

From dyads to collectives: a review of honeybee signalling

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1 **From dyads to collectives: a review of honeybee signalling**

2 Matthew J Hasenjager*¹², Victoria R Franks*¹³ and Ellouise Leadbeater^{1†}

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4 * *These authors contributed equally*

5 ¹*Department of Biological Sciences, Royal Holloway University of London, Egham, UK*

6 ²*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN USA (present*
7 *address)*

8 ³*Department of Biological Sciences, University of Chester, Parkgate Road, Chester UK (present address)*

9 [†]*Corresponding author: elli.leadbeater@rhul.ac.uk*

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17

18 **Abstract**

19 The societies of honeybees (*Apis spp*) are microcosms of divided labour where the fitness interests of
20 individuals are so closely aligned that, in some contexts, the colony behaves as an entity in itself. Self-
21 organization at this extraordinary level requires sophisticated communication networks, so it is not
22 surprising that the celebrated “waggle dance”, by which bees share information about locations outside
23 the hive, evolved here. Yet bees within the colony respond to several other lesser-known signalling
24 systems, including the *tremble dance*, the *stop signal* and the *shaking signal*, whose roles in coordinating
25 worker behaviour are not yet fully understood. Here, we firstly bring together the large but disparate
26 historical body of work that has investigated the “meaning” of such signals for individual bees, before
27 going on to discuss how network-based approaches can show how such signals function as a complex
28 system to control the collective foraging effort of these remarkable social insect societies.

29

30 **Keywords:** Waggle dance, tremble dance, stop signal, shaking signal, honeybee social networks

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32

33 1. Introduction

34 The honeybee waggle dance is arguably one of the most celebrated examples of communication within
35 the field of animal behaviour, and certainly one of the most fascinating. This symbolic communication
36 system was observed potentially as far back as the 4th century BC by Aristotle (Haldane 1955), but it was
37 not until the 20th century that the meaning of these dances was finally deciphered by Karl von Frisch (von
38 Frisch 1967), earning him a share of the 1973 Nobel Prize in Physiology. For many students of Animal
39 Behaviour, the waggle dance is familiar as a means by which individual honeybees can reduce investment
40 in searching for food and exploit the benefits of foraging alongside others with closely aligned fitness
41 interests. Perhaps less commonly understood are the mechanisms by which the dance, alongside other
42 communication signals (eg tremble dances: Seeley 1992; stop signals: Nieh 1993; shaking signals:
43 Schneider and Lewis 2004) and olfactory cues deriving from the scent of visited flowers (Farina et al 2005
44 2012), controls the collective foraging behaviour of the colony (Seeley 1995). The waggle dance does not
45 act alone, but is just one information source in a series of potentially interacting signal networks that
46 include positive and negative feedback loops and which direct colony behaviour such that the collective
47 makes group-level “decisions” about how to allocate the workforce and where to send foragers.

48 While the key signals that underpin these group decisions have now been the focus of several
49 decades of research (reviewed in Seeley 1995; Anderson and Ratnieks 1999; Couvillon 2012; Kietzman
50 and Visscher 2015), attempts to study the information flow networks that arise from them have been
51 logistically challenging. Tracking even a small proportion of the ~20 000 honeybees in a colony to detect
52 individual signals, cues, responses and typical behavioural roles is a major hurdle of scale, while analysing
53 the massive amounts of data that can arise from such work was almost impossible until recently (although
54 see Biesmeijer and Seeley 2005). However, advances in both processing power and network theory have
55 opened the door to understanding the behaviour of this complex system. In the first half of this review,
56 we draw together the literature on key movement and vibration-based signals that are produced by

57 foraging bees: the waggle dance, tremble dance, stop signal and shaking signal. In the second half, we go
58 on to explain how network theory can provide a unique avenue for understanding how these signals
59 translate behaviour from the individual to the colony level, introducing studies that have started to apply
60 this approach.

61

62 **2. Honeybee Signalling Systems**

63 *a. The waggle dance*

64 The waggle dance (von Frisch 1967) is arguably the single most well-known behaviour within the
65 honeybee repertoire (Dyer 2002; Grüter and Farina 2009; Couvillon 2012). A waggle dance is made up of
66 two alternating phases: a waggle run during which the forager moves in a straight line across the comb
67 while vigorously shaking its abdomen back and forth, and a return phase during which it circles around to
68 return roughly to the point at which its run began (Fig 1a). The duration of each waggle run correlates
69 with the distance of a given resource from the hive, and the angle of the run with respect to gravity
70 corresponds to the direction of the resource relative to the sun (von Frisch 1967).

71 While it is now firmly established that the spatial information encoded in the waggle dance is
72 transmitted to dance-followers (Gould 1975; Riley et al 2005), this hypothesis was at one time quite
73 controversial. Adrian Wenner and his colleagues in particular, while accepting that elements of the dance
74 correlated with the spatial location of the visited resource, proposed an alternative explanation for the
75 arrival of recruited bees at the advertised food source: that honeybees were guided to food primarily
76 through the transmission of olfactory information within the hive, which they matched to known or
77 sought-out scents of forage locations (Johnson 1967; Wenner et al 1969; Wenner and Wells 1990; Munz
78 2005). Ultimately Von Frisch's hypothesis was vindicated by James Gould, through a set of experiments in
79 which Gould manipulated foragers such that their dances indicated a site that they themselves had not

80 visited. Sufficient recruits arrived at the advertised site to unambiguously demonstrate that honeybees
81 were able to use dance-conveyed information to locate novel foraging sites (Gould 1975)

