The Superstatistics of confined ants: From serenity to panic

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Nonequilibrium systems with strong parameter fluctuations are difficult to describe with ordinary Statistical Mechanics. Superstatistics –that can be seen as statistics of an statistics– has emerged as a tool able to describe these complex systems. It has been successfully applied, for example, to hydrodynamic turbulence, internal convection, and even DNA architecture, but not to macroscopic biological systems. Here we present fully controlled laboratory experiments in confined ants both in normal and in “panic” conditions. Using a data-driven superstatistical model, we reproduce key signatures of their motion: from non-Gaussian velocity distributions driven by a Log-normal diffusion coefficient, to clustering away from the source of danger information.

Keywords: Superstatistics; Langevin; ants; panic; collective motion

SIGNIFICANCE STATEMENT

We introduce Superstatistics as a study tool in the animal world, and report its Log-normal variant in a living system. Our study suggests that “panicked” ants, when exposed to a threat, can transmit information to their nestmates through a barrier they cannot physically cross. We explain both normal and panic dynamics, identifying non-Gaussian velocity densities, time scale separation, and the statistics of the diffusion coefficient. We also reveal distinct behavioral regimes in the ants’ collective panic response and how it relates with the individual ant memory and cluster formation. Furthermore, our findings indicate that optical signals or simple antennation are not significant mechanisms for panic transmission. We believe that these discoveries provide a foundation to uncover the biological origin of Log-normal type diffusion in confined environments.

INTRODUCTION

Nature displays a diversity of collective biological behaviors ranging from the microscopic to the macroscopic scales, and from high confined environments to the open space: the movement of cells during wound heal [1–3] and the flocking of birds [4–6] illustrate quite well those scenarios.

Here, we focus on the collective motion of confined macroscopic individuals, which is a common scenario in eusocial organisms, such as ants, who often live in high density societies. Leaf-cutter ants like Atta Insularis build complex nests made of networks of tunnels and chambers within which they live, move, take care of eggs, and even harvest fungus. While there is an extensive body of work that qualitatively describes the activity of ants in both open and confined spaces, its detailed quantitative understanding is still challenging [7–9].

In terms of quantitative modelling, one may start invoking the Langevin equation, which captures the finding that animals tend to maintain their direction of motion during some characteristic (persistence) time [10–13]. Namely,

$$\frac{d}{dt}v_i(t) = -\gamma v_i(t) + \sigma \xi_i(t)$$

(1)

where \(v_i\) denotes the \(i\)-th component of velocity; \(\gamma\), a positive parameter that encloses directional persistence; and \(\sigma\), the intensity of a Gaussian white noise, \(\xi_i\). A more complete overview of the statistical properties of Equation (1) was made in 1931 and it is known as Ornstein-Uhlenbeck process [14], nowadays a reference in ecological models for persistent movement [10].

In addition to this, a superposition of different dynamics on different time scales often describes properties of driven nonequilibrium systems [15], e.g., the fast jiggly dynamics of a Brownian particle subject to slow environmental fluctuations of a given diffusivity [16, 17]. This is known as Superstatistics (which stands for superposition of statistics), and one of its key merits is the ability to explain the emergence of non-Gaussian densities [18, 19].

The theory is connected to Langevin systems and, within the framework of Statistical Mechanics, can be interpreted by considering a system that is composed of small regions or cells that are temporarily in local equilibrium, showing spatio-temporal fluctuations of some intensive quantity, such as the inverse temperature \(\beta = 2\gamma/\sigma^2\) in Equation (1). It is assumed that the system
reaches local equilibrium on a timescale $\tau_1$ much smaller than the time $\tau_2$ needed for $\beta$ to vary among cells. Consequently, within each region, $\beta$ could be considered approximately constant. Then, during time intervals of the order of $\tau_2$ and inside each cell of a system following the dynamics of Equation (1), local Gaussian velocity stationary distributions of the form:

$$p(v_i|\beta) = \left(\frac{\beta}{2\pi}\right)^{1/2} e^{-\beta v_i^2/2}$$

arise. This means that to describe the long-time behavior, the marginal distribution for the $i$-th component of velocity $v_i$,

$$p(v_i) = \int_0^\infty p(v_i|\beta)f(\beta)\,d\beta$$

should be computed. Here, $f(\beta)$ is the probability density function of $\beta$, and a relation such as Equation (3) explains the emergence of many non-Gaussian behaviors reported in the literature [20–24].

