Ants acknowledge information to control its rate of transfer

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Signals whose function is solely to coordinate communication are so far known only in human conversations[1] and telecommunication networks[2]. Utterances like "mm-hmm"[3], gestures such as the nodding of one's head, or "ACK" packets used in Internet protocols to confirm the reception of a message[4] all coordinate communication. Rather than carrying domain-specific information[5–7], these signals are generic acknowledgements used by receivers to control the flow of sender information when the rate of information transfer could possibly be overwhelming. Here, we show the first evidence of the use of acknowledgements to control information transfer rates outside human society. Quantitative comparison of information flows between sender-receiver pairs demonstrates that acknowledgements are used by pairs of ants during tandem running[8,9]—a social behaviour where the sender facilitates the receiver's intake of navigational information—but not by pairs of termites that also tandem run[10,11] to maintain cohesion but not to share large amounts of information. Our analysis provides a quantitative framework for identifying in other animal taxa hidden patterns of information flow with implications for uncovering cryptic signals within complex communication behaviours that are still poorly understood[12,13].

In animals that cooperate to share knowledge about valuable resources, individuals may communicate information-rich directions to reach a place of interest. Whereas some species reduce this burden by externalising individual memory through modifications to the environment (*e.g.*, using pheromone trails as a collective memory[8]), in other species, informed individuals communicate directly to naïve ones[14]. This includes the tandem runs of certain species of ants[8,9], such as the ant *Temnothorax rugatulus* (Fig. 1a), where one experienced individual leads a naïve follower through the environment so that the follower can learn navigational cues (Fig. 1b) to a valuable target (*e.g.*, rich food or a new home) and independently return to that location[15]. However, not all tandem runs have a route-learning function that requires information-rich messages. In certain termites[10,11], such as *Coptotermes formosanus* and *Reticulitermes speratus* (Fig. 1a), tandem runs serve only to maintain cohesion between a newly mated pair as they

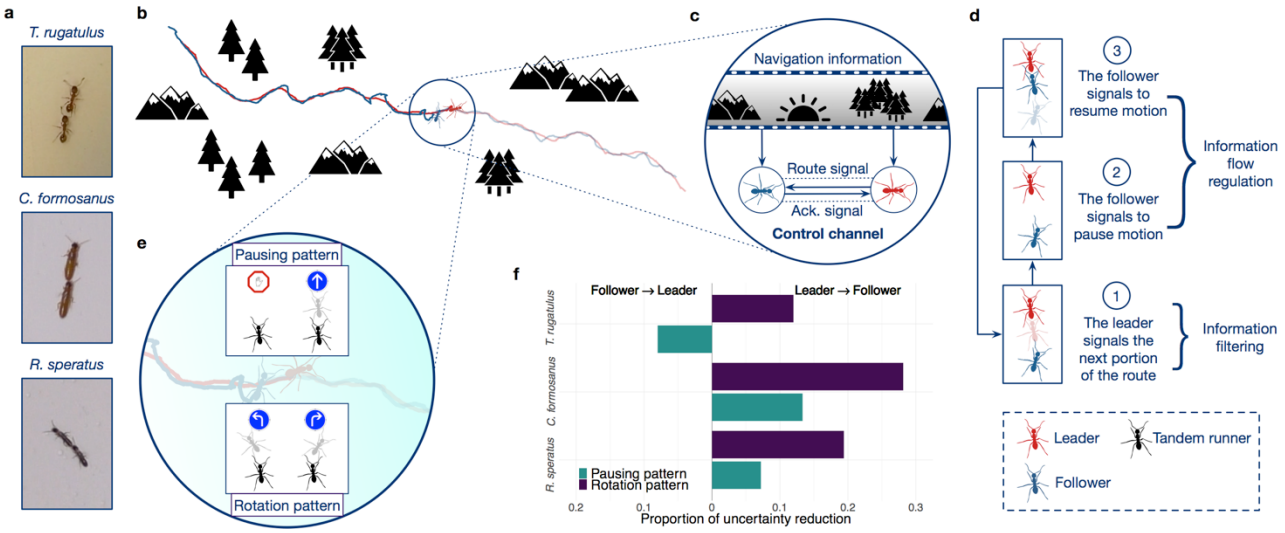

Figure 1. Alternative representations of tandem runs. Panel (a) shows pictures of tandem runs for T. rugatulus, C. formosanus, and R. speratus. Panel (b) shows a sampled tandem run trajectory within an idealised environment. Panels (c) and (d) give, respectively, a schematic and a mechanistic illustration of the regulation of information flow in ants' tandem runs. Panel (e) shows the encoding schema used to discretise spatial trajectories of each ant and each termite on the basis of both rotation pattern and pausing pattern. Panel (f) provides the proportion of uncertainty reduction explained by the interaction between leader and follower.