82 Nonetheless Gould pointed out that “only further work can establish whether the dance-language
83 communication is common or rare under normal circumstances” (Gould 1975), and it is now well
84 established that surprisingly little dance-following leads to arrival at a novel food source (Grüter and
85 Farina 2009). By tracking dance-following across foragers’ lifetimes, Biesmeijer and Seeley (2005)
86 estimated that under natural conditions only 12–25% of dance-following interactions are for this purpose.
87 The remaining 75–88% of dance-following interactions are thought to instead involve food sources that
88 are already known by the dance-followers (Biesmeijer and Seeley 2005)—for example, after a period of
89 interrupted foraging (eg nightfall), dance-following can reactivate experienced foragers to resume
90 collecting from familiar patches (Johnson 1967; Gil and Farina 2002; Grüter et al 2008; Hasenjager et al
91 2020). Dance-following is often cursory under these circumstances (Gil and Farina 2002; Biesmeijer and
92 Seeley 2005; Grüter et al 2013) suggesting that foragers are unlikely to be seeking detailed spatial
93 information (though see Wray et al 2012). Indeed, bees very often ignore the spatial information
94 altogether, following a dance but subsequently arriving at their own preferred site (Johnson 1967; Grüter
95 et al 2008; Hasenjager et al 2020). When dancers do finally choose to seek out new sites, they engage in
96 longer bouts of dance following (Grüter and Ratnieks 2011; Grüter et al 2013; Hasenjager et al 2022),
97 presumably to obtain accurate spatial information. Dance-following, though critically important for
98 locating the general vicinity of new foraging patches (Hasenjager et al 2020), thus often seems to serve as
99 a backup information source for foragers that know of no alternative patches (eg novice foragers or when
100 a previously visited site is no longer profitable; Biesmeijer and Seeley 2005; Grüter and Ratnieks 2011;
101 Grüter et al 2013).

102

103 *b. The tremble dance*

104 Resembling the waggle dance in some respects, the tremble dance is an additional signal employed by
105 honeybees in the hive during collective foraging behaviour. When tremble-dancing, a forager rapidly
106 shakes her body along its central axis and walks slowly across the comb with frequent changes of direction
107 (Seeley 1992; Fig 1b). The tremble dance was described alongside the waggle dance by von Frisch, who
108 thought that it had no communicative function (von Frisch 1967). However, while tremble dances are not
109 thought to have any translational aspect (eg they do not encode spatial information like waggle dances),
110 subsequent investigations beginning in the 1990s highlighted that this signal nevertheless plays a crucial
111 role in the communication of foraging conditions and the regulation of colony nectar processing.

112 Seeley (1992) provided vital evidence for a relationship between nectar processing and elicitation
113 of tremble dancing through a classic experiment in which he simultaneously trained two cohorts of
114 foragers from the same hive to separate feeders, and then experimentally increased forager numbers
115 collecting from one feeder. Bees from the unmanipulated cohort started to tremble dance despite having
116 experienced no change in the foraging conditions outside of the hive. The hive-internal cue that could
117 indicate such a processing shortfall was suggested to be a delay in finding a bee to unload nectar on arrival,
118 and indeed, the focal cohort experienced just such a delay. At the same time, Kirchner and Lindauer (1994)
119 found that a number of experimental conditions that had been previously observed to also elicit tremble-
120 dancing, such as capture at a food source, experiencing crowded feeders, or collection of salty nectar, also
121 led to unloading delays (potentially because nectar receivers detected alarm pheromone on the bodies of
122 foragers or were unwilling to receive strange-tasting nectar). As a result, it seemed clear that unloading
123 delays act to stimulate tremble dancing, and Seeley et al (1996) later demonstrated that increases in
124 nectar influx with associated tremble dancing subsequently lead to hive workers being recruited as nectar
125 receivers. When a colony's nectar processing capacity rises as a result, the delay experienced by incoming
126 foragers should decrease and tremble dancing should cease (Seeley 1995).

127 However, despite the elegance of this feedback loop, we now know that hive-internal unloading
128 delays cannot be the sole trigger for tremble dancing. This is because up to one half of natural tremble
129 dances start immediately upon entering the hive (Biesmeijer 2003b), when foragers have experienced no
130 delay. Many (but not all) of these dances occur on the first foraging trip of the day, so it is unlikely that
131 recent previous experience of long delays could have elicited the dance. Thom (2003) also showed that
132 crowded conditions at a food source can induce tremble dancing in the absence of an unloading delay,
133 casting into doubt the assertion (Kirchner and Lindauer 1994) that tremble dancing by captured crowded
134 or otherwise disturbed bees (Lindauer 1948) is a side-effect of the unloading delays that they experience.
135 Thus, there is currently no proposed trigger that can explain all reported incidences of tremble dancing,
136 which appears to be an adaptive reaction to changes in both internal and external foraging conditions,
137 the function of which is partly but not fully understood. In a later section of this text, we suggest how a
138 network-based approach could contribute to this issue.

139 Tremble dancing also has a secondary, indirect, consequence of reducing recruitment through
140 waggle dancing (Seeley 1992) because a bee that opts to tremble dance after foraging reduces the pool
141 of waggle dancers. However, this negative effect on waggle dancing is mediated more directly through a
142 third key signal involved in regulating honeybee collective foraging and which is closely associated with
143 tremble dancing—the “stop signal”—described below.

144

145 *c. The stop signal*

146 When stop-signalling, a honeybee abruptly “headbutts” another individual and emits a brief high-pitched
147 buzz by rapidly vibrating its thoracic muscles (Fig 1c). The sound component of stop signals produces a
148 distinctive waveform with a fundamental frequency of 350-450Hz lasting approximately 150ms (Kirchner
149 1993). Crucially, recipients “freeze” briefly, which is distinctive from other vibrational signals such as
150 piping signals or begging calls (Pastor and Seeley 2005). In the context of foraging, tremble-dancing bees

151 often also produce stop signals (Nieh 1993), but the association is not exclusive; indeed, under normal
152 foraging conditions the majority of stop signals appear not to be produced by tremble dancers but by bees
153 that have recently followed dances (Pastor and Seeley 2005). They are often directed at waggle dancers
154 (Nieh 1993; Pastor and Seeley 2005) but tremble dancers that produce stop signals also direct them to
155 other tremble dancers, food exchangers, dance followers and other bees (Nieh 1993).

