Revealing the structure of information flows discriminates similar animal social behaviors

Gabriele Valentini[1], Nobuaki Mizumoto[2], Stephen C. Pratt[2,6], Theodore P. Pavlic[2,3,4,5*◦], Sara Imari Walker[1,3,6*◦]

[1]Arizona State University, School of Earth and Space Exploration, Tempe, AZ 85827
[2]Arizona State University, School of Life Sciences, Tempe, AZ 85287
[3] Arizona State University, Beyond Center for Fundamental Concepts in Science, Tempe, AZ 85287
[4] Arizona State University, School of Computing, Informatics, and Decision Systems Engineering, Tempe, AZ 85287
[5]Arizona State University, School of Sustainability, Tempe, AZ 85287
[6]Arizona State University, ASU–SFI Center for Biosocial Complex Systems, Tempe, AZ 85287
*sara.i.walker@asu.edu; tpavlic@asu.edu ◦co-senior authors

Behavioral correlations over time are an essential but often neglected aspect of interactions among animals. These correlations pose a challenge to current methods, which can collect data at high frequency but lack effective means to analyze complex series of interactions. Experimental manipulations can readily decode short-term stimulus-and-response relationships, but they face difficulties with those that evolve over intermediate time scales. In these scenarios, non-invasive information-theoretic tools have the potential to transform the way in which causal interactions are revealed in behavioral ecology. Here we show that simultaneous observation of the flow of different types of information between subjects can reveal the communication protocols that guide complex social interactions over time. We demonstrate this approach by comparing tandem running in ants and termites. This behavior involves prolonged mutual signaling between the leader and follower of a pair as they walk through the environment. Although the signals in the two taxa are very similar when viewed at short time scales, they serve different purposes, with ants using them to transmit navigational information, and termites only to maintain cohesion of a mated pair. By separately analyzing information on direction and motion, we showed unidirectional information flow from leader to follower in termites, but bidirectional flow in ants, consistent with the follower ant using acknowledgement signals to regulate the flow of directional information from the leader. These results show the promise of information theory to uncover hidden signaling pathways and to offer a common language for comparisons across a wide taxonomic range.

Introduction

Social interactions among individuals unfold across different scales of space and time (Flack 2012). At short timescales, causal relationships can often be captured by experiments that manipulate an immediate stimulus to reveal its causal connection(s) to a stereotyped response, or fixed action pattern. In herring

gulls, for example, the feeding behavior of chicks is visually triggered by a red spot on the lower bill of adult gulls—a causal relationship revealed through experiments in which changes in the color of this spot were shown to affect the likelihood that chicks will engage in feeding behavior (Tinbergen 1953). However, interactions are often more complex than this, because they follow a protocol where rules are conditionally applied over time depending on the outcome of previous interactions. In these cases, where short-term histories may affect longer-term outcomes, the ability to make testable predictions requires quantitative tools that can capture the dynamics of the interaction protocol at an intermediate time scale. Considering only short-term interactions, like the stimulus-and-response of herring gull parent and chick, might not explain functional differences observed at long time scales in otherwise similar behaviors.

Consider the tandem-running behavior of many ants and termites, in which one individual leads a follower through the environment (Fig. 1a). At short time scales, tandem runs in the ant *Temnothorax rugatulus* appear identical to those in the termites *Coptotermes formosanus* and *Reticulitermes speratus*. They use similar signaling mechanisms, in which the leader releases a short-range pheromone that attracts the follower (Möglich, Maschwitz, and Hölldobler 1974; Bordereau and Pasteels 2010) while the follower taps the leader's body with its antennae to indicate its continued presence (Möglich, Maschwitz, and Hölldobler 1974; Franks and Richardson 2006; Nutting 1969; Vargo and Husseneder 2009). Upon removal of the follower, the leader stops and waits for the follower to resume contact, both in ants (Möglich, Maschwitz, and Hölldobler 1974; Franks and Richardson 2006) and in termites (Mizumoto and Dobata 2019). At long time scales, however, there are clear differences. Followers in *T. rugatulus* use tandem runs to learn a route, acquiring navigational information that allows them to later repeat the same journey independently of the leader (Fig. 1b). In contrast, termite leader–follower pairs use tandem runs only to maintain spatial cohesion; once a suitable location is found, the termites remain there to start a new colony, and neither partner ever retraces the route of their tandem run.

Given their similarity between ants and termites, short-term signaling mechanisms (i.e., their stimulus and response dynamics) cannot explain species differences in the function of tandem runs (i.e., route-learning versus spatial cohesion). These differences are likely encoded at intermediate time scales, where it becomes possible to detect the communication protocol (or set of interaction rules) that describe how and when leader and follower use each signaling mechanism. However, experimental manipulations that operate at intermediate time scales also interfere with and constrain the normal patterns of behavior over time. As we show in this study, information-theoretic methods can reveal the structure of information flow between subjects based only on observational data from many repeated interactions. Moreover, these model-free methods do not rely on a priori assumptions, and can be applied over different ecological scenarios allowing for comparisons across a wide taxonomic range (McCowan, Hanser, and Doyle 1999).

Information theory provides a model-free formalism to explicitly quantify the effects of the interaction between individuals across space and time (Cover and Thomas 2005; Lizier, Prokopenko, and Zomaya 2008). Whereas the generic concept of *entropy* quantifies the uncertainty in a distribution of outcomes, the derived construct of *transfer entropy* quantifies the reduction of uncertainty about the future state of a

