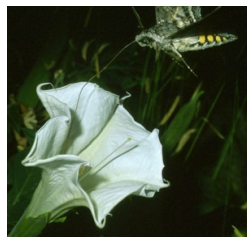


Hawkmoths: pollinators that are herbivores

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January 11th, 2015

TABLE OF CONTENTS

BACKGROUND

The System

Biological Facts

Objectives

MATHEMATICAL MODEL

System of Equations

Analytical Analysis

RESULTS

Analytical Solutions

Simulations

Graphics

CONCLUSIONS

BIBLIOGRAPHY

REFERENCE PAPER

Annals of Botany Page 1 of 9
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ANNALS OF
BOTANY
FOUNDED 1887

Reproductive biology of *Datura wrightii*: the benefits of a herbivorous pollinator

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THE SYSTEM

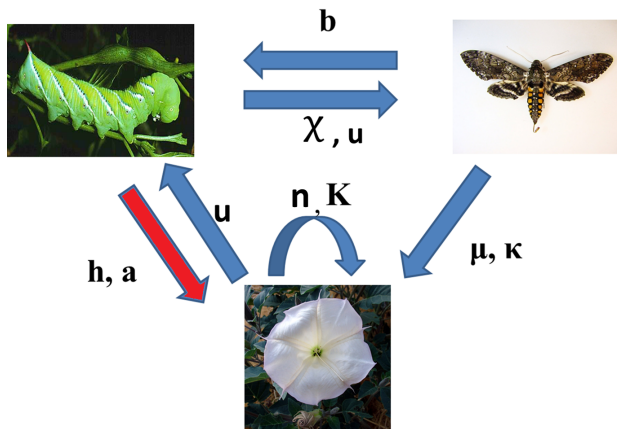


Figure: Model Diagram

BIOLOGICAL FACTS

- ▶ *Datura wrightii* (P) is highly self-compatible
- ▶ Plant leaves are the only food of *Manduca sexta* larvae (M_L)
- ▶ But *M. sexta* adults (M_A) don't depend exclusively on P
- ▶ Pollinated flowers by M_A produce more fruit and seeds
- ▶ The floral visitation component of the moth-plant interaction is mutualistic

OBJECTIVES

Identify the key biological aspects of the system.

Create a minimal model that describes the population dynamics of the system $P-M_L-M_A$.

Can this model predict coexistence of a plant and a pollinator that is also its herbivore?

SYSTEM OF EQUATIONS

$$\begin{aligned}\frac{dP}{dt} &= \left(n + \frac{\kappa M_A}{1 + \mu M_A} \right) P \left(1 - \frac{P}{K} \right) - \frac{a M_L P}{1 + ahP} \\ \frac{dM_L}{dt} &= b M_A - m_L M_L - \frac{\chi M_L P}{1 + uP} \\ \frac{dM_A}{dt} &= \frac{\chi M_L P}{1 + uP} - m_A M_A\end{aligned}$$

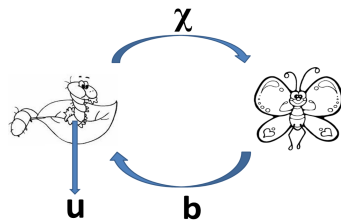
SYSTEM OF EQUATIONS

Setting some parameters:

$$\frac{dP}{dt} = \left(1 + \frac{3M_A}{1 + M_A}\right) P(1 - P) - \frac{M_L P}{1 + 0.3P}$$

$$\frac{dM_L}{dt} = bM_A - 0.2M_L - \frac{\chi M_L P}{1 + uP}$$

$$\frac{dM_A}{dt} = \frac{\chi M_L P}{1 + uP} - 0.2M_A$$



ANALYTICAL ANALYSIS

Now we search for equilibria:

$$\frac{dP}{dt} = \frac{dM_A}{dt} = \frac{dM_L}{dt} = 0$$

$$P^* = \frac{1}{\frac{\chi(b-m_A)}{m_L m_A} - u}$$

$$M_L^* = \left(n + \frac{3M_A^*}{1 + M_A^*} \right) (1 + hP^*)(1 - P^*)$$

$$M_A^* = \frac{\chi P^* M_L^*}{m_A (1 + uP^*)}$$

ANALYTICAL ANALYSIS

P solution:

Gives a condition in order to get a biologically relevant equilibrium:

$$P^* = \frac{1}{\frac{\chi(b-m_A)}{m_L m_A} - u} \Rightarrow \frac{u}{\chi} < \frac{b - m_A}{m_L m_A}$$

ANALYTICAL ANALYSIS

```
In [3]: s[1][1]
Out[3]: sqrt(152587890625.0*b**8*x**8 - 48828125000.0*b**7*u*x**7 - 366210937500.0*b**7*x**8 - 4882812500.0*b**6*h*x**7 + 6835937500.0
*b**6*u**2*x**6 + 97656250000.0*b**6*u*x**7 + 439453125000.0*b**6*x**8 + 4882812500.0*b**6*x**7 + 976562500.0*b**5*h*u*x**6 + 13671875
000.0*b**5*h*x**7 + 1953125000.0*b**5*h*x**6 + 5468750000.0*b**5*u**3*x**5 + 1132812500.0*b**5*u**2*x**6 - 91796875000.0*b**5*u*x**7 -
976562500.0*b**5*u*x**6 - 288085937500.0*b**5*x**8 - 13671875000.0*b**5*x**7 + 156250000.0*b**4*h**2*x**6 - 781250000.0*b**4*h*u**2*x**5 -
1914062500.0*b**4*h*u*x**6 - 312500000.0*b**4*h*x**5 - 107421875000.0*b**4*h*x**7 - 820312500.0*b**4*h*x**6 + 27343750.0*b**4*u*x**4
*x**4 + 783125000.0*b**4*u**3*x**5 + 7968750000.0*b**4*u**2*x**6 + 781250000.0*b**4*u*x**5 + 46875000000.0*b**4*u*x**7 + 19140625000.
0*b**4*u*x**6 + 109863281250.0*b**4*x**8 + 10742187500.0*b**4*x**7 + 156250000.0*b**4*x**6 - 125000000.0*b**3*h**2*u*x**5 - 125000000.0
*b**3*h**2*x**6 - 12500000.0*b**3*h**2*x**5 + 31250000.0*b**3*h*u**3*x**4 + 100000000.0*b**3*h*u**2*x**5 + 18750000.0*b**3*h*u**2*x**4 +
1140625000.0*b**3*h*u*x**6 + 750000000.0*b**3*h*u*x**5 + 3906250000.0*b**3*h*x**7 + 578125000.0*b**3*h*x**6 + 125000000.0*b**3*h*x**5 -
8750000.0*b**3*u**5*x**3 + 265625000.0*b**3*u**4*x**4 - 3687500000.0*b**3*u**3*x**5 - 31250000.0*b**3*u**3*x**4 - 3015625000.0*b**3*u**2*x
**6 - 1000000000.0*b**3*u**2*x**5 - 13671875000.0*b**3*u*x**7 - 1140625000.0*b**3*u*x**6 - 125000000.0*b**3*u*x**5 - 25195312500.0*b**3
*x**8 - 3906250000.0*b**3*x**7 - 1250000000.0*b**3*x**6 + 2500000.0*b**2*h**2*u**2*x**4 + 75000000.0*b**2*h**2*u*x**5 + 5000000.0*b**2*h**2
**2*x**4 + 375000000.0*b**2*h**2*x**6 + 75000000.0*b**2*h**2*x**5 + 2500000.0*b**2*h**2*x**4 - 62500.0*b**2*h*u**4*x**3 - 23750000.0*b**2
h*u**3*x**4 - 50000.0*b**2*h*u**3*x**3 - 41250000.0*b**2*h*u**2*x**5 - 21250000.0*b**2*h*u**2*x**4 - 3031250000.0*b**2*h*u*x**6 - 3750000
00.0*b**2*h*u*x**5 - 5000000.0*b**2*h*u*x**4 - 742187500.0*b**2*h*x**7 - 1656250000.0*b**2*h*x**6 - 75000000.0*b**2*h*x**5 + 17500.0*b**2
u**6*x**2 + 600000.0*b**2*u**5*x**3 + 96250000.0*b**2*u**4*x**4 + 625000.0*b**2*u**4*x**3 + 96250000.0*b**2*u**3*x**5 + 23750000.0*b**2
u**3*x**4 + 623437500.0*b**2*u**2*x**6 + 412500000.0*b**2*u**2*x**5 + 2500000.0*b**2*u**2*x**4 + 2281250000.0*b**2*u*x**7 + 3031250000.0
