

1 **Optimal foraging and the information theory of gambling**

2 Roland J. Baddeley¹, Nigel R. Franks², Edmund R. Hunt^{2,3}

3 ¹School of Experimental Psychology, University of Bristol, 12a Priory Road, Bristol, BS8 1TU, UK

4 ²School of Biological Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol, BS8 1TQ,
5 UK

6 ³School of Computer Science, Electrical and Electronic Engineering, and Engineering Mathematics, Merchant
7 Venturers Building, 75 Woodland Road, Bristol, BS8 1UB, UK

8 ORCIDS: RJB, 0000-0002-7431-6580; NRF, 0000-0001-8139-9604; ERH, 0000-0002-9647-124X

9 **Authors for correspondence:** email: edmund.hunt@bristol.ac.uk, roland.baddeley@bristol.ac.uk

10 **Abstract**

11 At a macroscopic level, part of the ant colony life-cycle is simple: a colony collects resources; these
12 resources are converted into more ants, and these ants in turn collect more resources. Because
13 more ants collect more resources, this is a multiplicative process, and the expected logarithm of the
14 amount of resources determines how successful the colony will be in the long run. Over 60 years
15 ago, Kelly showed, using information theoretic techniques, that the rate of growth of resources for
16 such a situation is optimised by a strategy of betting in proportion to the probability of payoff. Thus,
17 in the case of ants the fraction of the colony foraging at a given location should be proportional to
18 the probability that resources will be found there, a result widely applied in the mathematics of
19 gambling. This theoretical optimum generates predictions for which collective ant movement
20 strategies might have evolved. Here, we show how colony level optimal foraging behaviour can be
21 achieved by mapping movement to Markov chain Monte Carlo methods, specifically Hamiltonian
22 Markov chain Monte Carlo (HMC). This can be done by the ants following a (noisy) local
23 measurement of the (logarithm of) the resource probability gradient (possibly supplemented with
24 momentum, i.e. a propensity to move in the same direction). This maps the problem of foraging (via
25 the information theory of gambling, stochastic dynamics and techniques employed within Bayesian
26 statistics to efficiently sample from probability distributions) to simple models of ant foraging
27 behaviour. This identification has broad applicability, facilitates the application of information theory
28 approaches to understanding movement ecology, and unifies insights from existing biomechanical,

29 cognitive, random and optimality movement paradigms. At the cost of requiring ants to obtain
30 (noisy) resource gradient information, we show that this model is both efficient, and matches a
31 number of characteristics of real ant exploration.

32 **Key words:** Movement ecology, collective behaviour, Bayesian methods, Markov chain Monte Carlo,
33 Lévy foraging, sociobiology

34 **Introduction**

35 Life has undergone a number of major organisational transitions, from simple self-replicating
36 molecules into complex societies of organisms (Maynard Smith and Szathmary, 1995). Social insects
37 such as ants, with a reproductive division of labour between the egg-laying queen and non-
38 reproductive workers whose genetic survival rests on her success, exemplify the highest degree of
39 social behaviour in the animal kingdom: ‘true’ sociality or eusociality. The workers’ cooperative
40 genius is observed in diverse ways (Camazine et al., 2001) from nest engineering (Dangerfield et al.,
41 1998) and nest finding (von Frisch, 1967), to coordinated foraging swarms (Franks, 1989) and
42 dynamically adjusting living bridges (Reid et al., 2015). This has inspired a number of technological
43 applications from logistics to numerical optimisation (Dorigo and Gambardella, 1997; Karaboga and
44 Basturk, 2007). All of these behaviours may be understood as solving particular problems of
45 information acquisition, storage and collective processing in an unpredictable and potentially
46 dangerous world (Detrain et al., 1999). Movement (the change of the spatial location of whole
47 organisms in time) is intrinsic to the process. Here we consider how optimal information processing
48 is mapped to movement, at the emergent biological levels of the organism and the colony, the
49 ‘superorganism’. We develop a Bayesian framework to describe and explain the movement
50 behaviour of ants in probabilistic, informational terms, in relation to the problem they are having to
51 solve: the optimal acquisition of resources in an uncertain environment, to maximise the colony’s
52 geometric mean fitness (Orr, 2009). The movement models are compared to real movement
53 trajectories from *Temnothorax albipennis* ants.

54 ***Operationalizing conceptual animal movement frameworks***

55 Scientists have studied animal movement for many years from various perspectives, and in recent
56 years attempts have been made to unify insights into overarching frameworks. One such framework
57 has been proposed by Nathan et al. (Nathan et al., 2008). We describe it briefly to set the research
58 context for the reader. Their framework identifies four components in a full description: the
59 organism's internal state; motion capacity; navigational ability; and influential external
60 environmental factors. This framework also characterises existing research as belonging to different
61 paradigms, namely 'random' (classes of mathematical model related to the random walk or
62 Brownian motion); 'optimality' (relative efficiency of strategies for maximising some fitness
63 currency); 'biomechanical' (the 'machinery' of motion); and the 'cognitive' paradigm (how
64 individuals' brains sense and respond to navigational information). However, scientists have yet to
65 create a theoretical framework which convincingly unifies these components. Frameworks such as
66 Nathan et al. are also focused on the individual and so for group-living organisms, especially for
67 eusocial ones, they are incomplete. The concepts of search and uncertainty also need to be better
68 integrated within foraging theory so that the efficiency of different movement strategies can be
69 evaluated (Giuggioli and Bartumeus, 2010).

70 Here, we contend that animal foraging (movement) models should be developed with
71 reference to the particular information processing challenges faced by the animal in its ecological
72 niche, with information in this context referring to the realised distribution of fitness-relevant
73 resources: in particular the location and quality of foraging patches, which are unknown *a priori* to
74 the organism(s). Furthermore, an important 'module' in any comprehensive paradigm for animal
75 movement is the role of the group and its goals in determining individual movement trajectories;
76 there has been much research on collective behaviour in recent years, with information flow
77 between individuals identified as an important focus of research (Sumpter, 2006). Eusocial insects
78 like ants exhibit a highly advanced form of sociality, even being described as a 'superorganism', that
79 is, many separate organisms working together as one (Hölldobler and Wilson, 2009). Their

80 tremendous information processing capabilities are seen clearly in their ability to explore and exploit
81 collectively their environment's resources. Ants thrive in numerous ecological niches, and alone
82 account for 15–20% of the terrestrial animal biomass on average, and up to 25% in tropical regions
83 (Schultz, 2000).

84 The collective behaviour of tight-knit groups of animals like ants has been described as
85 collective cognition (Couzin, 2009). Because a Bayesian framework seems natural for a single
86 animal's decision-making (McNamara et al., 2006), an obvious challenge would seem to be applying
87 its methods to describe the functioning of a superorganism's behaviour. First, we identify a simple
88 model that describes the foraging problem that ants, and presumably other collectives of highly
89 related organisms, have evolved to solve.

90 ***Placing bets: choosing where to forage***

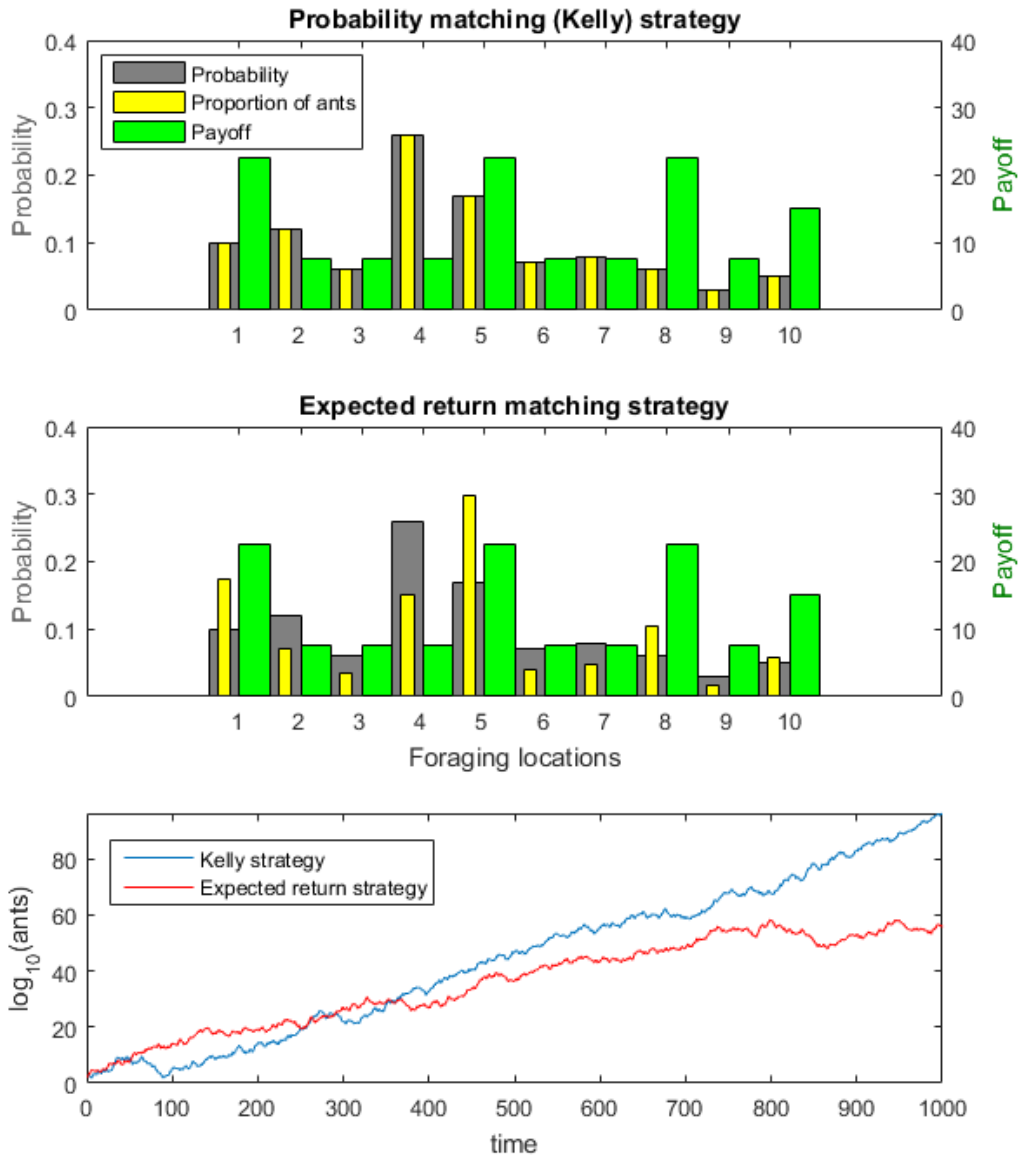
91 Evolution by natural selection should produce organisms that can be expected to have an efficient
92 foraging strategy in their typical ecological context. In the case of an ant colony, although it consists
93 of many separate individuals, each worker does not consume the food it collects and is not
94 independent, but there is rather a colony-level foraging strategy enacted without central control
95 that ultimately seeks to maximise colony fitness (Giraldeau and Caraco, 2000). Following the colony
96 founding stage comes the 'ergonomic' stage of a colony's life cycle (Oster and Wilson, 1978). This is
97 when the queen is devoted exclusively to egg-laying, while workers take over all other work,
98 including collecting food. Thus the colony becomes a 'growth machine' (Oster and Wilson, 1978),
99 whereby workers collect food to increase the reproductive rate of the queen, who transforms
100 collected food into increased biomass or more numerous gene copies. Ultimately, the success or
101 failure of this stage determines the outcome of the reproductive stage, where accumulated 'wealth'
102 (biomass) correlates with more offspring colonies. This natural phenomenon has parallels with
103 betting, where the winnings on a game may be reinvested to make a bigger bet on the next game. In
104 the context of information theory, John Kelly made a connection between the rate of transmission of

