Scale-free movement patterns in termites emerge from social interactions and preferential attachments

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As the number or density of interacting individuals in a social group increases, a transition can develop from uncorrelated and disordered behavior of the individuals to a collective coherent pattern. We expand this observation by exploring the fine details of termite movement patterns to demonstrate that the value of the scaling exponent μ of a power law describing the Lévy walk of an individual is modified collectively as the density of animals in the group changes. This effect is absent when termites interact with inert obstacles. We also show that the network of encounters and interactions among specific individuals is selective, resembling a preferential attachment mechanism that is important for social networking. Our data strongly suggest that preferential attachments, a phenomenon not reported previously, and favorite interactions with a limited number of acquaintances are responsible for the generation of Lévy movement patterns in these social insects.

termites | collective behavior | Lévy walks | social insects | preferential attachments

Global behavioral traits in social insects represent a trade-off between individual and collective actions. In termites, where neuter individuals (workers and soldiers) are blind, short-range local interactions among conspecifics are known to generate large-scale spatial and temporal patterns of organization including sophisticated nest mounds, tunneling systems, soil patterns, and worker survival and foraging strategies (1–7). At the heart of collective social patterns are individual behaviors that are amplified or modified in a process known as social facilitation. In recent years, it has become important to study the details of the individual basis of termite behavior to better understand socially facilitated patterns arising at a large scale (5, 8).

Regarding foraging and spatial exploration, it is well known that individual termite workers forage inside underground or wood-carved tunnels with a few examples of species foraging in the open (9). Laboratory observations have established that individual termite spatial exploration is highly directional with distances traveled following self-similar scale-free patterns (10) in a way that resembles passive floaters in near-chaos turbulent fluids, prompting the idea that generic physical phenomena may be at play. In ants, another social group, it was observed that density-dependent interactions among workers are responsible for a transition from chaos to periodic patterns of activity (11, 12), while in the gregarious locust a critical transition was observed in the coherence of the collective movement patterns when the size of the group was increased (13).

Lévy walks (LW) are random walks composed of clusters of multiple short steps with longer steps between them. This pattern is repeated across all scales with the resulting clusters creating fractal patterns that have no characteristic scale. Because there is no characteristic scale, the overall length of LW is dominated by the longest step taken and, while the step-length variance grows over time, it nonetheless remains finite even when unbounded by biological and ecological considerations. The hallmark of Lévy walks is a distribution of step lengths, l, with a heavy power-law tail as described by the formula $f(l) \sim l^{-\mu}$, where $\sim$ means "distributed as" and μ is the scaling exponent with $1 < \mu < 3$ as a condition which ensures that the distribution can be normalized with probabilities that sum to unity and is characterized by a divergent variance. When μ is close to 1, movements are close to being ballistic and when $\mu < 3$, they are effectively Brownian (scale finite rather than scale-free). It has been hypothesized that LW may be an efficient way of exploring space when searching (14–17). It is now well established that many social insects including bumblebees (18), honeybees (19), ants (20), and termites (10) perform LW when engaged in foraging activities. LW have also been identified in swarming bacteria (21) and in spider monkeys (22) which live in social groups. Similarly, theoretical studies have shown how LW might arise in systems composed of interacting individuals (23). However, most of the experimental studies in these insects—and in other animals in general—have focused on individuals acting in the absence of interactions with conspecifics. Here we report on an experimental study—with strong theoretical support—of collective patterns where the aim is to explore in detail how social interactions influence the motion mode of individuals in a social context.

Significance

When searching for food or conspecifics with whom to interact or merely meandering in a Petri dish, termites perform small displacements interspersed with a few long strides. This is known as Lévy walk, a pervasive movement pattern in animals. The extent to which this pattern is modifiable by the context is still under debate. We show that Lévy walks emerge from collective actions, being modified as the density of individuals in the group changes and absent when individuals interact with inert obstacles. Moreover, our data suggest strongly that preferential attachments, a phenomenon not reported previously, and favorite interactions with a limited number of acquaintances are responsible for the generation of Lévy movement patterns in these social insects.

SYSTEMS BIOLOGY

For this we discuss three complementary experimental designs, each aimed at exploring different aspects of interacting termite motion. The experiments detailed below are 1) social interactions and collective motion, 2) motion with passive obstacles, and 3) annular constrained motion. We also develop computer simulations to uncover the possible mechanism involved in the generation of LW from collective behaviors.

