Temperature effects on ant activity
Analysis of a mathematical model

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Abstract
It is now established that repeated interactions between individuals can give rise to a variety of spatial and temporal patterns in social insects. In this report, we study the effect of the temperature, playing the role of an external forcing, on the daily activity of an ant’s nest.

A mathematical model is developed and analyzed, first in absence of external forcing. Then the full model with a temperature dependent forcing is studied numerically. For large amplitudes and large frequencies of the forcing function, the system becomes entrained by the temperature oscillation. Finally, the model results are compared to experimental ones carried out on the field. The results are in good agreement with the data regarding timing, phase shift and asymmetry.

Keywords: collective animal behavior, ant activity, temperature, environmental variability, model analysis, Poincaré map, recurrence plot

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I. Introduction

Repeated social interactions between animals can give rise to patterns in nature (see Camazine et al. 2001). Migrating geese flying in V formation (Lissaman & Shollenberger 1970), a school of fishes that quickly spreads out and then immediately reorganizes to avoid the attacks from a predator (Sumpter 2010), or meerkats that take turn guarding when the group is feeding (Clutton-Brock et al. 1999) are just a few examples of this. The high level of organization makes it possible to describe the appearance of the group as a unit instead of a bunch of individual animals.

This field of science increased in the researchers interest during the middle of the 20th century. Based on theories from mathematics, physics and chemistry they developed models (e.g. using feedback mechanisms and the Navier-Stokes equation for fluid flow) to describe and understand how the patterns they observed are generated (see Nicolis & Prigogine 1977). Such models let us discern the basic factors that govern collective behavior and interestingly some of them turned out to be valid for many different kinds of animals and situations. Recently, some similar methodologies have also been applied to analyze human behavior in the study of modern sociology (Sumpter 2010).

Relatively simple kinds of interactions between individuals may be the origin of collective behavior, without any need to model at the individual level. For example, looking at isolated ants no rhythmical activity patterns are observed. On the other hand, the ant colony as a whole can be highly organized with periodic bursts of activity, see figure 1 (Cole 1991). This synchronization has many benefits, in particular concerning task allocation and information processing within an ant nest (Franks et al. 1990).

![Figure 1. Observations of activity (from Cole 1991). Individual ants (upper graph) do not show any periodical patterns whereas the colony (lower graph) does. One time unit is one minute.](image)

Many parameters in the environment, such as the light and the temperature cycles, have a period of about 24 hours which makes it natural that animal systems exhibit approximately the same periodicity. The most fundamental oscillation in the animal kingdom is therefore the circadian rhythm (Goldbeter 1996). On a somewhat larger time scale, changing weather conditions and seasons influence the animals and their collective behavior. Some studies have been made on this topic (see e.g. López-Olmeda, Madrid & Sánchez-Vázquez 2006, Moore & Rankin 1993, North 1993, Porter 1987) but still there is much to investigate.
II. Observations

The starting point for this report is temperature and ant activity data from Noda et al. (2006). They studied the leaf cutter ant, *Atta insularis*, endemic to Cuba, by installing an infrared sensor at one of the exits of the nests measuring the number of passing ants. The result of their observation is shown in figure 2 where the measured activity and temperature is plotted\(^1\). As seen in the figure there is a phase shift between activity and temperature, so that when the temperature reaches its maximum value during the day, the activity is at its lowest level. The change of activity is asymmetric in the sense that the increase of activity goes much faster than the decrease.

\[\text{Figure 2. Recorded ant activity (dashed line) and temperature (solid line) for 7 days. Data from Altshuler (2012).}\]

In this report, a model for collective ant activity is analyzed. The model incorporates a function describing the variability of the temperature. The analysis in section IV will show how this affects the dynamics of the system. The temperature part can easily be changed to any other environmental forcing (e.g. a varying food source). The model is kept as simple as possible with few coefficients and analyzed from a mathematical perspective using Matlab.

III. General model

Synchronization may be the consequence of two main factors: exogenous effects (e.g. temperature and sunlight) or endogenous effects (e.g. caused by the level of hunger).

