The Bayesian Superorganism III: externalised memories facilitate distributed sampling

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Abstract

A key challenge for any animal is to avoid wasting time by searching for resources in places it has already found to be unprofitable. This challenge is particularly strong when the organism is a central place forager – returning to a nest between foraging bouts – because it is destined repeatedly to cover much the same ground. Furthermore, this problem will reach its zenith if many individuals forage from the same central place, as in social insects. Foraging performance may be greatly enhanced by coordinating movement trajectories such that each ant visits separate parts of the surrounding (unknown) space. In this third of three papers, we find experimental evidence for an externalised spatial memory in *Temnothorax albipennis* ants: chemical markers (either pheromones or other cues such as cuticular hydrocarbon footprints) that are used by nestmates to mark explored space. We show these markers could be used by the ants to scout the space surrounding their nest more efficiently through indirect coordination. We also develop a simple model of this marking behaviour that can be applied in the context of Markov chain Monte Carlo methods (see part two of this series). This substantially enhances the performance of standard methods like the Metropolis–Hastings algorithm in sampling from sparse probability distributions (such as those confronted by the ants) with little additional computational cost. Our Bayesian framework for superorganismal behaviour motivates the evolution of exploratory mechanisms such as trail marking in terms of enhanced collective information processing.

Keywords: exploration, trail markers, spatial memory, Markov chain Monte Carlo, ants, superorganism

Introduction

Exploring an unfamiliar, changing environment in search of valuable resources such as food or potential nest sites is a challenge for many organisms. A memory of where one has already explored, to avoid revisiting unprofitable locations, would generally seem to be an advantage. Nevertheless, while having a spatial memory of e.g. foraging locations is clearly adaptive, developing such a memory is associated with physiological costs. These include the metabolic overhead of a bigger brain (memory storage capacity) and the cost of encoding and retrieving memories (brain activity); these costs have to be traded-off against the benefit of improved foraging performance (Fagan et al. 2013). One way to circumvent the cost of carrying memories internally is to store the information externally in the environment. Indeed, such externalised information storage may have been the historical precursor to the development of internalised memory storage and retrieval (Chung and Choe 2009; Chung et al. 2009). Use of external markers as memory has been demonstrated in arguably simple organisms, including the slime mould *Physarum polycephalum* (Reid et al. 2012). Markers may be left in the environment to signify the presence or absence of good foraging or nest-making prospects at that location, so that when an animal returns it can make an appropriate and timely decision about the expenditure of its efforts.

An analogous problem to animals searching for food sources in an unfamiliar environment is that of sampling efficiently from unknown probability distributions. Markov chain Monte Carlo (MCMC) methods have been developed to generate such samples but suffer from the same problem of potentially revisiting the same area of probability space repeatedly. Although methods such as the Metropolis–Hastings algorithm show random walk behaviour in their sampling trajectory, they are still popular techniques because of their ease of implementation and computational simplicity. As discussed in the second paper of our series on the 'Bayesian superorganism' (Baddeley et al. 2018), MCMC methods can be used as a model of animal movement that enacts the optimal probability matching strategy for collective foraging ('gambling') (Kelly 1956). There, we drew a parallel with advances in efficiency in MCMC methods, to more adaptive animal behaviours emerging in natural

history: for example, from the random-walk type behaviour of the Metropolis-Hastings algorithm (Metropolis et al. 1953; Hastings 1970) to the correlated random walks produced by Hamiltonian Monte Carlo (Duane et al. 1987). The performance boost provided by externalised memories, discussed here, may similarly be understood as an evolutionary advancement in collective information processing capabilities.

Here, we present two main findings: (1) evidence that *Temnothorax albipennis* worker ants avoid the footprints of nestmates during the reconnaissance of an unfamiliar space, and that this enhances the efficiency of the colony-level collective exploration; (2) we develop a bio-inspired trail avoidance method for the purpose of Markov chain Monte Carlo sampling that similarly uses a memory of where the walker has visited to obtain a representative sample more rapidly. This method is easy to implement and computationally simple, and offers significant improvements in performance for the sort of sparse distributions that ants and other organisms also have to sample from routinely. In the next section we introduce some more biological background on chemical markers (externalised memories), but the reader familiar with this topic may proceed to the Methods section.

Further biological background on chemical markers

In addition to expediting the process of environmental search, external markers can also have the purpose of communicating one's presence to friendly or competitor conspecifics. Some animals are well-known for marking territory: for instance wolves (*Canis lupus*) use scent marks to maintain their territories (Peters and Mech 1975) while mice (*Mus musculus*) use olfactory cues to help establish their territorial boundaries (Mackintosh 1973). In the Hymenoptera, the honeybee *Apis mellifera ligustica* marks visited flowers with a scent and rejects flowers that have been recently visited; it responds more strongly to its own markers than that of its nestmates (Giurfa 1993). Such repellent scent-marks should help the bee to forage more efficiently. As in the ants, these marks may simply be hydrocarbon footprints rather than costly signals (Eltz 2006). Ants are known to

engage in two distinguishable approaches to marking the area around their nest. In territorial marking, ants will defend the marked area against intra- and inter-specific intruders. By contrast, home-range markers label areas that the colony knows to be hospitable and available for foraging, but such areas are not defended against other ant colonies (Hölldobler and Wilson 1990). Major workers of the African weaver ant *Oecophylla longinoda* mark their territories with persistent pheromones that are distinguishable to the ants at the colony level (Hölldobler and Wilson 1977), whereas workers of the leafcutter ant *Atta cephalotes* deposit 'nest exit pheromones' in the vicinity of their nest entrances, helping to orient workers and hence enhancing the efficiency of leaf gathering (Hölldobler and Wilson 1986). *Lasius niger* ants have been found to engage in home-range marking, which rather than territorial marking may help them to enlarge their potential foraging space alongside other colonies, in a 'shared information' strategy (Devigne and Detrain 2002).