b**2*u*x**6 + 75000000.0*b**2*u*x**5 + 3437500000.0*b**2*x**8 + 7421875000.0*b**2*x**7 + 3750000000.0*b**2*x**6 - 1000000.0*b**2*h**2*u**2*x**
4 - 15000000.0*b**2*h**2*u*x**5 - 200000.0*b**2*h**2*u*x**4 - 5000000.0*b**2*h**2*x**6 - 15000000.0*b**2*h**2*x**5 - 1000000.0*b**2*h**2*x**4 + 500.0*b
h**5*x**2 + 25000.0*b**h*u**4*x**3 + 500.0*b**h*u**4*x**2 + 575000.0*b**h*u**3*x**4 + 20000.0*b**h*u**3*x**3 + 70000000.0*b**h*u**2*x**5 +
6250000.0*b**h*u**2*x**4 + 37812500.0*b**h*u*x**6 + 70000000.0*b**h*u*x**5 + 200000.0*b**h*u*x**4 + 718750000.0*b**h*x**7 + 21562500.0*b**h*x
**6 + 15000000.0*b**h*x**5 - 200.0*b**b**7*x - 7500.0*b**b**6*x**2 - 1350000.0*b**b**5*x**3 - 500.0*b**b**5*x**2 + 15375000.0*b**b**4*x**4 - 250
000.0*b**b**4*x**3 - 123750000.0*b**b**3*x**5 - 5750000.0*b**b**3*x**4 - 665625000.0*b**b**2*x**6 - 70000000.0*b**b**2*x**5 - 1000000.0*b**b**2*x
**4 - 2031250000.0*b**b**u*x**7 - 378125000.0*b**b**u*x**6 - 15000000.0*b**b**u*x**5 - 257812500.0*b**b**x**8 - 718750000.0*b**b**x**7 - 50000000.0*b**b
**x**6 + 100
00.0*h**2*u**2*x**4 + 100000.0*h**2*u*x**5 + 200000.0*h**2*u*x**4 + 2500000.0*h**2*x**6 + 1000000.0*h**2*x**5 + 10000.0*h**2*x**4 - 100.0
h**u**4*x**2 - 2500.0*h**u**4*x**3 - 100.0*h**u**4*x**2 - 45000.0*h**u**3*x**4 - 2000.0*h**u**3*x**3 - 4250000.0*h**u**2*x**5 - 55000.0*h**u
**2*x**4 - 18125000.0*h**u*x**6 - 4500000.0*h**u*x**5 - 200000.0*h**u*x**4 - 28125000.0*h**x**7 - 10625000.0*h**x**6 - 1000000.0*h**x**5 + u**8 + 4
0.0*u**7*x + 800.0*u**6*x**2 + 100000.0*u**5*x**3 + 100.0*u**5*x**2 + 912500.0*u**4*x**4 + 2500.0*u**4*x**3 + 6250000.0*u**3*x**5 + 45000
0.0*u**3*x**4 + 28750000.0*u**2*x**6 + 4250000.0*u**2*x**5 + 100000.0*u**2*x**4 + 75000000.0*u*x**7 + 18125000.0*u*x**6 + 1000000.0*u*x**5 +
8203125.0*x**8 + 28125000.0*x**7 + 2500000.0*x**6)/(156250.0*b**3*x**4 - 12500.0*b**2*u*x**3 - 93750.0*b**2*x**4 + 250.0*b**u**2*x**2 + 5
0000.0*b**u*x**3 + 18750.0*b**x**4 - 50.0*u**2*x**2 - 500.0*u*x**3 - 1250.0*x**4) - 0.02*(390625.0*b**4*x**4 - 62500.0*b**3*u*x**3 - 6250
00.0*b**3*x**4 - 12500.0*b**2*h*x**3 + 3750.0*b**2*u**2*x**2 + 62500.0*b**2*u*x**3 + 281250.0*b**2*x**4 + 12500.0*b**2*x**3 + 500.0*b
h**u*x**2 + 5000.0*b**h*x**3 + 500.0*b**h*x**2 - 100.0*b**b**3*x - 2000.0*b**b**2*x**2 - 17500.0*b**b**x**3 - 500.0*b**b**x**2 - 50000.0*b**b**x
- 50000.0*b**x**3 - 100.0*h**u*x**2 - 5000.0*h**x**3 - 100.0*h**x**2 + u**4 + 20.0*u**3*x + 250.0*u**2*x**2 + 1500.0*u*x**3 + 100.0*u*x**2
+ 3125.0*x**4 + 500.0*x**3)/(x**2*(5.0*b - 1.0)*(25.0*b*x - u - 5.0*x)**2)
```