105 information over a communications channel, which might be said to noisily transmit the outcome of
106 a game to a gambler while bets can still be made, and the theoretical maximum exponential growth
107 rate of the gambler's capital making use of that information (Kelly, 1956). To maximise the gambler's
108 wealth over multiple (infinite) repeated games, it is optimal to bet only a fraction of the available
109 capital each turn across each outcome, because although betting the whole capital on the particular
110 outcome with the maximum expected return is tempting, any losses would quickly compound over
111 multiple games and erode the gambler's wealth to zero. Instead, maximising logarithmic wealth is
112 optimal, since this is additive in multiplicative games and prevents overbetting. Solving for this
113 maximisation results in a probability matching or 'Kelly' strategy, where bets are made in proportion
114 to the probability of the outcome (Cover and Thomas, 2006). For instance, in a game with two
115 outcomes, one of 20% probability and one of 80% probability, a gambler ought to bet 20% of his
116 wealth on the former and 80% on the latter. This does not depend on the payoffs being fair with
117 respect to the probabilities of the outcome, or $\sigma_i = \frac{1}{p_i}$, which in the aforementioned case would be
118 5 and 1.25. Instead it simply requires fair odds with respect to some distribution, or $\sum \frac{1}{\sigma_i} = 1$ where
119 σ_i is the payoff for a bet of 1, so they could for instance be 2 to 1 or uniform odds in the case of a
120 game with two outcomes (see supplementary Methods). For the purposes of our foraging model, we
121 can simply impose the constraint of fair odds, and any distribution of real-life resource payoffs can
122 be mapped to this when renormalized.

123 In the case of ants choosing where to forage, the probability matching strategy can be
124 directly mapped onto their collective behaviour. With two available foraging patches having a 20%
125 and 80% probability of food being present at any one time, the superorganism should match this
126 probability by deploying 20% and 80% of foragers to the two sites (though it is also possible to follow
127 a Kelly strategy while holding back a proportion of wealth; see supplementary methods). Regardless
128 of the particular payoff σ_i available at each site, provided $\sum \frac{1}{\sigma_i} = 1$ this strategy is optimal over the
129 long term, with the evolutionary time scale of millions of years favouring its selection. Figure 1

130 shows a simulated comparison of the Kelly strategy where probabilities of receiving a resource
 131 payoff are matched, regardless of the payoff, with a strategy that allocates foragers proportional to
 132 the one-step expected return $p_i\sigma_i$, which does take the payoff into account.

Long term result of alternative foraging strategies for 100 ants



133

134 **Figure 1.** A comparison of the Kelly strategy with an expected return matching strategy, over the
 135 long term (identical one-step payoffs for a 'win' in both cases). In the top pane (probability
 136 matching) the proportion of ants 'bet' (yellow bars) matches the probability of success (grey). In the
 137 middle pane, the proportion of ants is allocated by the expected return (probability \times payoff). The
 138 Kelly strategy increasingly outperforms any other strategy as time goes by (bottom pane, example
 139 simulation).

140 Previous analysis of the behaviour of Bayesian foragers versus those modelled using the marginal
141 value theorem indicated that, rather than abandoning a patch when instantaneous food intake rate
142 equals foraging costs, a forager should consider the potential future value of a patch before moving
143 on, even when the current return is poor (Olsson et al., 2006). The priority of resource reliability
144 over immediate payoff in our model, when long-term biomass maximisation is the goal, is itself an
145 interesting finding about superorganismal behaviour; but here we go further and specify models of
146 movement to operationalize this strategy.

147 Certain methodologies designed to sample from probability distributions – Markov chain
148 Monte Carlo (MCMC) methods – may be used as models of movement that also achieve a
149 probability matching (Kelly) strategy. Exploring the environment and sampling from complex
150 probability distributions can be understood as equivalent problems. MCMC methods aim to build a
151 Markov chain of samples that draw from each region of probability space in correct proportion to its
152 density. A well-mixed Markov chain is analogous to a probability matching strategy. Once the
153 Markov chain has converged on its equilibrium distribution (the target probability distribution, or
154 resource quality distribution in our ant model) it spends time in each location proportional to the
155 quality or value (probability) of each point.

156 ***A colony-level strategy***

157 There is a central ‘social’ (colony-level) element in attempting to enact a Kelly strategy of allocating
158 ‘bets’ in proportion to the probability of their payoff. This is because it requires a ‘bank’ (collection
159 of individuals) that can be allocated. This logic does not seem to apply when one is thinking of a
160 single individual, which might instead prefer (or need) to pursue high expected returns to survive in
161 the short-term. Therefore, our model is relevant to groups of individuals who have aligned interests
162 in terms of their fitness function – this is notably true in the social insects such as the ants, because
163 workers are (unusually) highly related, or in clonal bacteria, for instance.

164 However, using MCMC as a model of movement does not, in itself, imply social interactions are
165 necessary. Multiple MCMC ‘walkers’ can sample in parallel from a space and still achieve sampling
166 (foraging patch visitation) in proportion to probability. Nevertheless, social interactions could be
167 highly advantageous in expediting an efficient sampling of the space, through for example ‘tandem
168 running’ (Franks & Richardson, 2006) to sample important areas (Hunt et al., in prep, 2018b), or
169 pheromone trails to mark unprofitable territory (Hunt et al., in prep, 2018c).

170 ***Ant trajectory data***

171 We use our data (Hunt et al., 2016a) from previous work examining the movement of lone
172 *Temnothorax albipennis* ants in an empty arena outside their colony’s nest (Hunt et al., 2016b). *T.*
173 *albipennis* ants have been used as a model social system for study in the laboratory, because
174 information flow between the environment and colony members, and among colony members, can
175 be rigorously studied. The ants typically have one queen and up to 200-400 workers (Franks et al.,
176 2006). The colony inhabits fragile rock crevices and finds and moves into a new nest when its nest is
177 damaged. With workers being only about 2mm long, relatively unconstrained trajectories of
178 individuals can be tracked on the laboratory workbench (for example, Hunt et al. 2016b).
179 Behavioural state-based models have been developed that account for the flow of individuals
180 between states with differential equations (Sumpter and Pratt, 2003; Pratt et al., 2005), but these
181 lack an account of the ants’ movement processes.

182 **Methods**

183 We run simulations of our Markov chain Monte Carlo movement models in MATLAB 2015b
184 (pseudocode is available in the supplementary material). Each new model is introduced to explain an
185 important additional aspect of the ants’ empirical movement behaviour.

186 In our movement data (Hunt et al., 2016a) there are two experimental regimes, one in which
187 the foraging arena was entirely novel to exploring ants, and one in which previous traces of the ants’

188 activities remained. We use the data from the former treatment, where each ant encounters a
189 cleaned arena absent of any pheromones or cues from previous exploring ants. We restrict our
190 analysis to the first minute of exploration, well before any of the ants have an opportunity to reach
191 the boundary of the arena. Log-binned root mean square displacement is calculated and a linear
192 regression made against log time. A gradient equal to a half indicates a standard diffusion process
193 (Brownian motion) whereas greater than a half indicates superdiffusive movements. This approach
194 to characterising ant search behaviour has been taken in e.g. Franks et al. (2010).

