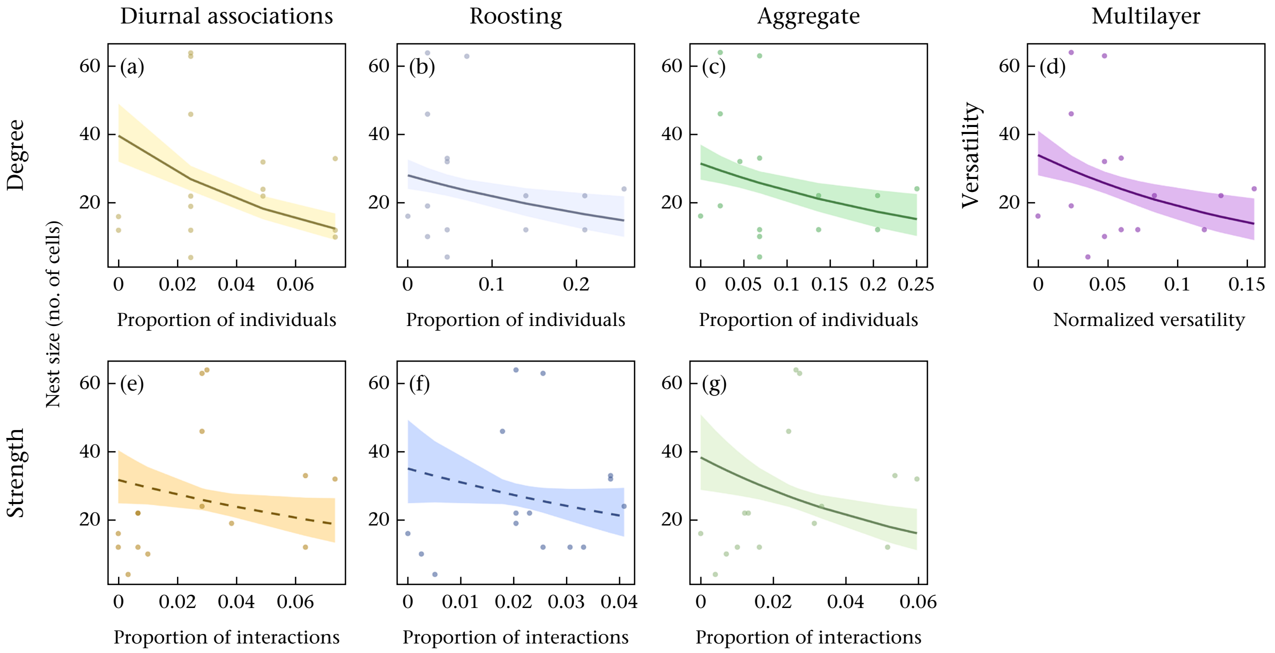

Figure 3. Relationship between final nest size (number of cells) and social position of dominant and solitary wasps during the 'establishment' period. The proportion of unique individuals a wasp interacted with (normalized degree) (a) in diurnal associations, (b) when roosting, (c) when both behavioural situations were aggregated into one network and (d) when both behavioural situations were integrated in a multilayer network. The proportion of social interactions (normalized strength) (e) in diurnal associations, (f) when roosting and (g) when both behavioural situations were aggregated into one network. Each point is a wasp; lines are the statistical model fit to the data; solid lines indicate significant relationships; dotted lines indicate insignificant relationships; shading shows the standard error. There is no plot for multilayer strength because it is the same as the aggregate strength.

Table 3

Output of statistical models examining the relationship between the nest size and social network position in diurnal associations, roosting, aggregate network and multilayer network during the 'establishment' period (second period of the breeding season)