Figure: M_L Solution

ANALYTICAL ANALYSIS

```
In [2]: s[1][0]
Out[2]: 25.0*x**2*(5.0*b - 1.0)*(sqrt(152587890625.0*b**8*x**8 - 48828125000.0*b**7*u*x**7 - 366210937500.0*b**7*x**8 - 4882812500.0*b**6*h*x**7 + 6835937500.0*b**6*u*x**7 + 2*x**6 + 97656250000.0*b**6*u*x**7 + 439453125000.0*b**6*x**8 + 4882812500.0*b**6*x**7 + 976562500.0*b**5*h*u*x**6 + 13671875000.0*b**5*h*x**7 + 1953125000.0*b**5*h*x**6 - 546875000.0*b**5*u**3*x**5 - 111328125000.0*b**5*u**2*x**6 - 91796875000.0*b**5*u*x**7 - 9765625000.0*b**5*u*x**6 - 280085937500.0*b**5*x**8 - 13671875000.0*b**5*x**7 + 156250000.0*b**4*h**2*x**6 - 781250000.0*b**4*h*u*x**5 + 1914062500.0*b**4*h*u*x**6 - 312500000.0*b**4*h*u*x**5 - 10742187500.0*b**4*h*x**7 - 8203125000.0*b**4*h*x**6 + 273437500.0*b**4*u*x**4 + 7831250000.0*b**4*u**3*x**5 + 79687500000.0*b**4*u**2*x**6 + 781250000.0*b**4*u**2*x**5 + 46875000000.0*b**4*u*x**7 + 1914062500.0*b**4*u*x**6 + 108963281250.0*b**4*x**8 + 10742187500.0*b**4*x**7 + 156250000.0*b**4*x**6 - 12500000.0*b**3*h**2*u*x**5 + 125000000.0*b**3*h**2*x**6 - 12500000.0*b**3*h**2*x**5 + 3125000.0*b**3*h*u**3*x**4 + 100000000.0*b**3*h*u**2*x**5 + 1875000.0*b**3*h*u**2*x**4 + 1140625000.0*b**3*h*u*x**6 + 750000000.0*b**3*h*u*x**5 + 3906250000.0*b**3*h*x**7 + 5761250000.0*b**3*h*x**6 + 125000000.0*b**3*h*x**5 - 8750000.0*b**3*u**5*x**3 - 265625000.0*b**3*u**4*x**4 - 3687500000.0*b**3*u**3*x**5 - 31250000.0*b**3*u**3*x**4 - 30156250000.0*b**3*u**2*x**6 - 100000000.0*b**3*u**2*x**5 + 75000000.0*b**3*u*x**7 - 1140625000.0*b**3*u*x**6 - 125000000.0*b**3*u*x**5 - 25195312500.0*b**3*x**8 - 39062500000.0*b**3*x**7 - 1250000000.0*b**3*x**6 + 2500000.0*b**2*h**2*u**2*x**4 + 75000000.0*b**2*h**2*u*x**5 + 5000000.0*b**2*h**2*u*x**4 + 375000000.0*b**2*h**2*x**6 + 75000000.0*b**2*h**2*x**5 + 2500000.0*b**2*h**2*x**4 - 625000.0*b**2*h*u**4*x**3 - 23750000.0*b**2*h*u**3*x**4 - 500000.0*b**2*h*u**3*x**3 - 412500000.0*b**2*h*u**2*x**5 - 212500000.0*b**2*h*u**2*x**4 - 3031250000.0*b**2*h*u*x**6 - 375000000.0*b**2*h*u*x**5 - 5000000.0*b**2*h*u*x**4 - 742187500.0*b**2*h*x**7 - 1656250000.0*b**2*h*x**6 - 75000000.0*b**2*h*x**5 + 175000.0*b**2*u**6*x**2 + 6000000.0*b**2*u**5*x**3 + 96250000.0*b**2*u**4*x**4 + 625000.0*b**2*u**4*x**3 + 962500000.0*b**2*u**3*x**5 + 23750000.0*b**2*u**3*x**4 + 623437500.0*b**2*u**2*x**6 + 412500000.0*b**2*u**2*x**5 + 2500000.0*b**2*u**2*x**4 + 22812500000.0*b**2*u*x**7 + 3831250000.0*b**2*u*x**6 + 75000000.0*b**2*u*x**5 + 34375000000.0*b**2*x**8 + 