195 A supplementary Methods section is at the end of the paper.

196

197 **Results**

198 We present simulation results from three different models of ant movement. Each model is directly
199 based on a known Markov chain Monte Carlo method (MCMC). This follows the recognition that we
200 can consider the problem of sampling from probability distributions of two continuous dimensions
201 as analogous between animal movement and statistics (for example). The trajectories produced by
202 each model are compared to real ant movement data. The development of MCMC methods from
203 the 1950s onward, to become more efficient, might be considered to parallel the evolutionary
204 history of animal foraging strategies. Some more details on the methods are found in the
205 supplementary Methods section.

206 ***Basic model: Metropolis-Hastings***

207 The first MCMC method to be developed was the Metropolis-Hastings (M-H) algorithm (Metropolis
208 et al., 1953; Hastings, 1970), which is straightforward to implement and still commonly used today.

209 We are trying to sample from the target probability distribution (resource quality
210 distribution) $P(x)$ which can be evaluated (observed) for any x , at least to within a multiplicative
211 constant. This means we can evaluate a function $P^*(x)$ such that $P(x) = P^*(x)/Z$. There are two

212 challenges that make it difficult to generate representative samples from $P(x)$. The first challenge is
213 that we do not know the normalising constant $Z = \int d^N x P^*(x)$, and the second is that there is no
214 straightforward way to draw samples from P without enumerating most or all of the possible states.
215 Correct samples will tend to come from locations in x -space where $P(x)$ is large, but unless we
216 evaluate $P(x)$ at all locations we cannot know these in advance (Mackay, 2003).

217 The M-H method makes use of a proposal density Q (which depends on the current state x)
218 to create a new proposal state to potentially sample from. Q can be simply a uniform distribution: in
219 a discretized environment these can be $x^{(\ell)} + [-1,0,1]$ with equal probability. After a given
220 proposed movement is generated, the animal compares the resource quality at this new location
221 with the resource quality at the previous location. If the new location is superior, it stays in its new
222 location. In contrast, if the resource quality is worse, it randomly ‘accepts’ this new location, or
223 ‘rejects’ this location based on a very simple formula based on the ratio of resource quality (if it is far
224 worse, the animal very rarely fails to return, whereas if it is not much worse, it often accepts this
225 mildly inferior location – see also supplementary methods). What is important about this extremely
226 simple algorithm is that, as long as the environment is ergodic (all locations can potentially be
227 reached), given time, the exploring animal will visit each location eventually. Visits will be made with
228 a probability proportional to its resource quality: it will execute an optimal Kelly exploration
229 strategy. The problem here, however, is the time taken. Whilst the M-H method is widely used for
230 sampling from high-dimensional problems, it has a major disadvantage in that it explores the
231 probability distribution by a random walk, and this can take many steps to move through the space,
232 according to $\sqrt{T}\epsilon$ where T is the number of steps and ϵ is the step length. *T. albipennis* ants were
233 found to be engaged in a superdiffusive search in an empty arena (supplementary Methods), and
234 similarly MCMC methods also have been developed to explore probability space more efficiently.

235

236 **Introducing momentum: Hamiltonian Monte Carlo (HMC)**

237 Random walk behaviour is not ideal when trying to sample from probability distributions, since it is
238 more time-consuming than necessary. One popular method for avoiding the random walk-like
239 exploration of state space is Hybrid Monte Carlo (Duane et al., 1987), also known as Hamiltonian
240 Monte Carlo (HMC). This simulates physical dynamics to preferentially explore regions of the state
241 space that have higher probability.

242 Unlike the M-H model of movement, HMC makes use of local gradient information such that
243 the walker (ant) tends to move in a direction of increasing probability. How *T. albipennis* may
244 measure this is explored in the Discussion. For a system whose probability can be written in the form

245
$$P(x) = \frac{1}{Z} \exp[-E(x)]$$

246 the gradient of $E(x)$ can be evaluated and used to explore the probability space more efficiently.

247 This is defined as:

248
$$E(x) = -\ln P(x)$$

249 Using this definition the local gradient $\nabla E(x)$ can be calculated numerically.

250 The Hamiltonian is defined as $H(\mathbf{x}, \mathbf{p}) = E(\mathbf{x}) + K(\mathbf{p})$, where $K(\mathbf{p})$ is a 'kinetic energy' which can
251 be defined as:

252
$$K(\mathbf{p}) = \mathbf{p}^T \mathbf{p} / 2$$

253 In HMC, this momentum variable \mathbf{p} augments the state space \mathbf{x} and there is an alternation between
254 two types of proposal. The first proposal randomises the momentum variable, with \mathbf{x} unchanged,
255 and the second proposal changes both \mathbf{x} and \mathbf{p} using simulated Hamiltonian dynamics. The two
256 proposals are used to create samples from the joint density

257
$$P_H(\mathbf{x}, \mathbf{p}) = \frac{1}{Z_H} \exp[-H(\mathbf{x}, \mathbf{p})] = \frac{1}{Z_H} \exp[-E(\mathbf{x})] \exp[-K(\mathbf{p})]$$

258 As shown, this is separable, so the marginal distribution of \mathbf{x} is the desired distribution
259 $\exp[-E(\mathbf{x})] / Z$, and the momentum variables can be discarded and a sequence of samples $\{\mathbf{x}^{(t)}\}$ is
260 obtained that asymptotically comes from $P(\mathbf{x})$ (Mackay, 2003).

261 We set the variable number of leapfrog steps (see supplementary Methods and Brooks et
262 al., 2011) to $L = 10$; after following the Hamiltonian dynamics for this number of steps a new
263 momentum is randomly drawn and a new period of movement begins. This behaviour of moving
264 intermittently in between updating the walker (ant) behaviour captures the behaviour observed in
265 real ants (Hunt et al., 2016b) (see Discussion on gradient sensing). We set the leapfrog step length
266 $\varepsilon = 0.3$ (see supplementary Methods for further introduction to L and ε).

267 For $N = 18$ simulated HMC ‘ants’ sampling from a sparse probability distribution (a gamma-
268 distributed noise; see supplementary Methods), for 600 iterations, the r.m.s. displacement was
269 again found and its log was regressed on log time. The gradient was found to be 0.567, 95%
270 confidence interval (0.528 0.606), which is significantly greater than 0.5, so in this respect it is more
271 similar to the superdiffusive search found in real ants (Franks et al., 2010).

272 We can also examine the correlation of velocities between successive movement periods.
273 Since momentum $\mathbf{p} = m\mathbf{v}$ is a vector in two-dimensional space, we can set $m = 1$ and find a
274 magnitude for the momentum to determine the ‘speed’ of each movement (over the course of $L =$
275 10 leapfrog steps). In previous research on ant movements (Hunt et al., 2016b) the correlation
276 between successive average event speeds in the cleaning treatment was found to be 0.407 ± 0.039
277 (95% CI). As expected for the HMC model, because the momentum is discarded and replaced with a
278 new random momentum after each movement, the correlation of successive event speeds is equal
279 to zero in this model. We can make the HMC model more ‘ant-like’ – and potentially more efficient –
280 by only partially refreshing this momentum variable after the end of a movement period.

281

282 ***Increasing correlations between steps: partial momentum refreshment (PMR)***

283 HMC with one leapfrog step is referred to as Langevin Monte Carlo after the Langevin equation in
284 physics (e.g. Kennedy, 1990) and was first proposed by Rossky et al. (1978). However, these
285 methods do not require $L = 1$, so we use $L = 10$ to enhance comparability with the previous HMC
286 model.

287 The momentum at the end of each movement can be updated according to the equation
288 $p' = \alpha p + (1 - \alpha^2)^{1/2} n$, where p is the existing momentum, p' the new momentum, α is a
289 constant in the interval $[-1, 1]$ and n is a standard normal random vector. With α less than one p' is
290 similar to p but with repeated iterations it becomes almost independent of the initial value. This
291 technique of partial momentum refreshment (PMR) was introduced by Horowitz (1991). Such
292 models are well-described in Brooks et al. (2011). Setting α equal to 0.65 (for example) and
293 simulating with $N = 18$ results in speed correlations equal to 0.387 ± 0.012 (95% CI) which
294 overlaps with the confidence interval for the real ant data.

295 The PMR method can be compared to an ant moving with a certain momentum (direction
296 and speed) and then intermittently updating this momentum in response to its changing position in
297 the physical and social environment, with a degree of randomness also included. The momentum
298 changes as per the HMC method along a single trajectory, according to its subjective perception of
299 foraging quality and potentially influenced by the pheromonal environment. If at the end of the
300 trajectory it does not find itself in a more attractive region than before, it returns to its previous
301 position: and with the correct model parameters (step size and number of leapfrog steps) this should
302 be a relatively infrequent occurrence (see methodological discussion in Brooks et al. (2011)). Real
303 ants have been predicted, and found, to leave 'no entry' markers when they turn back from an
304 unprofitable location (Britton et al. 1998; Robinson et al. 2005). Its starting momentum in a
305 particular direction is maintained to some degree but with some randomness mixed in – and so its
306 previous tendency to move toward regions of high probability (quality) is not discarded as in HMC
307 but used to make more informed choices about which direction to move in next. This is because

308 foraging patches are likely to show some spatial correlation in their quality, with high quality regions
309 more likely to neighbour other high quality regions (Klaassen et al., 2006; Van Gils, 2010). Previous
310 empirical research (Hunt et al., 2016b) found evidence that ant movements are predetermined to
311 some degree in respect of their duration. This implies that periods of movement are followed by a
312 more considered sensory update and decision about where to move to next. A series of smaller
313 movements (like 10 leapfrog steps) followed by a larger momentum update, as in the PMR model,
314 would seem to correspond well with this intermittent movement behaviour.

