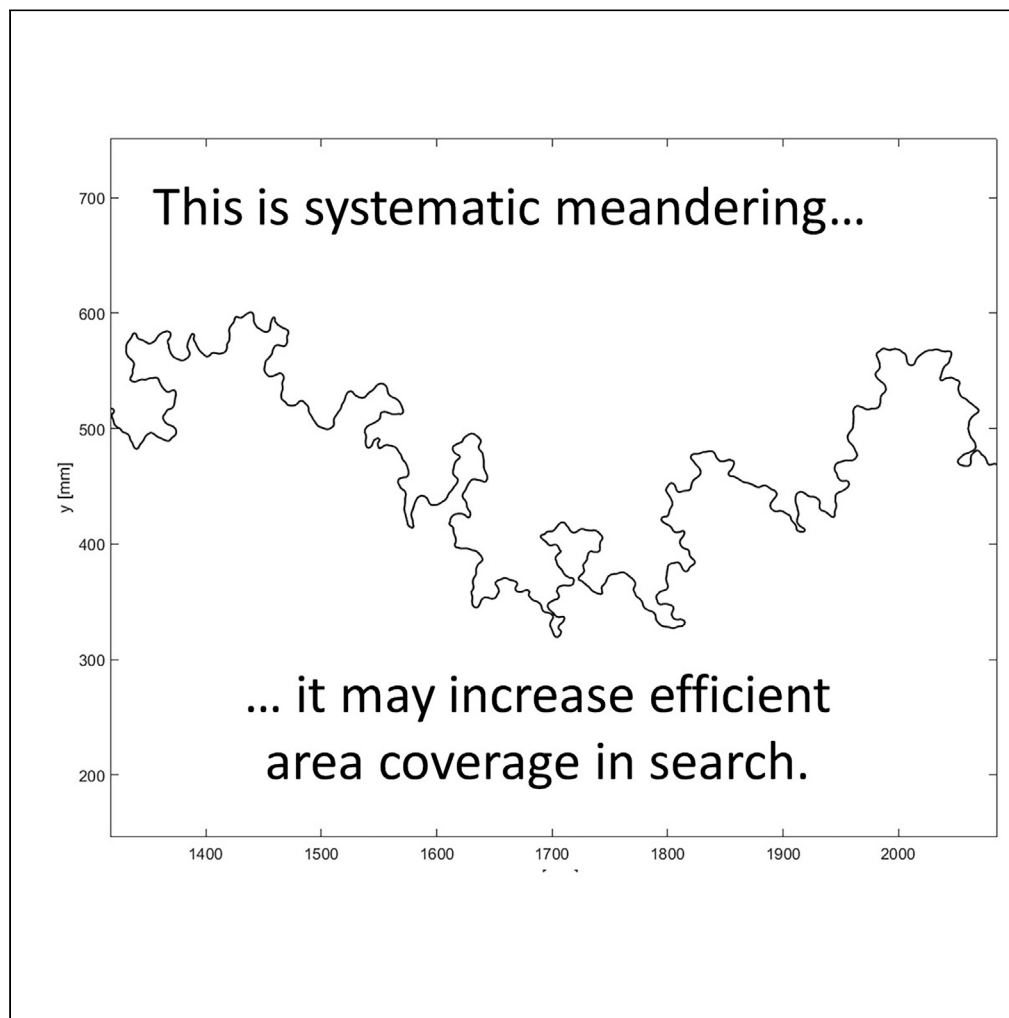


## Article

## Ants combine systematic meandering and correlated random walks when searching for unknown resources



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**Highlights**

Turn autocorrelations of ants in a large arena compared with those of simulated tracks

Ants meander regularly, changing turn direction roughly every 10 mm (3 body lengths)

This reduces self-crosses and dispersion from the nest, likely improving efficiency

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## Article

## Ants combine systematic meandering and correlated random walks when searching for unknown resources

Stefan Popp<sup>1,2,3,\*</sup> and Anna Dornhaus<sup>1</sup>

## SUMMARY

**Animal search movements are typically assumed to be mostly random walks, although non-random elements may be widespread. We tracked ants (*Temnothorax rugatulus*) in a large empty arena, resulting in almost 5 km of trajectories. We tested for meandering by comparing the turn autocorrelations for empirical ant tracks and simulated, realistic Correlated Random Walks. We found that 78% of ants show significant negative autocorrelation around 10 mm (3 body lengths). This means that turns in one direction are likely followed by turns in the opposite direction after this distance. This meandering likely makes the search more efficient, as it allows ants to avoid crossing their own paths while staying close to the nest, avoiding return-travel time. Combining systematic search with stochastic elements may make the strategy less vulnerable to directional inaccuracies. This study is the first to find evidence for efficient search by regular meandering in a freely searching animal.**

## INTRODUCTION

Mobile animals spend much of their life searching for resources, be it for food, water, mates, shelter, or group members. Typically, they need to stay in a particular area (habitat), and often even stay close to a 'central place', like a nest, to return quickly to it. If resources are unpredictably distributed, the animal must adopt a search strategy to maximize encounters with such resources. Systematic search patterns like spirals or meanders, where right and left turns of similar sizes alternate, are mathematically optimal in ideal scenarios, because they cover 100% of the area exactly once. However, their efficiency drops below that of random movements in the presence of navigational and locomotory inaccuracies<sup>1</sup> or unknown obstructions,<sup>2</sup> as small local deviations from the pattern can lead to long periods of overlapping search paths and unsearched areas close to the central place. Random movements are robust to these factors but less efficient than non-random strategies in low-noise scenarios. Here, we ask whether and how animals combine systematic and random elements in their search for resources.