Apart from pheromones, which are signals laid deliberately by ants at a cost to themselves, to influence the behaviour of other ants, ants have also been shown to respond to cues such as the cuticular hydrocarbon footprints left by other ants. These can also be used to distinguish between different colonies (Akino and Yamaoka 2005), and potentially also to recognize different castes, as in a study of *Reticulitermes* termites (Bagnères et al. 1998). They can also be detected by ant predators, and so this deposition is not without costs (Cárdenas et al. 2012). The response ants make to detecting such markers depends on whether the cue is from a nestmate, a competing colony, or a different species altogether, because depending on the relationship between sender and receiver, it could represent a threat or useful information about the location of foraging resources (Wüst and Menzel 2016). The role of the ant species (dominant or submissive) in the local community can be key in this respect (Binz et al. 2014).

In our study organism, the house-hunting rock ant *T. albipennis*, there is evidence for pheromone use in navigating to a new nest site (Pratt et al. 2001; McLeman et al. 2002) as well as in *T. curvispinosus* (Bowens et al. 2013). Other *Temnothorax* species are also known to use individual-specific trail pheromones for orientation outside their nests: *T. affinis* (Maschwitz et al. 1986) and *T.*

unifasciatus (Aron et al. 1988). *T. albipennis* is thought to use an individual-specific pheromone trail during the nest-site assessment process: to measure the floor area using the 'Buffon's needle' algorithm, an ant experiences a lower crossing rate of its own trail when the nest is larger. If its trail was not individual-specific only one ant could do this before the trail was confused with those of other scouting nestmates (Mallon and Franks 2000). *T. albipennis* colonies are also found to avoid conspecific colonies when choosing where to locate its nest, as a result of odour cues left by foreign colonies (Franks et al. 2007). Pheromones are also probably used by the ants when scouting potential new nest sites, since when previously assessed nest sites are replaced with clean nest sites, colonies are more likely to pick the poor option, having lost their reconnaissance information (Franks et al. 2007). *T. rugatulus* was found to use an alarm pheromone that elicits two different behaviours depending on the context: in an unfamiliar nest it causes ants to reject it as a potential new home, to avoid danger; while when released near the ants' home nest it attracts them to defend against a threat (Sasaki et al. 2014).

Chemical marks left by harvester ants (*Pogonomyrmex*) during exploration for new food have been suggested as a way of avoiding redundant repeat searches in that area (Holldobler and Wilson 1970; Carroll and Janzen 1973). The usefulness of an avoidance behaviour during the searching phase for food was commented upon by Nonacs in a study of *Lasius pallitarsis* ants. Such a behaviour was predicted to be more helpful for solitary foragers, than for species with mass recruitment to prey items that need teams of workers to carry them home. Experimental investigation found that the ants show a state-dependent avoidance of the path of previous nestmates (Nonacs 1991). This question has recently been revisited when evidence was found that *Myrmica rubra* (Myrmicinae) ants avoid the footprints of their nestmates, which suggests that they are using the information it conveys to inform their foraging or scouting decisions (Binz et al. 2014). However, this behaviour was not observed in the four other ant species in the study: *Formica polyctena* (Formicinae), *Formica rufibarbis* (Formicinae), *Lasius niger* (Formicinae), and *Tetramorium caespitum* (Myrmicinae). *T. albipennis* is also in the subfamily Myrmicinae, and we predicted that it

too uses cuticular hydrocarbon footprints left by previous exploring nestmates to scout an unknown area surrounding its nest more efficiently. Here, we present evidence that *T. albipennis* indeed avoids the footprints of nestmates during the reconnaissance of an unfamiliar space, and for the first time show that it enhances the efficiency of the colony-level collective exploration.

Methods

Data processing and analysis

We examine data from a previous study of *T. albipennis* ant movement patterns (Hunt et al. 2016). These data present two experimental regimes, one in which the foraging arena was entirely novel to exploring ants, because it was cleaned by the experimenter in advance, and one in which previous traces of the ants' activities remained. We call these treatments 'No cleaning' (NC) and 'Cleaning' (C). These were both applied to six ants each from three colonies, for a total of 36 ants. The colonies inhabited small artificial nests with a 2mm diameter entrance hole drilled into the centre of the top. A colony was placed into a 90×90cm arena and a 15×15cm white paper mask with a 1×1cm central hole affixed over the top, with a further 1.5×1.5cm white paper removable cover to block the nest entrance. This created a smooth surface (with a raised area over the nest) to allow continuous tracking of a single ant. The paper cover was removed to allow a single ant out of the nest, and the entrance cover was then replaced, so that the ant would explore freely in isolation for 45 minutes before being removed to a separate dish for the duration of the experiment. The exploration trajectory of the ant was recorded by a camera mounted on a motorised gantry system, which followed the ant's movements and recorded its path as a sequence of (x, y) points spaced by 0.1 seconds. In the NC treatment, six ants were consecutively released from the same colony on the same day, and pheromone signals and/or other cues such as cuticular hydrocarbon footprints were allowed to accumulate. In the C treatment, the arena surface was cleaned before the subsequent ant was allowed into the arena, to prevent chemical communication between successive ants (see

the ‘Methodology and apparatus’ section of (Hunt et al. 2016) for a more detailed description of the method).

