



# From dyads to collectives: a review of honeybee signalling

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## Abstract

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

**Keywords** Waggle dance · Tremble dance · Stop signal · Shaking signal · Honeybee social networks

## Introduction

The honeybee waggle dance is arguably one of the most celebrated examples of communication within the field of animal behaviour, and certainly one of the most fascinating. This symbolic communication system was observed potentially as far back as the fourth century BC by Aristotle (Haldane 1955), but it was not until the twentieth century that the meaning of these dances was finally deciphered by Karl von Frisch (von Frisch 1967), earning him a share of the 1973 Nobel Prize in Physiology. For many students of Animal Behaviour, the waggle dance is familiar as a means by which individual honeybees can reduce investment in searching for food and exploit the benefits of foraging alongside others

with closely aligned fitness interests. Perhaps less commonly understood are the mechanisms by which the dance, alongside other communication signals (e.g. tremble dances: Seeley 1992; stop signals: Nieh 1993; shaking signals: Schneider and Lewis 2004) and olfactory cues deriving from the scent of visited flowers (Farina et al. 2005; 2012), controls the collective foraging behaviour of the colony (Seeley 1995). The waggle dance does not act alone, but is just one information source in a series of potentially interacting signal networks that include positive and negative feedback loops and which direct colony behaviour such that the collective makes group-level “decisions” about how to allocate the workforce and where to send foragers.

While the key signals that underpin these group decisions have now been the focus of several decades of research (reviewed in Seeley 1995; Anderson and Ratnieks 1999; Couvillon 2012; Kietzman and Visscher 2015), attempts to study the information flow networks that arise from them have been logistically challenging. Tracking even a small proportion of the ~20,000 honeybees in a colony to detect individual signals, cues, responses and typical behavioural roles is a major hurdle of scale, while analysing the massive amounts of data that can arise from such work was almost impossible until recently (although see Biesmeijer and Seeley 2005). However, advances in both processing power and network theory have opened the door to understanding the

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behaviour of this complex system. In the first half of this review, we draw together the literature on key movement and vibration-based signals that are produced by foraging bees: the waggle dance, tremble dance, stop signal and shaking signal. In the second half, we go on to explain how network theory can provide a unique avenue for understanding how these signals translate behaviour from the individual to the colony level, introducing studies that have started to apply this approach.

## Honeybee signalling systems

### The waggle dance

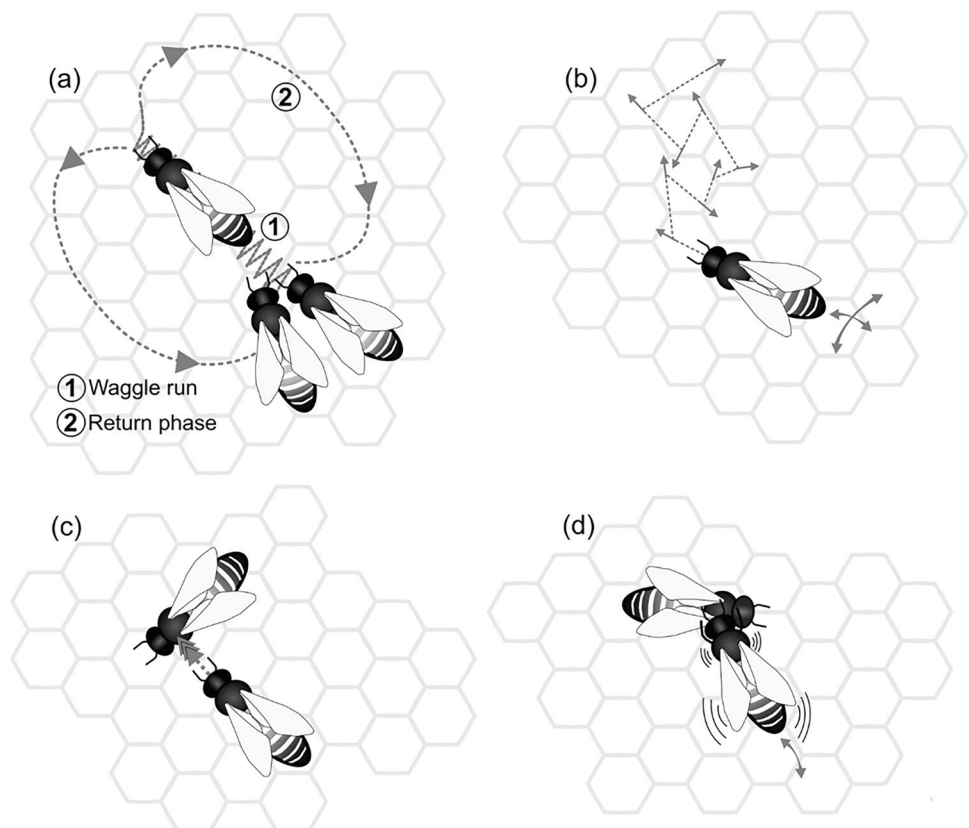
The waggle dance (von Frisch 1967) is arguably the single most well-known behaviour within the honeybee repertoire (Dyer 2002; Grüter and Farina 2009; Couvillon 2012). A waggle dance is made up of two alternating phases: a waggle run during which the forager moves in a straight line across the comb while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