Most studies of animal movement classically assume that animals move according to a 'Correlated Random Walk' (CRW).<sup>3</sup> In this framework, the movement path is typically represented by discrete steps between turns (but see<sup>4</sup>), where two consecutive steps point in similar directions (hence 'correlated').<sup>5</sup> Another often used type of random walk is the Lévy Walk, where step lengths are drawn from a power-law distribution and turn angles are uniformly distributed.<sup>6,7</sup> A Correlated Random Walk, and by extension animal movements, are typically described by the distribution of turn angles (usually a Wrapped Cauchy Distribution) at a defined step length (or with a defined step length distribution). Similarly, most of the work on the efficiency of search strategies analyzes the properties of different random walks, like turn angle distributions and combinations of different distributions in various resource environments,<sup>8,9</sup> rather than how systematic behaviors would change the resource finding efficiency.

Only recently have more studies focused on the non-random aspects of animal movement patterns beyond responses to external stimuli like gradients,<sup>10</sup> environmental structures,<sup>11</sup> or encounters with resources or conspecifics.<sup>12</sup> Although theoretical work suggests systematic search behaviors arising from interactions with resource patches,<sup>13,14</sup> we still have a limited understanding of systematic movements might be intrinsically generated and combined with random factors to create the search strategy before reacting to extrinsic cues.

On one extreme end, some animals like leaf-grazing moths or ancient seafloor dwellers move(d) in completely or mostly systematic, space-filling meanders (see Figure 1A). Such movement is theoretically

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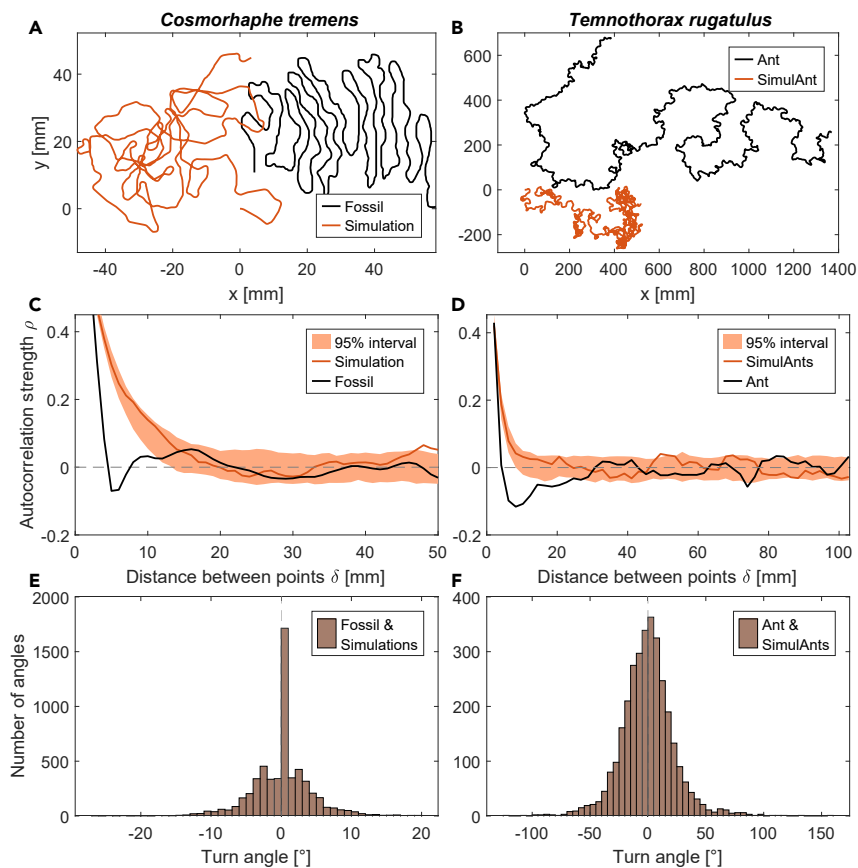
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**Figure 1. Ant meanders and fossil meanders are detectable through autocorrelation**

Left column: *Cosmorhaphie tremens* (fossilized trace, from Sims et al.<sup>25</sup>), right column: *Temnothorax rugatulus* ants. Simulations are created by shuffling turn angles (see [results: random walk simulations](#) for details).

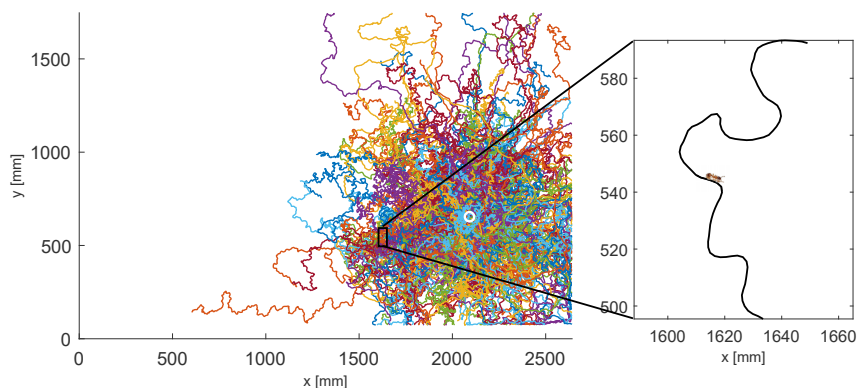
(A and B) Example tracks in black and one simulation of it in red.

(C and D) Correlograms of turn angle autocorrelations of the example tracks. An autocorrelation value toward 1 means that angles are always followed by very similar angles in the same direction, a value near  $-1$  means turns in opposite directions, and a value of 0 means equal likelihood of turns in the same or the opposite direction. The x-axis represents the time lags between the two angles being correlated. In (D), there is a negative autocorrelation between 4 and 22 mm, indicating that successive turns into the opposite direction are approx. 4 to 22 mm apart. Phases of significant positive and negative autocorrelation should appear alternatingly at multiples of this timeframe. That this is not the case here is because of sufficient noise in length and amplitude of meanders.

