All’s Fair in Love and Parasitism:

Modeling chemical espionage by Trichogamma wasps

SCUDEM 2019: Problem C

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Background: Chemical Espionage by *Trichogramma* wasps

T. brassicae wasps parasitize *P. brassicae* butterfly eggs

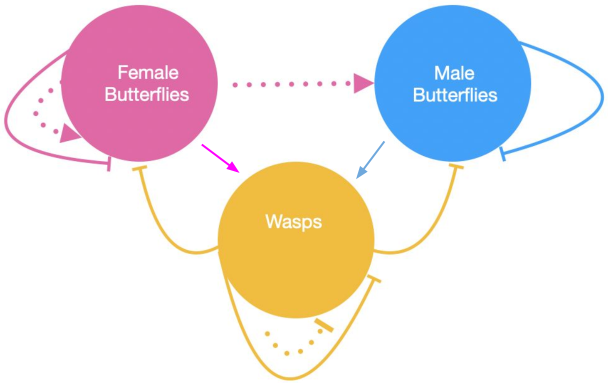
Detection of female butterflies is facilitated by exploitation of anti-aphrodisiac signal on mated females

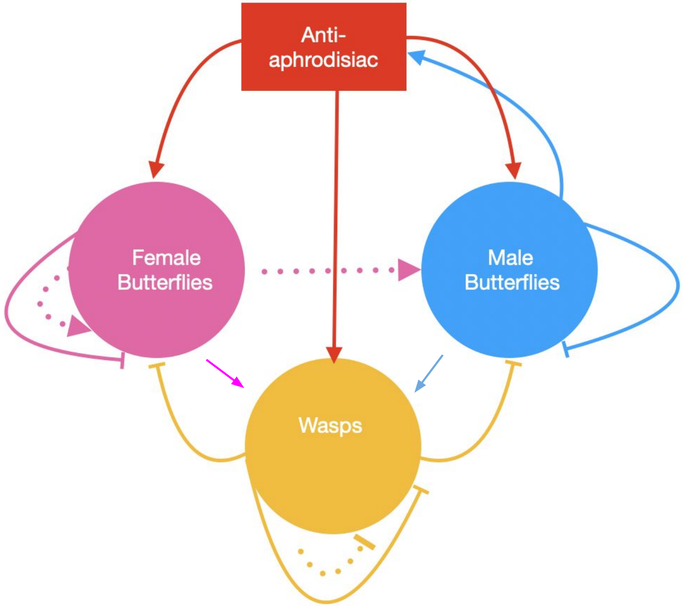
Goal: Model & interpret the dynamics of the espionage-and-hitchhike strategy of *T. brassicae* wasps on *P. brassicae* butterflies

T.brassicae caught in the act of parasitization of a *P. brassicae* egg

Net Effects of Interactions Between Populations

- Arrowheads = activation
- Blunted arrowhead = repression
- Dashed lines = linear effect





Part One: *A Basic Lotka–Volterra Model for Predator–Prey Interactions*

$$\frac{dX}{dt} = X\left(\beta_1 - \delta_1 - \frac{X}{K} \qquad \right)$$

$$\frac{dZ}{dt} = Z\left(-\delta_3 - cZ \qquad \right)$$

State-Dependent Variables

X – prey population

Z – predator population

Parameters:

$\boldsymbol{\beta_1}$ – prey birth rate

$\boldsymbol{\delta_1}$ – prey mortality rate

$\boldsymbol{\delta_3}$ – predator mortality rate

c – rate of competition between predators

K – carrying capacity for the prey population

Part One: *A Modified Lotka–Volterra Model for Holling Type II Predator–Prey Interactions*

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

$$\frac{dZ}{dt} = Z\left(-\delta_3 - cZ + \frac{\varepsilon X}{1 + \lambda(x + y)}\right)$$

<u>State-Dependent Variables</u>

X – prey population
Z – predator population

<u>Parameters:</u>

$\boldsymbol{\beta_1}$ – prey birth rate
$\boldsymbol{\delta_1}$ – prey mortality rate
$\boldsymbol{\delta_3}$ – predator mortality rate
c – rate of competition between predators
K – carrying capacity for the prey population
$\boldsymbol{\lambda}$ – handling time for each prey consumed
$\boldsymbol{\alpha}$ – rate at which predator-prey interaction affects prey population
$\boldsymbol{\varepsilon}$ – rate at which predator-prey interaction affects predator population.