156 Although once thought to be a begging signal that elicits food exchange (Esch 1964; von Frisch
157 1967), it is now clear that stop signals instead act in part to reduce forager dispatch (Pastor and Seeley
158 2005; Kietzman and Visscher 2015). Firstly, bees that stop signal rarely receive food from their target
159 colony-mates (Nieh 1993). Secondly, when stop signals are directed at waggle dancers, they stop dancing
160 and leave the dancefloor (Kirchner 1993; Nieh 1993); this same response can be triggered by synthesized
161 sounds produced at the same frequency as stop signals (Nieh 1993). Thirdly, there is also some evidence
162 from one honeybee species (*A. cerana*) that stop signals produced by guard bees at the nest entrance can
163 inhibit worker departures (Tan et al 2016).

164 The fact that tremble dancers often stop-signal (Nieh 1993) is congruent with a role as an
165 emergency brake that interrupts the cycle of positive feedback created by waggle dance recruitment,
166 allowing the colony time to build nectar processing capacity before recruitment recovers. Likewise it
167 makes sense that stop signal production by foragers drastically increases when they experience
168 conspecific attacks during food competition, predator attacks, or in the presence of alarm pheromone
169 (Nieh 2010; Jack-McCollough and Nieh 2015; Tan et al 2016), and become more intense when danger is
170 greater (Tan et al 2016; Dong et al 2019). For example, during nectar-robbing events, if a target colony is
171 proving competent at defending itself, shutting down recruitment in the robbing colony could be critically
172 important to limit the attack-associated costs (Johnson and Nieh 2010). Yet it is strange that such contexts
173 also typically elicit tremble dancing. If tremble dancing serves to recruit nectar processing power, why
174 does it occur in the predation/competition contexts that elicit stop signalling? And if the stop signals that

175 are directed at other tremble dancers, nectar receivers, dance followers or other non-foraging bees have
176 a function (Nieh 1993), what is it? Approaching these questions can be challenging because they require
177 a good assessment of the tasks that individual signallers and recipients had been engaged in prior to the
178 signalling interaction, and continued tracking to identify subsequent behavioural change. Automated
179 tracking of individuals, in combination with network-based analyses that can assign behavioural roles,
180 now offer a means to rise to this challenge that we discuss further below, after we introduce a final signal
181 that contributes to foraging: the shaking signal.

182

183 *d. The shaking signal*

184 In contrast to the signals described above, which often elicit relatively immediate and specific changes in
185 receiver behaviour, the shaking signal is thought to act as a modulatory communication signal that
186 modifies the overall arousal or activity of receivers but does not lead to one specific change in their
187 behaviour (Nieh 1998; Schneider and Lewis 2004). The shaking signal is delivered by the signaller grasping
188 another bee with its pro- and mesothoracic legs and proceeding to vibrate its own body dorso-ventrally
189 for 1–2 s at a frequency of ~16 Hz (Fig 1d). However, identifying the “message” being transmitted by the
190 shaking signal has proven challenging as it is produced in several contexts (eg the onset and cessation of
191 foraging swarming queen-rearing), and its effects on receivers appear to be highly context-specific and
192 dependent on recipients’ physiology, age, task performance and genetics (Schneider and Lewis 2004;
193 Koenig et al 2020). For example, recipients of shaking signals move faster and show elevated rates of cell
194 inspection, trophallaxis, waggle dance-following and grooming behaviour (Nieh 1998; Cao et al 2007;
195 Koenig et al 2020). In addition, some behavioural effects are only apparent 15–30 min after receiving the
196 signal (Schneider and Lewis 2004). Nevertheless several lines of evidence suggest that the shaking signal
197 plays an important role in regulating collective foraging activity.

198 In the context of foraging, most shaking signals are produced by foragers, often following previous
199 foraging success (Nieh 1998; Biesmeijer 2003a). Shaking signals are often produced in lieu of waggle
200 dances and following the first successful foraging trips of the day, when many bees in the hive remain
201 relatively inactive (Seeley et al 1998). In addition, bees that have experienced foraging success on previous
202 days will often produce shaking signals even before they begin foraging (Biesmeijer 2003a). As a result,
203 there is predictable diurnal variation in shaking signal production, with peaks of signalling activity
204 preceding production of waggle dances (Nieh 1998; Biesmeijer 2003a; Ramsey et al 2018). Shaking signal
205 production is often especially pronounced after bees have experienced a dearth of forage (Seeley et al
206 1998). The recipients of these forager-produced shaking signals are often younger and/or inactive bees
207 (Lewis et al 2002; Nieh 1998), yet as noted above, receiver responses can be highly idiosyncratic.

208 One possible function of the shaking signal is that by increasing receiver movement and activity,
209 shaking signals increase the likelihood of interaction with nestmates and other sources of task-relevant
210 information within the colony (eg contents of inspected cells; Biesmeijer 2003a; Cao et al 2007).
211 Consequently, recipients of shaking signals will more rapidly acquire up-to-date information about the
212 state of the colony and forage availability. Shaking signals thus could provide an indirect means by which
213 foragers can promote reallocation of work effort in response to changes in foraging conditions. Indeed,
214 although peaks in shaking signal production are generally observed in the early morning at the onset of
215 foraging, minor peaks in the afternoon have also been observed (Nieh 1998). These afternoon shaking
216 signals may aid in coordinating the cessation of colony foraging and food-processing activity by promoting
217 re-evaluation of current activity by recipients (potentially mediated through increased activity; Nieh 1998)
218 However as with the tremble dance and stop signal, a better understanding of the role of shaking signals
219 in coordinating colony foraging has awaited the ability to track the identities, work history and social
220 experiences of signallers and receivers across extended periods of time. We now turn to how tools

221 developed to study complex networks coupled with advances in tracking technologies offer a potentially
222 useful means to meet these challenges.

