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Emergent dynamical phases and collective motion in termites

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Termites which are able to forage in the open can be often seen, in the field or in the lab: (i) wandering around, forming no observable pattern, (ii) clustering themselves in a dense and almost immobile pack, or (iii) milling about in a circular movement. Despite been well reported patterns, they are normally regarded as independent phenomena whose specific traits have never been properly quantified. Evidence, however, favours the hypothesis that these are interdependent patterns, arisen from self-organized interactions and movement among workers. After all, termites are a form of active matter where blind cooperative individuals are self-propelled and lack the possibility of visual cues to spatially orientate and align. It follows that their non-trivial close-contact patterns could generate motion-collision-induced phase separations. This would then trigger the emergence of these three patterns (disorder, clustering, milling) as parts of the same continuum. By inspecting termite groups confined in arenas, we could quantitatively describe each one of these patterns in detail. We identified disorder, clustering and milling spatial patterns. These phases and their transitions are characterized aiming to offer refinements in the understanding of these aspects of self-propelled particles in active matter where close-range contacts and collisions are important.

1. Introduction

Active matter are systems made of a large number of interacting constituents (alive or not) able to convert some source of energy into directed motion [1–3]. In addition to being self-propelled, these constituents interact among themselves in such a way that their movement is both synchronized and correlated [4,5]. In doing so, collective behaviour and pattern formation spontaneously emerges. Pattern formation is a form of spatio-temporal self-organization that is ubiquitous in nature, spanning physical, chemical, biological and even social phenomena [6]. In living matter, it is regarded as a fundamental out-of-equilibrium process underlying morphogenesis at the cellular level [7–10], to quote an example. However it is also present as a product of the complex collective interactions of individuals in social groups. Swarms, fish schools and insect foraging trails are examples *par excellence* [11–13]. The distinct ordered and disordered phases exhibited by various artificial systems composed of active particles have been investigated [3,14]. For example, patterns found by evolving the original Vicsek model [15] present either a disordered phase or an ordered flocking state. For $N \rightarrow \infty$, in particular, a coexistence of two different phases is observed close to criticality [16].

Termites are, rightfully, biological active matter. They form groups of interacting individuals, and such interactions result in collective behaviours which translate into spatio-temporal emergent patterns [17–19]. Here we explore the

various emergent spatial patterns in individuals confined in arenas. These collective arrangements of termite individuals are commonly found in the field [20,21] as well as in the lab (as observed here; figure 1). Individuals in termite groups can be seen in the field and in the lab (i) wandering around, forming no observable pattern, or (ii) they cluster themselves in a dense and almost immobile pack, or (iii) mill about in a circular movement. Given the similarities between termite spatial organization and non-living active matter, we hypothesize that these collective arrangements of termites (i.e. disorder, clustering, milling) are parts of the same continuum, rather than behaviours originated from an independent selective pressure. In order to inspect this hypothesis, we parameterized phase changes in termite workers movement patterns in order to explore how interactions at a local smaller scale may control these changes, that is, the scale of the individual. Such a parameterization allowed us to inspect whether these changes lead to a change of one of these collective behaviours into another.

Besides a disordered phase, where termites are basically moving uncorrelated, collective-directed motion and stable spatial clusters in groups of workers can be clearly identified. The disorder is observed at the beginning of an experiment when termites are just deposited in the arenas and they are exploring the new surroundings. In this sense, the disordered phase is like the transient period of a dynamical system when the basis of attraction is being explored before arriving into the phase space attractor.

Collective-directed motion is known as milling or collective vortex where self-propelled particles rotate spontaneously in circular motion around a common centre. In termites, the formation of milling was first reported, and named ‘carrousel’, by Grassé and others in *B. natalensis* and *B. bellicosus* workers. Grassé noted that following a big perturbation, workers self-organize into a convoy, rotating in a circle for a very long time. He mentioned further that it was possible to often observe the spontaneous emergence of a second concentric circle of rotating termites but with the rotation direction inverted (see [20–22] and references therein).

Circling behaviours highly similar to termite milling are also observed in a variety of organisms: ants [23], caterpillar circles, bat doughnuts, amphibian vortex, duck swirl, and fish torus are just a few examples [24]. Milling is a kind of universal spatial phenomenon of abstract self-propelled particles, not necessarily alive, and is also present in simple computer models with or without spatial confinement, borders or walls [25–31]. In nature, when a scouting termite finds a profitable source of food, it returns to its nest laying an odour trail to be subsequently followed by its foraging nestmates. As these foragers follow these marks and find the resource, they reinforce this trail so that to keep track of the resource location. At a first glance, this could explain the milling observed by us in the lab and by Grassé [22] in the field. However, unprofitable sources of food do not stimulate scout termites to lay trails. Thence, providing that these field or lab circular paths do not lead to any food, it seems unwarranted to claim a role for trail pheromones in forming milling. Moreover, even if pheromones would play a role in maintaining the milling for some time, they would not explain the inception of milling. It seems thence reasonable to suspect that termite milling has some roots on the causes of milling spatial phenomena observed in abstract self-propelled particles which are not alive.