with respect to gravity corresponds to the direction of the resource relative to the sun (von Frisch 1967).

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

Nonetheless, Gould pointed out that “only further work can establish whether the dance-language communication is common or rare under normal circumstances” (Gould 1975), and it is now well established that surprisingly little dance-following leads to arrival at a novel food source (Grüter and

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



Farina 2009). By tracking dance-following across foragers' lifetimes, Biesmeijer and Seeley (2005) estimated that under natural conditions, only 12–25% of dance-following interactions are for this purpose. The remaining 75–88% of dance-following interactions are thought to instead involve food sources that are already known by the dance-followers (Biesmeijer and Seeley 2005)—for example, after a period of interrupted foraging (e.g. nightfall), dance-following can reactivate experienced foragers to resume collecting from familiar patches (Johnson 1967; Gil and Farina 2002; Grüter et al. 2008; Hasenjager et al. 2020). Dance-following is often cursory under these circumstances (Gil and Farina 2002; Biesmeijer and Seeley 2005; Grüter et al. 2013), suggesting that foragers are unlikely to be seeking detailed spatial information (though see Wray et al. 2012). Indeed, bees very often ignore the spatial information altogether, following a dance but subsequently arriving at their own preferred site (Johnson 1967; Grüter et al. 2008; Hasenjager et al. 2020). When dancers do finally choose to seek out new sites, they engage in longer bouts of dance following (Grüter and Ratnieks 2011; Grüter et al. 2013; Hasenjager et al. 2022), presumably to obtain accurate spatial information. Dance-following, though critically important for locating the general vicinity of new foraging patches (Hasenjager et al. 2020), thus often seems to serve as a backup information source for foragers that know of no alternative patches (e.g. novice foragers or when a previously visited site is no longer profitable; Biesmeijer and Seeley 2005; Grüter and Ratnieks 2011; Grüter et al. 2013).

## The tremble dance

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

Seeley (1992) provided vital evidence for a relationship between nectar processing and elicitation of tremble dancing through a classic experiment in which he simultaneously trained two cohorts of foragers from the same hive to separate feeders, and then experimentally increased forager numbers collecting from one feeder.

Bees from the unmanipulated cohort started to tremble dance despite having experienced no change in the foraging conditions outside of the hive. The hive-internal cue that could indicate such a processing shortfall was suggested to be a delay in finding a bee to unload nectar on arrival, and indeed, the focal cohort experienced just such a delay. At the same time, Kirchner and Lindauer (1994) found that a number of experimental conditions that had been previously observed to also elicit tremble-dancing, such as capture at a food source, experiencing crowded feeders or collection of salty nectar, also led to unloading delays (potentially because nectar receivers detected alarm pheromone on the bodies of foragers or were unwilling to receive strange-tasting nectar). As a result, it seemed clear that unloading delays act to stimulate tremble dancing, and Seeley et al. (1996) later demonstrated that increases in nectar influx with associated tremble dancing subsequently lead to hive workers being recruited as nectar receivers. When a colony's nectar processing capacity rises as a result, the delay experienced by incoming foragers should decrease and tremble dancing should cease (Seeley 1995).