(E and F) Turn angle distributions of the tracks. Distributions of empirical and simulated tracks overlap perfectly because turn angles of the empirical tracks are used to create the simulated tracks.

one of the most efficient ways of completely covering a given area,<sup>14</sup> but it is rarely performed perfectly in nature. However, elements of systematic movement patterns are present in many other trace fossils,<sup>15</sup> as well as extant species like hungry collembola<sup>16</sup> and roundworms,<sup>17</sup> or different species of amoeba.<sup>18</sup> Spirals as search strategies are often used by animals, but only when their target is known, as in homing isopods<sup>19</sup> and ants<sup>20,21</sup> or when returning to the location of a previous food find.<sup>22</sup> We would also expect larger animals to adopt a regular left-right pattern when searching for food, because of its high efficiency.<sup>18</sup> Smooth meandering, as observed in rivers, has been anecdotally observed in different ants, but never confirmed or quantified,<sup>23,24</sup> maybe due to the difficulty of accounting for the random elements and the continuous character of the movement.

Here, we use a Correlated Random Walk derived from empirical data as a null-model to identify meandering as a non-random, systematic movement in an ant likely to be generated without external cues. Specifically, we compare the turn autocorrelations between ant tracks and a realistic Correlated Random Walk. Turn autocorrelations are positive for a track when two turn angles some distance  $\delta$  away



**Figure 2. All included ant tracks of one 5h trial**

The white circle indicates the position of the nest entrance. Tracks are cut if they come close to one of the walls or after 3m. Zoom window shows a part of one track with an image of an ant to scale. See also [Figure S1](#).

from each other are similar, negative in the case of zig-zagging or meandering, and random movement contains no autocorrelation among turn directions ([Figure 1](#)). Turn autocorrelation is not to be confused with the heading angle correlation, also called ‘persistence’, namesake of the Correlated Random Walk. In previous studies, turn autocorrelations were also used to explain anomalous diffusion by explicitly incorporating them into random walk models.<sup>4,16,17,26–28</sup>

We use the ant species *Temnothorax rugatulus*, which has been the subject of studies on collective decision making and recruitment.<sup>29–31</sup> Their colonies are of typical size for ants<sup>31</sup> (50–300 workers) and do not employ group- or mass recruitment, leading to most resources being collected by individually searching foragers. Anecdotal evidence suggests they mostly forage on small living or dead arthropods and opportunistically lick up sugary liquids.<sup>32–34</sup> Individuals can discriminate their own pheromone from that of other ants<sup>35–37</sup> and are not attracted to or follow the trails of nestmates toward food.<sup>35,38</sup> Their traits of foraging individually, having a relatively small range compared to other ant species,<sup>32</sup> and small colony size make these ants a good study species to investigate search efficiency of Central Place Foragers.

Research on ant search is typically done in contexts where the goal location is already known, such as food baits or the nest entrance. Generally, ant search becomes more dispersed the less ‘confident’ ants are in their knowledge about the location of the goal.<sup>36–40</sup> A rare example of a study on search of *unknown* resource locations shows that *Cataglyphis bicolor* search is consistent with a correlated random walk with no systematic elements.<sup>41</sup>

## RESULTS

### Data acquisition

We filmed 5 colonies of *T. rugatulus* ants each exploring a large, empty arena (2 × 3m) for 5h with 25fps. All ants of one colony were free to exit and enter the nest at any time. We tracked ants in the videos using TRex.run<sup>42</sup> and processed the raw tracking data using custom routines to correct tracking errors. We then resampled the tracks with a constant step length of 2 mm to eliminate spurious movement angles because of tracking inaccuracies, while preserving the geometry of the track. To control for correlations between measured track characteristics and track length, we excluded tracks shorter than 60 cm and cut longer tracks to 3m (for details on all methods, see [STAR Methods](#) and provided code). This resulted in 1.5 million points in 1,384 tracks (see [Figure 2](#) for one colony and [Figure S1](#) for others) across all 5 colonies (range: 65k–452k points and 60–451 tracks per colony, [Figure S3](#)), with typically between 1 and 15 analyzed ants present simultaneously.

### Ant movement characteristics

Ants walked with a median speed of 8.3 mm/s and faster speeds were correlated with lower turning angles (Linear Model:  $F(451,519) = 9.2e+04$ ,  $p < 0.001$ ). Ants did not demonstrate a common turn bias toward either side (t-test whether the distribution of the sum of turn angles is different from 0:  $p = 0.19$ ,  $t: 1.31$  *df*: 1383, *SD*: 1367; [Figure S4](#)). Colonies achieved what seems to be near complete area coverage

in a short time, even in the far corners, which is as far away from the nest as some colony median foraging distances observed in nature.<sup>32</sup> Ant colonies in nature may thus achieve similar coverage, unless the three-dimensional aspect of natural surfaces, like leaf litter, increases the real foraging area experienced by ants in the field dramatically. Physical interactions with nestmates likely only play a small role in shaping the movement of ants. 69.8% of ants never physically interacted with other ants and only 0.6% of the total distance walked by all ants falls within 5 cm after interactions. In addition, only 62 interactions in 46 out of the 1,384 tracks happened farther than 60 cm (20%) away from the start or end of the tracks, with probability of interactions expectedly decreasing with distance to the nest and time from the start of the track. Finding systematic effects of physical interactions with other ants is thus difficult and not the focus of this study. We also find that ants from larger colonies tend to move faster, have higher dispersivity, and show more negative turn autocorrelation than ants from smaller colonies (see below; Linear Models, respectively:  $F(1382) = 610$ ,  $p < 0.001$ ;  $F(1382) = 13.6$ ,  $p < 0.001$ ;  $F(1382) = 9.27$ ,  $p = 0.002$ ).

