Analysis of a Mathematical Model for Egg Laying in a Seabird Colony

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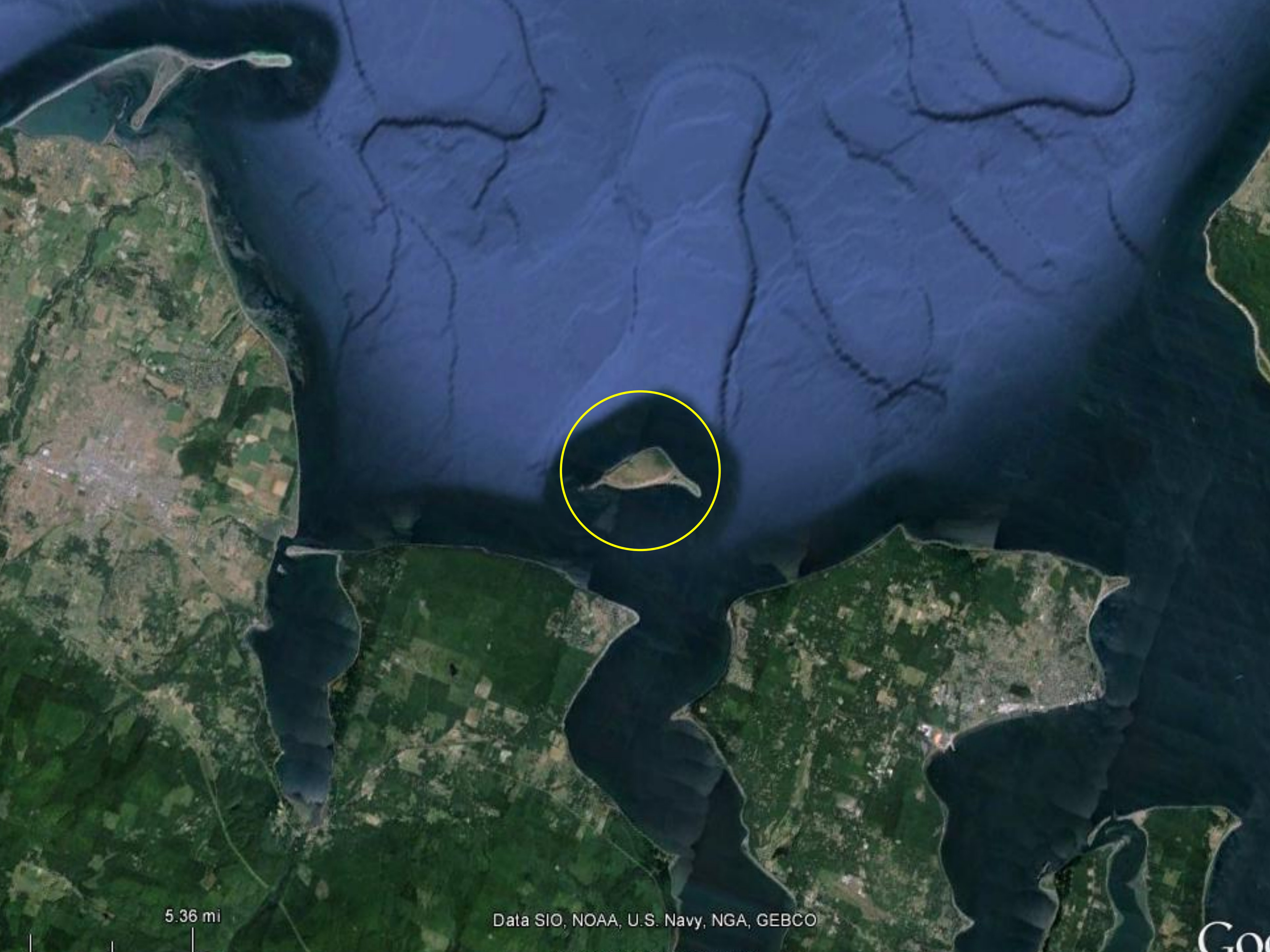
Outline

- Introduction/Context
- Research questions
- Specific mathematical objectives
- Methodology
- Results
- Conclusions/Summary

Introduction/Context

- Research of Glaucous-winged gull colony at Protection Island, Washington from 2006-2017
- Refuge established in 1988
- Hosts over 70,000 nesting seabirds


5.36 mi
Data SIO, NOAA, U.S. Navy, NGA, GEBCO


Protection
Island
National Wildlife Refuge
Established August 26, 1988
U.S. Fish and Wildlife Service
Department of the Interior

