SCUDEM 2019 - Executive Summary (Problem C)

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Introduction: Chemical Espionage by *Trichrogamma* wasps

Parasitic wasps belonging to the *Trichogramma brassicae* and *Trichogramma evanescens* species use a strategy of chemical espionage and hitchhiking to detect and parasitize eggs of the butterfly species *Pieris brassicae*. As a result, Trichogramma wasps are significant mortality factors in Pieris butterfly populations. In order to facilitate detection of the *P. brassicae* butterfly eggs, the wasps exploit the anti-aphrodisiac signal present on the female butterflies. This anti-aphrodisiac signal consists of a mixture of pheromones that are passed from males to females during mating, in an effort for male butterflies to enforce female butterfly monogamy. This reduces male intraspecific competition and allows females to place their eggs in a more suitable location. Wasps respond to the anti-aphrodisiac only when it is present in conjunction with other mated female odors, allowing them to distinguish between other anti-aphrodisiac compounds present in the environment [1].

Once the parasitic wasps have detected the anti-aphrodisiac-containing odor blend on mated females, they ride on the mated female butterfly to a host plant. Here, they proceed to parasitize the butterfly eggs by depositing their own eggs inside the butterfly's eggs. The wasp larvae then consume the butterfly larvae, and emerge from the butterfly eggs after full development [1].

T. brassicae innately understand how to hitchhike on mated female butterflies whereas *T. evanescens* are only able to consistently exhibit this behavior after the completion of one successful hitchhike. This discrepancy suggests a higher degree of host specialization for *T. brassicae,* implying that without butterfly *P. brassicae,* the *T. brassicae* population would decrease rapidly due to reduced ability in recognizing other anti-aphrodisiacs and parasitizing eggs of other butterfly species. On the other hand, *T. evanescens* are considered to be generalist-parasitic wasps; they are more adaptive and can respond to varied host cues [1].

Here, we model and interpret the dynamics of this espionage-and-hitchhike strategy on the populations of a wasp species, *T. brassicae*, and the large cabbage white butterfly, *P. brassicae*.

Methods: Modifying a Lotka-Volterra Predator-Prey Type Model to Account for Sex Specific Differences and Anti-Aphrodisiac Effects

Model:

$$\frac{dX}{dt} = \mathrm{A}\beta_1 Y - \delta_1 X - \frac{\frac{X}{1+\mathrm{A}} + Y}{K} X - \frac{\mathrm{A}\alpha Y Z}{1+\lambda(x+y)}$$

$$\frac{dY}{dt} = Y\left(\mathrm{A}\beta_2 - \delta_2 - \frac{X+Y}{K} - \frac{\mathrm{A}\alpha Z}{1+\lambda(x+y)}\right)$$

$$\frac{dZ}{dt} = Z\left(-\delta_3 - cZ + \frac{\mathrm{A}\varepsilon Y}{1+\lambda(x+y)}\right) \tag{1.1}$$

State Variables:
$\boldsymbol{X}$ − male butterfly population
$\boldsymbol{Y}$ − female butterfly population
$\boldsymbol{Z}$ − wasp population

Parameters (All are Positive):
$\boldsymbol{\beta_1}$ − female butterfly birth rate
$\boldsymbol{\beta_2}$ − male butterfly birth rate
$\boldsymbol{\delta_1}$ − male butterfly death rate
$\boldsymbol{\delta_2}$ − female butterfly death rate
$\boldsymbol{\delta_3}$ − wasp death rate

$\mathbf{A}$ − concentration of mated female odor blend (including Anti − Aphrodisiac)
$\boldsymbol{c}$ − rate of competition between wasps
$\boldsymbol{K}$ − carrying capactiy of butterfly population
$\boldsymbol{\lambda}$ − handling time for each prey consumed
$\boldsymbol{\alpha}$ − rate at which female butterfl − wasp interaction affects the male/ female butterfly population
$\boldsymbol{\varepsilon}$ − rate at which female butterfly − wasp interaction affects the wasp population

Explanation - We started by determining the effects of anti-aphrodisiacs emitted by male butterflies:

1. Since anti-aphrodisiacs dissuade other male butterflies from bothering an already-mated female butterfly, they allow the female butterflies to invest more time and energy in egg laying, thus stimulating the birth of both male and female butterflies.
2. Anti-aphrodisiacs make it more likely that a male is able to fertilize a female's eggs, thus reducing competition between male butterflies.
3. Since anti-aphrodisiacs facilitate detection of female butterflies by wasps, they increase predation of the butterfly eggs (thereby also increasing wasp birth rate).

