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# A Review on Foraging Trajectories in Termites: Insights from Lévy Walks to Ecological Behavior

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## Foraging in termites

Some termites species feed directly on wood within inner galleries while other forage on the ground surface. When foraging, [Grassé \(1986, p. 74, 86, 88\)](#) states that these surface-foraging species operate collectively in groups of soldiers and workers, without individual scouts relaying information to the colony. In laboratory settings, termites displaying individual behaviours were observed in lignicole species that do not forage in their natural habitat ([Grassé, 1986, p. 86](#)). In the field, it typically takes a few hours to locate a food source, after which more termites to join and, in some species, construct protective roofs along the food trail ([Mathews, 1977](#), cited by [Grassé, 1986, p.77](#)). In *Hodotermes mossambicus*, the first foragers are described as moving randomly, primarily using the sun for orientation and occasionally leaving pheromones on the ground ([Leuthold, 1973](#) ; [Leuthold, Bruinsma, Vanhuis 1976](#) ; both cited in [Grassé, 1986, p. 67-68](#)).

## Mathematical modelling of termite trajectories

Modeling the foraging trajectories of initial termite groups is limited. Several studies have shown that termites, such as *Cornitermes cumulans*, follow Lévy walk patterns ([Miramontes et al., 2014](#); [Paiva et al., 2021, 2022](#); [Castiblanco et al., 2022](#)). Lévy walks describe a distribution of step lengths that is neither uniform nor centered around a mean value, as seen in Brownian motion. Instead, the step lengths follow a power law of  $L^{-\mu}$ , where  $L$  represents the varying step length and  $\mu$  is a constant typically ranging from 1 to 3 (Figure 1). Lévy walks are observed across various scales, from the microscopic to the ecological, in phenomena such as molecular cell machinery, brain T-cell movements, bacteria, DNA, mollusks, honeybees, marine predators, birds, mammals, human hunter-gatherers, airborne dispersal of spores and seeds, collective animal movements, and trace fossils ([Reynolds, 2018](#)). While they are believed to enhance foraging efficiency, this is not always the case: “*Many insect herbivores must literally bump into a host plant before they recognise it is food and yet evidence for Lévy walks in insects is limited. [...] The key question is now is not whether some organisms have Lévy walk movement patterns, but when and why they do*” ([Reynolds, 2018](#)).

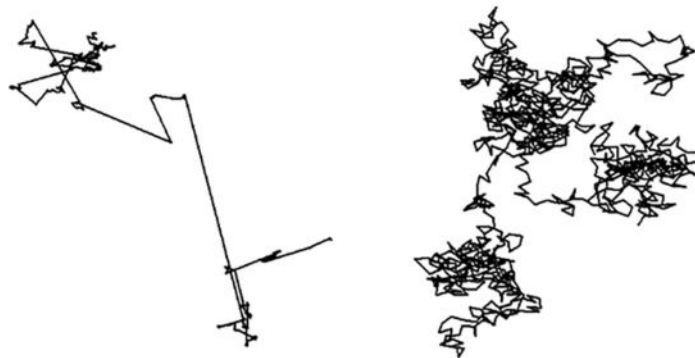


Figure 1. Lévy walk (left) and Brownian walk (right). From [Reynolds et al. \(2018\)](#)  
[doi:10.1242/bio.030106](https://doi.org/10.1242/bio.030106) ([CC-BY 3.0](https://creativecommons.org/licenses/by/3.0/))

Miramontes *et al.* (2014), Castiblanco *et al.* (2022), and Paiva *et al.* (2021, 2022) tracked *Cornitermes cumulans* termites in a free-range disk arena, using video cameras positioned above the arena at a rate of 2 images per second and Ethovision tracking software. The recordings captured the termites' movements along the arena's border, their free movement, and their static waiting times over several hours. Most of the termites' trajectories were concentrated near the arena's border, though the analysis appeared to include all walking behaviors (Figure 2). The arena's diameter was reported not to affect the results in Miramontes *et al.* (2014), which included arena sizes of 140 mm, 90 mm, and 55 mm. Castiblanco *et al.* (2022) and Paiva *et al.* (2022) chose the 55 mm diameter, bringing the arena borders very close together. Their analyses were based on the mean-square displacement during each sampling period, and they plotted the occurrence distribution (histogram) to estimate the fit with power-law scaling, including Lévy walk patterns.