Clusters in termites are groups of individuals in close proximity, often engaged in body-to-body interactions through antennations but with the body barely moving. Clustering formation resembles a gas–liquid transition [32] where initial free and uncorrelated moving termites condense (get trapped) into clusters by means of social interactions that act as the attractive and condensation force. Termites are polar-like particles, as they have distinct heads and tails, so disorder–order changes are expected. In fact, they interact through a combination of steric repulsion and alignment interactions. It is reasonable to expect that the clustering phase is more likely to be observed at higher densities. In these conditions, most of the workers stay in the cluster, but a few may escape executing long walks in the arena. These roles (trapped and escaped) are interchanged in a way that most of the termites will get trapped again giving up the free walks at some point [19]. It is remarkable that the step-size statistics of this process which includes mostly short movements but also few long walks is self-similar (Lévy-like) [18,19].

In this contribution, we explore several dynamical phases in the behaviour of confined termites. We identify disorder, clustering and milling. We aim to characterize these phases and their changes in order to achieve a deep understanding of self-propelled particles in active matter both in living and artificial systems where close-range contacts and collisions are important.

2. Methods

Termite workers (*Cornitermes cumulans*) were collected in the grounds of the UFSJ (Universidade Federal de São João del-Rei) at its ‘Alto Paraopeba’ campus, in the municipality of Ouro Branco, Minas Gerais, Brazil. Termites were then taken to an acclimatized laboratory as described in detail in [18]. Experimental arenas consisted of a glass Petri dish upside down over a filter paper. Within the arena, a variable number of termite workers was inserted and their movements were recorded continuously from above, with a video camera for 55 min (Sony FDR AX–53 4K). Termite trajectories were captured and digitized at a sample rate of one point every 0.333 s with an automatic video-tracking software (for more details, see electronic supplementary information of the ref. [19]). No obstacles or food were present in the arenas. The resulting time series contained x , y spatial coordinates used for numerical analysis.

3. Results and discussion

Figure 1 displays images of the arena, illustrating experiments that represent the typical phases observed during the temporal evolution of the experiments. Each panel of figure 1 pertains to a different experiment. The panels qualitatively illustrate the existence of three phases, with images of the disordered, clustering and milling phases from left to right. We witnessed time series

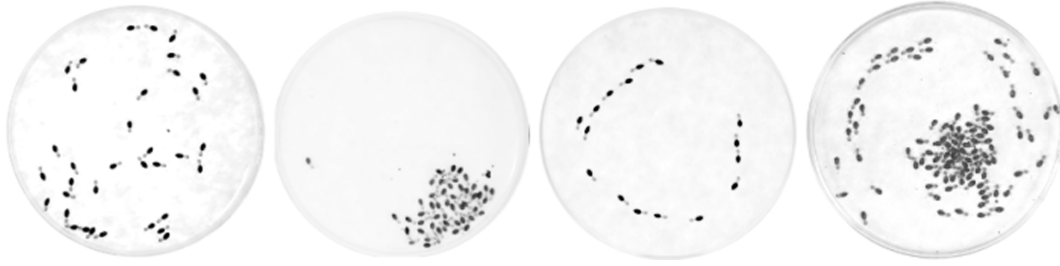


Figure 1. Examples of the typical dynamical phases observed in confined termites. Top view of the arenas and showing, from left to right, disorder, clustering, milling and an interesting coexistence of milling and clustering.