Network measure	Fixed effects	Estimate	SE	χ^2_1	P	VIF
Degree	**Diurnal degree**	**-15.854**	**3.057**	**29.16**	**<0.001**	**1.30**
	Roosting degree	**-2.512**	**0.918**	**8.09**	**0.004**	**1.28**
	Body mass	0.265	2.800	0.01	0.924	1.08
	Maximum stable group size	**0.699**	**0.093**	**61.27**	**<0.001**	**1.45**
	Nest choice day	0.010	0.006	2.31	0.128	1.41
Strength	Diurnal strength	-7.164	3.662	3.80	0.051	2.87
	Roosting strength	-12.494	7.878	2.58	0.108	3.49
	Body mass	-2.916	2.759	1.12	0.289	1.14
	Maximum stable group size	**0.674**	**0.125**	**28.97**	**<0.001**	**4.21**
	Nest choice day	-0.006	0.006	1.12	0.289	1.55
Aggregate degree	**Aggregate degree**	**-2.929**	**0.989**	**9.53**	**0.002**	**1.61**
	Body mass	-2.876	2.825	1.04	0.31	1.08
	Maximum stable group size	**0.433**	**0.075**	**36.29**	**<0.001**	**1.47**
	Nest choice day	0.004	0.006	0.41	0.522	2.04
Aggregate strength	**Aggregate strength**	**-14.595**	**5.191**	**7.92**	**0.005**	**3.29**
	Body mass	-3.479	2.702	1.67	0.197	1.09
	Maximum stable group size	**0.624**	**0.110**	**29.52**	**<0.001**	**3.30**
	Nest choice day	-0.008	0.005	2.42	0.119	1.30
Multilayer versatility	**Versatility**	**-5.830**	**1.853**	**10.80**	**0.001**	**1.79**
	Body mass	-2.277	2.838	0.65	0.422	1.10
	Maximum stable group size	**0.486**	**0.080**	**40.04**	**<0.001**	**1.69**
	Nest choice day	0.006	0.007	0.84	0.358	2.17

Bold values indicate significant relationships with a threshold of $P = 0.01$.

in a multilayer network did not predict nest size. Nest size was not significantly related to normalized degree (GLM: $\chi^2_1 = 0.355$, $P = 0.551$; Fig. 2c, Table 2) or normalized strength (GLM: $\chi^2_1 = 0.05$, $P = 0.824$; Fig. 2g, Table 2) in the aggregate network. Furthermore, nest size was not significantly related to versatility in the multilayer network (GLM: $\chi^2_1 = 0.56$, $P = 0.451$; Fig. 2d, Table 2). Nest size was positively linked with the maximum number of foundresses who joined a nest in all models (Table 2) and it was not linked with body mass or the day on which a nest was chosen in any models (Table 2).

During nest establishment, we found that social position in separate behavioural situations, aggregate networks and multilayer networks predicted nest size. Nest size was negatively linked with normalized degree encountered in diurnal associations (GLM: $\chi^2_1 = 29.17$, $P < 0.001$; Fig. 3a, Table 3) and roosting interactions (GLM: $\chi^2_1 = 8.09$, $P = 0.004$; Fig. 3b, Table 3). Nest size

