Do honeybees modulate dance-following according to foraging distance?

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Highlights

- Honeybee waggle dances indicate the direction of and distance to food sources.
- Whether dance-follower responses account for the indicated distance is unclear.
- Responses to waggle dances indicating different foraging distances were compared.
- Dance-following behaviour did not differ according to the dance-indicated distance.
- Results are consistent with honeybee foraging being driven by signalling rules.

Abstract

Honeybees famously use waggle dances to communicate foraging locations to nestmates in the hive, thereby recruiting them to those sites. The decision to dance is governed by rules that, when operating collectively, are assumed to direct foragers to the most profitable locations with little input from potential recruits, who are presumed to respond similarly to any dance regardless of its information content. Yet, variation in receiver responses can qualitatively alter collective outcomes. Here, we use network-based diffusion analysis to compare the collective influence of dance information during recruitment to feeders at different distances. We further assess how any such effects might be achieved at the individual level by dance-followers either persisting with known sites when novel targets are distant and/or seeking more accurate spatial information to guide long-distance searches. Contrary to predictions, we found little evidence that dance-followers’ responses depended on target distance over the foraging distances considered here (100 – 500 m). While dance information was always key to feeder discovery, its importance did not vary with feeder distance, and bees were in fact quicker to abandon previously rewarding sites for distant alternatives. These findings provide empirical support for the longstanding assumption that self-organized foraging by honeybee colonies relies heavily on signal performance rules with limited input from recipients.

Keywords: collective behaviour; honeybee; network-based diffusion analysis; social information; social insects; waggle dance

Introduction

Living in groups provides opportunities to pool information across multiple individuals in order to make accurate collective decisions (e.g. navigation in homing pigeons (Dell’Ariccia et al., 2008); predator avoidance in fish (Ward et al., 2011)). In the social insects, such decisions are the product of many (often thousands of) individual-level environmental assessments that are shared with nestmates through evolved communication signals. Simple rules that govern the production or longevity of these signals can generate non-linear feedbacks that produce accurate collective decisions (Detrain & Deneubourg, 2008; Seeley, 2010; Sasaki et al., 2013). A classic example involves waggle dance-based recruitment to foraging locations in the western honeybee (*Apis mellifera*), whereby energetically efficient trips elicit more waggle runs on return to the hive (Seeley & Towne, 1992; Seeley, 1994). This modulation of dance behaviour, coupled with shorter foraging trip durations for nearby sites, means that such sites should be over-represented on the dancefloor, and thus attract more recruits, relative to more distant alternatives that offer resources of similar quality. This straightforward performance rule could thus enable colonies to collectively optimize energetic efficiency without requiring that dance-followers use the spatial information contained in the dance to make any decision about the potential value of the trip that lies ahead of them (Detrain & Deneubourg, 2008).

In the above scenario, dance-followers are expected to respond similarly to any dance, regardless of its content. For example, the dance-indicated foraging distance is assumed not to impact decisions about whether to seek out the indicated site (Seeley & Towne, 1992; Grüter et al., 2013) or how many dance circuits should be followed to acquire sufficiently accurate spatial information (Tanner & Visscher, 2008). Yet research over the past decade has revealed the sophisticated ways in which insects acquire, process, store, retrieve, and use information (Giurfa, 2015), with potential impacts on how signals are both produced and used. Variation in learning among honeybee foragers, for instance, has been linked to differences in the likelihood and intensity of dancing (Cook et al., 2020). Similarly, there is growing evidence that signal recipients decide how to respond by weighing the costs and benefits of using the transmitted information. Ants generally ignore trail pheromones in favour of memories but will switch to trail-following if information indicates that doing so will lead to a higher quality food source (Czaczkes et al., 2019). Likewise, experienced honeybee foragers often discount the spatial information contained in dances in favour of returning to known foraging locations (Grüter et al., 2008; Grüter & Ratnieks, 2011; Hasenjager et al., 2020) and may devalue dance information when it repeatedly proves unreliable (I'Anson Price et al., 2019). Accounting for such individual variation in receiver responses can lead to qualitatively different outcomes in models of collective behaviour (Detrain & Deneubourg, 2008; Schürch & Grüter, 2014; Lemanski et al., 2019).

Here, we use network-based diffusion analysis (NBDA; Franz & Nunn, 2009; Hoppitt et al., 2010) to evaluate the relative influence of dances that indicate novel close or distant feeders on the likelihood that foragers successfully arrive at the indicated resource. NBDA can provide an integrative estimate (*s*) of the influence of each dance circuit followed over an individual's likelihood of arriving at a given resource, and we propose that this influence may decrease with distance to the target when dance-followers are unfamiliar with the target resource. We expect this reduced response to dances for distant targets because locating new sites can require multiple search trips and hence significant time costs that potentially increase with distance (Seeley & Towne, 1992; Biesmeijer & Seeley, 2005). Experienced foragers are thus expected to more strongly prioritize known foraging locations for which search costs are negligible. Additionally, foragers that attempt to locate the dance-indicated site may follow relatively more waggle runs for distant sites to acquire more accurate spatial information (Tanner & Visscher, 2008; Tanner & Visscher, 2009). Indeed, a previous study found that when dances for more distant locations contained more angular scatter (i.e. a low signal-to-noise ratio), followers compensated by following more waggle runs (Al Toufailia, Couvillon, et al., 2013). This study further found that bees followed fewer waggle runs for distant locations, though more time was spent following these dances overall (Al Toufailia, Couvillon et al., 2013).

However, interpreting these findings is challenging, as neither the previous foraging experience nor subsequent behaviour of dance-followers was known.