General Methods

Species. *Cornitermes cumulans* (Kollar) (Blattaria: Isoptera: Termitidae: Syntermitinae) workers were collected from wild colonies at the gardens of the Federal University of Viçosa, Minas Gerais, Brazil. In the wild, this species of neotropical termites lives in conspicuous mounds of moderate size (ca. 130 cm high and 110 cm in basal diameter) with almost all activity being subterranean. They move in an intricate network of tunnels and galleries inside the nest that are connected to the foraging sites via subterranean tunnels. In the field, these tunnels (sometimes 30 m long) depart from the nest in all cardinal directions, obeying a near-straight bearing at a near constant depth (ca. 10 cm below the surface) until reaching a resource, such as a tussock. At this point, the tunnels are sharply directed upward, ending at the food item where foragers spread themselves in a small radius around the tunnel tip, to explore the resource. This combination of near-straight long tunnels sharply changing direction in the proximity of resources has been also reported in the field for other termites, either foraging in subterranean tunnels (24), or within galleries built above ground (25).

Protocols and Data. Individuals (workers only) were obtained from field colonies, not more than 24 h before starting the experiments, and kept under controlled laboratory conditions before trials. The experimental setup consisted of arenas made of sand-blasted petri dishes mounted in a closed chamber with controlled illumination. Three types of arenas were used: 1) circular empty arenas in which termites moved freely, 2) circular arenas in which termite movement was hampered by obstacles, and 3) annular arenas in which termites performed a pseudo-one-dimensional movement. Termite movements in the arenas were video captured and the video fed to a tracking software. The specific methods, software, and procedures are given below for each of the experiments. Further details and data are given in *SI Appendix*.

Testing for Lévy Walks. Humphries et al. (26) noted that the projection of a Lévy walk is itself a Lévy walk and thereby identified another objective methodology for detecting Lévy walks in two-dimensional movement patterns which we adopt here when analyzing data from the circular arenas. Further details of the methodology can be found in ref. 27. In this approach movement patterns are first projected onto the *x* and *y* axes to create two one-dimensional movement patterns for each individual. Turns in these projections can then be identified in an unambiguous way as occurring where the direction of travel changes. Without projection, turns and so step lengths in two-dimensional movement patterns can be identified only by making reference to arbitrarily defined critical turning angles (26). For the annular arenas, movements are pseudo-one-dimensional and turns occur when the direction changes from clockwise to anticlockwise or vice versa.

Following a now well-established practice (28) we fitted our step-length distributions to power laws, biexponentials, and exponentials using maximum-likelihood methods (29) and the best model distribution was indicated using the Akaike information criterion (30).

The model distributions, and hence competing movement hypotheses, are given by

$$p_1(l) = N_1 l^{-\mu}, \, b \geq l \geq a \quad \text{[1]}$$

$$p_2(l) = A N_2 e^{-\lambda_2 l} + (1 - A) N_3 e^{-\lambda_3 l}, \, b \geq l \geq a \quad \text{[2]}$$

$$p_3(l) = N_4 e^{\lambda_4 l}, \, b \geq l \geq a, \quad \text{[3]}$$

where N_1, N_2, N_3, and N_4 are the normalization factors.

A power-law distribution of step lengths is indicative of LW patterns. Biexponentials are the expected distribution from two-state composite correlated random walks and can closely resemble power laws when, as in the current situation, the range of scales is limited and so can compete strongly with LW as models of movement pattern data (31). Exponentials indicate Brownian walks and are a null model.

Social Interactions and Collective Behaviors

Termites are social insects capable of producing and maintaining highly complex behaviors. The study of the mobility of termites is important because some species are agricultural, industrial, or residential pests. Moreover, mobility leads to interindividual interactions that are the basis for sociality, a trait shared by all termite species and a behavior that is in the upper end of evolutionary transitions (32). However, traditional studies have concentrated on the movements of isolated individuals and not those executed in a social context. In a previous study (10) it was established that isolated termite individuals walking in closed containers exhibit complex movement patterns with a very rich structure compatible with superdiffusive motion, self-similarity, and scale-free temporal activity.

Providing that interindividual encounters can temporarily impair free movement of workers, we hypothesized that social interactions will modify the walking patterns and that these modifications will be density dependent (Fig. 1). Such modification of the individual mobility potentially affects the efficiency of collective foraging, searching, nestmate encountering, and information spread, being hence essential to colony functioning.

Termites were observed in groups of different sizes so that density could be varied. We studied group sizes ranging from one up to 29 individuals. The mobility of a focal individual was recorded in video, at a rate of one Cartesian point every 0.5 s along 4 to 5 h, and its trajectory was analyzed to extract step lengths. A total of ca. 1.2 million datapoints have been obtained from individuals collected in 31 field colonies. Video trackings were fed to Ethovision (Noldus Technologies) software to extract these positional datapoints.

