

Automated monitoring of behavior reveals bursty interaction patterns and rapid spreading dynamics in honeybee social networks

Tim Gernat^{a,b}, Vikyath D. Rao^{a,c}, Martin Middendorf^b, Harry Dankowicz^d, Nigel Goldenfeld^{a,c}, and Gene E. Robinson^{a,e,f,1}

^aCarl R. Woese Institute for Genomic Biology, University of Illinois at Urbana–Champaign, Urbana, IL 61801; ^bSwarm Intelligence and Complex Systems Group, Department of Computer Science, Leipzig University, 04109 Leipzig, Germany; ^cDepartment of Physics, University of Illinois at Urbana–Champaign, Urbana, IL 61801; ^dDepartment of Mechanical Science and Engineering, University of Illinois at Urbana–Champaign, Urbana, IL 61801; ^eNeuroscience Program, University of Illinois at Urbana–Champaign, Urbana, IL 61801; and ^fDepartment of Entomology, University of Illinois at Urbana–Champaign, Urbana, IL 61801

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Social networks mediate the spread of information and disease. The dynamics of spreading depends, among other factors, on the distribution of times between successive contacts in the network. Heavy-tailed (bursty) time distributions are characteristic of human communication networks, including face-to-face contacts and electronic communication via mobile phone calls, email, and internet communities. Burstiness has been cited as a possible cause for slow spreading in these networks relative to a randomized reference network. However, it is not known whether burstiness is an epiphenomenon of human-specific patterns of communication. Moreover, theory predicts that fast, bursty communication networks should also exist. Here, we present a high-throughput technology for automated monitoring of social interactions of individual honeybees and the analysis of a rich and detailed dataset consisting of more than 1.2 million interactions in five honeybee colonies. We find that bees, like humans, also interact in bursts but that spreading is significantly faster than in a randomized reference network and remains so even after an experimental demographic perturbation. Thus, while burstiness may be an intrinsic property of social interactions, it does not always inhibit spreading in real-world communication networks. We anticipate that these results will inform future models of large-scale social organization and information and disease transmission, and may impact health management of threatened honeybee populations.

trophallaxis | temporal network | burstiness | barcode | tracking

Social life depends on intricate networks of interactions among conspecifics. This is especially true for highly social animals, such as humans and eusocial insects, who use these interactions to coordinate their activities (1, 2). Network science has provided a wealth of insights about how interaction patterns impact coordination, information exchange, and disease transmission in animal societies (e.g., refs. 3 and 4). Recently, this knowledge has been further enhanced by the use of temporal network models, which, in addition to representing individuals and their social connections, also record when the connections between individuals are active (5, 6). Temporal networks thus acknowledge that the connection between linked individuals is only available while these individuals interact and crucially account for the temporal ordering of interactions, making them particularly relevant for models of disease and information spreading (5, 6).

Spreading simulations are a powerful approach to quantifying how well an empirical temporal network supports transmission processes. Instead of tracking a particular piece of information or disease, such simulations probe the structure of the observed network and, by comparison against a randomized reference model, provide insight into how spreading dynamics reflect social interactions (5). For example, analysis of susceptible-infected (SI) spreading simulations on networks of face-to-face contacts, mobile phone calls, email, and internet communities revealed that in these

networks spreading is slower than expected (5–10), suggesting that they are not optimized for fast information or disease transmission.

The speed of spreading on a social network depends on the interplay of a variety of factors, such as its topology and the timing of successive contacts (5, 8). Human communication networks are characterized by an intermittent, unpredictable timing of interactions, with time intervals between successive social contacts described by a heavy-tailed distribution (burstiness) (8–11). Network theory predicts that the interplay of burstiness and other network properties could accelerate spreading (12–14). However, no fast and bursty human communication networks have been reported, and in other animal societies there are very few studies of temporally highly resolved communication networks that were conducted over long enough timescales to be able to explore the relationship between burstiness and spreading dynamics (15, 16).