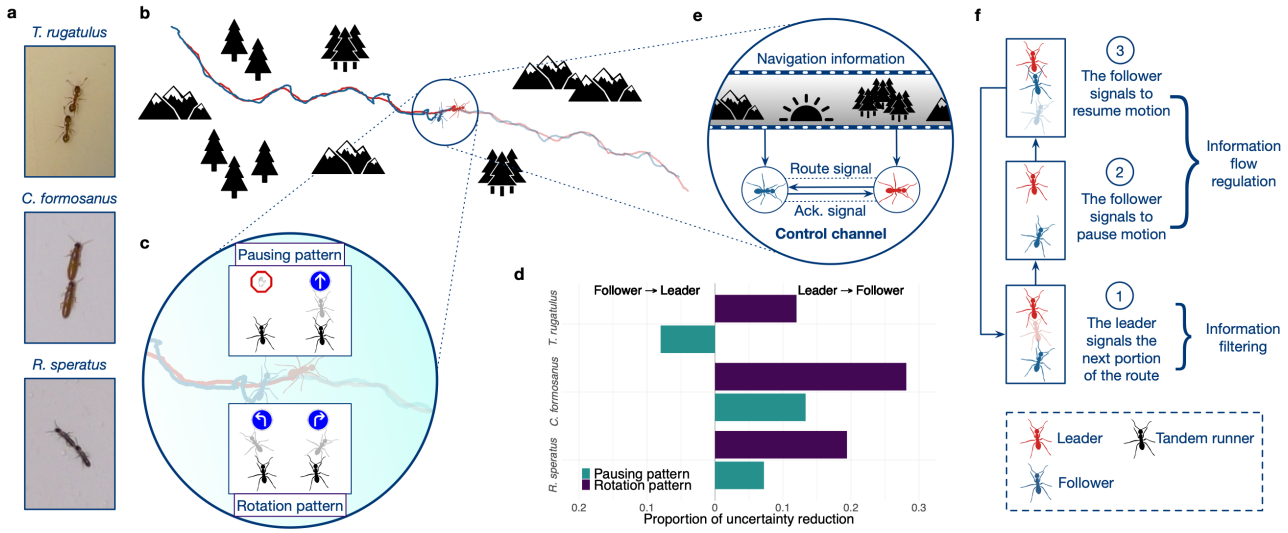

Figure 1. Information flow during tandem run recruitment by ants and termites. (a) Tandem running pairs of T. rugatulus, C. formosanus, and R. speratus. (b) A sampled tandem run trajectory within an idealised environment. (c) The encoding schema used to discretise spatial trajectories of each ant and each termite on the basis of both rotation pattern and pausing pattern. (d) The predominant direction of information flow measured as the proportion of uncertainty reduction explained by the interaction between leader and follower. (e) A schematic illustration, and (f) a mechanistic illustration of the regulation of information flow in ants' tandem runs.

putative receiver given knowledge of the present state of the corresponding sender (Schreiber 2000). Transfer entropy is well suited for studying message passing; it naturally incorporates temporal ordering, from the sender's present to the receiver's future, and quantifies the additional predictive power gained from the sender beyond what is contained in the receiver's past, thus accounting for autocorrelations that might otherwise affect behavioral data (Mitchell et al. 2019). Previous studies have used transfer entropy to reveal whether one animal is influencing another on the basis of a single representation of behavioral data (Orange and Abaid 2015; Butail, Mwaffo, and Porfiri 2016; Kim et al. 2018; Ward et al. 2018; Porfiri et al. 2019; Ray et al. 2019). We extend these methods by applying transfer entropy to multiple parallel information flows within the same behavior (*e.g.*, patterns embedded in the direction of motion as well as in the speed of motion as shown in Fig. 1c). That is, we use different symbolic representations of the same raw data, allowing us to uncover the complex structure of causal relationships between subjects. Following this approach, we provide evidence that the communication protocol used by leaders and followers over intermediate time scales explains the functional differences between the tandem runs of ants and termites, despite their using similar signaling mechanisms at short time scales.

Results

We first used transfer entropy to find whether the leader's or the follower's behavior better predicts the *direction of motion* of the other runner along the route. In ants, the leader is showing a known route to the follower (Franks and Richardson 2006) and in termites the leader is directing a random search for a new home across the environment (Nutting 1969; Vargo and Husseneder 2009). In both cases, the leader

is expected to be the best predictor of the direction of the pair's motion. Consequently, we expect the leader's behavior to be more informative about that of the follower both in ants and in termites. To test this hypothesis, we coarse-grained the spatial trajectories of each runner into sequences of clockwise and counterclockwise turns (Fig. 1c and Methods). We then measured the flow of information between the pair averaged over the entire duration of the tandem run (*i.e.*, over intermediate time scales). We found that, as expected, the leader better predicts the direction of motion of the follower than the other way around across all three species (Fig. 1d, rotation bars).

Next, we focused on the frequent brief interruptions that give tandem runs a distinctive stop-and-go appearance. During these interruptions, the follower breaks tactile contact with the leader, who then pauses while the follower performs a local random search (Franks et al. 2010; Mizumoto and Dobata 2019). When the follower again touches the leader, the latter resumes motion, and the pair continues on their way. In ants, these frequent interruptions are believed to regulate the speed of the run to better enable followers to acquire navigational information (Franks and Richardson 2006; Franklin et al. 2011). As termites do not use tandem runs to learn a route, interruptions may be more consistent with accidental chance separations from the leader. Thus, we hypothesize that in ants, but not in termites, followers better predict the cessation and resumption of motion than do leaders. Under this hypothesis, followers send acknowledgment signals (Figs. 1e and 1f) similar to the use of utterances (*e.g.*, "mm-hmm" see Jefferson 1984) or gestures (*e.g.*, the nodding of one's head) in human conversations as well as "ACK" packets in Internet protocols that confirm receipt of a message (Cerf and Kahn 1974). If our hypothesis is correct, we would expect the information-theoretic signature of the tandem pair's pausing pattern in ants to differ from that of termites. To test this, we analyzed the spatial trajectories using a different representation obtained by coarse graining them into sequences of *pauses and movements* (Fig. 1c). As expected, we found that the leader remains the best source of predictive information in termites, but in ants the follower instead controls the flow of information and better predicts the future pausing behavior of the leader (Fig. 1d, pausing bars).

Side-by-side comparison of tandem-run trajectories (Figs. 2a and 2d) shows that ants, but not termites, evince a tension between cohesion and information acquisition. Leader and follower ants repeatedly switch in and out of proximity regulation under the control of the follower (Figs. 2b and 2c). The predictive power of the leader's rotation pattern dominates at close distances up to two body lengths, when the pair is undergoing sustained motion and seeking cohesion (point 1, rotation regime); when their distance increases further, the follower becomes more informative, predicting pauses in the motion of the leader (point 2, pausing regime). Their separation then decreases as the follower approaches the stationary leader (point 3) and predicts her resumption of motion. When leader and follower are again in close proximity, the leader begins to move away (point 4) and this pattern repeats. Large separations are evidently generated by the follower ant and are unrelated to rotational course corrections.