We first created pools of unemployed yet motivated individually marked foragers and allowed their recruitment to a novel feeder located either close to or more distant from the hive. We then used NBDA to compare (i) the strength of social transmission through the resulting dance networks and (ii) the overall importance of dance information in explaining arrivals at novel distant versus nearby locations. We further monitored behaviour at the individual level to establish the mechanisms by which such collective effects might be achieved, predicting that (i) bees that follow dances for distant target recruitment sites may persist with known sites for longer, rather than attempting to locate the new food source, and that (ii) the same bees may invest in gaining more accurate location information by following more waggle runs pre-departure (Tanner & Visscher, 2008; Tanner & Visscher, 2009) or investing more time in following dances (Al Toufailia, Couvillon, et al., 2013). Finally, we monitored individual dancer behaviour to confirm our expectation, based on previous work (Seeley & Towne, 1992; Seeley, 1994), that closer resources will be over-represented on the dancefloor.

Methods

Colony housing

These experiments were carried out on the campus of Royal Holloway, University of London from July – September 2018. Three queen-right honeybee colonies were housed indoors within three-frame observation hives with unrestricted access via tunnels to the outdoors. Colonies contained 2000 – 3000 workers, brood, and reserves of pollen and honey. Each colony underwent both a short-distance and a long-distance recruitment trial, performed consecutively to minimise differences in colony and environmental conditions across trials (Table S1). For each colony, trial order (i.e. long- vs. short-distance) was randomly determined.

Training

Working with a single colony at a time, two groups of foragers (13 – 31 per group) were simultaneously trained using standard techniques (described in von Frisch, 1967; Seeley 1995) to two feeders providing unscented sucrose solution. In each case, one feeder was designated the *recruit feeder* (always 100m from the hive) and the other the *target feeder* (either 100m or 500m from the hive, depending on the trial) with an angular separation of ~110^o between the two feeders (Fig. 1). During training, foragers were assigned unique enamel paint marks (Humbrol™) upon first arriving at a feeder, meaning we could be confident that individuals trained to the recruit feeder had never visited the target feeder. Later, during the test period (see below), the recruit feeder would become depleted, creating a pool of marked potential recruits for the target feeder (Fig. 1).

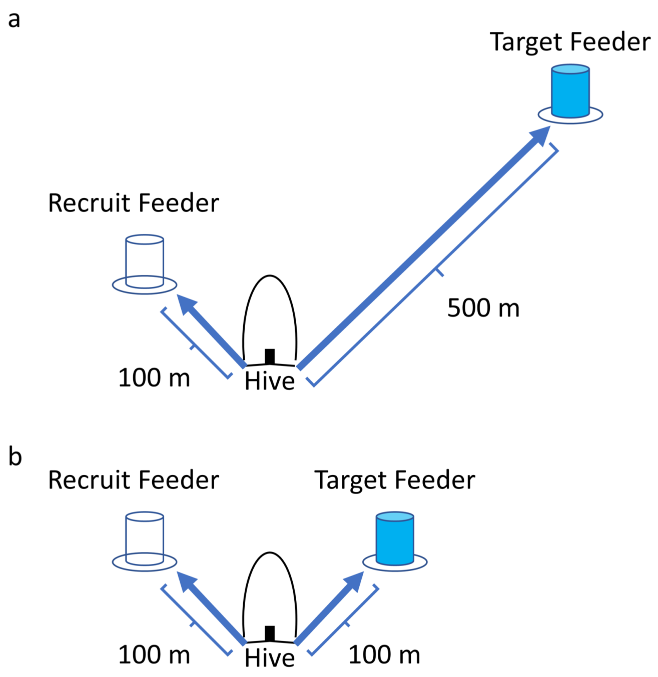

Figure 1. Feeder arrangements used during the (a) long-distance and (b) short-distance trials. Within each trial, cohorts were simultaneously trained to the recruit and target feeders. During trials, the recruit feeder was left empty to create a pool of potential recruits for the target feeder.

Training took place over 5 – 11 days per trial. Both feeders offered identically scented sucrose on the final day of training for one hour (following Seeley, 1995: 50 µL essential oil per L sucrose, plus reservoir of essential oil below the feeder; scents varied between trials; table S1) in order to promote greater interest in the target feeder during the trial (see Grüter & Ratnieks, 2011). Only individuals that visited the recruit feeder during either this odour presentation or during the previous training day were used as potential recruits during the trials. Although most potential recruits visited the recruit feeder multiple times during both of these training days, a small number of individuals only visited the feeder once during the odour presentation or were only observed during one 30 min census on the previous day. However, as excluding these 21 individuals did not qualitatively alter our findings or conclusions, we retained them in the full analysis.

Trials

Trials commenced between 0930 – 1000 on the following morning. During a trial, the target feeder continued to provide scented 2M sucrose, whereas the recruit feeder was left empty (Fig. 1), thus mimicking a common natural scenario in which one tree or patch of flowers comes into bloom at the same as another of the same species ceases to be rewarding. We allowed 10–12 foragers previously trained to the target feeder to collect from it, while any remaining members of this cohort were captured upon arrival. Successful recruits from the recruit feeder were also allowed to collect freely from the target feeder. We did not restrict the activities of other bees in the hive, but any that located the target feeder were captured on arrival; as these individuals were unmarked, it was not possible to track their in-hive behaviour. Using both video recordings and in-person observations, we recorded arrival and departure times for each marked individual at both the recruit and target feeder throughout the trial. Trials lasted either 120 min (colony A) or 180 min (colonies B and C); this change was implemented to allow recruits in the 500 m trials additional time to locate the target feeder.

