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Testing the level of ant activity associated with quorum sensing: An empirical approach leading to the establishment and test of a null-model

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ABSTRACT

On the basis of experimental observations, this paper develops two well-defined mathematical models for the level of activity of Pharaoh's ants within their nesting area, with the aim of providing a more general understanding of animal activity. Under specific conditions, we observe that the activity of ants within their nesting area appears to show no dependence on their density. Making the assumption that all ants move independently of one another, this behaviour can be mathematically modelled as a random process based on the binomial distribution. Developing the model on this basis allows an exponential distribution to be exposed that underlies the time-intervals between ants leaving the nesting area. Such a distribution is present, irrespective of whether the ant population in the nesting area remains constant or steadily depletes, and suggests that ant–ant interactions do not play any significant role in determining ant activity under the experimental conditions adopted.

The mathematical framework presented plays the role of a null model that will have a wide range of applications for detecting other determinants of activity-level (not addressed in this study) including environmental and social factors such as food availability, temperature, humidity, presence of pheromone trails, along with intraspecific and interspecific interactions outside the nest and, indeed, more generally. The null model should have applications to a range of organisms.

Lastly, we discuss our data in relation to a recent study of ants leaving their nest (Richardson et al., 2010) in which the null model was rejected in favour of *record dynamics*, where ant–ant interactions were conjectured to play a role.

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1. Introduction

Organisms frequently monitor the density of conspecifics in their immediate vicinity and modify their behaviour appropriately. For example, some bacteria secrete diffusible signals, for which they also express specific receptors, in order to signal and monitor their density. This mechanism was first discovered in the bacterium *Vibrio fischeri*; this species uses this technique to ensure that free-living bacteria, which are at low density in the sea, do not indulge in metabolically expensive luminescence, except when living symbiotically, at high density, in the light organs of some marine fish and squid. This mechanism was first called 'quorum sensing' by Fuqua et al. (1994). It has subsequently emerged that bacteria ubiquitously use both intra and inter-species communication to regulate a range of behaviours, notably co-ordinated control of pathogenicity towards their unfortunate host (Miller and Bassler, 2001).

Social insects also exhibit a number of clear examples of behavioural responses to the density of conspecifics. The Argentine

ant, *Linepithema humile*, tends to make convoluted exploratory pathways at high ant density, but these become straighter as ant density decreases (Gordon, 1995). This is in broad accordance with the predictions of models of behaviour, based on optimal searching (Adler and Gordon, 1992). The ant *Leptothorax albipennis*, after damage to its nest, sends out ants to find new nesting sites. When the number of ants at a potential new nest site first reaches a threshold value (or density), this triggers a local consensus decision to switch from recruitment by tandem running, to the speedier mechanism of carrying ants (and brood) from the old nest to the newly chosen site (Pratt et al., 2002). Scout bees from a swarm of *Apis mellifera* investigate potential new nest sites and, on returning to the swarm, communicate the quality of the new nest site by the vigour and duration of their waggle dances. The better sites therefore recruit more bees. Once a quorum of about 15 bees is established at a potential new site, those bees returning to the swarm perform a piping behaviour to prime the entire swarm for flight to the new site (Seeley et al., 2006; Visscher and Seeley, 2007).

Given these well documented cases, not least in ants, where the behaviour of organisms depends on their density, we have investigated whether there is any evidence that the density of Pharaoh's ants, *Monomorium pharaonis*, within a nest, has any significant influence on their level of activity.

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Our investigations, based on two different types of experiment, test whether there is an analogue of quorum sensing in Pharaoh's ants. In one experiment, we measured the times at which ants left their nesting area, when taking a specific foraging route, and were allowed to return to their nesting area. As a consequence, the mean ant density within the nesting area remained constant throughout the experiment. This rate of leaving was compared directly to a situation in which the ants were strictly prevented from returning to their nesting area after taking the foraging route, in which case the mean density of ants progressively decreased over time. As we shall argue, the measured rate at which ants leave their nesting area is a measure of their level of activity. Given this, our measurements probe the degree to which the level of activity of the ants is affected by their density.

To explore these issues in detail, we also formulated mathematical models. Rather than using models with deterministic rules for the behaviour of each ant, we constructed and tested two null statistical models, in which individual ants move randomly and *independently* of one another. These models yield results that show remarkable similarity to our direct behavioural observations. We conclude that under the experimental conditions we established, Pharaoh's ants move with a level of activity that is, to very high accuracy, independent of the number of other ants encountered in the nesting area. That is, they make decisions to move as independent agents without any hint of behavioural change associated with the density of ants.

The simple experimental methodology and null-model mathematical framework we present here provide a solid foundation for further investigations that can precisely determine the influence of controllable environmental and social perturbations on the activity of ants and other organisms. Examples of such perturbations include changes of food supply, temperature, humidity, along with intraspecific and interspecific interactions outside the nest. We finally note and discuss a recent study of ants leaving their nest (Richardson et al., 2010) in which data appear best fitted by more complex mathematics — a model of ants exiting that involves *record-dynamics*, implying some kind of ant–ant interactions.

2. Ant activity: an experimental approach

We used the Pharaoh's ant, *Monomorium pharaonis*, in our experiments. Pharaoh's ants are a well-studied, highly invasive, unicolonial species (Sudd, 1960; Fourcassie and Deneubourg, 1994) in which a number of seminal aspects of self-organising foraging behaviour has been elucidated (e.g. Jackson et al., 2004). The ants were kept at a constant temperature of 25°C and constant level of humidity of 40%, and deprived of sugar for a period of two days prior to an experiment. During an experiment, the ants were able to leave their nesting area (i.e., the brood chamber and its immediate vicinity), via a bridge. Application of a coating of *fluo*n (fluon PTFE, *Blades biological*) to the far end of the bridge, which was vertical, caused all ants walking on the coated region of the bridge to fall from the bridge.

In one experiment, the far end of the bridge was located within the nesting area, so that all ants falling off the bridge re-entered the nesting area (see Fig. 1). We call this 'leaving with replacement'. We observed that after falling, the ants carried out a range of different behaviours, and there was no evidence of the ants learning to repeatedly use the bridge.

In the second experiment, the far end of the bridge was located above a container that was physically inaccessible from the nesting area. Ants falling into this container were unable to return to the nesting area during the course of an experiment (see Fig. 1). We refer to this as 'leaving without replacement'.

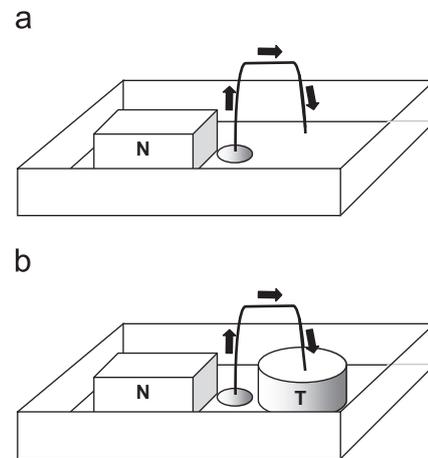


Fig. 1. Apparatus used to determine the rate that ants leave the nesting area. (a) Ants were able to climb the wire bridge (thick line) in the direction of arrows. On encountering the fluon covered vertical far end of the bridge, ants fell to the ground and hence directly returned to the nesting area in which the nest (N) was situated. (b) Ants walking along the bridge in the direction marked by the arrows fell into the trap (T) which had fluon coated walls; the ants were therefore unable to return to the nesting area during the period of the experiment. Rates of falling from the far end of the bridge were used as the proxy for ants leaving the nesting area in both experiments.

The times at which ants fell were recorded for experiments 'with replacement' and 'without replacement'; both types of experiments were repeated for 4 different colonies of Pharaoh's ants. Below we illustrate our findings with results and figures from (i) a single experiment 'with replacement' and (ii) a single experiment 'without replacement.' In Appendix A we present summary statistics for the experiments carried out on the different colonies. The quantitative results differ between colonies, due to differences in uncontrollable aspects, such as the precise colony size. However, for a given experimental set-up, the general conclusions, that we report hold for all experiments of that type that were carried out.