223

224 **3. From dyads to networks**

225 While the signals described above, amongst a plethora of olfactory cues (von Frisch 1967; Farina et al
226 2005; Thom et al 2007), allow individual bees to find food more quickly, recruit nectar receivers, and stop
227 foraging when needed, they also produce colony-level foraging behaviour that extends beyond the sum
228 of individual signalling dyads (Sumpter 2006). To provide an example of the somewhat abstract concept
229 of collective decision-making, consider the means by which colonies “choose” between nectar sources
230 without requiring that any single individual compares foraging sites. When a bee finds nectar forage that
231 exceeds a threshold concentration (the value of which is determined by seasonal forage availability; von
232 Frisch 1967), the dances that she performs on returning to the hive indicate its location but also reflect
233 the energetic efficiency of the foraging trip. This is because more efficient trips (“efficiency” deriving from
234 travel and collection time, factored by the calorific returns of sucrose collected) elicit more dance circuits
235 than less efficient equivalents (Seeley 1994). As a result, dance-followers are more likely to encounter
236 dances for those food sources, and thus are more likely to be recruited to them without requiring that
237 any individual judges a particular food source to be “better” than an alternative (Seeley and Towne 1992).
238 The colony, rather than the individual, makes a decision about where to allocate labour, collectively
239 favouring closer and sweeter nectar sources.

240 A similar example can be found in the context of nest-site choice by swarms, whereby waggle
241 dancers not only dance for the prospective nest sites that they have found (performing more dance
242 circuits for higher-quality sites just as for forage; Seeley and Visscher 2008), but also administer stop
243 signals to those dancers that advertise alternatives (Seeley et al 2012). In combination, the two signalling
244 networks achieve an outcome whereby information flows rapidly through the group, allowing recruitment

245 to poor sites to be shutdown rapidly, and reducing the likelihood of deadlocks over similar sites. While
246 the basic units that build this group-level behaviour are individual dyads—for example, a waggle dancer
247 and a dance follower who may later become a dancer herself—the group itself is a complex system built
248 through the properties of the networks that arise from such signals.

249 In recent years, the application of network theory to animal behaviour has greatly advanced
250 understanding of how complex social systems are structured and the consequences for behavioural,
251 ecological, and evolutionary processes (Hasenjager and Dugatkin 2015; Krause et al 2015). Network
252 theory offers a framework for describing systems of interacting agents (eg honeybee workers) as sets of
253 nodes linked together by edges that denote both the occurrence and strength of some form of
254 relationship. In the case of social insects, examples of networks include interactions between signallers
255 and recipients (eg tandem-running in ants: Richardson et al 2018), antennation (Gordon 2010), or even
256 stigmergic interactions (indirect communication via environmental modification; Richardson and
257 Gorochowski 2015). Representing social systems in this fashion enables the use of a mathematical toolkit
258 for establishing what their key elements are, and how their structure shapes the behaviour of the system
259 as a whole (Waters and Fewell 2012; Pinter-Wollman et al 2014; Farine and Whitehead 2015). While a
260 prominent drawback of network approaches has been the very substantial data requirements (Farine
261 2018; Finn et al 2019), recent advances in technologies to automatically track animal behaviour mean that
262 comprehensive high-resolution data on the behaviour of individual workers across entire colonies are now
263 within reach (Boenisch et al 2018; Gernat et al 2018; Wild et al 2021) including automatic detection of
264 particular communication interactions (eg trophallaxis: Gernat et al 2018; Wild et al 2021; waggle dances:
265 Wario et al 2017; Okubo et al 2019; shaking signals: Ramsey et al 2018).

266 It was certainly possible to explore colony-level behaviour in social insects before a network-
267 based toolbox became available (eg Heinrich 1981; Deneubourg et al 1990; Seeley and Buhrman 1999;
268 Mallon et al 2001). It is therefore reasonable to ask whether network science can contribute to

269 understanding the evolutionary function of honeybee signalling networks rather than simply describing
270 the proximate mechanisms that give rise to colony behaviour. We propose that it can, for the following
271 reasons. Firstly, as highlighted in the preceding sections, current empirical approaches have hit their limits
272 in describing the basic biological “meaning” of some signals (eg receiver responses to the tremble dance
273 and shaking signal are often highly idiosyncratic; Biesmeijer 2003b; Schneider and Lewis 2004). Network
274 approaches can make sense of detailed interaction histories to remedy this issue. Relatedly, explaining
275 why so much apparent redundancy exists in the system requires understanding of how signal types
276 interact with one another synergistically, additively, or antagonistically, and network tools have been
277 developed that can disentangle these effects (De Domenico et al 2016; Hasenjager et al 2021). Finally,
278 networks themselves are group-level behavioural phenotypes, and selection can shape them to achieve
279 specific aims. Network science provides a variety of metrics to capture these structural features (see
280 Table 1 for a list; Farine and Whitehead 2015) which can illustrate how selection may have acted to
281 promote (or reduce) processes such as information flow, disease transmission or division of labour within
282 groups, which would not be apparent through an individual-level approach (Otterstatter and Thomson
283 2007; Pinter-Wollman et al 2011; Mersch et al 2013; Hasenjager et al 2020; Easter et al 2022). We expand
284 each of these points below, highlighting how current network approaches could be used, introducing
285 studies that have begun to explore these approaches, and discussing extensions to the approach that
286 bring better fit to the honeybee system.