During trials, we filmed the dance floor within the observation hive. A wooden baffle directed foragers onto one side of the hive, meaning the vast majority of dances were visible. For each hive visit made by target feeder foragers (including recruits), we recorded its duration, whether dancing occurred, and the number of waggle runs produced. We also recorded all dance-following interactions between marked individuals, noting participant identities, when each interaction occurred, its duration (sec), and the number of waggle runs followed. A bee was defined as following a waggle run if its head was oriented towards the dancer within one antennal length. We further recorded the occurrence of waggle dances by other bees in the hive for natural food sources, whether these dancers carried pollen, the number of waggle runs produced, and any instances in which a marked individual followed one of these dances.

Statistical analysis

All analyses were carried out in R ver. 4.0.3 (R Core Team, 2020). To better account for model selection uncertainty, we employed an information-theoretic approach, allowing us to incorporate information from multiple candidate models when forming our inferences (Burnham & Anderson, 2002).

Network-based diffusion analysis (NBDA)

In an NBDA, the strength of social transmission per unit of network connection (e.g. per waggle run followed), relative to the rate of feeder discovery through individual exploration, is estimated by the social transmission parameter, s (Franz & Nunn, 2009; Hoppitt et al., 2010). In other words, s estimates the increased likelihood of successfully locating the target feeder for each waggle run that is followed by a potential recruit (or for each second of dance-following, depending on the model), where higher values of s correspond to stronger social influences. Conversely, if dance-guided search is no more effective than individual scouting, the estimated value of s would be 0. Crucially, s can be fitted separately for different sets of trials, allowing for transmission strengths to be compared across treatments (Hasenjager, Leadbeater, et al., 2021). For example, if each waggle run transmits more spatial information for longer foraging distances, then all else being equal, higher values of *s* would be expected for long-distance trials.

Here, we set out to compare estimates of *s* between the short- and long-distance trials, based on social networks constructed from our video records of dance-following interactions. Specifically, we used order-of-acquisition diffusion analysis, in which networks are used to predict the order in which individuals acquire a behaviour—here, discovery of the target feeder within each trial (Hoppitt et al., 2010). Network connections were directed from dancers to followers, and we included models where connections were weighted either by the number of waggle runs followed or the total duration (sec) of dance-following in our candidate model sets (described below). To capture the temporal ordering of dance-following interactions, we used dynamic networks that updated when individuals departed the hive for the target feeder (Hasenjager, Leadbeater, et al., 2021).

To compare the relative influence of dance-based transmission for recruitment across our distance treatments, we fit models in which *s* was either estimated separately for short- and long-distance trials ($s_{Short} \neq s_{Long}$) or in which *s* was constrained to be equal across these treatments ($s_{Short} = s_{Long}$). See the Supplementary Material for more details on specification of the NBDA models and for the complete candidate model set. Due to asymmetry in the uncertainty for parameter estimates, profile likelihood techniques were used to obtain 95% Cis (Morgan, 2009). The NBDA was carried out using the *NBDA* package (Hoppitt et al., 2020).

Individual-level analyses

Prior to seeking out a new feeder, honeybee foragers typically return to known sites (often extremely persistently), even if they know those sites to be unrewarding (Al Toufailia, Grüter, et al., 2013). To examine potential differences in this persistence, and in pre-departure information gathering, when the alternative target feeder was either close or distant, we classified trips where individuals were observed at the recruit feeder as “reactivation” trips. If instead that recruit left the hive for more than 90 seconds and either successfully discovered the target feeder or was not observed at either site, it was classified as searching for the target feeder (’search trip’).

A full description of the individual-level analyses, including all fixed and random effects in each global model, is provided in tables S2 and S3 and summarised here. Our primary analyses focussed on the effects of target distance on follower behaviour in terms of: (i) the number of waggle runs followed before departing the hive (zero-inflated negative binomial GLMM); (ii) the duration (sec) of dance-following per hive visit (zero-inflated negative binomial GLMM); and (iii) the probability of searching for the target feeder vs reactivating during hive absences (binomial GLMM). To confirm that longer target distances incur greater search costs, we also analysed (iv) the duration of hive absences (linear mixed-effects model); and (v) the number of unsuccessful searches prior to locating the target feeder (Poisson GLMM).

For completeness, we also analysed dancer behaviour across the short- and long-distance treatments, to compare how the two target feeders were represented on the dancefloor. We included (i) hive visit frequency (linear mixed-effects model); (ii) mean hive visit duration (linear mixed-effects model); (iii) the probability of dancing per visit (binomial GLMM);

and (iv) the mean number of waggle runs produced during visits with dancing (linear mixed-effects model).

In every model, *trial* and *colony* were included as a random intercept term and fixed effect respectively; *individual* was included as a random effect for analyses that included multiple observations per individual. All input variables were mean-centred and continuous variables were scaled by dividing by twice their standard deviation (Schielzeth, 2010; Grueber et al., 2011). LMMs were fitted using nlme (Pinheiro et al., 2018) to model heteroscedasticity in the residuals (Zuur et al., 2009) and GLMMs were fitted with glmmTMB (Brooks et al., 2017). Inspection of GLMM residuals was carried out using DHARMa (Hartig, 2020).

We performed model selection on all candidate models nested within each global model (tables S2 and S3) on the basis of AICc. As we had no *a priori* reason to believe that the different effects included in the global models could not operate together, all-subsets selection was deemed to be appropriate. To avoid selecting overly complex models, models were removed from the candidate set if they were more complex versions of a model with a lower AICc value (Burnham & Anderson, 2002; Richards, 2008; Grueber et al., 2011). From this reduced model set, we extracted a 95% confidence set of models and used these to obtain model-averaged parameter estimates (MAEs), unconditional standard errors (USEs), and unconditional 95% confidence intervals (Cis) (Burnham & Anderson, 2002). Where a single model received especially strong support ($w_i \geq 0.95$), inferences were based on this model alone. Multimodel inference was performed using the MuMIn package (Barton, 2019).

