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Letter to Editor

Comment on P. Nouvellet, J.P. Bacon, D. Waxman, “Testing the level of ant activity associated with quorum sensing: An empirical approach leading to the establishment and test of a null-model”

Nouvellet et al. (2010) report the results from two experiments with the Pharaoh’s ant, *Monomorium pharaonis* and test a null model. Their experimental set-up consists of a nest in an arena with a Γ-shaped object (like a hangman’s scaffold) placed close to the nest. The distal end of the Γ-object is vertical and slippery so that ants that reach it fall off. In the first experiment, ‘with replacement’, ants fall directly back into the arena. In the second experiment, ‘without replacement’, a container is placed under the far end of the Γ-object so that ants that have fallen from it are unable to go back to the arena. Each of the two experiments was repeated with 4 different ant colonies and the data reported covers about 1.5 h. Their null model has two versions corresponding to the two experiments. Both versions assume that ants move independently (i.e. do not interact) and drop randomly from the scaffold. However, the second model takes into account the diminishing number of ants that have the opportunity to climb the Γ-object. There is close agreement between the results from each of the two experiments and the respective version of the null model. For the experiment ‘with replacement’, the accumulated number of ants that have dropped increases linearly with time and the time intervals between drops are exponentially distributed. This is compatible with a model of independent Poissonian agents. For the experiment ‘without replacement’, the increase in the accumulated number of ants that have dropped slows down with time, the time intervals between drops increase with time and their distribution is different from exponential. However, when the time intervals between drops are scaled by their expected values, they are well fitted by an exponential distribution. This is compatible with a model of independent Poissonian agents where their diminishing number (finite-size effect) is taken into account.

Nouvellet et al. (2010) compare and contrast their results with those in Richardson et al. (2010a). We reported the results from one experimental and one control treatment on colonies of the ant *Temnothorax albipennis* as well as a null model very similar to theirs (Richardson et al., 2010a). In the experimental treatment, we removed every ant as it exited the nest in 13 colonies over periods ranging from 2 to 200 h. In the control treatment, we recorded the times previously unseen, ‘new ants’ leave the nest in 7 colonies over a period of 60 h. We found that in both cases the event rates decreased rapidly over time. This rapid decay was compatible neither with classical exponential decay (homogeneous Poisson process) nor with a heterogeneous Poisson process. The latter null model was based on experimental results of individual ant heterogeneity and also included the effect of a declining number of ants remaining in the nest, i.e. a finite-size effect (Richardson et al., 2010a). We tested the hypothesis that such exits follow record dynamics (Sibani and Littlewood, 1993). In record dynamics, events are triggered when a fluctuating, record, signal exceeds a historical ‘high water mark’. While exponential decay is characterised by Poisson statistics in linear time, record dynamics are characterised by Poisson statistics in logarithmic time (Sibani and Littlewood, 1993; Anderson et al., 2004). Our results demonstrate that under both experimental conditions the process of ants exiting their nests is compatible with a record dynamics process (Richardson et al., 2010a). Systems exhibiting record dynamics are charactrerised by strong interactions, non-stationarity and non-exponential deceleration over time.

Now we will comment specifically on that part of the paper by Nouvellet et al. (2010) where they compare and contrast their result that ants do not interact with our result that ants do interact.

(1) Nouvellet et al. (2010) state that their experiments are comparable to our experiments, see e.g. section 8, 1st paragraph.

We strongly disagree. We measure the exit times of all ants leaving the nest. Nouvellet et al. (2010) measure the time ants fall from the tip of the scaffold placed in an arena. Hence, the latter study concerns the activity of ants that have already left their nest and subsequently happen to reach the particular point in the arena with the Γ-shaped object, choose to climb it, reach its tip and fall from it. The ants in our experiments and the ants in the experiments by Nouvellet et al. (2010) make their decisions in two different environments: inside and outside the nest, respectively. These two environments differ according to both direct and indirect ant–ant interactions. For example, the colony inside the nest has a resilient social and spatial structure (Sendova-Franks and Franks, 1994). This affects direct interactions. The nest interior is associated with particular diffusion patterns of airborne pheromones and gases (Cox and Blanchard, 2000). This affects indirect interactions. For these reasons alone our experiments are not comparable. Furthermore, the set-up in the experiments by Nouvellet et al. (2010) is artificial because they have not taken into account indirect interactions outside the nest. Like many other ant species, Pharaoh’s ants rely heavily on indirect interactions via pheromone trails outside the nest and lay these trails during exploration (Jackson et al., 2006). Hence ants could also be using the density of pheromone trails to assess local density. These trails last for several days, so over the course of the experiments

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described (approximately 100 min) the density information from this source would not be expected to change. Therefore, one might predict that the two treatments would not differ according to indirect interactions.