All of the statistical analysis presented in this work was performed using the software package MATLAB (The MathWorks Inc., 2009).

3. Results

3.1. Ants leaving with replacement

When the number of ants that have left the nesting area 'with replacement' is plotted against time, it is found to closely correspond to a linear change (Fig. 2).

The distribution of *time-intervals* between adjacent ants leaving the nesting area (Fig. 3) has the appearance of an exponential distribution.

We cannot directly use a Kolmogorov–Smirnov test (Hogg and Tanis, 2006) to determine whether this distribution is genuinely exponential since the distribution contains a parameter (the inverse of the mean time-interval) which would need to be estimated from the data (Lilliefors, 1969; Broom et al., 2007). Instead, we used an Anderson–Darling test (Anderson and Darling, 1952; see also Kvam and Vidakovic, 2007) to determine whether the distribution of time-intervals follows an exponential distribution. The test revealed that there was no significant difference ($p=0.113$) between the observations ($N=585$) and an exponential distribution, and led to a value of a mean time-interval between ants leaving the nesting area of 8.283 s (see Table 1).

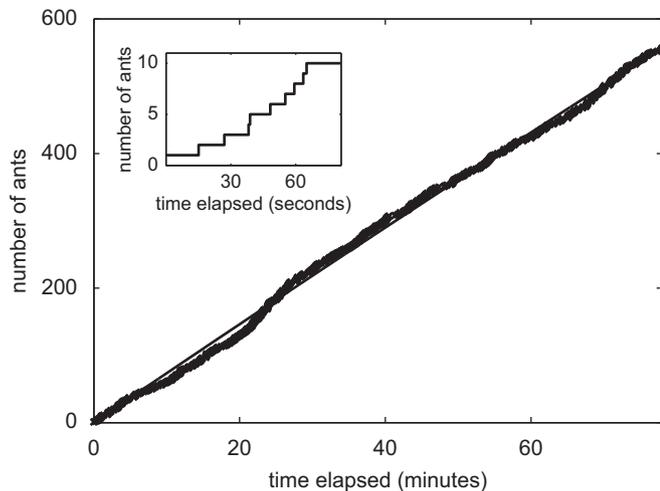


Fig. 2. A plot illustrating the cumulative number of ants (shown as a thick black line comprising individual data points) that have left the nesting area ‘with replacement’, as a function of time. The thin straight line was derived from linear regression. In this particular experiment, on average, 0.12 ants were leaving/second. The rate of activity, as characterised by the rate of leaving, did not appreciably change with either the time that had elapsed since the start of the experiment or the number of ants that had left the nesting area. A visual estimate indicated that approximately 300 ants were in the nesting area. Thus some ants must have left the nesting area at least twice during the experiment. The inset is a ‘zoom’ of the first 80 s of the main figure, to show the actual discrete unit changes in number. The horizontal lines in the inset figure represent the time-intervals between adjacent ants leaving.

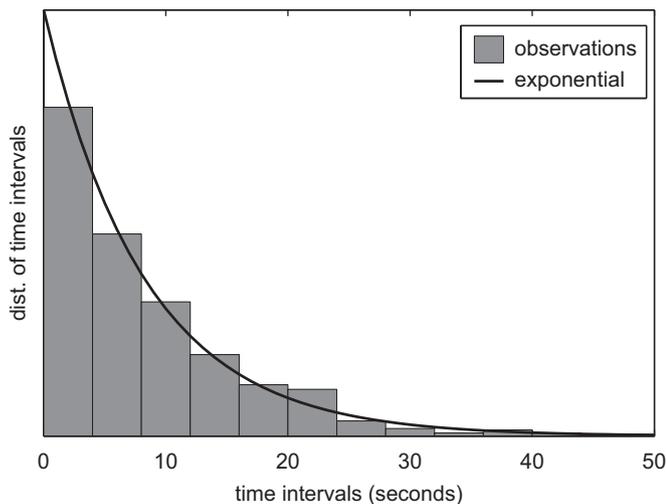


Fig. 3. A plot, for a single experiment, which illustrates the distribution of time-intervals between consecutive ants leaving the nesting area, under the scenario ‘leaving with replacement’. This distribution is found not to be significantly different from an exponential distribution (solid curve), using an Anderson–Darling test (see Table 1). The graph is consistent with ants moving independently of each other and performing a stochastic process (a Poisson process) that is ‘memoryless’ (Hogg and Tanis, 2006).

A plot of the time-intervals produced during the entire course of an experiment (Fig. 4) strongly suggests that the distribution of time-intervals is independent of the time elapsed since the start of the experiment; linear regression of time-interval against time elapsed from the start of the experiment confirmed the absence of a significant trend ($N=585$, $p=0.56$).

The simplest interpretation of these data is that the ants move independently within the nesting area, without any aggregation (Parrish and Edelstein-Keshet, 1999; Ame et al., 2004; Jeanson et al., 2005; Lauzon-Guay et al., 2008) or recruitment behaviour (Wilson,

1962), and some ants randomly encounter the bridge and use it to leave the nesting area. The mean rate with which ants fall from the bridge has, we assume, contributions from both the geometry of the problem (the larger the diameter of the wire, constituting the bridge, the larger the probability of encountering it) and the level of activity of the ants (the more active or fast-moving the ants, the greater the chance they have of encountering the bridge). Under a fixed experimental geometry, the mean rate with which ants leave the nesting area is used in the present work as a measure of ‘ant activity’.

The results obtained for ants leaving their nesting area ‘with replacement’ indicate that their activity remained essentially constant during the entire duration of the experiment. Furthermore, a linear increase over time of the mean number of ants leaving the nesting area and an exponential distribution of time-intervals between adjacent ants indicates that the ants leave the nesting area as a Poisson process (see e.g., Haigh, 2002).

3.2. Ants leaving without replacement

When ants left their nesting area ‘without replacement’, the number falling from the bridge per unit time decreased as the number of ants in the nesting area decreased. This is apparent in Fig. 5, in which the cumulative number of ants that had left the nesting area is plotted against the time elapsed since the start of the experiment.

A decrease in the rate of ants leaving the nesting area over time is expected if their level of activity remains independent of the density of ants in the nesting area, since as time proceeds there are fewer ants within the nesting area, and hence fewer likely to encounter the bridge. The question is whether the observed decrease in the rate of leaving is *fully explained* by simply a reduction in the number of ants, or whether the level of the ants’ activity is modulated beyond this – due to the decreasing *density* of the ants. We address this question later on, when we mathematically formulate a null model of the problem.

In experiments where ants leave their nesting area without replacement, we have verified that the distribution of time-intervals between consecutive ants leaving (Fig. 6) deviates significantly from an exponential distribution. Results of an Anderson–Darling test for one particular experiment, given in Table 1, illustrate this ($N=496$, $p < 0.001$).

However, we hypothesised that the distribution is fundamentally exponential in character, but the parameter characterising the distribution (the inverse of the mean time-interval) is a function of the time elapsed since the start of the experiment, and hence changes during the course of an experiment. The lengthening time distribution, as a function of elapsed time, is clearly shown in Fig. 7.

To investigate this hypothesis, we employed a statistical approach that tests only the underlying shape of the distribution, and is insensitive to time-dependence of the parameter in the distribution (Broom et al., 2007). This test uses the ratio of adjacent time-intervals, and this transformation of the data yields a new probability distribution which is independent of the parameter of the original distribution. We found no evidence to reject an underlying exponential *shape* of the distribution (Table 1, $N=496$, $p=0.35$). As a consequence, the overall distribution of time-intervals can be well-characterised as an exponential distribution, but with a parameter whose value depends on the time elapsed since the start of the experiment, and which changes during the course of an experiment.

