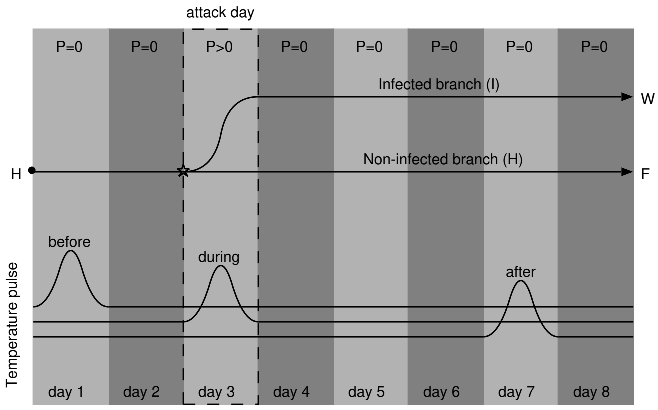
Heat wave model for "Timing of heatwaves matters: extreme heat during parasitism disrupts top-down control"

Nicholas A. Pardikes, Tomas A. Revilla, Gregoire Proudhom,
Melanie Thierry, Chia-Hua Lue, and Jan Hrcek

1 Mathematical model

The joint effect of parasitism and heat waves is modelled by projecting a cohort of hosts "H" over a span of 8 days like in the experiments. Exposure to parasitoid attack at day 3 creates an infected branch "I". At the end of day 8, surviving hosts emerge as flies "F" if uninfected, or as wasps "W" if infected, as illustrated below



Heat waves, shown as temperature pulses above, can occur before, during or after parasitoid attack, at day 1, 3 or 7, respectively like in the experiments.

Let H_t and I_t be, respectively, the number of uninfected and infected hosts at the end of day $t = 1, 2 \ldots, 8$. The cohort start with $H_0 = 50$ eggs and $I_0 = 0$ infected hosts, and subsequent numbers are obtained by the recurrences

$$H_{t+1} = H_t e^{-m(t)-a(t)} \tag{1}$$

$$I_{t+1} = I_t e^{-m(t)} + H_t \left(1 - e^{-a(t)}\right) e^{-m(t)}. \tag{2}$$

Hosts survive with with probability $e^{-m(t)}$, $m(t)$ is the *mortality rate* per capita on day t according to

$$m(t) = \begin{cases} m_0 & t \neq \tau \\ m_0 + m_\tau & t = \tau \end{cases}, \tag{3}$$

m_0 is a *intrinsic mortality* rate and m_τ is the *mortality differential* caused by the heat wave on day $\tau = 1, 3, 7$. The probability of escaping parasitism on day t is $e^{-a(t)}$ where

$$a(t) = \begin{cases} 0 & t \neq 3 \\ a_0 P & t = 3 \end{cases}, \tag{4}$$

a_0 is the attack rate by P parasitoids (3 females). The non escaping fraction $1 - e^{-a(t)}$ is used to increment the number of infected hosts.

At the end of day $t = 8$, uninfected hosts emerge as $F = H_8$ adult flies. $W = \varepsilon I_8$ parasitoids emerge from infected hosts which die, where ε is the conversion rate of wasps per infected host. Experiment data provides numbers of flies F and wasps W emerging on day 8 and after. Substituting (3, 4) in system (1, 2) and integrating from $t = 0$ to $T = 8$ gives

$$F = H_0 e^{-m_0 T - m_\tau - a_0 P} \tag{5}$$

$$W = \varepsilon H_0 e^{-m_0 T - m_\tau} \left(1 - e^{-a_0 P}\right). \tag{6}$$

Our model assumes that there is no interaction between attack rates, mortality and mortality differentials, e.g., m_0 and m_τ values are independent of the presence of parasitoids, and a_0 values are independent of heat waves occurences, before, during or after. This independence (*null hypothesis*) can be tested by comparing empirical outcomes with stochastic simulations based on host dynamics (1, 2). The comparissons require estimation of m_0, m_τ, a_0 and ε.

