Group dynamics and record signals in the ant *Temnothorax albipennis*

T. O. Richardson¹,²,*, K. Christensen³,⁴, N. R. Franks², H. J. Jensen³,⁵ and A. B. Sendova-Franks¹

¹Department of Mathematics and Statistics, BIT, University of the West of England, Coldharbour Lane, Bristol BS16 1QY, UK
²School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK
³Institute for Mathematical Sciences, Imperial College London, 53 Prince’s Gate, Exhibition Road, South Kensington Campus, London SW7 2PG, UK
⁴Blackett Laboratory, Department of Physics, and ⁵Department of Mathematics, Imperial College London, Prince Consort Road, South Kensington Campus, London SW7 2AZ, UK

Many purely physical complex systems, in which there are both stochasticity and local interactions between the components, exhibit record dynamics. The temporal statistics of record dynamics is a Poisson process operating on a logarithmic rather than a linear time scale (i.e. a log-Poisson process). Record dynamics often drive substantial changes in complex systems when new high water marks in partially stochastic processes trigger new events. Social insect colonies are exemplary complex biological systems in which many of the local interactions of the components have been moulded by natural selection for the common good. Here, we combine experimental manipulation of ant colony demography with modelling to test the hypothesis that social interactions are the mechanism underlying the record dynamics. We found that compared with the control, log-Poisson statistics were disrupted in colonies in which the pattern of interactions was modified by the removal of the brood, and disappeared completely in ‘callow’ colonies composed entirely of very young workers from the same age cohort. We conclude that a subtle interplay between the demography of the society and the pattern of the interactions between the ants is crucial for the emergence of record dynamics. This could help identify what makes an ant colony a cohesive society.

**Keywords:** social insects; aggregation; Poisson process; log-Poisson process; glassy behaviour; record dynamics

1. INTRODUCTION

There may be safety in numbers [1], so for many social animals, individuals are more likely to remain in a group the larger it is. Hence, when deciding whether to leave the safety afforded by the group, individuals may often take the size of the group into account [2–4].

Social insect colonies occasionally undertake emigrations in which the colony leaves the current nest and moves to a new one [5,6]. When the old nest is rendered uninhabitable and a new nest site is not immediately available, many species of ant form a temporary aggregation in which the ants cluster together in the open [7] or under a temporary shelter [8]. Experiments on temporary aggregation rarely include brood, which provide an attractive stimulus to adults [9], often use a small subset of a much larger colony [7,10,11] and tend to focus on individuals drawn from a single

¹Author for correspondence (tom.richardson@bristol.ac.uk).


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dominance interactions [20, 21], previous experience and spatial location [22].

In the context of a nest site in which queen and brood are present, it would be surprising if the probability of leaving increases when the number of ants remaining in the nest decreases. This scenario could lead to a positive-feedback ‘trap’, in which the loss of each nest-leaver results in an increased probability of those remaining also leaving. Indeed, recently Richardson et al. [23] showed that when ants are experimentally prevented from returning to the nest, the absolute rate at which those remaining leave the nest decreases rapidly over time (see also Nouvellet et al. [24]). In T. albipennis, the event rate shows the same qualitative decrease when ants are not removed and events are defined as the first exit of each individual (Richardson et al. 2010). Unlike classical relaxation processes, such as radioactive decay characterized by a constant rate, the event rate is proportional to the inverse of time. The log rather than the linear waiting times between exits are exponentially distributed, and the cumulative number of exits increases linearly in log rather than linear time (Richardson et al. 2010). Therefore, the temporal statistics of ant nest exits is compatible with a Poisson process in log rather than linear time. Such log-Poisson characteristics in turn suggest record dynamics [25, 26].

Complex systems in which events are governed by record dynamics exhibit rapidly, and crucially non-exponentially, declining event rates (the rates are proportional to the inverse of time, hence events accumulate at a constant rate in logarithmic time). Further, such systems always include strong interactions between the component parts. Record dynamics have been shown to govern rapidly declining event rates in a diverse variety of non-equilibrium systems, for example declining extinction rates [27–29], the ‘tangled nature’ model of macroevolution [25, 30], fluctuating commodity prices [31], type-II superconductors [32], colloidal gels [33] and relaxation of the angle of repose in vibrated sandpiles [34].