Some behaviors were noticeable: At low densities the mobility patterns of the individuals are mostly linear (ballistic) with few social interactions; as the density was increased, the process of social interactions was more evident since the rate of encounters increased as well. When a termite encounters a nestmate, it may ignore it, engage in a very time-short interaction, or come to a rest and engage in a prolonged interaction that may include a careful process of antennation or allogrooming. When a nestmate is ignored after an encounter, the trajectory of motion is not significantly modified beyond the readjustment due to the mechanical collision. At intermediate or high densities, the process of interactions may lead to the formation of termite clusters that significantly modify the nature of the walking patterns (see *SI Appendix* for more information).

We found that power-law distributions, the hallmark of LW, consistently produced the best fits to our step-length data. However, some clarifications are in order. At isolation or low densities, the focal individuals exhibited an LW scaling exponent $\mu \approx 3/2$. Two things were observed at intermediate or high densities. A focal individual may be observed retaining a scaling exponent $\mu \approx 3/2$ but the power-law distribution would fit even better (Fig. 1) or a focal individual would be recorded with a scaling exponent $\mu \approx 2.0$.
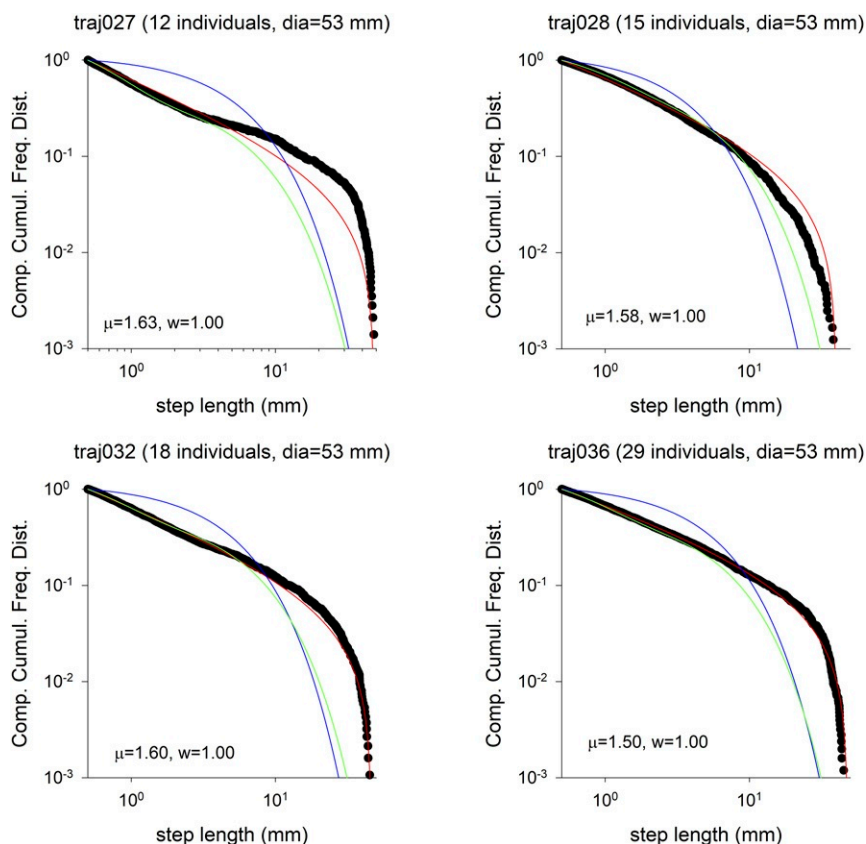
Fig. 1. Step-length distributions of measured trajectories are shown for a single focal individual confined with conspecifics in different group sizes. Red lines are fits with power laws. Blue lines are exponential fits, and the green lines are biexponential fits. In these examples, best fits are always power laws and the fits become even better as the number of individuals is increased. The scaling exponent found in this example is around 3/2.

Motion with Inert Passive Obstacles

When social interactions are disrupted, collective patterns cease to exist. In the blind worker termites the interactions happen at close range involving mechanical contact and chemical recognition. When a termite encounters a passive obstacle, for example a container wall, it will briefly explore it and then will ignore it. There cannot be any social interactions and certainly no collective behavior. With this in mind we designed an experiment where passive inert obstacles (metal poles) were located in the walking field of one termite, so that trajectories were truncated because of the obstacles but without the worker being able to engage in social interactions. This is then a null experiment to contrast results against those in an arena in the companion of nestmates as discussed above. Tracking procedures were the same as above.