287

288 *a. Linking signals to outcomes*

289 Inferring a signal’s function firstly requires an understanding of who produces it, who it is directed to, and
290 how it changes their behaviour. When interactions involve hive-based bees this can be challenging to
291 achieve because it requires knowledge of pre-interaction behavioural history, and so age has typically
292 been used as a proxy for behavioural role, based on temporal polyethism within honeybee workers (Free

293 1965). This method however cannot take into account the drastic variation among workers in
294 developmental trajectories that reflects genetics, brood requirements and external conditions. To remedy
295 this, Wild et al (2021) used automated tracking to follow a honeybee colony across 25 days, reconstructing
296 the daily interaction networks for each individual and using them to identify the fine-scale behavioural
297 role of each bee at distinct points in time. Importantly, tagging just 1% of the colony is sufficient to achieve
298 strong performance in inferring individuals' behavioural roles, and at 5% performance is equivalent to
299 that achieved by tagging the whole colony. Wild et al's methods offer a means to identify changes in
300 activity patterns that follow exposure to particular signals, such as repeated tremble dances, stop signals
301 or shaking signals. For example, such methods could prove useful in exploring the function of those stop-
302 signals that are delivered to or produced by non-foraging bees, or of those tremble dances that are
303 produced in a predation context. This approach could also facilitate investigation into how shaking signals
304 influence task allocation, given that their effects on receiver behaviour are thought to heavily depend on
305 individuals' past experiences and may only manifest some time after the interaction has occurred
306 (Schneider and Lewis 2004). However perhaps the most exciting potential application of Wild et al's
307 approach lies in its potential to capture interactions between signals whereby the impact of one signal
308 depends upon whether a bee has received another. By making available the entire behavioural history of
309 each individual, synergistic and antagonistic effects between signals could be investigated (eg using a
310 multilayer network framework, which we return to in the next section).

311 Network science also offers a means to quantify responses to signals, through a technique called
312 network-based diffusion analysis (NBDA; Franz and Nunn 2009; Hoppitt et al 2010). The core assumption
313 underlying NBDA is that if a particular type of interaction transmits information, then the corresponding
314 network of interactions should predict the order in which individuals begin to express a related
315 behavioural trait. For example, all else being equal, foragers that follow more waggle dance circuits for a
316 given site (and thus are more strongly connected in the dance-following network) are expected to locate

317 that site sooner than individuals that follow fewer circuits. The more closely that the pattern of arrivals
318 follows this dance-following network, the stronger the estimated social transmission effect of dance-
319 following. Crucially, multiple network types can be included in an NBDA allowing researchers to address
320 their relative contribution to a given response (Table 1). For example, although it has long been
321 established that bees are capable of using the spatial information in waggle dances, it is equally well-
322 established that olfactory cues are also key in directing bees towards food (Gould 1975; Johnson 1967;
323 Riley et al 2005; Grüter et al 2008), and we have recently employed NBDA to quantify the relative
324 contribution of waggle dance communication and olfactory cues in aiding recruits in locating new forage
325 sites (Hasenjager et al 2020).

326 To disentangle the influence of dance-based and olfactory communication pathways, we videoed
327 the in-hive interactions of a cohort of foragers whose familiar feeder had ceased to provide rewards, while
328 an alternative novel feeder was being advertised in the hive. From video records, we constructed
329 networks that captured waggle dance-following interactions and separate networks based on interactions
330 involved in transmitting olfactory information (eg trophallaxis antennation). Waggle dance-following
331 interactions alone were able to explain 97% of recruitment events to novel feeders, highlighting the
332 critical role that dances play in food source discovery despite the simultaneous availability of olfactory
333 cues (Hasenjager et al 2020). In contrast, when we compared the same networks in the context of
334 rediscovery of a familiar feeder, olfactory cues gained more importance, becoming approximately equally
335 as effective as dances in explaining feeder arrivals (Hasenjager et al 2020).

336 Traditionally, network analysis has often relied upon static networks that ignore the order in
337 which interactions occur—an approach that makes sense when studying, for example, stable social
338 relationships, but not when studying the consequences of signalling interactions (Blonder et al 2012;
339 Farine 2018). Thus, applying NBDA to honeybee signalling required that we use networks that could
340 change over time (Hasenjager et al 2020; 2021). Two principal approaches have been developed to model

341 temporal networks: time-aggregated networks, which are essentially a series of static networks, and time-
342 ordered networks, which yield a complete record of all interactions at all time points (reviewed in Blonder
343 et al 2012; Hasenjager et al 2021). Which approach is more useful will often depend on the research
344 question. For example, time-aggregated networks could be used to evaluate whether particular honeybee
345 foragers consistently occupy central positions in a signalling (eg dance-following) network across multiple
346 days, whereas investigating the potential role of receivers in modulating the production duration or
347 efficacy of forager signals is likely to benefit from the more fine-grained time-ordered approach (Table 1).
348 It is also possible to represent a time-aggregated network as a multilayer network, where each layer
349 represents a different time window (Finn et al 2019; Fisher and Pinter-Wollman 2021). We discuss the
350 concept of multilayer networks which capture combinations of different signals in the next section.