### Random walk simulations

We compared each empirical ant track to 1999 (following the '99 rule'<sup>43</sup>) simulations of this track under assumptions of random walking. We did not pool ants or compare the population means because of the (expectedly) large variation in track lengths and turn angle distributions and, importantly, some ants may not even be in the state of searching, but instead getting familiar with the surroundings.<sup>44</sup> This results in answering the questions for each ant separately.

Simulations were made by drawing with replacement from the set of turn angles of the ant track, while accounting for positive angle correlations of subsequent steps because of the relatively high sampling frequency of less than 1 body length (see [STAR Methods](#) for details). Our results hold up when we instead draw turn angles from the commonly applied Wrapped Cauchy Distribution (WCD) (e.g. Bartumeus et al.<sup>45</sup>) fitted to the turn angle data (see [STAR Methods](#) for details and [Figure S6](#) for main results).

For all three metrics, we define significant differences where the ant's measure was smaller (or greater) than >95% of her simulations.<sup>46</sup> To control for false-positive inflation due to calculating significance for each of the 1,384 ants individually, we employ the Benjamini-Hochberg correction of false discoveries.<sup>47</sup>

### Turn angles are negatively autocorrelated

A distinguishing property of meandering behavior is that turn angles at some point  $p$  are negatively correlated with angles at some other point  $p+\delta$  (where  $\delta$  stands for the distance walked between the two points). This means that turns separated by the distance lag  $\delta$  are likely in opposite directions. We calculated the turn autocorrelation over all lags from  $\delta = 2$  mm to  $\delta = 30$  mm after<sup>48</sup>, p. 176, as implemented by Berens.<sup>49</sup>

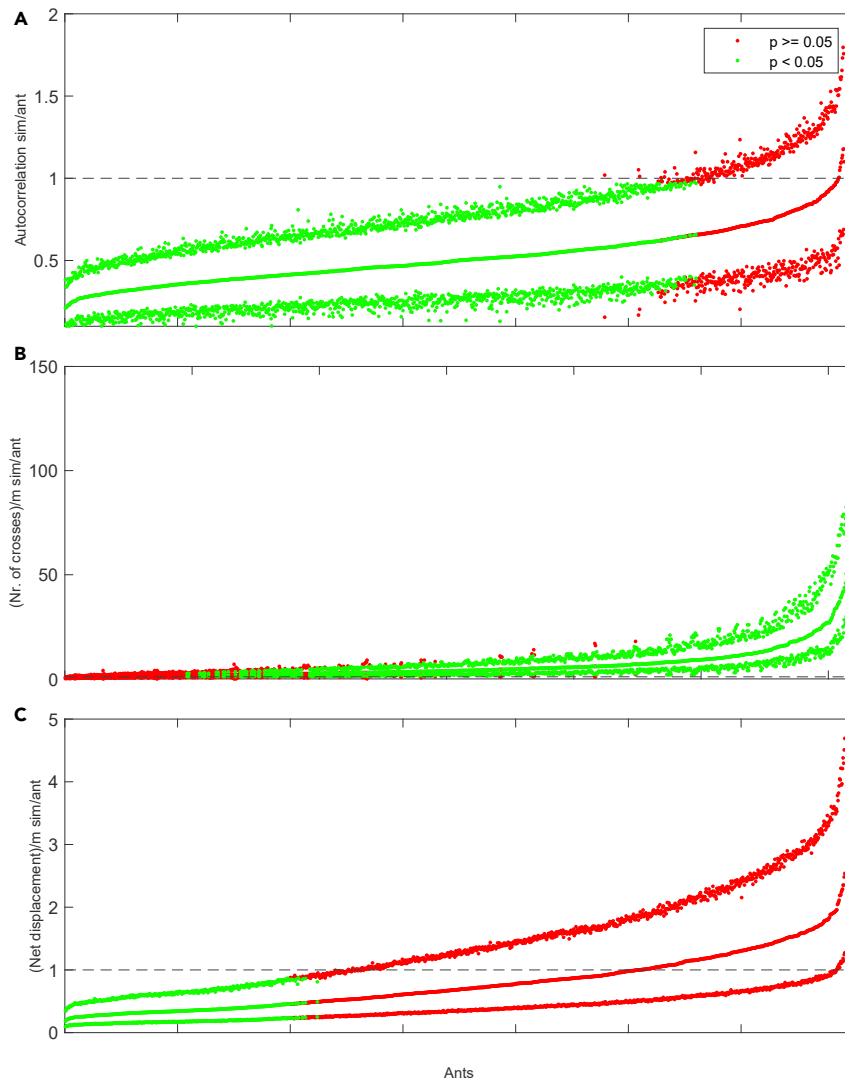
78.0% of tracks had significantly negative autocorrelation, indicating meandering behavior ([Figure 3A](#)). The lag distance where the most negative (i.e. minimum) turn angle autocorrelation occurs is around  $10.0 \pm 8.5$  mm, (mean  $\pm$  SD), which thus represents the typical half-wavelength of one meander (see [Figure S5](#) for the distribution of meander lengths).

### Most ants cross their paths less but are not more dispersive

Given the hypothesis that this meandering makes search more efficient than random walking, we also calculated as a crude measure of efficiency the number of times the path intersected itself. 73.8% of ant tracks cross themselves significantly less than random walk tracks ([Figure 3B](#)). The median number of path crosses per meter walked in ants is 4.65, whereas it is 21.24 in simulations.