From theoretical arguments (33–35) it follows that truncation of LW asymptotically approaches a Gaussian process, so that the power-law distribution of steps is lost in favor of an exponential distribution. This process becomes more and more evident as large steps are truncated into small steps. In our experiment given this reasoning, we do not expect LW to arise as strongly as in the collective motion experiment or be present at all.

Focal individuals were observed in containers with one metal pole on the field. After coming across it, colliding with it, and ignoring it, the isolated termites continued exploring their space, walking as usual in a mostly rectilinear fashion or close to the border. As the density of obstacles was increased (see *SI Appendix* for more details), the individual traveled across the interspaces with large trajectories being truncated; as a conse-

quence, no LW were detected. When the density of obstacles was high, the worker avoided exploring the tight labyrinth formed by the crowded metal poles and preferred to walk close to the border. This experiment confirms that a process involving social interactions is needed for the emergence of LW with μ other than 3/2 (Fig. 2).
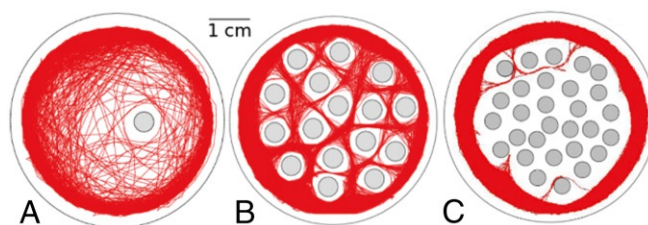

Fig. 2. Graphical dynamics of nonsocial interactions. In this arrangement, a single termite explores an arena with different metal pole numbers. In *A*, a single pole has been introduced. Most of the termite's movement happens away from the obstacle, confined to the border area. When the termite approaches the obstacle, it will change direction after colliding but otherwise ignore the pole in the sense that the worker does not invest time in trying to antennate or allogroom it, there is no waiting time, and the obstacle is largely ignored. In *B*, an intermediate sparse density formed by 16 obstacles provokes a termite's movement pattern where almost all of the arena has been explored; however, there is no attempt to engage in social interaction. In *C* the pole density is so high (26 obstacles) that the termite avoids entering the intricate labyrinth formed by the space between the obstacles. There were only a few trajectories recorded in the interspace between poles; however, the obstacles are largely ignored.

Annular Constrained Motion

In this section we develop and discuss two independent parsimonious theoretic models of termite movement to explore how LW emerge from collective behaviors. Model predictions are validated by examining the movement patterns of termites constrained to move in a circular corridor or in annular regions formed by the borders of two concentric petri dishes (see *SI Appendix* for more information). A total of 600,000 datapoints have been analyzed. This experimental setup allows step lengths not constrained by geometry. A distribution of step lengths spanning several decades allows us to discriminate reliably between LW and other competing hypotheses about movement patterns.

An Agent-Based Model for Annular Motion. Our first model is agent based with realistic rules for movement and interactions based on detailed experimental observations of termite behavior. N termites are described by a persistent random walk along an annular corridor of a given width a. Termites can stay in two states: active or inactive. An active termite becomes inactive with a probability p_w and stays inactive for a time interval τ (waiting time) or with complementary probability it tries to move. The waiting time is a random variable with a power-law distribution that decays with exponent γ because there is evidence that this is the real distribution (10). An alternative exponential decay for the waiting times was explored with no significant differences (see *SI Appendix* for more details).

When a termite i meets another j, they may enter the inactive state or the termite j reacts to this contact, engaging in further interaction or moving away. The evolution rules of the model are as follows:

1) The waiting time of all inactive termites is updated (subtracted $dt = 1/N$). If it becomes less than zero, the state of the termite is set to active.
2) An individual i is randomly selected. With probability p_w it becomes inactive and, with complementary probability, it tries to perform a step according to the correlated walk (see *SI Appendix* for more details). Since spatial overlapping is forbidden, the movement is stopped to avoid it and we consider that a meeting occurs.
3) The time is updated ($t = t + dt$), and we return to the rule 1.

Results of this model include the distances traveled that are power-law distributed with a decay exponent ranging from 3/2 to 2 (Fig. 3).

