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

Christiane Gallos
Department of Mathematics
Andrews University

J.N. Andrews Honors Program

Funded by the National Science Foundation
Outline

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

- Refuge established in 1988
- Hosts over 70,000 nesting seabirds
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

<table>
<thead>
<tr>
<th>Day 1</th>
<th>Day 2</th>
<th>Day 1</th>
<th>Day 2</th>
<th>Day 1</th>
<th>Day 2</th>
</tr>
</thead>
</table>

[Graph with peaks and valleys indicating data over days]
Eggs laid per day

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

\[
\begin{align*}
    w_{t+1} &= b + w_t \left(1 - e^{-cx_t}\right) \\
    x_{t+1} &= w_t e^{-cx_t} + py_t \\
    y_{t+1} &= x_t
\end{align*}
\]

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

\[ w = (1 - e^{-cx})w + b \]
\[ x = we^{-cx} + py \]
\[ y = x \]

\[ w_e = be^{1-p} \]
\[ x_e = \frac{b}{1-p} \]
\[ y_e = \frac{b}{1-p} \]
Methodology: Equilibrium

- Characteristic equation
  \[ \lambda^3 - \lambda^2 (q(c) - cb) - \lambda (p + cb) + pq(c) = 0 \]
  \[ q(c) \equiv 1 - e^{1-p} \quad \text{Note: } 0 < q(c) < 1 \]

- Found stability of equilibrium using mathematical conditions called Jury Conditions (Lewis 1970)
  
  J1. \((1 - p)(1 - q(c)) > 0\)
  J2. \((1 - p)(1 + q(c)) - 2bc > 0\)
  J3. \(pq(c) < 1\)
  J4. \(1 - p^2 q(c)^2 > |(p + cb) + pq(c)(cb - q(c))|\)
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 $c_1$.

\[
2b/(1 - p) \quad b/(1 - p) \quad x_e
\]

\[
C_1 \quad C
\]
Methodology: “two-cycle”

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

\[
w_{t+2} = b + (1 - e^{-c(py_t + w_t e^{-c_y})}) (b + (1 - e^{-c_y}) w_t)
\]

\[
x_{t+2} = px_t + (b + (1 - e^{-c_y}) w_t) e^{-c(py_t + w_t e^{-c_y})}
\]

\[
y_{t+2} = py_t + w_t e^{-c_y}
\]

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

- 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.
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 $c_1$. 

\[ \frac{2b}{1 - p} \]
\[ \frac{b}{1 - p} \]
\[ x_e \]
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

- Dr. Henson
- Photographs taken by Dr. Hayward
- Whitney Watson
- REU team members: Dorothea Gallos, Benjamin MacDonald, and Mykhaylo Malakhov
- Seabird Ecology Team
- National Science Foundation