In contrast to ants, the termite leader dominates both regimes of predictive information (Fig. 2d–f and Extended Data Fig. 6). Even more, these regimes are inverted with respect to ants with rotation being predicted at larger distances and pausing of motion at shorter distances. The distance between a leader

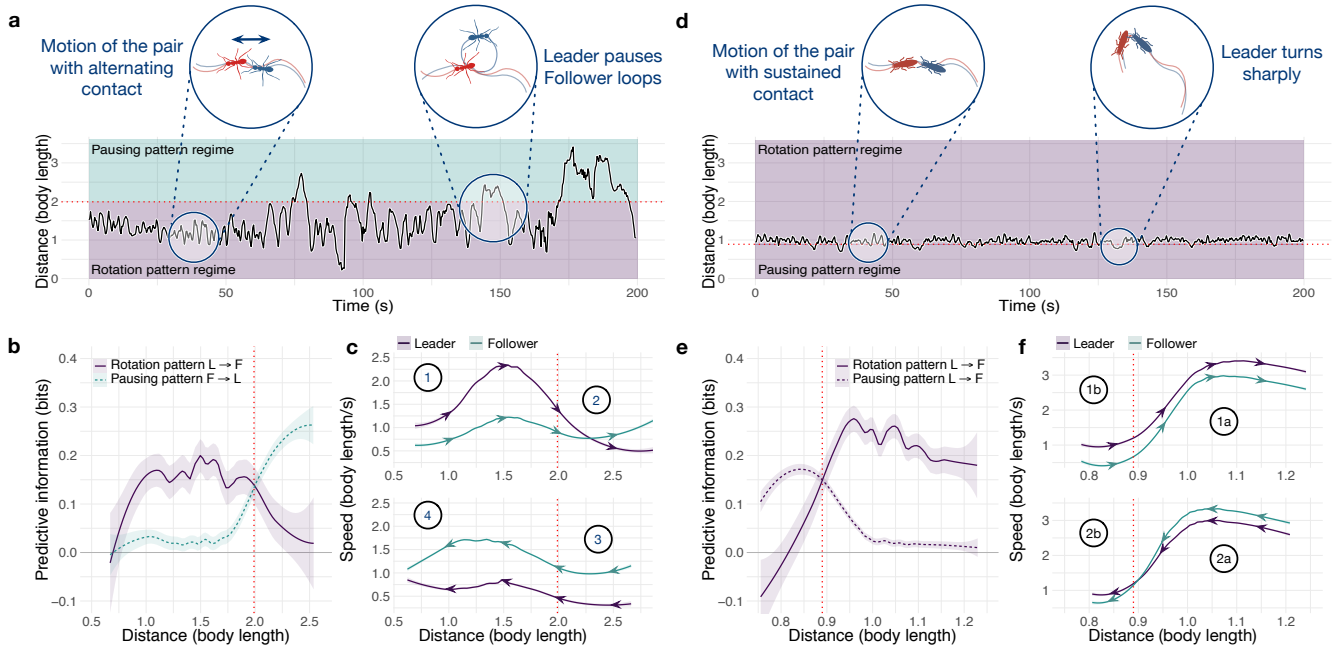

Figure 2. Spatiotemporal dynamics of tandem running. (a) and (d) Distance between the centroids of runners as a function of time. (b) and (e) Average predictive information as a function of the distance between centroids of runners. (c) and (f) Average speed of leader and follower as a function of the distance between their centroids for increasing and decreasing distance. Panels (a), (b), (c) show results for the ant T. rugatulus. Panels (d), (e), (f) show results for the termite C. formosanus. Purple represents the leader, green represents the follower.

and a follower is characterized by oscillations with higher frequency but lower amplitude than those of the ants (cf. Fig. 2a and Fig. 2d). These oscillations are largely within the rotation regime due to sustained motion. In this regime, tandem runners frequently alternate between a phase in which the leader is the faster of the two and their distance increases (point 1a) and a phase in which the follower moves faster than the leader, reducing the gap (point 2a). Sporadically, leader and follower can be found very close to each other (less than 0.89 body lengths, Fig. 2e) where they enter the pausing regime. When this happens, the leader's motion initially predicts the decrease and then the increase in speed of the follower (points 1b and 2b). The pausing regime is then quickly abandoned, and rotation information regains dominance. This behavior is consistent with relatively close proximity facilitating momentary large course corrections (Fig. 2d, right inset). Leader-initiated pauses in termites might serve some unknown function, *e.g.*, motor planning (Card and Dickinson 2008; Hunt et al. 2016); however, unlike the case of ants, we have no evidence that the termite pauses facilitate follower control over any aspects of the trajectory.

Discussion

Although both ants and termites have similar mechanisms for mutual signaling at short time scales, they use these mechanisms according to different communication protocols at intermediate time scales. In principle, both ant and termite followers can transfer information to their leaders by signaling their presence through physical contact; however, differently from ants, termite followers do so only when establishing

contact at the beginning of a run and, sporadically, after accidental breaks. Once contact is established and the run is proceeding steadily, termite followers cease to transfer information to their leaders who instead control both the direction and the speed of the run. Although manipulation experiments acting at short time scales can show bidirectional flow in all three species, we found evidence that communication at intermediate time scales is consistently bidirectional only in ants (from leader to follower for rotations and from follower to leader for pauses) whereas, with the exception of accidental breaks, it is consistently unidirectional in termites (from leader to follower for both rotations and pauses).

The communication protocol followed by termites can be likened to a person leading another by the hand. The protocol of ants reveals instead a more complex coordination of social behavior as leader and follower systematically alternate between close contact and separation. We suggest that the ants' intermittent motion and bidirectional feedback is akin to the pausing for acknowledgment observed between machines on a computer network. In this case, communication theory can aid in understanding the frequency of acknowledgments in terms of the receiver's informational capacity and the complexity of the information being received. The selective exposure of a follower to navigational information from the environment is akin to the sending of a complex message over a simple channel which, in machine-to-machine communication, requires flow control mechanisms to prevent overwhelming the receiver.