Here, we use experimental manipulations of colony structure in combination with modelling to investigate the mechanisms underlying the log-Poisson characteristics of nest exits when ants are experimentally prevented from returning home (Richardson et al. 2010). Our experiments compare (i) control colonies where worker and brood demographies have not been manipulated with (ii) ‘no-brood’ colonies where worker demography is not manipulated but the brood has been removed and (iii) colonies that have a full brood complement but all the workers belong to the same age-cohort of very young workers. Both worker developmental stage and experience influence, and are influenced, by social interactions. Hence, the motivation for this manipulation was to check whether a narrower distribution of probabilities for performing some action could still reproduce the log-Poisson statistics found in unmanipulated colonies.

2.1. Material and methods

Twenty-five T. albipennis ant colonies were collected on 3 May 2008 in Dorset, UK, and housed in 50 \times 35 \times 1 mm microscope-slide nests (figure 1) with food and water provided ad libitum. All colonies had a single queen that showed normal behaviour for a fertilized queen, for example a strong tendency to take up a central position within the colony.

Sixty-four hours prior to the beginning of the period when ants were removed as they left the nest, each colony was stimulated to emigrate to a new nest by removing the roof of their original nest. During this ‘settling-in’ period, no food or water was provided to the colonies, although they were allowed access to an exploration arena (100 \times 100 mm), which was accessible via a tube attached to the front of the nest (figure 1). During the period when ants were removed as they left the nest, the exploration arena was disconnected. Then, every time an ant walked to the glass tip of the access tube, its motion was detected by the high-resolution webcam (Logitech QC deluxe) positioned immediately above (figure 1). This webcam was attached to a PC running automated motion detection software, thus sensing the exit of the ant. When an ant was detected leaving the nest, the computer opened a valve, releasing a short (0.2 s) burst of pressurized air through the inner tube, hitting the ant from the rear, and resulting in the ant being blown out of the access tube, into a collection dish.
We tested the exit dynamics of *T. albipennis* ant colonies under the following three experimental conditions. Note, all colony-size statistics were collected in a census immediately prior to the commencement of removal of workers as they left the nest.

2.1.1. Control. Nine unmanipulated colonies with brood present (median $N$ adults = 90, inter-quartile range (IQR) = 34; median $N$ brood = 127, IQR = 111.8).

2.1.2. No-brood treatment. Eight unmanipulated colonies with all brood removed (median $N$ adults = 118, IQR = 24; median $N$ brood = 0.5, IQR = 4.8). The brood was removed during the enforced emigration into the experimental nest, that is 64 h prior to commencement of experimental ant removal. In some colonies, the queen laid a few eggs after the removal of the brood, hence the median $N$ brood is non-zero.

2.1.3. Callows treatment. Eight callow colonies were constructed (median $N$ adults = 101, IQR = 67, median $N$ brood = 77, IQR = 45.5) in the following way. The queen plus a retinue of 10 adults were removed from each of eight unmanipulated colonies, thus creating eight ‘proto-colonies’. Then, the 10 adult workers from each proto-colony were marked using Pactra paint. These adult workers were used to perform the crucial task of helping the late-stage pupae eclose into callows, after which the adult workers were removed. We then collected brood items from 20 donor colonies, and sorted them according to their developmental stage (eggs, larvae, pre-pupae and pupae). Each proto-colony received a complement of brood containing equal proportions of eggs, larvae and pupae. We aimed to ensure there were equal numbers of workers and brood in each colony. The modal length of time from the point at which the majority of the pupae had eclosed, until the emigration into the experimental nest, was 12 days. Newly eclosed callows are extremely sluggish, hence the delay to allow time for them to acquire some mobility. Although not all the late-stage pupae eclosed at exactly the same time, the variation was relatively low, with the delay between the first and last eclosions of approximately 2 days.