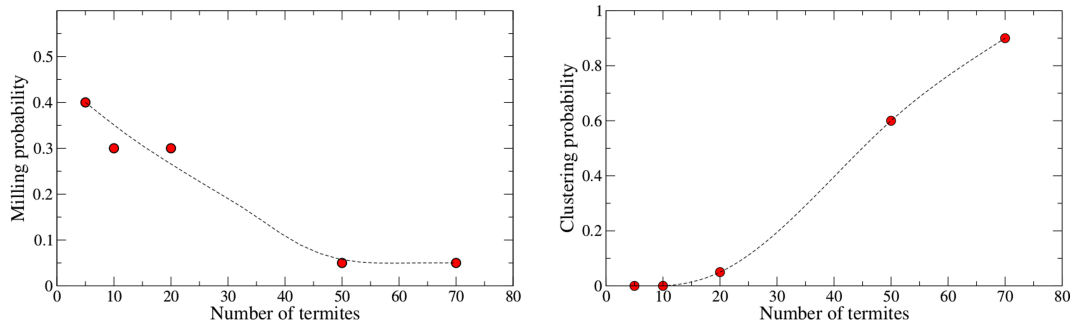


Figure 2. Role of the termite density in the emergence of two collective behaviours. Left is the probability of observing milling when density is varied in the containers. As the number of workers increases, the probability of milling decays because of overcrowding. At right, the probability of observing clustering increases along with the density. Each point in the plots corresponds to an average of 20 independent samples, always in 95 mm diameter arenas and about 1 h experiments. Dashed lines are a guide for the eyes only.

containing a single phase along all the observation time, as well as experiments exhibiting a change between phases, and occasionally the coexistence of multiple phases. The rightmost panel of [figure 1](#) presents an image exemplifying a scenario of phase coexistence (clustering and milling). One should emphasize that these phases can last from a few minutes to more than an hour.

3.1. Role of density

An individual may be recruited to a particular dynamical behaviour ([figure 2](#)) as a function of the number of individuals already committed to that behaviour [33], a phenomenon commonly known as social facilitation [34]. However, this may be a nonlinear response since the autocatalytic recruitment of individuals can be slowed down or halted when saturation happens beyond a given number or density of individuals. In ants, it was shown that a transition from a chaotic to a periodic state is a function of the density of individuals in a nest [35]. In termites, it was shown that density can regulate individual survival [17] or may enhance mating encounters by changing speed according to the density [36] and in robots, it may induce the formation of aggregation clusters [37]. Even vehicle traffic exhibits a phase transition as a function of density [12]. All this is because these are collective behaviours that depend on the number of participating individuals.

In our experiments ([figure 2](#)), we noticed that milling in these termites requires a low number of individuals to emerge. As a matter of fact, when the number is high and so is the density, we notice a low probability of milling formation. This seems counter-intuitive at first because high-density states would mean more social interactions to strengthen collective action; however, high density disrupts the formation of coherent spatial structures simply because of the lack of space due to the finite boundaries of the containers. On the opposite, the emergence of clustering needs a large number of participating individuals since it is an aggregative process ([figure 2](#)).

3.2. Time series

Termite walking and their movement patterns have been the subject of recent studies ranging from their anomalous diffusion properties [18,19] to the dynamics of turning angles [38,39]. It is precisely the analysis of turning angles that allows us to explore additional aspects of the emergence of behavioural phases. From the time series recordings, simple parameter measurements such as angular position were made and then used further to estimate a number of quantities as follows.

At each time step t , the i -termite position $\vec{S}_i(t) = (x_i(t), y_i(t))$ was recorded and the displacement was defined as

$$\Delta \vec{S}_i(t) = \vec{S}_i(t) - \vec{S}_i(t - dt), \quad (3.1)$$

as shown in [figure 3](#). The velocity was obtained using $\vec{v}_i(t) = \Delta \vec{S}_i(t)/dt$ where dt is the interval between the two consecutive positions. The turning angle $\Delta \theta_i(t) \in (-\pi, \pi)$ was defined as the angle variation between two consecutive displacements, as shown in

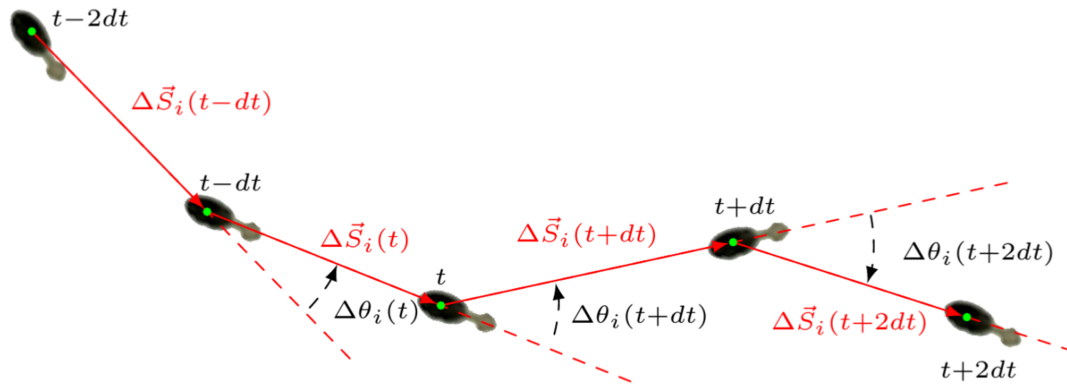


Figure 3. Schematic illustration of a sequence of steps of a termite between times $t - 2dt, t - dt, \dots, t + 2dt$. The red segments indicate the displacements between two consecutive positions. The red dashed lines indicate the turning angle or angular displacement, between the direction of a step and the next one. The dashed black arrows show the rotation direction.

