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RESEARCH ARTICLE

Coupled information networks drive honeybee (*Apis mellifera*) collective foraging

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Abstract

1. Collective behaviour by eusocial insect colonies is typically achieved through multiple communication networks that produce complex behaviour at the group level but often appear to provide redundant or even competing information.
2. A classic example occurs in honeybee (*Apis mellifera*) colonies, where both the dance communication system and robust scent-based mechanisms contribute to the allocation of a colony's workforce by regulating the flow of experienced foragers among known food sources.
3. Here we analysed social connectivity patterns during the reactivation of experienced foragers to familiar feeding sites to show that these social information pathways are not simply multiple means to achieve the same end but intersect to play complementary roles in guiding forager behaviour.
4. Using artificial feeding stations, we mimicked a natural scenario in which two forager groups were simultaneously collecting from distinct patches containing different flowering species. We then observed the reactivation of these groups at their familiar feeding sites after interrupting their foraging.
5. Social network analysis revealed that temporarily unemployed individuals interacted more often and for longer with foragers that advertised a familiar versus unfamiliar foraging site. Due to such resource-based assortative mixing, network-based diffusion analysis estimated that reactivation events primarily resulted from interactions among bees that had been trained to the same feeding station and less so from different-feeder interactions. Both scent- and dance-based interactions strongly contributed to reactivation decisions. However, each bout of dance-following had an especially strong effect on a follower's likelihood of reactivation, particularly when dances indicated locations familiar to followers.
6. Our findings illustrate how honeybee foragers can alter their social connectivity in ways that are likely to enhance collective outcomes by enabling foragers to

rapidly access up-to-date information about familiar foraging sites. In addition, our results highlight how reliance on multiple communication mechanisms enables social insect workers to utilise flexible information-use strategies that are robust to variation in the availability of social information.

KEYWORDS
collective behaviour, honeybee, network-based diffusion analysis, social insects, social network, social transmission

1 | INTRODUCTION

In eusocial insect species, the need to coordinate individual actions to achieve beneficial collective outcomes has favoured the evolution of sophisticated information-sharing networks that enable group-level coordination (reviewed in Gordon, 2010; Johnson & Linksvayer, 2010; Seeley, 1995). Perhaps the best known of these is the honeybee waggle dance communication system, by which successful foragers communicate the location of food resources to their nestmates (Couvillon, 2012; Dyer, 2002; Menzel, 2019; Riley et al., 2005; von Frisch, 1967). Although the waggle dance is best known for its role in recruitment to new food sources, the vast majority of bees that engage in dance-following are already familiar with one or more of the indicated resources, such that dance communication most commonly regulates the flow of workers among known food sources (Biesmeijer & Seeley, 2005). Through a series of internal feedback loops (Seeley, 1995), the colony thus controls the allocation of its workforce, reactivating bees at known sites for which profitability can be confirmed and passively shutting down those that have become unrewarding (Biesmeijer & Seeley, 2005; Grüter & Farina, 2009; von Frisch, 1967).

Powerful though the dance communication system is, it does not operate alone. A diverse array of olfactory cues are brought to the colony by returning foragers and contribute to information-sharing and forager recruitment (Esch & Bastian, 1970; Grüter & Farina, 2009; Hasenjager et al., 2020; Kirchner & Grasser, 1998; Tautz, 2022; Wenner et al., 1969) to the extent that they once rendered the idea of dance communication highly controversial (Gould, 1975; Wenner et al., 1969; Wenner & Wells, 1990). While there is no longer any serious doubt that forager bees can use the spatial information contained in dances to locate food sources (Gould, 1975), it is also clear that odour-based cues are key drivers of collective foraging. For example, exposure to the odour of a familiar food source in the hive through antennation of nestmates (Cholé et al., 2019; Gil & Farina, 2002) or during food-sharing interactions (i.e. trophallaxis; Farina et al., 2005; Grüter et al., 2006) can motivate foragers to seek out that same resource in the field (Balbuena et al., 2012; Gould, 1975; Grüter & Farina, 2009; Hasenjager et al., 2020; Johnson, 1967; Reinhard et al., 2004; Tautz, 2022; Tautz & Sandeman, 2003; von Frisch, 1967), even when dance information indicates a different site (Grüter et al., 2008). Indeed, it is not clear whether bees visiting a known foraging location extract any spatial information from the dances that they follow before leaving the hive. Dance-following is often brief in this context, and bees frequently arrive at their known food source even if the dance indicates a different location (Grüter et al., 2008, 2013; Grüter & Ratnieks, 2011). What, then, is the contribution of dance-following to motivating visits to known food sources?

Network-based diffusion analysis (NBDA) is a tool that can compare the relative influence of competing social information sources on the occurrence of a behaviour (such as arrival at a feeder) by quantifying its spread through potential transmission pathways, represented as social networks that capture different forms of social interaction (Franz & Nunn, 2009; Hasenjager et al., 2021; Hoppitt et al., 2010). Here, we employ NBDA to quantify the relative contribution of dance- and odour-based communication in motivating experienced but temporarily unemployed foragers to resume collecting from known food sources (i.e. reactivation; Biesmeijer & Seeley, 2005). We used artificial feeders to mimic a natural foraging context in which two cohorts from the same colony are simultaneously collecting from two resource patches containing different flowering species (and thus different scents). We then briefly interrupted foraging—as would occur naturally due to rain, nightfall or temporary nectar depletion (Nicolson et al., 2007)—by temporarily removing the feeders before allowing foraging to resume. Social networks were then constructed based on observed in-hive interactions during the reactivation process, with each network capturing a different form of interaction thought to drive reactivation (i.e. dance-following, trophallaxis or antennation) (Gil & Farina, 2002; Grüter et al., 2008; Hasenjager et al., 2020; Johnson, 1967; von Frisch, 1967). These networks were partitioned to distinguish information-sharing between nestmates that were familiar with the same feeder from instances in which the advertised feeder was unfamiliar to the receiver bee. In this way, we could not only establish the relative influence of dance-following and olfactory interactions in driving bees to their familiar feeder but also establish whether *any* dances or scents, regardless of their match to the target destination, could elicit the same effects. Our findings illustrate how dance- and scent-based pathways play complementary roles in motivating visits to known food sources and thereby contribute to regulating colony foraging efforts.