315 ***Measuring the performance of MCMC foraging models***

316 The performance of the three MCMC models developed here can be measured in the following way.
317 As discussed, the foraging ants should pursue a probability matching strategy, whereby they allocate
318 their numbers across the environment in proportion to the probability that it will return (any)
319 payoff. This will maximise the long-term rate of growth of the colony, or its biological fitness.
320 Matching the probability distribution of resources in the environment can be understood as
321 minimising the distance between it and the distribution of resource gatherers. In the domain of
322 information theory, the difference between two probability distributions is measured using the
323 cross-entropy

$$324 \quad H(p, q) = H(p) + D_{KL}(p||q)$$

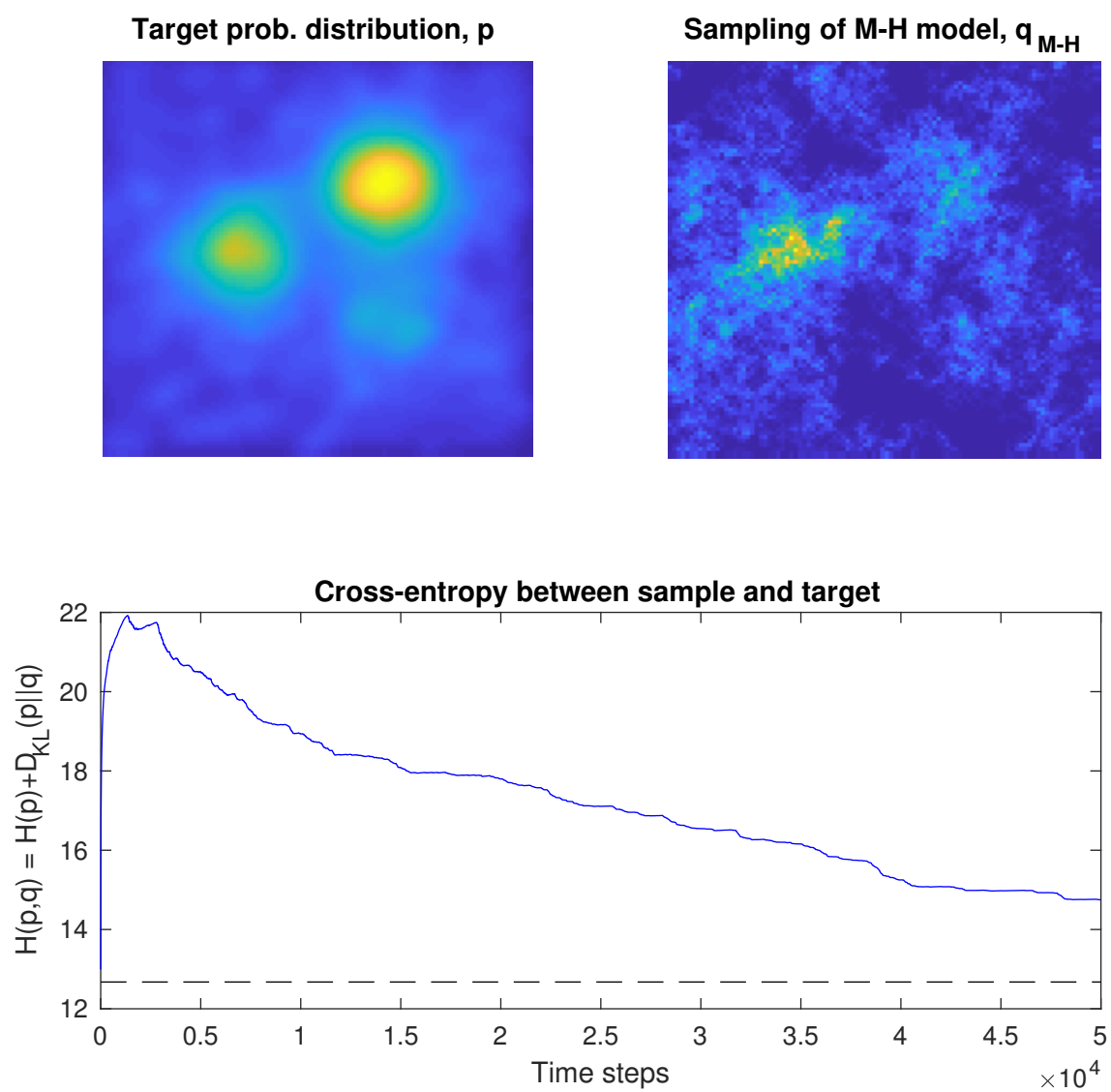
325 Where $H(p) = -\sum_i p(i)\log p(i)$ is the entropy of p and $D_{KL}(p||q)$ is the Kullback-Leibler (K-L)
326 divergence of q from p (also known as the relative entropy of p with respect to q). This is defined as

$$327 \quad D_{KL}(p||q) = \sum_i p(i) \log \frac{p(i)}{q(i)}$$

328 If we take p to be a fixed reference distribution (the probability of collecting resources in the
329 environment), cross entropy and K-L divergence are identical up to an additive constant, $H(p)$, and
330 is minimised when $q = p$, where the K-L divergence is equal to zero. Cross-entropy minimisation is a
331 common approach in optimization problems in engineering, and in the present case can be used to

332 represent the task the ant foragers are trying to perform: match their distribution q with the
333 distribution p of resources in the environment. The magnitude and rate of reduction of the cross-
334 entropy is therefore used to compare the effectiveness of the MCMC models (M-H, HMC, PMR)
335 presented here. However, as noted later, for dynamic environments (where the distribution of
336 resource probabilities p is not fixed), K-L divergence is the suitable cost function to minimise.

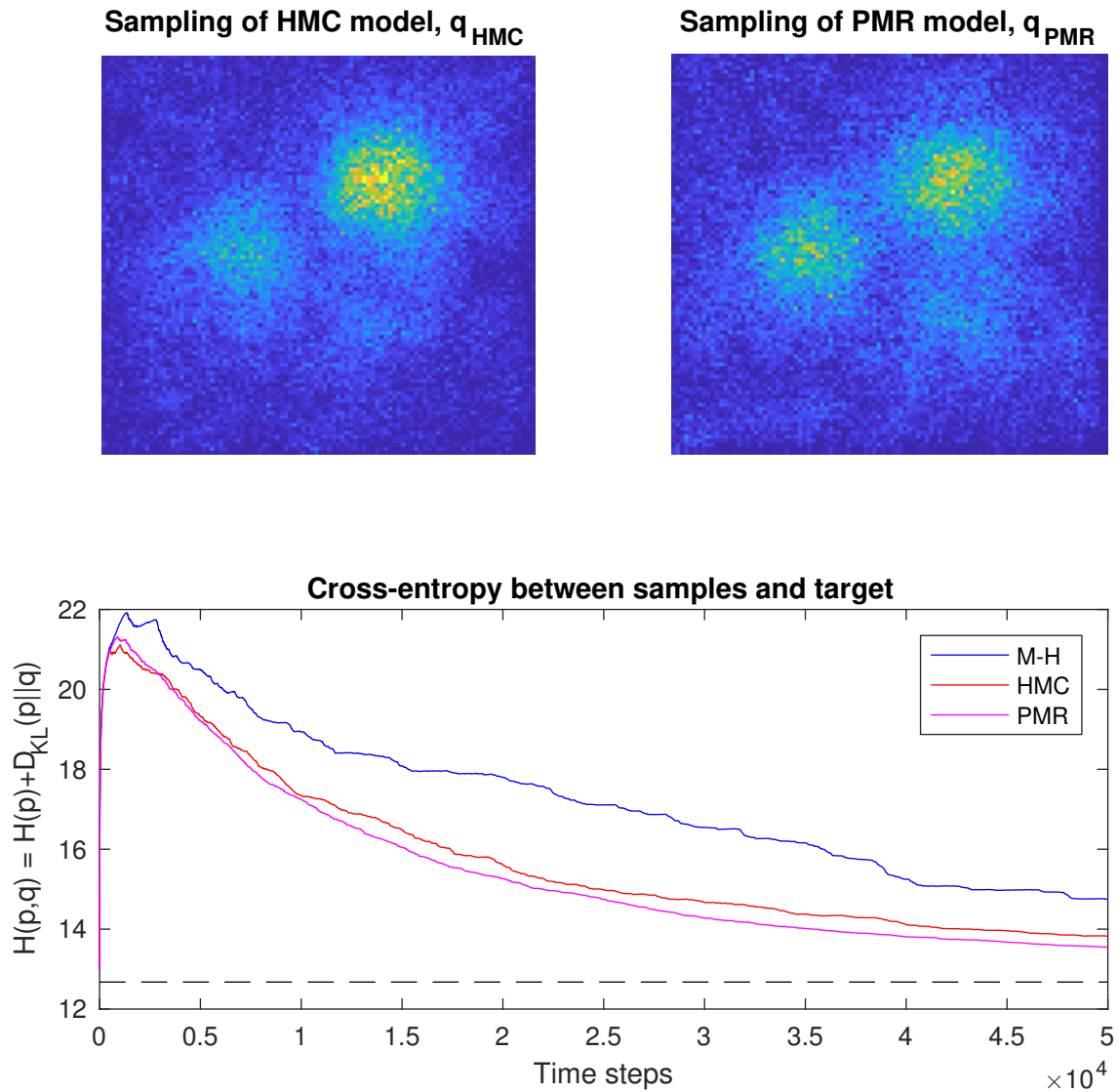
337 Example simulations for the three models sample from a target distribution p with three
338 simulated resources patches. This example distribution is generated by combining a gamma-
339 distributed background noise (shape parameter=0.2, scale parameter=1) on a 100×100 grid given a
340 Gaussian blur ($\sigma = 3$, filter size 100×100), what we refer to later as the ‘sparse distribution’, in
341 equal 50% proportion with three patches of resources, which are single points of increasing relative
342 magnitude of 1, 2, and 3 that have been given a Gaussian blur ($\sigma = 10$, filter size 100×100). The
343 distribution p is thus also on a 100×100 grid. The simulations are run for 50,000 time steps, a
344 reasonable period of time to explore this space of 10,000 points. Figure 2 shows the M-H model,
345 which converges rather slowly on the target environment p . Figure 3 shows the performance of the
346 HMC and PMR models, which show an improvement in the convergence rate because they avoid the
347 random walk behaviour of the M-H model.