Introduction/Context

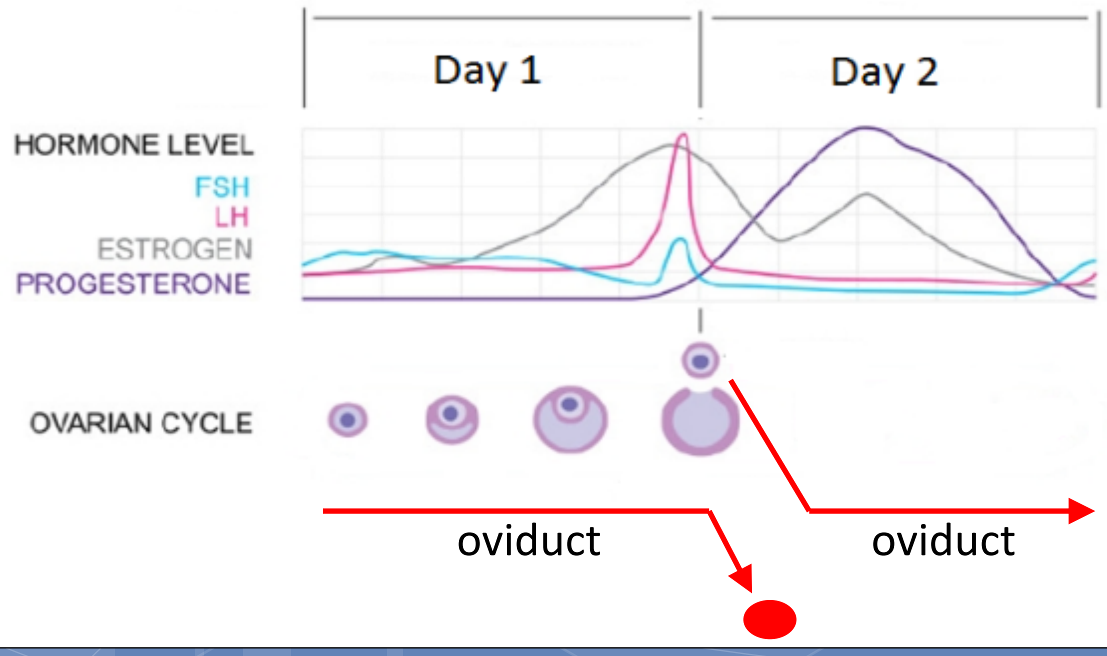
- Glaucous-winged gulls are "sentinels of climate change"
- Sensitive to small changes in climate
- Exhibit traditional animal behavior

Introduction/Context

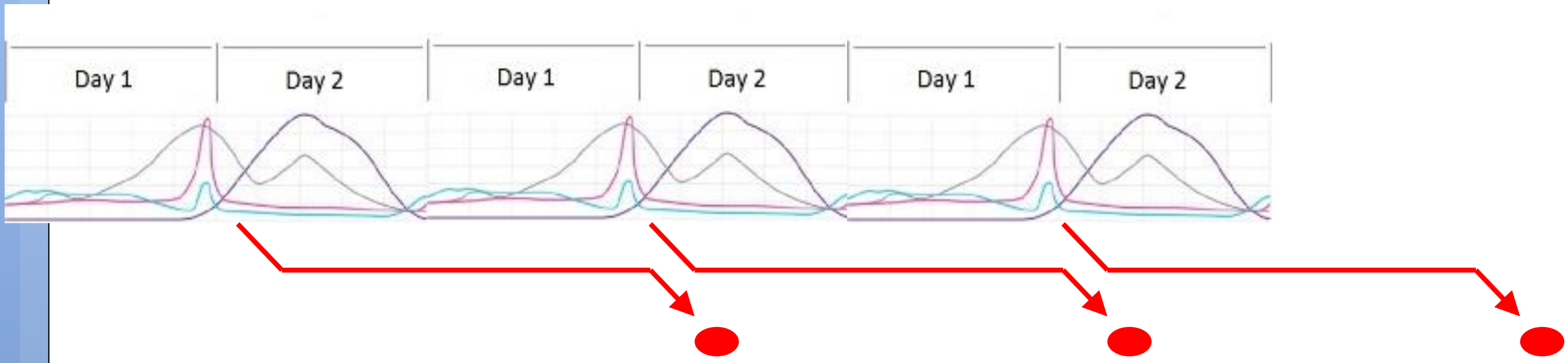
- High sea surface temperature (SST) associated with low food availability
- Combat food shortage through egg cannibalism
- Defensive response to cannibalism is egg-laying synchrony in dense parts of colony
- Synchrony: female gulls lay eggs together every other day
- Synchronization increases with increased colony density and social interaction

Female gull's ovulation cycle

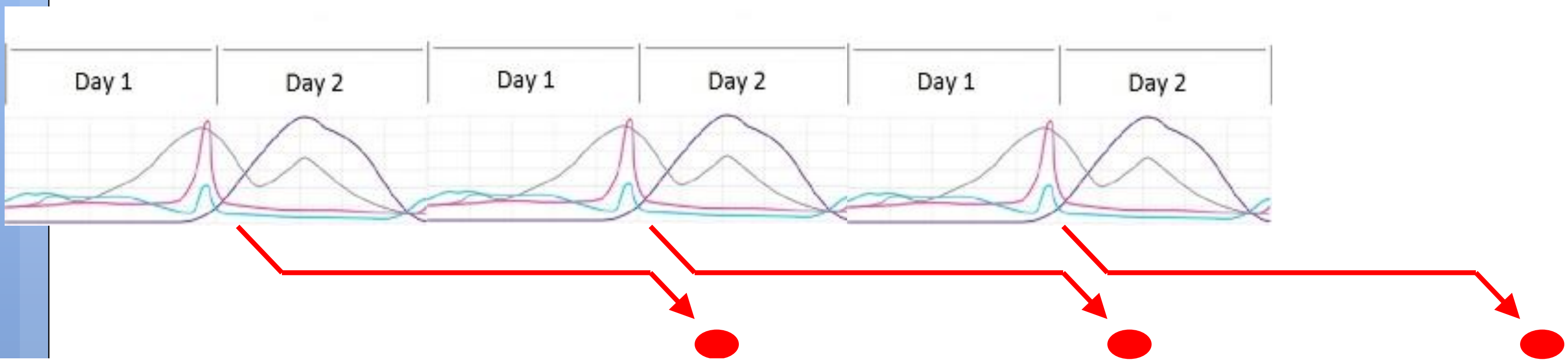
- Begin ovulating in spring at beginning of annual breeding season
- Ovulation cycle ~2 days long
- Results in an egg laid every two days
- About three eggs per nest