Part Two: *Modifications to Account for Sex-Specific Differences*

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

- Birth rate of males: linear with respect to the female population
  - Reproduction is restricted by female abundance
- Death rate of males: linear with respect to its population.
- Predation: determined by interaction between wasp and female butterfly

State-Dependent Variables

X – male butterfly (*P. brassicae*) population

Y – female butterfly (*P .brassicae*) population

Z – wasp (*T. brassicae*) population

Parameters:

$\boldsymbol{\beta_1}$ – male butterfly birth rate

$\boldsymbol{\delta_1}$ – male butterfly mortality rate

K –total carrying capacity for butterflies

λ – handling time for each prey consumed

α – rate at which wasp-female butterfly interaction affects the male/female butterfly population

Part Two: *Modifications to Account for Sex-Specific Differences*

$$\frac{dX}{dt} = \beta_1 Y - \delta_1 X - \left(\frac{X+Y}{K}\right)X - \frac{\alpha YZ}{1+\lambda(x+y)}$$

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

- Birth rate and death rate of females males is linear with respect to the population of females

State-Dependent Variables

X – male butterfly (*P. brassicae*) population
Y – female butterfly (*P .brassicae*) population
Z – wasp (*T. brassicae*) population

Parameters:

$\boldsymbol{\beta_1}$ – male butterfly birth rate
$\boldsymbol{\beta_2}$ – female butterfly birth rate
$\boldsymbol{\delta_1}$ – male butterfly mortality rate
$\boldsymbol{\delta_2}$ – female butterfly mortality rate

K –total carrying capacity for butterflies
$\boldsymbol{\lambda}$ – handling time for each prey consumed
$\boldsymbol{\alpha}$ – rate at which wasp-female butterfly interaction affects the male/female butterfly population

Part Two: *Modifications to Account for Sex–Specific Differences*

$$\frac{dX}{dt} = \beta_1 Y - \delta_1 X - \left(\frac{X+Y}{K}\right) X - \frac{\alpha YZ}{1+\lambda(x+y)}$$

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

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

- The wasps are dependent on butterflies for growth

State-Dependent Variables

X – male butterfly (*P. brassicae*) population
Y – female butterfly (*P .brassicae*) population
Z – wasp (*T. brassicae*) population

Parameters:

$\boldsymbol{\beta_1}$ – male butterfly birth rate
$\boldsymbol{\beta_2}$ – female butterfly birth rate
$\boldsymbol{\delta_1}$ – male butterfly mortality rate
$\boldsymbol{\delta_2}$ – female butterfly mortality rate
$\boldsymbol{\delta_3}$ – wasp mortality rate

c – rate of competition between wasps
K –total carrying capacity for butterflies
$\boldsymbol{\lambda}$ – handling time for each prey consumed
$\boldsymbol{\alpha}$ – rate at which wasp-female butterfly interaction affects the male/female butterfly population
$\boldsymbol{\varepsilon}$ – rate at which wasp-female butterfly interaction affects wasp population

Part Three: *Modifications to Account for Anti-Aphrodisiac Effects*

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

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

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

Reduces competition between male butterflies

State-Dependent Variables

X – male butterfly (*P. brassicae*) population
Y – female butterfly (*P .brassicae*) population
Z – wasp (*T. brassicae*) population

Parameters:

$\boldsymbol{\beta_1}$ – male butterfly birth rate
$\boldsymbol{\beta_2}$ – female butterfly birth rate
$\boldsymbol{\delta_1}$ – male butterfly mortality rate
$\boldsymbol{\delta_2}$ – female butterfly mortality rate
$\boldsymbol{\delta_3}$ – wasp mortality rate

A – concentration of mated female odor blend (including Anti-Aphrodisiac)

c – rate of competition between wasps
K –total carrying capacity for butterflies
$\boldsymbol{\lambda}$ – handling time for each prey consumed
$\boldsymbol{\alpha}$ – rate at which wasp-female butterfly interaction affects the male/female butterfly population
$\boldsymbol{\varepsilon}$ – rate at which wasp-female butterfly interaction affects wasp population

Part Three: *Modifications to Account for Anti-Aphrodisiac Effects*

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

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

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

Stimulates the birth of both male and female butterflies

State-Dependent Variables

X – male butterfly (*P. brassicae*) population
Y – female butterfly (*P .brassicae*) population
Z – wasp (*T. brassicae*) population

Parameters:

$\boldsymbol{\beta_1}$ – male butterfly birth rate
$\boldsymbol{\beta_2}$ – female butterfly birth rate
$\boldsymbol{\delta_1}$ – male butterfly mortality rate
$\boldsymbol{\delta_2}$ – female butterfly mortality rate
$\boldsymbol{\delta_3}$ – wasp mortality rate