explore in search of a nest site. Despite having different function, in both ants and termites the follower is attracted to volatile pheromones emitted by the leader[16,17] and the leader responds to the touch of the follower's antennae by resuming or continuing motion[16,18,19]. This mutual communication may serve merely to maintain proximity between the pair, but we hypothesize that it has an additional role in ants, because of their need to transfer a large amount of information[20,21]. Under this hypothesis (Figs. 1c and 1d), the leader acts as a filter of the environment, setting the path and directing the follower to useful navigational cues. The follower, in turn, actively regulates the speed of the run through acknowledgement signals, by interrupting and resuming physical contact with the leader, so that she can acquire information at a manageable rate.

Both the cohesion and acknowledgement hypotheses predict that leaders will pause and wait if the follower's tactile input is lost, consistent with the results of experiments[16,18,19] and with the occurrence of spontaneous pauses in unmanipulated tandems of both ants and termites. To distinguish between these explanations, we employ information theory[22] to formally quantify the directionality of information flow between leaders and followers. Given time series of behavioural observations of two parties that may be communicating, transfer entropy quantifies the reduction of uncertainty about the future state of the putative receiver given knowledge of the present state of the corresponding sender[23]. Transfer entropy is well suited for studying message passing as 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. It is a measure of predictive information[24] that allows us to make rigorous statements about the directionality of information flow without altering the studied behaviour through experimental interventions.

Using transfer entropy, we first studied whether the leader's or the follower's behaviour better predicts the direction of motion of the other runner along the route. We expect the leader's behaviour to be more informative about that of the follower both in ants, because the leader is showing a known route to the follower, and in termites, because the leader is directing a random search. To test this, we coarse-grained the spatial trajectories of each runner into sequences of clockwise and counter-clockwise turns (Fig. 1e and Methods). Then, we measured the flow of information between the pair and found that, as expected, the leader better predicts the rotation pattern of the follower than the other way around across all three species (Fig. 1f, rotation bars).

Next, to analyse the regulation of speed, 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[19,25]. When the follower again touches the leader, the latter resumes motion, and the pair continues on their way. If our hypothesis about acknowledgment signals is correct, we would expect the follower's pausing pattern of ants to differ from that of termites. This is because the ant follower likely triggers each pause by breaking contact to acquire navigational information[15,26], while the termite follower should not interrupt tandem runs deliberately but only as a result of accidental separation from the leader. To test this, we analysed the same spatial trajectories but instead coarse-grained them as sequences of pauses and movements (Fig. 1e). 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 behaviour of the leader (Fig. 1f, pausing bars). Communication is therefore bidirectional in ants (from leader to follower for rotations and from follower to leader for pauses) and unidirectional in termites (from leader to follower for both rotations and pauses).

Side-by-side comparison of tandem run trajectories (Figs. 2c and 2f) 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. 2a and 2b). 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 and the leader begins to move away (point 4), 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 leader and follower is characterised by oscillations with higher frequency but lower amplitude than those of the