2 | MATERIALS AND METHODS

The experiments described here were conducted in accordance with guidelines established by the Research Ethics Committee of Royal Holloway, University of London.

2.1 | Colony housing

Trials were conducted on the campus of Royal Holloway, University of London, from July to September 2019, using honeybees originally derived from a cross between *Apis mellifera mellifera* and *A. m. ligustica*. Four queen-right colonies were housed indoors within three-frame, glass-walled observation hives with uninterrupted, tunnel-based outdoor access. Each colony contained 2000–3000 workers, brood and sufficient reserves of pollen and honey such that supplemental provisioning was not required, yet enough empty cells remained to promote foraging. Each colony underwent two trials, carried out consecutively to minimise differences in colony and environmental conditions across trials, but with new cohorts of foragers trained for each trial. In one trial, a physical malfunction interfered with bees leaving the hive, resulting in a total of seven trials rather than eight (information on each trial is provided in Table 1).

2.2 | Training procedure

For a colony's first trial, two groups of individually marked foragers (~10 foragers per group) were simultaneously trained to two continuously monitored unscented sucrose feeders using standard techniques (Seeley, 1995; von Frisch, 1967). Once each feeder reached its final location 150 m southeast or southwest of the hive (Figure 1), these groups were used to recruit a new cohort of 15–27 foragers on each feeder (Table 1). These recruits served as the focal foragers during the trial (the initially trained group was captured and frozen since they had experienced their feeder at multiple locations). Each new recruit was individually marked with enamel paint (Humbrol®) upon first arriving at a feeder, and any individuals that switched between feeders during training were removed from the experiment. Each focal forager included in a trial was therefore familiar with the location of only one of the feeders. For a colony's second trial, the focal foragers from the first trial were used to recruit new, untested forager cohorts to the feeders before being captured and frozen themselves; training procedures were otherwise as previously described. As cohorts were recruited across multiple days, unscented sucrose was used throughout training to standardise individuals' exposure to the scents used during the trials (see below). On average, focal foragers collected from their familiar feeding station for 2.79 ± 1.34 days (mean ± SD) prior to each trial. Across seven trials conducted across four colonies, 281 individually marked focal foragers were trained in total, with each individual being included in only a single trial. Training focal foragers took 3–7 days per trial; each trial was carried out during a single day following the last day of training.

2.3 | Trial procedure

On the morning of each trial, both feeders offered a scented 2 M sucrose solution (50 μL essential oil per L sucrose solution; Figure 1a), with an additional 2 mL of essential oil added in a reservoir beneath each feeder (following Seeley, 1995). Different scents were used at each feeder, and different pairs of scents were used across reactivation trials for a given colony (Table 1). Scented feeders were available

TABLE 1 Overview of reactivation trials.

Trial	Colony	Date (2019)	Scents[a]	Trained	Reactivated[b]
1	A	July 22	SE: Lavender SW: Geranium	SE: 22 SW: 20	SE: 18 (17) SW: 11 (11)
2	A	August 2	SE: Peppermint SW: Lemon	SE: 27 SW: 25	SE: 27 (23) SW: 25 (25)
3	B	August 22	SE: Peppermint SW: Geranium	SE: 22 SW: 17	SE: 21 (19) SW: 15 (13)
4	C	August 30	SE: Lavender SW: Peppermint	SE: 15 SW: 20	SE: 12 (11) SW: 18 (16)
5	C	September 7	SE: Geranium SW: Lemon	SE: 17 SW: 26	SE: 16 (14) SW: 26 (25)
6	D	September 17	SE: Geranium SW: Peppermint	SE: 16 SW: 16	SE: 12 (10) SW: 16 (14)
7	D	September 26	SE: Lemon SW: Lavender	SE: 20 SW: 18	SE: 12 (11) SW: 13 (13)

[a] SE and SW refer to the direction (southeast or southwest) of the feeders relative to the hive. Feeders were located 150 m from the hive.

[b] The number of reactivation events that were included in the network-based diffusion analysis (NBDA) is provided in parentheses. This did not include individuals that either reactivated before opportunities for social transmission were available or did not visit the feeder during the odour presentation. The NBDA was thus restricted to the subset of reactivation events in which individuals could have engaged in the focal communication pathways and that had experienced opportunities to associate their feeder with the provided scent.