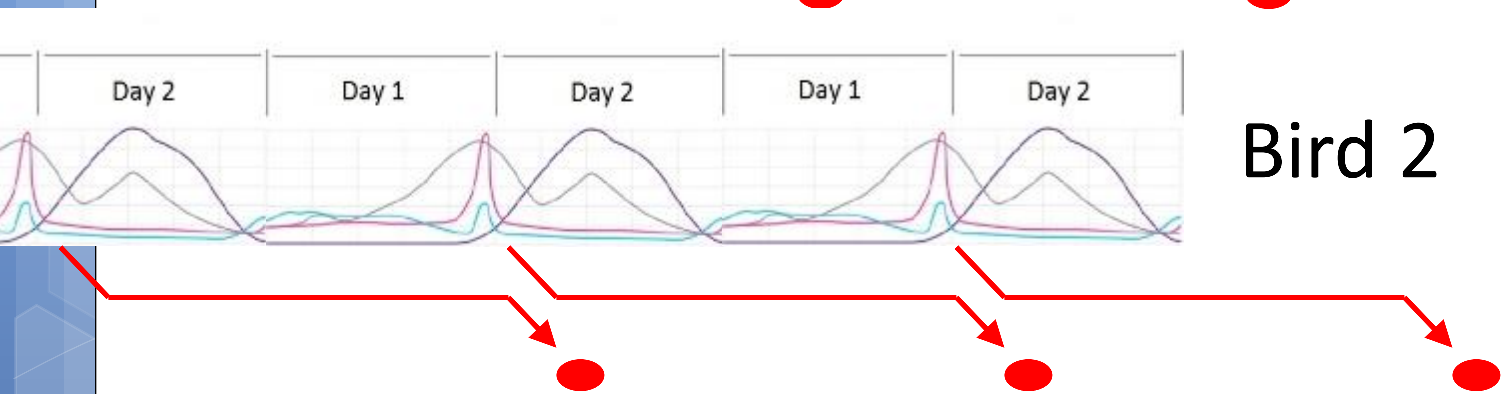


Bird 1



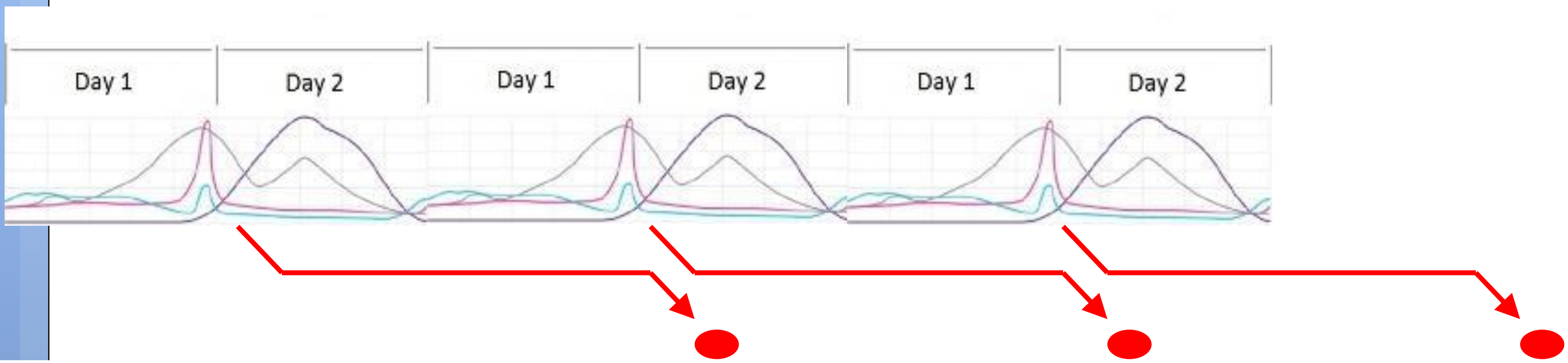
Bird 1



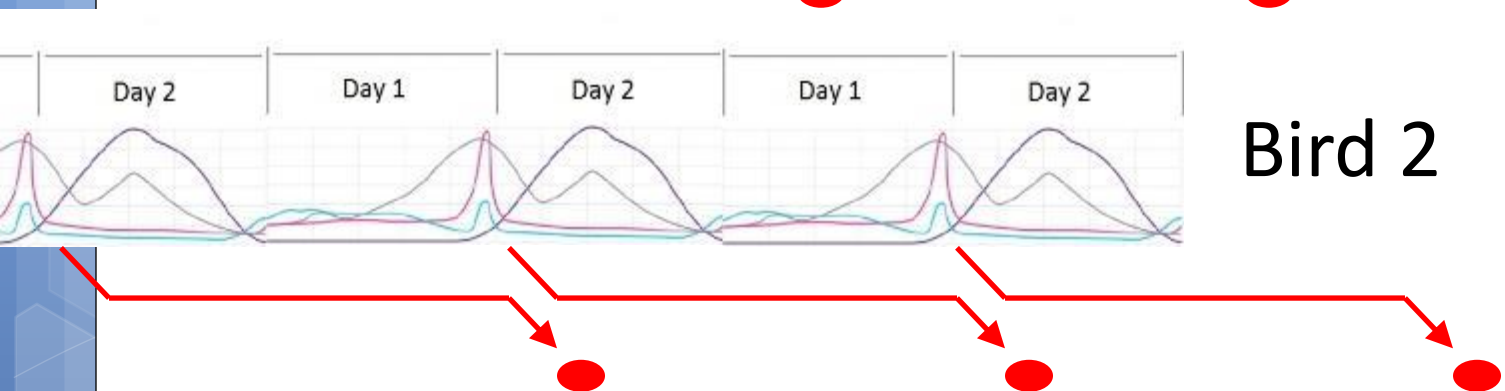


Bird 2

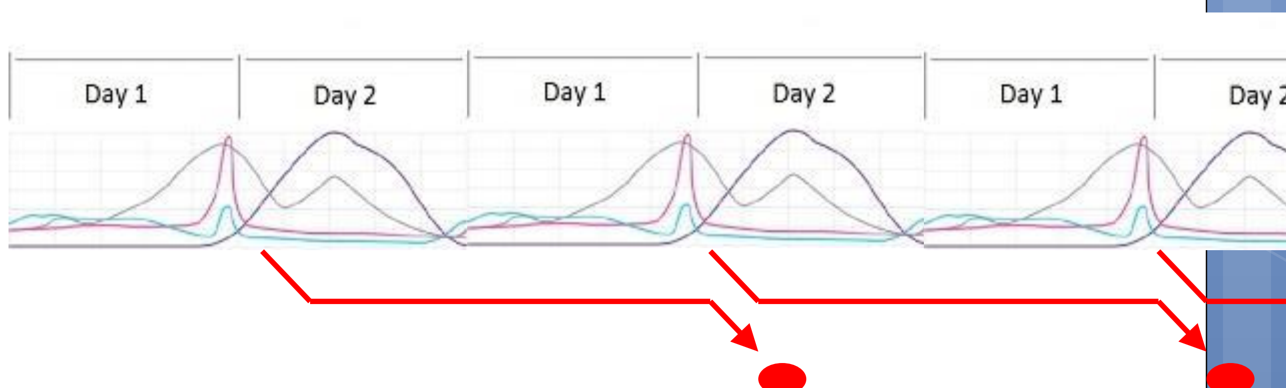
Bird 1

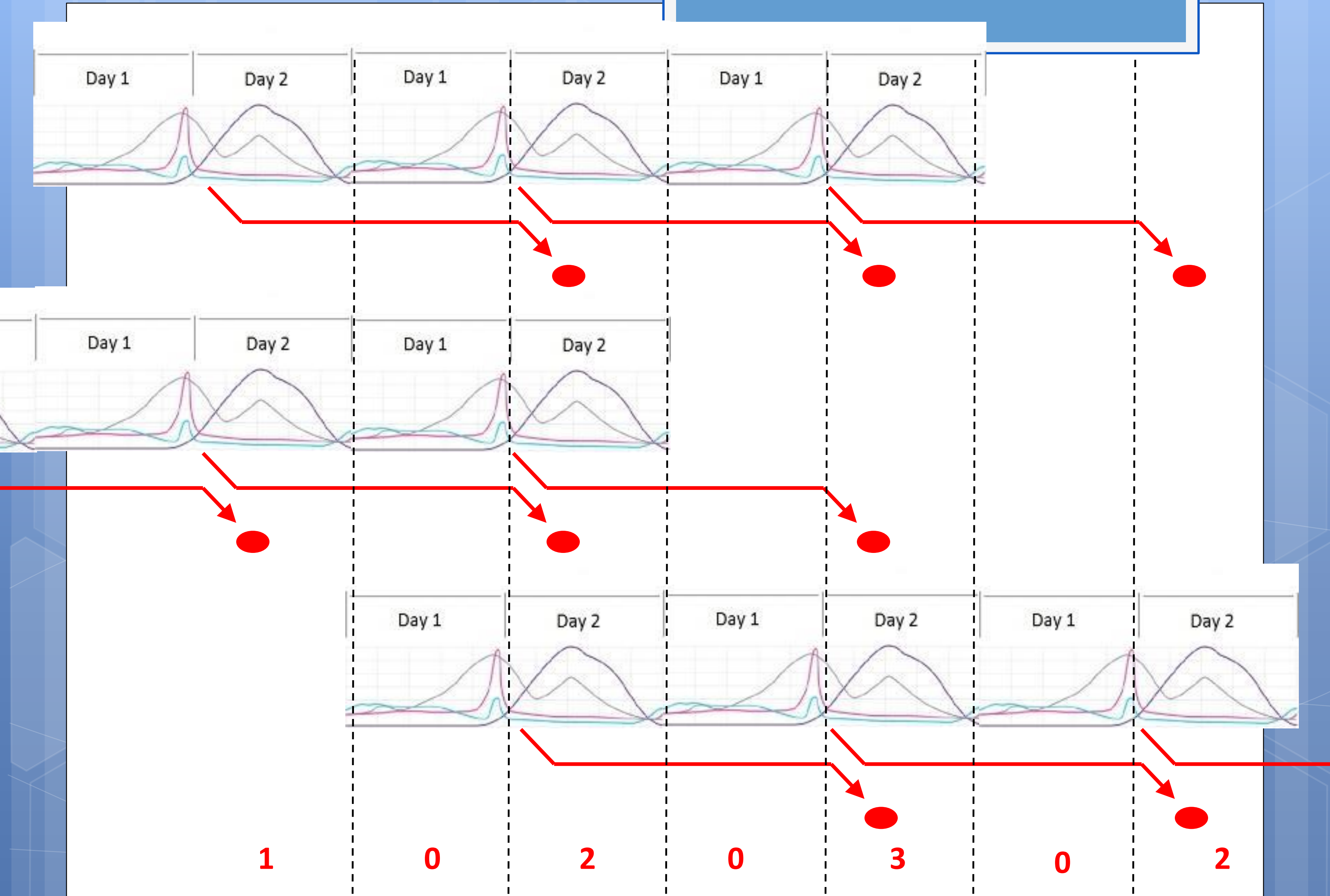


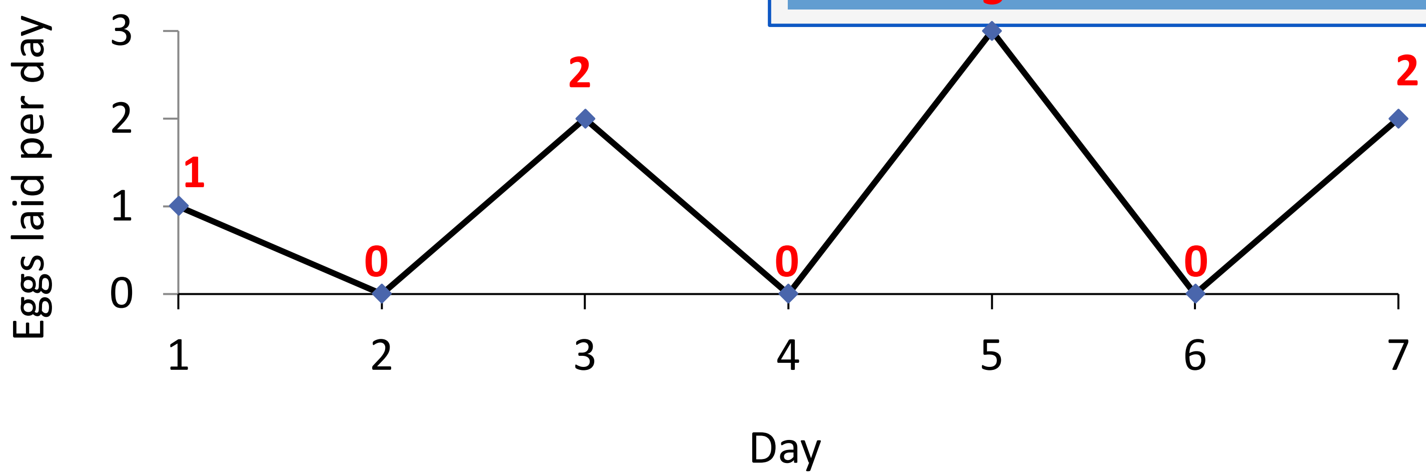
Bird 2

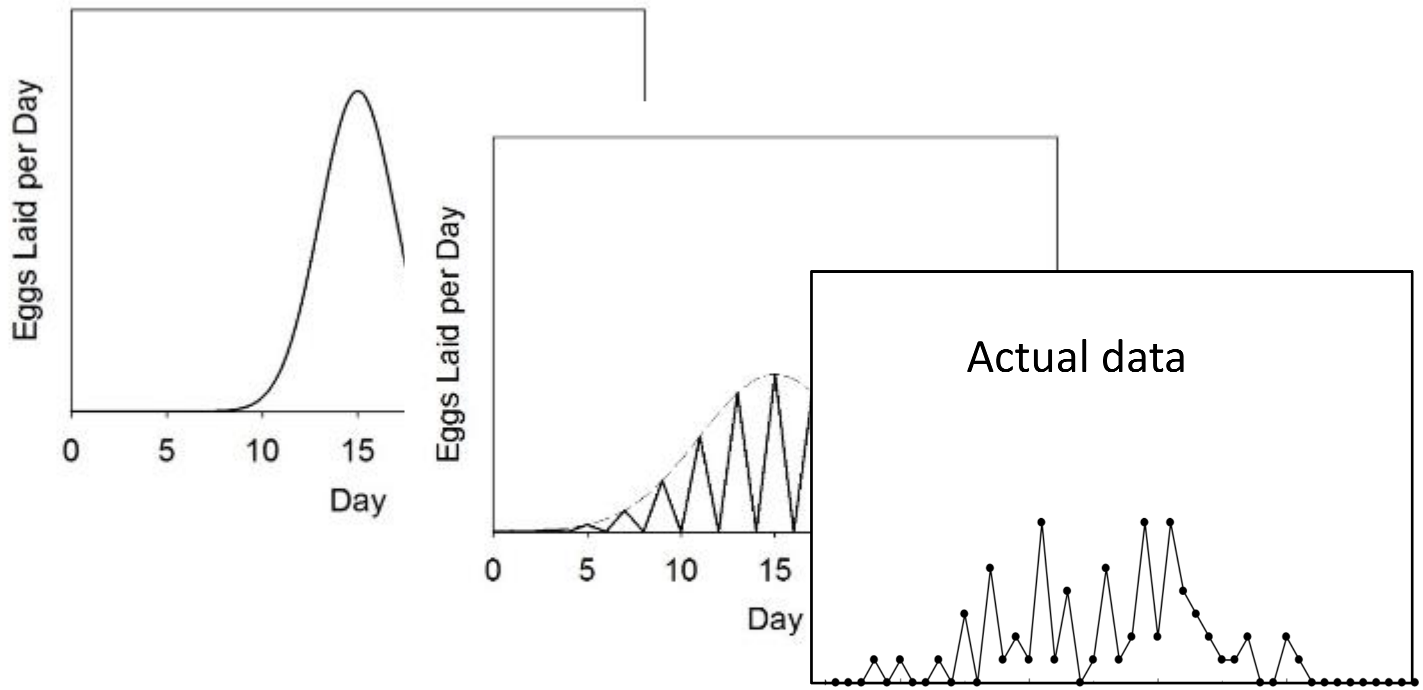


Bird 3




Day 1
Day 2
Day 1
Day 2
Day 1
Day 2
Day 1
Day 2
Day 1
Day 2
Day 1
Day 2
Day 1
Day 2