Ethical note

These experiments used free-flying honeybees housed in observation hives with tunnel-based access to the outdoors (see *Colony housing*). Honeybees freely arrived at the feeders during training and were given an individually specific enamel paint marking; this procedure often elicited self-grooming by the painted individuals, but no mortality was observed. During experimental trials, it was necessary to capture some individuals (e.g. unmarked recruits) upon their arrival at the feeding stations. Forceps were used to grasp individuals by a hind leg and quickly transfer them to an aerated container, which provided access to food and was kept out of direct sunlight. Individuals were released upon trial completion. All other individuals were allowed to freely interact with the feeding stations. The experiments described here were conducted in accordance with guidelines established by the Research Ethics Committee of Royal Holloway, University of London.

Results

Network-based diffusion analysis (NBDA)

In the short- and long-distance trials respectively, 49 and 25 recruits successfully located the target feeder (table 1). Dance information was key in guiding to foragers to the target feeder, regardless of its distance from the hive. Of our candidate set for the NBDA, two models received nearly all support (model probabilities: $w_1 = 0.91$; $w_2 = 0.09$). The top-ranked model included the dance-following network—with connections weighted according to the number of waggle runs followed—and constrained the estimated value of the social transmission parameters, *s*, to be equal across distance treatments (i.e. $s_{100\ m} = s_{500\ m}$). In other words, the acceleratory effects of dance-based transmission (per waggle run followed) over how rapidly individuals discovered the target feeder did not vary with foraging distance. The best-supported model estimated the strength of social transmission to be 2.42 x 10^7 (95% CI: 0.90, +∞), corresponding to an estimated 97 – 100% of recruitment events explained by dance-guided search, as opposed to individual scouting. The second-ranked model differed only in that the dance-following networks were weighted according to the total duration (sec) of dance-following, but otherwise yielded qualitatively identical results. In summary, the NBDA indicated that successful recruitment was predicted by an individual's investment in dance-following but provided no evidence that either the strength of social transmission through the dance-following networks or the overall contribution of dance-guided searches for recruitment differed between short- and long-distance trials. See table S4 for parameter estimates from both models.

Table 1. Summary of experimental trials (TF: target feeder; RF: recruit feeder).

Colony	TF distance	RF trained	TF recruits	Dancers: Waggle runs per hive visit	Followers: TF waggle runs followed per hive visit	
					Reactivation	Searching
A	100 m	21	16	11.4 ± 18.5	3.9 ± 4.2	7.4 ± 5.3
A	500 m	26	3	11.8 ± 15.3	2.3 ± 3.5	8.3 ± 6.4
B	100 m	31	22	15.5 ± 15.5	5.2 ± 6.9	14.4 ± 7.9
B	500 m	22	9	12.5 ± 13.6	3.6 ± 4.6	17.4 ± 10.2
C	100 m	28	11	4.6 ± 8.1	2.3 ± 3.3	4.7 ± 4.8
C	500 m	30	13	11.3 ± 13.6	4.1 ± 7.1	13.6 ± 8.5

Data provided as sample size or mean ± SD. Hive absences were labelled as 'reactivation' if a forager returned to the RF; otherwise, foragers were assumed to be searching for the TF.

Follower behaviour

As expected, individuals typically made multiple trips to the empty recruit feeder before searching for the new target (see also Grüter & Ratnieks, 2011), and the probability of abandoning the recruit feeder in favour of searching for the target feeder increased over time (binomial GLMM: hive visit: estimate ± SE = 2.65 ± 0.22 (95% CI: 2.21, 3.08); Fig. 2). However, contrary to our expectations, bees were more likely to engage in search trips when the target feeder was distantly located than when it was close to the hive, and this probability rose more steeply over time in the former (binomial GLMM: target feeder distance (500 m): estimate ± SE = 0.85 ± 0.21 (95% CI: 0.44, 1.26); target feeder distance * hive visit: estimate ± SE = 1.72 ± 0.43 (95% CI: 0.89, 2.56); Fig. 2). See table S5 for the full model summary.

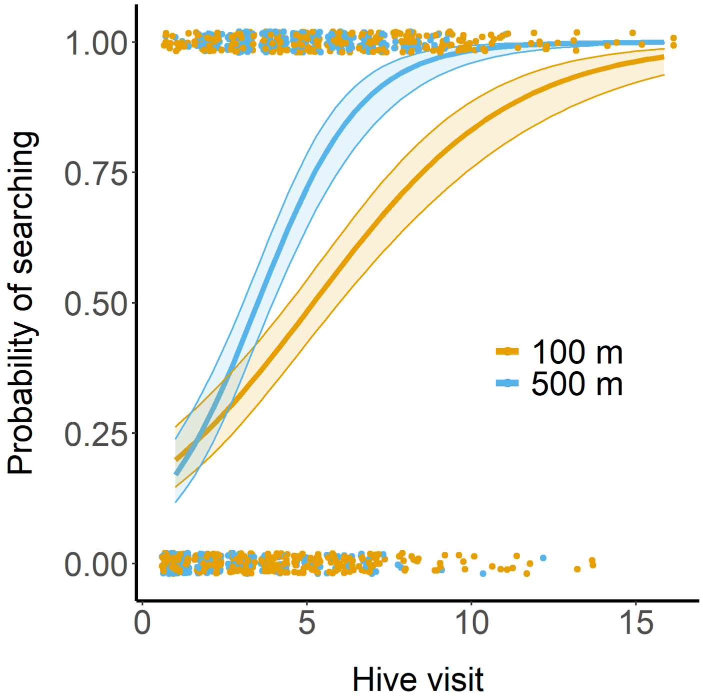

Figure 2. Probability of searching for the target feeder upon departing the hive. Observed data are jittered for clarity (0 = reactivation, 1 = searching). Lines and shaded regions respectively indicate predicted values and 95% CI calculated from GLMM fixed effects with all random effects set to 0.