Here we develop a model for activity patterns in the colony based on the possibility for an ant to be in one out of two states, either active (*A*) or inactive (*I*). When two active ants meet, the probability that they continue to be active increases. Active ants turn into inactive ants with the rate \(k\) and inactive ants become unavailable (“dead”) with the rate \(k'\). The parameters \(k\) and \(k'\) are positive. In mathematical notation this model can be expressed as a pair of coupled

\(\text{Paragraph continues...}\)

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\(^1\)In an article by Porter & Tschinkel (1987) it is concluded that rain can cause the foraging rate of ants to decrease by circa 40%. According to Altshuler (2012) the provided data is trustworthy in this sense. During the period of measurements some interruptions occurred, perhaps caused by rain, but the provided time series are uninterrupted and no significant rain fell during the measurements.
non-linear ordinary differential equations (odes):

\[
\frac{dA}{dt} = \alpha \frac{A^2}{1+I^2} - kA
\]

(1)

\[
\frac{dI}{dt} = kA - k'I
\]

where \( \alpha \) is a scaling factor. The model is only valid for cases when \( A \) and \( I \) are not both zero. Since ants can become “dead” the total number of ants in the model is not constant.

Before focusing on the analysis of the temperature dependent model (section IV), let us first analyze the system 1.

**Analysis of the general model**

The equilibrium points are found by calculating values for \( A \) and \( I \) that give \( \frac{dA}{dt} = 0 \) and \( \frac{dI}{dt} = 0 \) simultaneously. For given values of \( k \) and \( k' \) only one equilibrium point exists:

\[
(A_{eq}, I_{eq}) = \alpha \frac{(k')^2}{k^2 + (k')^2} \left( \frac{1}{k}, \frac{1}{k'} \right)
\]

In order to study how a small perturbation \((\delta A, \delta I)\) behaves in regions close to the equilibrium point the model has to be linearized. This is done by calculating the Jacobian matrix for the system of odes and evaluate it at each equilibrium point. The eigenvalues of these matrices determine if an equilibrium point is stable or unstable and what the phase portraits will look like.

The linearization about the equilibrium point \((A_{eq}, I_{eq})\) gives

\[
\begin{pmatrix}
\frac{d(\delta A)}{dt} \\
\frac{d(\delta I)}{dt}
\end{pmatrix} =
\begin{pmatrix}
\frac{k^2 - k'^2}{k^2 + (k')^2} - k'k & -2k^2k' \\
k & -k'
\end{pmatrix}
\begin{pmatrix}
\delta A \\
\delta I
\end{pmatrix}
\]

(3)

The eigenvalues \( (\lambda) \) of this matrix are found by solving the equation

\[
\lambda^2 + \lambda \left( k' - \frac{k^2 - (k')^2}{k^2 + (k')^2} \right) + k'k = 0
\]

(4)

\[
\lambda = -\frac{p(k, k')}{2} \pm \sqrt{\left(\frac{p(k, k')}{2}\right)^2 - k'k}
\]

(5)

where \( p(k, k') = k' - \frac{k^2 - (k')^2}{k^2 + (k')^2} k \)

The eigenvalues determine the stability of the system. If both eigenvalues have negative real parts the solution is stable and vice versa. The bifurcation point is the point where the transition between unstable and stable occurs, thus when \( p(k, k') = 0 \). Solving this third order equation gives that the bifurcation point appears when the ratio between \( k \) and \( k' \) is

\[
\frac{k}{k'} = \frac{1}{3} + \left( \frac{19}{27} + \frac{\sqrt{11}}{27} \right)^{1/3} + \left( \frac{19}{27} - \frac{\sqrt{11}}{27} \right)^{1/3} \approx 1.84
\]

(6)

In figure 3 two bifurcation diagrams are shown, one for fixed values of \( k \) and one for fixed \( k' \). Table 1 gives an overview of the intervals for \( k \) corresponding to different kinds of stability when the parameter \( k' \) is fixed \((k' = 0.01)\). The regions are found using the eigenvalues from equation 5.
Figure 3. Bifurcation diagrams (Hopf bifurcations) for active and inactive ants. (A) \( k = 0.01 \) is fixed. (B) \( k' = 0.01 \) is fixed. Dashed lines represent unstable solutions.