(2) Nouvellet et al. (2010) attempt to discredit our conclusion of log-Poisson statistics for exit time in our experiments, see e.g. section 9, 4th paragraph and Appendix C. They argue that they are not convinced by our conclusions because:

(2a) Nouvellet et al. (2010) show that the data from their first, 'without replancement' experiment do not follow a log-Poission process by noting that the number of "ants leaving their nest" (falling from the Γ-shaped object) is not what is expected from a log-Poisson process (Fig. 10).

We agree that the data from the experiments by Nouvellet et al. (2010) are not compatible with a log-Poisson process. However, we strongly disagree with their assumption that our experiments are comparable with their experiments. Hence their argument that because they do not find compatibility with a log-Poisson process, we should not find it either, is invalid.

(2b) Nouvellet et al. (2010) compare our Fig. 3 (Richardson et al., 2010a) with their Fig. 11a (Survivorship versus $\ln(T_k/T_{k-1})$) and our Fig. 4 (Richardson et al., 2010a) with their Fig. 11b (No. ants leaving versus ln(t)). Their argument is that by visual inspection the compared figures seem similar. Hence, they are arguing that even for data they have shown to follow a Poisson process, just by applying our plots, they could get a visual impression of a log-Poisson process, indicating this has happened in our case.

We strongly disagree. First, Fig. 11a was not plotted correctly in the online version of the paper. The y-axis had to be logged and the x-axis inverted. Even after these corrections were made in the published version of the paper, the survivorship plot is far from a straight line (as it must be for a log-Poisson process) and based on only a third of the scale for $\ln(T_k/T_{k-1})$ in our Fig. 3 (Richardson et al., 2010a). Second, Fig. 11b uses ln (natural logarithm) rather than logarithm base 10 as we do in Fig. 4 (Richardson et al., 2010a). This makes the region with a supposedly straight line in Fig. 11b appear larger. A close inspection, however, reveals that it is only 0.2–0.4 of an order of magnitude compared to the 3 orders of magnitude in our Fig. 4 (Richardson et al., 2010a). Neither of the plots in Fig. 11 provides evidence for a log-Poisson process. Hence, the argument by Nouvellet et al. (2010) that their data, which follows a Poisson process, looks similar to our data when plotted as survivorship versus $\ln(T_k/T_{k-1})$ and number of ants leaving versus $\ln(t)$ is invalid.

(2c) Nouvellet et al. (2010) examine our results in Table S1 (Richardson et al., 2010a) and conclude that 5 of the 13 colonies which underwent the treatment condition (38%) and 3 of the 7 colonies that underwent the control condition (42%) show evidence to reject the log-Poisson process (Appendix C).

We strongly disagree. The Anderson–Darling test we used does not compare our data for the survivorship of the log times in Fig. 3 and Table S1 (Richardson et al., 2010a) with an exponential distribution. Instead it tests whether the residuals from the linear regression models fitted to the data in Fig. 3 are compatible with a normal distribution. Not only were any deviations very small in the majority of cases but it is well known that linear regression is robust to small deviations from normality (Kleinbaum et al., 2008, p. 48). Such deviations would disappear had we used the much less sensitive Kolmogorov–Smirnov test applied several times by Nouvellet et al. (2010) in their study. Hence their argument that our statistical results reported in Table S1 show evidence to reject the log-Poisson process is invalid.

(2d) Nouvellet et al. (2010) also carry out a meta-analysis of all p-values from the Anderson–Darling tests for the 13 treatment and the 7 control colonies separately, using the weighted Z-method (Whitlock, 2005). They conclude that the overall p-value associated with the null hypothesis that the distribution of exit times is log-Poisson process is $p<0.001$ in both cases (Appendix C).