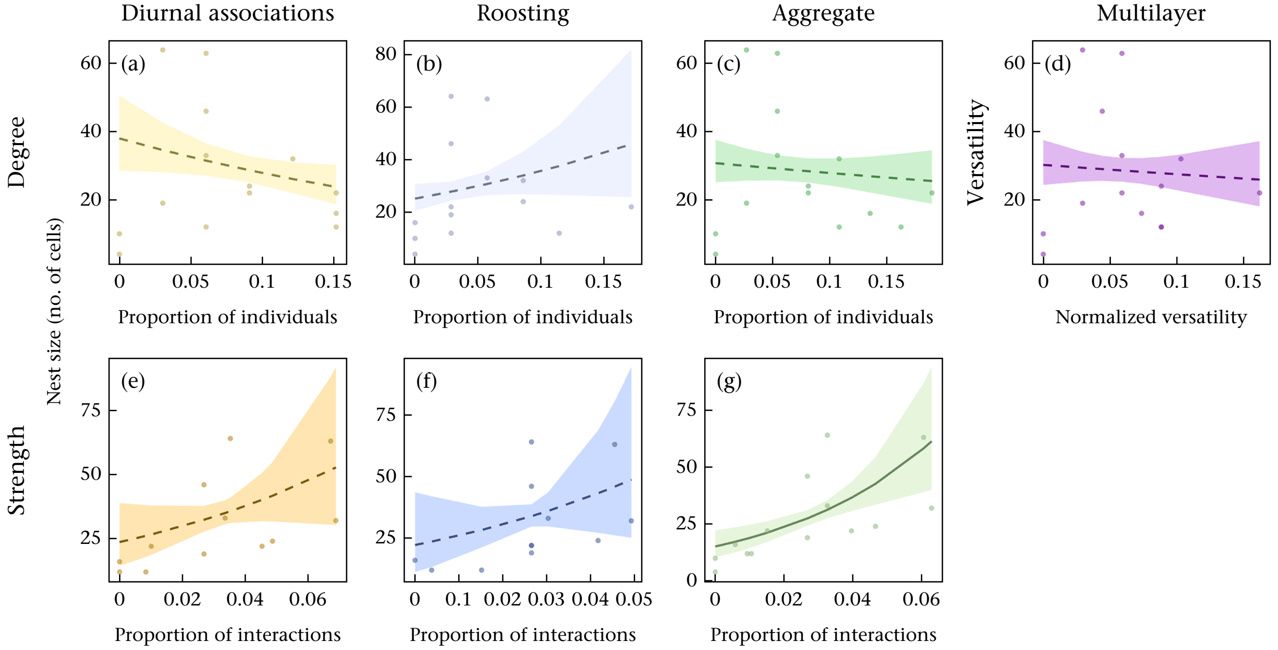

Figure 4. Relationship between final nest size (number of cells) and social position of dominant and solitary wasps during the 'growth' period. The proportion of unique individuals a wasp interacted with (normalized degree) (a) in diurnal associations, (b) when roosting, (c) when both behavioural situations were aggregated into one network and (d) when both behavioural situations were integrated in a multilayer network. The proportion of social interactions (normalized strength) (e) in diurnal associations, (f) when roosting and (g) when both behavioural situations were aggregated into one network. Each point is a wasp; lines are the statistical model fit to the data; solid lines indicate significant relationships; dotted lines indicate insignificant relationships; shading shows the standard error. There is no plot for multilayer strength because it is the same as the aggregate strength.

was negatively linked with normalized degree (GLM: $\chi^2_1 = 9.52$, $P = 0.002$; Fig. 3c, Table 3) and normalized strength (GLM: $\chi^2_1 = 7.92$, $P = 0.004$; Fig. 3g, Table 3) in the aggregate network. Finally, nest size was negatively linked with versatility in the multilayer network (GLM: $\chi^2_1 = 10.80$, $P = 0.001$; Fig. 3d, Table 3). However, we did not find that nest size was linked with the normalized strength in diurnal associations (GLM: $\chi^2_1 = 3.8$, $P = 0.051$; Fig. 3e, Table 3), or while roosting (GLM: $\chi^2_1 = 2.57$, $P = 0.11$; Fig. 3f, Table 3). Nest size was positively linked with the maximum number of foundresses who joined a nest (Table 3). We did not find that nest size was significantly linked with body mass or the day on which a nest was chosen in any models (Table 3).

During the growth period, we found that pooling social interactions together in an aggregate network predicted nest size. However, considering behavioural situations separately or integrating them in a multilayer network did not predict nest size.

Table 4
Output of statistical models examining the relationship between the nest size and social network position in diurnal associations, roosting, aggregate network and multilayer network during the 'growth' period (third period of the breeding season)

Network measure	Fixed effects	Estimate	SE	χ^2_1	*P*	VIF
Degree	Diurnal degree	-3.104	1.538	4.11	0.042	1.32
	Roosting degree	3.503	2.166	2.63	0.104	1.65
	Body mass	2.134	3.053	0.49	0.485	1.09
	Maximum stable group size	**0.323**	**0.092**	**12.43**	**<0.001**	**1.48**
	Nest choice day	**-0.019**	**0.007**	**7.15**	**0.007**	**1.55**
Strength	Diurnal strength	1.147	6.812	2.38	0.123	11.54
	Roosting strength	37.983	11.332	1.37	0.241	14.42
	Body mass	2.328	2.906	0.39	0.528	1.17
	Maximum stable group size	-0.348	0.187	3.08	0.079	9.05
	Nest choice day	**-0.025**	**0.006**	**14.38**	**<0.001**	**1.81**
Aggregate degree	Aggregate degree	-0.989	1.179	0.71	0.399	1.12
	Body mass	0.559	2.978	0.04	0.851	1.14
	Maximum stable group size	**0.414**	**0.070**	**36.72**	**<0.001**	**1.26**
	Nest choice day	-0.011	0.005	3.83	0.0504	1.29
Aggregate strength	**Aggregate strength**	**22.257**	**6.245**	**13.49**	**<0.001**	**6.43**
	Body mass	0.927	2.831	0.11	0.743	1.05
	Maximum stable group size	-0.109	0.167	0.43	0.511	7.11
	Nest choice day	**-0.016**	**0.005**	**8.49**	**0.004**	**1.33**
Multilayer	Versatility	-0.954	1.637	0.34	0.558	1.22
	Body mass	0.282	2.953	0.01	0.924	1.11
	Maximum stable group size	**0.433**	**0.073**	**38.29**	**<0.001**	**1.38**
	Nest choice day	-0.011	0.005	3.35	0.067	1.36

Bold values indicate significant relationships with a threshold of $P = 0.01$.