If the eigenvalues are complex of the form \( a \pm ib \), the solution will be periodic with periodicity \( 2\pi/b \). Exactly at the bifurcation point \( p = 0 \) the eigenvalues are \( \lambda_{bf} = 0 \pm \sqrt{0 - k'k} = \pm i\sqrt{k'k} \) and thus the period is given by \( 2\pi/\sqrt{k'k} \).

The time evolution of the disturbance \( \delta A \) (equation 3) and phase portraits for these regions are shown in figure 4A. The disturbances can have negative values, meaning that the number of ants is lower compared to the number at the equilibrium point. In all time development graphs it is sufficient to show only the number of active ants since the number of inactive ants changes in a similar way. Figure 4B shows the development of the non-linearized system (system 1) for the same values of \( k \). Similar graphs can be obtained if \( k \) is fixed and \( k' \) varied.

The bifurcation diagram (figure 3B) tells that the system should be unstable for \( k > 0.0184 \) when \( k' = 0.01 \) is fixed. However, this is not seen in figure 4B. The reason that the processes for these \( k \)-values are spiral sinks instead of spiral sources is probably that there is an attractor with stable solutions encircling the unstable line in the Hopf bifurcation.

IV. Temperature dependent model

The general model in equation 1 can be expanded to include changing environmental conditions by writing

\[
\frac{dA}{dt} = \phi(t) \frac{A^2}{A^2 + \tau} - kA
\]

\[
\frac{dI}{dt} = kA - k'I
\]

The function \( \phi(t) \) determines the significance of the encounters between the ants. For the temperature dependent model \( \phi(t) = \alpha (1 + T(t)) \) is used where \( T(t) \) is the temperature (in °C). When \( T(t) = 0 \) this is identical to the temperature independent model in equation 1.
Table 1. Different values of $k$ give different kinds of solutions ($k' = 0.01$ is fixed).

<table>
<thead>
<tr>
<th>STABLE</th>
<th>NEUTRAL</th>
<th>UNSTABLE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sink</td>
<td>Spiral sink</td>
<td>Center</td>
</tr>
<tr>
<td>0 &lt; $k &lt; 0.0041$</td>
<td>0.0042 &lt; $k &lt; 0.017$</td>
<td>$k = 0.0184$</td>
</tr>
<tr>
<td>$k = 0.019 &lt; k &lt; 0.063$</td>
<td>$k = 0.064 &lt; k$</td>
<td></td>
</tr>
</tbody>
</table>

![Figure 4](image1.png)

Figure 4. Time evolution (upper) and corresponding phase portraits (lower) for the disturbance $\delta A$ (figure (a)) and for the system in equation 1 (figure (b)) for different $k$-values corresponding to the regions in table 1. Initial conditions are $(A_0, I_0) = (10, 0)$. The parameters $\alpha = 1$ and $k' = 0.01$ are fixed for all the graphs.
Analysis of the temperature dependent model

The diurnal temperature changes can in a simplified way be described as a sine curve. This representation makes it easier to analyze how the system behaves for different forcings.

Different amplitudes of the forcing temperature sine function can change the dominant periodicity of the activity. For large amplitudes of the forcing, the mean period of the oscillation is shifted from the natural period of the system to the period of the forcing, see figure 5. For each amplitude the integration is run for 100,000 time steps. Then the mean period and standard deviation ($\sigma$) is calculated from the distances between the peaks.

During the transition from the natural period to the period of the forcing the deviation from the mean period is large because the oscillation is irregular with many periodicities at the same time. As the period of the forcing becomes dominant the deviation decreases, entailing a more periodic behavior of the system.

![Figure 5](image.png)

**Figure 5.** Mean period of the oscillation plotted for different amplitudes of the forcing function. For this graph $\alpha = 0.1$, $k = 0.01$, $k' = 0.0054$ (at the bifurcation point) and the forcing function is $T(t) = 30 + A \sin (0.005 \cdot t)$. The errorbars represent $\pm 1\sigma$.

Varying the frequency of the sine function also affects the time-dependent behavior. In figure 6 the dominant period for different frequencies is shown. The time evolution is calculated for 100,000 time steps for each frequency and then the mean periods and standard deviations are calculated from the distances between peaks.