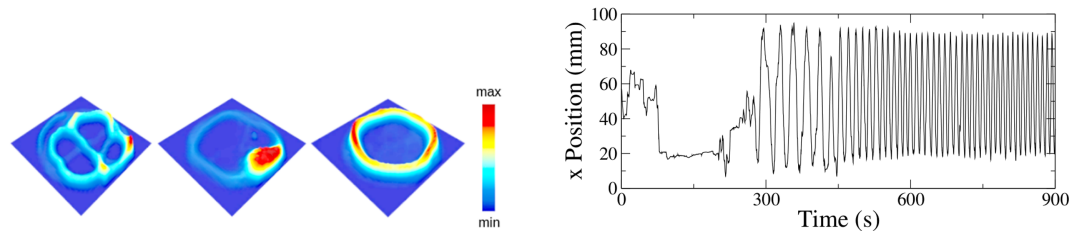


Figure 4. Typical temporal and spatial emergent patterns observed in confined termites. (Left) Accumulated activity in the arena as seen in a heat map; from left to right, disorder (45 termites, 105 mm-diameter arena), clustering (50 termites, 95 mm-diameter arena), and milling phases (20 termites, 100 mm-diameter arena). To build these plots, the arena area was divided into a square grid of size 40×40 units and the number of termites that entered and left each grid box during the experiment was recorded. (Right) Temporal evolution of the displacement x spatial coordinate exhibiting three phases, for one termite in an 100 mm-diameter arena together with other 19 termites. At around $t = 150$ s, there is an episode of clustering where the curve shows a plateau. At around 200 s, there is a disordered phase when the stable plateau is broken and from $t \approx 450$ s, there is a milling phase exhibiting typical periodicity.

figure 3 and using the following formula:

$$\theta_i(t) = \theta_i(t - dt) + \Delta\theta_i(t), \quad (3.2)$$

we have defined the angular position $\theta_i(t)$, a temporal measure of the displacement's direction, of the termite i .

Considering the observed phases, it is clear that the integrated trajectories of the termites exhibiting them are quite different. Therefore, it is important to examine quantitatively the spatial distribution of termites throughout the arena. To address this aspect, we defined a square that encloses the arena, splitting the area into a grid to determine the spatial distribution frequency. There are 40×40 bins in a grid that divides this square. Throughout the experiment, we kept track of how often termites visited each grid cell. Note that only the cells inside the circular arena were visited. The resulting plots, for each behavioural phase, are presented as examples in figure 4 left. In the disordered phase, several trajectories are visited. Meanwhile, in the clustering phase, the termites stay confined to a given region and, in the milling phase, a closed loop is more visited than other regions in the arena.

3.3. Displacement and turning angle fluctuations

To quantitatively characterize the termite behaviour and the emerging phase, we consider the individual displacement time evolution obtained from the recorded videos. Initially, we aim to illustrate the behaviour for each phase by examining the temporal displacement in the x spatial coordinate (displacement fluctuation). Each phase can be identified subjectively in a first approximation (see figure 4, right). In the disordered phase, the displacement fluctuates quite significantly; in the clustering case, we observe very small or no fluctuations; and finally, in the milling phase, the displacement exhibits periodic behaviour. For convenience and without loss of generality, the x position was analysed here using a fluctuation ratio r given by:

$$r = \langle x^2 \rangle / \langle x \rangle^2. \quad (3.3)$$

Results show that time series where a change from disorder to milling is present can be spotted easily because they exhibit the typical S-shaped curve of a phase change (figure 5). On the other hand, series without milling exhibit a rather flat fluctuation ratio along time. When a change from disorder to milling or to clustering is present, the value of r has the tendency to decay towards a lower value, suggesting a more coherent dynamical behaviour.

Another quantitative measure used to distinguish each phase and the changes from one phase to another is the turning angle. In particular, fluctuations of turning angles can be explored by means of a probability distribution of angle variations ($|\Delta\theta|$) as shown in the log-log plots in figure 6 containing typical examples of time series with different behavioural phases on them. While this is a very simple analysis, it captures well the differences in the temporal behaviour when there are regime changes and when not.