Day 1
Day 2
1
0
2
0
3
0
2


Eggs laid per day
3
2
1
0
1
2
3
4
5
6
7
Day
1
0
2
0
3
0
2


Eggs Laid per Day
0
5
10
15
Day
Eggs Laid per Day
0
5
10
15
Day
Actual data

Research Questions

Mathematical model: set of equations that describe biological system

We use a mathematical model to answer our research questions.

- Does our mathematical model predict the possibility of egg-laying synchrony?
- Does egg-laying synchrony lead to an increase in the number of eggs that survive cannibalism?

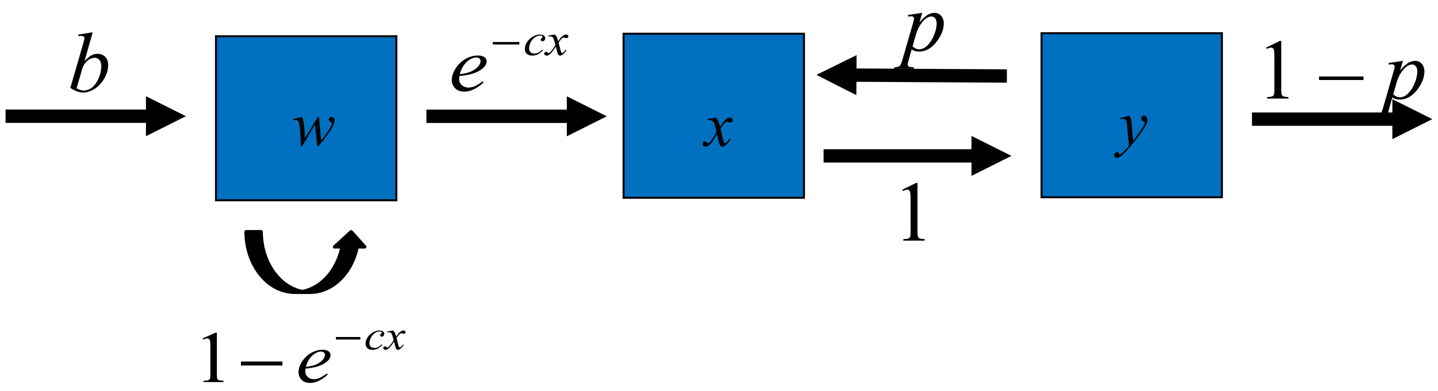
Specific mathematical goals

- Identify “steady states” of the model (states that persist over time)
- Find the “stability” of each steady state (Does the system tend toward the steady state or not?)
- Identify the effect of egg-laying synchrony on the total number of eggs produced by the colony

Methodology

- How mathematicians do research
  - Look for patterns
  - Make a claim about the pattern
  - Prove the claim
  - Proven claim is then called a theorem
- Our collaborative process
  - Worked together with Dorothea Gallos as part of National Science Foundation-funded REU
  - Did calculations individually to verify accuracy
  - Tried to keep in mind big picture/biological meaning
  - Used technology (graphing tools) to help visualize formulas
- Mathematical model