In the previous study (Hunt et al. 2016) the focus of the analysis was on the characteristics of movement ‘events’ – a period of non-zero speed followed by stopping – and the effect of treatments on metrics such as average speed and the correlation between the average speed of consecutive movement events. Here, we examine the effect of the treatment on exploration behaviour – how efficiently the ants reconnoitre an unfamiliar experimental arena – with the hypothesis that the ants use chemical information from previous exploring nestmates to do this more quickly, by avoiding moving through regions of the space that have already been somehow marked as explored. We test this hypothesis of enhanced exploration efficiency in the following way. In nature the ants might benefit from sampling preferentially from surrounding regions of higher quality, in the sense of being more likely to contain valuable resources such as food (Baddeley et al. 2018) or a potential new nest site (Hunt et al. 2018); and would want to spend less time in ‘empty’ regions of the space that contain little of relevance to their reproductive fitness. High-quality regions are likely to be associated with cues that help the ants navigate toward them: for instance, a good potential nest site may be more likely to be located in brighter regions of space than darker regions, because it could benefit from warmer ambient temperatures. Therefore, in a natural environment we would not expect the ants to explore uniformly in the region around their nest; and while we might naively suppose that an empty experimental arena represents a uniform environment, from an ant’s perspective it may be somewhat heterogeneous in terms of lighting and so forth, despite an experimenter’s best efforts. Therefore, rather than measure the ants’ exploration efficiency by reference to how quickly they fill *uniform* space, we take the ‘target distribution’ that ants are trying to sample from as being approximated by the actual exploratory trajectories taken by all 36 ants. Although this may seem an unconventional approach, it will account for any heterogeneity in terms of the lighting environment (though best efforts were taken to control it) and also differential responses to surrounding landmarks in terms of lateralized behaviour. For instance, a preference for

viewing landmarks with the right eye has been suggested (Basari et al. 2013), which may affect exploration behaviour, and also a leftward turning bias when exploring nest sites (Hunt et al. 2014), which may relate to these ants having slightly asymmetric eyes (Hunt et al. 2018).

We create a target distribution for the exploring ants in the following way, using MATLAB 2015b. The exploration trajectories for all 36 ants are combined (a total exploration time of 27 hours), and trajectory points located inside the central region where the 15 × 15 cm paper mask is located are removed, because many of the ants spend a significant proportion of their time familiarising themselves with their immediate surroundings and engaging in thigmotaxis (edge following) around the mask before beginning reconnaissance bouts away from the central region. The (x, y) coordinates were then transformed from a Cartesian to a polar system (θ, r), where $-\pi \leq \theta \leq \pi$ and $4.3 \leq \ln r < 6.5$ (the size of the arena in mm excluding the central area). A periodic boundary for angle θ was created by adding the points in the region $[-\pi, 0]$ into a new region $[\pi, 2\pi]$ and similarly copying $[0, \pi]$ into $[-2\pi\ , -\pi]$ to create a larger space $-2\pi \leq \theta \leq 2\pi$. The coordinates from all 36 trajectories were counted using a histogram on a grid 881 × 1257 (θ step size 0.01, $\ln r$ step size 0.0025). The periodic boundary prevented 'ringing' effects at the edge when a gaussian blur was then applied over all the points in the space, to create a continuous distribution. The gaussian blur has two parameters, filter size and σ which controls the width of the blur. In the results presented a filter of size 200 × 300 was used, to be roughly a quarter of the size. Since the ants are small (only 1mm wide) and hence only leave trails detectable in a surrounding space perhaps 3mm wide, around 0.3% of the arena width, a fairly large blur is necessary to transform their exploration trajectories into a continuous distribution. The σ used was set equal to 30, around 3% of the width of the new space, or ≈10 × the estimated trail width. After the blur was applied, the distribution was then truncated back to its original size such that $-\pi \leq \theta \leq \pi$ again, and normalised such that the sum of all the points was equal to 1 , as in a probability distribution where the value at each position represents the likelihood of an ant wanting to visit it.

To measure how quickly each treatment converged toward the final distribution, the exploration trajectories were combined by colony from all ants up to ant 1,2, … 6 out of the nest. For instance, to measure the progress by ant 2 of the NC treatment, the trajectories of 2 ants were combined (the first ant, and the second) to see its cumulative progress toward the goal. The process described above was then repeated to obtain a probability distribution, which was then compared against the final distribution using the cross-entropy (CE) as a measure of their similarity, where a lower CE signifies greater progress toward the equilibrium distribution of a well-explored arena (see also (Baddeley et al. 2018)). In the last step the three colony-level CE measures were averaged to obtain a mean cross-entropy for the NC treatment by ant 2. Our hypothesis that the ants use chemical information from preceding nestmates to explore more efficiently would correspond to a CE that falls faster in the NC treatment than the C treatment.

While the NC and C treatments measure the difference to exploration made by chemical information from nestmates, it is also quite possible that individual ants make use of their own pheromone markers or other cues left behind, like their own footprints, to avoid wasting time revisiting regions of space they have already walked through. To assess the benefit of individual-level memory (both internal and external), we constructed simulated trajectories by randomly sampling from a vector of the movements of all 36 ants. These 'Markov' ants provided a memoryless benchmark of exploration performance, as ants that do not avoid their own trails, because there is neither externalised memory (chemical markers) nor internal memory (in their brain) of where they have been. A trajectory of 45 minutes of exploration was constructed by concatenating 1 second periods of movement that stayed within the arena boundary (a 90×90cm space). The performance of 100 'colonies' of these Markov ants (6 per colony, as with the real colonies) was compared in the same way.

To assess the statistical significance of one treatment converging more quickly on the final distribution than the other, a permutation test was used, on ants 2-6 out of the nest. The first ant is not included in the test for statistical significance since it is expected that the two treatments are

equivalent at this stage: the first ant explores an arena empty of any chemical information. A non-parametric test is appropriate since the distribution of the CE for each treatment is unknown, and relatively few data points are being compared (15 from each treatment). A permutation test was also used to assess whether the average distance travelled by each exploring ant is different in the NC and C treatments.