We studied burstiness and spreading dynamics in the honeybee (*Apis mellifera*), a highly accessible and easily manipulated model system for social behavior and communication. Honeybees form large societies with tens of thousands of individuals, coordinated

Significance

Interaction patterns in human communication networks are characterized by intermittency and unpredictable timing (burstiness). Simulated spreading dynamics through such networks are slower than expected. A technology for automated recording of social interactions of individual honeybees, developed by the authors, enables one to study these two phenomena in a non-human society. Specifically, by analyzing more than 1.2 million bee social interactions, we demonstrate that burstiness is not a human-specific interaction pattern. We furthermore show that spreading dynamics on bee social networks are faster than expected, confirming earlier theoretical predictions that burstiness and fast spreading can co-occur. We expect that these findings will inform future models of large-scale social organization, spread of disease, and information transmission.

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Data deposition: Temporal network datasets were submitted as [Dataset S1](#) and are also publicly available at www.beemonitoring.igb.illinois.edu.

¹To whom correspondence should be addressed. Email: generobi@illinois.edu.

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via frequent information exchanges that are in part mediated by social interactions (17). One of these interactions is “trophallaxis,” during which two bees touch each other with their antennae while orally transferring liquid food (18). In honeybees and other social insects, all colony members engage in trophallaxis extensively (19–22) and it takes place more often than expected if its sole purpose is feeding (19). Trophallaxis has been implicated in disease transmission (23–25) and communication (17, 26), and recent findings report the occurrence of several types of communication-related molecules in trophallaxis fluid (27). Honeybee trophallaxis is thus an excellent system for exploring the relationship of burstiness and spreading in a nonhuman animal society, permitting a cross-species comparison with human communication networks. This comparison enables us to explore whether highly social animals have similar interaction patterns and whether their networks function in a similar way.

We developed a method to automatically monitor trophallaxis with high spatiotemporal resolution over extended periods of time (Figs. 1–3 and *SI Materials and Methods*). Similar to other high-throughput approaches for tracking insects (15, 28–30), we based our method on a custom matrix barcode, called “bCode” (Fig. S1). Attached to the thorax, bCodes enabled reliable identification and tracking of every individual in a colony from sequences of digital images (*SI Materials and Methods*). To detect trophallaxis, our software first uses information about each bee’s position and orientation to identify pairs of bees that were in the proper position (Fig. 2). Custom computer vision algorithms then determine for each pair the exact position, shape, and orientation of the bees’ heads (Fig. S2) and verify trophallaxis by confirming that the heads are connected by a shape that resembles a proboscis (tongue) or antenna (Fig. 3).

We monitored five honeybee colonies for 8–11 d each (Table S1). To standardize the colonies, they were each established with 1,200 1-d-old adult worker bees and a queen. Such colonies have been shown to develop the basic elements of colony social organization despite an atypical age demography (31). Bees were housed in a single-sided, glass-walled observation hive designed to prevent them from obscuring each other’s barcodes (Fig. S3). The observation hive was kept in a dark, temperature-controlled room (Fig. 14) and connected to the outside for normal foraging. Barcoded bees were imaged once per second by a computer-controlled high-resolution camera under infrared light invisible to the bees (32).

Results and Discussion

Trophallaxis interactions were analyzed as temporal networks (5), with nodes representing individuals, and time-stamped edges connecting nodes if the corresponding individuals interacted at least once. These networks revealed that honeybee interactions are bursty, as seen in the distribution of waiting times τ between successive interactions of individual bees (Fig. 4A and Fig. S4A). This distribution can be represented by a power law fit $P(\tau) \sim \tau^{-\alpha}$ (Fig. 4A, Table 1, and Fig. S4A), although other functional forms are also possible. Most importantly, this distribution is not consistent with an exponential or other short-tailed distribution expected from a memoryless process, suggesting the presence of non-Markovian, long-ranged temporal correlations whose origin is presently unclear. By contrast, the waiting times in ensembles of 100 temporally randomized networks, in which the times of the original interactions were randomly permuted, were approximately exponentially distributed (Fig. 4A and Fig. S4A). The coefficient of burstiness for honeybee networks (Table 1) was similar to that observed for human telephone and email communication (33), demonstrating a striking parallel between the interaction patterns of both species.