7421875000.0*b**2*x**7 + 375000000.0*b**2*x**6 - 1000000.0*b**h**2*u**2*x**4 - 15000000.0*b**h**2*u*x**5 - 2000000.0*b**h**2*u*x**4 - 5000000.0*b**h**2*x**6 - 15000000.0*b**h**2*x**5 - 1000000.0*b**h**2*x**4 + 500.0*b**h*u**5*x**2 + 25000.0*b**h*u**4*x**3 + 500.0*b**h*u**4*x**2 + 5750000.0*b**h*u**3*x**4 + 20000.0*b**h*u**3*x**3 + 70000000.0*b**h*u**2*x**5 + 6250000.0*b**h*u**2*x**4 + 378125000.0*b**h*u*x**6 + 70000000.0*b**h*u*x**5 + 2000000.0*b**h*u*x**4 + 718750000.0*b**h*x**7 + 21562500.0*b**h*x**6 + 15000000.0*b**h*x**5 - 200.0*b**u**7*x - 7500.0*b**u**6*x**2 - 1350000.0*b**u**5*x**3 - 500.0*b**u**5*x**2 - 15375000.0*b**u**4*x**4 - 250000.0*b**u**4*x**3 - 123750000.0*b**u**3*x**5 - 5750000.0*b**u**3*x**4 - 666525000.0*b**u**2*x**6 - 70000000.0*b**u**2*x**5 - 1000000.0*b**u**2*x**4 - 203125000.0*b**u*x**7 - 378125000.0*b**u*x**6 - 15000000.0*b**u*x**5 - 257812500.0*b**u*x**8 - 718750000.0*b**x**7 - 50000000.0*b**x**6 + 10000.0*h**h**2*u**2*x**4 + 1000000.0*h**h**2*u*x**5 + 200000.0*h**h**2*u*x**4 + 2500000.0*h**h**2*x**6 + 1000000.0*h**h**2*x**5 + 100000.0*h**h**2*x**4 - 100.0*h**h*u**5*x**2 - 2500.0*h**h*u**4*x**3 - 100.0*h**h*u**4*x**2 - 450000.0*h**h*u**3*x**4 - 2000.0*h**h*u**3*x**3 - 4250000.0*h**u**2*x**5 - 550000.0*h**u**2*x**4 - 18125000.0*h**u*x**6 - 4500000.0*h**u*x**5 - 200000.0*h**u*x**4 - 28125000.0*h**x**7 - 10625000.0*h**x**6 - 1000000.0*h**x**5 + u**8 + 40.0*u**7*x + 800.0*u**6*x**2 + 100000.0*u**5*x**3 + 100.0*u**4*x**4 + 91250.0*u**4*x**2 + 2500.0*u**4*x**3 + 625000.0*u**3*x**5 + 450000.0*u**3*x**4 + 28750000.0*u**2*x**6 + 4250000.0*u**2*x**5 + 100000.0*u**2*x**4 + 75000000.0*u*x**7 + 18125000.0*u*x**6 + 1000000.0*u*x**5 + 8203125.0*x**8 + 28125000.0*x**7 + 25000000.0*x**6)/(156250.0*b**3*x**4 - 12500.0*b**2*u*x**3 - 93750.0*b**2*x**4 + 250.0*b**u**2*x**2 + 5000.0*b**u*x**3 + 18750.0*b**x**4 - 50.0*u**2*x**2 - 500.0*u*x**3 - 1250.0*x**4) - 0.02*(390625.0*b**4*x**4 - 5025000.0*b**3*u*x**3 - 6250000.0*b**3*x**4 - 12500.0*b**2*h*x**3 + 3750.0*b**2*u**2*x**2 + 625000.0*b**2*u*x**3 + 2812500.0*b**2*x**4 + 125000.0*b**2*x**3 + 500.0*b**h*u*x**2 + 5000.0*b**h*x**3 + 500.0*b**h*x**2 - 100.0*b**u**3*x - 20000.0*b**u**2*x**2 - 175000.0*b**u*x**3 - 500.0*b**u*x**2 - 500000.0*b**x**4 - 50000.0*b**x**3 - 100.0*h**u*x**2 - 500.0*h**x**3 - 100.0*h**x**2 + u**4 + 20.0*u**3*x + 250.0*u**2*x**2 + 1500.0*u*x**3 + 100.0*u*x**2 + 3125.0*x**4 + 500.0*x**3)/(x**2*(5.0*b - 1.0)*(25.0*b*x - u - 5.0*x)**2)/(25.0*b*x - u - 5.0*x)**2
```

