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A Note on Cannibalism and Synchrony in Seabird Egg-Laying Behavior

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A Note on Cannibalism and Synchrony in Seabird Egg-laying Behavior

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ABSTRACT

During years of high sea surface temperature, food resources for glaucous-winged gulls (*Larus glaucescens*) are scarce. In response, male gulls cannibalize the eggs of neighbors. When this occurs, female gulls in dense areas of the colony adopt a tactic of egg-laying synchrony, in which they lay eggs synchronously on an every-other-day schedule. Field observations show that the first-laid egg of each clutch is the most likely to be cannibalized. In this paper, we analyzed a discrete-time model of egg-laying behavior that tracks egg order in the nest. Using Jury Conditions, we found that the equilibrium destabilizes into a two-cycle as colony density increases through a critical value, and that the two-cycle becomes increasingly synchronous as density increases further. We demonstrated that synchronous colonies produce more eggs than non-synchronous colonies in the presence of egg cannibalism.

KEYWORDS

Two-cycle bifurcation; egg cannibalism; egg-laying synchrony; glaucous-winged gulls; mathematical model; sea surface temperature; ovulation synchrony

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1. Introduction

Protection Island National Wildlife Refuge, Washington, USA is home to a large colony of glaucous-winged gulls (*Larus glaucescens*) [11]. These birds are sensitive to environmental conditions and are considered indicators of climate change [6]. The behaviors of the occupants of this colony have been studied extensively as functions of environmental variables [3] [4] [5] [8] [9] [10] [11] [12] [15] [16] [17].

In the spring, female gulls begin ovulating on an approximately two-day cycle [7]. An initial luteinizing hormone (LH) surge is followed by ovulation, and the ovum moves into the oviduct. Approximately forty-eight hours later, the gull experiences another LH surge, ovulates again, and lays the previous egg, which has traveled through the oviduct. Each female repeats this cycle approximately three times, resulting in an average of three eggs per clutch [7]. We refer to these as "first", "second", and "third" eggs to denote the order in which they were laid in the clutch. In general, this pattern of every-other-day egg laying is not synchronized across individuals on a daily timescale.

In years of high sea surface temperature (SST), the colony experiences low food availability. When SST is high, plankton and forage fish descend to cooler depths, and surface-feeding seabirds such as glaucous-winged gulls go hungry. This low food availability leads to cannibalism of neighbors' eggs as a way to access energy [5]. Gull cannibals tend to take the first egg in a nest (the egg laid at clutch initiation) in the first twenty-four hours after it is laid [19]. The susceptibility of the first-laid eggs likely is due to the parents becoming increasingly protective as more eggs are laid in the nest. In addition, the probability that a first-laid egg is cannibalized within twenty-four hours after it is laid is inversely related to the number of clutch initiations that day. That is, the more first eggs laid on a particular day, the less chance each first egg has of being cannibalized, likely due to predator satiation [19].

High levels of egg cannibalism lead to an adaptive strategy of egg-laying synchrony, in which females lay eggs together on an every-other-day schedule. Henson et al. [11] showed empirically that egg-laying synchrony increases as colony density increases and is strongest for clutch initiation, meaning gulls tend to lay first eggs synchronously on an every-other-day schedule, which entrains the eggs that follow at two-day intervals.

These two behavioral consequences of high SST, cannibalism and synchrony, beg the question of colony survival as average temperatures continue to rise. Indeed, SSTs in the North American Pacific Northwest have risen approximately 1°C in the last few decades [13][18].

Two previous studies used proof-of-concept models to probe the population-level consequences of synchronous egg laying.

Burton and Henson [1] analyzed the following egg-laying model:

$$\begin{aligned}x_{t+1} &= be^{-cx_t} + py_t \\y_{t+1} &= x_t.\end{aligned}\tag{1}$$

Here, the time step is one day, x is the number of gulls in the first day of the ovulation cycle, y is the number of gulls in the second day of the ovulation cycle, $b > 0$ is the inherent number of birds that enter the system each day, e^{-cx} is the probability of the incoming gulls joining the x class, $c > 0$ represents colony density, $p \in (0, 1)$ is the probability that a bird in the y class returns to the x class, and $1 - p$ is the probability that a bird leaves the system. The value of p controls the expected number of ovulation cycles experienced per female, which is empirically three. Burton and Henson [1], using c as a bifurcation parameter, proved the existence and uniqueness

of an equilibrium solution which bifurcates at a critical value c_{cr} into a two-cycle that becomes increasingly synchronous as colony density c increases.