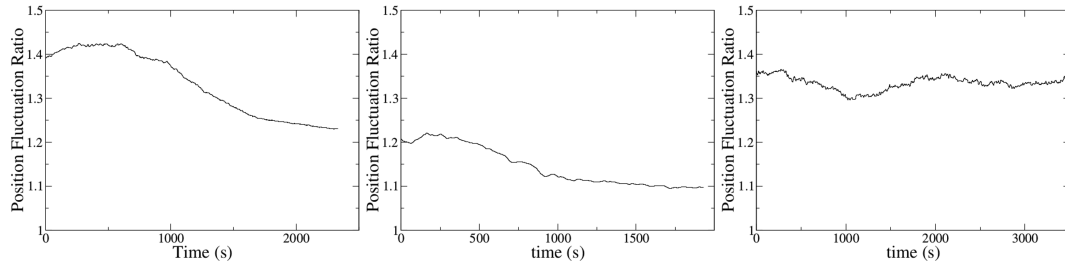


Figure 5. Typical examples of a position fluctuation ratio analysis (r). (Left and centre) Nine time series containing 50 006 points each were analysed and their r was calculated using a moving average window of size 1.5×10^4 . The average of all these points is shown as the black S-shaped curve that resembles a characteristic curve of a phase change. Left panel is a change from disorder to milling and the centre panel depicts a change from disorder to clustering. (Right) Seven time series containing 48 772 points each were analysed and their r was calculated using a moving average window of size 1.5×10^4 . The average is shown as the black curve exhibiting a nearly flat response. This is the case of disorder with no transition.

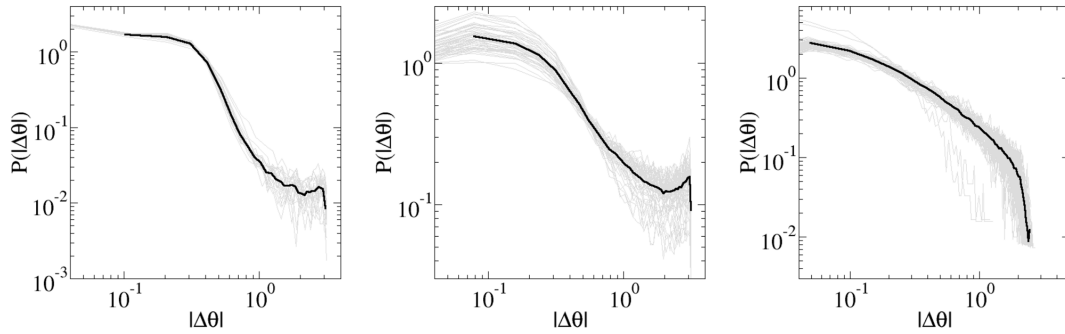


Figure 6. Typical plot examples of termite time series containing the probability distribution of angle fluctuations ($|\Delta\Theta|$) for different behavioural phases. Grey curves on each of them are individual termites in the arena and the black curve is the average of them. From left to right side: change from disorder to milling (20 time series containing 10 866 points each), change from milling to clustering (50 time series containing 10 374 points each) and disordered behaviour (78 time series with 2505 points each). Black S-shaped curve is obtained when there is a behavioural change. However in its absence, when there is just disordered behaviour, the average curve exhibits a simple decay response.

3.4. Mean velocity and Hurst exponent

The mean velocity of the termites increases when a change from clustering to disorder or from disorder to milling is observed. This could be expected, as the termites undergoing milling follow a path while in the disordered scenario, they are meandering through the arena. When they are in the clustering configuration, although a few termites break away from the cluster and walk around the arena, most of the termites are doing only small displacements around their position, so the mean velocity should be small.

The left panel of figure 7 shows the time evolution of the angular position obtained for all termites in one experiment. We analyse the curves obtained for the angular position considering the local roughness defined as the standard deviation of $\delta\theta_i(t)$ in relation to the mean inside a box of size ε :

$$w^2(\varepsilon) = \left\langle \frac{1}{N_\varepsilon} \sum_t (\theta_i(t) - \langle \theta \rangle)^2 \right\rangle_\varepsilon \quad (3.4)$$

where $\langle \theta \rangle$ is the mean value of $\theta_i(t)$ and N_ε the number of points inside the window of size ε . $\langle X \rangle_\varepsilon$ denotes a mean over the various windows of size ε . We consider 10 sectors to measure the local roughness (the sectors are indicated by the vertical lines in the left panel of figure 7).

Through the scaling analysis of the local roughness (w) as the window size ε increases, we observed that

$$w(\varepsilon) \sim \varepsilon^H, \quad (3.5)$$

where H is the Hurst exponent, which provides information related to autocorrelation in time series [40].