Model



- w: number of females not yet ovulating
- x: number of females in first day of ovulation cycle
- y: number of females in second day of ovulation cycle
- c: nest density
- Simplifying assumptions
  - The breeding season has no end
  - Number of females entering w class has no limit

Model equations

- Mathematical equations that describe biological system

$$\begin{cases} w_{t+1} = b + w_t\left(1 - e^{-cx_t}\right) \\ x_{t+1} = w_t e^{-cx_t} + py_t \\ y_{t+1} = x_t \end{cases}$$

Time step = 1 day

$$b, c > 0$$

$$0 < p < 1$$

Definitions: “equilibrium” & “2-cycle”

- Equilibrium: state in which the system does not change through time
  - Example: constant egg laying
- Two-cycle: state in which system oscillates between two values

  - Example: synchronous egg laying

Methodology: Equilibrium

- Found equilibrium equations and then solved for equilibrium

$$w = (1 - e^{-cx})w + b$$

$$x = we^{-cx} + py$$

$$y = x$$

$$\longrightarrow$$

$$w_e = be^{\frac{cb}{1-p}}$$

$$x_e = \frac{b}{1-p}$$

$$y_e = \frac{b}{1-p}$$

Methodology: Equilibrium

- Characteristic equation

$$\lambda^3 - \lambda^2\left(q(c) - cb\right) - \lambda\left(p + cb\right) + pq(c) = 0$$

$$q(c) \equiv 1 - e^{\frac{-bc}{1-p}} \qquad \text{Note}: \ 0 < q(c) < 1$$

- Found stability of equilibrium using mathematical conditions called Jury Conditions (Lewis 1970)

$$\text{J1.} \ (1-p)(1-q(c)) > 0$$

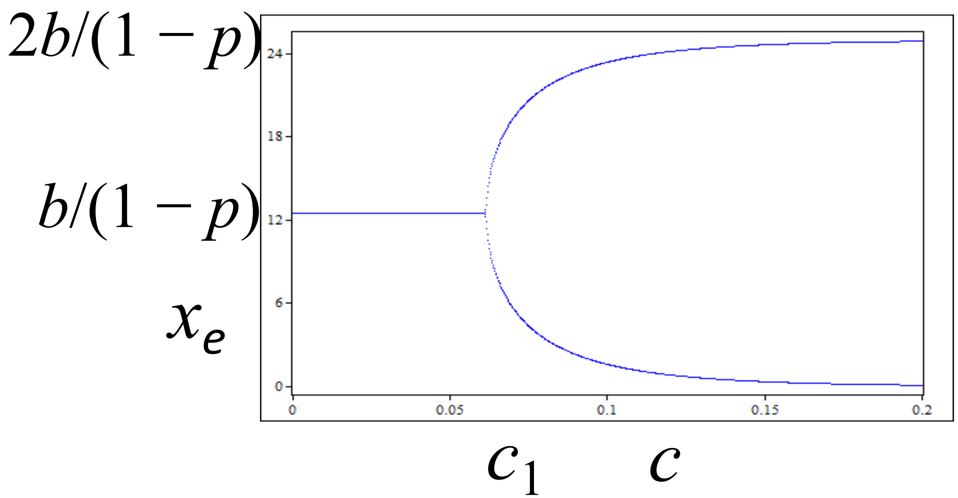
$$\text{J2.} \ (1-p)(1+q(c)) - 2bc > 0$$

$$\text{J3.} \ pq(c) < 1$$

$$\text{J4.} \ 1 - p^2 q(c)^2 > \left|\left(p + cb\right) + pq(c)\left(cb - q(c)\right)\right|$$

Results: Equilibrium

- Equilibrium (constant egg laying) is stable when nest density value is less than critical value c_1 and unstable when nest density is greater than c_1.



Methodology: “two-cycle”

- Found first composite map by modifying model equations that “see” only every other time step

$$w_{t+2} = b + (1 - e^{-c(py_t + w_t e^{-cx_t})})(b + (1 - e^{-cx_t}) w_t)$$

$$x_{t+2} = px_t + (b + (1 - e^{-cx_t}) w_t) e^{-c(py_t + w_t e^{-cx_t})}$$

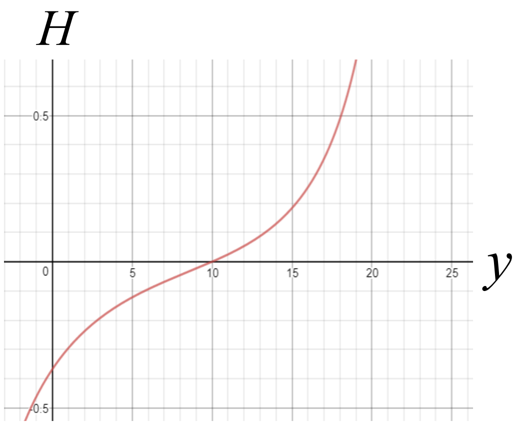
$$y_{t+2} = py_t + w_t e^{-cx_t}$$

$$H(y) \equiv \frac{y(1-p)}{b(2e^{cy} - 1) + y(1 - e^{cy})(1-p)} - e^{\frac{-2cb}{1-p} + cy}$$

