

Problem 3

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Introduction

Nature is riddled with contending pressures to pass on genetic information. This evolutionary molding is epitomized by the dynamics between large cabbage white butterfly and parasitic wasps. After mating, male butterflies secrete anti-aphrodisiac pheromones onto impregnated females.¹ This increases the male's chances of fertilizing a mate and allows the female to focus on caretaking. Through chemical espionage, phoretic wasps are able to sense these pheromones to identify impregnated females, hitch a ride to butterfly nests on the butterfly's backs, and lay larvae in the nests to feed off of the butterfly's eggs.¹ Ultimately, this leads to an interesting trade-off between competing interests. This paper functions to model the long term population dynamics of butterflies and wasps based on the aforementioned interactions between these species and evaluate long term equilibria based off of variational parameters. The dispersion of anti-aphrodisiac pheromones from impregnated butterflies, propagation of resultant action potentials in wasps due to stimulation of olfactory receptor neurons from these pheromones, and the physical trajectory of wasps onto impregnated butterflies are also modelled.

Assumptions and Models

In order to succinctly model this natural phenomenon, the following assumptions were made; there is no genetic variation in the butterflies that results in changes of pheromone secretion; once a wasp hitches a ride on an impregnated butterfly, if the butterfly survives it will lay a consistent number of eggs and the wasp will infect all eggs resulting in death of all butterfly larvae and the birth of a consistent number of wasps; a non-parasitized butterfly will have a consistent number of offspring achieve adulthood; there is a consistent percentage of the butterfly population that is impregnated at any time; there is no migration in or out of the environment being evaluated; and a wasp only reproduces through the parasitism of a butterfly.

Table 1: Variables and Constants Related to Population Dynamics

| Symbol | Meaning | Symbol | Meaning |
|------------|------------------------------|--------|--|
| B | Number of butterflies | e_i | Eggs per impregnation |
| B_{max} | Maximum butterfly population | w_e | Number of wasps born per egg parasitized |
| W | Number of Wasps | i | Percentage of butterfly population impregnated |
| d_B, d_W | Death rates of the insects | I_w | Number of butterflies that are impregnated and parasitized by a wasp |
| α | Rate of wasp parasitism | | |

Under these assumptions, the rate of change of the butterfly population can be defined as

$$\frac{\partial B}{\partial t} = [(iB - I_w) e_i - d_B B] (B_{max} - B).$$

And the total wasp population is given by

$$\frac{\partial W}{\partial t} = I_w e_i w_e - d_W W.$$

Where the total number of impregnated butterflies that are under attack from wasps is given by

$$\frac{\partial I_w}{\partial t} = (\alpha W - d_B I_w)(iB - I_w).$$

According to these equations, the butterfly population undergoes logistic growth limited by the carrying capacity of their environment. In the long term, if the attack rate of the wasps (α) is low, the butterfly population will maintain slight oscillations below the carrying capacity. If the attack rate of the wasps is high, all butterflies and wasps will eventually die off. If the attack rate is moderate, the populations of the wasps and the butterflies will oscillate back and forth.

The anti-aphrodisiac pheromones randomly accelerate (a) outwards from the impregnated butterfly based on its mass (m) and a friction coefficient (γ) according to the following equation

$$\mathbf{a} = \frac{\partial \mathbf{v}}{\partial t} = -\frac{\gamma}{m} \mathbf{v}.$$

The friction coefficient is given by the following equation

$$\gamma = 6\pi\eta a.$$

Where η is the viscosity of air and a is the radius of the pheromones. Additionally, the pheromones travel at a velocity described by

$$\mathbf{v} = \frac{\partial \mathbf{x}}{\partial t} = e^{-mt/\gamma} \mathbf{v}(0)$$

And are at a given radial position (r) according to time described by

$$\mathbf{r} = -\frac{\gamma}{m} e^{-mt/\gamma} \mathbf{v}(0).$$

These released pheromones are registered in the form of electric potentials within olfactory receptor neurons of the antennae of the wasps. When the additive value of these electric potentials is greater than the threshold value, an action potential is produced in the neuron that causes an excitatory signal. If this threshold electric potential is not reached, then no signal is formed. From the assumption that the neuronal system of olfactory receptor neurons and stimulated synaptic modules and resultantly stimulated motor neurons and muscles has little to no resistance or signal loss, the system can be modelled as a lossless transmission line. Voltage (V) and current (I) of the propagated electrical signal is given as a function of the self-inductance (L) and the capacitance (C), respectively, within the neurons and can be defined as

$$\frac{\partial V}{\partial x} = -L \frac{\partial I}{\partial t} \text{ and } \frac{\partial I}{\partial x} = -C \frac{\partial V}{\partial t}.$$

Using these definitions and a standard wave equation,

$$\frac{\partial^2 V}{\partial t^2} - u^2 \left(\frac{\partial^2 V}{\partial x^2} \right) = \frac{\partial^2 I}{\partial t^2} - u^2 \left(\frac{\partial^2 I}{\partial x^2} \right).$$

The propagation speed (u) can be defined by solving the previous wave equation, yielding

$$u = 1/\sqrt{LC}.$$

Resultant trajectory of the wasp is defined by the force (F) at which the wasp propels forward as given by Newton's second law. Considering both air resistance and gravity, the acceleration of the wasp in three dimensions is given by

$$\begin{aligned} \mathbf{a}_x &= \frac{dv_x}{dt} = \frac{F_x}{m} - \frac{c}{m} (\mathbf{v}_x^2 + \mathbf{v}_y^2 + \mathbf{v}_z^2)^{1/2} \mathbf{v}_x \\ \mathbf{a}_y &= \frac{dv_y}{dt} = \frac{F_y}{m} - \mathbf{g} - \frac{c}{m} (\mathbf{v}_x^2 + \mathbf{v}_y^2 + \mathbf{v}_z^2)^{1/2} \mathbf{v}_y \\ \mathbf{a}_z &= \frac{dv_z}{dt} = \frac{F_z}{m} - \frac{c}{m} (\mathbf{v}_x^2 + \mathbf{v}_y^2 + \mathbf{v}_z^2)^{1/2} \mathbf{v}_z. \end{aligned}$$

Where the determination of the velocity and position of the wasp is confined to numerical solutions due to the coupling of these equations.

Limitations and Future Directions

Although these equations describe the aforementioned phenomena, there are certainly limitations and room for improvement. The proposed model for random dispersion of pheromones is only valid within the short term. Also, the assumptions that all males release the same amount of pheromones, all females lay the same number of eggs, and the same number of eggs always achieve adulthood under non-parasitic conditions simplify modelling, but make the model less realistic when describing the variant nature of life. Equations related to aerodynamic specifics of wasp flight should be explored in future studies. Also, other factors such as disease, natural disasters, and migration should be incorporated into the population dynamics equations.

References

- Huigens, M. E., Woelke, J. B., Pashalidou, F. G., Bukovinszky, T., Smid, H. M., & Fatouros, N. E. (2010). Chemical espionage on species-specific butterfly anti-aphrodisiacs by hitchhiking *Trichogramma* wasps. *Behavioral Ecology*, 21(3), 470-478.