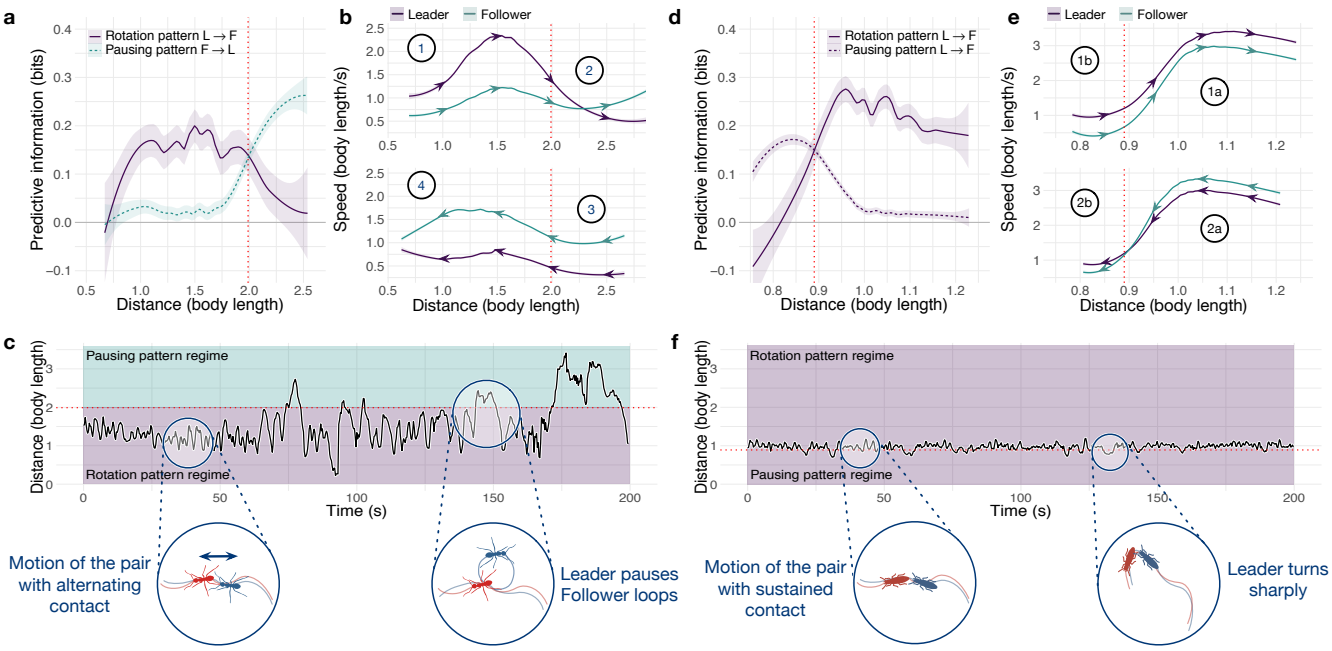

Figure 2 Spatiotemporal dynamics of tandem running. Average predictive information as a function of the distance between centroids of runners, average speed difference between leader and follower as a function of the distance between their centroids for increasing and decreasing distance, and distance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

ants (cf. Fig. 2c and Fig. 2f). 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. 2d) 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 behaviour is consistent with relatively close proximity facilitating momentary large course corrections (Fig. 2f, right inset). Leader-initiated pauses in termites might serve some unknown function (*e.g.*, motor planning[27,28]); however, we have no evidence that they facilitate follower control over any aspects of the trajectory.

Both ants and termites rely on physical contact as a feedback mechanism to maintain cohesion. However, whereas termites separate sporadically and can be likened to a person leading another by the hand, ants show a more complex coordination of social behaviour as they 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 is the sending of a complex message over a simple

channel which requires control of information flow for similar reasons as in machine-to-machine communication. Tandem running by the ant *T. albipennis* has also been likened to teaching—a social behaviour often used to distinguish humans from other animals—because the leader modifies her behaviour in the presence of a naïve follower at some cost and as a result of bidirectional feedback[15,18]. Regulation of information flow might be a required component of teaching. This assumption could be investigated by applying the methodology we put forward to other examples of teaching known in the animal kingdom[29].

Although social insects use cue-based mechanisms to regulate the flow of physical material (*e.g.*, food or nesting material[30,31]), our study is the first to reveal signalling mechanisms that control the flow of a non-physical quantity—information—in a non-human organism. This opens questions about the evolution of flow regulation: tandem running has evolved multiple times in the ants, and not all instances necessarily require acknowledgment signals[32]; thus a comparison across systems may provide insights into how signals that regulate other signals evolve. The methodology we put forward, which applies advanced information-theoretic measures to different coarse-grainings of the same dataset, can enable the discovery of cryptic signalling behaviours in other taxa and can reveal deeper insights into behaviours that have poorly or partially understood functions (e.g., turn-taking[12,13], complex coordinated dances in avian[33]).