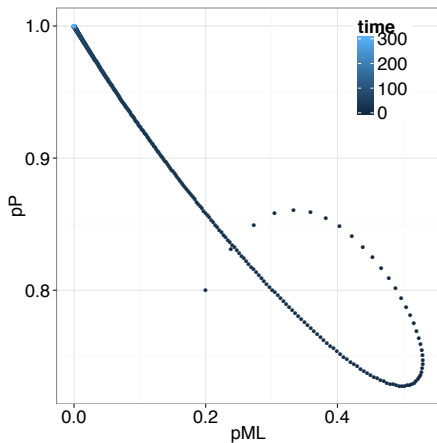
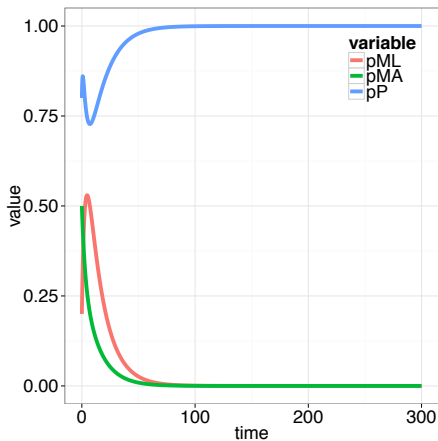
Figure: M_A Solution

ANALYTICAL ANALYSIS

$$J = \begin{pmatrix} -P^* \left(1 + \frac{3M_A^*}{1+M_A^*} + \frac{0.3M_L^*}{(1+hP^*)^2} \right) & \frac{-P^*}{1+hP^*} & \frac{3P^*(1-P^*)}{(1+M_A^*)^2} \\ \frac{-\chi M_L^*}{(1+uP^*)^2} & -0.2 - \frac{\chi P^*}{1+uP^*} & b \\ \frac{\chi M_L^*}{(1+uP^*)^2} & \frac{\chi P^*}{1+uP^*} & -0.2 \end{pmatrix}$$

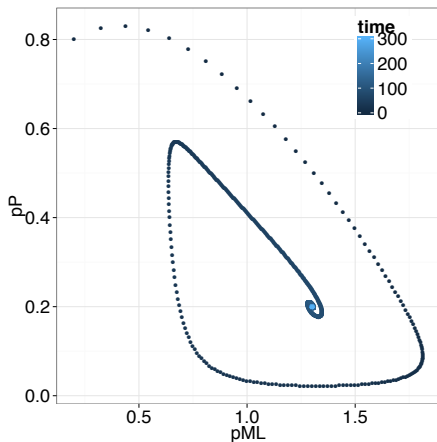
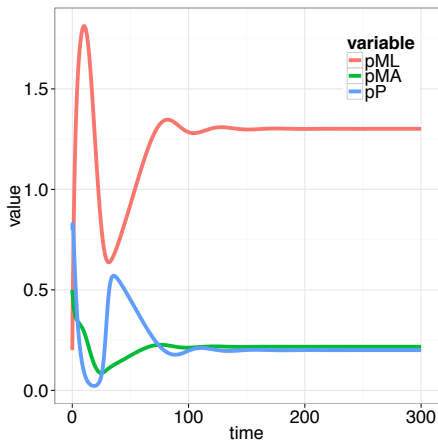
GRAPHICS