348

349 Figure 2. Performance of the M-H model as it generates a sample distribution q that approximates
350 the target distribution p , the location of resources in the environment. The minimum cross entropy,
351 where $q = p$, is shown as a dotted line.

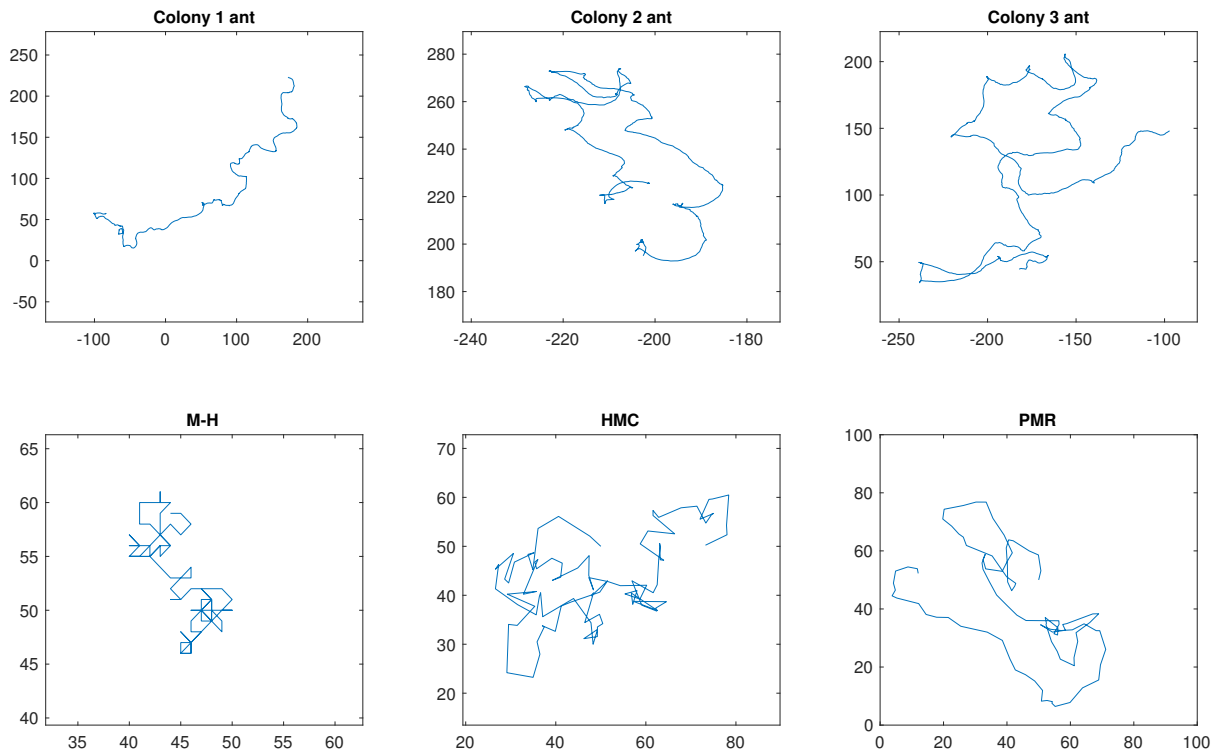
352



353

354 Figure 3. Performance of the HMC and PMR models, compared to that of M-H. In general, HMC and
355 PMR outperform M-H because random walk type exploration of probability space is avoided, by
356 following local gradient information and making larger steps. Their performance depends on the
357 nature of the target distribution and choosing suitable values for step length ϵ and number of steps
358 L .

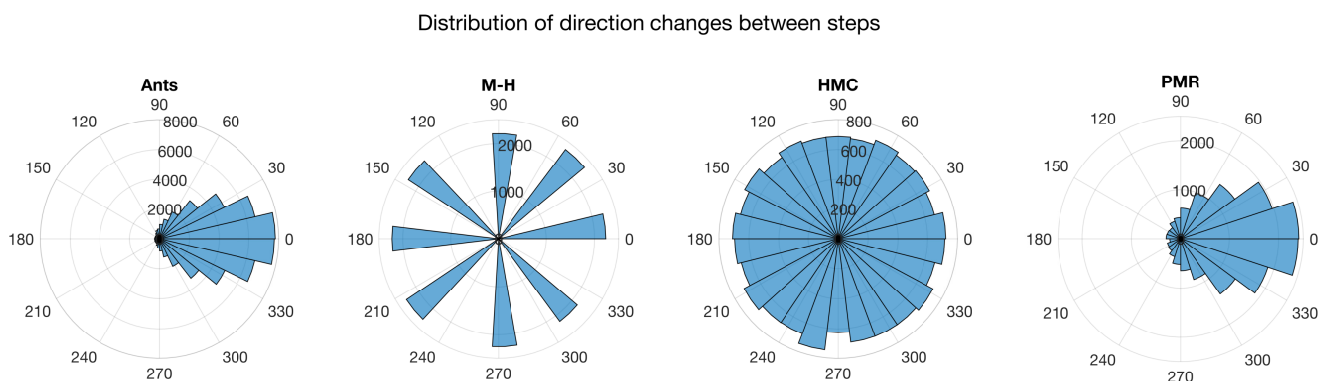
359



360

361 Figure 4. Comparison of example trajectories from real ants and for the 3 MCMC models (100
362 simulated timesteps). The model trajectories become increasingly superdiffusive.

363 Figure 4 shows example trajectories from real ants (Hunt et al. 2016a) for a period of 100 s, and for
364 100 timesteps of the 3 models. The ants are in an empty arena and the models are sampling from a
365 sparse distribution (supplementary Methods). The random walk behaviour of the M-H model is
366 evident, while the greater tendency to make longer steps in one direction is evident in the PMR
367 model in comparison to the HMC model.



368

369 Figure 5. The distribution of direction changes between steps in real ants (N=18) and the three
370 MCMC models (simulated for N=18 'ants' for 1000 timesteps).

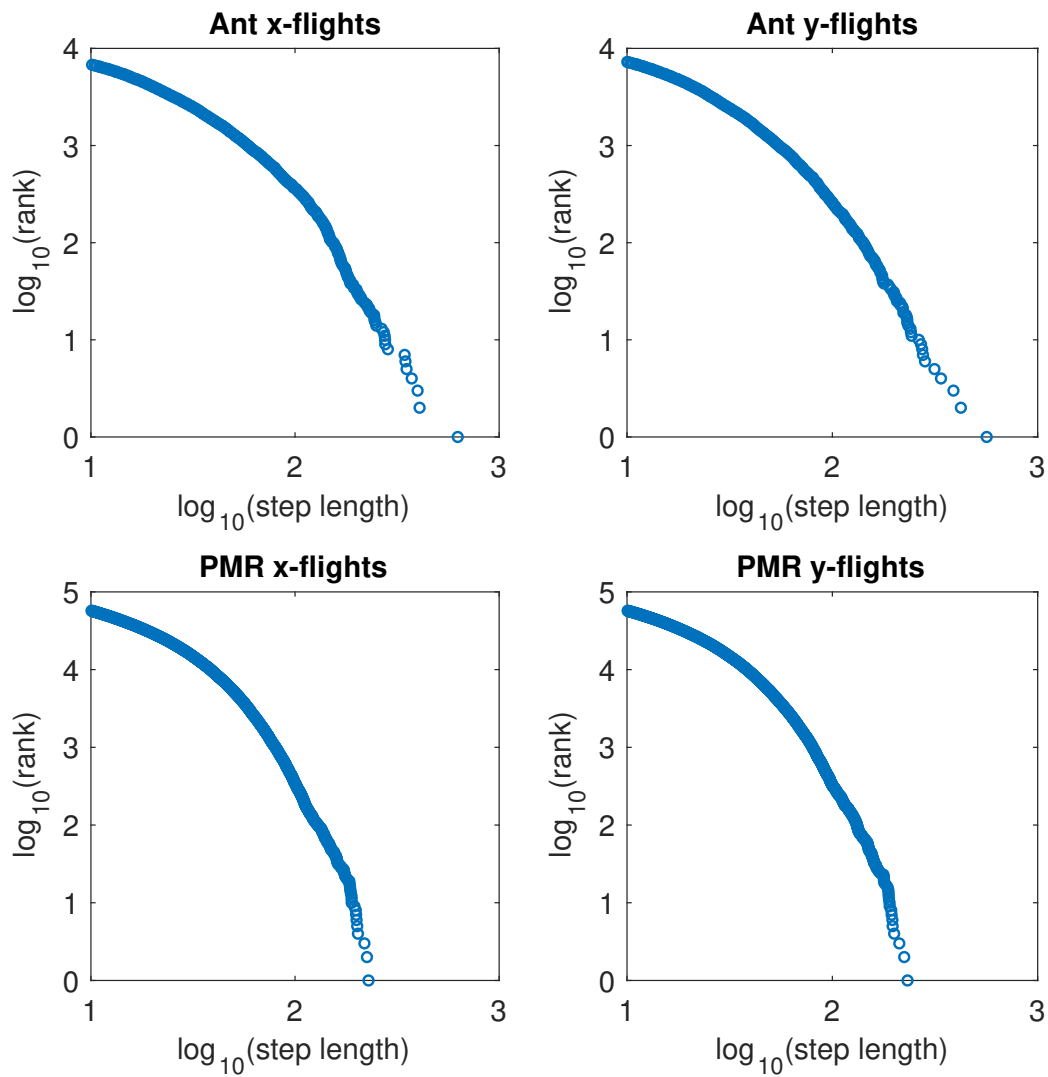
371 Figure 5 shows the distribution of directional changes (change in angle heading) between steps. The
372 distribution of direction changes is known as the phase function in statistical physics and has been
373 applied to ant trajectory analysis by for instance Khuong et al. (Khuong et al. 2013). Real ants can
374 make large changes of direction, of course, but this is rarely done with an abrupt heading shift. The
375 M-H model moves grid-wise in single steps; the HMC model has no correlation between step
376 directions; while the PMR model tends to make each new step in a similar (correlated) direction to
377 the prior one. In this respect, too, PMR is a better model of ant movement.