H values fall in the range $[0,1]$, interpreted as follows. A value $0.5 < H \leq 1$ indicates what is commonly termed ‘statistically persistent behaviour’; that is, whatever the past trend in the series, it is likely to continue in the future, implying a strong degree of predictability and correlation. A value $0 < H \leq 0.5$ represents ‘anti-persistent behaviour’ with low predictability.

Since termites in milling are performing a persistent behaviour over a closed trajectory, it is expected that the Hurst exponent of their steps be close to 1 while termites in the disordered state will be smaller. For each experiment, we split in ten equal parts all the time series (each one corresponding to one of the termites in the arena). Then, we averaged H and the velocity v over all termites in each time interval. In doing so, we obtain 10 consecutive pairs of values ($\langle v \rangle$, $\langle H \rangle$) for each experiment. In figure 8, these pairs are plotted, and it becomes evident that the region occupied by them can be associated with each of the emergent behavioural phases. There is a clear pattern where milling is characterized by high values of $\langle H \rangle$ and high-velocity values and clustering is characterized by low $\langle H \rangle$ values and low-velocity values. Disordered behaviour is associated with intermediary

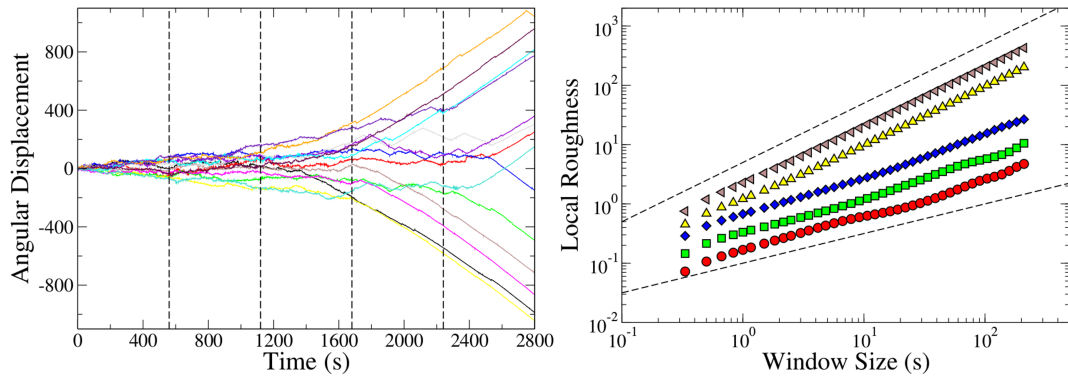


Figure 7. Angular displacement (left panel) and local roughness (right panel) for an experiment in which the termites change their behaviour from disordered to milling after 30 min (there were 14 termites in a 100 mm diameter arena). In left panel, each colour represents a different individual in the same arena. The vertical dashed lines in the left panel indicate five regions used to evaluate the local roughness (only five regions are shown for clarity). In right panel, each colour corresponds to the local roughness in one of the those regions (the first region in red circles, the second one in green squares, the third one in blue, the yellow triangles corresponds to the fourth region and the grey ones to the last region). The dashed lines in the right panel, which represent power laws with exponents of 0.5 (bottom) and 1.0 (top), should serve as a visual guide.

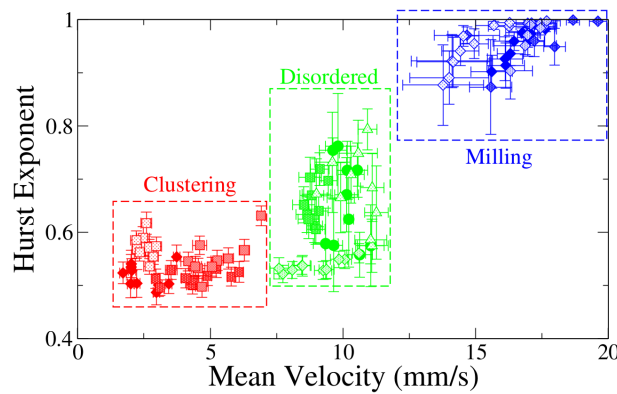


Figure 8. A graph depicting the mean Hurst exponent against mean velocity. Each point is an average from the measures of all termites in the arena in a time window. Same symbols correspond to the different time windows in the same experiment, and their colours were choose based on the emergent behaviour observed. One can see single phases well separated into defined regions as indicated by the dashed rectangles. Each experiment was divided into 10 time windows, within which we evaluated the Hurst exponent and the mean velocity. So, for a 55 minute video, this resulted in the analysis of 10 short series, each lasting 5.5 min. This allows us to detect changes in emergent behaviour over time. Data are from 12 independent experiments that range from 3 to 70 termites, in arenas with diameters between 90 and 105 mm.

values of both $\langle H \rangle$ and $\langle v \rangle$. It is interesting to note that, since our measurements were taken in a range of time windows, it allows us to identify the behavioural transitions across time.