A Solvable Model for Annular Motion. Our second model is a minimal generic model that is mathematically solvable. It is very different from the more specific and realistic agent-based model we presented above. However, the fact that two very different models generate Lévy walks shows dramatically that their emergence is robust with respect to how the interactions are modeled, so that they are not artifacts of specific kinds of interactions. In this model, the movements of N individuals around an annular track are modeled. Some individuals are moving clockwise around the track. Some are moving anticlockwise. Occasionally, an individual will change its direction of motion. The turning rate (i.e., the likelihood of turning) increases if an individual encounters conspecifics moving in the opposite direction. It decreases if neighboring conspecifics are moving in the same direction. This simple form of interaction leads to movement patterns resembling Lévy walks, as explained below (Fig. 4).

Real termites switch directions when walking, reversing their direction. We may model this with a switching rate R. If R is constant, then the distances, x, traveled between reversals are theoretically known to be exponentially distributed according to
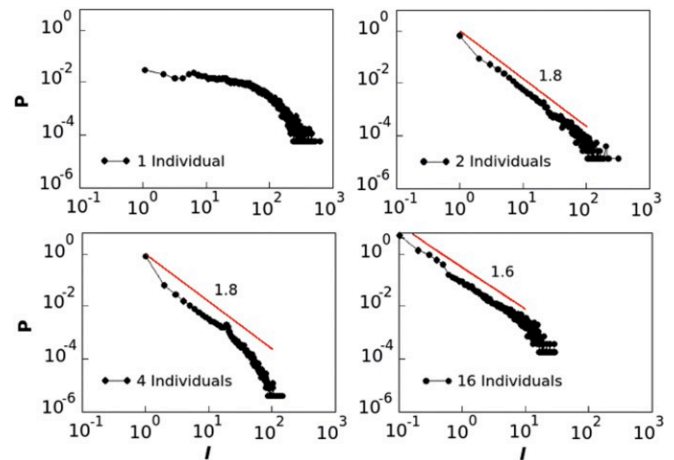

Fig. 3. Agent-based model. Shown are examples of step-length (l) distributions (P) showing clear signs of a power-law decay indicative of Lévy walks when the number of modeled individuals increases, from 1 to 16. The scaling exponents μ were found to be in the range 3/2 to 2. No power law is evident for one individual.

$p(x) = \mathrm{Re}^{-xR}$. However, real termites have switching rates with some distribution $f(R)$. In our model, the overall distance distribution, $P(x)$, is then obtained by integrating $f(R)p(x)$ over all R. Simulations indicate that $f(R)$ is complex with resonances but that typically $f(R) \to R^p$ as $R \to 0$. Exponentials and gamma distributions, which are standard distributions for the statistics of switching rates, have the same asymptote. It follows (e.g., using the saddle point approximation) that $P(x)$ have power-law tails $x^{(-2-p)}$. This is the hallmark of LW. Our simulations support this prediction, i.e., support the predicted connection between p and the Lévy exponent $\mu = 2 + p$. This simple analysis might explain why LW emerge largely irrespective of how interactions are modeled. LW appear to be almost inevitable.

Selective Social Interactions. There is a very important and crucial prediction arising from our formalism. In this simple model the emergence of random walks with power-law step-length distributions is characterized by $\mu = 1 + (N_e - 1)/2$, where $N_e < N$ is the effective number of nestmates among N with whom the focal individual interacts only. It is then the number of particular interactions, hereafter called "favorite" individuals. As a consequence, LW are not expected for $N_e \geq 5$, because $\mu \geq 3$ effectively corresponds to Brownian walks. Analysis of our data suggests that LW are mostly absent when $N_e \geq 4$ and that at these relatively high densities a few individuals have movement patterns resembling 3/2 LW. We may hypothesize that it could be that these termites are responsive only to a few termites in the arena and "ignore" most of their cohort so that N_e is effectively a low number. It follows also that $N_e = 1$ to 4 are like "goldilocks" numbers that allow for the emergence of LW per se rather than random walks with power-law exponents outside of the Lévy range. We typically observed that $N_e = 2$ to 4 (in groups of 4 to 8); this is very intriguing indeed and invited us to conjecture that termites tend to interact as if preferentially with a low number of favorites $N_e = 2$ to 4 because that facilitates the execution of LW (see next section). This finding seems to be similar to Dunbar's number, a property of social networks that limits the number of friends or acquaintances a given human individual has (38).