Methods

Ant experiments. We used 6 colonies of *T. rugatulus* ants (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[34]. 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 hole over the centre of the nest cavity to allow ants to enter and leave the nest. We conducted emigration experiments to induce ants to perform tandem runs. To obtain sufficiently long tandem runs, we used a large experimental arena (370 mm by 655 mm) delimited by walls (37 mm tall) and subdivided by 5 barriers (10 mm by 310 mm) placed to form a contiguous corridor with alternating left and right turns (see Extended Data Fig. 1b). Both walls and barriers were coated with Fluon to prevent ants from leaving the experimental arena. A new nest was placed at one extremity of the corridor and was covered with a transparent red filter to encourage the ants, which prefer dark cavities[35], to move in. The nest housing a colony was transferred from its plastic box and placed at the other extremity of the corridor. Colony emigration was induced by removing the top slide of the occupied nest. We performed 6 experiments, one for each colony, and recorded them at 30 frames per second using a video camera with 1K resolution. For each colony, we then selected between 1 and 6 pairs of ants performing tandem runs obtaining a total of 20 samples. Selected tandem runs last more than 15 minutes and have the same pair of ants travelling between the two nests with no or minimal interaction with other members of the colony.

Termite experiments. Experiments with *C. formosanus* and *R. speratus* were performed as part of a recent study on sexually dimorphic movements of termites during mate search[19]. Alates from 2 colonies of *C. formosanus* were collected in Wakayama, Japan, in June 2017; alates from 5 colonies of *R. speratus* were collected in Kyoto, Japan, in May 2017. After controlled nuptial flight experiments, termites that shed their wings were selected and used for tandem run experiments. Experiments were performed in a Petri dish (145 mm Ø) filled with moistened plaster whose surface was scraped before each trial. A female and a male termite were introduced in the experimental arena with the opportunity to tandem run for up to 1 hour. A total of 17 experiments were performed for *C. formosanus* and 20 experiments for *R. speratus* using different individuals. Tandem runs were recorded at 30 frames per second using a video camera with a resolution of 640 by 480 pixels.

Data extraction. We extracted motion trajectories from video recordings of tandem runs by automatically tracking the position over time of leaders and followers. Motion tracking was accomplished using the UMATracker software[36]. As we tracked the centroids of each runner's body, the distance between individuals is always greater than zero even when leader and follower are in contact with each other. All trajectories were sampled at 30 frames per second and shortened to a duration of 15 minutes. Trajectories were then converted from pixels to millimetres using a scaling factor estimated by measuring known features of the experimental arena with ImageJ[37]. Body size of each runner was measured from video recordings of the experiments using ImageJ.

Encoding behavioural patterns into time series. We considered three possible behavioural patterns for each runner: *pausing pattern*, *rotation pattern*, and their combination *pausing & rotation pattern*. We did so by discretising the space-continuous trajectories of each leader and each follower using three different coarse-grainings. 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 discrete time series $X = (x_1, x_2, \dots)$. To capture the time interval where the sender best predicts the behaviour of the receiver, we subsampled spatial trajectories in time before encoding the behavioural 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 *counter-clockwise* (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, counter-clockwise 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 behavioural outcomes, we also considered a compound pausing & rotation pattern that simultaneously encodes for 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 *counter-clockwise* (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 counter-clockwise following the same methodology used for the rotation pattern.

Measuring predictive information. Our analysis of communication in tandem running is grounded on the theory of information[22] and on its constructs of entropy, conditional entropy, and transfer entropy. We aim to quantify how knowledge of the current behaviour of the sender allows us to predict the future behaviour of the receiver. We consider the behavioural 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 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[38] $H(F^{i+1}) = -\sum_{f_{i+1}} p(f_{i+1}) \log_2 p(f_{i+1})$. 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 behaviour $F^{(k)}$ 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 behaviour of the follower given what we know about its past behaviour.

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[23]. It measures the amount of information about the future behaviour of the receiver given by knowledge of the current behaviour 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[24]. 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[39] 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[40]. 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 dividing it by the conditional entropy as in

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

Normalised transfer entropy[40] is a dimensionless quantity that captures the proportion of the future behaviour 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 normalised 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[41].