In line with previous work (Grüter & Ratnieks, 2011; Grüter et al., 2013), we found that foragers on average followed more waggle runs before departing in search of the target feeder than when re-visiting the empty feeder, though this effect lessened over time (zero-inflated negative binomial GLMM: search trip: MAE ± USE = 0.75 ± 0.06 (95% CI: 0.63, 0.87); searching * hive visit: MAE ± USE = -0.51 ± 0.13 (95% CI: -0.76, -0.27)). In line with our predictions, bees tended to follow more waggle runs before searching for a more distant feeder (Table 1; Fig. 3). However, the evidence for this effect was weak, with the 95% confidence intervals spanning 0 (same GLMM: TF distance (500 m) * search trip: MAE ± USE = 0.16 ± 0.15 (95% CI: -0.12, 0.45); Fig. 3). Similar results were found when investment in dance-following was measured by dance-following duration (sec). Bees spent more seconds per hive visit following dances for the more distant feeder (zero-inflated negative binomial GLMM: TF distance (500 m): MAE ± USE = 0.55 ± 0.18 (95% CI: 0.19, 0.91)), reflecting the positive relationship between waggle run duration and foraging site distance. However, there was little evidence that they invested disproportionately more time in following long-distance dances prior to searching (same GLMM: TF distance (500 m) * search trip: MAE ± USE = 0.15 ± 0.14 (95% CI: -0.12, 0.42)). See tables S6–S9 for full model summaries.

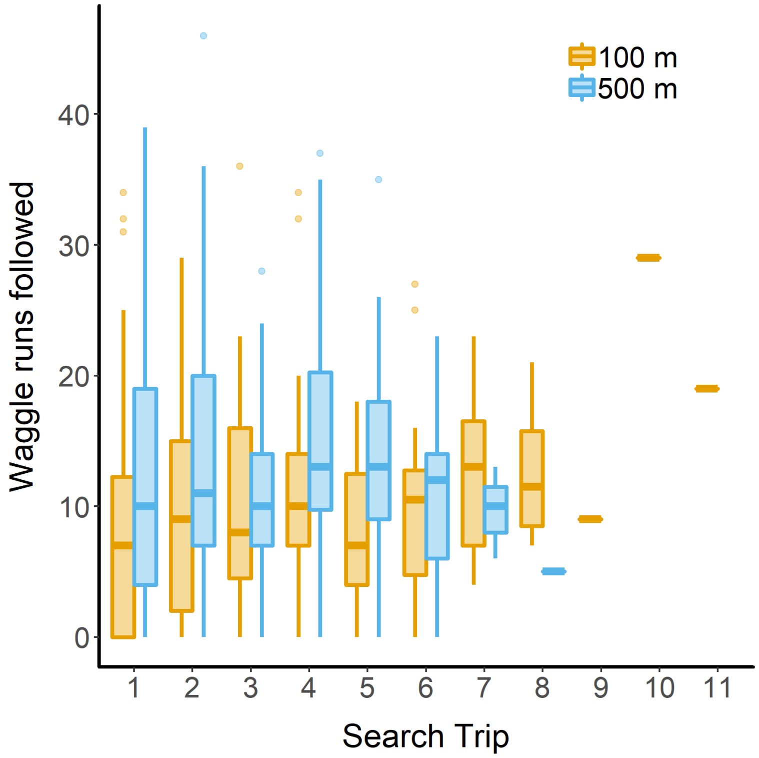

Figure 3. The number of waggle runs followed prior to searching for the target feeder. Thick lines indicate medians, boxes enclose the interquartile range, and whiskers extend to up to 1.5x this range.

As expected if long-distance searches are more costly, search trips into the field were longer in duration than reactivation trips only when the target feeder was more distant (LMM: target feeder distance (500 m) * search trip: MAE ± USE = 0.6 ± 0.06 (95% CI: 0.48, 0.72); Fig. 4a; tables S10 & S11). Comparing the mean duration of searches for the target feeder vs. collection trips made by employed foragers (minus time spent at the feeder) confirmed that both search and collection trips took more time when the target feeder was more distant from the hive (LMM: target distance (500 m): estimate ± SE = 0.63 ± 0.03 (95% CI: 0.5, 0.76); table S12) and that search trips were longer in duration than collection trips (LMM: trip type (collection): estimate ± SE = -0.6 ± 0.05 (95% CI: -0.69, -0.51); table S12)). However, searches were not disproportionately longer at 500 m than at 100 m (the best-supported model, $w_i >$ 0.99, did not include an interaction between target feeder distance and trip type; table S12). Regardless of distance, successful recruits undertook a similar number of unsuccessful searches before eventually locating the target feeder (Poisson GLMM: target feeder distance (500 m): MAE ± USE = -0.24 ± 0.22 (95% CI: -0.67, 0.18); Fig. 4b; tables S13 & S14).

In addition to dances for the target feeder, we observed 122 dances for natural food sources. These dancers produced 8.74 ± 12.37 (mean ± SD) waggle runs per dance and carried pollen in 56 of these dances. Although our focal bees occasionally followed these natural dances, these following events were brief in duration (mean ± SD = 1.13 ± 0.35 waggle runs followed; n = 40 dance-following events). Out of 519 prospective search flights, only 10 (i.e. 1.9%) involved a focal bee following a dance for a natural food source (mean ± SD = 1.8 ± 1.03 waggle runs followed).