2.2. Results

In the control, and to a lesser extent also in the no-brood colonies, the mean of the cumulative number of exits, $N(t)$, divided by the starting colony size, $n_{t=1}$ grows at a constant rate over four orders of logarithmic time; hence, the proportion remaining in the nest decreases, such that

$$1 - \frac{N(t)}{n_{t=1}} \approx \log_{10} t$$

as in a log-Poisson process (figure 2a). However, in the callow colonies, the proportion of the original colony remaining declines exponentially in linear time (figure 2b), as

$$1 - \frac{N(t)}{n_{t=1}} \approx e^{-At},$$

which is the expectation from a homogeneous Poisson process, such as radioactive decay.

Under all experimental conditions, the waiting times between exits increased disproportionately through time (figure 2). As expected (Richardson et al. 2010), in the control colonies, the instantaneous exit rate, given by the reciprocal of the waiting time between any two exits, $r_k = (T_k - T_{k-1})^{-1}$, fell off rapidly over time, like $P(r_k = t) \propto t^{-\beta}$. Furthermore, the size of the colony relative to its size at the beginning of the removal, $(1 - N(t)/n_{t=1})$, is a better predictor of the per capita instantaneous rate, $r_k/n_t$, than the absolute number of ants in the nest. The per capita instantaneous rate corrects for any finite-size effect, that is, it corrects for the decline of the absolute rate, $r_k$, that occurs simply due to there being fewer and fewer ants ‘available’ to leave the nest.

We found social inhibition under both control and no-brood conditions, that is, $r_k/n_t$ significantly decreased as the proportion of the original colony remaining fell (figure 3, top row). If the coefficient $m$ in the regression, $\log_{10}(r_k/n_t) \sim m^*(1 - N(t)/n_{t=1})$ is negative, this indicates social amplification, that is, the smaller the aggregate, the higher the exit rate and hence the shorter the residence times of those remaining. However, we found $m > 0$, so the smaller the aggregate, the lower the exit rate and hence the longer the residence times, which we term social
inhibition. The rate $r_j/n_j$ decreased significantly more rapidly in the controls compared with the no-brood colonies (table 1). So, the unmanipulated colonies showed a greater decrease in the per capita exit rate as a function of the proportion remaining than did the no-brood colonies. We again found a qualitatively different pattern in the callow colonies, in which the per capita exit rate was not a function of the proportion of the original colony remaining, that is, the coefficient $m$ in the regression $\log_{10} (r_j/n_j) \sim m(1 - N(t)/n_{o-1})$ was not significantly different from zero (figure 3, top row; table 1; electronic supplementary material, figure S4). In other words, when colonies were constructed so as to minimize the variation in the ants’ exit probabilities, the per capita exit rate was stationary, and thus the absolute exit rate was dependent only upon the finite number of ants in the nest.

Both the control and no-brood colonies showed a power-law relationship between per capita exit rate and time, that is, $\log_{10}(r_j/n_j) \sim -\beta \log_{10} t$, hence $r_j/n_j \propto t^{-\beta}$ (figure 3, row 2; table 1; electronic supplementary material, figure S3). However, as the callow colonies showed a qualitatively different decrease in the event rate that was not well described by linear regressions of the form $\log_{10}(r_j/n_j) \sim -\beta \log_{10} t$ (figure 3, row 2; table 1; electronic supplementary material, figure S3). We did not include these colonies in statistical comparisons of $\beta$. The controls had a significantly greater $<\beta>$ than the no-brood colonies (table 2), that is, the waiting time between exits increases more rapidly when the brood is present, compared with when the brood is absent.

For the controls and to a lesser extent also in colonies without brood, after an initial transient, the ensemble average of the variance : mean ratio, $<\text{VMR}>$ is fairly constant over logarithmic time (figure 3, row 3). A Poisson process has the property of equivalence of mean and variance ($\sigma^2$) of the accumulated number of events, that is, the VMR is equal to one, and does not vary over time. If the event rate is only proportional to a Poisson process, the variance and mean will not necessarily be equal, but the VMR will still be constant in time [23]. Hence, for both the control and no-brood colonies, the occurrence of exits is proportional to a log-Poisson variable. However, the same cannot be said for callow colonies, in which the $<\text{VMR}>$ increases rapidly over time.