By performing careful experiments, here we use the behavior of confined ants in normal and panic conditions as a case study for superstatistical analysis. We quantify the motion of ants that are confined into a square, quasi-2D cell. A number of interesting features arise: from non-Gaussian ant velocity distribution heavily influenced by speed-dependent noise intensity, to the existence of a fluctuating diffusivity, characteristic of non-Gaussian diffusion emergence in single-particle tracking experiments performed in soft and biological matter [24, 25]. Then, we expose the confined ants to the effect of danger information: ants in a neighbouring cell that are chemically excited transmit “panic information” to the individuals under study through a specially-designed barrier that cannot be physically crossed. A collective output is built within minutes: in spite of their short individual memory [8], the ants form a cluster whose center shifts away from the barrier through which the danger information has emerged. In other words, the individual short-term memory has become a long-term collective memory when danger information is turned on. We propose a superstatistical model able to quantitatively reproduce all the experimentally observed features, both before and after panic. To the best of our knowledge, this is the first documented occurrence of Superstatistics in the animal world and Log-normal Superstatistics in any living system.

**EXPERIMENTAL DETAILS**

A system consisting in two 3D-printed cells, each of $6 \times 6 \times 1 \text{cm}^3$ and separated by a barrier, was designed to investigate the possible transmission of danger information by ants from one cell to another (see Figure 1).

Ants are placed in both cells and filmed during 5 minutes. Then, an insect repellent is added at the center of the left cell and another 10 minutes of film is taken. The left and right cells will be referred to as DANGER and SAFE, respectively. In a CONTROL experiment the same procedure is followed, except no ants are introduced into the DANGER arena. We hypothesize that, if ants in the SAFE arena move away from the barrier after the addition of the repellent a significantly larger distance than they do during a CONTROL experiment, danger information has been transmitted by the “panicked” ants in the DANGER cell to the ants in the SAFE cell beyond any “passive” diffusion of the repellent through the barrier.

In an attempt to isolate the possible mechanisms of danger information transmission, various types of barriers were employed (lower panel of Figure 1A). The glass barrier consists of a transparent glass wall aimed at filtering optical signals as the primary mechanism for the transfer of panic information. The thick barrier is made in such a way that ants on both sides can make contact with their extremities (e.g., their respective antennas) but cannot antennate the bodies of individuals in the opposite arena. In contrast, the thin barrier allows such contacts (see Figure 1C). We term our protocols GLASS, THICK and THIN, corresponding to each type of barrier.

A total of 10 repetitions for each protocol was made and ants were used only once in order to avoid any effects
associated to previous individual experience [26]. The experiments were performed in workers of the ant species *Atta insularis*, called bibijagua in Cuba, that have been extensively studied both in natural and laboratory conditions [27–32] (see Figure S1 in Supplementary Information for a high resolution picture of a typical individual).

**COLLECTIVE MOTION: TRACKING THE CENTER OF MASS**

Using image processing techniques, we tracked the center of mass (CM) in both cells for each protocol. Data was processed using yupi, a Python library to handle (tracking, transform, generate, store, analyze, visualize) trajectory data [33]. As illustrated in Figure 2A-C for typical experiments, the motion of the CM at the DANGER cell is always near its geometrical center, independently from the protocol used. A similar situation holds for the SAFE cell, with the conspicuous exception of THIN, where the CM tends to move away from the barrier after the repellent is added into the DANGER arena. Figure 2E-H shows the time evolution of the $x$-coordinate of the CM at the SAFE cell with respect to its starting position, corresponding to an average between the repetitions of each type of experiment.

The net displacement of the CM, defined as the difference between its final and initial $x$-coordinate averaged over the 15th and 5th minutes, was computed (see Figure S2 on Supplementary Information). A non-parametric Mann-Whitney test [34] was used to test the hypothesis that the pair of samples THIN-GLASS, THIN-THICK and THIN-CONTROL come from populations with identical means. We find that the three p-values are 0.0017, 0.0004 and 0.0373, respectively. Hence, we argue that only in the THIN protocol the addition of repellent induces an “escape response” in the ants trapped in the SAFE cell.