Trail avoidance model

In previous research (Baddeley et al. 2018; Hunt et al. 2018) we have proposed that a central challenge that an ant colony confronts, that of trying to identify regions of value in an unknown surrounding environment, is analogous to the problem found in statistics, physics, etc. of efficiently sampling from complex probability distributions or computing numerical integrations. This is because in order to sample from a probability distribution efficiently, one must identify regions of high probability density, but these are not known *a priori* but only after evaluating the probability density function at those locations. Similarly, an ant needs to find regions of high quality, but does not know where they are unless it expends effort (time, energy) in exploration (Baddeley et al. 2018; Hunt et al. 2018). An ant colony has a key advantage over a solitary animal: it is composed of many workers, which can cooperate to benefit the colony as a whole, working together as one 'superorganism' (Hölldobler and Wilson 2009). Each worker could set off in a different direction to that of its nestmates, and hence all of the surrounding area could be quickly explored. However, the ants lack any central controller to direct their movements so as not to overlap and waste time exploring the same region several times; instead they must make their decisions about where to move based only on locally available information (Camazine et al. 2001). A key feature of the Markov chain Monte Carlo (MCMC) movement models we have proposed is the use of local quality gradient information in deciding where to move next: it would seem reasonable to expect ants (and other organisms) preferentially to move toward regions of increasing quality (Baddeley et al. 2018). What we have not yet considered is that this gradient may be modified by the ants themselves, by making

use of their sophisticated chemical communication systems (Hölldobler and Wilson 1990). We suggest that ants may leave behind chemical markers, either deliberately (i.e. pheromones) or incidentally (such as hydrocarbons from their footprints), that convey information about where they and their nestmates have already explored. Such markers may be thought of as 'negative', in the sense that an ant seeking to explore the environment will seek to avoid them, and as reducing the quality gradient in that direction, such that other alternative directions have a relatively higher gradient.

In a simple encapsulation of this exploration and trail avoidance behaviour, we can say that an ant trying to sample from unknown resource quality distribution P also leaves behind a consistent marker at every step that it takes, which corresponds to its subjective experience or model of the world M (but which does not require any internal memory in the ant itself). M starts off as a uniform prior of the world (e.g. a distribution of ones for each location) but then is added to (e.g. $+1$) at each visited location. This is equivalent to Bayesian updating with a Dirichlet prior, because this is the conjugate to the multinomial distribution (Frigyik et al. 2010). M can be renormalised at each time step to be a probability distribution that sums to 1. Over time, as the ant more thoroughly explores the distribution P, this model will converge $M \rightarrow P$, with more markers accumulating in regions of higher probability. Since the objective of the ant is to sample from regions of high probability first, one way to prioritise such regions is to sample from P^2, since this will substantially increase the relative value of high probability regions over low probability regions. For instance, an ant would rather visit a region of 0.2 probability over a region of 0.1, with the former being of $2 \times$ the quality as the latter. If this is squared, this becomes a relative value of $\frac{0.2^2}{0.1^2} = \frac{0.04}{0.01} = 4 \times$ higher, making this region of P space much more attractive, with a sharper gradient toward it too. Therefore, an effective objective for ant exploration (or indeed MCMC methods) is to sample from:

$$P \times \frac{P}{M}$$

which converges in time to sample from P as $P/M \rightarrow 1$, but which should sample from high probability regions first as a combination of the P^2 (attractive) and M (repulsive) terms. Such an objective function for the ant or MCMC method to sample from does not require a change in the method itself: it can be applied in conjunction with the most basic approaches such as Metropolis–Hastings, which are computationally simple. A 'pseudocode' representation of our approach is shown in Table 1.

```
Pseudocode for self-avoiding MCMC method applied to M–H algo.
input: target probability distribution P, α
output: ant's model of world M
M = α × ones (size ( P ) ) Dirichlet prior of world, e.g. α =1
for t=1: simulation time
x _proposed = x _current + random ( -1,0,1 ) (same for y _prop.)
ratio = P ( x _prop, y _prop) / P ( x _curr, y _curr) (classic M–H criterion)
R1 = P ( x _prop, y _prop) / M ( x _prop, y _prop)
R2 = P ( x _old, y _old) / M ( x _old, y _old)
ratio = ratio * (R1/R2) (this obtains P 2 /M )
if ratio > 1, accept = 1; elseif ratio > rand(1), accept = 1; else accept = 0
if accept = 1, ( x,y ) = proposed, else ( x,y ) = current (unchanged)
M( x,y ) = M( x,y ) + 1 deposit 'negative pheromone'
M=M/ ∑ M renormalise to probability distribution summing to 1
end for loop
```

Table 1. Pseudocode for the self-avoiding MCMC method.

Simulations of this 'trail-MCMC' model of ant exploration (or sampling approach) are presented in the results, using a Metropolis–Hastings (M–H) method to sample from both a random distribution (corresponding to a noisy, sparse world) and a distribution with three patches of differing qualities. The random distribution was Dirichlet-distributed, generated by sampling from a gamma distribution of shape k and scale parameter $\theta = 1$. The probability density function (p.d.f.) for this distribution is shown in Figure 1. This results in mostly low-probability cells with a few higher-probability cells, which corresponds to the ants' ecology where most space is unsuitable for locating the colony's nest.