In a Poisson process, the average waiting time is fixed, so the ratio $X = (T_k - T_{k-1})/T_{k-1}$ decreases rapidly over time. However, since in a log-Poisson process $X$ is stationary [23], the waiting time increases at a constant rate, $T_k - T_{k-1} \propto t$. Indeed, under control conditions, $<X>$ is rather constant over approximately one order of magnitude (figure 3, row 4). To a lesser extent this is also the case for the no-brood colonies, and the rate at which $<T_k - T_{k-1}>$ increases in log time is significantly slower than in the control (table 2). However, for the callow colonies, $T_k - T_{k-1}$ is stationary as in a Poisson process. That is, the coefficient $\sigma$ in the regression $\log_{10}(T_k - T_{k-1}) \sim \sigma^2 (1 - N(t)/n_{o-1})$ is not significantly different from zero (table 1) and hence the ratio $X$ should show a rapid non-exponential decay over time, that is $X \propto 1/T_{k-1}$. Indeed, in the callows, $<X>$ decreases continuously over the entire period of observation (figure 3, row 4).

In the Poisson process, the waiting time is stationary, exponentially distributed (i.e. $P(T_k - T_{k-1} > x) = e^{-\lambda x}$) and there is no correlation between successive waiting times. Similarly, in a log-Poisson process, the
logarithmic waiting times \( (\ln T_k - \ln T_{k-1} = \ln(T_k/T_{k-1}) = \tau) \) are stationary, exponentially distributed \([23]\) \( (i.e., P(\tau > z) = e^{-\lambda \tau}) \) and without temporal correlation. However, here we wish to compensate for the falling colony size by calculating the logarithmic waiting times on a \textit{per capita} basis. Indeed, control colonies have \textit{per capita} logarithmic waiting times that are stationary (electronic supplementary material, figure S5), are well fitted by the exponential distribution, \( P(\tau/n_i > x) = e^{-\lambda x} \) (figure 4), and are not temporally correlated (electronic supplementary material, figure S1). However, in the callow colonies,
\[
\log_{10}(r_{k}/n_{k}) \sim m \left(1 - N(t)/n_{t-1}\right)
\]

Table 1. Comparing the coefficients \(m\), \(\beta\) and \(a\) in the controls against those in the no-brood and callow colonies. We used GLMs of the form, \(\text{response} \sim \text{colony} + \text{experiment} + \text{covariate} + \text{experiment} \times \text{covariate}\), where \(\times\) denotes interaction. This interaction term determines whether the coefficients (i.e. \(m\), \(\beta\) or \(a\)) are significantly different in the no-brood and callow colonies, compared with the control. The standardized residuals from the above GLMs were slightly more right skewed than a GLMs of the same form as in Table 1 were used. Both the \(\text{per capita}\) rate and the waiting times were significantly different in the control versus no-brood colonies.

<table>
<thead>
<tr>
<th>response</th>
<th>GLM term</th>
<th>(R^2) (adj)</th>
<th>d.f.</th>
<th>(F)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\log_{10}(r_{k}/n_{k}))</td>
<td>colony</td>
<td>36.4</td>
<td>15,855</td>
<td>15.46</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>experiment</td>
<td></td>
<td>32.97</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(1 - N(t)/n_{t-1})</td>
<td>1,855</td>
<td>294.62</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(\text{experiment} \times (1 - N(t)/n_{t-1}))</td>
<td>1,855</td>
<td>41.62</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>(\log_{10}(r_{k}/n_{k}))</td>
<td>colony</td>
<td>49.0</td>
<td>15,855</td>
<td>5.25</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>experiment</td>
<td></td>
<td>6.31</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(\log_{10} T_{k})</td>
<td>1,855</td>
<td>582.50</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(\text{experiment} \times \log_{10} T_{k})</td>
<td>1,855</td>
<td>11.18</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>(\log_{10}(T_{k} - T_{k-1}))</td>
<td>colony</td>
<td>53.2</td>
<td>15,838</td>
<td>5.77</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>experiment</td>
<td></td>
<td>22.13</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(\log_{10} T_{k-1})</td>
<td>1,838</td>
<td>645.14</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(\text{experiment} \times \log_{10} T_{k-1})</td>
<td>1,838</td>
<td>30.53</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>

\(\pi/n_{t}\) are considerably more right-skewed, non-stationary and temporally correlated, while in the no-brood colonies these metrics are again intermediate between Poisson and log-Poisson.