With this we are also saying that the CONTROL experiment shows that the mere diffusion of the repellent from DANGER to SAFE does not produce a significant shift of the CM in the SAFE cell. So, the escape response is mediated by some kind of information transmitted by panicked ants from DANGER to SAFE. (A video containing an example of each kind of experiment, including the evolution of the CM, can be found in Movie S1 as Supplementary Information).

Figure 2C,G also reveals an interesting behavior of the ants in the SAFE arena as they escape from the barrier. Immediately following the repellent injection, the velocity of the CM rapidly spikes, indicating a fast dynamic response that lasts for about one minute. This is followed by a slower process in which the ants form a stable cluster at a certain distance from the barrier, a retreat that is quite distinct from the immediate reaction seen when ants are directly exposed to insect repellent [27]. Further details of this behavior will be discussed later.

**MOTION ANALYSIS BEFORE PANIC**

Having established that the THIN protocol promotes the propagation of danger information through the barrier, we studied individual trajectories of ants confined in the SAFE cell only using thin barriers. We used the CONTROL experiments to establish a “baseline” model of how ants behave when confined in the SAFE cell, considering only their interactions with each other and with the cell walls. We chose CONTROL protocol because, in this setup, ant interactions with the left wall (i.e., the barrier) are influenced solely by the barrier itself, without interference with the ants in the DANGER arena. Then, in the next section, we will build upon this model and extend it to the case where ants also interact with those in the DANGER cell and get danger information.

Data consists in approximately 20 randomly selected ants that were tracked manually during different repetitions of the CONTROL protocol. Trajectories were taken...
deviation of both components, however, are not independent of velocity, as demonstrated in the upper part of the same figure, and within their error bars, they exhibit the same non-linear dependence on \( v \). Therefore, for the mean of the parallel component, \( \langle a^\parallel \rangle \), and the intensity of both the parallel and perpendicular fluctuations, \( \langle (a^\parallel)^2 - (a^\perp)^2 \rangle \Delta t^{1/2} \), which we denote as \( \mu(v) \) and \( \sigma(v) \), respectively, we propose the following relations:

\[
\mu(v) = -\gamma v \tag{4a}
\]
\[
\sigma(v) = \Sigma + \Delta \Sigma (1 - e^{-v/v\gamma}) \tag{4b}
\]

where \( \gamma^{-1} \) is a persistence time. The first term, \( \Sigma \), accounts for the intensity of acceleration fluctuations at rest, while the second term describes its increase with the velocity, mediated by a characteristic speed \( v_{\gamma} \) and a proportionality factor, \( \Delta \Sigma \). Note that, in order to obtain \( \sigma(v) \), the standard deviation of acceleration time series was scaled by \( \Delta t^{1/2} \) to ensure dimensional consistency with a continuous stochastic process, where the white noise has units of \( s^{-1/2} \). We also tested other models for the function \( \sigma(v) \), such as general power laws of the form \( a + b v^c \), but none performed better than the exponential model in Equation (4b), as they could, for instance, produce unphysical values for \( \sigma(v = 0) \). Equation (4b) was fitted and the numerical values of the parameters are reported in Table I. These results strongly suggest to begin with a Langevin equation such as Equation (1) as a model for ant movement, with a slight modification that allows for \( \sigma \) to be expressed as \( \sigma(v) \), a function of speed.

Alongside, the temporal correlation of ant velocities decay exponentially, as shown in a plot of the velocity autocorrelation function (VACF) depicted in Figure 4B. With this, we found a persistence time of \( \gamma^{-1} = 0.53 \) s (also reported in Table I), which is consistent with the inverse of the slope of parallel acceleration plot shown in Figure 4A. Let’s now look in more detail into the stochastic part of accelerations.

Figure 5A shows the probability density function (PDF) for the zero-mean parallel and perpendicular acceleration components, i.e., \( a^\parallel - (a^\parallel) \), in units of its standard deviation. The non-Gaussian shape highlights the need for a model with non-Gaussian noise. A straightforward assumption is to allow the noise intensity to be stochastic. This leads us to the domain of Su-
perstatistics, as the more basic consideration following a constant noise intensity is that it should be a slowly varying process. Note that in Figure S3, the noise autocorrelation function (NACF) appears as a flat function of time close to zero, so acceleration fluctuations are not correlated at the time scales under study.