378

379 ***Optimal foraging and Lévy flights***

380 We have presented a new class of foraging models based on MCMC methods, which operationalise
381 movement for a Kelly strategy (probability matching) in two-dimensional space. There is an
382 extensive theoretical and empirical literature examining the distribution of step lengths for foraging
383 animals that considers the hypothesis that a Lévy distribution is optimal (Bartumeus, 2007;
384 Benhamou, 2007; Humphries et al., 2010; Viswanathan et al., 2008). Lévy flights are a particular
385 form of superdiffusive random walk where the distribution of move step-lengths fits an inverse
386 power law such that the probability of a move of length l is distributed like $(l) \approx l^{-\mu}$, where $1 <$
387 $\mu \leq 3$.

388 We use the method of Humphries et al. (2013) to identify individual movement steps in two
389 dimensional data, treating monotonic movements in a certain direction in one dimension (i.e., x or
390 y) as a step. We estimate the exponent using maximum likelihood estimation (White et al., 2008).
391 The distribution of ranked step length sizes in both real and simulated data is shown in Figure 6.



392

393 Figure 6. The (apparently) power-law distributed step lengths for both real ants and simulated PMR
394 walkers.

395 There are similar exponents estimated (Table 1) for both the real ant data in an empty arena (N=18
396 ants from 3 colonies) and PMR trajectories (100 'ants' for 5000 iterations) sampling from a sparse
397 probability distribution (supplementary Methods). The exponent μ in both cases is in the right region
398 for a Lévy flight $1 < \mu \leq 3$. This would seem to be evidence for a Lévy strategy in the ants (though
399 variation in individual walking behavior can also contribute to the impression of a Lévy flight
400 (Petrovskii et al. 2011)), but we suggest an alternative in the next section of this paper.

401

Dimension of steps	Maximum likelihood estimate of exponent, truncated Pareto distribution	
	Empirical data	PMR data
x	2.41	2.26
y	2.55	2.26

406 Table 1. Power-law exponents in both empirical and PMR simulated trajectories potentially indicate
407 a Lévy walk

408

409

410 Discussion

411 *MCMC models and existing movement paradigms*

412 The framework we develop here is an important step in integrating key perspectives in movement
413 research, as described for example by Nathan et al. (2008). It incorporates elements of randomness,
414 producing correlated random walks in certain environments; it quantifies optimality in respect of
415 foraging strategies via cross-entropy (Kullback-Leibler divergence); it includes an important aspect of
416 common animal behaviour, namely intermittent movement (Kramer and McLaughlin, 2001), and
417 specifically for the ants' neural and/or physiological behaviour, apparent motor planning (Hunt et al.,
418 2016a); and it makes explicit the information used by the animal step-by-step. Finally, and crucially,
419 it explicates cognition at the emergent group level, because individual movement is at the service of
420 a group-level Kelly strategy. One component of Nathan et al.'s framework is the internal state of the
421 organism. This is not included in the models here, though state-dependent behaviours such as
422 tandem running (Franks and Richardson, 2006) could be included by analogy with particle filtering
423 (e.g. Gordon et al., 1993), for instance (Hunt et al., in prep, 2018b). Our use of the Markov
424 assumption (movement being memoryless, depending only on the current position) is justifiable
425 with respect both to the worker ant's individual cognitive capacity, and its single-minded focus on

426 serving the colony through discovering and exploiting resources. Its motion capacity is linked to the
427 specification of a partial momentum refreshment model; while we specify the navigation capacity in
428 its ability to measure the quality gradient, which is also an externally determined factor.

429 ***The mechanisms and challenges of gradient sensing***

430 We may consider further the ability of ants to use local gradient information, as in the HMC and
431 PMR models, with respect to the ants' sensory system. *Temnothorax albipennis* is well-known for
432 relying heavily on visual information in movement (McLeman et al., 2002; Pratt et al., 2001) and in
433 common with most (or perhaps all) ants on olfactory information. It may be that the intermittent
434 movement examined in Hunt, Baddeley et al (Hunt et al., 2016b) is associated with limitations in the
435 quality of sensory information when moving (Kramer and McLaughlin, 2001). We suggest that *T.*
436 *albipennis* workers have relatively good eyesight for a pedestrian insect and their small size, having
437 around 80 ommatidia in each compound eye (Hunt et al., 2018a) and may be assumed
438 conservatively to have an angle of acuity of 7 degrees (Pratt et al., 2001). Therefore, movement
439 would seem unlikely to make much difference to how well they can see. Since our model highlights
440 the importance of gradient following, this may be more difficult to measure for the olfactory system
441 during movement. Indeed, in Hunt et al. (2016b) we suggest that social information from
442 pheromones or other cues is only fully attended to during periods of stopping because of motor
443 planning, with the duration of movements being predetermined by some endogenous neural and/or
444 physiological mechanism. This may be therefore a mechanistic reason for the stepwise movement in
445 the PMR model, in addition to its informational efficiency which is its evolutionary origin. Even more
446 sophisticated MCMC models that rely on the second derivative of the probability distribution, such
447 as the Riemann Manifold Langevin method (Girolami and Calderhead, 2011), may be relevant,
448 because this property (the rate of change of the gradient) may be only measured with adequate
449 accuracy when the ant is at rest.

450

451 ***Lévy step length distributions indicate a world with little gradient information***

452 In a ‘flat’ quality landscape, or sparse world, our model generates Lévy-like behaviour as seen for
453 instance in Reynolds et al., 2013. This remains an adaptive response, but it is not a true Lévy
454 distribution, because there is a finite variance. Much interest has been generated by Lévy flight
455 based foraging models which theoretically optimise mean resource collection for certain random
456 worlds; and this would seem to be evidence for just such a strategy in *T. albipennis* ants. Yet here we
457 make a simple point that rather than being a deliberate strategy, Lévy-like behaviour may result
458 from an organism lacking cues about which way to move. Scale-free reorientation mechanisms have
459 indeed been suggested as a response to uncertainty in invertebrates (Bartumeus and Levin, 2008).
460 Yet the generation of a Lévy -like distribution from our gradient-following model suggests that such
461 observations may not really be scale-free. The empirical distribution of momentums provides insight
462 into the length-scales on which the world remains smooth.

463 ***Measuring efficiency, selecting for unpredictability***

464 The rate of resource collection can be straightforwardly calculated by finding the cross-entropy
465 (Kullback-Leibler divergence) between the spatial distribution of resources, and the realised foraging
466 distribution resulting from the foraging strategy. The distribution of resources is seen from a ‘genes-
467 eye’ view of the animal or superorganism, with respect to maximising the long-term biomass or
468 number of copies of genes in the environment: this focuses on a location’s probability of yielding
469 resources, or reliability, as opposed to the one-off payoff. The foraging strategy is that chosen by
470 natural selection. Minimising the cross-entropy (Kullback-Leibler divergence) is achieved by obeying
471 the matching law: foraging proportional to the probability finding the best resources at each
472 available location. This strategy is especially suited to a superorganism like an ant colony, because it
473 can forage in multiple locations simultaneously by allocating worker ants in numbers proportional to
474 the location’s reliability, through self-organisation (Camazine et al., 2001).

475 There has been some intimation before that MCMC could be a model for biological
476 processes (Neal, 1993), with some query about whether the requisite randomness is possible in
477 organisms. We think that not only is spontaneous (i.e. non-deterministic, ‘random’) behaviour
478 present, it is necessary for survival in terms of being unpredictable around predators, prey or
479 competitors (Brembs, 2010), or for finding food using a ‘strategy of errors’ (Deneubourg et al.,
480 1983). Indeed, the Bayesian framework developed here allows predictions to be developed
481 regarding the optimal amount of ‘randomness’ in behaviour at both the level of the individual and
482 colony (in the partial momentum refreshment model, this is adjusted with the α parameter) that can
483 be tested in future empirical research. Further predictions arise from the momentum reversal step in
484 MCMC PMR (Brooks et al., 2011), which may be compared to observations of U-turning in ants
485 (Beckers et al., 1992; Hart and Jackson, 2006). Recent literature (Hoffman and Gelman, 2014) has
486 developed methods to adjust the path length dynamically, while removing the need to have a
487 parameter L for the number of leapfrog steps. Observing how ants (and other organisms) adjust
488 their step lengths according to different resource distributions will be instructive of their underlying
489 movement model.