Tandem running by the ant *T. albipennis* has also been likened to teaching—a social behavior often used to distinguish humans from other animals—because the leader modifies her behavior in the presence of a naïve follower at some cost and as a result of bidirectional feedback (Franks and Richardson 2006; Richardson et al. 2007). Regulation of information flow might be an underappreciated requirement of teaching. This assumption could be investigated by applying the methodology we put forward here to other examples of teaching known in the animal kingdom (Hoppitt et al. 2008). Moreover, although social insects use cue-based mechanisms for flow and congestion control of physical quantities, such as food or nesting material (Seeley 1989; Prabhakar, Dektar, and Gordon 2012), our study is the first to reveal a protocol for the application of signal-based mechanisms to control the flow of information (*i.e.*, a non-physical quantity) in a non-human organism. Furthermore, tandem running has evolved multiple times in the ants but not all instances necessarily require acknowledgment signals (Kaur et al. 2017) and so comparing across taxa may reveal the ecological context that led to the evolution of signals that regulate other signals. Thus, being able to formally quantify differences in information flows in social interactions not only provides mechanistic insights but also allows for investigating questions about the evolution of information processing itself.

Conclusions

Temporal correlations manifesting over intermediate time scales represent an important but often neglected aspect in behavioral ecology (Mitchell et al. 2019). Complex spatiotemporal interactions among individuals (*i.e.*, those interactions evolving over intermediate time scales) are difficult to study by direct manipulation in highly controlled laboratory settings. Instead, quantitative and non-interventional methods

applied over longer observational periods can be used to capture the dynamical aspect of social interactions, but these methods are generally underdeveloped and sporadically used in behavioral ecology. As we have shown in this study, information theory offers tools such as transfer entropy that can disentangle the temporal structure of the interaction between individuals.

Whereas the construct of transfer entropy has seen extensive applications in the neurosciences, particularly to study effective connectivity in the brain (Vicente et al. 2011), its application in the field of animal behavior is less frequent and has focused primarily on revealing leader–follower relationships in fish (Butail, Mwaffo, and Porfiri 2016; Kim et al. 2018; Ward et al. 2018) and bats (Orange and Abaid 2015), with more recent applications in the study of decision-making in humans (Grabow et al. 2016; Porfiri et al. 2019) and slime molds (Ray et al. 2019). These previous applications set out to answer the generic question of whether one subject is influencing another on the basis of a single symbolic representation of raw data (e.g., a single encoding that carries information only about the direction of motion). Such uses of transfer entropy and other information-theoretic measures (McCowan, Hanser, and Doyle 1999) cannot disentangle the complex structure of information flow between subjects when different simultaneous aspects of their interaction carry different forms of information in potentially different directions. By quantifying multiple, concurrent informational patterns (i.e., variation over time in both direction and speed) and subsequently relating the findings to each other, we have shown how to uncover more complex communication protocols as opposed to simply identifying distinguished individuals within a social interaction.

The methodology we put forward, which applies advanced information-theoretic measures to different symbolic representations of the same dataset, has allowed us to show differences in the communication protocol used by tandem running ants and termites and to explain the disparity in their function. This approach is sufficiently generic to enable the discovery of cryptic signaling behaviors in other taxa and to provide deeper insights into behaviors whose function is poorly or partially understood (*e.g.*, turn-taking (Flack 2013; Pika et al. 2018) and complex coordinated dances in birds (Ota, Gahr, and Soma 2015)). Furthermore, we have shown how the generality of this approach can extend traditional information-theoretic analysis from a mechanistic focus on one species toward a comparison across a wide taxonomic range. Such a common language of information processing can enable the posing of questions, hypotheses, and predictions for the evolution of information processing itself.

Materials and Methods

Ant experiments. We used 6 colonies of *T. rugatulus* (between 30–60 individuals each) collected in the Pinal Mountains near Globe, Arizona, during September 2017. Each colony was kept in a plastic box (110 mm by 110 mm) with a nest, a water tube, and an agar-based diet (Bhatkar and Whitcomb 1970). Nests (50 mm by 75 mm) were composed of a balsa-wood slat with a central rectangular cavity (30 mm by 50 mm) and sandwiched between two glass slides (see Extended Data Fig. 1a). The top slide had a 2 mm

228 hole over the center of the nest cavity to allow ants to enter and leave the nest. We conducted emigration
229 experiments to induce ants to perform tandem runs. To obtain sufficiently long tandem runs, we used a
230 large experimental arena (370 mm by 655 mm) delimited by walls (37 mm tall) and subdivided by 5 barriers
231 (10 mm by 310 mm) placed to form a contiguous corridor with alternating left and right turns (see Extended
232 Data Fig. 1b). Both walls and barriers were coated with Fluon to prevent ants from leaving the experimental
233 arena. A new nest was placed at one extremity of the corridor and was covered with a transparent red filter
234 to encourage the ants, which prefer dark cavities (Franks et al. 2003), to move in. The nest housing a colony
235 was transferred from its plastic box and placed at the other extremity of the corridor. Colony emigration was
236 induced by removing the top slide of the occupied nest. We performed 6 experiments, one for each colony,
237 and recorded them at 30 frames per second using a video camera with 1K resolution. For each colony, we
238 then selected between 1 and 6 pairs of ants performing tandem runs obtaining a total of 20 samples.
239 Selected tandem runs last more than 15 minutes and have the same pair of ants travelling between the two
240 nests with no or minimal interaction with other members of the colony.
241
242 **Termite experiments.** Experiments with *C. formosanus* and *R. speratus* were performed as part of a study
243 on sexually dimorphic movements of termites during mate search (Mizumoto and Dobata 2019). Alates
244 from 2 colonies of *C. formosanus* were collected in Wakayama, Japan, in June 2017; alates from 5 colonies
245 of *R. speratus* were collected in Kyoto, Japan, in May 2017. After controlled nuptial flight experiments,
246 termites that shed their wings were selected and used for tandem run experiments. Experiments were
247 performed in a Petri dish (145 mm Ø) filled with moistened plaster whose surface was scraped before each
248 trial. A female and a male termite were introduced in the experimental arena with the opportunity to tandem
249 run for up to 1 hour. A total of 17 experiments were performed for *C. formosanus* and 20 experiments for
250 *R. speratus* using different individuals. Tandem runs were recorded at 30 frames per second using a video
251 camera with a resolution of 640 by 480 pixels.
252
253 **Data extraction.** We extracted motion trajectories from video recordings of tandem runs by automatically
254 tracking the position over time of leaders and followers. Motion tracking was accomplished using the
255 UMATracker software platform (Yamanaka and Takeuchi 2018). Because we tracked the centroids of each
256 runner's body, the distance between individuals was always greater than zero even when leader and
257 follower were in contact with each other. All trajectories were sampled at 30 frames per second and
258 shortened to a duration of 15 minutes. Trajectories were then converted from pixels to millimeters using a
259 scaling factor estimated by measuring known features of the experimental arena with ImageJ (Schneider,
260 Rasband, and Eliceiri 2012). Body size of each runner (average ± standard deviation) was measured from
261 video recordings of the experiments using ImageJ (*T. rugatulus*: 2.34 ± 0.3 mm, *C. formosanus*: 8.89 ±
262 0.42 mm, *R. speratus*: 5.5 ± 0.3 mm).
263