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

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

## The stop signal

When stop-signalling, a honeybee abruptly “headbutts” another individual and emits a brief high-pitched buzz by rapidly vibrating its thoracic muscles (Fig. 1c). The sound component of stop signals produces a distinctive waveform with a fundamental frequency of 350–450 Hz lasting approximately 150 ms (Kirchner 1993). Crucially, recipients “freeze” briefly, which is distinctive from other vibrational signals such as piping signals or begging calls (Pastor and Seeley 2005). In the context of foraging, tremble-dancing bees often also produce stop signals (Nieh 1993), but the association is not exclusive; indeed, under normal foraging conditions, the majority of stop signals appear not to be produced by tremble dancers but by bees that have recently followed dances (Pastor and Seeley 2005). They are often directed at waggle dancers (Nieh 1993; Pastor and Seeley 2005) but tremble dancers that produce stop signals also direct them to other tremble dancers, food exchangers, dance followers, and other bees (Nieh 1993).

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

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

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

## The shaking signal

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

In the context of foraging, most shaking signals are produced by foragers, often following previous foraging success (Nieh 1998; Biesmeijer 2003a). Shaking signals are often produced in lieu of waggle dances and following the first successful foraging trips of the day, when many bees in the hive remain relatively inactive (Seeley et al. 1998). In addition, bees that have experienced foraging success on previous days will often produce shaking signals even before they begin foraging (Biesmeijer 2003a). As a result, there is predictable diurnal variation in shaking signal production, with peaks of signalling activity preceding production of waggle dances (Nieh 1998; Biesmeijer 2003a; Ramsey et al. 2018). Shaking signal production is often especially pronounced after bees have experienced a dearth of forage (Seeley et al.



1998). The recipients of these forager-produced shaking signals are often younger and/or inactive bees (Lewis et al. 2002; Nieh 1998), yet as noted above, receiver responses can be highly idiosyncratic.

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

## From dyads to networks

While the signals described above, amongst a plethora of olfactory cues (von Frisch 1967; Farina et al. 2005; Thom et al. 2007), allow individual bees to find food more quickly, recruit nectar receivers and stop foraging when needed, they also produce colony-level foraging behaviour that extends beyond the sum of individual signalling dyads (Sumpter 2006). To provide an example of the somewhat abstract concept of collective decision-making, consider the means by which colonies “choose” between nectar sources without requiring that any single individual compare foraging sites. When a bee finds nectar forage that exceeds a threshold concentration (the value of which is determined by seasonal forage availability; von Frisch 1967), the dances that she performs on returning to the hive indicate its location but also reflect the energetic efficiency of the foraging trip. This is because more efficient trips (“efficiency” deriving from travel and collection time, factored by the calorific returns of sucrose collected) elicit more dance circuits than less efficient equivalents (Seeley

1994). As a result, dance-followers are more likely to encounter dances for those food sources, and thus are more likely to be recruited to them without requiring that any individual judges a particular food source to be “better” than an alternative (Seeley and Towne 1992). The colony, rather than the individual, makes a decision about where to allocate labour, collectively favouring closer and sweeter nectar sources.

A similar example can be found in the context of nest-site choice by swarms, whereby waggle dancers not only dance for the prospective nest sites that they have found (performing more dance circuits for higher-quality sites just as for forage; Seeley and Visscher 2008), but also administer stop signals to those dancers that advertise alternatives (Seeley et al. 2012). In combination, the two signalling networks achieve an outcome whereby information flows rapidly through the group, allowing recruitment to poor sites to be shutdown rapidly, and reducing the likelihood of deadlocks over similar sites. While the basic units that build this group-level behaviour are individual dyads—for example, a waggle dancer and a dance follower who may later become a dancer herself—the group itself is a complex system built through the properties of the networks that arise from such signals.