490 ***Selection for collective foraging phenotypes***

491 The major evolutionary transitions (Maynard Smith and Szathmary, 1995) can be seen as successive
492 leaps forward in information processing efficiency. The Bayesian framework developed here permits
493 the evaluation and prediction of alternative movement strategies, for groups of high-related
494 organisms, in quantitative, informational terms, in relation to environmental resource distributions.
495 Our framework permits us to make the simple statement that for a movement strategy to be
496 favoured under natural selection:

$$497 \qquad D_{KL}(p||q_{new}) < D_{KL}(p||q_{old}) \qquad (1)$$

498 i.e. the Kullback-Leibler divergence (measuring the similarity of two distributions) between a
499 potential (genetically accessible) collective movement strategy that results in the equilibrium

500 distribution of foragers q_{new} , and the organism's resource environment p , has to be lower than
501 under the current strategy found in the population that results in distribution q_{old} . This reduction
502 may indeed be achieved by more sophisticated, coordinated, collective behaviour, notwithstanding
503 higher individual energetic cost. Future research could relate such an expression to concepts in
504 evolutionary genetics such as fitness landscapes (Orr, 2009). The theoretical relationship between
505 the level of relatedness within a social group, and the relevance of the Kelly strategy, could be
506 explored in future research.

507

508 **Conclusion**

509 We described the foraging problem as a repeated multiplicative game, where an ant colony has to
510 place 'bets' on which foraging patches to visit, with an ultimate payoff of more colonies or copies of
511 their genes being created. Ants are very successful in terms of their terrestrial biomass (Schultz,
512 2000), and so it would seem likely that they are following a highly evolved strategy. We suggest the
513 theoretical optimum is a 'Kelly' or probability matching strategy, which maximises the long term
514 'wealth' or biomass of the colony rather than the resource collection of single ants. By mapping the
515 foraging problem to a set of methods designed to effectively sample from probability distributions,
516 we present models of ant movement that achieve this matching behaviour. These MCMC-based
517 models thus provide spatially explicit predictions for movement that describe and explain how
518 colonies optimally explore and exploit their environment for food resources. We also show how Lévy
519 -like step length distributions can be generated by following a local gradient that is uninformative,
520 suggesting that contrary to being an evolved strategy, Lévy flight behaviour may be a spontaneous
521 phenomenon. While we do not include interactions between ants in the model, past theoretical
522 analysis of information use in collective foraging suggests that totally independent foraging is
523 actually optimal for a broad range of model parameters when the environment is dynamic. This is

524 because information about food patches may not be worth waiting for if they are short lived
525 (Dechaume-Moncharmont et al., 2005).

526 Understanding the logic of information flow at the level of the gene and the cell has been
527 identified as a priority (Nurse, 2008). However, given that no level of organisation is causally
528 privileged in biology (Noble, 2011), explicating this at the organismal and super-organismal level
529 should also advance our understanding. Our Bayesian framework operationalizes earlier proposed
530 frameworks (such as that of Nathan et al., 2008) for movement in a coherent and logical way,
531 accounting for the uncertainty in both the individual ant and the colony's cognition in relation to the
532 foraging problem. It also allows quantification of the system's emergent information processing
533 capabilities and hypothesis generation for different organisms moving in different environments.
534 Our MCMC models can be used as a foundation upon which further organismal and ecological
535 complexity can be explained in future research; and suggest that the movement strategies of animal
536 collectives may be instructive for biomimetic improvements to MCMC methods.

537

538 **Author contributions.** ERH drafted the paper, produced the analysis and simulations, and suggested
539 eqn. (1); NRF advised on social insect biology; RJB proposed the Bayesian framework and its specific
540 theoretical concepts; all authors contributed to the present draft.

541 **Funding statement.** E.R.H. thanks the UK Engineering and Physical Sciences Research Council (grants
542 no. EP/I013717/1 to the Bristol Centre for Complexity Sciences, EP/N509619/1 DTP Doctoral Prize).

543 **Ethics statement.** The ant *Temnothorax albipennis* is not subject to any licencing regime for use in
544 experiments. The ants were humanely cared for throughout the experiment.

545 **Competing interests.** We have no competing interests.

546

547 **References**

- 548 Bartumeus F, 2007. Levy processes in animal movement: An evolutionary hypothesis. *Fractals*
549 15:151-162. doi: 10.1142/s0218348x07003460.
- 550 Bartumeus F, Levin SA, 2008. Fractal reorientation clocks: Linking animal behavior to statistical
551 patterns of search. *Proceedings of the National Academy of Sciences of the United States of*
552 *America* 105:19072-19077. doi: 10.1073/pnas.0801926105.
- 553 Beckers R, Deneubourg JL, Goss S, 1992. Trails and U-turns in the selection of a path by the ant
554 *Lasius niger*. *Journal of Theoretical Biology* 159:397-415. doi: 10.1016/s0022-
555 5193(05)80686-1.
- 556 Benhamou S, 2007. How many animals really do the Levy walk? *Ecology* 88:1962-1969. doi:
557 10.1890/06-1769.1.
- 558 Brembs B, 2010. Towards a scientific concept of free will as a biological trait: spontaneous actions
559 and decision-making in invertebrates. *Proceedings of the Royal Society B: Biological Sciences*
560 278:930-939. doi: 10.1098/rspb.2010.2325.
- 561 Britton NF, Stickland TR, Franks NR, 1998. Analysis of ant foraging algorithms. *Journal of Biological*
562 *Systems*, 6(04), 315-336. doi: 10.1142/S0218339098000212.
- 563 Brooks S, Gelman A, Jones G, Meng XLE, 2011. *Handbook of Markov Chain Monte Carlo*. CRC press.
- 564 Camazine S, Deneubourg JL, Franks NR, Sneyd J, Bonabeau E, Theraulaz G, 2001. *Self-organization in*
565 *biological systems*. Princeton University Press.
- 566 Couzin ID, 2009. Collective cognition in animal groups. *Trends in Cognitive Sciences* 13:36-43. doi:
567 10.1016/j.tics.2008.10.002.
- 568 Cover TM, Thomas JA, 2006. *Elements of information theory*. New Jersey: John Wiley & Sons.
- 569 Dangerfield JM, McCarthy TS, Ellery WN, 1998. The mound-building termite *Macrotermes*
570 *michaelseni* as an ecosystem engineer. *Journal of Tropical Ecology* 14:507-520.
571 doi: 10.1017/s0266467498000364.
- 572 Dechaume-Moncharmont F-X, Dornhaus A, Houston AI, McNamara JM, Collins EJ, Franks NR, 2005.
573 The hidden cost of information in collective foraging. *Proceedings of the Royal Society B:*
574 *Biological Sciences* 272:1689-1695. doi: 10.1098/rspb.2005.3137.
- 575 Dempster ER, 1955. Maintenance of genetic heterogeneity. *Cold Spring Harb. Symp. Quant. Biol.*
576 20:25-32.
- 577 Deneubourg JL, Pasteels JM, Verhaeghe JC, 1983. Probabilistic behaviour in ants: A strategy of
578 errors? *Journal of Theoretical Biology* 105:259-271. doi: 10.1016/s0022-5193(83)80007-1.
- 579 Detrain C, Deneubourg JL, Pasteels JM, 1999. *Information processing in social insects*. Springer
580 *Science & Business Media*.
- 581 Dorigo, M. and L.M. Gambardella, Ant colony system: a cooperative learning approach to the
582 traveling salesman problem. *Evolutionary Computation, IEEE Transactions on*, 1997. 1(1): p.
583 53-66. doi: 10.1109/4235.585892.
- 584 Duane S, Kennedy AD, Pendleton BJ, Roweth D, 1987. Hybrid Monte Carlo. *Physics Letters B*
585 195:216-222. doi: 10.1016/0370-2693(87)91197-x.
- 586 Franks NR, 1989. Army ants: a collective intelligence. *American Scientist* 77:138-145.
- 587 Franks NR, Dornhaus A, Best CS, Jones EL, 2006. Decision making by small and large house-hunting
588 ant colonies: one size fits all. *Animal Behaviour* 72:611-616. doi:
589 10.1016/j.anbehav.2005.11.019.
- 590 Franks NR, Richardson T, 2006. Teaching in tandem-running ants. *Nature*, 439(7073), 153. doi:
591 10.1038/439153a
- 592 Franks NR, Richardson TO, Keir S, Inge SJ, Bartumeus F, Sendova-Franks AB, 2010. Ant search
593 strategies after interrupted tandem runs. *Journal of Experimental Biology* 213:1697-1708.
594 doi: 10.1242/jeb.031880.
- 595 Giraldeau L-A, Caraco T, 2000. *Social foraging theory*: Princeton University Press.