Encoding behavioral patterns into time series. We considered three possible behavioral patterns for each runner: *pausing pattern*, *rotation pattern*, and their combination *pausing & rotation pattern*. We did so by coarse-graining the space-continuous trajectories of each leader and each follower using three different symbolic representations. Each spatial trajectory consists of a sequence $(q_1, q_2, \dots)$ of 2-dimensional points, $q_i = (q_i^x, q_i^y)$, representing spatial coordinates over time which are then encoded into a symbolic time series $X = (x_1, x_2, \dots)$. To capture the time interval where the sender best predicts the behavior of the receiver, we subsampled spatial trajectories in time before encoding the behavioral patterns of each runner. We considered different sampling periods, starting from a short period of one sample every 33.3667 ms (29.97 Hz) to a long period of one sample every 1.5015 s (0.666 Hz) with an interval between each period of 33.3667 ms (*i.e.*, sampling period $\in \{0.0334s, 0.667s, \dots, 1.5015s\}$).

The pausing pattern is encoded using two states: the *motion state* (M) and the *pause* state (P). The motivation for this coding scheme is to capture when a tandem runner pauses while waiting for the other to re-join the tandem run or to react to physical contact. Pauses, small adjustments of the position of the runner, or changes due to noise in the sampled trajectories may each accidentally be considered as genuine acts of motion. To prevent these spurious classifications, we used a threshold to distinguish segments of the trajectory into those identifying motion and those identifying pauses. The distribution of step sizes, *i.e.*, the distance travelled by a runner between two consecutive sampled positions q_i and q_{i+1}, shows two distinct modes: short steps representing pauses and long steps representing sustained motion (see Extended Data Fig. 2). The 10th percentile was used as a threshold for separating the two modes for all sampling periods. We therefore encoded steps in the trajectory in the 10th size percentile as pause states and the remaining steps as motion states. This threshold was varied in the interval $\{5\%, 6\%, \dots, 15\%\}$ during a perturbation analysis of predictive information (see Computation of statistics).

The rotation pattern is also encoded using two states: *clockwise* (CW) and *counterclockwise* (CCW). The direction of rotation at time i is obtained by looking at three consecutive positions, q_{i-1}, q_i, q_{i+1}, in the spatial trajectory of each runner. The rotation is clockwise when the cross product $\overrightarrow{q_{i-1}q_i} \times \overrightarrow{q_i q_{i+1}}$ is positive, counterclockwise when it is negative, and collinear when it is zero. In the rare occurrences of collinear motion, the direction of rotation at the previous time step, $i-1$, is copied over in the time series.

As a control for our choices of possible behavioral outcomes, we also considered a compound pausing & rotation pattern that simultaneously encode both components of tandem running. The pausing & rotation pattern is defined using a ternary coding scheme that encodes motion bouts in the states *pause* (P), *clockwise* (CW) and *counterclockwise* (CCW). As for the pausing pattern, the shortest 10% of steps in the spatial trajectories are encoded as pausing (see Computation of statistics for a perturbation analysis of this parameter). The remaining 90% of steps are encoded using states clockwise and counterclockwise following the same methodology used for the rotation pattern.

Measuring predictive information. Our analysis of communication in tandem running is grounded in the theory of information (Cover and Thomas 2005) and its constructs of entropy, conditional entropy, and

transfer entropy. We aim to quantify how knowledge of the current behavior of the sender allows us to predict the future behavior of the receiver, that is, to measure causal interactions in a Wiener-Granger sense (Bossomaier et al. 2016). We consider the behavioral patterns of leaders and followers as the series of realizations $(l_i, i \geq 1)$ and $(f_i, i \geq 1)$ of two random variables, L and F. For simplicity, the following presentation focuses on predicting the future of the follower, $F^{i+1} = (f_{i+1}, i \geq 1)$, from the present of the leader, L, but leaders and followers cover both roles in our analysis.

The overall uncertainty about the future F^{i+1} of the follower is quantified by the (marginal) entropy (Shannon 1948) $H(F^{i+1}) = -\sum_{f_{i+1}} p(f_{i+1}) \log_2 p(f_{i+1})$. Entropy measures the average amount of information necessary to uniquely identify an outcome of F^{i+1}. Knowing the history of the follower may reduce the uncertainty in the distribution of possible outcomes for the future of the follower, and the reduction in uncertainty can be quantified by the difference between the marginal entropy and the entropy after the historical information is considered. Let $f_i^{(k)} = \{f_{i-k+1}, \dots, f_{i-1}, f_i\}$ represent the finite history with length k of F up to the current time i and $F^{(k)}$ a new random variable defined over a series $\left(f_i^{(k)}, i \geq 1\right)$ of k-histories. The amount of uncertainty about F^{i+1} that is left after accounting for its past behavior $F^{(k)}$ is given by the conditional entropy

$$H\left(F^{i+1} \middle| F^{(k)}\right) = -\sum_{f_i^{(k)}, f_{i+1}} p\left(f_i^{(k)}, f_{i+1}\right) \log_2 \frac{p\left(f_i^{(k)}, f_{i+1}\right)}{p\left(f_i^{(k)}\right)},$$

for history length $1 \leq k < \infty$. $H(F^{i+1}|F^{(k)})$ represents the average amount of information necessary to uniquely identify the future behavior of the follower given what we know about its past behavior.