What are the consequences of termites responding to particular individuals? In this picture LW seem to be inevitable and accidental but could nonetheless outperform straight-line and Brownian-like movements when searching and so have adaptive values. These searching patterns may not be optimal
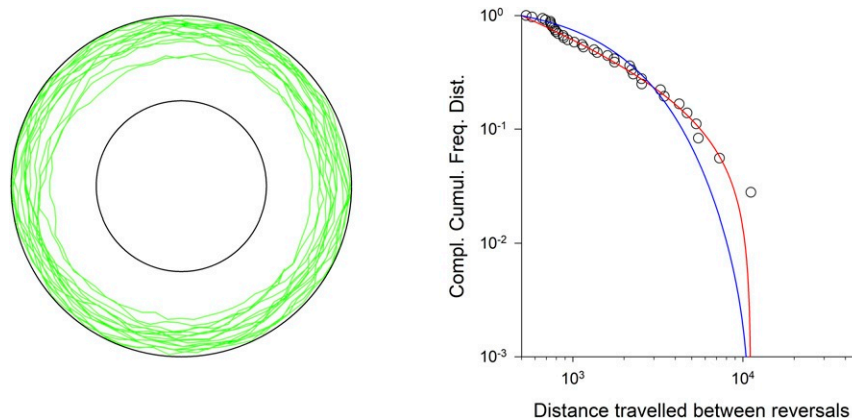
Fig. 4. A termite walks around the annulus with constant angular speed (*Left*), while randomly meandering in the radial direction resembling a real movement pattern. When two termites meet, they interact and their movement around the annulus is temporarily disrupted. Distances traveled between consecutive disruptions define a "step length." For the case of $N = 2$ interacting individuals in the annulus, the model can be solved because the time intervals between consecutive encounters will be power-law distributed with exponent 3/2 by virtue of the Sparre–Andersen theorem (36, 37). It is therefore not surprising to find evidence of 3/2 LW in simulation data, as indicated at *Right* where the distribution of simulated step lengths is seen to be well represented by the best-fit, $\mu \approx 3/2$, power-law distribution (red line). Shown for comparison is the best-fit exponential (blue line).

(μ different from 2) but optimality might not be achievable because they do not have an individual mechanism for generating such LW unless they can choose to interact with, say, just 3 particular termites ($\mu = 1 + (3 - 1)/2 = 2$). This theoretic result suggests that if the focal termite interacts with just one favorite, then its movement patterns will be a LW with Lévy exponent $\mu = 3/2$. We see LW with $\mu \approx 3/2$ when there are not just 2 individuals in the arena but more. Intriguingly, the theory predicts the occurrence $\mu = 2$ LW if the focal termite interacted with just 2 favorites. It follows that if termites could "choose" the number of favorites, then the LW would be plastic and could be tuned by selection pressures for advantageous searching. We could hypothesize that when there are many individuals in the arena, focal individuals with a low number of favorites perform LW with μ in the range 3/2 to 2, while those with many favorites have diffusive walks.

Preferential Attachments

Favoritism, or preferential attachment, is a previously undocumented characteristic of termites that we predict. We describe in what follows our experimental approach to implement an annular arena and the statistics of individual interactions that allow us to confirm both results, the emergence of collective LW and the presence of preferential attachments.

It has been suggested that preferential interactions actually exist in the social networks of ants (39–41). However, there are no specific studies addressing the consequences of favoritism on the patterns of collective motion. We show that preferential interactions are pervasive among *C. cumulans* termites: such a behavior was observed in individuals randomly sampled among their thousands of nestmates. Moreover, it was a behavior consistently occurring in assays independently performed for distinct colonies. In general, it is known that preferential attachments are a ubiquitous and crucial characteristic of social networks, including those of humans (42, 43).

As intriguing as it is, we still have no evidence on what makes a favorite termite in these experiments. At this point, our cursory observations while running the assays allow us to state that favorites do not seem to be a "trap" for the focal termite, at least in the sense of a static cluster attracting this individual. This is because favorites also kept moving around the assay, hence escaping any eventual cluster to which they belong at a given time of a given interaction with the focal

termite. New experiments, specifically designed, are needed to address this.

Annulus Experiments and Collective LW. We set up an "annular arena," placing a small petri dish inside a bigger one, thereby creating a circular corridor where termites were allowed to walk. This design was filmed with termite groups of different sizes and then a focal individual was selected on the video track using an open-source algorithm (developed by us) for tracking its position and potential interactions with all of the nestmates (44). This allowed us to identify when a trajectory around the circular corridor is truncated due to spontaneous reversals, stops, or social interactions. We predict that distributions of these distances are heavy power-law tails. This is the hallmark of a LW.