2 Parameter estimation

Experiment data is used to calculate empirical mortality per host per day using the formula

$$\mu = \frac{1}{T} \ln\left(\frac{H_0}{F}\right) \approx \frac{2.3026}{T} \log_{10}\left(\frac{H_0}{F}\right). \tag{7}$$

There was small fraction of experiments where all hosts got infected and $F = 0$. For these cases we set $F = 1$ in order to perform calculations. Thus μ overestimates real pre-adult mortality rates. According to (5), daily mortality follows the linear model

$$\mu = m_0 + \frac{m_\tau}{T} + \frac{a_0 P}{T}, \tag{8}$$

which facilitates parameter estimations. Intrinsic mortality rate m_0 corresponds to mortality recorded from double control experiments

$$m_0 = \mu_{00},$$

i.e., without heat waves (1st sub-index is 0) and without parasitoids (2nd sub-index is 0). Mortality differentials m_τ are obtained using difference between the mortality with the heat wave minus mortality in the double control (no heat wave and no parasitoids)

$$m_\tau = (\mu_{\tau 0} - \mu_{00})T, \tag{9}$$

and a_0 is obtained using the difference between the mortality under attack without heat wave, minus mortality in the double control

$$a_0 = (\mu_{03} - \mu_{00})T/P. \tag{10}$$

According to equation (6) the number of emerging wasps without heat waves is

$$W_{03} = \varepsilon_0 \left(He^{-m_0 T} - He^{-m_0 T - a_0 P}\right) = \varepsilon_0 \left(F_{00} - F_{03}\right)$$

where the quantity $He^{-m_0 T}$ is expected to match the empirical number of flies F_{00} that emerge under the double control (no heat wave and no parasitoids), whereas $He^{-m_0 T - a_0 P}$ is expected to match the empirical number of flies F_{03} that emerge if parasitoid attack happened but heat waves didn't. From this we get

$$\varepsilon = \frac{W_{03}}{F_{00} - F_{03}}, \tag{11}$$

Since m_0, m_τ's, and a_0 are linear related, it is very easy to derive expected values and variances

$$\begin{aligned}
E[m_0] &= E[\mu_{00}] \\
V[m_0] &= V[\mu_{00}] \\
E[m_\tau] &= T\left(E[\mu_{\tau 0}] - E[\mu_{00}]\right) \\
V[m_\tau] &= T^2\left(V[\mu_{\tau 0}] + V[\mu_{00}]\right) \\
E[a_0] &= T\left(E[\mu_{03}] - E[\mu_{00}]\right)/P \\
V[a_0] &= T^2\left(V[\mu_{03}] + V[\mu_{00}]\right)/P^2
\end{aligned}$$

where $T^2 = 8^2 = 64$, $P^2 = 3^2 = 9$. The experiments from which the μ's are sourced are independent, so any potential covariances are implied to be zero. In practice, μ's expectations and variances are given by corresponding sample means and sample variances.

For the host to wasp conversion rate ε it is not possible obtain closed formulas for their variances because the relations between W's and F's are not linear. Instead, we estimate ε using sample averages $\bar{W}_{03}, \bar{F}_{00}, \bar{F}_{03}$ in (11).

3 Simulation

We implement the following stochastic simulation protocol

1. Set $H_0 = 50$ and $I_0 = 0$
2. From day $t = 1$ to day $T = 8$ calculate
   a) Deaths: draw m from a normal distribution with mean $E[m_0]$ and variance $V[m_0]$. If a heat wave occurs, add a mortality differential drawn from a normal distribution with mean $E[m_\tau]$ and variance $V[m_\tau]$, with $\tau = t$. For each host $i = 1, \ldots, H + I$, draw x_i uniformly between 0 and 1: if $x_i > e^{-m}$, subtract 1 from H or from I, which one depends whether i is non-infected or infected respectively.
   b) Attacks: set a equal to $P = 3$ (female wasps) times a number drawn from a normal distribution with mean $E[a_0]$ and variance $V[a_0]$. For each non-infected host $i = 1, \ldots, H$, x_i is drawn from a uniform distribution between 0 and 1, if $x_i > e^{-a}$ then subtract 1 from H and add 1 to I.
3. Set $F = H_8$ and draw W from a Poisson distribution with parameter εI_8.

This is protocol applies to each combination of: (i) host species; (ii) parasitoid species, including no parasitoid; and (iii) timing of heat wave (including no parasitoid and/or no heatwave as controls). The number of replicas for each combination matches the corresponding data sample size. The 95% confidence intervals for number of emerging adult flies F and wasps W are visually compared with corresponding 95% confidence intervals from the data.

The simulations were run using Matlab R2024a. All necessary commands are listed and executed by the single m-file: `simulation_script.m`