4. Conclusions from the experimental approach

In the first experiment, where replacement is allowed, the ants appear to display behaviour that is consistent with them moving

Table 1

In this table, we test the exponential nature of the distribution of time-intervals between ants leaving their nesting area. In the top row, the exponential nature of the distribution, when replacement is allowed, is shown to be consistent with the data, using an Anderson Darling (AD) test. The following rows show the distribution of time-intervals when replacement is not allowed. First, the “raw” distribution of time-intervals is shown not to be exponentially distributed. Then using a different method (Broom et al., 2007), we find evidence for the underlying exponential shape of the distribution, but with a parameter that slowly changes with time, employing a Kolmogorov Smirnov (KS) test. Our model for this predicts a changing parameter, and furthermore, predicts the nature of the change. We transformed the time-intervals, by rescaling them by their expected value, and the resulting distribution was predicted to be exponential with a parameter of unity. We tested this using a Kolmogorov–Smirnov test (final row).

Summary of statistical tests					
Test		Outcome	AD-statistic	KS-statistic	P-value
Replacement	Exponential	Not rejected	1.02	–	0.113
No replacement	Exponential	Rejected	9.8	–	< 0.001
	Underlying exponential shape	Not rejected	–	0.058	0.35
	Exponential, with shifting parameter according to Eq. (8)	Not rejected	–	0.025	0.92

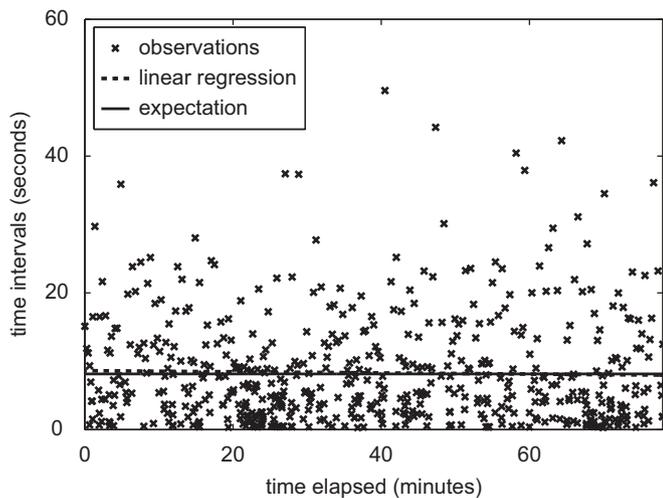


Fig. 4. A plot of the relationship, in a single experiment, between the time-intervals of consecutive ants leaving the nesting area and the time elapsed since the start of the experiment. The ants left ‘with replacement’. The time-intervals appear to be drawn from the same distribution (i.e., a stationary distribution) for the full duration of the experiment. See Fig. 8 for additional details. The horizontal line represents the mean time-interval derived from the exponential distribution of Fig. 3, while the dashed line (which is virtually indistinguishable from the horizontal line) represents a linear regression of the time-intervals against time. The linear regression confirms the absence of significant trend in the time-intervals over time.

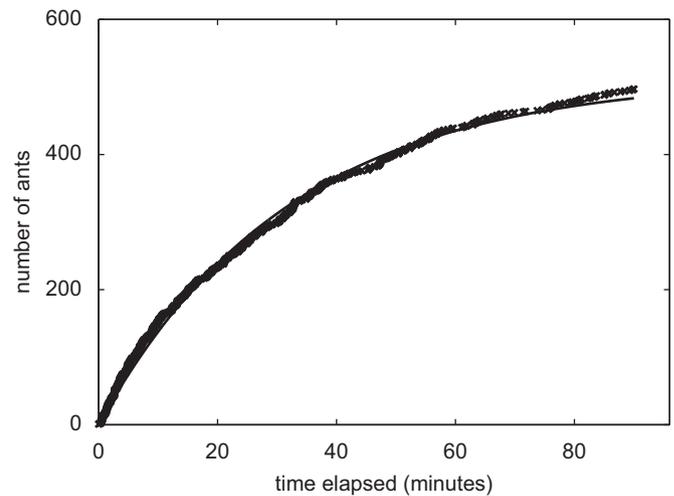


Fig. 5. A plot of the cumulative number of ants that fell as a function of time. Ants fell into a new area and were not allowed to return to their nesting area, hence this is a ‘with replacement’ experiment. Initially, there were an average of 0.21 ants leaving/second, but this rate of exploration decreased over the course of the experiment, as the number of ants within the nesting area decreased. The solid curve, derived from the mathematical model (see Eq. 6), represents the expected cumulative number of fallen ants.

independently of one another with a behaviour characterised by (i) a mean rate of leaving that does not change during the course of an experiment and (ii) with an exponential distribution of time-intervals between adjacent ants leaving the nesting area. While (ii) implies (i), we note that *any* stationary distribution of time-intervals would, by definition, lead to a constant value of the mean time-interval. The exponential distribution obtained shows that, under these experimental conditions, the way the ants leave the nesting area is a memoryless stochastic process (i.e., a random process where past events have no impact on the present; see e.g., Hogg and Tanis, 2006).

In the second experiment where ants leave their nesting area without being replaced, the ants’ rate of leaving decreased with time, as the number of ants in the nesting area also decreased. While this might be consistent with some level of communication or collective behaviour, e.g., ants being less active as they ‘sense’ that the ant density within the nesting area decreases, the exponential nature of the distribution of time-intervals that arises (albeit with a time-dependent parameter) suggests that a random, memoryless stochastic process also underlies the observations in this second experiment.

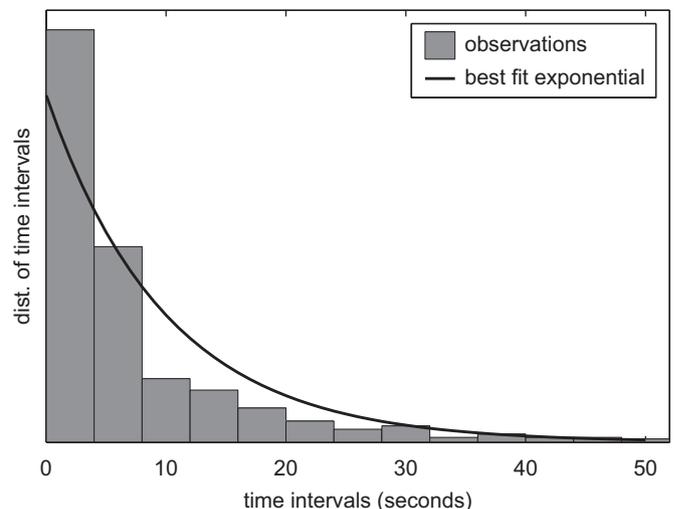


Fig. 6. Distribution of time-intervals between ants leaving ‘without replacement’. The solid curve is the best-fit exponential distribution (by fitting the distribution from the data). It is apparent that the data (histogram) deviates from the exponential distribution and an Anderson–Darling test (Table 1) confirms that this difference is statistically significant.

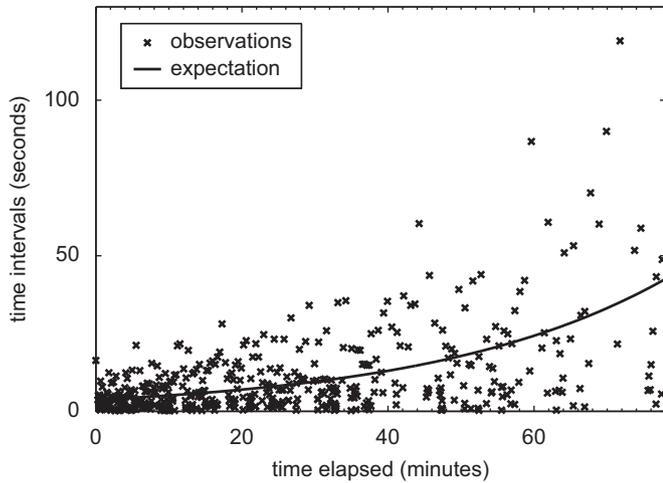


Fig. 7. A plot, in a single ‘without replacement’ experiment, of the time-intervals of consecutive ants leaving as a function of the time elapsed since the start of the experiment. The time-intervals clearly increase during the course of the experiment – as the number of ants remaining in the nesting area decreases. The values for the expected mean time-intervals (curved line) were derived from the mathematical model (see Eq. 8).