Further explanation on proposed model:

To begin, our state variables are the male butterfly population, female butterfly population, and parasitoid wasp population. We assumed that reproduction is limited only by the abundance of females in the population. Therefore, both the male and female butterfly birth rate to be a linear correlation with the number of females in the population, as used by previous two-sex models [2], [3]. Death rates for the male and female populations, however, are only linearly dependent on the male and female population, respectively. In addition, butterfly birth rates are positively affected by anti-aphrodisiac concentration, so we included this parameter in the linear butterfly birth terms, while having no effect on the linear death terms.

We also assumed that the population of butterflies has a total carrying capacity of K. This is relevant to the modelling equations for both the male and female populations, because total carrying capacity indicates that competition for resources between butterflies is not sex specific. However, because anti-aphrodisiac concentrations can decrease competition between male butterflies, this is reflected in our model for male butterfly dynamics.

We assumed that the wasps are dependent on butterflies for population growth, because wasp growth requires parasitization of butterfly eggs. In the absence of the butterflies, wasps die off; thus their inherent growth rate is negative (given by their mortality rate). The only positive terms given in the equation for modeling wasp growth is given by the amount of predation on the butterfly populations. Furthermore, there is also intraspecies competition within the wasp population; this is given by the parameter c. (There is no relevant carrying capacity, because the wasp population cannot get big enough to become limited by resources). We further assumed that the wasp eggs are 100% successful at killing female butterfly eggs and surviving gestation once they have successfully "hitchhiked" with a mated female butterfly.

The effect of the wasp population on the butterflies is given by the predation term (last term in each equation). Here, we assumed that predation is not sex-specific. In our modification, the amount of predation in both male and female butterfly populations is only an interaction between female butterfly population and the wasps, since the wasps only directly interact with the female butterflies via chemical espionage and hitchhiking. We chose to use Lotka-Volterra with Holling type II response to model the predation, since the parasitoid relationship of these wasps is similar to that of predation.

The parasitic behavior from the wasps occurs without the presence of anti-aphrodisiac. However, because wasps use it to facilitate detection of female butterflies, the scale of such behavior increases in the presence of anti-aphrodisiac. Therefore, the predation term is a quadratic of the interaction between female mated butterflies and wasps, in relation with the death rate of wasps to butterfly eggs and anti-aphrodisiac. There is also a holding term (λ), which symbolizes the amount of time between predation, thereby allowing for the possibility of bounded solutions with respect to predation.

These systems of Lotka-Volterra equations allow for the possibility of stable solutions to exist, with the parameters we chose.

Results - Model Analysis

In order to analyze the given model, we elected to choose parameter values for all parameters except for the parameter A (where A represents the concentration of the mated female odor blend, including anti-aphrodisiac). This will allow us to analyze the effects of different values of A on the dynamics.

Specifying Parameters:

We take time t to be in units of gestational period. Then:

- Since *P. brassicae* deposit between 20 and 50 eggs per oviposition (an average of 35 eggs), and we assume that there is an equal amount of male and female eggs laid, $\boldsymbol{\beta_1} = \boldsymbol{\beta_2} = 17.5 \approx 18$. [1]
- Studies have shown the gestational period of *P. brassicae* to be 4.6 days [5]. The average time between a parasitoid wasp finding a mated female and the eggs hatching and killing the butterfly eggs is then 1.74 gestational periods (λ).
- We could not find relevant data or studies to help determine values for the other parameters. We therefore made educated guesses, that are summarized in the table below. Here we took $\boldsymbol{\varepsilon}$ to be larger than $\boldsymbol{\alpha}$, because many wasp larvae can parasitize a single butterfly egg.