3. MODELLING

A natural initial step in modelling the decision to leave the nest is to construct a null model that assumes the exit decisions are purely probabilistic. Then, the nest-leaving decision is not made in response to extrinsic stimuli. This scenario is essentially an example of parallel dice-rolling by independent Poissonian agents; in every time step, every ant makes a probabilistic decision to leave or to stay based entirely on its own instantaneous exit probability. Thus, each ant’s decision is completely independent of the actions of its nestmates. If all the ants have the same exit probability and if the number of ants is very large, the number remaining in the nest will decrease exponentially over time. The classic example of this is radioactive decay, which is essentially a homogeneous Poisson process. The specific distribution of the individual probabilities of performing some action is crucial in determining how these individual waiting times are distributed across the population. For example, a fixed population of homogeneous Poissonian agents (one in which there is no reduction in the population over time, nor any variation in the probability of performing an action) will produce a distribution of individual mean waiting times that follows an exponential. However, if the agents are heterogeneous, then the distribution of individual mean waiting times can be more skewed than exponential, and potentially even scale-free [39]. Similarly in an ant colony, the components—the ants—are not homogeneous. For example in *T. albipennis* [14] and also in *Pogonomyrmex badius* [40], the more corpulent the ant, the lower its instantaneous probability of leaving. So within the ant society there is a *distribution* of individual exit probabilities. We tested whether the log-Poisson statistics could be reproduced by appropriately parametrizing the exit probability distribution in the null model. From an existing dataset [14], we calculated the empirical distribution of individual exit rates and used this as the source of heterogeneity in the null model. If this model reproduced the non-exponential decay during ant removal, then we could conclude...
that exit decisions are influenced only by the intrinsic tendency of the individual to leave the nest, and that social interactions, including the non-return of external workers, have no effect on the individual exit decisions.

The mechanism described above is a natural null model because it is so simple, and also because the Poisson statistics it produces are well studied. However, the temporal statistics of a Poisson process operating on a logarithmic time scale, that is ‘log-Poisson’ statistics, characterizing the nest exit dynamics in unmanipulated colonies (Richardson et al. 2010), suggest an alternative mechanism of record dynamics (25,26) derived from the statistical mechanics of complex systems. In this scenario, individual ants are triggered when a fluctuating variable, the ‘record signal’, reaches a never-before-seen (record) level. If the record signal is uncorrelated in time, the increment between successive record values will rapidly decrease, and the interval between successive records will rapidly increase. Clearly, there are strong interactions between ants [41–43], and the interaction rate—measured by the collective activity—fluctuates non-periodically over time [44–46].

3.1. Material and methods

3.1.1. The null model. Here we assume that within each colony there is a distribution of intrinsic decay probabilities, and that a ‘decay’ event is equivalent to an exit. Then, the declining exit rate will be because of the diminishing number of ants, but also because on average the more ‘unstable’ ants leave the nest before those with lower exit probabilities. This model is essentially a non-homogeneous Poisson process that incorporates a finite-size effect.

From a previous dataset in which individually marked T. albipennis ants were allowed to freely leave and return to the nest [14], we obtained the times that each ant left the nest over a 5 day period. From this, for each ant, we calculated the mean waiting time between successive exits. It should be emphasized that here the waiting time refers to the time elapsed between successive exits by the same ant. We then took the inverse of each ant’s mean waiting time, giving the mean exit rate for each ant. Thus, we obtained the distribution of the instantaneous decay probabilities (exit rates) within each of seven colonies. These rate distributions were well fitted by a log-logistic distribution. A variable that follows a log-logistic distribution is one in which the logarithm of the variable is logistically distributed (electronic supplementary material, figure S2). At the start of each run of the simulation, every ‘ant’ in the colony was assigned an individual exit rate from the distribution. In every time step, each ant decided whether to leave the nest by comparing its exit probability to a uniformly distributed random number between 0 and 1. If the ant’s exit probability was greater than this random number, the ant leaves the nest. We recorded the same statistics for these simulated ants, as for the real ants. For comparison, we also ran the model without any individual variation, by assigning the mean instantaneous decay probability from the log-logistic distribution to all the ants, which is a homogeneous Poisson process.