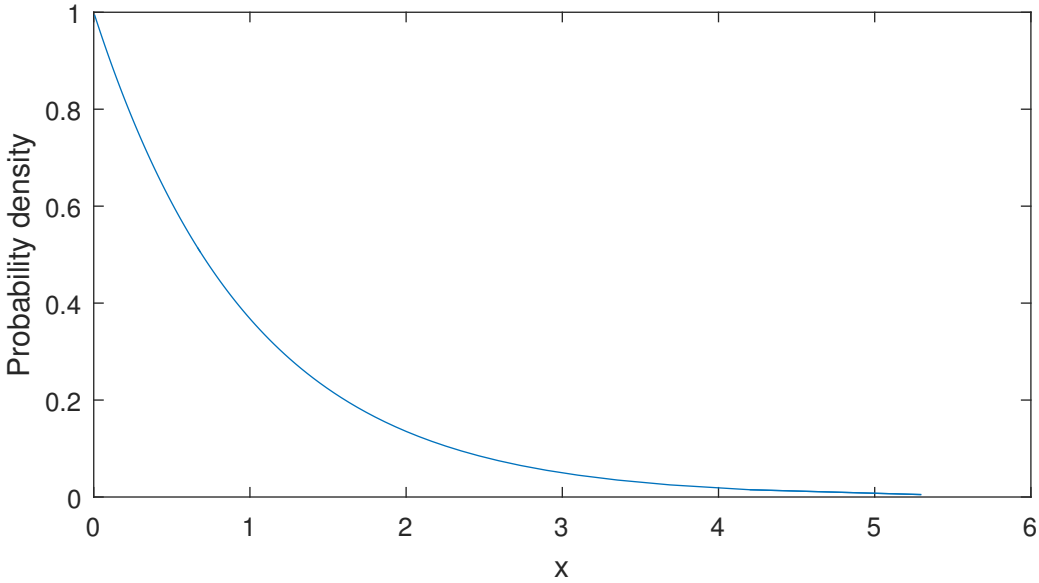

Figure 1. Probability density function for the gamma distribution with $k = 1$, $\theta = 1$.

The distribution with three patches had values of increasing relative magnitude of 1, 2, and 3 which were given a Gaussian blur ($\sigma = 10$, filter size 100×100) and combined in equal proportion with a gamma-distributed background noise, of $k = 0.2$, $\theta = 1$. Shape $k = 0.2$ results in a very sparse distribution, with a few cells of higher probability. This background noise was given a Gaussian blur ($\sigma = 3$, filter size 100×100), which gave some local structure to the background noise (around the higher probability cells). This resulted in the same distribution of 'nests' as featured in previous papers on decision-making (Hunt et al. 2018) and foraging (Baddeley et al. 2018).

The M–H method samples from the distributions using periodic boundary conditions. To assess the effect of cleaning (that is, removing the externalised spatial memory of the ants) the simulations are also run under a 'cleaning' condition where the memory is reset five times, to correspond to the five cleaning bouts in the experimental study (after each ant has explored, for six ants). To ease this comparison the simulations are run for T=60,000 time steps, or 10,000 time steps per 'ant'. The performance is compared to a M–H method sampling from the standard objective distribution P by examining the rate of fall in cross-entropy between the sample and the target P (as previously discussed in (Baddeley et al. 2018)).

Results

Ant exploration trajectories

The rate of convergence of the exploring ants toward the final distribution is shown in Figure 2; the ants in the no cleaning treatment converge significantly more quickly than those in the cleaning

treatment (p=0.0161, permutation test on ants 2-6 across the 3 colonies. The analysis was repeated for Gaussian blur size $\sigma = 20$, resulting in p=0.0394, and $\sigma = 40$, resulting in p=0.0098). This is despite the average distance travelled by the ants from each treatment not being significantly different. The average distance is 18.58 ± 0.77 m (s.e. of the mean) in the NC treatment and 17.57 ± 0.77 m in the C treatment (p=0.21, permutation test). As expected, without any memory (externalised or internal) the simulated Markov ants converge on the target more slowly than either of the experimental treatments, because they are essentially engaged in a random walk around the arena.

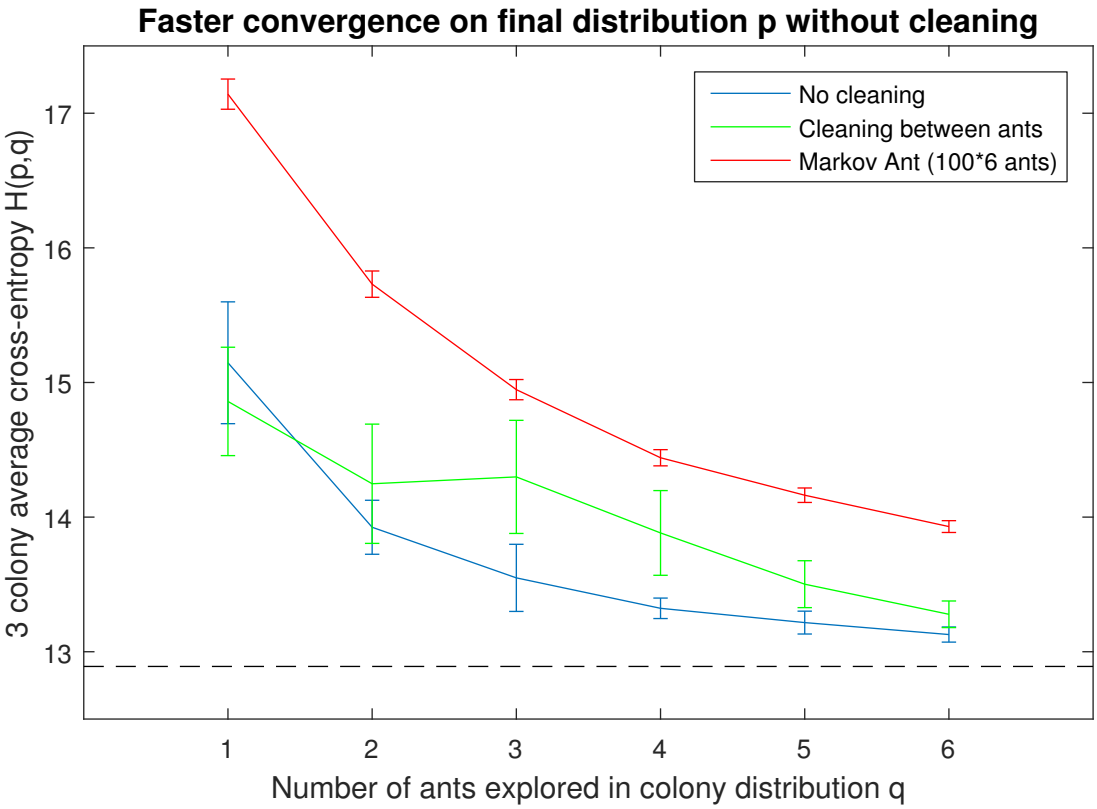

Figure 2. The ants in the no cleaning treatment converge fastest toward the final distribution, indicating that they benefit from chemical information left by preceding nest mates. The error bars indicate one standard error of the mean; a permutation test on ants 2-6 indicate that the cross-entropy is significantly lower in NC than C (p=0.0161). The 'Markov ant' converges slowest, because it benefits neither from the chemical markers (externalised spatial memory) nor internal memory about where it has already visited. The cross-entropy minimum is indicated by the dashed black line.