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[40]. To do so, we randomly paired the behavioural 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 randomisation 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 maximise 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 behavioural 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

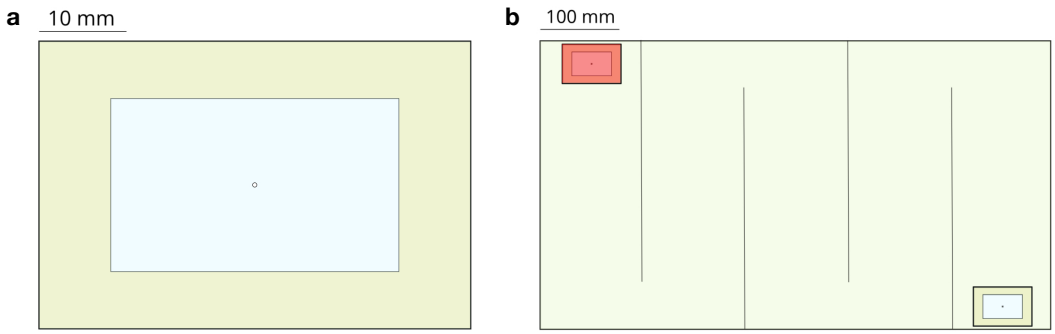
Conceptualization, G.V., T.P.P., S.I.W., and S.C.P; Methodology, G.V.; Formal Analysis, G.V.; Investigation, G.V. and N.M.; Writing–Original draft, G.V. and T.P.P.; Writing–Review & Editing, S.C.P, S.I.W., and N.M.; Funding acquisition, S.I.W., S.C.P, and T.P.P.

Additional information

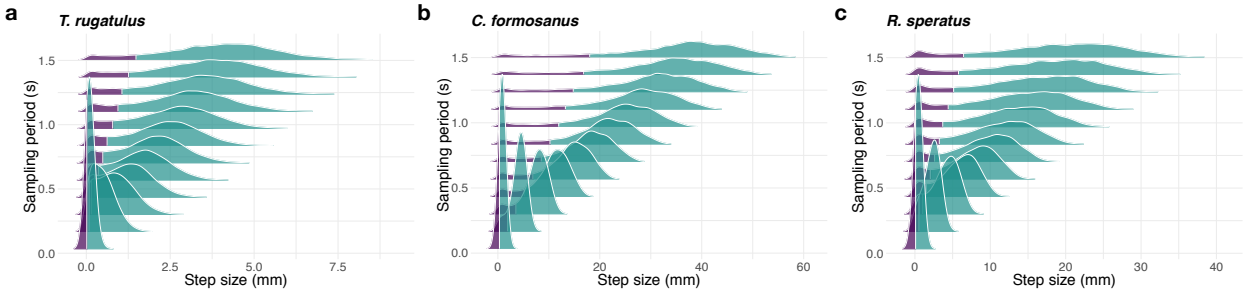
Accession codes: Data that support the findings of this study will be available in "figshare" with identifier "10.6084/m9.figshare.9786260" upon acceptance of the manuscript.

Competing interests: The authors declare no competing interest.