A dynamical reason for the non-Gaussian behavior seen in Figure 5A has been proven to be due to Superstatistics whenever a superposition of local Gaussians (2) whose variance fluctuates on a large spatio-temporal scale arise. Therefore, it is needed to check if time series does contain separate time scales. For that, as suggested by [35], a time average of the local flatness, $\kappa_i$, of velocity components, $v_i$, was computed for computing time intervals, $\tau$:

$$\kappa_i(\tau) = \frac{1}{T-\tau} \int_0^{T-\tau} \frac{\langle (v_i - \langle v_i \rangle)^4 \rangle}{\langle (v_i - \langle v_i \rangle)^2 \rangle^2} dt'$$  \hspace{1cm} (5)

Here, $T$ is the overall measurement time and $\langle v_i \rangle$ is the average of the $i$-th velocity component on a time window, $\tau$. The result is shown in Figure 4C, where a dashed line was drawn to indicate the flatness of the Gaussian. The time $\tau_2$ at which this line intercepts $\kappa_i(\tau)$ corresponds to a time scale $\tau_2 = 3.3s$. Having pointed out that the time scale at which velocity fluctuates is $\tau_1 \equiv \gamma^{-1} = 0.53s$, the ratio $\tau_2/\tau_1 \approx 6$ implies that there exist some intensive parameter, $\beta(t)$, that fluctuates on a temporal scale 6 times larger than the one of the velocity, $v(t)$.

The slowly varying stochastic process $\beta(t)$ can then be determined by noticing that $\beta^{-1}$ is the variance of the local Gaussians (2). Namely,

$$\beta(t) = \frac{1}{\langle v_i^2(t) \rangle_{\tau_2} - \langle v_i(t) \rangle_{\tau_2}^2}$$  \hspace{1cm} (6)

where $\langle \cdot \rangle_{\tau_2}$ means that the average is taken over a time window of the order of $\tau_2$. So, we looked for a suitable power $p$ such that $\beta^p$ could make the dynamics fall into one of the universality superstatistical classes, e.g., $\chi^2$ or Log-normal [36]. We found that, indeed, when $p = -1$, it is the diffusion coefficient, $D \propto \beta^{-1}$, the slowly varying intensive parameter. Furthermore, Figure 4D shows that it follows a Log-normal density that, in its standardized form, looks like:

$$f(D) = \frac{1}{Dv(2\pi s^2)} \exp \left( -\frac{\log^2 D}{2s^2} \right)$$  \hspace{1cm} (7)

and whose shape parameter, $s$, is given in Table 1. Note that the fit was performed within a range of up to 15 standard deviations (inset of Figure 4D). Caution must be exercised when fitting experimental data as Log-normal Superstatistics and stretched exponentials since they can produce similar fits and typical experimental conditions often do not reach the asymptotic tails [36]. In the inset plot of Figure 4C typical realizations of $v_x(t)$ and $D(t)$ are depicted, and the time scale separation can be qualitatively verified by observing how one process changes faster than the other.

Based on these results, and without introducing free parameters, we used the persistence time $\gamma^{-1}$, the speed-dependent noise intensity $\sigma(v)$, and the slowly varying diffusion coefficient $D(t)$—which follows a Log-normal distribution with $s$ as the shape parameter—to develop a superstatistical Langevin equation to model the velocity component $v_i(t)$ of ants in the SAFE cell prior to the induction of danger, taking the form:

$$\frac{d}{dt}v_i(t) = -\gamma v_i(t) + \sigma(v)\sqrt{2\gamma^2D(t)}\xi_i(t)$$  \hspace{1cm} (8)

Here, at any time instant $t$, the diffusion coefficient $D(t)$...
and the Gaussian $ξ_i(t)$ are used to generate the stochastic variable $η(t) = \sqrt{2τ_D(t)}ξ_i(t)$. Then $η(t)$ is standardized by dividing by its standard deviation to be finally scaled by $σ(v)$. A Runge-Kutta method of strong order 1.5 within a Milstein scheme to compute Stratonovich-type integrals was used for numerical integration \cite{37}.