A major shortcoming in model (1) is that the synchronizing mechanism e^{-cx} depresses the average number of eggs laid per day when c is large. Thus, Burton and Henson were not able to compare the effect of cannibalism on synchronous ($c > c_{cr}$) and non-synchronous ($c < c_{cr}$) colonies [1][2].

To avoid this problem, Gallos et al. [2] added a pre-ovulation compartment to model (1):

$$\begin{aligned}w_{t+1} &= b + (1 - e^{-cx_t})w_t \\x_{t+1} &= py_t + w_t e^{-cx_t} \\y_{t+1} &= x_t.\end{aligned}\tag{2}$$

Here, w is the number of gulls in the colony that are not yet ovulating. The other parameters and variables retain their meaning from model (1). Gallos et al. showed that model (2) also has a two-cycle bifurcation at a critical value of c and that the two-cycle becomes more synchronous as c increases. In model (2), however, unlike in model (1), the average number of eggs laid per day is constant as a function of c . Hence, it was possible to investigate whether egg-laying synchrony is beneficial to the population in the presence of cannibalism in terms of egg survival, which in fact it was shown to be [2]. A major shortcoming of model (2) is that it does not track the order in which eggs are laid in a nest. Hence, it is impossible to use this proof-of-concept model to probe the population-level effects of cannibalism and synchrony of first-laid eggs.

In this paper we modify model (2) by adding state variables to account for egg laying order and limiting the number of ovulation cycles to three, implementing the observation that most gulls lay three eggs per clutch [7]. Tracking the order in which eggs are laid in the nest allows us to incorporate the cannibalism behavior on first-laid eggs [19].

Our egg-laying model, without cannibalism, is

$$\begin{aligned}w_{t+1} &= b + (1 - e^{-cx_t})w_t \\x_{t+1} &= w_t e^{-cx_t} \\y_{t+1} &= x_t \\z_{t+1} &= p_0 y_t \\r_{t+1} &= z_t \\s_{t+1} &= p_1 r_t \\u_{t+1} &= s_t.\end{aligned}\tag{3}$$

Here w is the number of females not yet ovulating, x and y are the number of females in the first and second day of the first ovulation cycle, respectively, z and r are the number of females in the first and second day of the second ovulation cycle, respectively, and s and u are the number of females in the first and second day of the third ovulation cycle, respectively. $b > 0$ is the inherent number of birds that enter the w class each day when x is small, $p_0 \in (0, 1)$ is the probability that a bird in the y class will move to the z class, and $p_1 \in (0, 1)$ is the probability that a bird in the r class will move to the s class. In other words, $p_0 \in (0, 1)$ is the probability that a bird in the first ovulation

cycle will continue on to the second ovulation cycle and $p_1 \in (0, 1)$ is the probability that a bird in the second cycle will continue on to the third cycle. For simplicity, we assume that each ovulation leads to an egg-laying event, and that the number of first, second, and third-laid eggs in the colony corresponds to x_t , z_t , and s_t , respectively.

In this Short Communication we study the dynamics of proof-of-concept model (3) as a function of the colony density $c \geq 0$. In Section 2, we investigate the stability of the equilibrium solution, and demonstrate a two-cycle bifurcation at a critical value of c , which corresponds to the onset of egg-laying synchrony. In Section 3, we study the existence and behavior of the bifurcating branches. In Section 4, we incorporate cannibalism of first-laid eggs into the model and compare egg survival in synchronous colonies vs. non-synchronous colonies. This study, although heavily motivated by field work, is a theoretical proof-of-concept investigation that probes the dynamic consequences of the two behaviors of egg cannibalism and synchrony in the context of warming SST and its effect on seabird colonies.