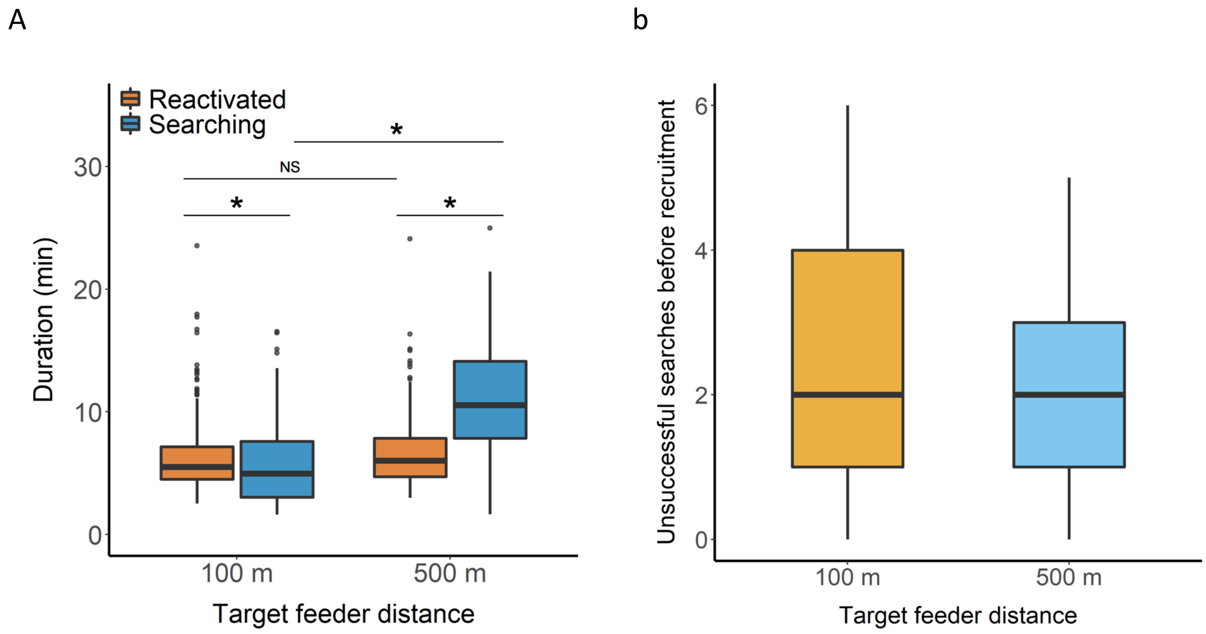

Figure 4. (a) Duration of hive absences and (b) number of unsuccessful searches before discovering the target feeder. Absences were labelled as reactivations if foragers returned to the empty recruit feeder and searches for the target feeder otherwise. The y-axis in (a) has been truncated to enhance clarity; an additional reactivation was observed in both the short- and long-distance trials with respective durations of 64.9 and 35.7 min. Thick lines indicate medians, boxes enclose the interquartile range, and whiskers extend up to 1.5x this range. *P* values for contrasts were adjusted using the Bonferroni method: *: $P < 0.001$.

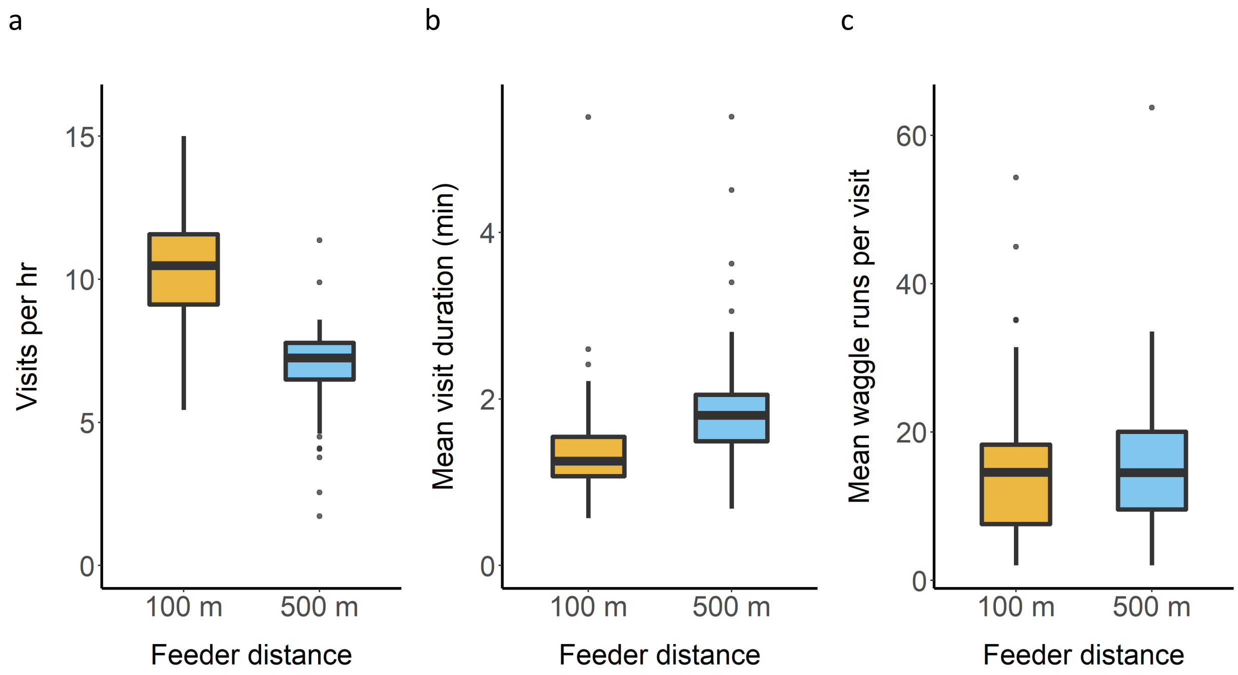

Figure 5. (a) Hive visit frequency, (b) mean visit duration, and (c) mean waggle runs produced per visit with dancing by foragers collecting from the target feeder. Thick lines indicate medians, boxes enclose the interquartile range, and whiskers extend up to 1.5x this range.