351

352 *b. Understanding interactive effects*

353 A problem for traditional approaches to understanding signal “meaning” is that the impact of a signal may
354 depend upon the other signals that an individual has received. For example, Thom and colleagues (2003)
355 hypothesize that stop-signals may sometimes serve to lower receivers’ response thresholds to the tremble
356 dance. Likewise, an individual’s likelihood of following a waggle dance can depend on whether it
357 previously received a shaking signal (Nieh 1998), which in turn are often produced by the same individuals
358 that produce waggle dances. Documenting these types of synergistic, antagonistic or additive interactions
359 is fundamental to understanding how communication evolves within highly eusocial groups. As we have
360 described above, the detailed interaction histories that automatic tracking has brought within reach (Wild
361 et al 2021) will be key here, but tools that can make sense of this huge body of information are also critical.

362 To this end, animal network studies are no longer limited to networks in which all connections
363 represent the same form of interaction (eg trophallaxis spatial proximity), or in which an aggregated
364 behavioural measure is generated from multiple interaction types. Instead, multilayer network

365 approaches combine multiple networks into a single mathematical structure while maintaining the
366 distinctiveness of each network type (ie layer; Silk et al 2018; Finn et al 2019; Hasenjager et al 2021). For
367 example, a multilayer network can be constructed in which each layer is a network capturing a different
368 interaction type (eg waggle dances tremble dances stop signals), with individuals connected to themselves
369 across layers (Fig 2). A multilayer framework enables researchers to address questions that are not
370 accessible using traditional monolayer approaches (Table 1). For example, one could ask: is an individual's
371 role in applying negative feedback on waggle dance-based recruitment via stop signals best captured by
372 its network position in the stop-signal layer alone, or by a measure of multilayer centrality (eg eigenvector
373 versatility; De Domenico et al 2015) that simultaneously incorporates information on its connectivity in
374 the stop-signal layer and its targets' connectivity in the waggle-dance layer? In other words, do only the
375 stop-signallers need to be well-connected to transmit their information effectively, or do they also need
376 their waggle dancing recipients to be well-connected too? Multilayer approaches could also be used to
377 investigate how strongly interaction dynamics are coupled across layers and whether the strength of this
378 coupling varies across contexts (Bianconi 2013; Table 1). For example, both tremble-dances and stop-
379 signals have been implicated in slowing forager recruitment (Seeley 1992; Nieh 1993) yet also appear to
380 have additional potentially unrelated functions (Nieh 1993; Seeley et al 1996). Comparing the structure
381 of these networks within and across contexts could highlight conditions in which their functions align or
382 diverge. Finally, multilayer representation of different network types can be further combined with an
383 additional set of layers that capture each time window (Fig 2), enabling investigation into how interactions
384 at one point in time (eg tremble dancing stop-signalling) may cascade out to influence interaction patterns
385 within and across layers (eg waggle dance-following) at subsequent time points (Bonnell et al 2021; Table
386 1).

387

388 *c. Adaptive structure of honeybee networks*

389 As we have seen, the signals employed by honeybee foragers do not simply transmit information between
390 dyads, but enable coordinated group-level behaviour such as matching foragers' nectar collection rate
391 with the colony's capacity to process incoming nectar (Seeley et al 1996). A more subtle means by which
392 selection might act upon collective activity is through the properties of the interaction network itself,
393 which arise from the patterning of interactions among workers (Gordon 2010; Naug 2015). For example,
394 differentiated interactions among particular age classes of honeybees can lead to sub-clusters in a
395 network that subsequently determine transmission dynamics and may allow information (for example
396 about foraging sites) to be targeted at foraging-age cohorts, while simultaneously isolating younger bees
397 for whom the information is less relevant and which could be exposed to pathogens transmitted via those
398 same interaction pathways (Naug 2008).

399 Among-individual variation in behaviour has also often been associated with enhanced collective
400 outcomes, including increased foraging rate and colony productivity in honeybees and other social insects
401 (Jandt et al 2014; O'Shea-Wheller et al 2021). Network theory offers a variety of metrics that can capture
402 this variation and link it to group-level behaviour (Farine and Whitehead 2015; Table 1). For example,
403 eigenvector centrality accounts for both an individual's direct connections and how well-connected its
404 network neighbors are, and thus can reflect a worker's importance in transmitting information throughout
405 the network. Such metrics can be further combined with simulation modelling to predict and evaluate
406 potential mechanisms of how observed patterns of variation influence colony dynamics (Gordon 2010;
407 Gernat et al 2018). For instance, previous research suggests that highly interactive individuals can emerge
408 as network hubs with acceleratory effects on signal propagation (Pinter-Wollman et al 2011). What might
409 be the potential consequences for collective processes if such 'hub'-like individuals are present across
410 different signaling networks with potentially synergistic (eg tremble dances and shaking signals) or
411 antagonistic (eg waggle dances and stop signals) effects (Table 1)? Predictions generated from models can
412 subsequently be tested through experiments that manipulate worker variation and/or signal production

413 (eg removal of foragers with high- vs low centrality: Crall et al 2018; artificial production of signals: Koenig
414 et al 2020). Multilayer network approaches also enable further comparison of individual variation within
415 and across signaling systems. Are networks that are constructed from different signaling systems similarly
416 organized? Is a forager's importance in the network correlated or highly variable across different signaling
417 layers? How stable is a worker's centrality in the network over time?

418 A final promising approach for identifying functional elements in the structure of colony
419 interaction networks is searching for recurrent patterns, or motifs, across subsets of individuals (Milo et
420 al 2004; Easter et al 2022). One such motif is the feed-forward loop, characterized as a pair of directional
421 pathways between two nodes (eg A and C) involving both a direct pathway and an indirect one mediated
422 by a third node (ie $A \rightarrow C$ and $A \rightarrow B \rightarrow C$ respectively). Feed-forward loops are potentially well-suited for
423 regulating colony behaviour by efficiently directing information flow through the network (Mangan and
424 Alon 2003). Indeed, this motif has been found in both the antennation networks of harvester ants
425 *Pogonomyrmex californicus* and in the dominance networks of the wasp *Ropalidia marginata*, potentially
426 reflecting the role of these networks in regulating colony functioning (Waters and Fewell 2012; Nandi et
427 al 2014). Likewise, by searching for feed-forward loops and other motifs within the signalling networks of
428 honeybee foragers it might be possible to gain insight into the networks' functional properties and how
429 selection has acted on forager behaviour.