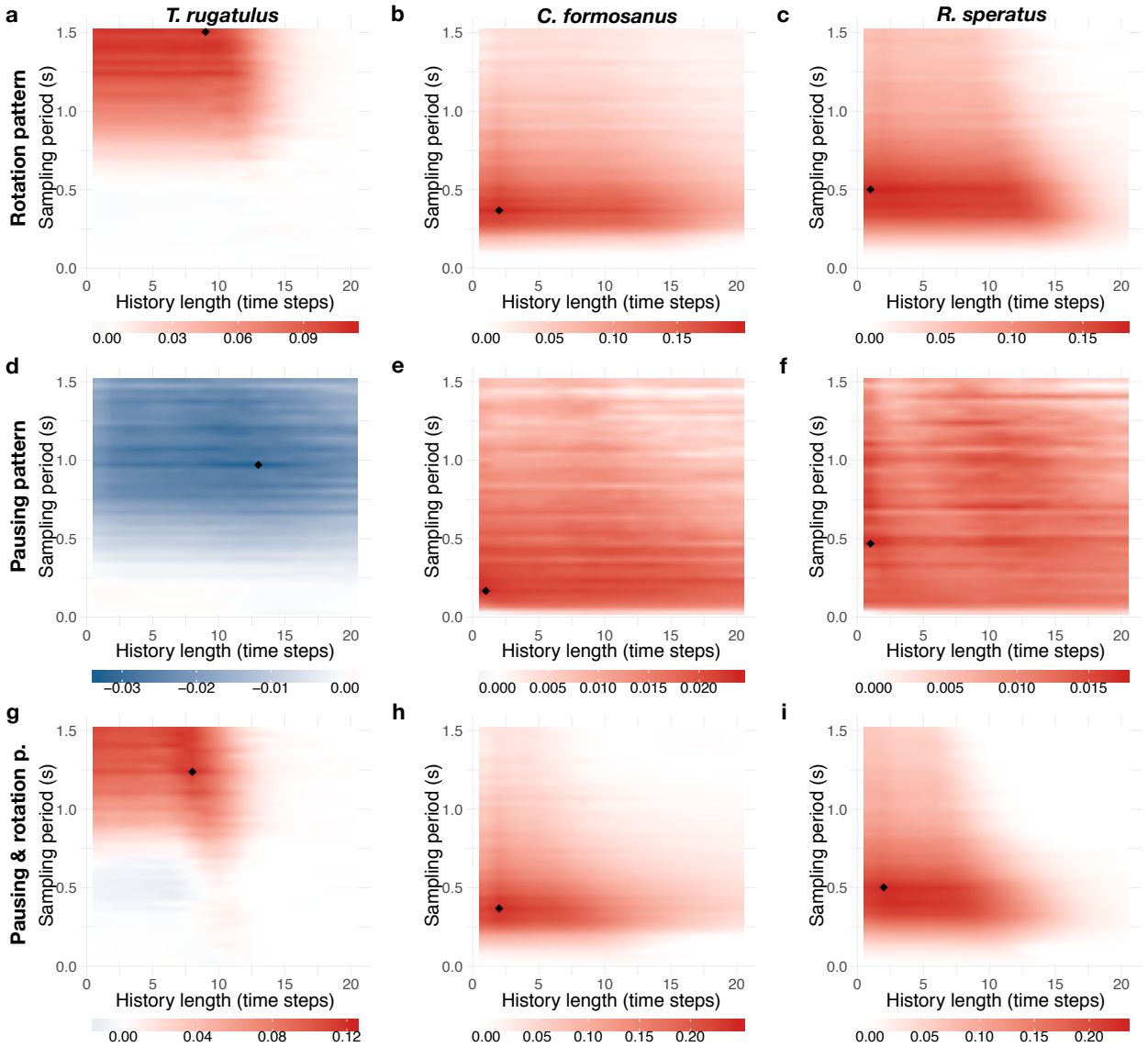
Extended data



Extended Data Figure 1 Experimental setup for T. rugatulus. Panel (a) shows the nest architecture with the entrance in its centre. Panel (b) shows the experimental setup partitioned into a corridor with the old nest (bottom right) and the new nest (top left) positioned at the extremities.



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

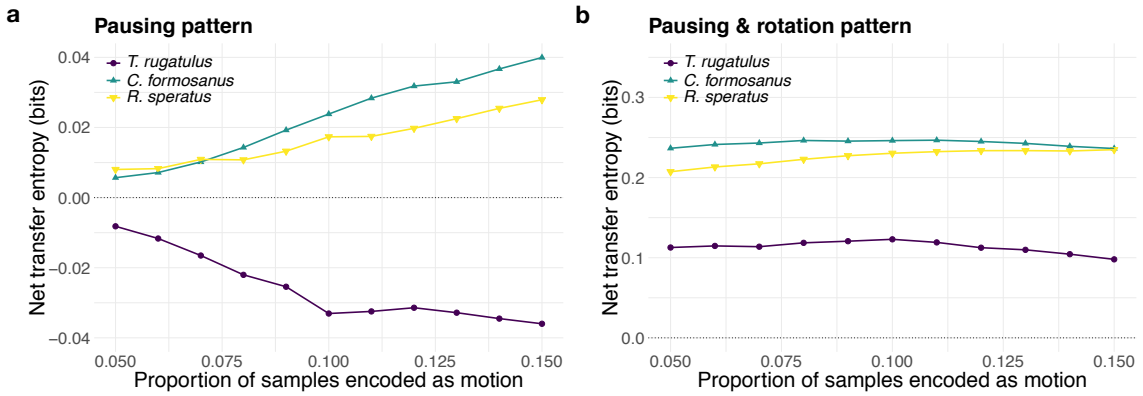


Extended Data Figure 3 Landscape of net information transfer. Panels show the landscape of net information transfer computed using net transfer entropy (bits) as a function of the sampling period and of the history length. Panels (a), (b), and (c) show the results for the rotation pattern, panels (d), (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. Colours 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.