3.1.2. The record dynamics model. Here we present an alternative phenomenological explanation for the production of the observed log-Poisson statistics. We assume that an event occurs (an ant leaves the nest) whenever a fluctuating record signal hits a new maximum (or minimum) value. Then, the temporal stochasticity of the signal itself is responsible for regulating the exit rate, rather than the variation across individuals, as in the null model. Time series created in this manner are known as ‘white noise’. As each instance of the signal is randomly chosen, the value of the signal at time \( T_k \) is not correlated with that at \( T_{k+1} \). If this number is the largest observed since the observation began, it is a new record (figure 5). Then, the rate at which new record events accrue is constant in logarithmic time, irrespective of the distribution from which the signal values are drawn [47–49].

It should be emphasized that the above statistical mechanism is a macroscopic summary of the processes occurring at the microscopic level. It does not describe the specific microscopic processes. However, record dynamics have been described in a wide variety of complex systems, all of which differ substantially in the...
were non-stationary (figure 6), accumulate at a constant rate in logarithmic time. Specifically, the exits did not of mean individual waiting times, we did not obtain exit rates was parameterized from the ants distribution by the callow colonies. Model qualitatively reproduces the statistics produced the ratio

\[ \frac{N_{t}}{T_{k}} \]

underlying microscopic details \([25,30,31,33,49]\), so knowledge of the precise microscopic details, though desirable, is not strictly necessary. However, in such complex systems, the microscopic processes always involve strong short-range interactions between the components. In social insect colonies, there are obviously strong interactions between the individual components \([42,45,50,51]\). However, biological systems of the sort we explore here are considerably more complex than the purely physical condensed-matter systems, and consequently the exact mechanisms responsible for regulating the interactions between the component parts are relatively less well understood. Thus, we do not attempt to reproduce log-Poisson statistics via a model that includes interactions between the components.

3.2. Results

When there was no individual variation in the exit rates, or rather, when the exits were organized by a homogeneous Poisson process operating on a finite population, we found typical Poisson statistics. Specifically, the number of events did not accumulate at a constant rate in logarithmic time (figure 6a) because the mean waiting time, \( T_{k} \), was fixed, causing the ratio \( X \) to decrease rapidly (figure 6c). Thus, this model qualitatively reproduces the statistics produced by the callow colonies.

Similarly, when the distribution of individual mean exit rates was parameterized from the ants distribution of mean individual waiting times, we did not obtain log-Poisson statistics. Specifically, the exits did not accumulate at a constant rate in logarithmic time (figure 6b), and both the VMR for \( N(t) \) and the ratio \( X \) were non-stationary (figure 6b,d).

We do not give further evidence of the log-Poisson nature of the event rate statistics generated by the record dynamics model as it has been demonstrated elsewhere \([25,47–49]\) that a fluctuating record signal produces log-Poisson statistics.

4. DISCUSSION

If social amplification of residence times were operating in complete ant colonies inhabiting established nests, the \( \text{per capita} \) exit rate would increase as the colony size decreased. However, in contrast to cockroach aggregations \([8,11,13]\), or temporary aggregations in other ants \([4,7,9,10,12]\), the more \( T. albipennis \) foragers that leave a nest (where there is brood present), the less likely are the remaining ants to leave. Intuitively, if colony size is falling, it is probably a bad strategy to leave the safety of an established nest because the declining colony size may indicate the external conditions are currently unfavourable. Furthermore, as the number of ants in the nest declines, the relative value of each individual remaining in the nest increases, hence the possible consequences of leaving it become more severe. Although the fluctuation of colony size may indeed be related to individual decisions to leave or to stay, the effect of fluctuating colony size on amplification or inhibition of residence times is also highly pertinent to the cohesion of the entire colony. For example, if the residence times of the individuals at a nest were subject to social amplification \([11]\), the entire colony could become trapped in a positive-feedback cycle, in which the absence of nest-leavers that for whatever reason have not returned increases the probability that those remaining also leave. As nest sites may be a limiting resource \([52]\), social amplification at nest sites would be rather maladaptive. By contrast, in the context of temporary aggregations, an increased propensity to leave a declining group of conspecifics may be a reasonable strategy because a declining aggregation affords less protection, and may indicate an alternative aggregation site may have been found.