In the next section, we construct formal models for the problem, and derive expressions for (i) the rate of ant departure from the nesting area and (ii) the distribution of time-intervals, and proceed to fit these model predictions to the data and compare the level of agreement.

5. Stochastic process underlying ant activity

We present idealised models of the above experiments which allow a complete mathematical description of the outcomes (details are given in Appendix B). In the models, individual ants are assumed to move independently of one another within the nesting area (as they appear to do so outside a nest; see Nouvellet et al., 2009).

In the experiments, ants left the nesting area if they encountered the bridge, climbed it and then fell off. To express all of this in a succinct way, we shall describe the ants as ‘leaving’ the nesting area via an ‘exit.’ We shall explore two models associated with two different exiting scenarios:

- (i) Ants randomly leave the nesting area by the exit, but are then immediately returned to the nesting area. This is ‘leaving with replacement’.
- (ii) Ants randomly leave the nesting area by the exit, but are prevented from returning. This is ‘leaving without replacement’.

We shall establish a statistical description of the two different scenarios to predict how the number of ants leaving their nesting area changes with time, under the null assumption that ant activity does not change, irrespective of whether the ants are replaced or prevented from returning to the nesting area.

To describe the problem, it helps to think of time as occurring in a discrete set of steps; the discrete step-size could have a genuine reality, such as the smallest time-interval that can be resolved in an experiment. We initially formulate the problem in this way (Appendix B) but do not pursue the implications of discrete time-steps in this work (although this may have applications elsewhere). Thus all results presented below hold when the time-step size is vanishingly small (i.e., when time is continuous).

Two parameters characterise the problem:

$$n = \text{the number of ants initially present in the nesting area} \quad (1)$$

$$r = \text{the probability of any individual ant leaving the nesting area per unit time (assumed to be the same for every ant)} \quad (2)$$

The probability of an individual ant leaving per unit time, r , encapsulates both the geometry of the problem, and also the level of ant activity. In principle, r need not be a constant, but could depend on quantities such as the corpulence of the ants (Robinson et al., 2009) or their density. For the mathematical analysis we present, we shall assume r is a constant, corresponding to a constant level of activity, and shall investigate the degree to which the data is compatible with this assumption.

The number of ants leaving during a time-step is the outcome of random sampling, where every ant in the nesting area has an equal probability, r , of finding and using the exit.

When leaving occurs with replacement, the number of ants that have exited by a time t from the start of the experiment, $N(t)$, is found to be a random variable with a Poisson distribution with parameter nrt (see Appendix B for details). Thus with $P(k,t)$ the probability that k ants have exited by time t since the start of the experiment, we have

$$P(k,t|\text{with replacement}) = (nrt)^k e^{-nrt} / k! \quad (3)$$

where $k=0, 1, 2, \dots$, and k can be arbitrarily large.

When replacement is prevented, the number of ants that are present in the nesting area decreases with time. Thus if, by time t , a total of $N(t)$ ants have exited then $n - N(t)$ ants remain in the nesting area and the random sampling, which determines which ants leave the nesting area, leads to $n - N(t)$ having a binomial distribution with parameters n and e^{-rt} (see Appendix B for details). The form of the probability parameter e^{-rt} , that occurs in the binomial distribution, yields the intuitively plausible result that the probability of an ant remaining in the nesting area decreases exponentially with time.

Given the distribution of the number of ants remaining in the nesting area, it directly follows that the number of ants that have left by time t , namely $N(t)$, which is the observable quantity in these experiments, has a binomial distribution with parameters n and $1 - e^{-rt}$.

The probability that k ants have left without replacement by a time t since the start of the experiment is shown in Appendix B to be given by

$$P(k,t|\text{without replacement}) = \binom{n}{k} (1 - e^{-rt})^k e^{-(n-k)rt}. \quad (4)$$

Here $\binom{n}{k}$ is a binomial coefficient, and $k=0, 1, 2, \dots, n$, hence k has a largest value equal to the total number of ants in the colony.

The models presented here rely heavily on the assumption of independence of movement of different ants within the nesting area (hence the validity of binomial sampling and the constancy of r). In particular, it is assumed that the departure of one ant does not statistically influence other ants to leave. Thus the models presented are equivalent to a particular null hypothesis, namely independence of movement within the nesting area and random exiting. If there are significant differences between the predictions of the models and the observations then it will be an indication of non-independence of the movements of the real ants.

Having characterised the process of ants leaving their nesting area, it is possible to derive how the expected number of ants that have left the nesting area depends on the time, t , that has passed since the start of the experiment. When replacement is allowed, it

is a standard property of the Poisson distribution of Eq. (3) that the expected number of ants that have left is

$$E[N(t)|\text{with replacement}] = nrt \quad (5)$$

(see e.g., Haigh, 2002).

In a similar way, it follows from Eq. (4) that when replacement is not allowed, the expected number of ants that have left is given by

$$E[N(t)|\text{without replacement}] = n(1 - e^{-rt}). \quad (6)$$

When rt is small ($rt \ll 1$) Eqs. (5) and (6) yield similar results but when rt becomes large compared with unity the two results become quite different. In particular, the result of Eq. (5) can reach any size, whereas that of Eq. (6) can only reach a maximum of n because there are only a total of n ants in the nesting area.

Finally given the processes of departure from the nesting area – described above – the distribution of time-intervals between two individual ants leaving, written $\varphi(\Delta T)$, can also be inferred (see Appendix B).

With replacement, the distribution of time-intervals follows an exponential distribution:

$$\varphi(\Delta T|\text{with replacement}) = nre^{-nr\Delta T}. \quad (7)$$

Without replacement, the distribution of time-intervals follows an exponential distribution, with a time-dependent parameter:

$$\varphi(\Delta T, t|\text{without replacement}) = \lambda(t)e^{-\lambda(t)\Delta T} \quad (8)$$

where

$$\lambda(t) = nre^{-rt}. \quad (9)$$

Thus without replacement, the observed time-intervals are drawn from an exponential distribution that *depends on the actual time of observation*. For example, the probability of observing a time-interval larger than 1 s, at the start of an experiment, will be different to the probability of observing a time-interval larger than 1 s at 60 min into the experiment. However, this dependence of the distribution on the time of observation can, by a simple time-dependent rescaling of observed time-intervals, be removed. The procedure is to divide a time-interval that is observed at time t , written $\Delta T(t)$, by its expected value (written $E[\Delta T(t)]$ and equal to $1/\lambda(t)$) at this particular time. We thus define the rescaled time-interval, $R = \Delta T(t)/E[\Delta T(t)]$ and this can be verified to have an exponential distribution, similar to that of Eq. (8), but with a parameter that is not of the form of $\lambda(t)$ of Eq. (9), but rather with a parameter that has the time-independent value of unity.

6. Contrasting data with the predictions of the models

Given the data and the null-models proposed above, we now re-analyse the data to estimate the parameter-values of the models and compare the level of agreement between models and data.

6.1. With replacement

When ants fell with replacement, the model for this case predicts that they leave the nesting area at a constant mean rate that follows from Eq. (5): $E[N(t)] = nrt$. Linear regression yielded the thin straight line in Fig. 2 with $nr = 0.12$ ($N = 585$, $p < 0.001$, $R^2 = 0.997$). In this situation it is not possible to obtain separate estimates of n and r ; only the product of the two can be estimated, representing the number of individuals falling per second (and thus depending on both the size of the colony and the level of activity of the ants). The observed time-intervals between individual ants leaving thus appear to be drawn from a distribution that is indistinguishable from an exponential distribution

(solid line in Fig. 3, Table 1). The mean time-interval between individual ants leaving appears uncorrelated with time (Fig. 4, straight line). We observe a very close agreement in the estimation of nr using either (i) the number of ants that have left as a function of time: $nr = 0.12$ (via linear regression) or (ii) from the distribution of time-intervals: $nr = 0.12$.