Dancer behaviour

In line with previous work (von Frisch, 1967; Seeley, 1994), dances representing the more distant (and thus less energetically efficient) 500 m feeder were underrepresented on the dancefloor relative to those for the closer feeder. This occurred because dancers visited the hive less frequently when the target feeder was more distantly located (LMM: target feeder distance (500 m): estimate ± SE = -3.58 ± 0.37 (95% CI: -5.15, -2.01); table S15). On average, dancers made 10.3 visits hr^{-1} when the feeder was located 100 m from the hive, but only 6.9 visits hr^{-1} when it was 500 m away (Fig. 5a). This is in part because travel to and from the distant feeder took longer (table S12), but foragers collecting at 500 m also tended to remain in the hive for longer on each visit (LMM: target feeder distance (500 m): estimate ± SE = 0.51 ± 0.09 (95% CI: 0.12, 0.89); Fig. 5b; table S16). In contrast to our expectation that bees foraging at the distant feeder would be less likely to dance upon returning to the hive, there was no evidence that foraging distance influenced foragers' propensity to dance (table S17). If anything, foragers in long-distance trials tended to be more likely to dance during hive visits (binomial GLMM: target feeder distance (500 m): estimate ± SE = 0.72 ± 0.71 (95% CI: -0.67, 2.11)), though the best-supported model ($w_i > 0.99$) did not include this effect (table S17). There was also no evidence that dancers for more distant feeders produced fewer waggle runs (LMM: target feeder distance (500 m): MAE ± USE = 0.31 ± 1.79 (95% CI: -3.2, 3.82); tables S18 & S19; Fig. 5c).

Discussion

The traditional view of insects as mere stimulus-response "machines" has given way to a growing recognition that despite their miniature brains, insects possess sophisticated cognitive capabilities (Giurfa, 2015). Accordingly, although empirically derived theoretical models have shown how simple rules that govern the production of waggle dances are sufficient to generate adaptive collective responses by honeybee colonies without requiring that dance-followers evaluate the transmitted spatial information (Seeley, 1995; Detrain & Deneubourg, 2008), dance-followers may in principle be able to fine-tune their responses according to this information. Here, we used NBDA to first ask whether the influence of dance information over the likelihood that foragers successfully arrive at a novel site varied depending on the indicated foraging distance. In contrast to our predictions, the NBDA supported no difference between short- and long-distance trials in either the likelihood of recruitment per dance circuit followed nor in the proportion of recruitment events that involved the use of dance information. In other words, reliance on dance information during recruitment was similar across the foraging distances studied here. We further found only weak evidence to suggest that foragers searching for more distant sites invested more in dance-following, either in terms of the number of dance circuits followed or the duration of dance-following, and foragers were in fact quicker to abandon a depleted site when the alternative was more distantly located. Taken together, these findings are consistent with the hypothesis that dance-followers do not evaluate the distance information contained in a dance when deciding how to respond to it, at least across the range of distances used here.

Although honeybees have been known to forage from sites that are located upwards of 10 km from the hive (Seeley, 1995; Beekman & Ratnieks, 2000), dance decoding studies have shown that the median distance travelled under natural conditions is often an order of magnitude lower than this (Couvillon et al., 2014). For example, we recently found the median distance indicated by dances across an entire season in southern England to be 492m and 743m for urban and agricultural sites respectively (Samuelson et al., 2019). Nonetheless, our feeder locations, at 100 and 500m from the hive, clearly do not represent the full foraging range of honeybees (Visscher & Seeley, 1982; Steffan-Dewenter & Kuhn, 2003; Couvillon et al., 2014). Additionally, dancers produced similar numbers of waggle runs and were equally likely to dance in both our short- and long-distance trials, suggesting that they did not perceive a difference in energetic efficiency between our treatments. Nevertheless, we note that our distance treatments were distinct enough to drive observable differences in search costs for dance-followers that had not yet located the feeders, and that previous work has detected modifications to dance behaviour between sites at 250 and 500m (Seeley, 1994). Thus, while we cannot conclude that dance followers do not take the indicated distance into account when deciding whether to seek out more distant sites than we considered here (see also Al Toufailia, Couvillon, et al., 2013), we are confident that our treatments should have elicited an effect if one exists within this range.

As foraging distances increase, searches require progressively greater investments in time and energy, exacerbated by the fact that dance-guided searches often fail (Fig. 4b; Seeley & Towne, 1992; Biesmeijer & Seeley, 2005). Why then did we not observe greater reticence to accept recruitment to distant novel sources? Dances are followed both by bees that have never visited the target site (recruitment) and bees that know its location (reactivation), with only the former incurring search costs. Since dancers do not know for which purpose their audience is following, we expected the behavioural rules that translate the energetic efficiency of a foraging trip into the number of waggle runs performed to ignore these additional search costs, allowing instead for dance-followers to fine-tune their responses depending on their informational status. However, it may be that the increasing search costs elicited by distant resources are already sufficiently accounted for through their under-representation on the dancefloor and that additional receiver responses are not needed to achieve adaptive collective foraging, especially given that we found that although search costs do increase with distance, they are not disproportionately large at greater distances. It also is possible that differences in follower responses depend on the ability to compare competing options on the dancefloor, an option which our experimental design specifically precludes (Fig. 1). Previous work suggests, however, that followers do not compare dances, at least on the basis of resource quality (Seeley & Towne, 1992).