Since bursty interactions have been associated with slow spreading dynamics in human communication networks, we expected that spreading in the bee networks is also inhibited. To test this hypothesis, we simulated spreading in each empirical trophallaxis network

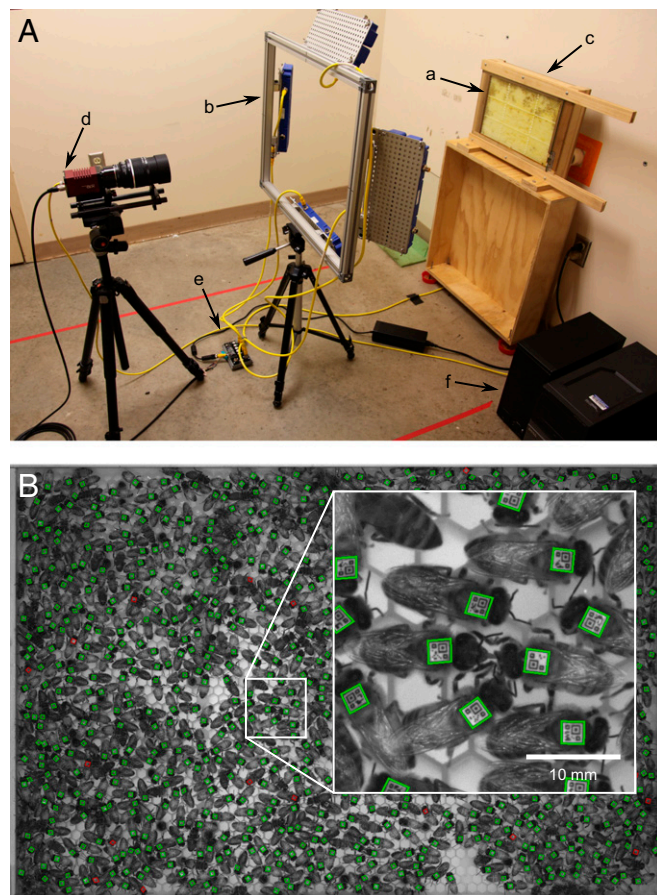
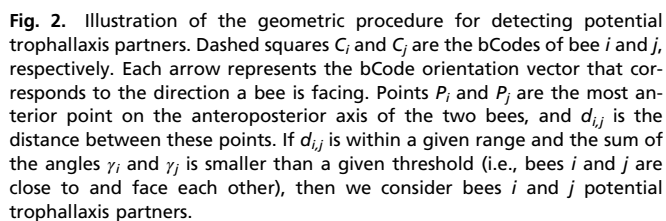


Fig. 1. Assay for automatically monitoring social interactions (trophallaxis) in honeybee colonies. (A) Experimental setup. Bees were housed in a glass-walled observation hive (a) that contained a one-sided honeycomb and was connected to a hole in the wall allowing unlimited access to the outdoors for foraging. The hive was illuminated with eight infrared LED lights mounted on an aluminum frame (b). To facilitate automatic image analysis, the honeycomb was backlit with an array of infrared lights mounted behind the hive (c, hidden). Images were recorded with a high-resolution monochrome camera (d) that controlled the infrared lights via a breakout board (e). A standard personal computer (f) controlled the camera and stored images. Some cables are omitted for visual clarity. (B) Typical image obtained from this system, showing barcoded bees inside the observation hive. Outlines reflect whether a barcode could be decoded successfully (green), could not be decoded (red), or was not detected (no outline). The hive entrance is in the lower-right corner. (Inset) Close-up of two bees that were automatically detected performing trophallaxis.

and in the ensembles of temporally randomized networks, using the deterministic SI model (34) (see *Materials and Methods* for details). This model is commonly used to explore how well the temporal pattern of human social contacts supports spreading processes through a network (reviewed in refs. 5 and 7), enabling us to readily compare results across species.