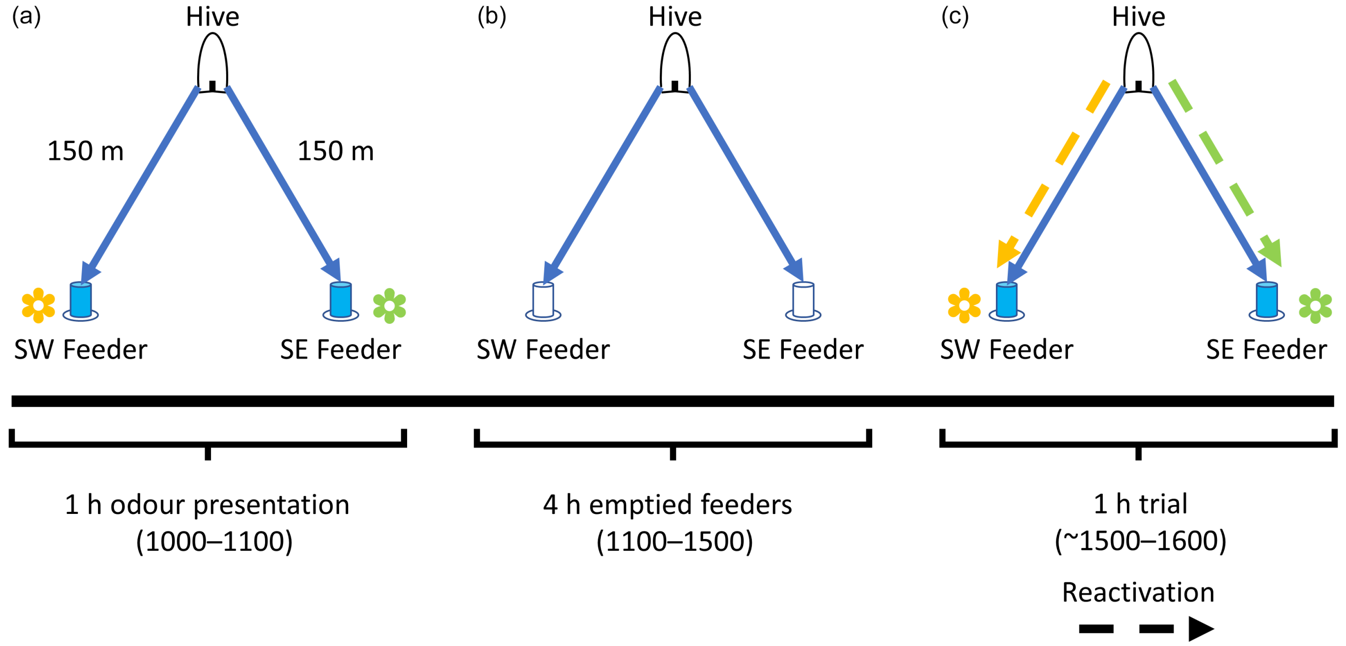

FIGURE 1 Experimental design. (a) Forager cohorts were trained to separate feeders located 150 m from the hive with an angular separation of 95°. On the morning of the trial, feeders provided scented sucrose solution for 1 h, with a different scent provided at each feeder (indicated by flower colour). (b) Following this odour presentation, feeders were replaced with unscented empty feeders for 4 h. (c) Scented feeders were reinstalled at 1500. A 1-h trial commenced when the first marked individual returned to either feeder (i.e. reactivated).

for 1 h from 1000 to 1100 h. During this time, individuals completed an average of 7.1 ± 3.3 (mean ± SD) trips to their feeder, providing sufficient exposure to form an association between the offered scent and their familiar feeding site (Villar et al., 2020). Feeders were then replaced with empty, unscented feeders for 4 h (Figure 1b), mimicking the temporary depletion of profitable nectar sources. Scented feeders were reinstalled at each site at 1500 h and provided the same scents as had been used that morning. Once the first marked individual returned to either feeder, the reactivation trial commenced and continued for 1 h. Using a combination of in-person observations and video recordings, arrival and departure times were recorded for each marked individual collecting from its familiar feeder during the trial. An individual was considered 'reactivated' once it visited its familiar feeder for the first time. Any unmarked individuals were captured upon arrival at the feeder and later frozen. One marked individual was recruited during the trial to the opposite feeder to which it had been trained; this individual was captured upon arrival at the feeder and was not included in the analysis.

During the trial, we also filmed in-hive behaviour on the dance-floor (i.e. the region of comb adjacent to the hive entrance where the majority of interactions with returning foragers occur). A wooden baffle directed foragers to one side of the observation hive. From these in-hive video recordings, we recorded all instances of dance-following, trophallaxis or antennation that occurred between marked individuals that had reactivated and those that had yet to reactivate. The timing of each interaction bout and its duration were recorded, as were the number of waggle runs followed for each dance-following bout. Dance-following was defined as being oriented towards and within one antennal length of a dancing, reactivated forager. Trophallaxis was defined as an unreactivated forager contacting the mouthparts of a reactivated forager with its extended proboscis. Antennation was defined as being oriented towards and within one antennal length of a reactivated forager, excluding any periods of antennation that occurred during or immediately following trophallaxis or dance-following. This was done to help disentangle antennation from these other forms of interaction. Summing across all individuals, this restriction excluded 38.5 ± 30.5% (mean ± SD) of the time spent engaged in antennation. However, our findings are broadly similar if the unadjusted antennation networks are used in the analysis (Tables S8 and S9).

2.4 | Network construction

For each trial, separate networks were constructed for dance-following, trophallaxis and antennation interactions. Links in these networks were directed and aggregated from time-stamped interactions, with each interaction originating at an employed forager collecting from its familiar feeder and directed towards a forager that had not yet reactivated at the time when that interaction occurred. In other words, for each individual, the networks included all of its interactions with already reactivated foragers prior to its own reactivation and, if it reactivated, any subsequent interactions it had with nestmates that had not yet reactivated. In this way, the networks capture all interactions among and between the individually marked forager cohorts that could have contributed to their reactivation. For each interaction type, two network variants were constructed, where network edges were weighted either by interaction duration or by the number of interaction events (i.e. ignoring their duration). For the trophallaxis and antennation networks, interaction duration was measured in seconds. The duration of dance-following bouts was measured by the number of waggle runs followed, as this provides an estimate of the amount of spatial information potentially transmitted during that bout. Interaction bouts that were interrupted by less than 5 s were counted as a single bout; this threshold generally provided sufficient time for an individual to reestablish contact when it appeared motivated to do so.