Setting $b = 0.5, u = 10$ (real part of eigenvalues negative):



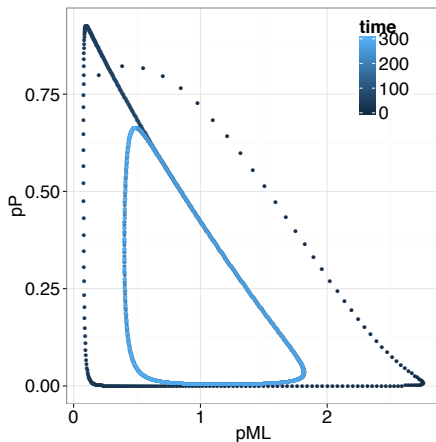
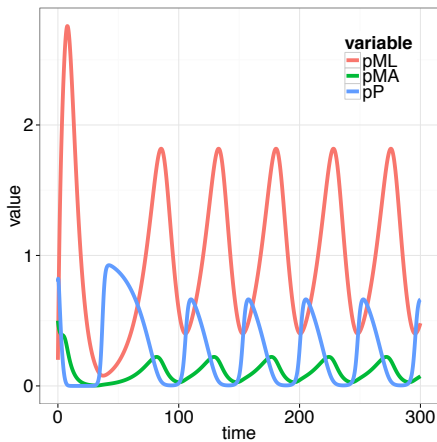
GRAPHICS

Setting $b = 1.4, u = 10$ (real part of eigenvalues negative):

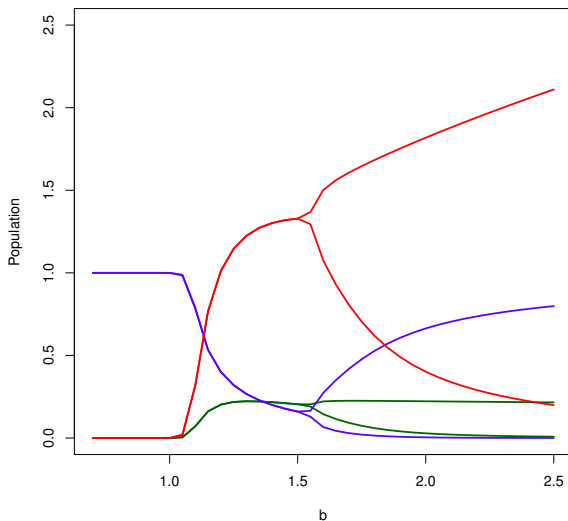


GRAPHICS

Setting $b = 2.0, u = 10$ (at least one eigenvalue positive):

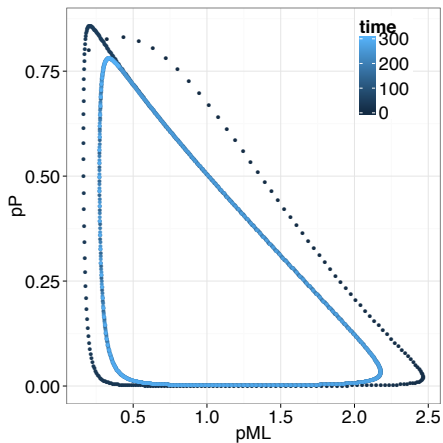
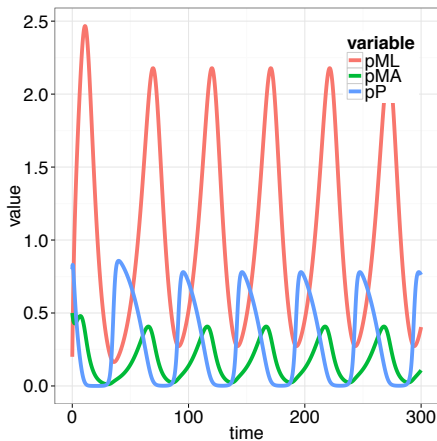