We strongly disagree. First, as pointed out above, these p-values relate to the compatibility of residuals from linear regression models with the normal distribution. Second, the meta-analysis tests the null hypothesis that all p-values should be uniformly distributed between 0 and 1 rather than give an overall p-value (Whitlock, 2005). To illustrate this point we carried out meta-analysis tests on data from Nouvellet et al. (2010). This is not to intimate that we doubt their claim that the results from their own study are compatible with a Poisson process. Rather we wish to demonstrate that the meta-analysis is a heterogeneity test because the null hypothesis could be rejected even when the p-values of individual tests are greater than 0.05 as in Nouvellet et al. (2010). When the weighted Z-method for meta-analysis (Whitlock, 2005) is applied to the p-values for the 4 Anderson–Darling tests for their first experiment, 'with replacement' (Tables 1 and 2), the p-value is less than 0.05. We used the p-value for the first colony $p=0.113$ weighted by the number of observations, $N=585$ (section 3, third paragraph, Nouvellet et al., 2010) and the p-values 0.1, 0.08 and 0.4 weighted by the respective estimated number of the ants in the nesting area, Ne, namely 500, 300 and 100 (Table 2, Nouvellet et al., 2010). The result for such a weighted Z-method is $Z_w=-2.16$, $p=0.015$, one-tailed (Whitlock, 2005). We also applied Stouffer's method: $Z_s=-2.08$, $p=0.019$, one-tailed and Fisher's combined probability test: $\chi^2_F=15.85$, $df=8$, $p<0.05$ (Whitlock, 2005). In other words, if we take the p-value in each of these three methods to represent an overall p-value, we would reject the null hypothesis that the data for the first 'with replacement' experiment in Nouvellet et al. (2010) is compatible with a Poisson process. This would not make sense because none of the individual p-values is less than 0.05. However, if we correctly interpret the meta-analysis as a test of heterogeneity, the results are not surprising because the p-values for the Anderson–Darling test for the first experiment, 'with replacement' in Nouvellet et al. (2010) are heterogeneous. The meta-analysis is sensitive to this heterogeneity even though it involves only 4 colonies compared to our sample sizes of 13 and 7 colonies. For this reason, their meta-analysis of our data is misplaced and their argument that our statistical results reported in Table S1 show evidence to reject the log-Poisson process is invalid.

Finally, we note that data from new experiments and analyses based on per-capita statistics, which thus control for finite-size effects (Richardson et al., 2010b) are also consistent with record dynamics, that is, log-Poisson statistics. However, for colonies with a manipulated demographic structure, and hence by proxy also manipulated interaction structure, the data are consistent with Poisson, rather than log-Poisson, statistics (Richardson et al., 2010b). This is further evidence that our conclusion of record statistics originating from ant–ant interactions is sound.

In summary, the claim by Nouvellet et al. (2010) that their results are comparable to those obtained by Richardson et al. (2010a) is invalid because the experiments in the two studies were carried out in two different environments, outside and inside the nest, respectively. Ant–ant interactions in these two environments differ but also the experimental design in Nouvellet et al. (2010) does not take into account indirect ant–ant interactions. Furthermore, the plot of their data in the format of our data, even after correction, shows no evidence of log-Poisson statistics. Their meta-analysis of the p-values in our study is misguided and incorrectly applied. Our null model (Richardson et al., 2010a), which includes the finite-size effect of the declining colony size and is therefore a numerical version of the analytical null model of Nouvellet et al (2010), shows that log-Poisson statistics cannot be obtained from a heterogeneous Poisson process with a finite number of components. For all these reasons, each and every argument Nouvellet et al. (2010) make against our results is invalid. In our experiments ant exits are compatible with a log-Poisson process.

Nouvellet et al. (2010) have set up an experiment using a hangman's scaffold that minimises the ants' ability to interact with one another. They then conclude that in this regime ants do not interact. This is analogous to an ichthyologist who uses dynamite for fishing and then concludes that fish do not swim. Benjamin Franklin once said (in the Continental Congress just before signing the Declaration of Independence, 1776) "We must, indeed, all hang together, or most assuredly, we shall all hang separately." In the experiments of Nouvellet et al. (2010) the ants may indeed hang separately but their criticisms of our work simply do not hang together.

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T.O. Richardson
Department of Engineering Design and Mathematics, University of the West of England, Coldharbour Lane, Bristol BS16 1QY, UK

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

E.J.H. Robinson
Department of Biology and York Centre for Complex Systems Analysis, University of York, Heslington,York YO10 5DD, UK

K. Christensen, J.H. Jensen
Institute for Mathematical Sciences, Imperial College London, 53 Prince's Gate, Exhibition Road, South Kensington Campus, London SW7 2PG, UK

K. Christensen
Department of Physics, Blackett Laboratory, Imperial College London, Prince Consort Road, London SW7 2AZ, UK

H.J. Jensen
Department of Mathematics, Imperial College London, South Kensington Campus, London SW7 2AZ, UK

N.R Franks
School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK

A.B. Sendova-Franks*
Department of Engineering Design and Mathematics, University of the West of England, Coldharbour Lane, Bristol BS16 1QY, UK
E-mail address: ana.sendova-franks@uwe.ac.uk

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* Corresponding author.