The PDF of parallel and perpendicular acceleration fluctuations can be successfully explained by Equation (8), as shown in Figure 5A. The model captures the non-Gaussian essence of the stochastic part that characterizes changes in velocity. Furthermore, Figure 5B displays experimental probability densities for the $x$ and $y$ velocity components. Apart from fluctuations due to the finite nature of experimental data, no discrepancies are observed between the shapes of the distributions, which is consistent with the spatial homogeneity and isotropy of the surface of the arena. The model also predicts the observed peak at low velocities and tails that extend far from a Gaussian yet bellow a power law, in line with the intensity of the parallel and perpendicular fluctuations of acceleration components, $σ(v)$, was the only observable that appeared to be significantly affected following the onset of panic. Figure 6D shows the time evolution of $σ(v)$ along with the fitting according to Equation (4b). Both components still remain indistinguishable over time. To further analyze their time-dependent behavior, we inspect the evolution of the parameters in Equation (4b). Figure 6E shows that the three parameters may be assumed nearly constant until around the 9th minute of the experiment, when two of them, $ΔΣ(t)$ and $ν_σ(t)$, increase suddenly and quickly relaxes back to its initial value, while $Σ(t)$ stays invariant. For later simulations, $ΔΣ(t)$ and $ν_σ(t)$ were fit to contiguous back-to-back exponential functions with matching growth and relaxation rates, selected for their simplicity in characterizing rapid changes. The timing at which this peak occurs will subsequently be used as a key measure of one of the most significant timescales in the ants’ mechanism in response to panic.

As mentioned previously, the collective behavior of ants in the SAFE cell is mediated by a fast dynamics that
span approximately one minute as soon as the repellent is injected. Before that, ants were dispersed throughout the arena. Therefore, when panic is induced in the 5th minute of the experiment, it can be assumed that an ant at the barrier in SAFE is immediately informed and becomes “activated”. After a certain characteristic time, $\tau_f$, this ant communicates the danger information to another nestmate, resulting in two activated ants. This cascade continues, and it ends after $T = 1$ min when the total number of individuals, $N_T = 20$, in the arena are informed. Consequently, the number of activated ants at time $t$, $N(t)$, obeys the differential equation $\dot{N} = \lambda_f N$ with the initial condition $N(0) = 1$, which implies that $\tau_f = T/\ln N_T = 20$ s.

While it is true that between minutes 5 and 6 more than one ant reaches the barrier, the process would then be mediated by multiple ants seeking information, retaining it, and triggering a cascade. This, along with the finite nature of information retention, leads us to conclude that a more simplified mechanism explaining the shift in the CM can be understood as a single “effective ant” representing several informed ants. From the moment this effective ant reaches the barrier, it remains activated and triggers a panic avalanche among its nestmates.

When all ants are informed in the 6th minute of the experiment, a slower dynamics arises. It can be characterized by the time between the moment when all members were activated and the peak observed in Figure 6E at minute 9.2, i.e., by a characteristic time $\tau_s = 3.2$ min. Hence, an extended model based on (8) that incorporates boundary effects and panic dynamics mediated by the times $\tau_f$ and $\tau_s$, was evaluated as follows:

\[
\frac{d}{dt} v_i(t) = -\gamma(v_i(t) - \bar{v}_i(t)) + \sigma(v, t)\sqrt{2\gamma^2D(t)}\xi_i(t) + F_w(r_i) \tag{9a}
\]

\[
\sigma(v, t) = \Sigma(t) - \Delta\Sigma(t)e^{-v/v_0(t)} \tag{9b}
\]

\[
F_w(r_i) = a_0e^{-r_i/\ell_w} - e^{-(r_i - L)/\ell_w} \tag{9c}
\]

\[
\bar{v}(t) = \left(\frac{F_w(x)}{\gamma} \frac{1 - e^{-(t - \tau_p)/\tau_s}}{1 - e^{-(t - \tau_p)/\tau_f}}, 0\right) \tag{9d}
\]

Here, $r_i$ stands for the $x$-$y$ components of the ants’ position. $F_w(r_i)$ in (9c), with units of acceleration, mimics the wall forces as shown in Figure 3A (main plot) with intensity $a_0 = 1.0$ cm/s$^2$ resulted from the fitted line shown in the inset plot, and $L = 6.0$ cm being the length of the arena.