A second step to obtain additional information about the future of the follower is to consider the time-delayed effects of its interaction with the leader. Transfer entropy was introduced for this purpose (Schreiber 2000). It measures the amount of information about the future behavior of the receiver given by knowledge of the current behavior of the sender—information that is not contained in the receiver's past. Due to its time directionality (*i.e.*, from the present of the sender to the future of the receiver), it is considered a measure of information transfer or predictive information (Lizier and Prokopenko 2010). Transfer entropy is defined as

$$T_{L \to F} = \sum_{f_{i+1}, f_i^{(k)}, l_i} p(f_{i+1}, f_i^{(k)}, l_i) \log_2 \frac{p\left(f_{i+1} \mid f_i^{(k)}, l_i\right)}{p\left(f_{i+1} \mid f_i^{(k)}\right)}$$

and measures the reduction of uncertainty of F^{i+1} given from knowledge of L which is not already given by $F^{(k)}$. The logarithm in the above equation is known as local transfer entropy (Lizier, Prokopenko, and Zomaya 2008) and tells us whether, at time i, the interaction $l_i \mid f_i^{(k)} \to f_{i+1} \mid f_i^{(k)}$ between the two processes is informative (> 0) or misinformative (< 0). In our analysis, we look at local transfer entropy averaged over the distance between leader and follower to understand the spatiotemporal dynamics of communication during tandem running.

Due to the asymmetry of transfer entropy, $T_{L\to F} \neq T_{F\to L}$, we can obtain the predominant direction and the magnitude of predictive information by studying the difference

$$T_{L\to F} - T_{F\to L}.$$

This quantity is positive when information flows predominantly from L to F and negative when it flows from F to L. Its absolute value is known as net transfer entropy (Porfiri 2018). Finally, as transfer entropy can be rewritten as $T_{L\to F} = H\left(F^{i+1}\middle|F^{(k)}\right) - H(F^{i+1}|F^{(k)}, L)$, we can normalise this quantity in the interval $[0; 1]$ simply by dividing it by the conditional entropy as in

$$\frac{T_{L\to F}}{H\left(F^{i+1}\middle|F^{(k)}\right)} = \frac{H\left(F^{i+1}\middle|F^{(k)}\right) - H(F^{i+1}\middle|F^{(k)}, L)}{H\left(F^{i+1}\middle|F^{(k)}\right)}.$$

Normalized transfer entropy (Porfiri 2018) is a dimensionless quantity that captures the proportion of the future behavior F^{i+1} of the follower that is explained by the interaction with the leader at time i. When F^{i+1} is completely predicted by L, the conditional entropy $H(F^{i+1}\middle|F^{(k)}, L)$ is zero and normalized transfer entropy is maximal and equal to 1; instead, when F^{i+1} is independent of L, $H\left(F^{i+1}\middle|F^{(k)}\right) = H(F^{i+1}\middle|F^{(k)}, L)$ and normalised transfer entropy is minimal and equal to 0.

Computation of statistics. We computed information-theoretic measures for both leaders and followers. In our computations, we assume that the pausing and rotation patterns of ants and termites are peculiar features of the species rather than of specific pairs of tandem runners. As such, rather than treating each trial separately and then aggregating the results, we estimated the necessary probabilities from all experimental trials together and obtained a single estimate of transfer entropy for each considered species and parameter configuration. Our measures of predictive information are therefore averaged over all trials of the same species. All information-theoretic measures were computed in R 3.4.3 using the `rinform-1.0.1` package (Moore et al. 2018).

To prevent possible artefacts that may arise due to finite sample sets, we discounted transfer entropy by a correction factor computed over pairs of independent time series, therefore obtaining conservative estimates (Porfiri 2018). To do so, we randomly paired the behavioral patterns of leaders and followers belonging to different tandem runs and computed transfer entropy in both directions. For each species and parameter configuration, we repeated this randomization process 50 times and estimated the correction factor as the average transfer entropy of the synthetic dataset.

The sampling period of continuous spatial trajectories and the history length of transfer entropy define the parameter space of our study. To choose a suitable parameter configuration and control for its robustness, we computed net transfer entropy for 900 different parameter configurations for each species (history length $k \in \{1, \dots, 20\}$ and sampling period $\{0.0334s, \dots, 1.5015s\}$). From the resulting landscapes of information transfer, which show robustness to variation of parameters, we then selected the parameter configurations that maximize the net transfer of information (see Extended Data Fig. 3 and Extended Data Table 1). Next, we performed a perturbation analysis of the probability threshold used to separate pauses from motion in the pausing pattern and in the pausing & rotation pattern ($\{5\%, 6\%, \dots, 15\%\}$). Although the

magnitude is subject to some variation, the direction of information transfer that represents our primary observable remains unaltered (see Extended Data Fig. 4). Finally, we also controlled for our choices of possible outcomes in the behavioral patterns by considering a compound pausing & rotation pattern. Extended Data Fig. 5 show the results of this analysis which closely resemble those shown in Fig. 2, for *T. rugatulus* and *C. formosanus*, and Extended Data Fig. 6, for *R. speratus*.

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Acknowledgements

This work was supported by NSF grant No. PHY-1505048. N.M. is supported by a JSPS Overseas Research Fellowship. The authors would like to thank Dr. Anna Dornhaus for constructive criticism of the manuscript.

Author contributions statement

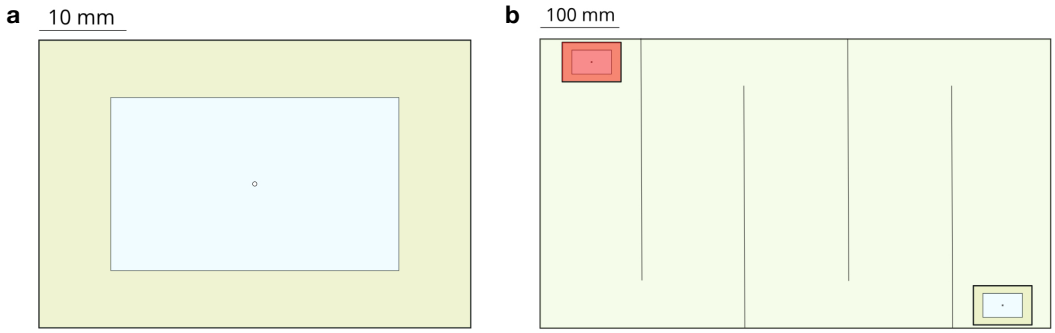
Conceptualization, G.V., T.P.P., S.I.W., and S.C.P; Methodology, G.V.; Formal Analysis, G.V.; Investigation, G.V. and N.M.; Writing–Original draft, G.V. and T.P.P.; Writing–Review & Editing, S.C.P, S.I.W., and N.M.; Funding acquisition, S.I.W., S.C.P, and T.P.P.