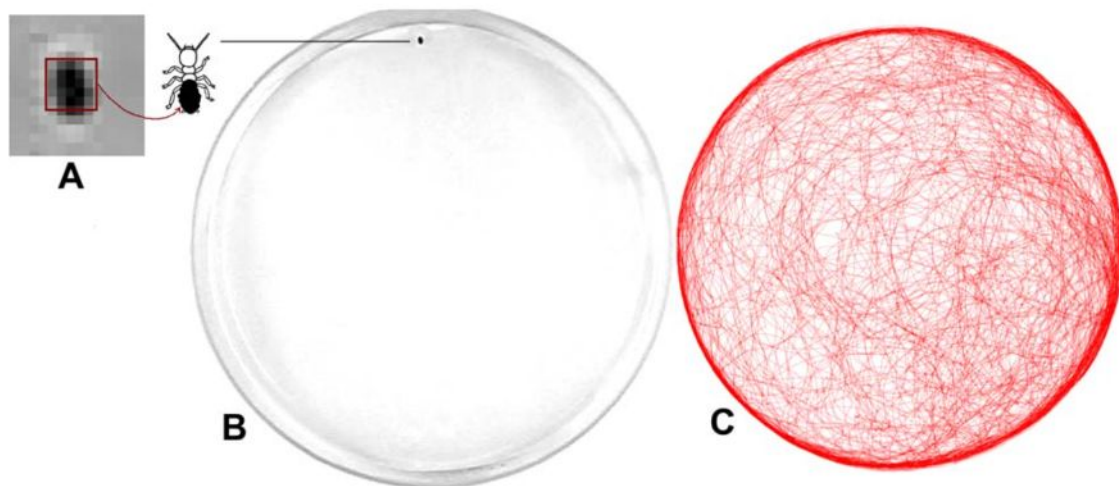


Figure 2. Experimental setup in Miramontes *et al.* (2014) [doi:10.1371/journal.pone.0111183.g001](https://doi.org/10.1371/journal.pone.0111183.g001) (CC BY 4.0). (A) A *Cornitermes cumulans* worker with a painted abdomen. (B) 205 mm diameter dish. (C) Tracked trajectory of 2-Hz individual steps.

Miramontes *et al.* (2014) studied individual termites, while Castiblanco *et al.* (2022) focused on groups of workers and soldiers comprising at least 6 individuals. Both studies found evidence of a Lévy walk process, where the distribution of step distances does not exponentially decrease around a mean value, as seen in Brownian motion. In other words, termites tend to stay in a particular direction for longer periods than Brownian particles would. The mean distance in Brownian motion is influenced by the density of other moving particles. However, in high-density termite populations, where they could behave similarly to particles, Brownian motion is not observed—96% of the movement is Lévy-like. That said, as termite density and the proportion of workers increase, the displacements tend to be shorter compared to the longer steps, making the movement less Lévy-like and more Brownian-like (Castiblanco *et al.*, 2022). Paiva *et al.* (2022) employed a different analytical approach, which suggested “a qualitative change in the foraging behavior between isolated and grouped termites (phase separation), where the latter display more complex patterns, closer to Lévy walk phenomenology”, with an optimal pattern observed at an intermediate termite density.

In single termites, a strong correlation over time was found between step distances, suggesting “a process akin to long memory”; no preferential turning angles were observed, but there was a directional tendency to move forward, along with a power-law waiting time distribution (Miramontes *et al.*, 2014). The scale power of the step

distance distribution was found to be between 2.1 and 2.2 for single termites ( $n=4$ ) (Miramontes *et al.*, 2014), and between 1.05 and 1.96 (with a mean of 1.5) for groups of  $\geq 6$  termites ( $n=3$  for each of 22 distinct caste compositions) (Castiblanco *et al.*, 2022). Paiva *et al.* (2021) observed a scale power of 1.5 in isolated termites or at low densities, while values ranged from 1.5 to 2 at higher densities, for groups of 1–26 individuals in a 55 mm Petri dish.

Shimoji *et al.* (2020) studied several motion parameters in isolated damp-wood termites (*Hodotermopsis sjostedti*), including mean, maximum, and mode speeds, acceleration standard deviation, total pausing time, number of pauses, as well as the peak and shape of the turning angle distribution. They found caste-dependent profiles in the movement patterns. In *Cornitermes cumulans*, termite density was shown to increase the mean speed, which ranged from 1.7 mm/s (0.5 to 4.9 mm/s), i.e. 0.2 body lengths per second (given that the termites are 8 mm long).

### Discussion and possible future works

In the studies on Lévy walks in *Cornitermes cumulans* termites (Miramontes *et al.*, 2014; Paiva *et al.*, 2021, 2022; Castiblanco *et al.*, 2022) and movement dynamics in *Hodotermopsis sjostedti* termites (Shimoji *et al.*, 2020), the termites were collected from the same colonies and placed in confined arenas. This setup means that the insects' behavior was not controlled and may not reflect their natural ecological context. Are they foraging? Are they searching for their nest? The experimental protocol does not allow these questions to be answered. The research focus of these studies is on identifying general principles that transcend species and behaviors, much like the aims of physics. While interesting behaviors emerge from these studies, their ecological relevance may be lost, and such rules can sometimes be speculatively applied when interpreting termite behavior. For example, Paiva *et al.* (2022) describe the behavior of their isolated termites as “*perform[ing] foraging patterns (innate foraging behaviour)*” which could be questioned given the experimental methods used.

Modeling the trajectories of *foraging* termites can only be done if they are free to walk from a healthy, well-established nest. Haifig *et al.* (2015) used a tracking system to study the dynamics of foraging trails in *Velocitermes heteropterus*, but their setup involved a stick-like bridge between the nest and the foraging arena, which constrained the termites' movement. Studying the trajectories of the first foraging groups from nocturnal species would help eliminate the variable of light direction in the experiment. The goal of such a study would be to determine whether the first foragers move randomly and whether this random walk could be characterized as a Lévy walk, similar to the behaviour observed in experiments where the termites' behaviour is uncontrolled (e.g., walks that do not start from the nest) and conducted with a single termite species.

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