On the other hand, the drift velocity $\bar{v}(t)$ in (9d) is a
vector with a null y component since the repellent effect causes asymmetries only in the direction perpendicular to the barrier. In contrast, the x component accounts for some drift dominated by the fast and slow time scales, $\tau_f$ and $\tau_s$, respectively. The function is an asymmetric sigmoid centered at the midpoint of the fast dynamics (i.e., at $t_p = 5.5 \text{ min}$) and saturates at a certain velocity $\frac{F_{ui}(\tilde{x})}{\gamma}$. This implies that there is a balance of forces for large $t$: the force to the left from the right wall and the “panic force” that continues pushing to the right. This is why the drift velocity has been expressed in terms of the position $\tilde{x}$, which is the only free parameter of the model and was fixed at the distance where the ant cluster remains at rest at the end of the experiment.

With this, we have quantitatively reproduced the experimental motion of the CM using the superstatistical model with parameters directly measured from the experiments. Figure 6F presents the $x$-coordinate of the CM from its initial position (as shown earlier in Figure 2G) alongside the prediction of the extended model (9), plotted as a dark green solid line. The numerical values for all model parameters are provided in Table I.

In addition, it is worth noting that not only does the diffusion coefficient fluctuates on the same time scale before and after panic is induced, but its Log-normal statistics also remains invariant. This leads to the idea that the emergence of a Log-normal type diffusion might be a fundamental feature in the interaction of ants under confinement, and thus it “survives” even in states of danger, which is revealed in the robustness of the PDFs of the acceleration over the whole length of the experiments, shown in Figure 6B.

Similarly, the fact that $\Sigma(t)$ remains nearly constant after the repellent is injected indicates that panic does not significantly alter the noise intensity at rest. Furthermore, the total noise intensity, $\Sigma + \Delta \Sigma$, appears to be “remembered”, as $\Delta \Sigma(t)$ returns to its pre-peak value after its sharp rise, maintaining the overall noise level.

It is instructive to condense the superstatistical treatment into a narrative of the ants response to panic in the SAFE cell, as time goes by. Immediately after the injection of the repellent in the DANGER cell, there is a period from minute 5 to minute 6 that can be identified in Figure 6F as the onset rising of the blue curve from zero. It corresponds to a “cascade dynamics” where individual ants get danger information from nestmates in the DANGER cell through the barrier, and pass it to other ants in the SAFE cell within a characteristic time $\tau_f = 20 \text{s}$. Interestingly, this number is of the order of the “ant memory” time reported in the literature [8]. A second stage occurs from minute 6 to minute 9.2 approximately, where the blue curve in Figure 6F increases steeply, with a characteristic time $\tau_s = 3.2 \text{ min}$. Within that stage, informed ants “rectify” their fluctuating motion in the direction away to the barrier, thus provoking a rightward shift of the CM. A final stage takes place from minute 9.2 to minute 15, where the ants cluster stabilizes, and the CM reaches its final position due to the saturation of the $V(t)$ “force”. This results from the balance between the rightward “panic repulsion” from the barrier due to the input of danger information, and the leftward “mechanical repulsion” due to the presence of the right wall of the right cell.

Finally, there is a remaining puzzle that we have not discussed yet: the time stability of the cluster, in spite of the short “individual memory” of each ant. A possible explanation is suggested by the fact that our clusters are not absolutely static: individual ants eventually separate from the group, explore, and return. We hypothesize that the information feedback provided by those ants from the boundaries of the right cell is rapidly transmitted to the rest of the densely-packed ants, so the cluster-formation behavior is constantly reinforced. This can be better understood by inspecting Figure S5, which shows the decrease in the probability of excursions to the barrier. Given that the left edge of the cluster is qualitatively observed at a distance no less than approximately 2 cm from the barrier, Figure S5 depicts the probability of finding an ant at a distance less than or equal to 2 cm from the barrier, as a function of time. After the repellent is introduced, barrier exploration decreases, though it never completely reaches zero. So, the establishment of the cluster within the last 5 minutes of the experiments illustrated in Figure 6F, is associated to the analogous portion of Figure S5, where a small (but steady) ant traffic between the cluster and the barrier is minimally “refreshing” the panic information.

CONCLUSIONS

We have presented controlled laboratory experiments with confined leaf-cutter ants of the species *Atta insularis*, where ants in a confined space were studied in “normal” conditions for 5 minutes, and in the presence of panic information emerging from the left side of the cell, for another 10 minutes. The experiments show a shift of the center of mass of the ants towards the right as panic is switched on, and the formation of a stable cluster in the last minutes of the experiment.