Parameter	Designated Value
$\boldsymbol{\beta_1}$	18
$\boldsymbol{\beta_2}$	18
$\boldsymbol{\delta_1}$	0.25
$\boldsymbol{\delta_2}$	0.25
$\boldsymbol{\delta_3}$	0.25

Parameter	Designated Value
$\boldsymbol{c}$	.01
$\boldsymbol{K}$	20,000
$\boldsymbol{\lambda}$	1.74
$\boldsymbol{\alpha}$	0.05
$\boldsymbol{\varepsilon}$	0.15

Even with these considerations, we were unable to calculate any equilibrium solutions for the model. We then decided to analyze a simpler model, which is as follows:

$$\begin{aligned}
\frac{dX}{dt} &= \mathrm{A}\beta_1 Y - \delta_1 X - \frac{\frac{X}{1+\mathrm{A}} + Y}{K} X - \mathrm{A}\alpha Y Z \\
\frac{dY}{dt} &= Y\left(\mathrm{A}\beta_2 - \delta_2 - \frac{X+Y}{K} - \mathrm{A}\alpha Z\right) \\
\frac{dZ}{dt} &= Z(-\delta_3 - cZ + \mathrm{A}\varepsilon Y) \qquad (1.2)
\end{aligned}$$

(All parameters are same as those in (1.1))

Calculating and Analyzing Equilibria:

Using MATLAB we calculated the equilibria at the previously specified values of the parameters, while varying the value of A. We found that when A<3, there are two relevant equilibria (ie, equilibria that have a zero or positive values in their components): these are in the form of (X,Y,Z) = (0 ,0, 0) or (positive real number, positive real number, 0). However, when A≥3, there is an additional relevant equilibrium: (positive real number, positive real number, positive real number). Hence, in order for there to be an equilibrium in which all species exist, A≥3, indicating that a certain amount of anti-aphrodisiac is needed in order for this steady state to exist in the model.

Also, we noticed that at large values of anti-aphrodisiac, in the equilibrium (positive real number, positive real number, positive real number), the populations of male and female butterflies were very low, which aligns with the interaction of the species in the wild: butterfly populations have strong selective pressure to minimize anti-aphrodisiac.

The equilibrium (positive real number, positive real number, 0) also aligns with our model, since without predation, the male and female butterfly populations should still be able to thrive. The positive equilibrium at (positive real number, positive real number, positive real number) also has significantly less male and female butterfly populations compared to the equilibrium (positive real number, positive real number, 0), which is corresponds with the model, since it indicates that predation is valid of the wasps on controlling the butterfly population.

Case Study: A=5

We set A=5 and determined the equilibria at this value (where all other parameters were designated values mentioned before). In order to determine the stability of these equilibria, we linearized by calculating the eigenvalues of the Jacobian of the system evaluated at each of the equilibria. The results are summarized below:

Equilibrium Point	**Eigenvalue 1**	**Eigenvalue 2**	**Eigenvalue 3**	**Stable?**
(0,0,0)	-25	-25	11	NO (semi)
(36.8, 36.8, 260)	**-25**	**-17+16.8i**	**-17-16.8i**	**YES**
(797062, 502938, 0)	150856.4	-87.85	-68	NO (semi)

The results indicate that the (positive real number, positive real number, positive real number) equilibrium is the only one that is stable.

Limitations:

While we recognize the wasps only parasitize mated female butterflies, in the given model, we assume that the all the female butterflies are mated. The only unmated female butterflies accounted for are those that are included in the birth rate function as premature eggs, some of which are parasitized by the wasps, others which develop into adults females which become mated by males by the next gestation period. In the future, perhaps we should separate the dynamics of the mated and unmated female butterflies, wherein unmated female butterflies are able to migrate into the population of mated butterflies.

Furthermore, given more time, we would also use a state-dependent parameter function to describe birth rates, as [6] had done, to show the effect of the male population on birth rate of both males and females. This is because it is perhaps inaccurate to assume that the abundance of females is what limits reproduction of *P. brassicae* butterflies.

We also would separate the two parasitoid wasp species into two functions: *T. brassicae* would have the same Holling type II function of predation, whereas *T. evanescens* would have a Holling type III function of predation to model its learning curve in discovering the anti-aphrodisiac hijacking, since it is not innate[1], and then becoming more able at predation of *P. brassicae* with time. *T. brassicae* and *T. evanescens* would also exists in a competitive state, where they compete for parasitization of *P. brassicae.*

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