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

It was certainly possible to explore colony-level behaviour in social insects before a network-based toolbox became available (e.g. Heinrich 1981; Deneubourg et al. 1990; Seeley and Buhrman 1999; Mallon et al. 2001). It is therefore reasonable to ask whether network science can contribute to understanding the evolutionary function of honeybee signalling networks rather than simply describing the proximate mechanisms that give rise to colony behaviour. We propose that it can, for the following reasons. Firstly, as highlighted in the preceding sections, current empirical approaches have hit their limits in describing the basic biological “meaning” of some signals (e.g. receiver responses to the tremble dance and shaking signal are often highly idiosyncratic; Biesmeijer 2003b; Schneider and Lewis 2004). Network approaches can make sense of detailed interaction histories to remedy this issue. Relatedly, explaining why so much apparent redundancy exists in the system requires understanding of how signal types interact with one another synergistically, additively, or antagonistically, and network tools have been developed that can disentangle these effects (De Domenico et al. 2016; Hasenjager et al. 2021a). Finally, networks themselves are group-level behavioural phenotypes, and selection can shape them to achieve specific aims. Network science provides a variety of metrics to capture these structural features (see Table 1 for a list; Farine and Whitehead 2015) which can illustrate how selection may have acted to promote (or reduce) processes such as information flow, disease transmission or division of labour within groups, which would not be apparent through an individual-level approach (Otterstatter and Thomson 2007; Pinter-Wollman et al. 2011; Mersch et al. 2013; Hasenjager et al. 2020; Easter et al. 2022). We expand each of these points below, highlighting how current network approaches could be

used, introducing studies that have begun to explore these approaches, and discussing extensions to the approach that bring better fit to the honeybee system.

### Linking signals to outcomes

Inferring a signal’s function firstly requires an understanding of who produces it, who it is directed to, and how it changes their behaviour. When interactions involve hive-based bees, this can be challenging to achieve because it requires knowledge of pre-interaction behavioural history, and so age has typically been used as a proxy for behavioural role, based on temporal polyethism within honeybee workers (Free 1965). This method however cannot take into account the drastic variation amongst workers in developmental trajectories that reflects genetics, brood requirements, and external conditions. To remedy this, Wild et al. (2021) used automated tracking to follow a honeybee colony across 25 days, reconstructing the daily interaction networks for each individual and using them to identify the fine-scale behavioural role of each bee at distinct points in time. Importantly, tagging just 1% of the colony is sufficient to achieve strong performance in inferring individuals’ behavioural roles, and at 5%, performance is equivalent to that achieved by tagging the whole colony. Wild et al.’s methods offer a means to identify changes in activity patterns that follow exposure to particular signals, such as repeated tremble dances, stop signals or shaking signals. For example, such methods could prove useful in exploring the function of those stop-signals that are delivered to, or produced by, non-foraging bees, or of those tremble dances that are produced in a predation context. This approach could also facilitate investigation into how shaking signals influence task allocation, given that their

**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 (e.g. 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 (e.g. task performance)?	Compartmental models; NBDA; experience-weighted attraction models	Barrett et al. 2017; De Domenico et al. 2016; Hasenjager et al. 2021a
(7) How strongly coupled are interaction patterns across different signalling systems?	Global overlap	Bianconi 2013

effects on receiver behaviour are thought to heavily depend on individuals' past experiences and may only manifest some time after the interaction has occurred (Schneider and Lewis 2004). However, perhaps the most exciting potential application of Wild et al.'s approach lies in its potential to capture interactions between signals whereby the impact of one signal depends upon whether a bee has received another. By making available the entire behavioural history of each individual, synergistic and antagonistic effects between signals could be investigated (e.g. using a multilayer network framework, which we return to in the next section).

Network science also offers a means to quantify responses to signals, through a technique called network-based diffusion analysis (NBDA; Franz and Nunn 2009; Hoppitt et al. 2010). The core assumption underlying NBDA is that if a particular type of interaction transmits information, then the corresponding network of interactions should predict the order in which individuals begin to express a related behavioural trait. For example, all else being equal, foragers that follow more waggle dance circuits for a given site (and thus are more strongly connected in the dance-following network) are expected to locate that site sooner than individuals that follow fewer circuits. The more closely that the pattern of arrivals follows this dance-following network, the stronger the estimated social transmission effect of dance-following. Crucially, multiple network types can be included in an NBDA, allowing researchers to address their relative contribution to a given response (Table 1). For example, although it has long been established that bees are capable of using the spatial information in waggle dances, it is equally well-established that olfactory cues are also key in directing bees towards food (Gould 1975; Johnson 1967; Riley et al. 2005; Grüter et al. 2008), and we have recently employed NBDA to quantify the relative contribution of waggle dance communication and olfactory cues in aiding recruits in locating new forage sites (Hasenjager et al. 2020).