2.5 | Network assortativity

Assortativity coefficients were obtained for each network using the *assortnet* package in R (Farine, 2014; R Core Team, 2022). The assortativity coefficient, *r*, measures the proportion of network edge weights that occurred between individuals trained to the same feeder relative to those that occurred between individuals trained to different feeders. Coefficients could range from −1 to 1, where positive values indicate that same-feeder interactions were more likely to occur and/or were of longer duration than different-feeder interactions. Mean assortativity was calculated across the seven trials for each network type, with network edges weighted either according to the number of interaction bouts between two individuals or their total interaction time.

To evaluate whether observed mean assortativity differed from random expectations, we performed randomisation tests, where observed mean assortativity was compared to expected distributions of *r* in the absence of assortative mixing. This procedure accounts for structural features of the data that could influence observed patterns of assortment apart from assortative mixing by the bees themselves. We constructed randomised reference networks in the following manner: First, for each antennation event, we maintained its start and stop times and the identity of the reactivated individual, but randomly selected the recipient of that interaction from the pool of individuals across both feeder cohorts that had not yet reactivated at the time when that event occurred. For example, an individual that departed the hive to reactivate 600 s into the trial was included in this pool of potential recipients only for interactions that ended prior to 600 s. As in the empirical data, an individual could be the recipient of multiple antennation events. Next, to take into account that trophallaxis and/or dance-following events were necessarily associated with an antennation event, for any antennation event in which this was the case, we created the corresponding trophallaxis or dance-following link between the reactivated forager and its randomised recipient. Finally, the randomised antennation network was filtered in the same manner as the empirical data (see 'Trial procedure'). In this way, we generated a set of randomised networks for each trial and calculated the mean assortativity per network type across trials. This process was repeated 1000 times to generate a set of null distributions of expected values in the absence of assortative mixing. If the observed mean assortativity coefficient was situated in the lower or upper 2.5% of the corresponding null distribution, this was taken as evidence of a significant pattern of negative or positive assortment, respectively.

2.6 | Network-based diffusion analysis

To evaluate the relative contribution of different forms of interaction in eliciting reactivation, we used NBDA (Franz & Nunn, 2009; Hoppitt et al., 2010). NBDA infers social transmission if the spread of a focal behavioural pattern through a group follows a social network that reflects opportunities for social learning. In the present study, the behavioural pattern of interest was the order in which individuals first arrived at their familiar feeder (i.e. reactivated). Thus, if bees that were quicker to reactivate were relatively strongly connected to reactivated foragers in a given network (e.g. dance-following, trophallaxis), the NBDA takes this as evidence of social transmission via that form of interaction. An NBDA estimates two key pieces of information: the strength of social transmission (relative to individual learning) per unit of network connection (estimated by the parameter, *s*) and the corresponding proportion of acquisition events (i.e. reactivations) that are explained by social transmission (%ST). Notably, we use an NBDA variant that can simultaneously incorporate multiple network types (Hasenjager et al., 2021), allowing us to compare *s* and %ST across different networks (e.g. dance-following, trophallaxis, antennation) and with those networks partitioned into same- versus different-feeder interactions (Figure 2). Such an approach allows us to estimate, for example, the relative strength of transmission across dances that indicate familiar versus unfamiliar sites. For a mathematical description of the NBDA model, see (Hasenjager et al., 2021; Hoppitt et al., 2010).

NBDA can take into account either the order or timing of acquisition events. We employed the former variant (known as order-of-acquisition diffusion analysis or OADA), as it requires less stringent assumptions be made about how acquisition rates change over time (Hoppitt et al., 2010). In order to increase our power to detect social transmission patterns, we rendered the OADA sensitive to between-group differences in learning rate by including all individuals within the same diffusion, taking as data the order of reactivation across all trials, but setting all between-trial connections in the networks to 0 (Hasenjager et al., 2021). To capture the temporal ordering of in-hive interactions, we used dynamic networks that updated when individuals departed the hive prior to arriving at the feeder of interest (as in Hasenjager et al., 2020).

We further included several individual-level variables (ILVs) in the NBDA to estimate their effects on the rate of asocial discovery and social transmission. These included the location of an individual's familiar feeder relative to the hive (SE/SW), the scent provided at its feeder (lavender/geranium/peppermint/lemon), the number of visits it made to its feeder during the 1 h odour presentation earlier in the day and the number of days of foraging experience at its familiar feeder prior to the trial. The latter two variables were standardised by subtracting the mean and dividing by the standard deviation. Trial number (7 levels) and colony (4 levels) were further

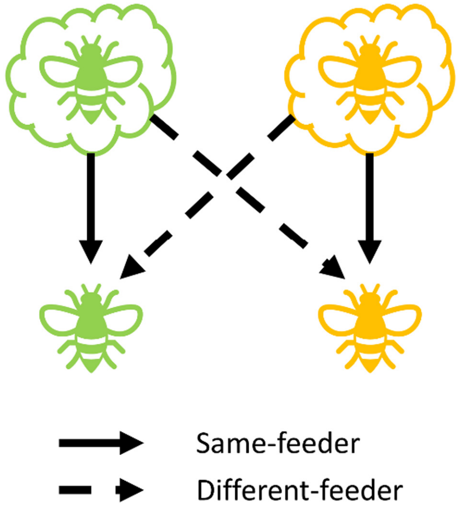

FIGURE 2 Interaction networks were partitioned according to whether interactions occurred between foragers trained to the same feeder or different feeders (see Figure 1 for details). Clouds around signallers represent the presence of site-specific olfactory cues.

included as random intercepts. Trained individuals that either never visited during the odour presentation or reactivated early in the trial before opportunities for social transmission were available were excluded as learners in the NBDA but were still allowed to transmit information to nestmates once they reactivated. This was done to restrict the analysis to those individuals that could have engaged in the focal communication pathways and that had experienced opportunities to associate the provided scent with their feeder.