If the temperature oscillation is too slow the system is unaffected by the forcing and will oscillate with its internal frequency. Increasing the frequency also increases the standard deviation until the frequency of the forcing function is adopted by the system. As seen in the figure, the system reestablishes its internal periodicity for the forcing frequencies 0.014 and 0.015. These frequencies corresponds to periods of 449 and 419 i.e. approximately half of the natural period ($2\pi/\sqrt{K' E} = 855$). In the region where the forcing frequency is close to half of the natural frequency a sub-harmonic resonance is expected.

It should be possible to find a forcing that causes resonance. With a frequency of the forcing sine function close to the the natural frequency of the oscillation, the outbreaks of activity could be amplified in the model. Some attempts have been made to find this resonance frequency but without success.
Figure 6. Mean period of the oscillation as a function of different frequencies of the forcing sine function. The parameters are $\alpha = 0.1$, $k = 0.01$, $k' = 0.0054$ (at the bifurcation point) and the forcing function is $T(t) = 30 + 5 \sin (f \cdot t)$. The errorbars represent $\pm 1\sigma$.

To visualize the results and find patterns in the output generated by different temperature forcings, four different kinds of graphs are used: time evolution, phase portrait, Poincaré map and recurrence plot.

The Poincaré map is created by finding the average period $\psi$ in the time series and then $I(n \cdot \psi)$ is plotted versus $A(n \cdot \psi)$ where $n = 0, 1, 2, ...$. The generated graphs show patterns that would be hard to interpret in a classical phase space plot.

A recurrence plot is useful to find structures in a chaotic system. Each value $A(t_i)$ is matched with all other $A(t_j)$ that have the same value within a tolerance. In a graph with time on both axes these indices are marked with points, creating a reflected pattern about the line $t_i = t_j$. Thus a recurrence plot shows the times where the trajectory in the phase space visits roughly the same area. Marwan (2003) gives the following interpretations of the textures that can be observed in a recurrence plot:

- **Single points:** if a state is rare.
- **Vertical or horizontal lines:** the state does not change or changes very slowly with time.
- **Diagonal lines, checkerboard structures:** oscillating systems. The system returns to the same state multiple times. If the spacing between the lines differs, the oscillation is quasi periodic. If the lines are orthogonal to the line $t_i = t_j$ the states have the same evolution but with reverse time. If the lines are parallel to $t_i = t_j$ the process could be deterministic, but if there are single points close to the line it could be chaotic.
- **Long bowed lines:** similar states reached at different times and with different velocity. The dynamics of the process could be changing.
- **White areas or bands:** abrupt changes in the dynamics.
- **Bright corners:** slowly varying parameters, the time series contains a trend.
In figure 7 the time evolutions, phase portraits, Poincaré maps and recurrence plots are shown for four different temperature forcings. All graphs have the same parameter settings using $\alpha = 0.1$, $k = 0.01$ and $k' = 0.0054$ (at the bifurcation point). The upper row of plots can be used for reference and displays the solution without temperature forcing (when $T = 0$). For the graphs in the second row the temperature is given by $T(t) = 30 + 11 \sin(\tau \cdot t)$ where $\tau = \sqrt{k/k'}$ is the natural frequency of the unforced oscillation. For the third row the forcing $T(t) = 30 + 5 \sin(0.5\tau \cdot t)$ is used and for the fourth row $T(t) = 30 + 5 \sin(1.25\tau \cdot t)$ is used. The integration time was 30 000 time steps and the initial settings $(A_0, I_0) = (10, 0)$ were used.

The equilibrium point, calculated using equation 2, gives $(A_{eq}, I_{eq}) \approx (2.28, 4.20)$ for the graphs in the upper row. For the other rows the mean temperature 30 in the temperature functions increases the number of active ants. A constant temperature $T(t) = 30$ gives the equilibrium point $(68.4, 126)$ and this point is also central in the phase portraits for varying temperatures.

The times series are plotted for the whole integration time. In the upper graph it is seen that it takes some time before the effect of the initial conditions is damped and the system has adjusted to a natural oscillation. To avoid the transients from the initial conditions, the phase portraits and Poincaré maps only use data from the second half of the integration time. For the recurrence plots, data from the last 5 000 time steps are used (except for the recurrence plot on the second row where 10 000 time steps are used).