We observed non-Gaussian probability density functions for both the ants’ acceleration fluctuations and velocities, a slowly varying diffusion coefficient and distinct behavioral regimes in the ants’ collective response to panic. Furthermore, our findings indicate that optical signals or simple antennation do not play a significant role in this panic transmission, raising the possibility of more complex communication mechanisms at work.

We were able to quantitatively reproduce all the above observations using a superstatistical, data-driven model involving a robust Log-normal type diffusion, with all relevant parameters extracted from experimental data.
The model suggests that, when panic is triggered, individual ants gather information at the source of danger and transmit it to others within a time scale expected for the memory of an individual. This leads to a cascade of events, which turn on a collective motion away from the source of panic and the emergence of a stable cluster over a larger characteristic time. Future research may focus on identifying which biological hidden “degrees of freedom”—perhaps corresponding to the precise ant-ant communication mechanism—potentially acts in a cascade-like fashion to give rise to the Log-normal diffusion.

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[1] Søren Vedel, Savas Tay, Darius M Johnston, Henrik Bruus, and Stephen R Quake, “Migration of cells in a social context,” Biophysical Journal 104, 147a (2013).
[2] Thomas E Angelini, Edouard Hannezo, Xavier Trepat, Manuel Marquez, Jeffrey J Fredberg, and David A Weitz, “Glass-like dynamics of collective cell migration,” Proceedings of the National Academy of Sciences 108, 4714–4719 (2011).
[3] He-Peng Zhang, Avraham Be’er, E-L Florin, and Harry L Swinney, “Collective motion and density fluctuations in bacterial colonies,” Proceedings of the National Academy of Sciences 107, 13626–13630 (2010).
[4] Andrea Cavagna, Alessio Cimarelli, Irene Giardina, Giorgio Parisi, Raffaele Santagati, Fabio Stefanini, and Massimiliano Viale, “Scale-free correlations in starling flocks,” Proceedings of the National Academy of Sciences 107, 11865–11870 (2010).
[5] Michele Ballerini, Nicola Cabibbo, Raphaël Candelier, Andrea Cavagna, Evaristo Cisbani, Irene Giardina, Alberto Orlandi, Giorgio Parisi, Andrea Procaccini, Massimiliano Viale, et al., “Empirical investigation of starling flocks: a benchmark study in collective animal behaviour,” Animal behaviour 76, 201–215 (2008).
[6] Daniel JG Pearce, Adam M Miller, George Rowlands, and Matthew S Turner, “Role of projection in the control of bird flocks,” Proceedings of the National Academy of Sciences 111, 10422–10426 (2014).
[7] Bert Hölldobler and Edward O Wilson, The ants (Harvard University Press, 1990).
[8] Deborah M Gordon, Ant encounters: interaction networks and colony behavior (Princeton University Press, 2010).
[9] David JT Sumpter, “The principles of collective animal behaviour,” Philosophical transactions of the royal society B: Biological Sciences 361, 5–22 (2006).
[10] Víceñ Ménndez, Daniel Campos, and Frederic Bartumeus, Stochastic foundations in movement ecology (Springer, 2016).
[11] Gandhimohan M Viswanathan, Marcos GE Da Luz, Ernesto P Raposo, and H Eugene Stanley, The physics of foraging: an introduction to random searches and biological encounters (Cambridge University Press, 2011).
[12] Eliezer Guraire, Christen H Fleming, William F Fagan, Kristin L Lairde, Jesús Hernández-Pliego, and Otso Ovaskainen, “Correlated velocity models as a fundamental unit of animal movement: synthesis and applications,” Movement ecology 5, 1–18 (2017).
[13] JV Santana-Filho, EP Raposo, AMS Macêdo, GL Vasconcelos, GM Viswanathan, Frederic Bartumeus, and MGE da Luz, “A langevin dynamics approach to the distribution of animal move lengths,” Journal of Statistical Mechanics: Theory and Experiment 2020, 023406 (2020).
[14] George E Uhlenbeck and Leonard S Ornstein, “On the theory of the brownian motion,” Physical review 36, 823 (1930).
[15] Christian Beck, “Dynamical foundations of nonextensive statistical mechanics,” Physical Review Letters 87, 180601 (2001).
[16] Bo Wang, Stephen M Anthony, Sung Chul Bae, and Steve Granick, “Anomalous yet brownian,” Proceedings of the National Academy of Sciences 106, 15160–15164 (2009).
[17] Aleksei V Chechkin, Flavio Seno, Ralf Metzler, and Igor M Sokolov, “Brownian yet non-gaussian diffusion: from superstatistics to subordination of diffusing diffusivities,” Physical Review X 7, 021002 (2017).
[18] Christian Beck and Ezhechiel GD Cohen, “Superstatistics,” Physica A: Statistical mechanics and its applications 322, 267–275 (2003).
[19] Ralf Metzler, “Superstatistics and non-gaussian diffusion,” The European Physical Journal Special Topics 229, 711–728 (2020).
[20] Silvio M Duarte Queirós, “On superstatistical multiplicative-noise processes,” Brazilian Journal of Physics 38, 203–209 (2008).
[21] Salvo Rizzo, Andrea Rapisarda, and CACTUS Group, “Environmental atmospheric turbulence at florence airport,” in AIP Conference Proceedings, Vol. 742 (American Institute of Physics, 2004) pp. 176–181.
[22] Amilcare Porporato, Giulia Vico, and Philip A Fay, “Superstatistics of hydro-climatic fluctuations and interannual ecosystem productivity,” Geophysical Research Letters 33 (2006).
[23] Keith Briggs and Christian Beck, “Modelling train delays with q-exponential functions,” Physica A: Statistical Mechanics and its Applications 378, 498–504 (2007).
[24] L Leon Chen and Christian Beck, “A superstatistical model of metastasis and cancer survival,” Physica A: Statistical Mechanics and its Applications 387, 3162–3172 (2008).
[25] Bo Wang, James Kuo, Sung Chul Bae, and Steve Granick, “When brownian diffusion is not gaussian,” Nature materials 11, 481–485 (2012).
[26] Christoph Grütter and Tomer J Czaczkes, “Communication in social insects and how it is shaped by individual
experience,” Animal Behaviour (2019).