3.5. Momentum and s.d. of turning angle

To further characterize the collective behaviour of the termite groups and their behavioural phases, we use two order parameters based on previous measures discussed elsewhere in simulation models and studies of schooling fish [41–43]. First, the rotation order parameter describes the rotation around the centre of the arena for each time, it is defined as

$$O_L = \frac{(1/N) \sum_{i=1}^N |\vec{u}_i \times \vec{r}_i|}{\max\{\sum_{i=1}^N (1/N) |\vec{u}_i \times \vec{r}_i|\}}, \quad (3.6)$$

here, $\vec{u}_i$ and $\vec{r}_i$ are velocity and position vectors in relation to the center of the arena of the i -th termite, respectively. As in previous works, $O_L \in \{0, 1\}$ by construction, where 0 corresponds to no-rotation and 1 to strong rotation about the centre of the arena. The absolute values are important here because, in contrast to most of the organisms that perform milling, termites do not necessarily move all of them in the same direction: some of them can move in the clockwise direction while others are anticlockwise, changing directions eventually. As one can see in figure 9, when the termites are in the milling phase, one observes strong rotation. In the clustering phase, there is a weak rotation and in the disordered phase, one observes intermediate values of the mean value of the absolute angular momenta. In the second-order parameter, we consider the s.d. value of the turning angle of the termites. In contrast to angular momenta, this parameter decreases as we go from clustering to disorder to milling, as can be seen in figure 9. The construction of this order parameter considers a normalization by the maximum value in order to get $O_{\Delta\theta} \in \{0, 1\}$.

To demonstrate more clearly these dynamically stable states, figure 10 shows a two-dimensional phase space spanned by the order parameter related to the variance of the turning angle $O_{\Delta\theta}$ and the one related to the angular momentum O_L . The mean turning angle of all termites analysed is zero (data not shown), and values of $O_{\Delta\theta}$ close to 1 are associated with a meandering

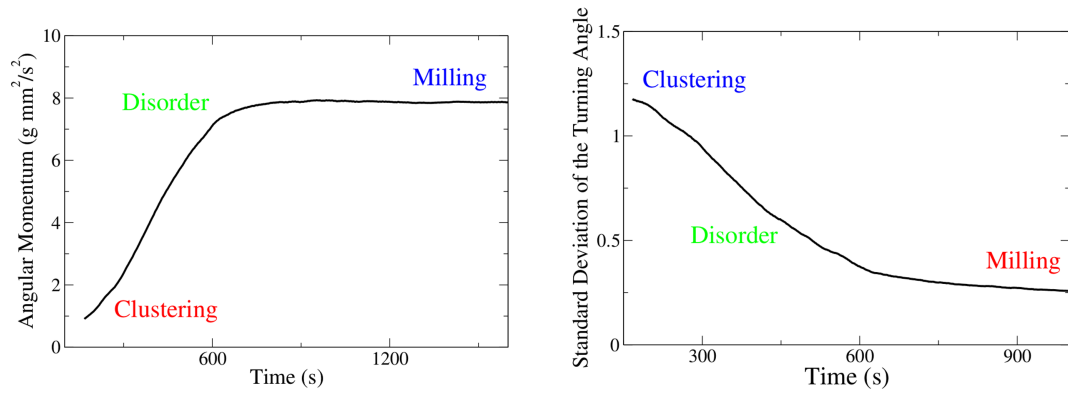


Figure 9. Typical behaviours of the absolute value of the angular momenta (left) and of the s.d. value of the turning angle (right), averaged in all termites in the arena, in an experiment where the three phases were observed (in this particular experiment, there were 20 termites in a 100 mm-diameter arena).