A straight-forward way of achieving fewer path crosses is to turn less, and thus move more quickly away from the nest (= disperse more). This comes with the costs of being in potentially riskier areas (because of competitors) and an increased return travel distance after a resource find. To test whether quicker movement away from the nest can explain the lower number of path crosses, we computed as a measure of 'dispersivity' the mean of the straight-line distances from the nest of each point in the track for ants and simulations. 29.8% of ants were more dispersive than their random walk and no ant was less dispersive ([Figure 3C](#)).

More non-random meandering indeed improves the tradeoff between fewer path crosses and more dispersivity by reducing the number of path crosses more than increasing dispersivity (see [Figure S7](#) for a



**Figure 3. Turn angles of ant tracks are more negatively autocorrelated (A), ants cross their paths less (B), and some ants are more dispersive than random walks (C)**

Ants are sorted by their median of the respective response variable in the three panels and represented each by the median, 5%, and 95% values of their simulations. Green dots indicate significantly different values between the ant and her simulations. Note that significance does not always switch at 0 because of the statistical correction for multiple comparisons.

(A) The minimum autocorrelation value of each set of simulations relative to its respective ant. The greater the value, the more pronounced the ant's meandering behavior. Note that some red medians are covered by green dots and 3 outlier points of values greater than 5 are excluded.

(B) Number of path self-crosses of simulations relative to ant tracks. The greater the value, the fewer the ant crosses her own path compared to her simulations.

(C) Mean displacement from the nest of simulations relative to ants. The greater the value, the closer to the nest the ant stayed compared to her simulations. This result thus shows that some ants went away farther from the nest than a similar random walk would have done. See also [Figure S6](#) for results using a Wrapped Cauchy Distribution null-model, and [Figure S7](#) for the same data, but where all tracks sorted by their autocorrelation value.

replication of [Figure 3](#) where ants are sorted by their autocorrelation median in all three panels; linear model of number of path crosses times dispersivity predicted by autocorrelation:  $F(1382) = 25$ ,  $p < 0.001$ , shown in [Figure S8](#), linear model of number of path crosses predicted by autocorrelation:  $F(1382) = 20$ ,  $p < 0.001$ , dispersivity predicted by autocorrelation:  $F(1382) = 35.8$ ,  $p < 0.001$ .

### Factors correlating with movement behavior

Slower tracks have more negative turn autocorrelations (Linear Model:  $F(1384) = 5.11$ ,  $p = 0.024$ ). Ants of larger colonies move with less turn autocorrelation (LM:  $F(1384) = 6.27$ ,  $p = 0.002$ ) and fewer crosses per meter (LM:  $F(1384) = 33.5$ ,  $p < 0.001$ ), and are faster (LM:  $F(1384) = 610$ ,  $p < 0.001$ ) and more dispersive (LM:  $F(1384) = 13.6$ ,  $p < 0.001$ ). See also [Figure S9](#). Ants entering the arena at later times of the experiment are faster (LM:  $F(1384) = 44.4$ ,  $p < 0.001$ ), and more dispersive (LM:  $F(1384) = 172$ ,  $p < 0.001$ ), and show more negative autocorrelation (LM:  $F(1384) = 5.18$ ,  $p = 0.023$ ) and fewer crosses per meter (LM:  $F(1384) = 40.5$ ,  $p < 0.001$ ).

### DISCUSSION

We found evidence that *Temnothorax* ants systematically meander left and right on a scale of around 5.4 mm (a half ‘wavelength’ of  $\sim 1.5$  body lengths). This is the first time such meandering behavior has been shown in ants or in any central place forager. We also find that ant tracks cross themselves less often than random walk tracks, while being as or more dispersive than them. This lends credence to the idea that the meandering seen here is an element of systematic search which allows ants to cover an area more efficiently than pure random walking.

### How this changes our view on systematic/random search

This study adds to the body of literature showing that even relatively ‘simple’ organisms employ more sophisticated movement patterns than simple correlated (or biased) random walks or purely reacting to the environment.<sup>18,50,51</sup> Instead, the ant species studied here employs a combination of random and systematic elements which are combined in a way to substantially decrease path self-crosses. This finding has implications for both the methods used in trajectory analysis and our conceptual understanding of animal search. Models of animal movement generally assume independence of successive turn angles and process empirical tracks in a way to account for this assumption. However, this processing discards a lot of important and interesting information, which may lead to drawing false conclusions. For example, our results indicate that the non-random component of the movement behavior is important for high search efficiency. Systematic behaviors are probably widespread in animals and including them in process models of animal movement might increase not only the fit of the generated behavior, but also the simplicity of the algorithm. In the example of meandering ants, this could be a formulation of a turn direction oscillator, removing the need to explicitly specify angle distributions. The field of search and area surveying using drones and robots currently mostly use regular patterns.<sup>52</sup> In particular, swarms of such agents could greatly benefit from combining random with systematic elements, solving some of the problems of robustness and adaptability.<sup>53</sup>

### Turn autocorrelation as a metric

Our main finding corroborates the anecdotal reports of a meandering behavior in other ant species<sup>23,24</sup> and a desert isopod.<sup>19</sup> Our simple but powerful approach could also be applied to these datasets and give evidence for a meandering behavior in other moving organisms. We analyzed the autocorrelation of turning angles, which is long known to be an important part of movement. However, it requires including data over a large range of scales,<sup>54</sup> which is why turn autocorrelation analysis is still comparatively rare. Here, we collect such a dataset, and use turn autocorrelations to quantify systematic elements and to specifically discover regular meandering during search. Turn autocorrelation analysis can be a useful descriptor of any high frequency sampled movement paths, similar to its use in Gurarie et al., 2017.<sup>4</sup> This measure can add information to other trajectory metrics describing, for example, sinuosity, space use, and behavior changes.<sup>55</sup> Our approach is in stark contrast to most movement analysis, where the turn angle autocorrelations are seen as a nuisance and avoided by track resampling, because these methods assume a pure Correlated RandomWalk<sup>56,57</sup> and might give spurious results if this assumption is not met.<sup>58</sup>