We adopted a Bayesian formulation for the NBDA, employing a Markov chain Monte Carlo (MCMC) procedure. The main advantage of this approach was that it allowed us to incorporate random effects more easily into our model. As the posterior distribution for a parameter takes into account the uncertainty in the plausible effects of other parameters included in the model, we based inferences on a global model that included all networks of interest and ILVs. However, to select the weighting method to be used for each network (i.e. interaction duration or the number of bouts), we compared eight candidate models using the Watanabe Akaike Information Criterion (WAIC) (Whalen & Hoppitt, 2016), where the candidate set included every combination of weighting method across the three interaction types (dance-following, trophallaxis and antennation). This analysis indicated that the best-supported model weighted the edges for all three network types by the number of interaction bouts rather than total duration (Table S3)—that is, a bout of dance-following, regardless of the number of dance circuits followed, counts as a single interaction. We base our inferences in the main text on this best-supported model, but we also provide parameter estimates from all candidate models with ΔWAIC <10 in the Supporting Information (Tables S5–S7).

We specified weakly informative prior distributions for the candidate models. Specifically, for both *s* parameters and random effect standard deviations (which can only take on non-negative values), we used uniform priors: $s \sim U(0,1000)$ and $\sigma \sim U(0,10)$. For ILV parameters, we used normal priors with a mean of 0 and variance of 1000. Inspection of the posterior distributions showed that for ILVs, the estimated variance was less than that of the prior and that the upper 95% highest posterior density interval (HPDI) for s and σ was situated well away from the upper limit of the prior distributions.

MCMC was performed using the *runjags* package in R (Denwood, 2016; R Core Team, 2022), enabling multiple chains to be run in parallel. We ran four chains with initial values randomly drawn from the associated prior distributions. Based on inspection of trace plots (Kruschke, 2015), we ran the chains in adaptive mode for 1000 iterations, followed by a further 60,000 burn-in iterations. We then ran 84,000 iterations with a thinning interval of 40 for a posterior sample of 10,500, providing an effective sample size of at least 1500 for all parameters. For the best-supported model, the effective sample size ranged from 2450 to 11,266. Inferences were based on 95% HPDIs, which indicate the range of values for each parameter that contain 95% of the posterior distribution. If zero was situated well outside the 95% HPDI for a parameter, this was taken as reasonable evidence for an effect. The NBDA was carried out using the *NBDA* and *bayesNBDA* packages in R (Hoppitt, 2020; Hoppitt et al., 2020; R Core Team, 2022).

3 | RESULTS

Out of the 281 marked individuals that were trained to the feeders, 242 (86%) reactivated during their trial (Table 1). Across all trials, we observed 294 dance-following bouts, 226 trophallaxes and 1094 antennation bouts. Across 864 observed pairs of interacting individuals, 27.5% engaged in dance-following, 22.8% engaged in trophallaxis and 83.7% engaged in antennation (note that pairs often engaged in multiple forms of interaction). Over half of pairs (57.3%) engaged in antennation exclusively.

3.1 | Resource-based assortment in forager networks

Prior to reactivation, unemployed foragers preferentially antennated nestmates collecting from their familiar feeder and followed their dances. Comparing observed assortativity coefficients, *r*, to expected distributions in the absence of assortative mixing revealed that both the dance-following and antennation networks were positively assorted by feeder (Tables S1 and S2; Figure S1). For dance networks, this was true regardless of whether connection strengths were based on the number of dance bouts or the number of waggle runs that were followed (dance-following networks: number of dance-following bouts: mean $r=0.145$, $p=0.004$; number of waggle runs followed: mean $r=0.234$, $p=0.002$). Likewise, for antennation networks, it did not matter whether connections were weighted by number or duration of contacts (antennation networks: number of contacts: mean $r=0.159$, $p=0.001$; duration of contact: $r=0.241$,