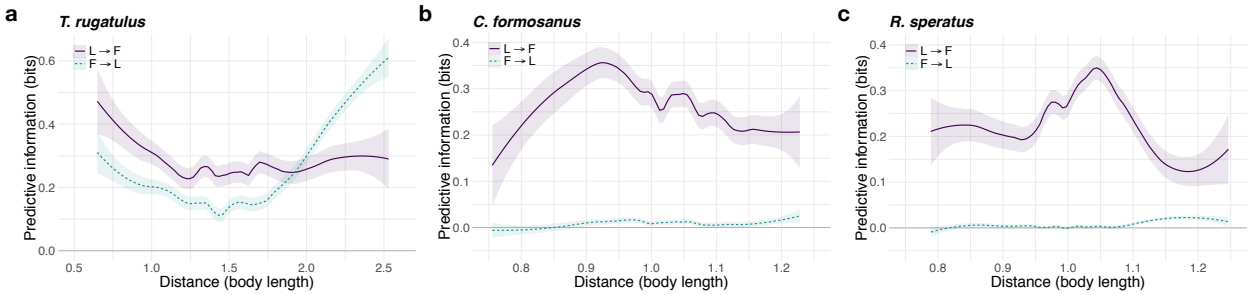
Extended Data Table 1 Selected parameter configurations for each species and behavioural pattern.

Species	Behavioural 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

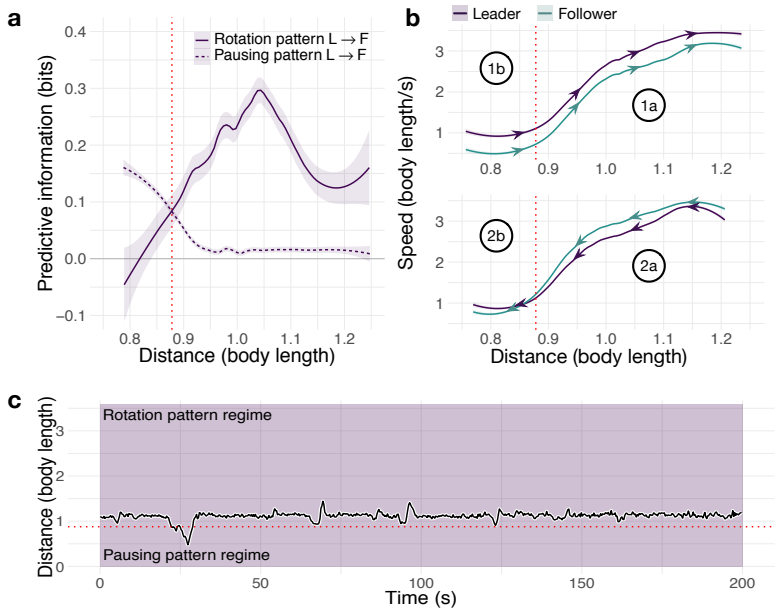
	Pausing & Rotation	0.3670	2
R. speratus	Rotation	0.5005	1
	Pausing	0.4671	1
	Pausing & Rotation	0.5005	2



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. Panel (a) show the results for the pausing pattern, panel (b) shows 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. Panels (a), (b), (c) show results, respectively, for the ant T. rugatulus, and the termites C. formosanus and R. speratus.



Extended Data Figure 6 Spatiotemporal dynamics of tandem running for R. speratus. Panel (a) shows the average predictive information as a function of the distance between centroids of runners, panel (b) shows the average speed difference between leader and follower as a function of the distance between their centroids for increasing and decreasing distance, and panel (c) shows the distance between the centroids of runners as a function of time. Colour purple represents the leader, colour green represents the follower.