### Other species

‘Zig-zagging’ is a common behavior, observed mostly in insects. It is present, e.g., in flying insects approaching objects,<sup>59,60</sup> probably to gain spatial information about them, moths following a pheromone plume,<sup>61</sup> ants following a pheromone trail,<sup>62,63</sup> or ants visually navigating toward a goal location.<sup>64,65</sup> However, these examples are rather different from searching for resources of unknown locations in a gradient-free environment. In such a scenario, zig-zagging has been suspected in harvester ants but

could not be confirmed.<sup>24</sup> Highly regular and tight meandering without a goal is observed, for example, in some worms in sediment (see [introduction](#)), leaf-mining or leaf-grazing insect larvae,<sup>66</sup> and bark beetles.<sup>67</sup> These cases have in common that the foraging space is severely restricted, and the visited surface or substrate is permanently altered. The combination of these factors may increase the value of highly regular patterns for the mover.<sup>14</sup> However, regular movement patterns may be underreported in species which do not leave such conspicuous trails. In fact, meandering elements in search might be widespread, as it can be found across a large portion of the Tree of Life, from slime molds,<sup>18</sup> over worms<sup>25</sup> to ants, despite these organisms having different foraging environments, life histories, and substrate of behavior. This suggests that this behavior either arose multiple times or is very ancient, but in either case does not require a brain.

### Area coverage efficiency

We also showed that ant tracks 1) cross themselves less than random walks, and 2) sometimes disperse more than random walks. The first property indicates that the area coverage efficiency of ant movements is higher than that of a random walk because ants waste less time searching the same places multiple times. Although the higher dispersivity leads to longer return trips once a resource is found, it leads ants more quickly away from areas near the nest, which are probably well-searched on a colony level. However, modeling studies are necessary to show in which resource and cost scenarios this behavior is indeed significantly more efficient. Random search, for example, might be just as efficient when resources replenish or change position quickly or when the probability of detecting resources is low,<sup>68</sup> or when navigational noise is high.<sup>1</sup> Likewise, more dispersive movements tend to improve search in resource sparse or patchy environments, where they are ideally combined with more tortuous local search within patches.<sup>8,69,70</sup> Systematically testing resource scenarios and specific meander properties, such as amplitude and frequency, will be useful to create a framework of when which pattern is theoretically optimal and generate hypotheses about ant navigation and foraging ecology. A meandering-like pattern can also be found in certain space-filling curves, which are mathematically ideal ways of filling spaces without curve-intersections.<sup>71</sup> This property is important for applications like land surveillance drones, which need to gather information about a given area in a time- and energy efficient manner, similarly to ants.<sup>52</sup> However, the currently employed rigid, *a priori* path planning is difficult in complex bounding shapes and impossible for unknown environments. A more ant-like area coverage strategy incorporating stochasticity is a possible solution to this problem.

### Coordination with nestmates

Because ants need to coordinate with their nestmates to maximize colony efficiency, it is likely that even solitary ant searchers are influenced by the movements of other ants of their colony.<sup>23,72,73,74</sup> We find that ants in larger colonies and those entering the arena later in the experiment meander less strongly, cross their paths less, and move faster and farther away from the nest. These movement characteristics likely reduce the repeated coverage of the same area by different ants of the same colony and seem to be upregulated with increasing number of ant steps in that area. This could be facilitated by the perception of the concentration of chemical marks on the ground. It is also plausible that properties of the meandering behavior, like turn length and amplitude are modulated by physical interactions with nestmates or perceiving their pheromone traces. Although we are not able to test this hypothesis here, it could be done systematically in a future study by controlling interactions and pheromone deposition.

### Conclusion and limitations of the study

We found that ants meander regularly, cross their own paths less, and disperse from the nest more than expected at random. We assume that ants in the arena are searching for targets, but cannot infer what they are searching for, if at all. Different targets or 'states' could explain the relatively large variation in meandering behavior. Nevertheless, the combination of systematic and random search by these ants is an argument against the widely used assumption of animals moving in random-only walks and indicates that the search strategies of many animals are more sophisticated than currently assumed. Our findings show that theoretical work and empirical analyses of animal movement behavior should pay more attention to non-random elements in ants and other species. With more such data, it will be possible to create and test hypotheses about the behavior's efficiency in real-life resource scenarios, its evolution, and generating processes. Incorporating non-random elements in movement models could lead to more accurate models and a richer understanding of these processes.



## STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- [KEY RESOURCES TABLE](#)
- [RESOURCE AVAILABILITY](#)
  - Lead contact
  - Materials availability
  - Data and code availability
- [EXPERIMENTAL MODEL AND SUBJECT DETAILS](#)
- [METHOD DETAILS](#)
  - Arena setup
  - Experimental procedure
  - Random walk null-model
  - Wrapped Cauchy Distribution null-model
- [QUANTIFICATION AND STATISTICAL ANALYSIS](#)

## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2022.105916>.