2. Equilibria and Stability

The equilibrium of model (3) is

$$\begin{aligned} w &= be^{cb} \\ x &= b \\ y &= b \\ z &= p_0b \\ r &= p_0b \\ s &= p_1p_0b \\ u &= p_1p_0b, \end{aligned}$$

and the Jacobian at the equilibrium is

$$\begin{pmatrix} 1 - e^{-bc} & bc & 0 & 0 & 0 & 0 & 0 \\ e^{-bc} & -bc & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & p_1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix}.$$

The characteristic equation is

$$\lambda^5(\lambda^2 + \lambda(e^{-bc} + bc - 1) - bc) = 0. \quad (4)$$

Application of the Jury Conditions in Lewis [14] leads to three conditions for the

stability of the equilibrium:

$$e^{-bc} > 0 \tag{5}$$

$$e^{-bc} + 2bc < 2 \tag{6}$$

$$bc < 1. \tag{7}$$

Condition (5) is true for $c \geq 0$, and condition (7) fails for $c \geq \frac{1}{b}$. We now show that condition (6) fails at a critical value of $c < \frac{1}{b}$.

Lemma 2.1. *There exists a unique $c_1 > 0$ such that $e^{-bc_1} + 2bc_1 = 2$. Furthermore, $e^{-bc} + 2bc < 2$ for all $c \in [0, c_1)$, and $e^{-bc} + 2bc > 2$ for all $c \in (c_1, \infty)$.*

Proof. Define $f(c) = e^{-bc} + 2bc$. Then $f'(c) = -be^{-bc} + 2b = b(2 - e^{-bc}) > 0$, so $f(c)$ is continuous and increasing for $c > 0$. $f(0) = 1$, and $\lim_{c \rightarrow \infty} f(c) = \infty$, and so there exists a unique $c_1 > 0$ such that $f(c_1) = 2$. Also, $f(c) < 2$ for $c < c_1$ and $f(c) > 2$ for $c > c_1$ \square

Lemma 2.2. $c_1 < \frac{1}{b}$.

Proof. Define

$$g(c) = e^{-bc} + (bc - 1).$$

Now $g'(c) = b(1 - e^{-bc}) > 0$, and so $g(c)$ is increasing for $c > 0$. Since $g(0) = 0$, we have

$$0 < g(c) = e^{-bc} + (bc - 1), \forall c > 0.$$

Thus,

$$bc - 1 < e^{-bc} + 2(bc - 1), \forall c > 0.$$

By Lemma 2.1, we have

$$bc_1 - 1 < e^{-bc_1} + 2(bc_1 - 1) = 0,$$

and so

$$c_1 < \frac{1}{b}.$$

\square

Lemmas 2.1 and 2.2 establish the following theorem:

Theorem 2.3. *The equilibrium is locally asymptotically stable for $c \in [0, c_1)$ and unstable for $c \in (c_1, \infty)$, where c_1 is the unique value that satisfies $e^{-bc_1} + 2bc_1 = 2$. \square*

An inspection of the characteristic equation (4) shows that $\lambda = -1$ corresponds to $e^{-bc} + 2bc = 2$. Hence, an eigenvalue exits the unit circle in the complex plane at $\lambda = -1$ when $c = c_1$. This suggests that a two cycle bifurcation occurs at $c = c_1$. We must check whether λ exits the unit circle with non-zero speed in order to verify the

bifurcation. Taking the derivative of the characteristic equation (4) with respect to c and evaluating at $\lambda = -1$ leads to

$$\frac{d\lambda}{dc}(7 - 6(e^{-bc} + bc - 1) - 5bc) + b(2 - e^{-bc}) = 0.$$

Note that $\frac{d\lambda}{dc} = 0$ leads to the contradiction $2 = e^{-bc}$. Thus, $\frac{d\lambda}{dc}\Big|_{\lambda=-1} \neq 0$.

This shows that

Theorem 2.4. *The equilibrium branch undergoes a 2-cycle bifurcation at $c = c_1$. \square*

In the next section we show that the 2-cycle is unique and explore the behavior of its branches as $c \rightarrow \infty$.