6.2. Without replacement

When ants left without replacement, the expected number of ants that had left and the observed number (as a function of elapsed time), showed a high level of agreement (Fig. 5), and allowed us to estimate that there were initially $n = 515$ (95% CI [511, 518]) ants present in the nesting area, and the probability of any ant leaving, per second, was found to be $r = 5.2 \times 10^{-4} \text{ s}^{-1}$ (95% CI [5.1×10^{-4} , 5.3×10^{-4}]). Additionally, the underlying distribution of time-intervals was predicted to be an exponential distribution with a time-dependent parameter. From the data, the exponential nature of the underlying distribution was demonstrated (Table 1). The time-dependence in the parameter of the distribution is illustrated by the curved line in Fig. 7.

Finally, given a distribution with an underlying form that is exponential, but with a time-dependent parameter, the scaling of each observed time-interval by its expected value leads to a new random variable, R , that has a distribution that is predicted to be exponential, with a parameter of unity. Fig. 8 shows the distribution of time-intervals, when scaled by their expected values.

The scaled time-interval values, i.e., the R values, cannot be distinguished from exponentially distributed values (solid line Fig. 8, Table 1) using a Kolmogorov–Smirnov test. We note that ants continue to behave in this statistically predictable fashion, despite their density decreasing to approximately 10% of its starting value during the course of an experiment.

7. Event based analysis

So far the analysis presented has been in terms of the relation between ants leaving a nesting area and the time elapsed since the start of an experiment. In Appendix B we show that direct predictions of the models, resulting from focussing on ‘events’,

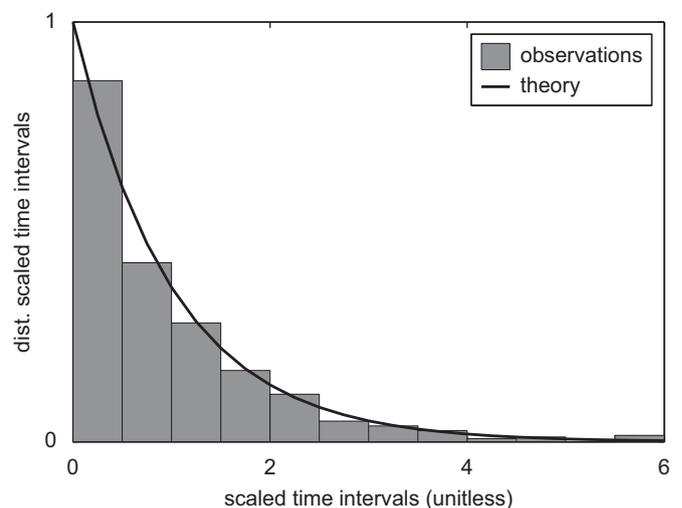


Fig. 8. Distribution of time-intervals between ants leaving without replacement. Each time-interval has been scaled by its expected value (given by $1/\lambda(t)$ of Eq. (9)). The model for this predicts that such scaled time-intervals are drawn from an exponential distribution with an expected value of the scaled time-interval of unity. The distribution of the scaled values is not significantly different from an exponential distribution, as confirmed by a Kolmogorov–Smirnov test (Table 1).

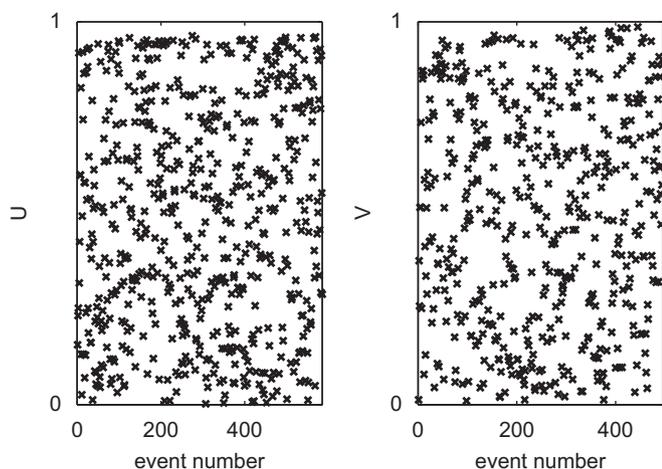


Fig. 9. Transformed time-intervals for the ant escape with replacement, U , and for no-replacement, V , are plotted against event number. If the predictions of the models were exact, U and V would be drawn from uniform distributions over the range 0 to 1. The distributions of U and V are found to not be significantly different from uniform distributions using a Kolmogorov–Smirnov test.

i.e., the dropping of individual ants without regard to the time they occurred, are the following:

- (i) In the case of ‘leaving with replacement,’ where ΔT_j is the random time-interval to the next ant dropping after the j ’th event (the j ’th ant dropping), the quantity $U_j = \exp(-nr\Delta T_j)$ is predicted to be a random number that is drawn from a uniform distribution on the interval 0 to 1. This property follows from the ΔT_j being predicted to be exponentially distributed.
- (ii) In the case of leaving without replacement, the quantity $V_j = \exp(-(n-j)r\Delta T_j)$ associated with the j ’th event is also a random number that is drawn from a uniform distribution on the interval 0 to 1.

The set of ‘event’-based quantities U_j and V_j from experiments with and without replacement is shown in Fig. 9.

The quality of the uniform distributions obtained provides further evidence of a Poisson process-like stochasticity underlying ants leaving their nesting area. Statistically, a Kolmogorov–Smirnov test (test statistic K) indicates that there is no significant deviation of the distribution of the U_j and V_j from a uniform distribution (for the U ’s: $K \approx 0.04$ giving $p \approx 0.37$; for the V ’s: $K \approx 0.02$ giving $p \approx 0.95$).

8. Comparing our model with a log Poisson process

Our findings are quite different from a recent study by Richardson et al. (2010) on the ant *Temnothorax albipennis*. By RFID tagging ants in each colony, these authors were able to examine the timing of ants leaving the nest when not allowed to return (so directly comparable to our non-replacement experiment) and the case in which ants were allowed to return but only those ants leaving the nests for the first time were recorded. They claim their data were better modelled by *record dynamics* (a Poisson process in logarithmic time, suggesting strong interactions between the components of the system – i.e., the ants) rather than a null model of exponential decay (Poisson statistics in linear time, where components of the system act independently).

A detailed comparison of the log Poisson process and our model is presented in Appendix C. In this section we merely

discuss the main findings of this Appendix and propose an objective way by which future studies could distinguish between the two processes.

The defining property of a log Poisson process is that the difference of the logarithm of the time of adjacent events is exponentially distributed. This leads us, under a reasonable approximation, to conclude that in a log Poisson process, the time intervals are exponentially distributed and the mean time interval, between adjacent events, increases linearly with time (see Appendix C). This can be contrasted with our study in which time intervals are also time dependent and exponentially distributed, but the mean time intervals increase exponentially with time. Thus while there is similar qualitative behaviour of the mean time interval of both models, there is a genuinely quantitative difference.

For future research on similar system, we propose the following steps:

- (1) Observe the fit in a plot of the number of individuals that leave, against time, with the predictions from each model. For our model, one would need to use a non-linear fit of the data to Eq. (6) of our model (thus obtaining estimates of r and n). For a log Poisson process (see e.g., Sibani and Dall, 2003 and Appendix C), one would need to fit the data to $E[T_k] = (1-c)^{-k} \approx \exp(ck)$ (i.e., estimate the value of c when k is the number of individuals that had left).
- (2) (a) Observe and test the nature of the distribution of the time intervals divided by their expected value, $R = \Delta T(t) / E[\Delta T(t)] = \Delta T(t) n r e^{-rt}$, using a Kolmogorov–Smirnov test. Under our model, the distribution is expected to be exponential with a parameter that has the time-independent value of unity.
 - (b) Observe and test nature of the distribution of the time intervals in log time, $\ln(T_{k+1}) - \ln(T_k)$, using an Anderson–Darling test. Under a log Poisson process, this distribution is expected to be exponential.