430

431

432 **6. Discussion**

433 On an evolutionary level, the ultimate value of collective foraging by honeybees remains a topic
434 of debate (l'Anson Price et al 2019). It has proved surprisingly hard to identify contexts in which waggle-
435 dancing—the key communication system that underlies collective decision-making—improves colony
436 foraging success. Attempts to do so have typically involved manipulations that render the spatial

437 information provided by dances meaningless, which sometimes negatively impacts food collection in
438 more patchy challenging landscapes (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Donaldson-
439 Matasci et al 2013), but not universally so (Donaldson-Matasci and Dornhaus 2012; Nürnberger et al 2017;
440 l’Anson Price et al 2019). Such manipulations are laborious to perform at scale (but see Nürnberger et al
441 2017), and identifying those circumstances under which dance followers choose to use the information in
442 dances may represent a fruitful alternative. For example, as we described above, Hasenjager et al 2020
443 used NBDA to show that dances drive bees to food when they move between similar forage sources;
444 extending this paradigm to transitions between food sources that differ in their scents (mimicking
445 between-species shifts) might find dances to be less important and hence highlight a need for rapid
446 within-species (*cf* between-species) shifts between flowering trees as a potential driver of dance
447 evolution.

448 While current computer vision approaches for long-term tracking of honeybee behaviour are
449 providing unprecedented access to the social lives of bees (Wario et al 2017; Gernat et al 2018; Wild et al
450 2021), many signals and cues that are employed by honeybees cannot be captured by visual-based
451 methods (Seeley 1998), including forager-produced pheromones (Thom et al 2007), acoustic signals
452 broadcast by queens (Michelsen et al 1986), and electrostatic charge accumulated during flight and other
453 activities (Greggers et al 2013). Developing methods that would allow for integrating these and other
454 forms of interaction into network models could further enhance understanding of honeybee collective
455 organization. Potentially promising approaches include integrating visual tracking with automated
456 monitoring of other sensory modalities (vibrational: Ramsey et al 2018; electrostatic: Paffhausen et al
457 2021), incorporation of stigmergic interactions (Richardson and Gorochowski 2015), and network-based
458 extensions that explicitly allow for the type of one-to-many interaction involved in broadcasting
459 pheromones (Greening et al 2015).

460 The wealth of research that has focused on honeybee signalling behaviour since the work of von
461 Frisch and his students in the mid-20th Century (von Frisch 1967) is impressive. This body of work has
462 documented in detail the individual-level impacts of signals at the dyadic level, and discussed (or in some
463 cases modelled) how such impacts scale up to the colony level (Seeley 1995; Nieh 2010; Couvillon 2012;
464 Kietzman and Visscher 2015). Now, network approaches offer a toolkit that may link individual and group-
465 level behaviour. Network analysis can help identify whether signals have multiple functions, and how
466 different signals overlap in functionality, thereby contributing to understanding how colony-level
467 responses remain robust across diverse environmental contexts and despite substantial variation in
468 worker experiences (Hebets et al 2016; Hasenjager et al 2020). In other words, the honeybee colony is a
469 complex system whereby signals interact and feed back into one another to control group behaviour, and
470 network science offers a means to both make sense of these previously impenetrable mechanisms and to
471 understand how selection shapes communication systems within a highly eusocial group.