Trail avoidance model simulations

An example simulation of the models (standard M–H, trail-avoidance M–H with and without cleaning) for the sparse distribution is shown in Figure 3. Such a distribution corresponds to a region of empty space where the ants would wish to avoid sampling from the same parts of the distribution repeatedly. It might be thought of as a 'zoomed-in' patch of empty space in the ants' environment, as opposed to the distribution of three patches in Figure 4, which is 'zoomed-out' and shows all available resources. Figure 3 shows that the standard M–H method converges slowly to the target distribution when all the space needs to be sampled from roughly equally: with a random walk considerable time is wasted going over previous ground. By contrast, the trail-avoidance M–H methods converge much more quickly, as seen in a more rapidly falling cross-entropy. In a way similar to the experimental result shown in Figure 2, the advantage of not cleaning the pheromone trail is not immediately apparent but becomes obvious by 'ant 3' ($t = 3 \times 10^4$ on the x -axis), because more pheromone has been accumulated for the no cleaning ant to avoid.

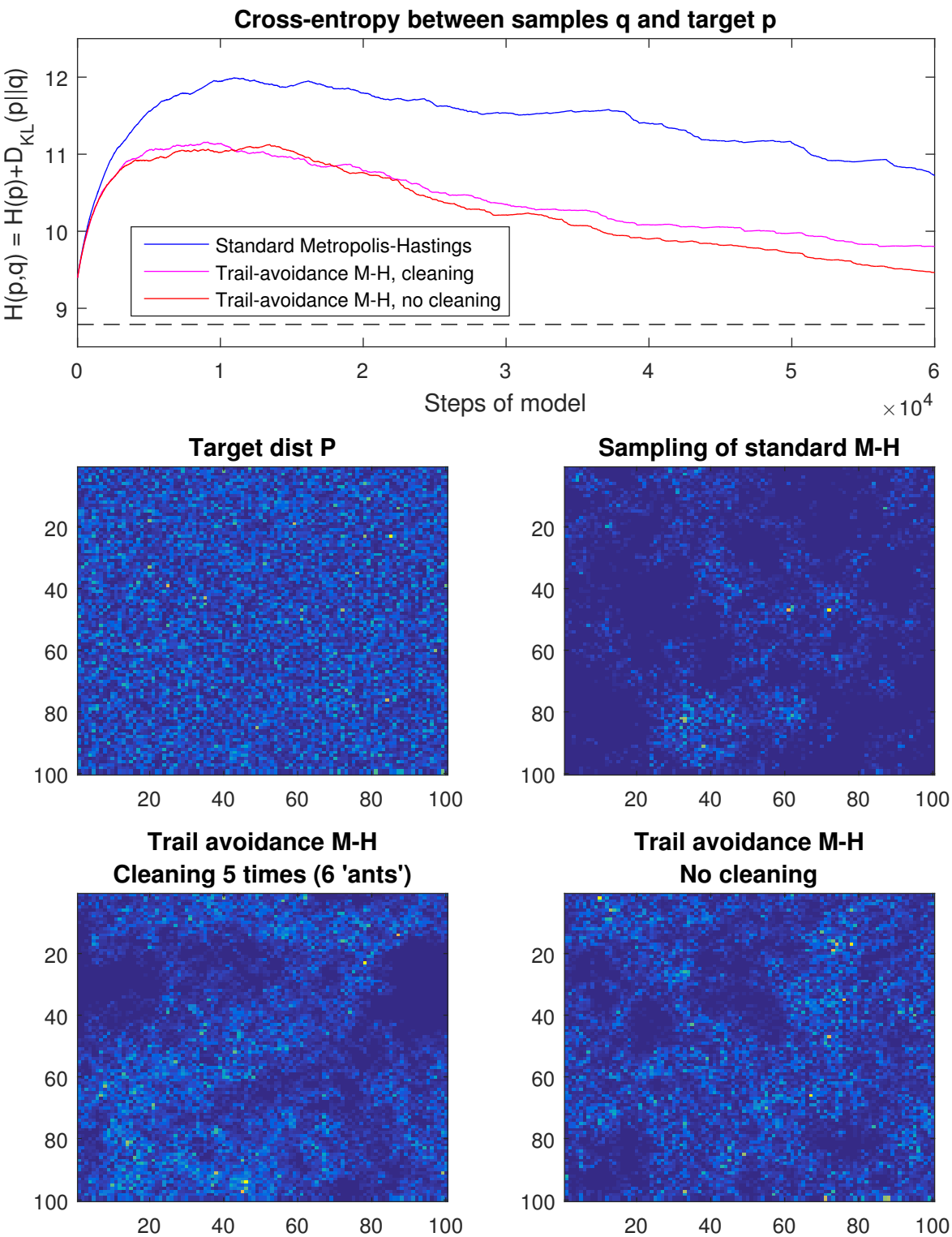

Figure 3. The trail avoidance model converges much more quickly to the target distribution, while cleaning slows its progress somewhat. The target (cross-entropy minimum) is shown by the dashed black line.

The result of a set of simulations sampling from three patches of different quality is shown in Figure 4. This does not show such a large improvement in performance for trail-avoidance M–H over standard M–H, because significant portions of the probability mass are more readily accessible to

random walk-like behaviour. Nevertheless, the standard M–H method is seen to have spent more time in the medium quality patch than the highest quality patch, in keeping with the general problem the ants also face of prematurely favouring a local, rather than a global, quality maximum. In comparison, the no cleaning trail-avoidance M–H samples from the three patches in the correct proportion to their quality in this example, and converges most quickly to the target distribution as a result. The cleaning simulation shows intermediate performance, sampling from the two main patches but not exploring the whole distribution as effectively as when the pheromone memory is allowed to accumulate.