Statistical analysis of these step-length distributions is illustrated in Fig. 5, *Top*. The other panels show the step-length distributions together with fits to exponentials (blue lines), which are indicative of scale-finite Brownian-like walks, and fits to power laws (red lines) which are indicative of scale-free LW. Fittings were done using maximum-likelihood methods. Encouragingly, the hallmark of LW (good fits to the red lines) becomes more pronounced as the number of termites within the arenas increases (as predicted), and with 16 termites the maximum-likelihood estimate for the Lévy (power-law) exponent is 1.82, which is close to the theoretical expectation of 2.0.

Analyses of Preferential Attachments. To inspect whether termites confined in the annular arenas would preferentially contact some of their nestmates over others we filmed and tracked each individual termite in the arenas along ca. 30 min at 30 fps. Then we tallied the number of time steps this focal termite spent contacting a given target termite along the whole footage, to estimate the proportion of contacts a target termite would receive from its conspecifics in that arena. These proportions were then submitted to a χ^2 test to inspect whether they would depart from a uniform distribution and, if so, to point to the existence of focal-target preferred attachments (Fig. 6*A*).

The number of preferred target termites in each arena (y-var) was then regressed against the number of termites therein confined (x-var), to inspect how preferential attachments would correlate with group size. Analysis consisted in contrasting the model thereby obtained with a model with zero intercept and slope = 1, that is, a model in which favoritism was absent.
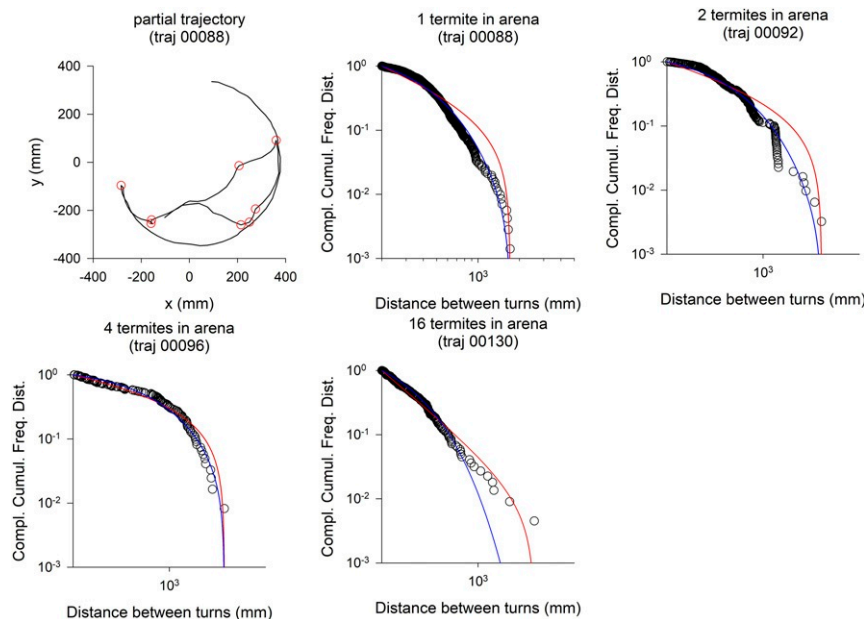
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Fig. 5. Distribution of the step lengths of real termites in the annulus experiment as the number of individuals is increased from 1 to 16.

Modeling was performed in R, under generalized linear modeling and normal error distribution, followed by residual analysis. Contrasts were made using the Akaike information criterion (AIC) (Fig. 6*B*).

Please see *SI Appendix, Preferential Interactions* for better detail and external links for all computational and statistical procedures employed in these analyses.

Conclusions

Despite the overwhelming evidence showing that animal search movement patterns are a multiscale and often free-scale process, very little is known about the internal physiological mechanisms that generate such patterns (however, see ref. 45). Even less is understood about how Lévy walks can emerge from collective behaviors. Swarming bacteria (21) and midge swarms (46) are two candidates but these systems appear to be very specific and rather complex. The mechanism we explore here in termites could operate across taxa. It is worth emphasizing that Lévy walks were found in two different experimental setups: circular arenas and annular arenas. Moreover, we accounted for these two sets of observations with two different models of social interactions. In one model, movements are two dimensional and interspersed with occasional pauses. In the other model, movements are one dimensional and continuous. This suggests that the emergence of Lévy walks in termites is not sensitively dependent upon the way in which individuals interact with one another and more generally that it is not specific to termites. This robustness gives our results added significance, as they could apply to other social animals.