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

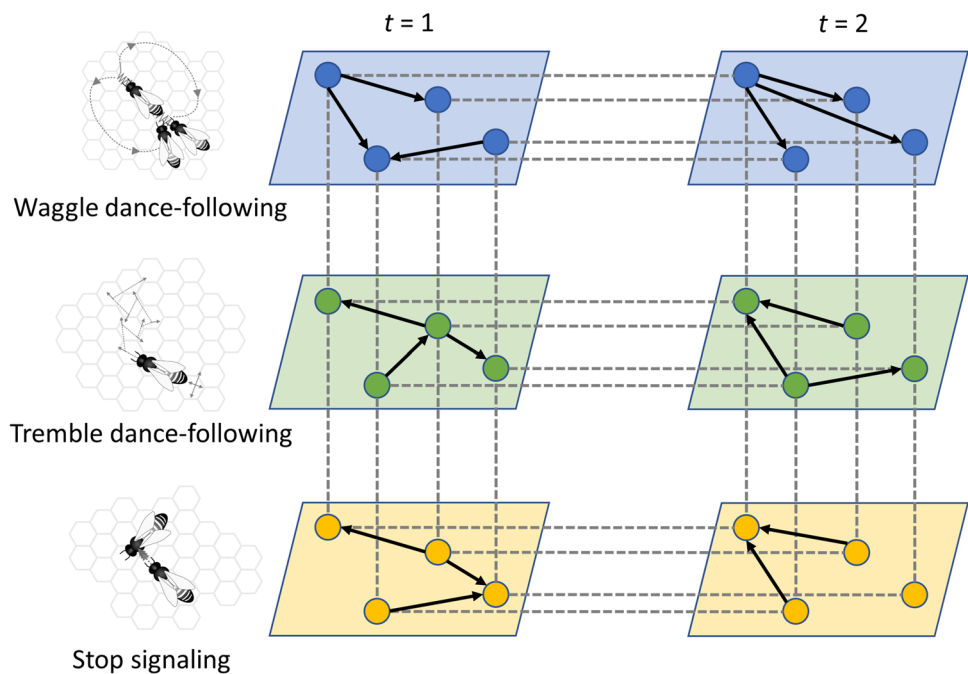
Traditionally, network analysis has often relied upon static networks that ignore the order in which interactions occur—an approach that makes sense when studying, for example, stable social relationships, but not when studying the consequences of signalling interactions (Blonder et al. 2012; Farine 2018). Thus, applying NBDA to honeybee signalling required that we use networks that could change over time (Hasenjager et al. 2020; 2021a). Two principal approaches have been developed to model temporal networks: time-aggregated networks, which are essentially a series of static networks, and time-ordered networks, which yield a complete record of all interactions at all time points (reviewed in Blonder et al. 2012; Hasenjager et al. 2021a). Which approach is more useful will often depend on the research question. For example, time-aggregated networks could be used to evaluate whether particular honeybee foragers consistently occupy central positions in a signalling (e.g. dance-following) network across multiple days, whereas investigating the potential role of receivers in modulating the production duration or efficacy of forager signals is likely to benefit from the more fine-grained time-ordered approach (Table 1). It is also possible to represent a time-aggregated network as a multilayer network, where each layer represents a different time window (Finn et al. 2019; Fisher and Pinter-Wollman 2021). We discuss the concept of multilayer networks which capture combinations of different signals in the next section.

## Understanding interactive effects

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

To this end, animal network studies are no longer limited to networks in which all connections represent the same form of interaction (e.g. trophallaxis, spatial proximity), or in which an aggregated behavioural measure is generated from multiple interaction types. Instead, multilayer network approaches combine multiple networks into a single