If after performing these tests, both processes are compatible with the data, then Occam’s razor would dictate that our model should be adopted because it is more parsimonious. Indeed using an analogy to a physical system, Richardson et al. (2010) argue that a log Poisson process reflects underlying interactions between individuals while our model does not make such an assumption. Furthermore, we add that our model is derived from a concrete mathematical description of the process (leading to biologically interpretable parameters) rather than an analogy to a physical phenomenon.

9. Discussion

In this work, we have made observations of animal activity, and modelled this phenomenon from basic principles. Specifically, we have focussed on the rate at which individual Pharaoh’s ants (*Monomorium pharaonis*) leave their nesting area. We have found a high level of agreement between observations and two null models presented here, which assume both independence of ant movement and random departure of ants from the nesting area. Our observations, within the context of the models, have allowed us to produce an estimate of the size of a colony and consistent estimates of the value of the parameter linked with the activity-level of the study organisms.

The models presented here treats the dynamics of ants leaving their nesting area as being the outcome of a set of independent ‘actions’ where the action of one ant leaving does not affect the actions of other ants. While we do not deny the presence of interactions between individual ants within the nesting area, the

high level of agreement between observations and theory (such as an exponential distribution of time-intervals) indicates that such interactions do not have any significant impact on the level of ant activity – at least under the experimental conditions investigated here.

In our first experiments, in which ants were allowed to return to the nesting area, the constant density of ants cannot trigger any density/quorum sensing mechanisms, and hence cannot activate any behavioural changes. However in the second set of experiments, where individuals were not allowed to re-enter the nesting area, the density of ants declined substantially; by the end of the experiment the density had a value of about 10% of the value at the start of an experiment. It would, *a priori*, have been reasonable to expect some behavioural effect because ants have been shown to be sensitive to the density of conspecifics in their vicinity (Wilson, 1984), and a change in their density, alone, could have acted as a form of feedback impinging on their level of activity and hence on their stochastic leaving-behaviour. This would manifest itself in the probability of any single ant leaving per unit time, r , depending on the number of ants in the nesting area. In the data analyses presented, we assumed a constant value of r and obtained an extremely high level of agreement between models and data. Furthermore, under 'leaving without replacement', Fig. 9 illustrates the values taken by the random variable V that was introduced in an event based analysis, and was predicted to have a uniform distribution under the assumption of constant r . The distribution of V does not significantly change with the number of events; a Kolmogorov–Smirnov test indicates that the distribution of the 50 first elements of V is not significantly different from that of the last 50 elements ($p \approx 0.50$). This implies that for the experiment without replacement, no density dependence was observed, suggesting that these Pharaoh's ants were leaving their nesting area as independent agents, seemingly oblivious to the dramatic decrease in ant density that was occurring within the nesting area during the course of an experiment.

A recent paper (Richardson et al., 2010), suggested a log Poisson process might underlie the dynamics of ants leaving their nest. Using an analogy to a physical system, they concluded that this was evidence for interactions between individuals. Based on our comparison of the two models (see Appendix C), we remain largely unconvinced by their conclusions. However, possible differences between the two studies might be due to intrinsic interspecies differences or ecology but could also be related to the feeding status of the animals. In our experiments, hungry ants may well default to behaving autonomously with a high tendency to forage. But when fed *ad libitum* (Richardson et al., 2010), interactions between returning fed ants and nest mates, signalling levels of food availability outside the nest, will be important in determining the rate of subsequent exploration (Hölldobler and Wilson, 1990). Similarly honeybees (Seeley, 1995) and bumblebees

(Dornhaus and Chittka, 2004) increase their exit rate from the hive/nest in response to returning bees signalling bountiful nectar availability in the environment.

We conclude that the level of activity observed, under the experimental conditions of the present work, in which ants were deprived of sugar for the 48 h prior to the observations, can be well explained by individual ants acting independently of each other, i.e., with a fixed probability of leaving the nesting area/unit time. Interestingly, for experiments without replacement, this leads to the distribution of time-intervals between individual ants leaving the nesting area being exponential, but with a mean value that changes with time, as the number of ants remaining in the nesting area varies with time. If, for example, we had used the distribution of time-intervals over the entire course of an experiment, then we would not have discovered the underlying exponential distribution. This character of the distribution could thus be termed cryptic, since it is not readily apparent from the overall results of an experiment. Using our model for this, this cryptic exponential distribution can be exposed, via a time-dependent rescaling of time-intervals. The fundamental nature of the stochasticity in this situation was therefore revealed.

Despite the somewhat counterintuitive predictions of our models for real organisms, their predictive power underlines their utility. Our experimental set-up and models may offer interesting opportunities for further exploration into other determinants of activity level, which could likely include both environmental and social factors, e.g., food availability, temperature, humidity, presence of pheromone trails, intraspecific and interspecific interactions outside the nest.

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Appendix A

This Appendix contains two tables which summarise the results for the different runs of experiments carried out. The general conclusions we draw in the main text (for experimental run 1) hold for all experiments.

In Table 2 we present the results of experiment where replacement is permitted. In this situation we can, for each run, determine the product of the parameters n and r , but not each parameter separately. We verify the exponential nature of the distribution of time-intervals using the Anderson–Darling test (test statistic AD). We also note that a visual estimate of the total number of ants in a nesting area is denoted N_e and is accurate within $\times 50$ ants.

In Table 3 we summarise the results of the second set of experiment where replacement was not allowed. In this situation,

Table 2

	nr	N_e	Exp. Dist.
Run 2	0.08	~500	$P \sim 0.1$ (AD~1.0)
Run 3	0.06	~300	$P \sim 0.08$ (AD~1.1)
Run 4	0.19	~100	$P \sim 0.4$ (AD~0.5)

Table 3

	N	$r \times 10^4$	Exp. Dist.	Shift exp. dist.
Run 2	529 (526–533)	6.8 (6.7–6.9)	$p < 0.001$ (AD~29.0)	$p \sim 0.2$ (KS~0.05)
Run 3	527 (523–532)	3.9 (3.8–4.0)	$p < 0.001$ (AD~4.2)	$p \sim 0.9$ (KS~0.02)
Run 4	214 (211–218)	5.2 (5.1–5.4)	$p < 0.05$ (AD~1.4)	$p \sim 0.4$ (KS~0.06)

estimates of both n and r are given. The distribution of time-intervals appears not to follow an exponential distribution (Anderson–Darling test, test statistic: AD), but cannot be distinguished from a distribution that would be exponential in shape with a shifting parameter (using a Kolmogorov–Smirnov test, test statistic: KS, on transformed time-intervals according to Broom et al., 2007).

Appendix B

In this Appendix we determine the statistical properties of the number of ants that have left the nesting area, as predicted by the models of the main text. We use a discrete-time description to derive results, where time t can take only the discrete values $t = j \times \tau$ where $j = 0, 1, 2, \dots$ and τ is the value of a discrete-time-step. While the results presented for a finite time-step may have some utility in their own right, we do not employ the finite step results here. Thus, at the end of the calculations, we take the time-step to zero, so time becomes continuous. We note that the models presented have close connections with ‘pure death’ models of population biology (Renshaw, 1993).

The probability of any particular ant to leave/unit time is r , hence the probability of any ant to leave in a time-step is taken as $r\tau$ (and we only consider $r\tau < 1$). The number of ants leaving during any time-step is the outcome of random sampling, where every ant in the nesting area has an equal probability of being chosen to leave. Hence the number of ants leaving is drawn from an appropriate binomial distribution.