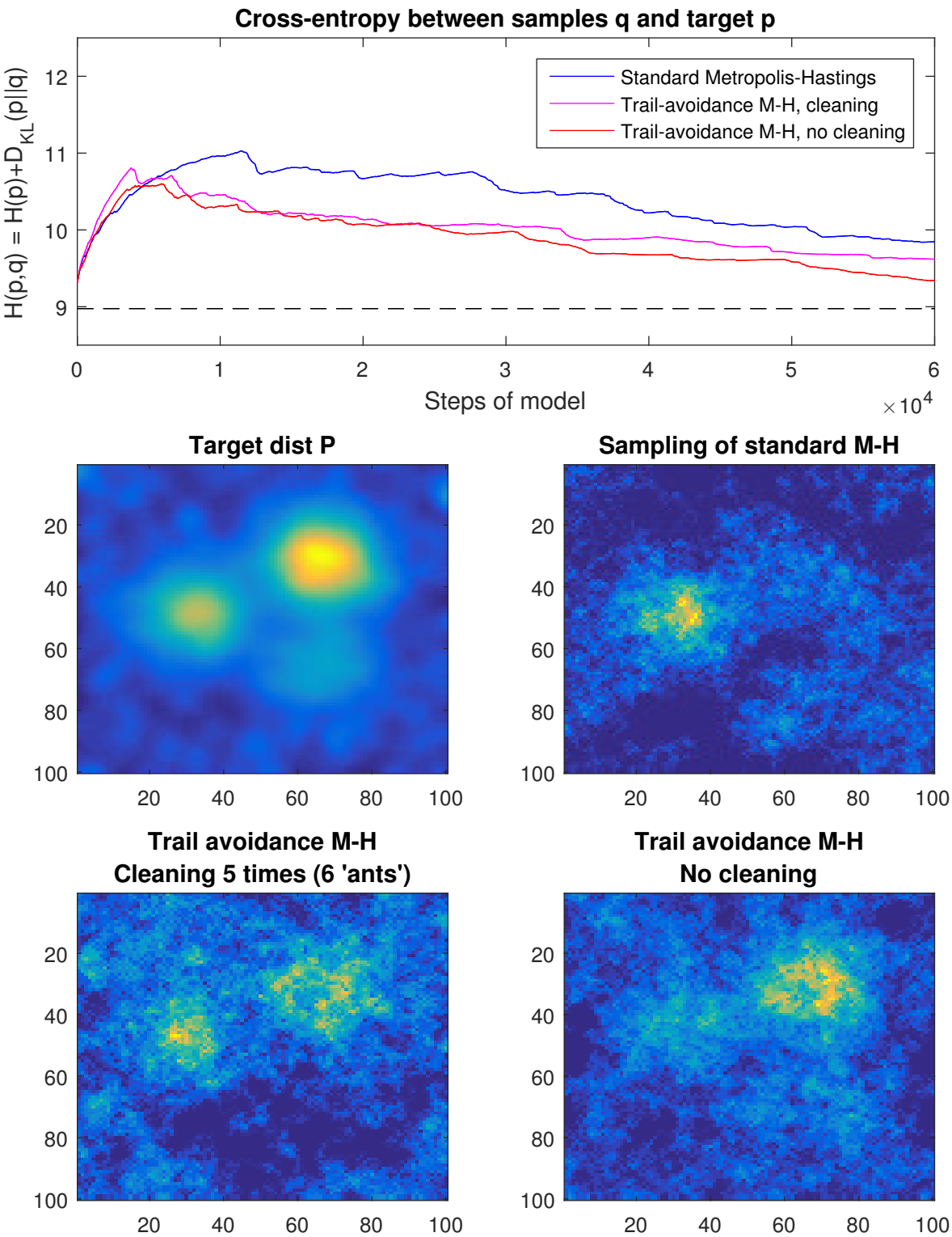

Figure 4. The trail avoidance model again converges more quickly to the target. The M–H model is more likely to get 'stuck' in higher probability regions and take longer to get to other important parts of the distribution. However, the performance gain is less obvious than in the preceding gamma distribution example.

381 **Discussion**

382 Ants and other organisms confront the challenge of having to explore unknown environments while
383 avoiding wasting time and incurring other costs and risks, which would occur if there are repeated
384 visits to the same unprofitable areas. One strategy to avoid time-wasting would be for the animal to
385 maintain an internal memory of where it has been, by using techniques such as learning the
386 configuration of local landmarks (allothetic navigation), or counting steps in a certain direction from
387 the nest (path integration, or other idiothetic mechanisms such as optic flow). However, the ants are
388 pre-eminent manipulators of terrestrial chemical information (Hölldobler and Wilson 1990). Analysis
389 of experimental data (Hunt et al. 2016) presented here provides evidence that *Temnothorax*
390 *albipennis* ants use chemical depositions – either pheromones or cues such as cuticular hydrocarbon
391 footprints – to explore an unknown arena more efficiently. This is because the ants in the treatment
392 where chemical information is allowed to accumulate converge on the colony's target distribution
393 more quickly than when that information is systematically cleaned away.

394 Our finding of collective exploration complements previous research on another Myrmicine
395 ant, *Myrmica rubra*, that found evidence for nestmate footprint avoidance though did not
396 demonstrate enhanced search efficiency (Binz et al. 2014). The avoidance behaviour is seen to be
397 such that the trajectories of two successive ants will nevertheless intersect several times: persistent
398 avoidance would, in effect, paint an ant into a corner. Instead the suggestion of a previous ant's
399 reconnaissance leads to a reweighting of exploration toward a different region of space. In practice,
400 where an ant holds private information about a source of food, for instance, that conflicts with social
401 information (an exploratory marker) it is likely to dominate the decision about whether to return to
402 the space when it is held with high confidence (probability) (Grüter et al. 2011). When there is a
403 coherence between private memory and social information, this may help to boost ants'
404 'confidence' in their own memories and walk more directly (straighter and faster) toward their goal
405 (Czaczkes et al. 2011).