In this article, we have explored the movement patterns of groups of termites walking in circular arenas. As the density of workers is increased, a clear group effect emerges, because the number of interactions increases as well. Termites engage in social contacts that truncate their otherwise almost rectilinear trajectories. As the density is increased, the workers tend to form dynamically changing clusters that act as social traps. Individuals in these clusters are not necessarily standing still but rather moving slowly in short steps. This seems to provide the mechanism of having large steps and short steps that together exhibit statistics conforming to power laws. We have observed focal individuals having scaling exponents μ in the range 3/2 to 2. As the density

increases, we observed that the goodness of fit to a power law gets better.

To test this mechanism we devised a null experiment where partner termites are replaced by inert metal poles to provide the possibility of mechanical contacts but no social interactions. As expected, a focal individual moving under such an arrangement where there are no social contacts tends to show Brownian statistics, as expected from theoretical results on the physics of truncated Lévy walks.

To investigate even further the role of social contacts, we designed another experiment where individuals move along two concentric petri dishes so as to be confined in an annular region. This increased the possibility of long trajectories while increasing the odds of social contacts. Emergent LW were observed here as well. A next step was the setting of two models for computer simulations that are very different in their implementations and assumptions. The first model is agent based where steps of a single individual are not Lévy but became Lévy after engaging in social interactions with other individuals. We witness the spontaneous formation of clusters in the model. The
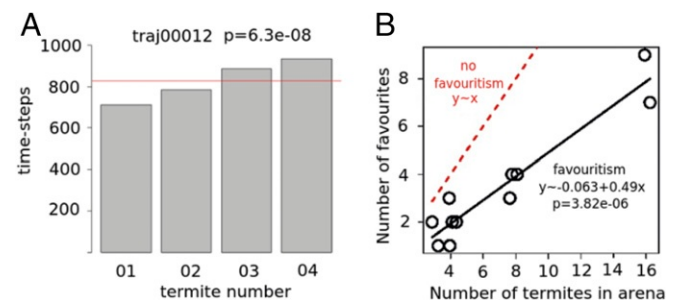

Fig. 6. (*A*) Average number of time steps (*y* axis) a given target termite (*x* axis) was contacted by the other termites in an annular arena. The red line depicts the expected frequency of attachments between focal and target termites in the absence of preferred mates. Here we show the results for arena traj00012. (*B*) The growth of the number of target termites favored by focal termites performing interactions in annular arenas as a function of group size. The dashed red line depicts the expected number of targets if favoritism was absent.

second simpler model is analytically tractable and predicted that the emergence of LW is dependent on the number of nestmates (Dunbar-like number) that the individual interacts with. It predicted the existence of a preferential attachment mechanism that we have identified and measured experimentally. This is an undocumented feature of termites that shows how rich and sophisticated the social networking can be in these insects. We predict from our model that low Dunbar-like numbers are important for the generation of LW with exponent μ close to the predicted optimal 2.0. We also conjecture that such a preferential attachment with low numbers of favorites is in fact a mechanism that allows for the slowing down of close contact transmission of diseases since allogrooming is not carried out with an arbitrary large number of individuals but preferentially with those in the social neighborhood having then a selective value. It helps also in the understanding of why a rapid flux of information is not carried out on an individual-to-individual basis but by the use of alarm pheromones released to the air. A word of caution is needed here: Despite being certain that focal termites tend to return to the same conspecifics over the experimental period, we do not know whether they would remain favoring these same conspecifics over their whole lifetime. That is, within the time frame studied (assays ca. 30 min long), there were favorites, and that is consistent over our replicates. Since these replicates came from distinct nests, it seems that this behavior is biologically consistent. Thus, the above conjectures on the selective advantages of "favoritism" must take into consideration these experimental limits.

More research on this topic would be desirable, as our results point to an entirely different set of questions on termite behavior in particular and social interactions in general. From ref. 8 we already know that 1) termite movement may be triggered by the rate of contacts with nestmates and 2) this rate depends on density. From our current results we know that Lévy walks emerge when termites contact a finite number of nestmates. It follows that density would have a strong potential to trigger Lévy (or non-Lévy) movements in termites. Termites may therefore use density as a clue, allowing them to switch from Lévy walks to other forms of displacement according to their distinct daily life demands (e.g., foraging, nursing, nest maintenance, etc.). These hypotheses clearly require proper testing. We present them only to highlight the multiple research pathways opened up by our current results.

Ethical Statement

The authors of this paper hold a permanent permit from IBAMA (The Brazilian Institute for the Environment and Renewable Natural Resources) to collect termites. Tacit approval from the Brazilian Government is implied by the authors being hired as scientific researchers. This species is not protected. No genetic information was assessed.

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