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



mathematical structure while maintaining the distinctiveness of each network type (i.e. layer; Silk et al. 2018; Finn et al. 2019; Hasenjager et al. 2021a). For example, a multilayer network can be constructed in which each layer is a network capturing a different interaction type (e.g. waggle dances, tremble dances, stop signals), with individuals connected to themselves across layers (Fig. 2). A multilayer framework enables researchers to address questions that are not accessible using traditional monolayer approaches (Table 1). For example, one could ask: is an individual's role in applying negative feedback on waggle dance-based recruitment via stop signals best captured by its network position in the stop-signal layer alone, or by a measure of multilayer centrality (e.g. eigenvector versatility; De Domenico et al. 2015) that simultaneously incorporates information on its connectivity in the stop-signal layer and its targets' connectivity in the waggle-dance layer? In other words, do only the stop-signallers need to be well-connected to transmit their information effectively, or do they also need their waggle dancing recipients to be well-connected too? Multilayer approaches could also be used to investigate how strongly interaction dynamics are coupled across layers and whether the strength of this coupling varies across contexts (Bianconi 2013; Table 1). For example, both tremble-dances and stop-signals have been implicated in slowing forager recruitment (Seeley 1992; Nieh 1993) yet also appear to have additional potentially unrelated functions (Nieh 1993; Seeley et al. 1996). Comparing the structure of these networks within and across contexts could highlight conditions in which their functions align or diverge. Finally, multilayer representation of different

network types can be further combined with an additional set of layers that capture each time window (Fig. 2), enabling investigation into how interactions at one point in time (e.g. tremble dancing, stop-signalling) may cascade out to influence interaction patterns within and across layers (e.g. waggle dance-following) at subsequent time points (Bonnell et al. 2021; Table 1).

### Adaptive structure of honeybee networks

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

Among-individual variation in behaviour has also often been associated with enhanced collective outcomes, including increased foraging rate and colony productivity in honeybees and other social insects (Jandt et al. 2014;



O'Shea-Wheller et al. 2021). Network theory offers a variety of metrics that can capture this variation and link it to group-level behaviour (Farine and Whitehead 2015; Table 1). For example, eigenvector centrality accounts for both an individual's direct connections and how well-connected its network neighbours are, and thus can reflect a worker's importance in transmitting information throughout the network. Such metrics can be further combined with simulation modelling to predict and evaluate potential mechanisms of how observed patterns of variation influence colony dynamics (Gordon 2010; Gernat et al. 2018). For instance, previous research suggests that highly interactive individuals can emerge as network hubs with acceleratory effects on signal propagation (Pinter-Wollman et al. 2011). What might be the potential consequences for collective processes if such "hub"-like individuals are present across different signalling networks with potentially synergistic (e.g. tremble dances and shaking signals) or antagonistic (e.g. waggle dances and stop signals) effects (Table 1)? Predictions generated from models can subsequently be tested through experiments that manipulate worker variation and/or signal production (e.g. removal of foragers with high centrality vs low centrality; Crall et al. 2018; artificial production of signals: Koenig et al. 2020). Multilayer network approaches also enable further comparison of individual variation within and across signalling systems. Are networks that are constructed from different signalling systems similarly organized? Is a forager's importance in the network correlated or highly variable across different signalling layers? How stable is a worker's centrality in the network over time?

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

## Discussion

On an evolutionary level, the ultimate value of collective foraging by honeybees remains a topic of debate (I'Anson Price et al. 2019). It has proved surprisingly hard to identify contexts in which waggle-dancing—the key communication system that underlies collective decision-making—improves colony foraging success. Attempts to do so have typically involved manipulations that render the spatial information provided by dances meaningless, which sometimes negatively impacts food collection in more patchy, challenging landscapes (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Donaldson-Mataschi et al. 2013), but not universally so (Donaldson-Mataschi and Dornhaus 2012; Nürnberger et al. 2017; I'Anson Price et al. 2019). Such manipulations are laborious to perform at scale (but see Nürnberger et al. 2017), and identifying those circumstances under which dance followers choose to use the information in dances may represent a fruitful alternative. For example, as we described above, Hasenjager et al. (2020) used NBDA to show that dances drive bees to food when they move between similar forage sources; extending this paradigm to transitions between food sources that differ in their scents (mimicking between-species shifts) might find dances to be less important and hence highlight a need for rapid within-species (*cf* between-species) shifts between flowering trees as a potential driver of dance evolution.

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

The wealth of research that has focused on honeybee signalling behaviour since the work of von Frisch and his students in the mid-twentieth century (von Frisch 1967) is

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

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## Declarations

**Competing interests** The authors declare no competing interests.

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