Alternatively, it may be the case that while sensitivity to distance information by followers could increase colony foraging efficiency, the mechanisms by which it could be achieved have diminishing returns. For example, beyond a certain point, the extra time spent following additional dance circuits may not appreciably increase the likelihood of locating a site. Moreover, the positive relationship between foraging site distance and waggle run duration means that as foraging distances increase, foragers must invest ever more time in dance-following to follow the same number of waggle runs (von Frisch, 1967; Al Toufailia, Couvillon, et al., 2013). Indeed, we observed that potential recruits spent more time overall following dances in the long-distance trials, though not disproportionately so prior to searching. The use of dance information may involve a speed-accuracy trade-off (Chittka et al., 2009), such that setting out with reasonably accurate spatial information may often be preferable to investing further time in waiting for and following dances.

It remains unknown whether a similar amount of spatial information is transmitted per waggle run for nearby versus more distant food sources. The value of *s* does not directly estimate this information, as *s* is also shaped by bees' motivation when following a dance (i.e. reactivation vs. recruitment). However, current evidence suggests a trade-off: as foraging distance increases, there is less imprecision in the directional component of the dance, but more imprecision in the distance component (Couvillon et al., 2012; Al Toufailia, Couvillon, et al., 2013). As *s* serves as an integrative measure of the effect of each waggle run on the likelihood of successful recruitment, these opposing effects may have also contributed to the lack of difference observed across our treatments.

In agreement with earlier studies (Grüter & Ratnieks, 2011; Grüter et al., 2013; Hasenjager et al., 2020), most foragers visited the empty recruit feeder several times before searching for the target feeder. Yet rather than foragers being more reluctant to abandon this site when alternatives were more distant (as predicted), the opposite pattern was observed (Fig. 2). It is possible that this finding simply stems from how foraging trips were labelled—i.e., during reactivations, it was assumed that bees did not also search for the target feeder. However, studies using harmonic radar to track bees' foraging flights have revealed the occurrence of such cross-trips between familiar and unfamiliar foraging locations (Menzel et al., 2013), potentially allowing individuals to gain up-to-date information on familiar foraging sites while also making use of dance information to seek out novel locations without requiring that they first return to the hive. If joint reactivation-search trips occurred more often in short-distance trials when feeders were relatively close together (Menzel et al., 2013), this could be reflected in our analysis as a lower likelihood of searching when the target was nearby. However, although we cannot rule out that such trips occurred, our data suggest that they were unlikely to be especially common (see Supplementary Material, tables S20 & S21). Alternately, the dance-indicated location in long-distance trials may have been easier to identify as a novel site, as neither the distance nor directional components matched that of the recruit feeder (von Frisch, 1967; Grüter et al., 2013). Regardless, our results complement previous reports that honeybees' persistence to familiar sites depend more on previous profitability than on the availability of alternatives (Al Toufailia, Grüter, et al., 2013).

Although we assumed that during departures from the hive, potential recruits were either returning to the recruit feeder or searching for the target feeder, individuals may also have engaged in alternative foraging behaviours, including visiting other known foraging locations or searching for natural food sources. However, trials took place during the late summer and early autumn when few natural food sources are available to bees in southern England (Couvillon et al., 2014). Accordingly, foragers were highly persistent in visiting the feeders during training, limiting their opportunities to learn about other foraging sites prior to the trial. In addition, there were relatively few dances for natural sources during the trials and these were rarely followed by our focal individuals. When natural dances were followed, these bouts were always brief in duration, indicating that foragers were not attempting to decode the dance's spatial information (Grüter & Farina, 2009). Individuals may also have attempted to locate other foraging sites through individual scouting. However, previous reports have found that scouting is relatively rare when dances are readily available in the hive (Biesmeijer et al., 2005; Beekman et al., 2007), as was the case in our study. We therefore feel confident that most searching events represented attempts to locate the target feeder. Nevertheless, we repeated our analysis of: (i) the duration of searching events and (ii) the number of waggle runs followed prior to each search using only the subset of successful recruitment events. Our findings were consistent with our more inclusive analysis: in long-distance trials, searches were longer in duration and recruits followed more waggle runs prior to a successful search, but this latter difference was not significant at the 95% level (tables S22 & S23).

Given that the colony represents the reproductive unit in honeybees, natural selection is expected to have acted on the heuristics that guide behaviour at the individual level in order to produce adaptive colony-level responses (Detrain & Deneubourg, 2008). Although such individual-level algorithms could in principal lead recruits to differentially respond to dances according to the indicated distance, we found no evidence that this is the case, at least across the foraging distances considered here. Rather, our results provide empirical support to the long-standing assumption that the effective allocation of recruits among foraging sites does not depend on information processing by dance-followers, but on the rules that govern the production of dances themselves, the tempo of foraging, and the abandonment of foraging sites (Seeley, 1995). However, due to the challenges involved in studying decision-making in bees foraging on natural sources, most studies (including our own) have used artificial food sources located relatively near to the hive that offer an unrestricted flow of sucrose. Additional investigations into how the production of dances is modulated under more naturalistic foraging conditions and how dance-followers respond to this information would be worthwhile.

Data accessibility. Raw data and code to reproduce all analyses are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8kprr4xn8 (Hasenjager, Hoppitt, et al., 2021).

Authors' contributions. M.J.H. and E.L. designed the study. M.J.H. collected the data and M.J.H. and W.H. analysed it. M.J.H. wrote the initial draft and all authors contributed to revisions.

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