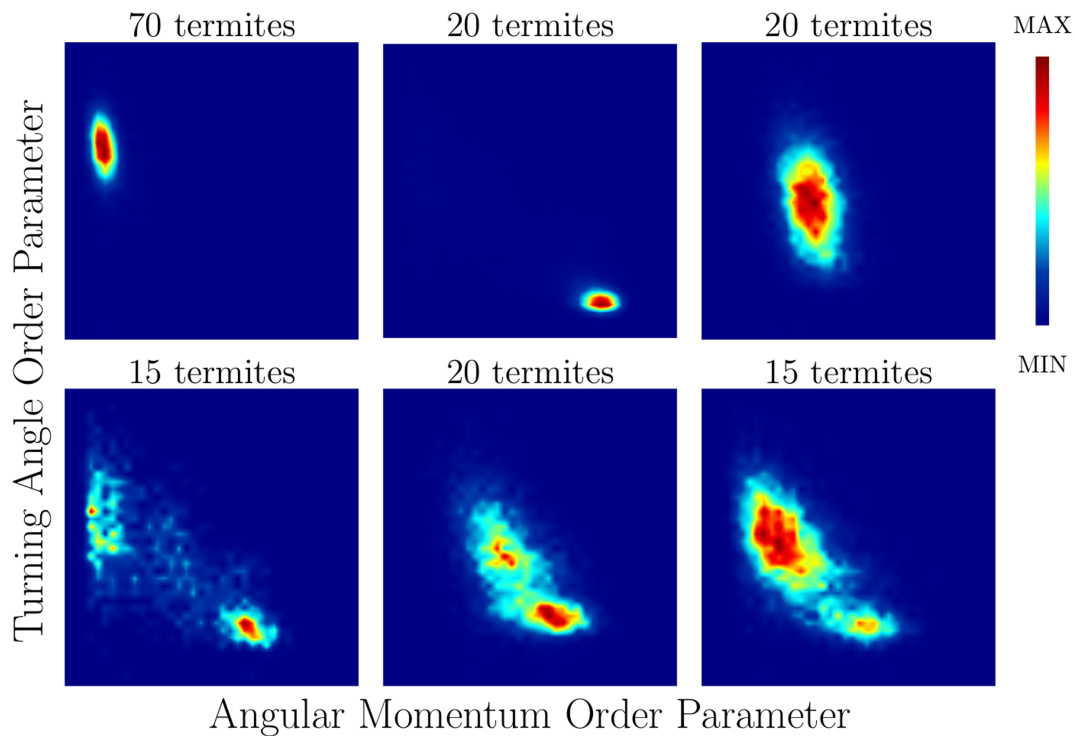


Figure 10. Density plots of the variance of the turning angle versus angular momentum order parameters from six independent experiments, both variables in the interval $[0, 1]$ by construction in each plot. The data show typical cases of each phase (top panels, from left to right: clustering, milling and disordered) and also cases where behavioural transitions are observed (bottom panel, from left to right side: from milling to clustering, from disordered to milling, and from clustering to disordered to milling). Each plot was built using time series with between 10^4 and 10^5 data points. The experiments correspond to (right to left side, top to bottom): 70 termites in a 95 mm arena, 20 termites in a 100 mm arena, 20 termites in a 95 mm arena, 15 termites in a 100 mm arena, 20 termites in a 100 mm arena and 15 termites in a 90 mm arena.

behaviour. Higher values of O_L are associated with stronger rotation about the centre of the arena. In this figure, we consider the proportion of time spent in different regions of this phase space, with red representing more time spent in a given region and blue the least time.

The top panels of figure 10, from left to right, display typical cases where we observe clustering, milling and disordered, during the entire trial. Some examples of the transition between different phases are shown in the bottom panels. Specifically, the changes from milling to clustering, disordered to clustering, and clustering to disordered to milling are displayed (from left to right, respectively).

Understanding the emergence of collective behaviour in active matter and the transitions from one state or phase to another from the interactions of many individual self-propelled constituents is challenging, especially in biological systems. In termites, under laboratory confinement, there are at least three detectable dynamical phases: disorder, clustering and milling with transitions from disorder to clustering and disorder to milling. The explanations of what triggers these transitions remain elusive and largely unknown [24]. Density, velocity, alignment and collisions (termites are blind [44]) are factors worth exploring and we have produced in the present study a number of experiments aimed at identifying parameters that can characterize the phases and their changes). However, it is important to remember that milling (vortex behaviour) is ubiquitous to many organisms and artificial systems under very different spatial situations [24] and so the importance to provide new insights on termites is relevant. The same applies to the other phases we describe here. Grassé [20] could not point the causes of milling but he did point out that it

was a natural event that occurred in the field. Our experimental setup was able to replicate, in the lab, these three field behaviours and that gave us confidence in drawing biological meaning from our assays.

We hope that this study could be helpful for improving our understanding of diverse behavioural aspects of self-organized patterns and phase transitions in active matter including other social living species and artificial systems such as swarm models [45], programmable robots [46] and engineering and interdisciplinary applications such traffic flows [47], smart aggregates [48] and shape-memory materials [49].

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Time series containing examples of termite walking trajectories are available at the FAIR-aligned Harvard Metaverse repository: [50].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. L.R.P.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; S.G.A.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; O.DeS.: funding acquisition, investigation, resources, supervision, validation, writing—original draft, writing—review and editing; O.M.: formal analysis, funding acquisition, investigation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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