3. Existence of the 2-cycle for $c > c_1$

The values of the 2-cycle branches of model (3) are equilibria of the first composite map. The equilibrium equations of the first composite map lead to the following equations for w, x , and y :

$$w = b + (1 - e^{-cy})(b + (1 - e^{-cx})w) \quad (8)$$

$$x = (b + (1 - e^{-cx})w)e^{-cy} \quad (9)$$

$$y = we^{-cx}. \quad (10)$$

The equilibrium values for z, r, s , and u are easily computed from w, x , and y . From equations (10) and (9), we obtain

$$x = be^{-cy} + ye^{cx}e^{-cy} - ye^{-cy}. \quad (11)$$

Solving equation (8) for w yields

$$w = \frac{2b - be^{-cy}}{e^{-cx} + e^{-cy} - e^{-cy}e^{-cx}}. \quad (12)$$

Using equation (10) on the left hand side of equation (12) we can write

$$ye^{cx} = \frac{2b - be^{-cy}}{e^{-cx} + e^{-cy} - e^{-cy}e^{-cx}}. \quad (13)$$

Solving equation (13) for x leads to

$$x = \frac{1}{c} \ln \frac{b(2e^{cy} - 1) + y(1 - e^{cy})}{y}. \quad (14)$$

Equating equations (11) and (14), and writing e^{cx} in terms of y by means of equation (14), gives

$$\frac{1}{c} \ln \frac{b(2e^{cy} - 1) + y(1 - e^{cy})}{y} = be^{-cy} + y \frac{b(2e^{cy} - 1) + y(1 - e^{cy})}{y} e^{-cy} - ye^{-cy}. \quad (15)$$

Simplification leads to

$$\frac{b(2e^{cy} - 1) + y(1 - e^{cy})}{y} = e^{2bc-cy}. \quad (16)$$

Rearranging, we obtain an equation for y :

$$B(y) \equiv y - \frac{b(2e^{cy} - 1) + y(1 - e^{cy})}{e^{2bc-cy}} = 0.$$

The roots of $B(y)$ correspond to the y -equilibria of the first composite map. The equilibrium values of x and w can then be computed from equations (14) and (12), respectively. In the next three lemmas, we examine the behavior of $\frac{dB}{dy}$ as a function of c and then determine the number of roots of $B(y)$ as a function of c . Our goal is to show that $B(y)$ has exactly one root for $c \leq c_1$ and exactly three roots for $c > c_1$ (see Figs. 1-2).

Lemma 3.1. *When $c = c_1$, $\frac{dB}{dy}$ has exactly one root $y = b$, with $\frac{dB}{dy} > 0$ for $y \neq b$. When $c > c_1$, $\frac{dB}{dy}$ has exactly two roots at $y = y_1, y_2$, with $\frac{dB}{dy} > 0$ for $y \in [0, y_1)$, $\frac{dB}{dy} < 0$ for $y \in (y_1, y_2)$, and $\frac{dB}{dy} > 0$ for $y \in (y_2, \infty)$.*

Proof.

$$\begin{aligned} \frac{dB}{dy} &= 1 - \frac{(2bce^{cy} + 1 - e^{cy} - cye^{cy}) - (-c)[b(2e^{cy} - 1) + y(1 - e^{cy})]}{e^{2bc-cy}} \\ &= \frac{1}{e^{2bc-cy}} (2cye^{cy} - 4bce^{cy} + e^{cy} - cy + bc - 1 + e^{2bc-cy}). \end{aligned} \quad (17)$$

Therefore, the roots of $\frac{dB}{dy}$ are the same as the roots of

$$V(y) \equiv 2cye^{cy} - 4bce^{cy} + e^{cy} - cy + bc - 1 + e^{2bc-cy}. \quad (18)$$

We will find the roots of $V(y)$. The derivative of $V(y)$ is

$$\frac{dV}{dy} = ce^{cy}(3 + 2cy - 4bc - e^{-cy} - e^{2bc-2cy}), \quad (19)$$

and so the sign of $\frac{dV}{dy}$ is determined by the sign of

$$W(y) \equiv 3 + 2cy - 4bc - e^{-cy} - e^{2bc-2cy}.$$

Note that

$$\frac{dW}{dy} = 2c + ce^{-cy} + 2ce^{2bc-2cy} > 0$$

for all $c > 0$, and so $W(y)$ is always increasing as a function of y . Note that

$$\begin{aligned} \lim_{y \rightarrow -\infty} W(y) &= -\infty, \\ \lim_{y \rightarrow \infty} W(y) &= \infty. \end{aligned}$$