Nest size was positively linked with normalized strength in the aggregate network (GLM: $\chi^2{}_1 = 13.49$, $P < 0.001$; Fig. 4g, Table 4) and negatively linked with the day on which a nest was chosen (GLM: $\chi^2{}_1 = 8.49$, $P = 0.004$; Table 4). However, nest size was not significantly related to the normalized degree in the aggregate network (GLM: $\chi^2{}_1 = 0.71$, $P = 0.39$; Fig. 4c, Table 4). We did not find a significant relationship between nest size and normalized degree in diurnal associations (GLM: $\chi^2{}_1 = 4.11$, $P = 0.042$; Fig. 4a, Table 4) or while roosting (GLM: $\chi^2{}_1 = 2.64$, $P = 0.104$; Fig. 4b, Table 4). Nest size was not significantly related to the normalized strength in diurnal associations (GLM: $\chi^2{}_1 = 1.37$, $P = 0.241$; Fig. 4e, Table 4) or while roosting (GLM: $\chi^2{}_1 = 2.38$, $P = 0.122$; Fig. 4f, Table 4). Nest size was not significantly related to versatility in multilayer networks (GLM: $\chi^2{}_1 = 0.343$, $P = 0.558$; Fig. 4d, Table 4). Nest size was linked with nest choice day and the maximum number of foundresses who joined a nest in several models (Table 4).

DISCUSSION

Both the timing and the behavioural situation of sociality impacted the fitness of paper wasps. The relationship between social position and fitness changed as the season progressed. As we predicted, wasps that interacted with more individuals when roosting early in the season had greater fitness. However, later in the season, wasps that had stronger social bonds in the aggregate social networks had higher fitness. It seems that wasps sample the population early in the season to determine who to partner with, and as the season progresses, they strengthen the relationships with the partners they select. Contrary to our predictions, participation in diurnal associations, in which wasps may gain more active information about conspecifics, was less predictive of fitness than were roosting interactions. We did not find that social interactions in either behavioural situation, pooled in an aggregate network or integrated in a multilayer network, predicted whether wasps joined nests.

Excitingly, our results suggest that starting with a large social network and then pruning ties may be beneficial (Supplementary Fig. S1). We found that wasps received a fitness benefit from being more social early in the season, but fitness was reduced when wasps were socially central later in the season (Fig. 3). Thus, wasps that were more socially integrated during the time of greatest social partner sampling were more successful. Adding to our interpretation that wasps prune social networks across the breeding season but strengthen existing connections, Supplementary Fig. S2 shows that wasps tended to strengthen ties during nest establishment with a subset of individuals with whom they interacted during shopping. Some associations dissolved during nest growth, which could be explained by nest failures. A previous study of the same wasp species we studied here (*P. fustcatus*) revealed that foundresses who engage in more partner sampling throughout the entire breeding season suffer fitness costs (Laub et al., 2024). Our results add that the timing of social interactions is as important for fitness as the social interactions themselves. In other species, such as chimpanzees, *Pan troglodytes* (Machanda & Rosati, 2020), and vultures (Acácio et al., 2024), individuals prune social networks as they age and invest in established relationships to strengthen them. Wasps might benefit from large roosting social networks during the shopping period because they have a large pool of potential partners from which to choose enduring nestmates. Another possible explanation for the benefit of large networks during partner sampling is that roosting with many others early on indicates social tolerance, as wasps cannot move away from other co-roosting wasps once roosts are selected for the night. Social tolerance in the form of affiliative personality is linked with fitness (Laub et al., 2024); therefore, being socially tolerant during the shopping period may be associated with more cooperation and higher fitness once nests form.