A – concentration of mated female odor blend (including Anti-Aphrodisiac)

c – rate of competition between wasps
K –total carrying capacity for butterflies
λ – handling time for each prey consumed
α – rate at which wasp-female butterfly interaction affects the male/female butterfly population
ε – rate at which wasp-female butterfly interaction affects wasp population

Part Three: *Modifications to Account for Anti-Aphrodisiac Effects*

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

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

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

Increased predation of butterfly eggs

State-Dependent Variables

X – male butterfly (*P. brassicae*) population
Y – female butterfly (*P .brassicae*) population
Z – wasp (*T. brassicae*) population

Parameters:

$\boldsymbol{\beta_1}$ – male butterfly birth rate
$\boldsymbol{\beta_2}$ – female butterfly birth rate
$\boldsymbol{\delta_1}$ – male butterfly mortality rate
$\boldsymbol{\delta_2}$ – female butterfly mortality rate
$\boldsymbol{\delta_3}$ – wasp mortality rate

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

Results: Part One – Specifying Parameters

Parameter	Designated Value
β_1	18
β_2	18
δ_1	0.25
δ_2	0.25
δ_3	0.25
c	.01
K	20,000
λ	1.74
α	0.05
ε	0.15

Parameters:

- β_1 – male butterfly birth rate
- β_2 – female butterfly birth rate
- δ_1 – male butterfly mortality rate
- δ_2 – female butterfly mortality rate
- δ_3 – wasp mortality rate
- **c** – rate of competition between wasps
- **K** –total carrying capacity for butterflies
- λ – handling time for each prey consumed
- α – rate at which wasp-female butterfly interaction affects the male/female butterfly population
- ε – rate at which wasp-female butterfly interaction affects wasp population

Results: Utilizing a Simplified Model

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

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

$$\frac{dZ}{dt} = Z(-\delta_3 - cZ + \mathrm{A}\varepsilon Y)$$

Result: 8 Steady State Solutions :

- Most are nonsignificant (Contain negative values for X, Y, Z)

Relevant Equilibria (X, Y, Z):

- (0,0)
- (positive real number, positive real number, positive real number)
- (positive real number, positive real number, 0)
- Correlates with model

Analysing effects of parameter “A” on of Equilibria

- Presence of (positive real number, positive real number, positive real number) equilibrium depends on value of A.
  - Bifurcation at A=2.99 (with chosen parameter values)
  - A>3 ⇒ this equilibrium exists

- Large values of anti-aphrodisiac —> (positive real number, positive real number, 0) has very small butterfly population
  - Butterfly populations have strong selective pressure to minimize anti-aphrodisiac.

Example: checking stability of relevant equilibria for A=5

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)

Other Considerations

- Account for differences in mated and unmated female populations
- Account for competition between different wasp species (*T. brassicae* and *T. evanescens*)
- Incorporate the effect of the male population on birth rate of both males and females
    - What if there are not always enough males for mating?

Additional Issue: Problem C-1

Additional Predator: Birds

(preys on both wasps and butterflies)

$$\frac{dX}{dt} = A\beta_1 Y - \delta_1 X - \frac{\frac{X}{1+A} + Y}{K} X - \frac{A\alpha YZ}{1+\lambda(x+y)} - \mu_1 XR$$

$$\frac{dY}{dt} = Y\left(A\beta_2 - \delta_2 - \frac{X+Y}{K} - \frac{A\alpha Z}{1+\lambda(x+y)} - \mu_1 R\right)$$

$$\frac{dZ}{dt} = Z\left(-\delta_3 - cZ + \frac{A\varepsilon Y}{1+\lambda(x+y)} - v_1 R\right)$$

$$\frac{dR}{dt} = R(-\delta_4 - dR + \mu_2(X+Y) + v_2 Z)$$

State Variables:

$\boldsymbol{X}$ – *male butterfly population*

$\boldsymbol{Y}$ – *female butterfly population*

$\boldsymbol{Z}$ – *wasp population*

$\boldsymbol{R}$ – *Bird population*

Parameters (All are Positive):

$\boldsymbol{\delta_4}$ – *Bird death rate*

$\boldsymbol{\mu_1}$ – *rate at which bird – butterfly interaction affects butterfly population*

$\boldsymbol{\mu_2}$ – *rate at which bird – butterfly interaction affects bird population*

$\boldsymbol{v_1}$ – *rate at which bird – wasp interaction affects wasp population*

$\boldsymbol{v_2}$ – *rate at which bird – wasp interaction affects bird population*

Analysis

- Relevant Equilibria Found (a, b, c) are positive real numbers
    - (0, 0, 0, 0)
    - (a, b, 0, 0)
    - (a, b, c, 0)

References

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Thank you!

Questions?