BIFURCATION DIAGRAM FOR b



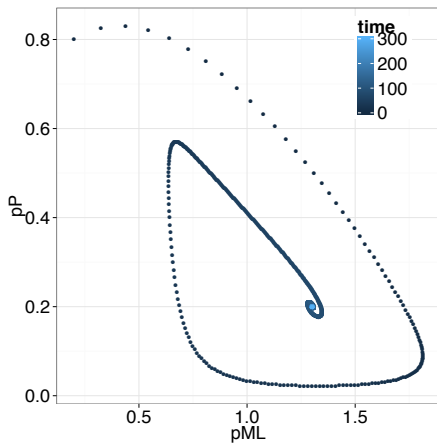
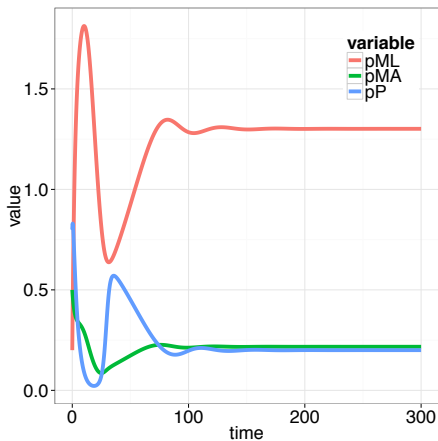
GRAPHICS

Setting $b = 1.4, u = 5$ (at least one eigenvalue positive):



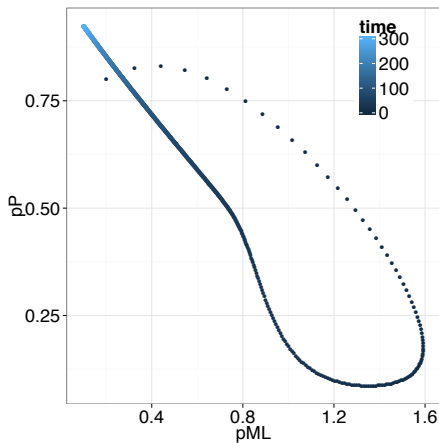
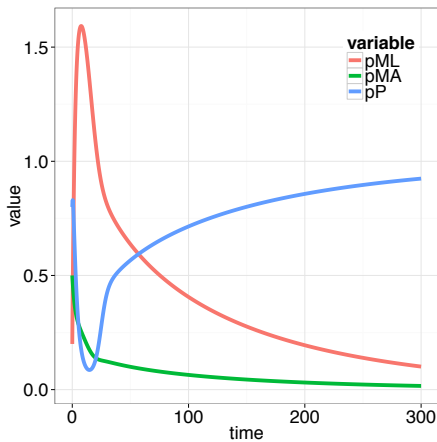
GRAPHICS

Setting $b = 1.4, u = 10$ (real part of eigenvalues negative):

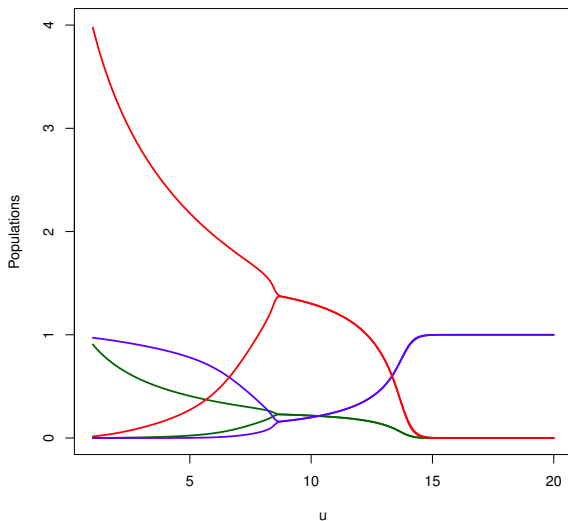


GRAPHICS

Setting $b = 1.4, u = 14$ (real part of eigenvalues negative):



BIFURCATION DIAGRAM FOR u



CONCLUSIONS

- ▶ This model can describe the population dynamics of the system $P-M_L-M_A$
- ▶ We identified three parameters (b, u, χ) that drive different dynamics of the system:
 - ▶ Extinction of the moth
 - ▶ Coexistence
 - ▶ Oscillations

FUTURE STEPS

- ▶ Evaluate the effects of K varying with M_A instead of being a fixed value
- ▶ Rescale the variables
- ▶ Make an exhaustive exploration of parameter values' variation

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