472

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479

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703

704

705 **Figure Legends**

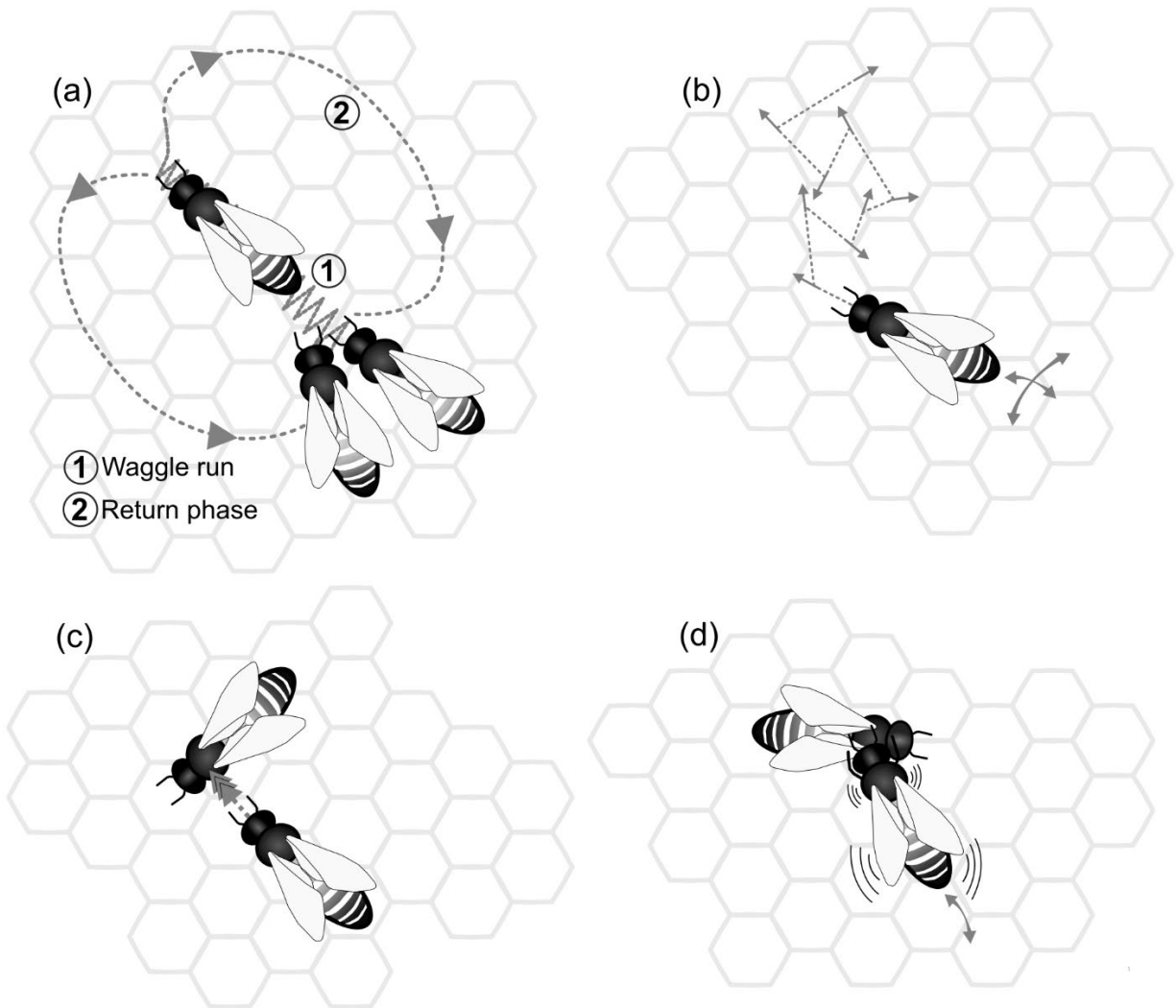
706 **Fig 1** Four key signals employed by honeybees during collective foraging: (a) Waggle dances are composed
707 of information-rich waggle runs separated by return phases (often alternating to the left and right); (b)
708 During a tremble dance a honeybee travels in an erratic trajectory across the comb while vibrating its
709 body side-to-side and occasionally front-to-back; (c) The stop signal involves the signaller “headbutting”
710 a receiver while simultaneously producing a brief pulse of sound; (d) When giving the shaking signal, a
711 worker grasps hold of a nestmate and vibrates her own body dorsoventrally.

712
713 **Fig 2** A multilayer network of four individuals encompassing three behaviours and two time periods.
714 Within a particular layer (denoted by the shaded parallelograms) individuals are represented by nodes,
715 and interactions between them by solid lines. Each row corresponds to a different form of interaction
716 (waggle dances tremble dances stop signals) and columns correspond to time periods. Individuals are
717 connected to themselves within and across time periods via interlayer edges (dotted lines).

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720 **Figures**

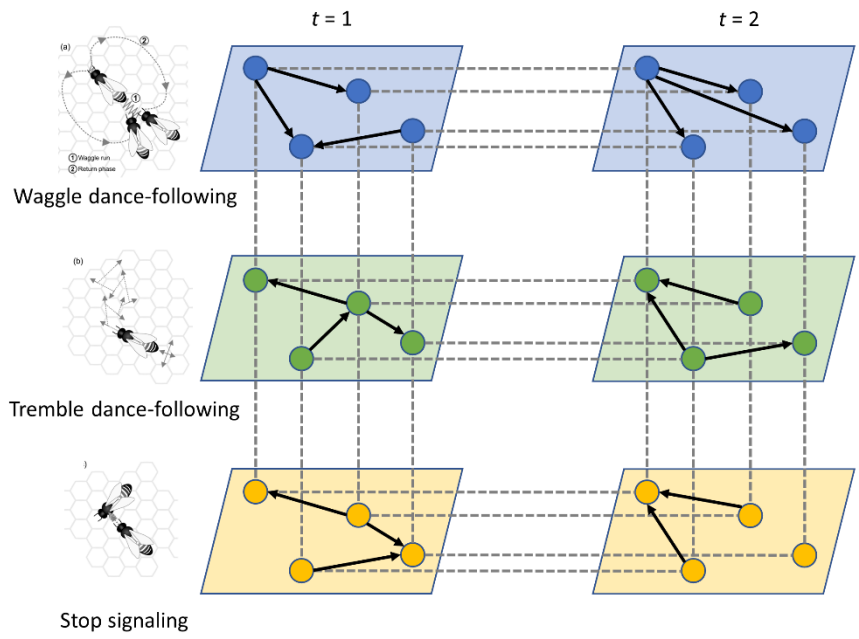
721 Figure 1



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724 Figure 2



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727 **Tables**728 **Table 1** Example questions that could be addressed using social network approaches

Questions	Network approaches	References
(1) Are there individual differences in the propensity to produce or receive particular signals (eg tremble dances stop signals)?	Centrality metrics	Farine and Whitehead 2015
(2) Are individual differences in signalling behaviour correlated across different types of signals?	Multidegree	Bianconi 2013
(3) How stable are individual differences in signaller or receiver behaviour?	Temporal networks	Blonder et al 2012
(4) How do signalling interactions at one point in time shape future interaction patterns within and across communication pathways?	Co-evolving multiplex networks	Bonnell et al 2021; Vijayaraghavan et al 2015
(5) What role do receivers play in modulating signal production duration or efficacy?	Temporal networks; simplicial complexes	Blonder et al 2012; Greening et al 2015
(6) Which communication pathway or combination of pathways best correlates with individual behaviour (eg task performance)?	Compartmental models; NBDA; experience-weighted attraction models	Barrett et al 2017; De Domenico et al 2016; Hasenjager Leadbeater et al 2021
(7) How strongly coupled are interaction patterns across different signalling systems?	Global overlap	Bianconi 2013

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