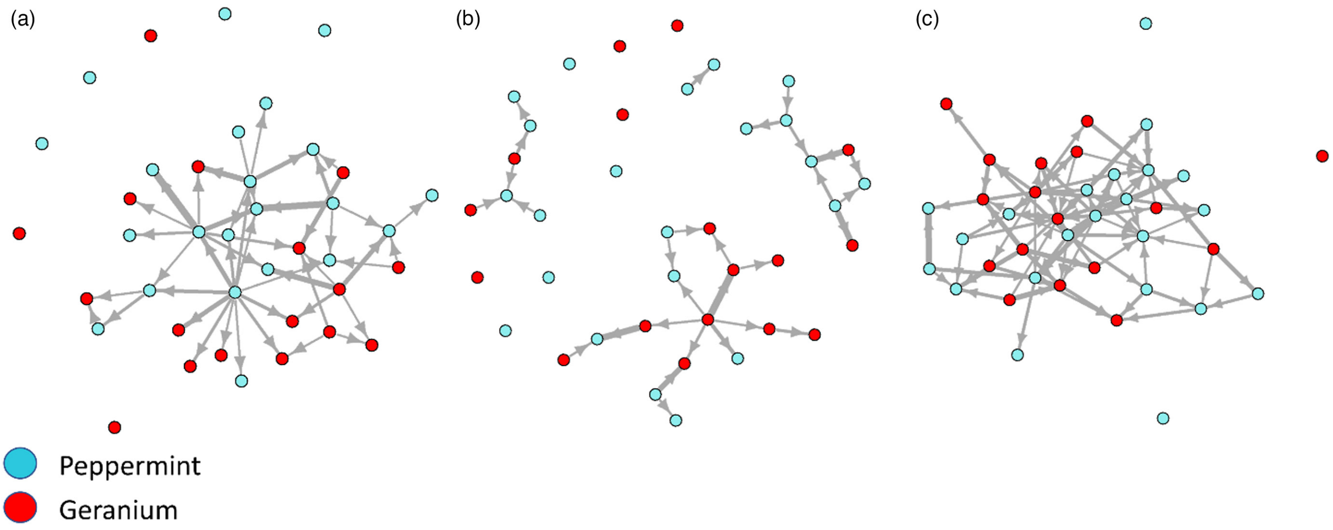

FIGURE 3 Example networks of (a) dance-following, (b) trophallaxis and (c) antennation events from the same trial, with edges weighted according to interaction duration (represented by edge thickness). Edges are directed from signaller to receiver (e.g. from dancer to dance-follower). Node colours indicate individuals' familiar feeding stations and are labelled with the scents offered at those stations. The networks shown here were selected to emphasise positive assortment by feeding site, with more and stronger connections between same-coloured nodes. Network visualisations for all trials are provided in Figures S2–S8.

$p=0.001$; Figure 3). For trophallaxis, observed assortativity values (though also positive) were well within the range expected in the absence of assortative mixing, particularly when contacts were weighted by duration (trophallaxis networks: number of contacts: $r=0.121$, $p=0.066$; duration of contact: $r=0.085$, $p=0.354$). Put simply, bees engaged in antennation and dance interactions relating to their known target feeder more often and for longer relative to interactions indicating the alternative feeder, but this was not necessarily true of trophallaxis.

3.2 | Variation in social transmission strength across networks

Bees were more likely to follow dances for their known feeder, but the NBDA revealed that such dances were also more powerful in motivating reactivation. For each network (e.g. dance-following, antennation), NBDA estimates the social transmission parameter, s, indicating the acceleratory effect on reactivation time per unit interaction (e.g. per bout of dance-following). Overall, following waggle dances for either feeder type significantly increased the likelihood that a bee would reactivate (Figure 4a; Table 2; dance-following: same-feeder: $s=328.4$ (95% HPDI: 36.19–777.15); different-feeder: $s=140.4$ (95% HPDI: 11.31–367.39)), but this effect was much greater for dances that indicated familiar resources (Table 2; estimated difference in s between dances indicating familiar vs. unfamiliar feeders = 188.01 (95% HPDI: 2.64–502.67)). Conversely, antennation exerted a weaker influence on reactivation per interaction bout than either type of dance (Figure 4a; Table 2; antennation: same-feeder: $s=58.67$ (95% HPDI: 6.93–145.93); different-feeder: $s=61.6$ (95% HPDI: 5.76–149.78)) with no evidence of a difference between same- and different-feeder interactions (Table 2; estimated difference in s between same- and different-feeder antennation bouts = −2.92 (95% HPDI: −59.84–56.46)). For trophallactic interactions, the lower limits of the 95% HPDIs for s were essentially zero for both same- and different-feeder interactions (Table 2; trophallaxis: same-feeder: $s=29.9$ (95% HPDI: 0.02–91.08); different-feeder: $s=32.81$ (95% HPDI: 0–106)), providing at best only weak evidence for a motivational effect in either case.

3.3 | Relative importance of different interactions during reactivation

Estimated rates of social transmission, s, can be further combined with the number and strength of interactions to estimate the percentage of the 222 reactivation events that resulted from social transmission via each interaction type (%ST) (Hasenjager et al., 2021). Combining all three interaction types, interactions among individuals that had been trained to the same feeder explained substantially more reactivation events than different-feeder interactions (same-feeder: 52.4% (95% HPDI: 47.8–56.8); different-feeder: 32.6% (95% HPDI: 27.9–37)). Consistent with dance-following instances for the familiar, target feeder being both more frequent and more effective, such dances explained substantially more reactivations (24.9% (95% HPDI: 21.5–28.2)) than those that indicated the alternative feeder (Figure 4b). Nonetheless, dance-following for the alternative feeder still explained some proportion of arrivals (11.6% (95% HPDI: 7.2–15.6)), in keeping with a potential motivational role even when spatial information is not a match (Grüter et al., 2008; Johnson, 1967). Antennation interactions explained a similar proportion of reactivation events as same-feeder dances (antennation:

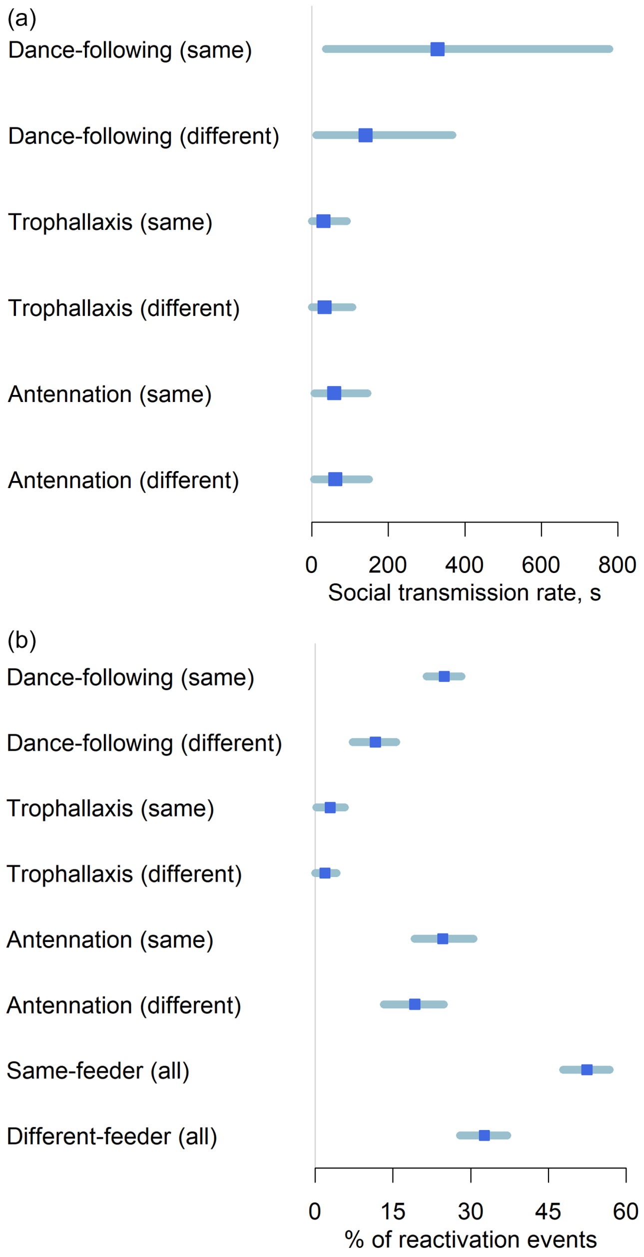

FIGURE 4 (a) Estimated social transmission parameters and (b) percentage of reactivation events explained by each transmission pathway from the network-based diffusion analysis. Points indicate means, and bars show 95% highest posterior density intervals.

same-feeder: 24.6% (95% HPDI: 19.2–30.5); different-feeder: 19.2% (95% HPDI: 13.2–24.8)), but in this case, there was little evidence for a difference between familiar- and unfamiliar-feeder interactions (Figure 4b; estimated difference in %ST between same- versus different-feeder antennation interactions: 5.46% (95% HPDI: −4.08–15.1)). Trophallactic interactions explained very few reactivation events, irrespective of whether interactions indicated a familiar or unfamiliar feeder (trophallaxis: same-feeder: 2.9% (95% HPDI: 0.2–5.7); different-feeder: 1.9% (95% HPDI: 0–4.1); estimated difference: 1.04% (95% HPDI: −2.49–4.66)). An estimated additional 14.97% of reactivations were not preceded by interactions with reactivated individuals, reflecting spontaneously initiated inspection trips and/or responses to other bees in the hive.

4 | DISCUSSION

The waggle dance is a key regulatory element that functions in part to control the allocation of a colony's foraging force across multiple resources (Seeley, 1995), yet it is just one of an array of diverse signals and cues that are utilised by honeybee foragers (Grüter & Farina, 2009; Michelsen et al., 1986; von Frisch, 1967). Here, we applied social network techniques to understand the interplay between dance- and scent-based interactions during a key foraging context: the reactivation of experienced honeybee foragers to familiar foraging sites (Biesmeijer & Seeley, 2005). Analysis of assortment patterns showed that site-specific cues guide the formation of forager communities in the hive (Figure 3). Consequently, temporarily unemployed foragers were not only more likely to interact with nestmates collecting from a familiar resource but also to be reactivated by them (Figure 4b). Social transmission rates estimated by the NBDA revealed that dance-following was particularly effective in eliciting reactivation, especially when dances indicated a familiar resource (Figure 4a). However, whereas each dance-following bout had an especially strong effect on reactivation, antennation explained more instances of reactivation overall due to its more frequent occurrence (Figure 4b). Scent- and dance-based pathways thus operate in concert to allow bees to rapidly access up-to-date information about familiar foraging sites and facilitate collective foraging efforts.

Groups of foragers advertising different resources are often closely clustered within the hive with relatively little spatial

Parameter	*M*	SD	95% HPDI
s: dance-following, same-feeder	328.4	211.6	36.19, 777.15
s: dance-following, different-feeder	140.4	110.8	11.31, 367.39
s: trophallaxis, same-feeder	29.9	30.75	0.02, 91.08
s: trophallaxis, different-feeder	32.81	37.75	0, 106
s: antennation, same-feeder	58.67	42.73	6.93, 145.93
s: antennation, different-feeder	61.6	44.0	5.76, 149.78

TABLE 2 Posterior means, standard deviations and 95% highest posterior density intervals (HPDIs) for social transmission parameters. Parameter estimates for individual-level variables and random effects are provided in Table S4.

segregation among them (Seeley, 1994; Seeley & Towne, 1992); nevertheless, both the dance-following and antennation networks in our study were positively assorted by foraging site. The fact that dances were followed for longer when they indicated a location familiar to the dance-follower suggests that followers may have been responding to the match between their navigational memories and the transmitted spatial information (as reported in von Frisch, 1967). However, such dances were also followed more often, potentially due to individuals being initially attracted to incoming foragers bearing familiar, feeder-associated scents. Indeed, the fact that foragers distinguish between potential interaction partners on the basis of scent is supported by the positive assortment observed in the antennation networks (see also Grüter et al., 2008; von Frisch, 1967). That said, we found little evidence for feeder-based assortative mixing in the trophallaxis networks. It may be that other functions of trophallaxis (e.g. nectar unloading, sampling the quality of incoming nectar; Farina & Grüter, 2009) obscured resource-specific assortative preferences.

Dances for familiar sites were not only more attractive to dance-followers but also had a stronger motivational effect on their likelihood of reactivation. The NBDA estimated that following a dance for a familiar site was over twice as effective in eliciting reactivation as following a dance for an unfamiliar site (Figure 4a). Given that same- versus different-feeder interactions for scent-based pathways (i.e. trophallaxis and antennation) were similarly effective in promoting reactivation (Table 2), this result suggests that dance-followers attended to the spatial information conveyed by the dance and were especially likely to reactivate when this matched their personal navigational memories. It is important to note, however, that we cannot say whether food-associated scents further enhanced the effectiveness of dances for familiar sites since scent- and dance-based information were never in conflict during our study.