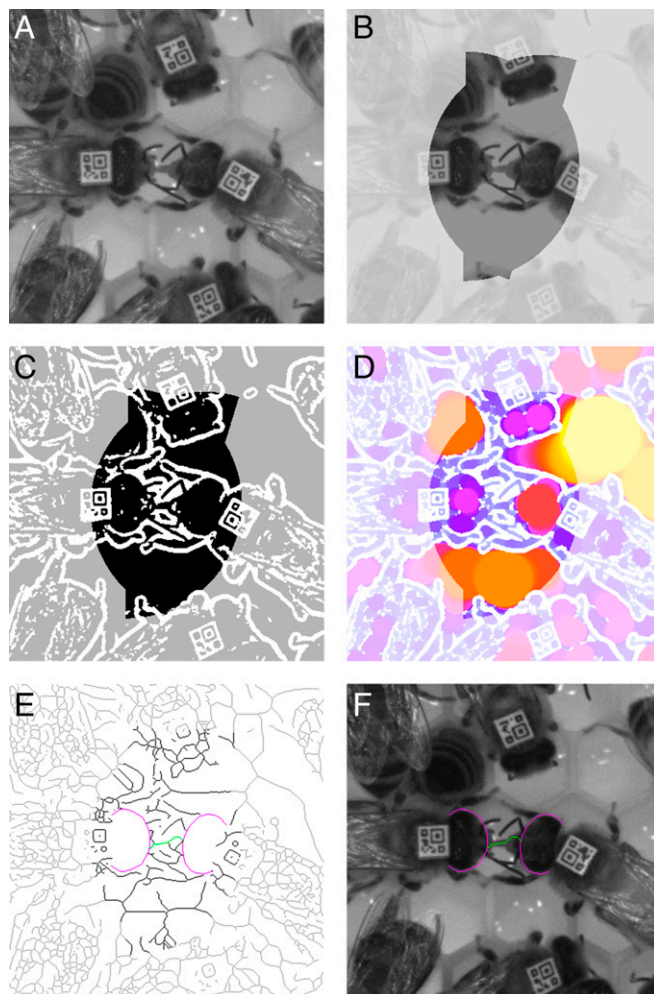
In contrast to human communication networks, spreading was faster in the bee networks than in the temporally randomized reference networks (Fig. 4B and Fig. S4B). The difference in prevalence varied over time (Fig. S5), with accelerated spreading seen until most individuals ($\bar{p} = 78.2 \pm 7.3\%$, mean \pm SD, $n = 5$) were “infected” (Fig. 4B, Table 1, and Fig. S4B). Following ref. 8, we used the time at which 20% of the bees were “infected” to quantify spreading speedup. Spreading was almost 50% faster than in the corresponding ensemble of randomized reference networks ($s = 46.7 \pm 13.7\%$, $n = 5$; conditional uniform graph test, $n = 100$, $P < 0.01$ for all trials) (Fig. 4C, Table 1, and Fig. S4C).



To test whether the speedup of spreading is resilient to perturbation, we collected returning foraging bees as they attempted to reenter their hives on the seventh day of the experiment; 13–46% of each colony was depopulated (Table S1). In all five trials, spreading continued to be faster in bee networks constructed from the interactions that took place on the day after the forager removal relative to the temporally and topologically randomized reference networks (conditional uniform graph test, $n = 100$, $P < 0.01$ for all trials). This demonstrates that accelerated spreading is robust to a strong perturbation and manifests even on the timescale of a single day. We speculate that the observed resiliency is in part rooted in individual anonymity in the hive; social insect workers living in large colonies apparently do not recognize each other as individuals (35). This means that bees interact opportunistically, which likely contributes to the resiliency of the trophallaxis network.