Additional information

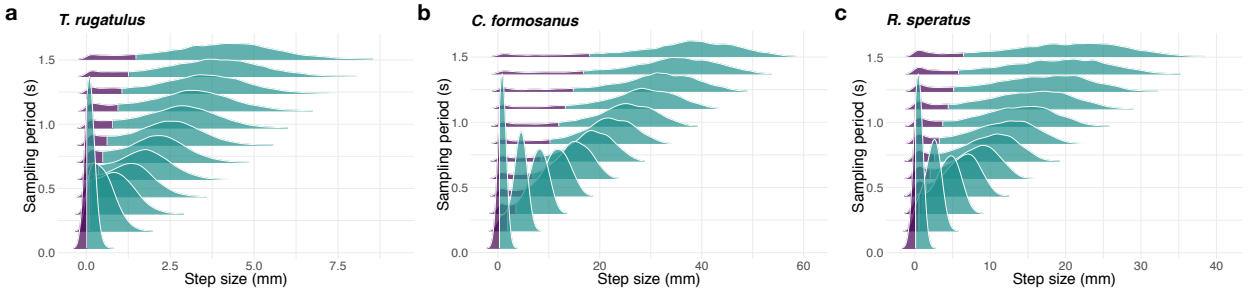
Accession codes: Data that support the findings of this study will be available in "figshare" with identifier "10.6084/m9.figshare.9786260" upon acceptance of the manuscript; data can be privately accessed by reviewers at "https://figshare.com/s/91986a474d89938e8239".

Competing interests: The authors declare no competing interest.

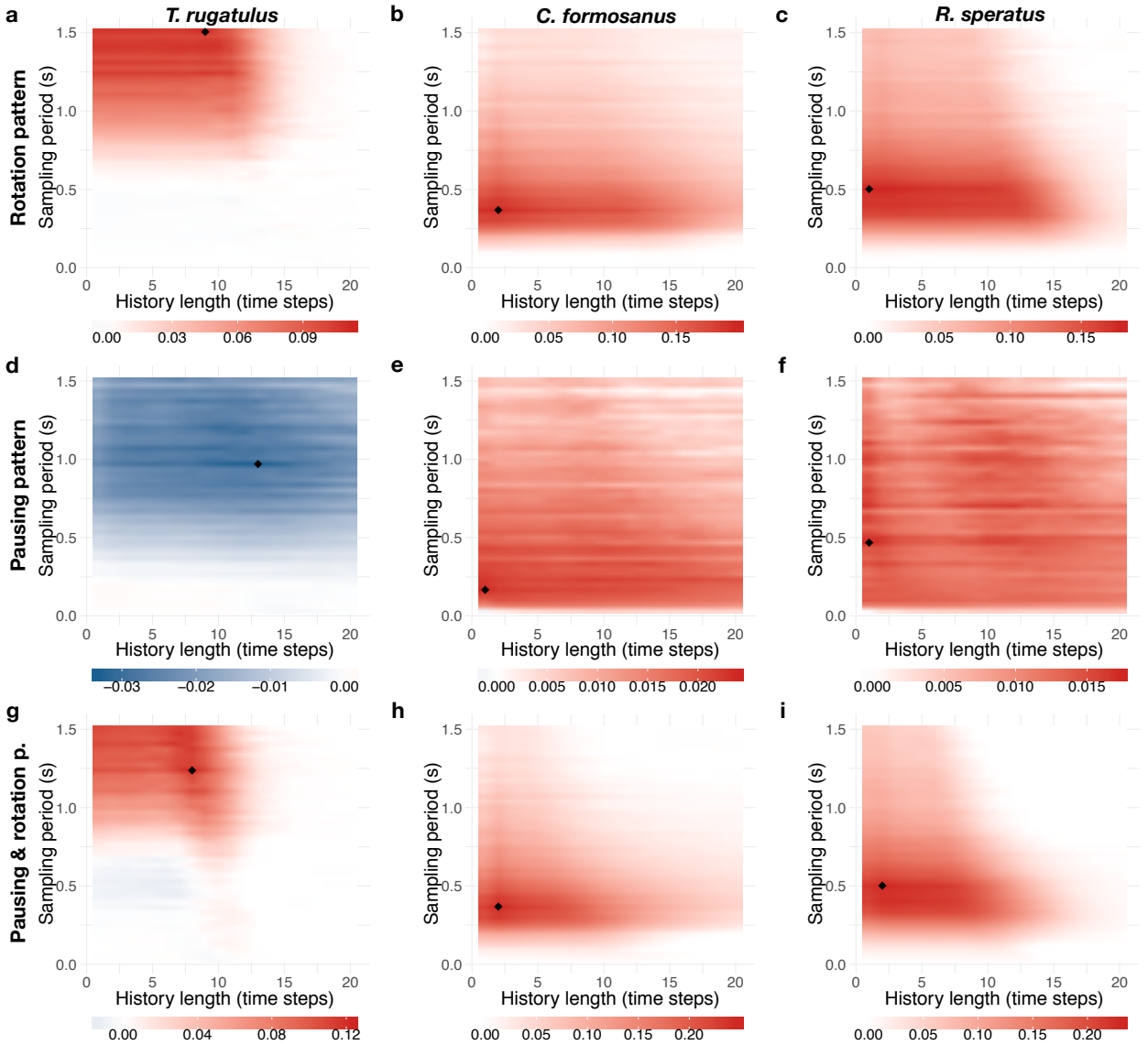
Extended data



Extended Data Figure 1 Experimental setup for T. rugatulus. (a) Nest architecture with the entrance in the center of the roof. (b) Experimental arena partitioned into a corridor with the old nest (bottom right) and the new nest (top left) positioned at the extremities.



Extended Data Figure 2. Probability density function of the step size as a function of the sampling period for (a) T. rugatulus, (b) C. formosanus, and (c) R. speratus. Blue represents the 10% probability mass used to define the pausing state; Green represents the remaining 90% of the probability mass defining the motion state.