Whereas some studies (including our own) have reported higher reactivation success for dances that indicate sites familiar to dance-followers (von Frisch, 1967; Wray et al., 2012), others have found no such relationship (Grüter et al., 2008). Increasing evidence suggests that information-use strategies in honeybees and other insects are often flexible and can be highly sensitive to experimental conditions (Gould, 1975; Grüter & Leadbeater, 2014). Indeed, such flexibility can be a key source of robustness supporting collective behaviour within social insect colonies (I'Anson Price et al., 2019). Additional studies aiming to tease apart the contributions of individual experience and environmental context in shaping how signals are used and combined with other information sources to guide forager decision-making would be valuable (Grüter & Czaczkes, 2019; Hasenjager, Franks, et al., 2022). For example, in honeybee feeder experiments, how scent is deployed during training can alter how strongly bees rely on dances to locate food (Gould, 1975; Grüter & Farina, 2009). In the current study, we used unscented feeders during training to standardise bees' exposure to scents used in the trials, but longer periods of exposure could conceivably impact bees' relative reliance on our focal communication pathways. We leave this as an interesting direction for future work.

Despite the stronger motivational effect per bout of dance-following relative to antennation (Table 2), bouts of antennation occurred more frequently, such that they accounted for more reactivation events overall (51% vs. 31%). Previous work has demonstrated that reactivation can be elicited simply by introducing familiar, food-associated scents into the hive, triggering recall of associated foraging locations (Johnson, 1967; Reinhard et al., 2004; von Frisch, 1967). Our findings, however, indicate that antennal interactions with bees bearing a scent not directly experienced in the field are similarly effective (Table 2; Figure 4b). Foragers may have learned to associate that scent with nectar rewards (though not a specific location) through earlier in-hive interactions during the initial odour presentation period (Farina et al., 2007) (Figure 1a). Reactivation can also be triggered in response to behaviourally active pheromones produced by foragers returning from a profitable site (Gilley et al., 2012; Thom et al., 2007), regardless of its scent. In either case, these findings indicate that reactivation through scent-based cues is not dependent on interacting with bees collecting from a specific resource. The communication systems underpinning reactivation are thus robust to stochastic variation in the occurrence of dances and in the timing and frequency of visits to the hive from foragers collecting from multiple flower species dispersed across potentially hundreds of square kilometres.

The ability of honeybees and other social insects to coordinate such robust and flexible collective responses, despite each worker possessing only limited information and cognitive capability, has long fascinated scientists and inspired advances across several disciplines, including engineering, robotics and cyber systems (Fefferman, 2019; O'Shea-Wheller et al., 2021). Here, we show how up-to-date information on resources is funnelled towards foragers that are familiar with those resources and therefore best able to rapidly act on that information due to the organisation of resource-specific communities on the dancefloor. By revealing how social insects alter their social connectivity to promote more effective collective outcomes, advances in network analysis and tracking technologies (Mersch et al., 2013; Stroeymeyt et al., 2018) promise to generate novel insights that not only will enhance understanding of how social groups function but may even be harnessed to address current challenges in applied science (Dorigo et al., 2021; O'Shea-Wheller et al., 2021).

AUTHOR CONTRIBUTIONS

Matthew J. Hasenjager and Ellouise Leadbeater designed the study. Matthew J. Hasenjager, Iona Cunningham-Eurich and Victoria R. Franks collected the data and Matthew J. Hasenjager and William Hoppitt analysed it. Matthew J. Hasenjager wrote the initial draft. All authors contributed to revisions and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data and code necessary to reproduce the results reported in this manuscript are available at figshare (Hasenjager, Hoppitt, et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Distributions of expected mean assortativity in the absence of resource-based assortative mixing.

Figure S2. Dance-following (a, d), trophallaxis (b, e), and antennation (c, f) networks from trial 1.

Figure S3. Dance-following (a, d), trophallaxis (b, e), and antennation (c, f) networks from trial 2.

Figure S4. Dance-following (a, d), trophallaxis (b, e), and antennation (c, f) networks from trial 3.

Figure S5. Dance-following (a, d), trophallaxis (b, e), and antennation (c, f) networks from trial 4.

Figure S6. Dance-following (a, d), trophallaxis (b, e), and antennation (c, f) networks from trial 5.

Figure S7. Dance-following (a, d), trophallaxis (b, e), and antennation (c, f) networks from trial 6.

Figure S8. Dance-following (a, d), trophallaxis (b, e), and antennation (c, f) networks from trial 7.

Table S1. Assortativity coefficients ± SE for networks with edges weighted according to the number of interaction bouts.

Table S2. Assortativity coefficients ± SE for networks with edges weighted according to interaction duration—i.e., number of waggle runs followed for the dance-following networks or duration (s) for the trophallaxis and antennation networks.

Table S3. Watanabe Akaike Information Criterion for candidate network-based diffusion analysis models.

Table S4. Posterior means, standard deviations, and 95% highest posterior density intervals for individual-level variables and random effects included in the network-based diffusion analysis reported in the main text.

Table S5. Posterior means, standard deviations, and 95% highest posterior density intervals from the network-based diffusion analysis using the dance-following (Int), trophallaxis (Dur), and antennation (Int) networks.

Table S6. Posterior means, standard deviations, and 95% highest posterior density intervals from the network-based diffusion analysis using the dance-following (Dur), trophallaxis (Int), and antennation (Int) networks.

Table S7. Posterior means, standard deviations, and 95% highest posterior density intervals from the network-based diffusion analysis using the dance-following (Dur), trophallaxis (Dur), and antennation (Int) networks.

Table S8. Watanabe Akaike Information Criterion for candidate network-based diffusion analysis models when using unadjusted antennation networks (see 'Section 2' in main text).

Table S9. Posterior means, standard deviations, and 95% highest posterior density intervals for the best-supported candidate network-based diffusion analysis model (Table S9) using unadjusted antennation networks (see 'Section 2' in main text).

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