We have discovered a strong similarity (burstiness) between the temporal structure of communication networks of honeybees and humans. A similarity in species separated by over 600 million years of evolution likely reflects a fundamental property of social interactions. However, despite this commonality, the networks of the two species appear to operate differently in terms of spreading

Although in our simulations most bees were “infected” quickly, spreading dynamics exhibited an interesting dichotomy. On short timescales, spreading was faster than expected while on longer



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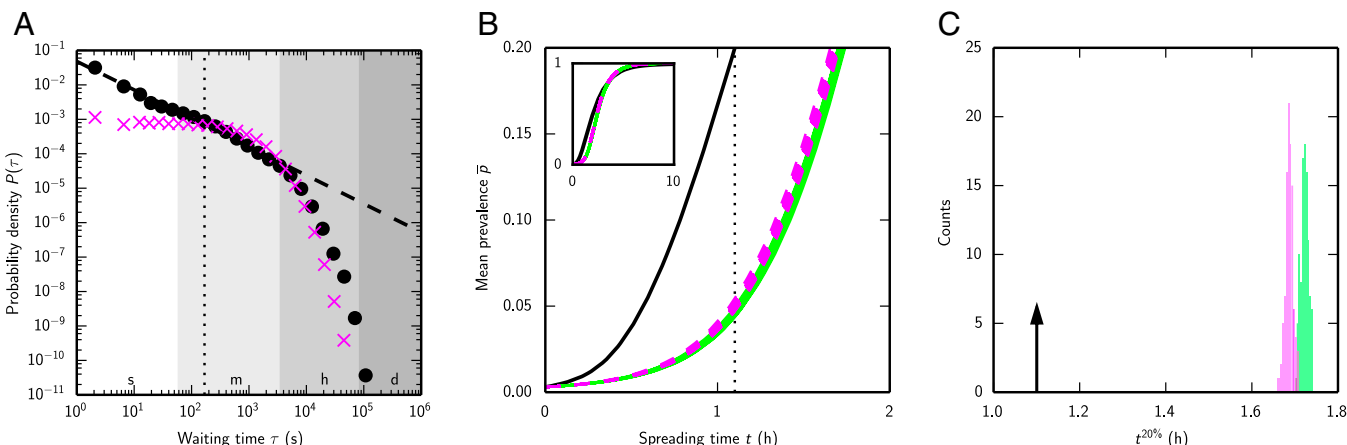


Fig. 4. Simulated spreading in honeybee trophallaxis networks is faster than in randomized reference networks, despite bursty interaction patterns. Panels show data from trial 1; see Fig. S4 for trials 2–5, which yielded similar results. (A) Distribution of log-binned waiting times between interactions for the empirical network of trial 1 (black circles) and 100 temporally randomized reference networks (magenta crosses). Dashed line: power law fit to the empirical waiting times (see Table 1 for exponents of the fit). The dotted line highlights the threshold $W = 168$ s that distinguishes short waiting times from long waiting times. (Lanes labeled s, m, h, and d denote seconds, minutes, hours, and days, respectively). (B) Mean fraction of bees “infected” via deterministic SI spreading (mean prevalence, controlled for mortality), averaged over 1,000 simulation runs, as a function of spreading time. Solid black line: empirical trophallaxis network; magenta dashed lines: 100 temporally randomized reference networks; green lines: 100 temporally and topologically randomized reference networks; dotted black line: time when the mean prevalence reaches 20% in the empirical network. (Inset) Mean prevalence as a function of spreading time until almost all bees have been “infected.” (C) Histogram of the mean time required to reach 20% prevalence ($t^{20\%}$) for the 100 temporally randomized reference networks (magenta) and the 100 temporally and topologically randomized reference networks (green). Arrow indicates when the prevalence reaches 20% in the empirical network.

timescales it was inhibited. Such spreading dynamics were also observed in *Temnothorax rugatulus* ants (36) but with a different reference model. Although the ant spreading dynamics were classified as slow, the early-time behavior appears qualitatively similar to our results (see figure 2 in ref. 36). It is therefore tempting to speculate that dichotomous spreading dynamics may be characteristic of highly social insects.