Changes in social tolerance seem to drive changes in paper wasp sociality. In other taxa, individuals often become less socially integrated as they age due to a reduction in their activity and movement in their environment, making them less likely to encounter conspecifics (Acácio et al., 2024; Albery et al., 2022; Almeling et al., 2017). However, in paper wasps, it seems more likely that changes in sociality are affected by changes in social tolerance. Wasps who join nests late in the breeding season are more likely to usurp dominant individuals, leading to social conflict, which harms nest productivity; therefore, wasps become less socially tolerant later in the season. Our previous work suggests that choosing partners and establishing a nest quickly is beneficial (Laub et al., 2024). Having many different social partners later in the season, when colonies are established, may indicate that wasps were unable to form stable relationships, perhaps because they were unsuccessful at choosing partners. If wasps do not choose partners, they may continue sampling partners throughout the season, which could lead them to interact with individuals that are less desirable as social partners by other wasps.

In the work presented here, we consider the number of foundresses with whom wasps form stable relationships as a continuous variable. When including solitary-foundress nests versus multiple-foundress nests as a discrete category in the statistical models, our overall conclusions were unchanged, but pruning diurnal interactions seems more important than pruning roosting interactions (Supplementary Table S1—S3). Founding a nest as a solitary foundress was predictive of building a smaller nest in almost all models, an unsurprising result as previous work found that the number of foundresses on a nest influences nest size (Tibbetts & Reeve, 2003). Further work is needed to understand how early shopping behaviour may be linked with cooperative behaviour on established nests.

In addition to finding that the number of social contacts impacted fitness, we also found that the number of social interactions across social situations were related to fitness. The number of interactions in the aggregate network, which combined interactions from both diurnal and roosting situations (normalized aggregate strength), were negatively related to fitness during nest establishment but positively related to fitness during the period of colony growth towards the end of the breeding season (Fig. 4). Excitingly, finding a positive relationship between fitness and strength in the aggregate network demonstrates that the greatest ‘payout’ of strong social relationships across behavioural situations is experienced at the end of the season, suggesting that wasps may need to maintain relationships for a relatively long period before they receive the most benefit. While this study did not directly test the behavioural mechanisms by which cooperation increases success, previous work suggests that cooperative larvae feeding and nest defence are important in *Polistes* nests (Donaldson et al., 2014; Karsai & Hunt, 2002). Therefore, interactions in aggregate networks during the growth period may capture the importance of both relationship stability indicated by roosting and the opportunity to engage in active cooperative interactions during the day. Work in other species, including primates (Silk et al., 2010) and birds (Riehl & Strong, 2018), found that long-term and consistent relationships confer fitness benefits, and our work suggests that strong social relationships provide fitness benefits in relatively short-lived organisms as well.

Summing interactions from different social situations in an aggregate network or integrating them in a multilayer network revealed links between the number of social interactions and fitness that were not detected when considering diurnal or roosting behavioural situations separately. We found that, during the shopping period, roosting social interactions, but not diurnal associations, predicted nest size. When summing these interactions in an aggregate network or integrating them in a multilayer network, social interactions did not predict nest size, perhaps because the effect of interactions while roosting on nest size was diluted by the lack of relationship between diurnal associations and nest size during shopping. However, as the season progressed, aggregate and multilayer network measures began to predict fitness outcomes. This suggests that, early in the season, interactions in roosting and diurnal associations have opposing impacts on fitness, but the impact of social interactions in both situations begins to act in the same direction and may be amplified towards the end of the breeding season. Overall, we found that if social interactions have opposing impacts on fitness, they may negate each other's effects when combined. However, when behaviours across situations impact fitness in the same direction, relationships that are not statistically significant when considering situations separately, become amplified and are significant when examining the interactions in an aggregate network. Thus, interactions in different social situations may have synergetic amplifying effects on fitness, as suggested by other studies examining the explanatory power of multilayer networks (van der Marel et al., 2021).

Our study demonstrates that both the timing and the behavioural situation of social interactions have important fitness consequences. Considering multiple types of interactions provides an opportunity to understand what information animals may gain in different situations and when interactions across situations may result in amplified fitness outcomes. Examining interactions over time provides information on when social interactions are most impactful. In a rapidly changing world, considering both the timing and situation of behavioural interactions may provide insight on how animals adjust their social behaviour to overcome new environmental challenges.

Author Contributions

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

Data Availability

All data and code are available at the corresponding author's GitHub profile (https://github.com/EmilyLaub/Timing-and-context-of-social-interactions).

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 at https://doi.org/10.1016/j.anbehav.2026.123583.

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