Replacement model

When replacement is allowed, the number of ants present in the nesting area is constant and equal to the initial number, n . The number of ants that have left by time t , namely $N(t)$, is determined by the stochastic difference equation

$$N(t + \tau) = N(t) + B(n, r\tau) \tag{10}$$

with

$$N(0) = 0. \tag{11}$$

In Eq. (10) the quantity $B(n, r\tau)$ represents a random variable that is independently drawn, each time-step, from a binomial distribution with parameters n and $r\tau$. Since a sum of independent and identically distributed binomial random variables is also a binomial random variable, the number of ants that have left after time t also has a binomial distribution. Consequently, we can write $N(t) = B(nt/\tau, r\tau)$. Allowing τ to tend to zero (so time becomes continuous) results in $N(t)$ having a Poisson distribution

$$N(t) \sim \text{Poisson}(nrt). \tag{12}$$

This has a mean, $E[N(t)]$, and a variance, $\text{Var}(N(t))$, of nrt . To derive the distribution of time-intervals, we note that given a dropping event occurs at time $j\tau$, the next event will occur at time $(j+k)\tau$ with a probability that results from $k-1$ ‘failures’ followed by a ‘success’. A failure occurs with probability $(1-r\tau)^n$ and a success occurs with probability $1-(1-r\tau)^n$. Hence the distribution of time-intervals between successive events follows a geometric distribution:

$$\psi(k; \tau) = [1-(1-r\tau)^n](1-r\tau)^{n(k-1)}. \tag{13}$$

As τ tends toward zero, we can neglect the probability of more than one ant leaving at any step and an event can be interpreted as a single ant leaving. For a time-interval of ΔT the number of time-steps is $k = \Delta T/\tau$. The probability density of time-intervals arises from the small τ limit of $\psi(\Delta T/\tau; \tau)/\tau$ and from Eq. (13) we

obtain the exponential distribution

$$\varphi(\Delta T) = nre^{-nr\Delta T}. \tag{14}$$

The last result we shall determine for the replacement model concerns the distribution of exponentially distributed random numbers. If U is a random variable with a uniform distribution on $[0, 1]$ then $Y = -\ln(U)/\lambda$ has an exponential distribution with mean $1/\lambda$. Conversely, if Y has an exponential distribution with mean $1/\lambda$, then $e^{-\lambda Y}$ is uniformly distributed on $[0, 1]$. It follows from Eq. (14) that if ΔT_j is a random variable with an exponential distribution with mean $1/(nr)$ then $U_j = e^{-nr\Delta T_j}$ is uniformly distributed on $[0, 1]$.

Without replacement model

When replacement is not allowed, and $N(t)$ ants have left from the nesting area, the number of ants present in the nesting area is $n - N(t)$. This is the number from which a random sample is selected to leave in the next time-step. It follows that the analogue of Eq. (10) is

$$N(t + \tau) = N(t) + B(n - N(t), r\tau). \tag{15}$$

The solution is subject to Eq. (11). To determine the distribution of $N(t)$ it is convenient to define $M(t) = n - N(t)$, and Eq. (15) becomes equivalent to

$$M(t + \tau) = B(M(t), 1 - r\tau) \tag{16}$$

with

$$M(0) = n. \tag{17}$$

We write the probability distribution of $M(t)$ as $\psi_t(m)$ and Eq. (16) leads to

$$\psi_{t+\tau}(m) = \sum_{k=0}^n f_{1-r\tau}(m, k) \psi_t(k) \tag{18}$$

where $f_s(a, b) = \binom{b}{a} s^a (1-s)^{b-a}$ and $\binom{b}{a}$ denotes a binomial coefficient. It may be verified that $\sum_{b=0}^n f_s(a, b) f_s(b, c) = f_{ss}(a, c)$ and this property, combined with Eqs. (17) and (18) leads to $\psi_t(m) = f_{(1-r\tau)^{t/\tau}}(m, n)$ and hence to $M(t)$ having a binomial distribution with parameters n and $(1-r\tau)^{t/\tau}$. As a consequence $N(t)$, has a binomial distribution with parameters n and $1 - (1-r\tau)^{t/\tau}$. As we allow τ to tend to zero (and time becomes continuous) we obtain a binomial distribution for $N(t)$ with parameters n and $1 - e^{-rt}$

$$N(t) \sim \text{Binomial}(n, 1 - e^{-rt}). \tag{19}$$

This is characterised by a mean value of

$$E[N(t)] = n(1 - e^{-rt}) \tag{20}$$

and a variance of $\text{Var}(N(t)) = ne^{-rt}(1 - e^{-rt})$.

To determine the distribution of time-intervals between individual ants leaving at time t , we note that when j ants have left, the mean time to the next ant leaving follows from Eq. (14) with n replaced by $n - j$ and is given by $1/[(n - j)r]$. At time t we approximate the mean time-interval between ants leaving by $1/[(n - E[N(t)])r]$. Combining this result with Eq. (20) leads to a mean time-interval between ants leaving that depends on time t according to

$$E[\Delta T(t)] \approx e^{rt}/(nr). \tag{21}$$

Similar considerations to the ‘with replacement’ case, where we first assume j ants have left, and then replace j by $E[N(t)]$, leads to an exponential distribution of time-intervals that depends on the time t and is given by

$$\varphi(\Delta T, t) = nre^{-rt} e^{-nre^{-rt}\Delta T}. \tag{22}$$

Furthermore, in the limit of small τ , we have that after j events (j ants having dropped), the time to the next event is an

exponential random variable with mean $1/[(n-j)r]$. Writing this random time as ΔT_j we have, following the arguments in the ‘with replacement’ case, that the random variable $V_j = e^{-(n-j)r\Delta T_j}$ is uniformly distributed on $[0, 1]$.

Appendix C

In this Appendix, we compare the random process, which is used in this work to describe the departure of ants from a nest, with the random process adopted by Richardson et al. (2010) for their experiments. We note that all experiments and analysis of the present work, with the exception of this Appendix, were completed prior to learning of the work by Richardson et al. (2010).

To proceed, let T_k denote the time the k ’th ant left the nest. Richardson et al. (2010) assumed that differences of the natural logarithms of the times ants left a nest, namely $\ln(T_{k+1}) - \ln(T_k)$, had an exponential distribution. This leads to so called ‘record dynamics’ and, for some physical systems, is known to imply long range correlations (see e.g., Sibani and Dall, 2003). The logic of Richardson et al. (2010) is that if $\ln(T_{k+1}) - \ln(T_k)$ has an exponential distribution then this is evidence of interactions (of some kind) between the ants in their experiments. We note that these workers are therefore reasoning by analogy, and are not deriving the dynamics of the ants from a concrete mathematical model of ant behaviour.

By contrast, the results of the present paper are based on the detailed analysis of a specific mathematical model of ant behaviour. This model does not include any interactions between the ants and it predicts that the time intervals between ants leaving the nest without replacement, namely $T_{k+1} - T_k$, are exponentially distributed. A non-trivial outcome of this model is that the mean time interval $E[T_{k+1} - T_k]$ depends on the value of k (i.e., on the number of ants that have left the nest).

Description of a log-Poisson process adopted by Richardson et al.

The model of Richardson et al. (2010) is based on the assumption that $\ln(T_{k+1}) - \ln(T_k)$ has an exponential distribution, which is termed a log Poisson process. We shall derive some approximate properties of this process.

To begin, we note that a log Poisson process can be expressed as $\ln(T_{k+1}) - \ln(T_k) = -c \ln(U_k)$ (23)

where c is a constant (the expected value of $\ln(T_{k+1}) - \ln(T_k)$), and the U_k are, for different k , independent random variables which are uniformly distributed over $[0, 1]$. We make the assumption that the distribution of $\log(T_k)$ changes slowly with k so that the parameter c in Eq. (23) is small:

$$c \ll 1. \tag{24}$$

To fully define the log Poisson process, we need to specify the time of the initial event and we take T_0 to have the value of unity, so all times are measured from time 1 (we cannot take it as zero due to the properties of logarithms).