At first blush, one might hypothesize that the spreading dichotomy observed here could be the result of the bee's inability to structure social interactions so as to reach everyone quickly, or a reflection of their ability to respond differently at different timescales, for example in the context of foraging. In the latter viewpoint, the trophallaxis network could play a role in mediating different response times by communicating changes in food resource availability quickly to foragers, but more slowly to hive bees. However, we caution against interpreting our results in this way, because the apparent inhibition at long timescales naturally follows from the fact that the waiting time probability density is fat-tailed, so that the approach to saturation is generally slower than for a purely memoryless process (13, 14). Thus, the dichotomous spreading dynamics might be an epiphenomenon of the heavy-tailed waiting time distribution discovered here and remains to be understood more fully in future theoretical work.

A social network that supports spreading well can be expected to benefit communication and coordination, but also the transmission of disease. Accelerated spreading is therefore seemingly at odds with some ideas of organizational immunity, which predict that interactions among members of insect societies should be structured to slow down disease transmission (37). Perhaps honeybee colonies self-organize to achieve a trade-off—fast information spreading and reduced disease transmission—by dynamically adapting interaction patterns to the health status of individual bees. The techniques we reported here will allow researchers to study this and other topics related to the mechanisms and ecology of communication networks in nonhuman societies.

Materials and Methods

Experiments. Colonies were established with 1,200 barcoded, 1-d-old worker bees and one unrelated, naturally mated queen that was also barcoded. Each colony was provided with the same amount of honey and artificial “bee

bread.” We provided sufficient honey to feed the entire colony for the duration of the experiment and enough bee bread for 2 d. After sundown on the second or third day of the experiment, we opened the hive entrance to allow workers to begin foraging. Five days later, we removed as many foragers as possible from the colony. We performed five separate trials of this experiment in summer and autumn of 2013. Further details are described in [SI Text](#).

Networks. We constructed one temporal network from the trophallaxis detections in each trial. Each node in such a temporal network corresponds to one bee. Pairs of distinct nodes (i, j) were connected with an undirected edge if the corresponding individuals interacted at least once during the observation period. We assigned a list of elapsed times $\theta_{i,j}$, counting from the beginning of the experiment and with a resolution of 1 s, to each edge to specify when each trophallaxis contact was initiated. These times enabled our spreading simulations to maintain the precise time order of interactions.

Bees that did not interact were not included in the networks. This led to the omission of at most one individual per trial. In the networks used in the primary analysis, the queen was always excluded, because social interactions with the queen are different from worker–worker interactions (17) in ways that resulted in a high number of false-positive trophallaxis detections (*SI Text*). However, to explore the sensitivity of our results to the exclusion of the queen, we also performed a subset of our analyses on networks in which interactions with the queen were retained (*SI Text*).

Burstiness. Bursty event sequences follow non-Poissonian statistics, characterized by bouts of rapidly occurring events that are separated by potentially long periods of inactivity. To quantify the burstiness of trophallaxis, we considered the

Table 1. Honeybee trophallaxis network features

Trial	V	E	I	T, d	B	α	s	c	\bar{p}
1	1,164	200,723	302,221	11	0.33	1.18	0.53	3.99	0.82
2	1,140	143,571	205,787	8	0.32	1.18	0.44	3.21	0.73
3	1,138	129,653	191,795	9	0.27	1.18	0.24	1.92	0.68
4	1,174	174,317	259,923	10	0.34	1.18	0.57	4.21	0.83
5	1,170	212,685	329,170	10	0.39	1.19	0.56	4.06	0.85

For each trial we show: the number of nodes (V), edges (E), and interactions (I); sampling time in days (T); burstiness coefficient of trophallaxis (B); exponent of the power law fit to the waiting time distribution (α); speedup of spreading in terms of time (s) and mean prevalence (c); and grand mean prevalence at the end of the period of accelerated spreading (\bar{p}).

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