In the time evolution graph in the second row, the slow oscillation of the forcing function acts as an overlying function. The natural frequency is constantly shifted by the frequency of the forcing creating the wave pattern. The third time series displays a pattern with a smaller peak that is followed by a larger peak. From about $t = 22 500$ this is reversed with the high peak coming first and this behavior is continued if the integration time is increased. When the forcing oscillation is rapid, as in the fourth row, the time evolution of the system becomes irregular.

The phase portraits in the second, third and fourth rows show trajectories crossing each other. In a two dimensional system like ours, this is only possible in a system subject to external forcing. The two-periodicity in the time evolution in the third row appears in the phase portrait as two equilibrium points approached alternately.

The Poincaré map in the upper row basically consists of a single point as can be expected for a regular oscillation. In the second row the slow oscillation causes the points to fall on a line in the Poincaré map. The map in the third row shows two separate lines, a characteristic of a two-periodic oscillation. The fourth Poincaré map shows a spiraling structure. A deformed circle in the Poincaré map, as in this case, is a sign of chaos.

All of the recurrence plots have diagonal lines and checkerboard structures since they represent oscillating processes. The larger structural elements seen in the plots in the second row indicate the overlying slow oscillation. Inside these larger boxes the pattern from the upper row recurrence plot is recognized. This tells us that the fast oscillation has the same simple wave form as the unforced oscillation. The recurrence plot in the third row contains more white areas than the others. This is because of the large spacing between the rapid visits to the lowest minimum. It also has both horizontal and vertical lines which implies slow changes with time.
FIGURE 7. Time evolutions, phase portraits, Poincaré maps and recurrence plots for four temperature forcings. The applied forcing is stated in the time series to the left on each row. Note the different scales for the graphs in the upper row and for the recurrence plot on the second row.
V. Comparing model with observations

To test the quality of the model, an attempt was made to recreate the observed time series of activity (see figure 2) using the measured temperature as the forcing function. The parameters $k$ and $k'$ were set to give the system a natural period of about one day so that the nest has a built-in circadian rhythm ($k = 0.0039$ and $k' = 0.002$ were used). $\alpha$ primarily affects the amplitude of the oscillation and was set to 0.0025 and the initial conditions were $(A_0, I_0) = (18, 0)$ to replicate the observed starting point of the measurements.

The result of the integration with the actually measured temperature is shown in figure 8 with the observed activity for comparison. Most of the peaks are adequately modeled regarding timing and length of activity bursts but the amplitude is not modeled very well. The important things to note is that both the phase shift between the activity and temperature and the asymmetric shape of the activity curve (both described in section II) can be modeled. As seen in figure 2 the small amplitudes of the peaks at 144 h and 168 h are not caused by a low temperature but rather by some other factor. This makes them impossible to predict using our deterministic model. One then has to account for the variability and stochasticity of individuals and the environment and use Monte Carlo simulations. This is however out of the scope of this project.

VI. Discussion

In this report a model where ants can be in two states (active or inactive) was created and analyzed to better understand the activity patterns in an ant colony. Then a forcing function was added to this general model to study the effects on the system for different sinusoidal forcings. Figures 5 and 6 shows that the mean period of the system goes from its natural period to the period of the external forcing when the amplitude or the frequency of the forcing function is increased. Four different kinds of graphs (time evolution, phase portrait, Poincaré map and recurrence plot) were discussed and used to represent the behavior of the forced system (figure 7). At last, observed temperature was used as the forcing function and the output of the model was compared with the actual measurements of activity (figure 8). The results are in good agreement with data concerning the phase shift and the asymmetry.

It should be checked how the model works for other forcings in nature, such as a varying food source. Other meteorological parameters, such as relative humidity,
pressure changes, cloud cover etc., could be measured to find the best set of parameters that could be used to model the activity. It should also be investigated how important temperature is for other ant species.

Figure 8 shows that, using the described model with temperature as the only environmental parameter, it is impossible to predict the amplitude of the activity outbreaks. Since both the time when the activity reaches its maximum and the length of the activity bursts can be reproduced reasonably well, the major improvement of the model is to be able to get the correct amplitudes. To do this, a stochastic model and more knowledge about which environmental factors that are important is needed.

Finally, the model should be compared with longer time series of measurements.
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