From Eq. (23) it follows that $\log(T_1) = -c \ln(U_0), \ln(T_2) = -c \ln(U_1) - c \ln(U_0)$ and generally $\ln(T_k) = -c \sum_{j=0}^{k-1} \ln(U_j)$, or equivalently

$$T_k = U_{k-1}^{-c} U_{k-2}^{-c} \dots U_0^{-c}. \tag{25}$$

Thus

$$\Delta T_k \equiv T_{k+1} - T_k = (U_k^{-c} - 1) U_{k-1}^{-c} U_{k-2}^{-c} \dots U_0^{-c} = (U_k^{-c} - 1) T_k. \tag{26}$$

To obtain an indication of the content of this process, we make two approximations to Eq. (26): (i) we approximate $(U_k^{-c} - 1)$ by $-c \log(U_k)$ which applies for $c \ll 1$; (ii) we replace T_k by its

expected value, $E[T_k] = (1 - c)^{-k} \approx \exp(ck)$. Thus

$$\Delta T_k \approx -c e^{kc} \log U_k. \tag{27}$$

Lastly, we wish to infer the distribution of time intervals not after k events, but rather, after time t . It may be shown that for the log Poisson process, the mean number of events up to time t is $\log(t)/c$. Thus to convert Eq. (5) to the time domain we replace k by $\log(t)/c$ and obtain $\Delta T(t) \approx -ct \log U$ which means the time intervals, at time t , have an exponential distribution with mean ct :

$$E[\Delta T(t)] \approx ct \quad \text{Prediction of model of Richardson et al.} \tag{28}$$

Eq. (28) has been checked by simulations and works reasonably for $c < 0.5$.

Eq. (28) is to be contrasted with the prediction of the model of the present work, which is given in Eq. (21) of Appendix B, namely $E[\Delta T(t)] \approx e^{rt}/(nr)$.

We can thus say that the log Poisson model adopted by Richardson et al. (2010) and the non-interaction model, used in the present work, both predict that mean time intervals increase with the time that has elapsed since the start of an experiment, but that the manner of increase is different.

Experimental evidence

We have subjected data from our ‘without replacement’ experiments to statistical tests, to see if they can be described by a log Poisson process. We reject a log Poisson process for our data, based on two simple analyses. Firstly, the distribution of logged time intervals ($\ln(T_{k+1}) - \ln(T_k)$) differs significantly from an exponential distribution (Anderson–Darling test, $N=495$, $p < 0.001$). Secondly, and perhaps more strikingly, we plotted the cumulative number of events (ant departures) against time, and used a non-linear fitting procedure to determine the ‘best choice’ for the parameter c in the prediction of a log Poisson process, namely: $E[T_k] = (1 - c)^{-k} \approx \exp(ck)$. Fig. 10 illustrates how ants exit the nest in our ‘without replacement’ experiments, along with the ‘best fit’ from a log Poisson process. The significant absence of a good fit contrasts very strongly with Fig. 5 in the main body of this paper, which plots data and a curve from our mathematical model.

We note that Richardson et al. (2010) pointed out that, under a log Poisson process, the survivorship function (calculated as $1 -$ cumulative distribution) of the logged time intervals and the cumulative number of exits should be linear in log scale. Thus they plotted those functions in their Figs. 3 and 4 as evidence to

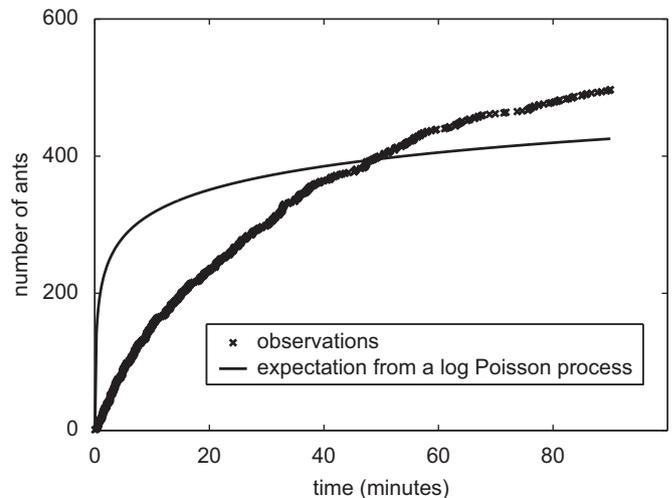


Fig. 10. Observed number of ants that leave their nest, as a function of time, and its expectation under a log Poisson process (solid curve).

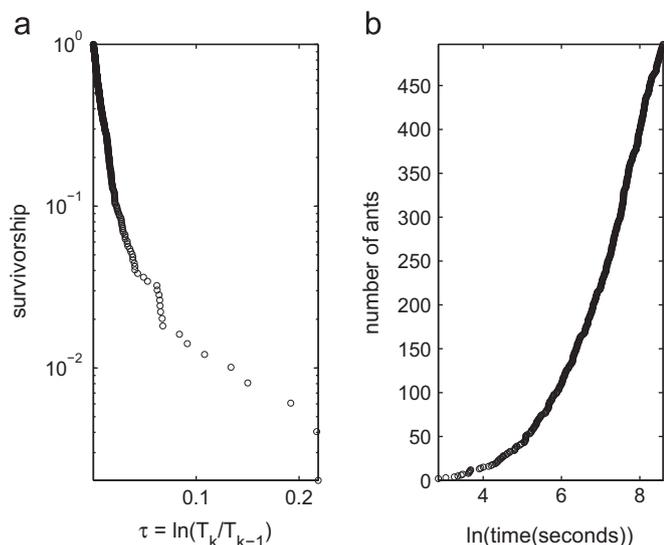


Fig. 11. (a) A plot of survivorship as a function of the difference of log times. (b) A plot of the cumulative number of ants that had left their nest against the logarithm of time.

support their model. While we conclude that, for our experiments, a log Poisson process is not a good description of the data (see above), we have plotted survivorship for our data (Fig. 11a) in the same format as Fig. 3 of Richardson et al. (2010) (i.e., survivorship plotted as a function of $\ln(T_{k+1}/T_k)$). We have also plotted the cumulative number against log time for our data (Fig. 11b) in the same format of Fig. 4 in Richardson et al. (2010). A visual inspection of these gives little reason to reject a log Poisson process, even though the analysis presented above does, indeed, clearly reject this process. Our view is that adopting a log scale might not be the most appropriate way to plot the data, since it does tend to smooth differences.

Let us, finally, consider the most important evidence adduced by Richardson et al. (2010) in favour of a log Poisson process. This is the test that the difference of the logarithm time intervals has an exponential distribution (the basic assumption underlying their analysis). In particular the result of the Anderson–Darling test presented in Table S1 of their work. In their ‘removal situation’ (equivalent to ‘without replacement’ in the present work), out of the total of 13 experiments, we observe that 5 (38%) show evidence to reject the log Poisson process at the 5% confidence level. In their non-removal situation, out of the 7 experiments, 3 (42%) show evidence to reject the log Poisson process. On the assumption that the experiments presented by Richardson et al. (2010) are independent on one another, it is possible to perform a small meta-analysis of their results. We used a weighted Z method (Whitlock, 2005) to obtain an overall p value that is associated with the null hypothesis of Richardson et al. (2010) that the distribution of exit times is a log Poisson process. This overall p value takes into account the p values from each independent experiment. The Z values (back-calculated from the p values) were weighted by number of exits from the nest. We found that both in the removal situation of Richardson et al. (2010) and in their non-removal situation, there was significant evidence to reject the null hypothesis of a log Poisson process (in both cases, $p < 0.001$).

Overall, we conclude that in our experiments, there is very strong statistical evidence to reject a log Poisson process. Additionally, on the basis of a limited meta-analysis, we find

some statistical evidence to reject the log Poisson process in the experiments of Richardson et al. (2010).

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