In the callow and no-brood colonies, ant exits accumulated at a markedly lower rate than in the controls (figure 2a). In the callows, this is most likely due to lower activity because overall activity rates increase with age \([53]\). In the no-brood colonies, the absence of hungry brood may have removed stimuli that trigger foraging and thus contributed to the observed reduction in the overall exit rate.

It is clear from the null model that individual variation is not, by itself, sufficient to reproduce event rates that decelerate according to record dynamics. Merely assigning individual nest-leaving rates (derived from previous empirical observations of unimpeded nest leaving) to the non-interacting ‘ants’ did not reproduce the log-Poisson statistics (figure 6b,d). Therefore, the scenario in which the decision to leave the nest is a purely probabilistic consequence of the individual exit rate is inaccurate.

The log-Poisson character of the \( \text{per capita} \) statistics in the control colonies demonstrates that the log-Poisson deceleration is not merely an artefact of the declining colony size. Colonies composed entirely of a
single age-cohort of very young and inexperienced callows differed qualitatively from the log-Poisson statistics described in the control and, to a lesser extent, in the no-brood conditions. In the callow colonies, the per capita exit rate was not a function of the number in the nest (electronic supplementary material, figure S4) or the time elapsed (electronic supplementary material, figure S3), events did not accumulate at a constant rate in logarithmic time (figure 2) and the per capita logarithmic waiting times were not exponentially distributed (figure 4) or stationary (electronic supplementary material, figure S5). Instead of the ‘normal’ log-Poisson temporal statistics found in unmanipulated colonies, the timing of nest exits in callow colonies was more like a homogeneous Poisson process (figure 6a,c). So, when the society lacks variation in age and task experience among the component parts, it displays none of the interesting dynamics exhibited by systems in which events are regulated by record dynamics.

The importance of the structuring of social interactions is supported further by the result that no-brood colonies show statistics that are intermediate between log Poisson and Poisson. We hypothesized that the removal of the brood would change the spatial distribution of the interactions between the workers within the colony, so causing a loss of log-Poisson temporal statistics. Indeed, the loss of the log-Poisson behaviour suggests that the particular pattern of ant–ant interactions mediated by the presence of brood of various developmental stages sorted into an annular structure is important for the generation of log-Poisson statistics. In summary, to explain the production of the log-Poisson statistics, it is necessary but not sufficient to invoke only the natural variation in the ants’ nest-leaving tendencies or the nature of the interactions between the workers.

So what then would be sufficient? It is reasonable to suppose that decreasing the density of ants within the nest might cause a reduction in the rate at which ants
encounter another. Then, if individual exit probabilities were downregulated (i.e. inhibited) as the encounter rate decreases, the exit rate would decline more rapidly than if there were no density effects. Clearly, in order to construct an individual-level model that reproduces the collective log-Poisson statistics, we will need a much more detailed understanding of how ant–ant interactions within the nest influence subsequent decisions to leave it.

Our results demonstrate how analysing the behaviour of social insect colonies using the tools of record dynamics brings new insights in their organization and opens up the prospect of developing a new theory to help identify what makes an ant colony a cohesive system. Substantial and irreversible changes in complex systems can originate from the combination of temporal stochasticity and strong interactions between the components. In the physical sciences there is strong evidence for the role of such record dynamics in a wide range of condensed-matter systems. The application of record dynamics to complex systems in biology promises to be fruitful because both stochasticity and agent–agent interactions are ubiquitous at all levels of biological organization.

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REFERENCES


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