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## AUTHOR CONTRIBUTIONS

S.P. and A.D.: Conceptualization, Methodology, Project administration; S.P.: Software, Formal analysis, Investigation, Resources, Data Curation, Writing – Original Draft, Visualization; A.D.: Writing – Review and Editing, Supervision, Funding acquisition.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

## INCLUSION AND DIVERSITY

One or more of the authors of this paper self-identifies as a gender minority in their field of research. We support inclusive, diverse, and equitable conduct of research.

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## STAR★METHODS

## KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper	<a href="https://osf.io/ew5ak/?view_only=c34545f6907842dcba485b8adebfb2aa">https://osf.io/ew5ak/?view_only=c34545f6907842dcba485b8adebfb2aa</a>
Experimental models: Organisms/strains		
<i>Temnothorax rugatulus</i> (Cole 1934)	Santa Catalina Mountains, AZ, USA	N/A
Software and algorithms		
ffmpeg	Tomar <sup>75</sup>	<a href="https://ffmpeg.org">ffmpeg.org</a>
TRex.run	Walter and Couzin <sup>42</sup>	<a href="https://trex.run">trex.run</a>
MATLAB R2021a	The MathWorks, Inc., Natick, MA, US	<a href="https://mathworks.com/products/matlab.html">mathworks.com/products/matlab.html</a>
Custom MATLAB routines	This paper	<a href="https://osf.io/ew5ak/?view_only=c34545f6907842dcba485b8adebfb2aa">https://osf.io/ew5ak/?view_only=c34545f6907842dcba485b8adebfb2aa</a>

## RESOURCE AVAILABILITY

## Lead contact

Further information and requests for resources, raw data, and code should be directed to and will be fulfilled by the lead contact, Stefan Popp ([popp@arizona.edu](mailto:popp@arizona.edu)).

## Materials availability

This study did not generate new unique reagents.

## Data and code availability

- Datasets of tracks and analysis data are available at the Open Science Framework. The DOI is listed in the [key resources table](#).
- All code described above is available at the open Science Framework. The DOI is listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.
- Video conversion was done in Ffmpeg,<sup>75</sup> tracking with TRex.run,<sup>42</sup> and all following processing was done in MATLAB (Release 2021a., The MathWorks, Inc., Natick, Massachusetts, United States) using custom routines, which can be found at Open Science Foundation: [https://osf.io/ew5ak/?view\\_only=c34545f6907842dcba485b8adebfb2aa](https://osf.io/ew5ak/?view_only=c34545f6907842dcba485b8adebfb2aa).

## EXPERIMENTAL MODEL AND SUBJECT DETAILS

For our experiments in July and September 2019, we used five colonies of *T. rugatulus*, which were collected in March 2019 in the Santa Catalina Mountains near Tucson, AZ, USA, above 2200m. Colonies had ca. 50–250 workers, 1 or several queens, and brood in all stages. Ants were housed in flat nests of a 2 mm thick cardboard ring (ø8cm) sandwiched between two plastic disks. The nest entrance was a 2 mm hole in the center of the top disk. Nests were placed in plastic boxes (20 × 15cm), where ants had access to *ad libitum* water and were provided with 1:10 honey water solution and cockroach halves for 24h once every week. One week prior to their participation in the experiment, colonies were deprived of food to ensure high foraging motivation without severely starving them.<sup>33,34</sup>

## METHOD DETAILS

## Arena setup

We followed all foragers of a colony simultaneously with high precision, in a large (2 × 3m) arena ([Figure S10](#)). The size of the arena is thus ca. 1000 ant body lengths and as long as the median foraging distance

of this species.<sup>32</sup> 5 cm high PVC walls covered in Fluon prevented ants from escaping. The arena was evenly lit by four LED panels mounted on a PVC-pipe framework. Four Sony  $\alpha$ 6300 cameras mounted on the same framework captured the whole arena in 25fps, 4K (3840x2160) mp4 video, resulting in a resolution of at least four pixels per mm<sup>2</sup>. For experiments, nests were placed under a layer of white butcher paper covering the whole arena floor and a small hole was pinched at the position of the nest entrance. This ensured no surface features which could influence the movement of the ants were present.

### Experimental procedure

We let each of the 5 *T. rugatulus* colonies explore the arena for 5h. Nests were placed underneath the paper cover and ants could freely exit and enter the nest through a hole in the paper directly over their nest entrance. Immediately after recording ended, ants were gently placed back inside the nest. Paper covers were exchanged between trials to remove any chemical markings from other colonies.

#### Video conversion

To facilitate tracking accuracy and data handling we used FFmpeg<sup>75</sup> (command routines can be requested from the corresponding author) to 1) cut the videos up into 30 min sections, avoiding tracking errors due to minimally changing lighting and camera angles over the course of the experiment, and 2) convert them to grayscale and reduce their bitrate to an average of 4 Mbps, resulting in greatly reduced file size with negligible information loss for tracking.

#### Tracking

To obtain ant positions in every frame for every camera, we used the tracking software TRex.run.<sup>42</sup> It first identifies objects through background subtraction and then links them into tracks based on positional predictions using an adapted Kalman filter. This tracking resulted in a temporal resolution of 25fps and an estimated maximal spatial error of  $\pm 0.5$  mm. Tracking parameters and routines can be requested from the corresponding author.

#### Joining tracks across cameras

We obtained one set of 10 track files for each camera for every colony. We thus had to synchronize and spatially join the tracks across camera views. This was achieved by 1) correcting lens distortion using the Computer Vision Toolbox (Release 2021a), 2) shifting and rotating tracks, and 3) blending and connecting tracks moving from the view of one camera into that of another through a positional averaging method.

#### Manual corrections

Some high-contrast features of the arena like dust particles or paper edges were falsely identified as objects and some tracks were interrupted, mostly when ants met each other or left the tracked frame. These errors were manually corrected using custom interactive plots, taking circa 200 undergraduate research assistant hours.