The experimental evidence for path avoidance of nestmates helped to inspire a new approach to tackling an analogous problem in the world of MCMC methods: slow convergence times owing to repeated sampling of the same region of probability space. The original MCMC method, Metropolis–Hastings, is well known for its random walk behaviour, yet is still a popular method because of its ease of implementation. We have shown that its efficiency can be substantially enhanced if it samples from the distribution $P \times {}^{P}/_{M}$, where M is a model (distribution) of where the MCMC walker has visited in the space, rather than simply P (the target distribution). The performance gain is particularly noticeable when sampling from sparse distributions, where the need to avoid revisiting previous parts of the space is especially acute. *T. albipennis* ants live in just such environments – where most of their surroundings hold little of relevance in terms of fitness, either food or potential nest sites – and hence such a mechanism should indeed be favoured by evolution. A shared substrate may serve effectively as a collective memory store, boosting the information-processing capability of the colony beyond the bottleneck of a single ant's memory. Here we have just examined the enhancement to sampling performance for a single walker (ant) – of course in real colonies there will be many simultaneous walkers (ants). More sophisticated MCMC methods that deploy parallel walkers can be compared to our approach, e.g. Wang and Landau (2001).

The model presented here retains a perpetual memory of where the ant has walked, although ongoing movement and pheromone deposition will lessen the relative weighting of past trails as pheromone accumulates elsewhere. In reality, pheromones will decay in strength over time. Although this is unavoidable, in a dynamic foraging environment it may well be preferable that repellent markers decay over time in any event, because they may quickly lose their relevance and even be maladaptive if they inhibit an ant from returning to an area where food has become available. Similar considerations may apply as with animals deciding how to weigh past observational memories with current ones; an exponential weighting is suitable in a Bayesian analysis (McNamara and Houston 1987). It would be straightforward to introduce a reduction to the

potency of the markers over time by multiplying the model by a decay factor, as in $e^{-\lambda t}M$, where λ is the decay constant. Theoretical consideration may be given to the optimal decay constant for different environments (or probability distributions), with sparse environments with a lower chance of opportunistic (randomly appearing) food favouring a lower constant, i.e. a slower decay. Such predictions may be readily tested in different ant species associated with different ecologies.

Theoretical consideration of self-organised behaviours such as ant collective foraging had predicted the value of inhibitory (negative) signals, before their empirical confirmation (Britton et al. 1998). In certain circumstances they could make the foraging process much more efficient (Stickland et al. 1999). As anticipated, a 'no entry' signal has been found in Pharaoh's ants *Monomorium pharaonis* to mark the unrewarding branch on a trail bifurcation. Concentrated at decision points – where the path branches – it could be used to complement attractive trail pheromones or to prevent an attractive pheromone becoming too strong through runaway positive feedback (Robinson et al. 2005). These ants are thought to have at least three types of foraging trail pheromone: one long-lasting attractive pheromone, thought to mark out the overall foraging network, and two short-lived attractive and repellent pheromones, to mark out short term food locations. The repellent pheromone was found to last more than twice as long as the short-lived attractive pheromone (Robinson et al. 2008). Simulations indicate that repellent pheromone increases the robustness and flexibility of the colony's overall foraging response (Robinson et al. 2008). The usefulness of such negative or repellent markers has also been demonstrated in a swarm robotics context, in simulation (Fossum et al. 2015; Schroeder et al. 2017) or digitally on the robots themselves (Payton et al. 2001; Van Dyke Parunak et al. 2005). Just as theoretical models of self-organisation predicted the value of negative markers before they were empirically confirmed, it is possible that advancements in Markov chain Chain Monte methods may inadvertently explain, or pre-empt the discovery of, certain behavioural mechanisms. Similarly, the biology of collective exploration is potentially a rich source of bio-inspiration for MCMC.

Conclusion

Many organisms face the challenge of identifying and exploiting food sources in an unfamiliar and changing environment. A common pitfall in the search process is revisiting previously explored regions of space that do not contain anything of value. An evolutionarily ancient way of avoiding this problem is to leave an externalised 'memory' of the previous visit by depositing a chemical marker that can be used to make a quick decision not to re-enter that space when it is encountered later. For superorganisms like ants, that seek to maximise their foraging performance at the level of the colony, pheromone signals or cues such as cuticular hydrocarbon footprints may be used to coordinate the movement decisions of their nestmates (i.e. through stigmergy) such that an unfamiliar space is quickly explored. Here, we presented evidence for avoidance of the paths of previous nestmates in *Temnothorax albipennis* ants, solitary foragers who would indeed particularly benefit from such a behaviour. We also demonstrated that this path avoidance phenomenon enhances the exploration efficiency of the ants at the colony level.

In addition to empirical findings, after noting the analogy between ant exploration and sampling from unknown probability distributions, we developed an ant-inspired enhancement to Markov chain Monte Carlo methods, whereby a memory is kept of where a walker has moved through the probability space. Such a method was shown to significantly enhance the efficiency of the Metropolis–Hastings method (Metropolis et al. 1953; Hastings 1970) when sampling from sparse probability distributions, because the random walk type behaviour of the method is reduced, but at little computational cost in comparison to more advanced momentum-based methods such as Hamiltonian Monte Carlo (Duane et al. 1987). When the 'superorganism' (Hölldobler and Wilson 2009) is examined using our Bayesian framework (Baddeley et al. 2018; Hunt et al. 2018), behavioural mechanisms such as individual trail markers become better understood in an ultimate sense (Tinbergen 1963) in relation to their facilitation of adaptive collective information-processing capabilities.

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