- 596 Girolami M, Calderhead B, 2011. Riemann manifold Langevin and Hamiltonian Monte Carlo
597 methods. *Journal of the Royal Statistical Society Series B-Statistical Methodology* 73:123-
598 214. doi: 10.1111/j.1467-9868.2010.00765.x.
- 599 Giuggioli L, Bartumeus F, 2010. Animal movement, search strategies and behavioural ecology: a
600 cross-disciplinary way forward. *Journal of Animal Ecology* 79:906-909. doi: 10.1111/j.1365-
601 2656.2010.01682.x.
- 602 Gordon NJ, Salmond DJ, Smith AF, 1993. Novel approach to nonlinear/non-Gaussian Bayesian state
603 estimation. In: *IEEE Proceedings F - radar and signal processing* 140(2): 107-113 doi:
604 10.1049/ip-f-2.1993.0015
- 605 Hart A, Jackson DE, 2006. U-turns on ant pheromone trails. *Current Biology* 16:R42-R43. doi:
606 10.1016/j.cub.2006.01.015.
- 607 Hastings WK, 1970. Monte Carlo sampling methods using Markov chains and their applications.
608 *Biometrika* 57:97. doi: 10.2307/2334940.
- 609 Hoffman MD, Gelman A, 2014. The No-U-Turn Sampler: Adaptively Setting Path Lengths in
610 Hamiltonian Monte Carlo. *Journal of Machine Learning Research* 15:1593-1623.
- 611 Hölldobler B, Wilson EO, 2009. *The superorganism: the beauty, elegance, and strangeness of insect*
612 *societies: WW Norton & Company.*
- 613 Horowitz AM, 1991. A generalized guided Monte Carlo algorithm. *Physics Letters B* 268:247-252.
614 doi: 10.1016/0370-2693(91)90812-5.
- 615 Humphries NE, Queiroz N, Dyer JRM, Pade NG, Musyl MK, Schaefer KM, Fuller DW, Brunnschweiler
616 JM, Doyle TK, Houghton JDR, Hays GC, Jones CS, Noble LR, Wearmouth VJ, Southall EJ, Sims
617 DW, 2010. Environmental context explains Levy and Brownian movement patterns of marine
618 predators. *Nature* 465:1066-1069. doi: 10.1038/nature09116.
- 619 Humphries NE, Weimerskirch H, Sims DW, 2013. A new approach for objective identification of turns
620 and steps in organism movement data relevant to random walk modelling. *Methods in*
621 *Ecology and Evolution* 4:930-938. doi: 10.1111/2041-210x.12096.
- 622 Hunt ER, Baddeley R, Worley A, Sendova-Franks A, Franks NR, 2016a. Data from: Ants determine
623 their next move at rest: motor planning and causality in complex systems. *Royal Society*
624 *Open Science* 3:150534. doi: 10.5061/dryad.jk53j
- 625 Hunt ER, Baddeley RJ, Worley A, Sendova-Franks AB, Franks NR, 2016b. Ants determine their next
626 move at rest: motor planning and causality in complex systems. *Royal Society Open Science*
627 3:150534. doi: 10.1098/rsos.150534.
- 628 Hunt ER, Dornan C, Sendova-Franks, AB, Franks NR, 2018a. Asymmetric ommatidia count and
629 behavioural lateralization in the ant *Temnothorax albipennis*. *Scientific Reports* 8:5825.
630 doi: 10.1038/s41598-018-23652-4.
- 631 Hunt ER, Franks NR, Baddeley RJ, 2018b. The Bayesian Superorganism I: collective probability
632 estimation. bioRxiv preprint 468942. doi: 10.1101/468942.
- 633 Hunt ER, Franks NR, Baddeley RJ, 2018c. The Bayesian Superorganism III: externalised memories
634 facilitate distributed sampling. bioRxiv preprint 504241. doi: 10.1101/504241
- 635 Karaboga, D. and B. Basturk, A powerful and efficient algorithm for numerical function optimization:
636 artificial bee colony (ABC) algorithm. *Journal of Global Optimization*, 2007. 39(3): p. 459-471.
- 637 Kelly JL, 1956. A new interpretation of information rate. *Bell System Technical Journal* 35:917-926.
- 638 Kennedy AD, 1990. The theory of hybrid stochastic algorithms. *Probabilistic Methods in Quantum*
639 *Field Theory and Quantum Gravity* 224:209-223.
- 640 Khuong A, Lecheval V, Fournier R, Blanco S, Weitz S, Beziau, J-S, Gautrais, J, 2013. How Do Ants Make
641 Sense of Gravity? A Boltzmann Walker Analysis of *Lasius niger* Trajectories on Various
642 Inclines. *PLOS ONE* 8(10): e76531. doi: 10.1371/journal.pone.0076531
- 643 Klaassen RHG, Nolet BA, van Gils JA, Bauer S, 2006. Optimal movement between patches under
644 incomplete information about the spatial distribution of food items. *Theoretical Population*
645 *Biology* 70:452-463. doi: 10.1016/j.tpb.2006.04.002.

- 646 Kramer DL and McLaughlin RL, 2001. The behavioural ecology of intermittent locomotion. *American*
647 *Zoologist* 41(2) doi: 10.1093/icb/41.2.137
- 648 MacArthur RH, 1965. Ecological consequences of natural selection, In: *Theoretical and mathematical*
649 *biology*. New York: Blaisdell.
- 650 Mackay DJ, 2003. *Information theory, inference and learning algorithms*: Cambridge University
651 Press.
- 652 Maynard Smith J, Szathmary E, 1995. *The major transitions in evolution*. Oxford, England: W. H.
653 Freeman and Co.
- 654 McLeman MA, Pratt SC, Franks NR, 2002. Navigation using visual landmarks by the ant *Leptothorax*
655 *albipennis*. *Insectes Sociaux* 49:203-208. doi: 10.1007/s00040-002-8302-2.
- 656 McNamara, J. M., R. F. Green and O. Olsson (2006). "Bayes' theorem and its applications in animal
657 behaviour." *Oikos* 112(2): 243-251. doi: 10.1111/j.0030-1299.2006.14228.x
- 658 Metropolis N, Rosenbluth AW, Rosenbluth MN, Teller AH, Teller E, 1953. Equation of state
659 calculations by fast computing machines. *Journal of Chemical Physics* 21:1087-1092.
660 doi: 10.1063/1.1699114.
- 661 Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE, 2008. A movement
662 ecology paradigm for unifying organismal movement research. *Proceedings of the National*
663 *Academy of Sciences of the United States of America* 105:19052-19059. doi:
664 10.1073/pnas.0800375105.
- 665 Neal RM, 1993. Probabilistic inference using Markov chain Monte Carlo methods. Technical Report
666 CRG-TR-93-1: Dept. of Computer Science, Univ. of Toronto.
- 667 Noble D, 2011. A theory of biological relativity: no privileged level of causation. *Interface Focus* 2:55-
668 64. doi: 10.1098/rsfs.2011.0067.
- 669 Nurse P, 2008. Life, logic and information. *Nature* 454:424-426. doi: 10.1038/454424a.
- 670 Olsson O, Brown JS, Lundberg P, 2006. The Foraging Benefits of Information and the Penalty of
671 Ignorance. *Oikos* 112:260-273.
- 672 Orr HA, 2009. Fitness and its role in evolutionary genetics. *Nature Reviews Genetics* 10:531-539.
673 doi: 10.1038/nrg2603.
- 674 Oster GF and Wilson EO, 1978. *Caste and Ecology in the Social Insects*. Princeton University Press.
- 675 Petrovskii S, Mashanova A, Jansen VA, 2011. Variation in individual walking behavior creates the
676 impression of a Lévy flight. *Proceedings of the National Academy of Sciences*, **108**(21), 8704-
677 8707. doi: 10.1073/pnas.1015208108.
- 678 Pratt SC, Brooks SE, Franks NR, 2001. The Use of Edges in Visual Navigation by the Ant *Leptothorax*
679 *albipennis*. *Ethology* 107:1125-1136. doi: 10.1046/j.1439-0310.2001.00749.x.
- 680 Pratt SC, Sumpter DJT, Mallon EB, Franks NR, 2005. An agent-based model of collective nest choice
681 by the ant *Temnothorax albipennis*. *Animal Behaviour* 70:1023-1036. doi:
682 10.1016/j.anbehav.2005.01.022.
- 683 Reid CR, Lutz MJ, Powell S, Kao AB, Couzine ID, Garnier S, 2015. Army ants dynamically adjust living
684 bridges in response to a cost-benefit trade-off. *Proceedings of the National Academy of*
685 *Sciences of the United States of America* 112:15113-15118. doi: 10.1073/pnas.1512241112.
- 686 Reynolds AM, Lepretre L, Bohan DA, 2013. Movement patterns of Tenebrio beetles demonstrate
687 empirically that correlated-random-walks have similitude with a Levy walk. *Scientific Reports*
688 3. doi: 10.1038/srep03158.
- 689 Robinson EJ, Jackson DE, Holcombe M, Ratnieks FL, 2005. 'No entry' signal in ant foraging. *Nature*,
690 **438**(7067), 442. doi: 10.1038/438442a
- 691 Rossky PJ, Doll JD, Friedman HL, 1978. Brownian dynamics as smart Monte Carlo simulation. *Journal*
692 *of Chemical Physics* 69:4628-4633. doi: 10.1063/1.436415.
- 693 Schultz TR, 2000. In search of ant ancestors. *Proceedings of the National Academy of Sciences*
694 97:14028-14029. doi: 10.1073/pnas.011513798.
- 695 Sumpter DJT, 2006. The principles of collective animal behaviour. *Philosophical Transactions of the*
696 *Royal Society B-Biological Sciences* 361:5-22. doi: 10.1098/rstb.2005.1733.

- 697 Sumpter DJT, Pratt SC, 2003. A modelling framework for understanding social insect foraging.
698 Behavioral Ecology and Sociobiology 53:131-144. doi: 10.1007/s00265-002-0549-0.
699 Van Gils JA, 2010. State-dependent Bayesian foraging on spatially autocorrelated food distributions.
700 Oikos 119:237-244. doi: 10.1111/j.1600-0706.2009.17497.x.
701 Viswanathan GM, Raposo EP, da Luz MGE, 2008. Levy flights and superdiffusion in the context of
702 biological encounters and random searches. Physics of Life Reviews 5:133-150.
703 doi: 10.1016/j.plrev.2008.03.002.
704 von Frisch K, 1967. The dance language and orientation of bees. Cambridge, MA: Harvard University
705 Press.
706 White EP, Enquist BJ, Green JL, 2008. On estimating the exponent of power-law frequency
707 distributions. Ecology 89:905-912. doi: 10.1890/07-1288.1.