#### Track interpolating

When the ant was intermittently not detected, and the gap did not exceed 1 cm, missing points of those frames were interpolated using a Bezier function. With the subsequent smoothing, this leads to a well-approximated path.

#### Track smoothing

We had to smooth the tracks, since the ant's tracking positions tend to wobble within the outlines of the ants due to fluctuations in pixel brightness between frames ('optic wobble'). This results in considerable spurious turning angles and displacements, especially during periods of slow or no movement, given that an ant may only be represented by 6–9 pixels. We used locally weighted scatterplot smoothing (LOWESS)<sup>76</sup> with a quadratic function and a window width of 10 points. We did not use robust LOWESS smoothing since it resulted in negligible improvements and increased the computing time 130-fold. All values were determined by visual comparison between the video and the track of an ant.

#### Equidistant resampling

To completely eliminate the effect of optic wobble in pausing periods, we resampled the track such that each point is  $2 \text{ mm} \pm 0.05 \text{ mm}$  away from the previous point. We did this by linearly interpolating 10 points

between each raw point and then selecting the first interpolated or raw point which is farther than 2 mm away from the previous point.

### Wall-following exclusion

We excluded all points of a track after the ant came close to a wall (up to ~4 cm). Ants exhibit wall-following behavior which is different from the obstacle-free behavior this paper is focused on.

### Interactions

When ants meet, they tend to antennate each other for a few seconds before continuing their paths. To estimate rates of such physical interactions, we defined them as when two ants come within 6.7 mm (2 distances from the ant centroid to the antennal tips) of one another. False positives are unlikely but ants which barely missed each other might be counted as meeting.

### Stationarity

Our autocorrelation analysis over whole tracks assumes stationarity of behavior, meaning that the behavior does not trend in a certain way over the time of the experiment. We thus tested for stationarity using Augmented Dickey-Fuller tests<sup>77</sup> on speed and absolute values of turning angles of each track. All tracks' turning angles were stationary and only 3.25% of tracks showed a trend of increasing speed over the course of the track, after accounting for multiple comparisons with the Benjamini-Hochberg<sup>47</sup> method.

### Track length standardization

Turn autocorrelations become less pronounced with increasing track length. However, this is mainly not due to differences between ants, but rather due to capturing more variation in meander lengths when more points are considered (see S2). Similarly, we found that longer tracks are increasingly more different from their random walk simulations (see below), leading to track length being a potentially confounding factor when comparing meandering with dispersivity. We thus cut all tracks after 3m distance walked and excluded tracks which were shorter than 60 cm, greatly reducing the track length variation while keeping the majority of points.

### Random walk null-model

We recreated ant tracks by selecting a turning angle  $\alpha$  at every point  $p$  from the ant data, for a number of  $P$  points equal to that of the focal empirical track. Due to the equidistant resampling, each point is 2 mm away from its predecessor. However, due to the relatively short sampling distance of  $<1$  body length, there are strong autocorrelations between two consecutive  $\alpha$ <sup>4</sup>. Drawing for each step independently could thus lead to a sharp left turn being immediately followed by a sharp right turn, which is very rarely done and not to be expected by any real (calm) ant, and which would make the null model less useful to identify a potential systematic search behavior.<sup>58</sup> We thus account for likely accelerations and turnspeeds by adopting the following procedure.

1. For the set of  $\alpha$  values, create 10 bins of an equal number of points.
2. Define the set of  $\alpha$  which follow any of the  $\alpha$  in a given bin as the set of plausible  $\alpha$ .
3. Set the first point's angle ( $\alpha_1$ ) equal to the ant track's first angle.
4. For each point  $p$  (up to  $P$ , the number of points in the empirical track), draw  $\alpha_p$  from the set of plausible  $\alpha$ , given the  $\alpha$  bin of the previous point,  $\alpha_{p-1}$ . Written in an equation:  $\alpha_p = P(\alpha_p|\alpha_{p-1})$ .

### Wrapped Cauchy Distribution null-model

To test whether our results hold with a random walk model more commonly used, we repeated the analyses with a null model where angles are not drawn from the tracks themselves, but from a Wrapped Cauchy Distribution (WCD) fitted to the turn angle data. WCDs are routinely used for animal movement analysis models.<sup>1</sup> Therefore, we first estimated the mean  $\mu$  and concentration parameter  $\rho$  of the WCD for each track separately and then sampled a matching number of angles from the resulting distribution. We create tracks by connecting turns with the 2 mm step lengths present in the ant tracks.

## QUANTIFICATION AND STATISTICAL ANALYSIS

Statistical significance was defined as <5% of the  $n = 1999$  simulations (=99) having a value of the respective metric relative to that of the ant which rejects the alternative hypothesis, according to Ref. 46. To control for false-positive inflation due to calculating significance for each of the 1384 ants individually, we employ the Benjamini-Hochberg correction of false discoveries.<sup>47</sup>

We wanted to measure the cost of the homing distance, without considering other factors like increased risk of predation, competition, or getting lost when farther away from the nest. Assuming a linear increase in cost with distance to the nest, this cost is the expected homing distance after finding a resource:

$$\sum_{p=2}^P \text{mm} \sqrt{(x_p - x_{\text{nest}})^2 + (y_p - y_{\text{nest}})^2}.$$

This measure is higher the more steps an agent spends farther away from the origin of the walk. The high sensitivity of this metric to track length is not relevant here, since we only compare tracks of equal lengths (ant track with its simulations).

All tracks which did not start within 5 cm of the nest (= segments of broken-up tracks) were excluded, additionally to track parts which followed the point of an ant coming within ~4 cm to one of the arena walls to exclude wall-following behavior.