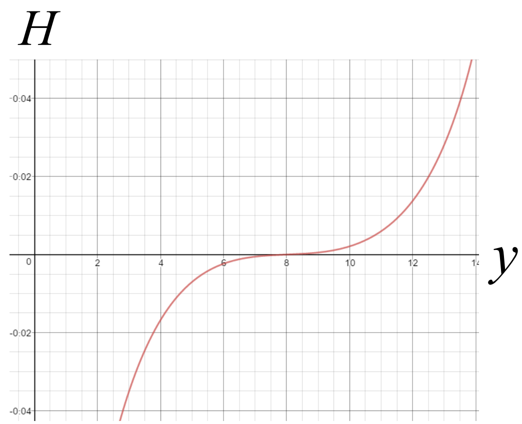
- The roots of H (y values that make H equal 0) are equilibria of composite map and therefore points of 2-cycle

Results: Roots of H(y)

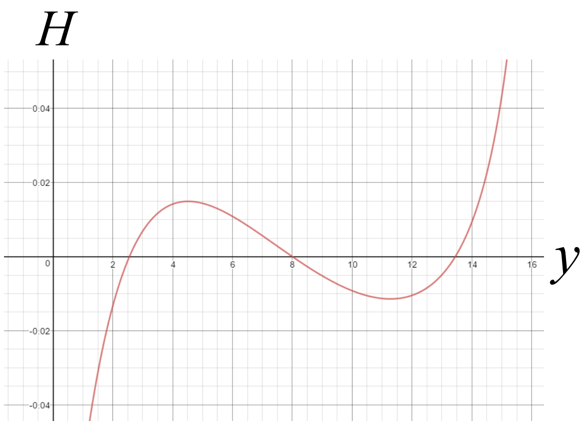
Theorem $H(y)$ has exactly one or exactly three roots.



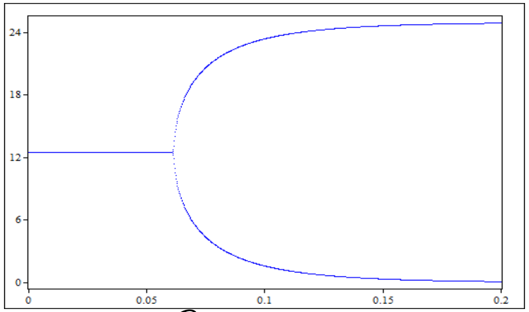
$c < c_1$



$c = c_1$



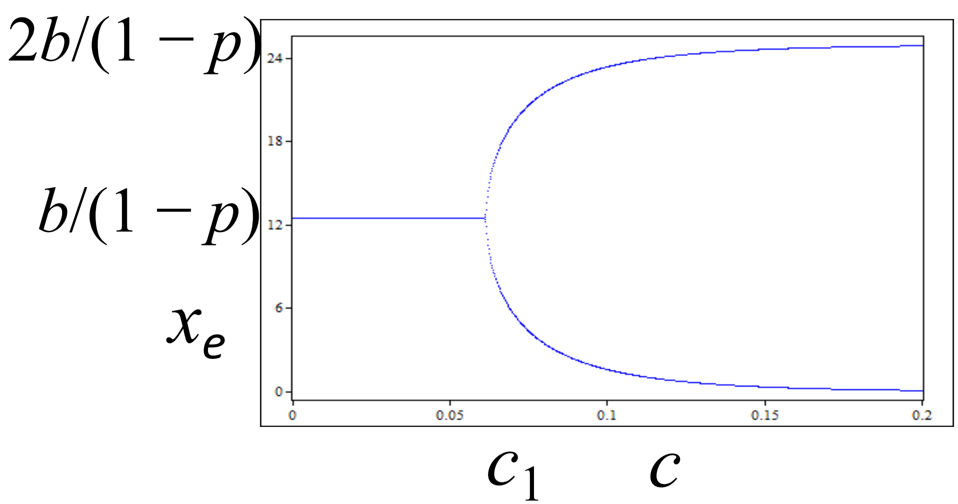
$c > c_1$



c_1

Results: Two-cycle

- Equilibrium (constant egg laying) is stable when nest density value is less than critical value c_1 and unstable when nest density is greater than c_1.
- Two cycle (every-other-day egg laying) is stable when nest density value is greater than critical value c_1.



Results: effect of egg-laying synchrony

- A greater number of eggs in the colony survive cannibalism if females lay eggs synchronously than if they do not lay eggs synchronously.
- Egg has less chance of being cannibalized if laid in synchrony with many other eggs.

Conclusions/Summary

- Two steady states: equilibrium & two-cycle
- Does our mathematical model predict the possibility of egg-laying synchrony?
  - When nest density is less than critical value, equilibrium is stable, i.e., a constant number of eggs is laid in the colony.
  - When nest density is greater than critical value, two-cycle is stable, i.e., eggs are laid every other day in the colony.
  - Every-other-day egg laying becomes increasingly synchronized as nest density increases further
- Is synchronous egg laying beneficial to the colony?
  - Egg-laying synchrony allows more eggs to survive cannibalism than would survive without synchrony

Acknowledgments

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- REU team members: Dorothea Gallos, Benjamin MacDonald, and Mykhaylo Malakhov
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