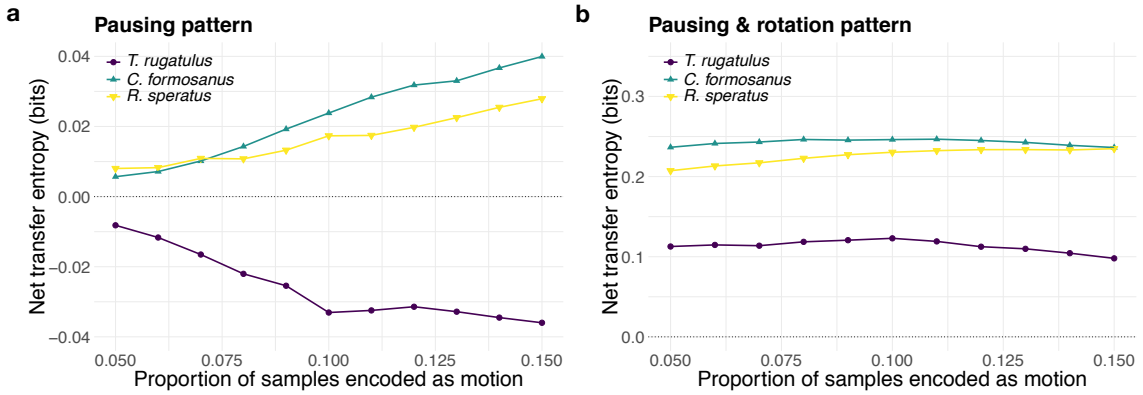


Extended Data Figure 3. Landscape of net information transfer computed using net transfer entropy (bits) as a function of the sampling period and of the history length. Panels (a), (b), and (c) show the results for the rotation pattern, panels (d), (e), and (f) show the results for the pausing pattern, and panels (g), (h), and (i) show the results for the compound pausing & rotation pattern. The first, second, and third columns show the results, respectively, for T. rugatulus, C. formosanus, and R. speratus. Colors indicate the intensity and predominant direction of information transfer (red for leader to follower, blue for follower to leader); the diamond symbol indicates the configuration with maximum magnitude.

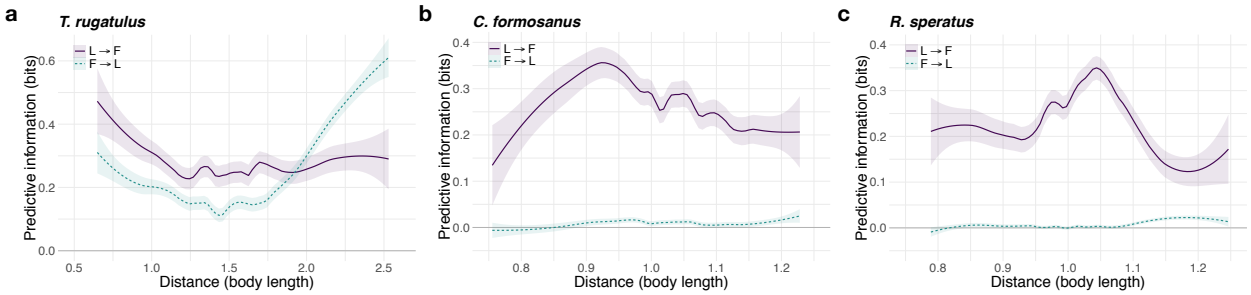
Extended Data Table 1. Selected parameter configurations for each species and behavioral pattern.

Species	***Behavioral pattern***	***Sampling period (s)***	***History length k***
T. rugatulus	Rotation	1.5015	9
	Pausing	0.9676	13
	Pausing & Rotation	1.2346	8
C. formosanus	Rotation	0.3670	2
	Pausing	0.1668	1

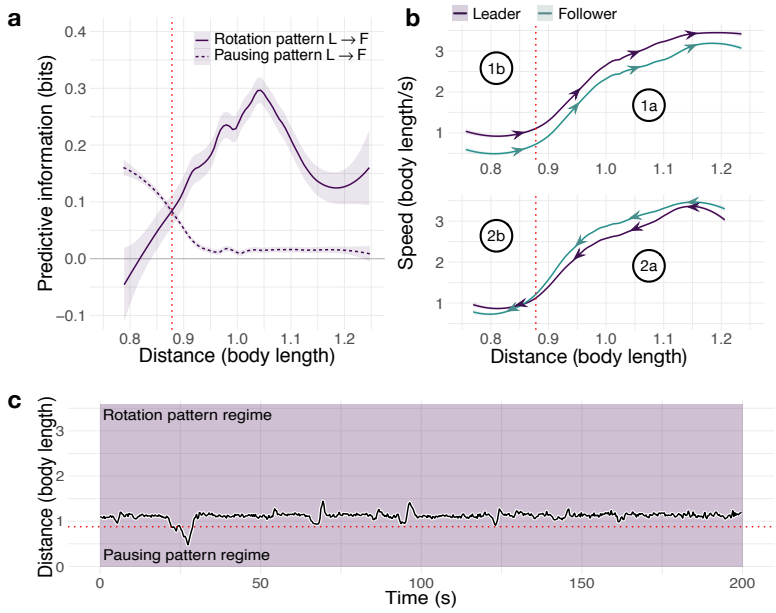
	Pausing & Rotation	0.3670	2
R. speratus	Rotation	0.5005	1
	Pausing	0.4671	1
	Pausing & Rotation	0.5005	2



Extended Data Figure 4. Perturbation analysis. Net transfer entropy as a function of the probability threshold used to encode step sizes into the motion state and pausing state. (a) The results for the pausing pattern. (b) The results for the compound pausing & rotation pattern. Sampling period and history length correspond to the selected parameters used for the entire analysis. Positive values represent information transfer from leader to follower, negative values represent information transfer from follower to leader.



Extended Data Figure 5. Average predictive information as a function of the distance between centroids of runners for the compound pausing and rotation pattern. Results are shown for (a) the ant T. rugatulus, and the termites (b) C. formosanus and (c) R. speratus.



Extended Data Figure 6. Spatiotemporal dynamics of tandem running for R. speratus. (a) The average predictive information as a function of the distance between centroids of runners. (b) The average speed of leader and follower as a function of the distance between their centroids for increasing and decreasing distance. (c) The distance between the centroids of runners as a function of time. Purple represents the leader, Green represents the follower.