[27] Ernesto Altshuler, O Ramos, Y Núñez, J Fernández, A J Batista-Leyva, and C Noda, “Symmetry breaking in escaping ants,” The American Naturalist 166, 643–649 (2005).

[28] Stamatios C Nicolis, J Fernández, Carlos Pérez-Penichet, Claro Noda, F Tejera, O Ramos, David JT Sumpter, and E Altshuler, “Foraging at the edge of chaos: Internal clock versus external forcing,” Physical review letters 110, 268104 (2013).

[29] C Noda, J Fernández, C Pérez-Penichet, and E Altshuler, “Measuring activity in ant colonies,” Review of scientific instruments 77 (2006).

[30] F Tejera, A Reyes, and E Altshuler, “Uninformed sacrifice: Evidence against long-range alarm transmission in foraging ants exposed to localized abduction,” The European Physical Journal Special Topics 225, 663–668 (2016).

[31] A Serrano-Muñoz, S Frayle-Pérez, A Reyes, Y Almeida, E Altshuler, and G Viera-López, “An autonomous robot for continuous tracking of millimetric-sized walkers,” Review of Scientific Instruments 90 (2019).

[32] A Reyes, Frank Tejera, and Ernesto Altshuler, “Flux-density traffic diagrams of foraging ants suggest absence of jamming even under external perturbations,” Revista Cubana de Física 33, 44–46 (2016).

[33] A Reyes, G Viera-López, JJ Morgado-Vega, and E Altshuler, “yupi: Generation, tracking and analysis of trajectory data in python,” Environmental Modelling & Software 163, 105679 (2023).

[34] Henry B Mann and Donald R Whitney, “On a test of whether one of two random variables is stochastically larger than the other,” The annals of mathematical statistics 18, 50–60 (1947).

[35] Christian Beck, Ezechiel GD Cohen, and Harry L Swinney, “From time series to superstatistics,” Physical Review E 72, 056133 (2005).

[36] Christian Beck, “Stretched exponentials from superstatistics,” Physica A: Statistical Mechanics and its Applications 365, 96–101 (2006).

[37] Kevin Burrage and Pamela Marion Burrage, “High strong order explicit runge-kutta methods for stochastic ordinary differential equations,” Applied Numerical Mathematics 22, 81–101 (1996).