Therefore $W(y)$ must have exactly one root at $y = y_1$ with $W(y) < 0$ when $y < y_1$ and $W(y) > 0$ when $y > y_1$. In the same way, $\frac{dV}{dy}$ must have exactly one root at $y = y_1$ with $\frac{dV}{dy} < 0$ when $y < y_1$ and $\frac{dV}{dy} > 0$ when $y > y_1$. Therefore, $V(y_1)$ is the minimum value of $V(y)$, and $V(y)$ is decreasing for $y < y_1$ and increasing for $y > y_1$. Note that

$$\begin{aligned} \left. \frac{dV}{dy} \right|_{y=b} &= ce^{cb}(2 - 2bc - e^{-bc}) \\ V(b) &= e^{bc}(2 - 2bc - e^{-bc}). \end{aligned}$$

From Lemma (2.1),

$$\begin{aligned} \left. \frac{dV}{dy} \right|_{y=b} &= V(b) = 0, \text{ for } c = c_1 \\ \left. \frac{dV}{dy} \right|_{y=b}, V(b) &> 0, \forall c < c_1 \\ \left. \frac{dV}{dy} \right|_{y=b}, V(b) &< 0, \forall c > c_1. \end{aligned}$$

- (1) When $c = c_1$, $V(y)$ has exactly one root which also corresponds to its minimum. Therefore $\frac{dB}{dy}$ has exactly one root $y = b$ at its minimum, with $\frac{dB}{dy} > 0$ for $y \neq b$.
- (2) When $c > c_1$, $\left. \frac{dV}{dy} \right|_{y=b} < 0$. Then, since $\frac{dV}{dy}$ is always increasing, $\left. \frac{dV}{dy} \right|_{y=y_1} = 0$ at some $y_1 > b$. Therefore, when $c > c_1$, the minimum of $V(y)$ occurs at $y_1 > b$. $V(b) < 0$ means that $V(y_1) < 0$ which implies that there are two roots of $V(y)$. Thus, $\frac{dB}{dy}$ has exactly two roots at $y = y_1, y_2$, with $\frac{dB}{dy} > 0$ for $y \in [0, y_1)$, $\frac{dB}{dy} < 0$ for $y \in (y_1, y_2)$, and $\frac{dB}{dy} > 0$ for $y \in (y_2, \infty)$.

□

Lemma 3.2. $\frac{dB}{dy} > 0$ when $c \in [0, c_1)$.

Proof. From equation (17),

$$\frac{dB}{dy} = \frac{1}{e^{2bc-cy}}(2cye^{cy} - 4bce^{cy} + e^{cy} - cy + bc - 1 + e^{2bc-cy}).$$

The roots of $V(y)$, equation (18), are the same as the roots of $\frac{dB}{dy}$. It is then enough to show that $V(y) > 0$ when $c < c_1$. Note that

$$\begin{aligned}
V(y) &= 2cye^{cy} - 4bce^{cy} + e^{cy} - cy + bc - 1 + e^{2bc-cy} \\
&= e^{cy}((2cy - 4bc - e^{-cy}) + 1 - cye^{-cy} + bce^{-cy} + e^{2bc-cy}).
\end{aligned} \tag{20}$$

From the proof of Lemma 3.1, the root of $\frac{dV}{dy}$, equation (19), corresponds to the minimum of $V(y)$. Let y_0 be the root of $\frac{dV}{dy}$. Then

$$\frac{dV}{dy} = 0 = ce^{cy_0}(3 + 2cy_0 - 4bc - e^{-cy_0} - e^{2bc-2cy_0})$$

and hence

$$2cy_0 - 4bc - e^{-cy_0} = e^{2bc-2cy_0} - 3. \tag{21}$$

Combining (20) and (21), the minimum of $V(y)$ is

$$\begin{aligned}
V(y_0) &= e^{cy_0}((e^{2bc-2cy_0} - 3) + 1 - cy_0e^{-cy_0} + bce^{-cy_0} + e^{2bc-cy_0}) \\
&= e^{cy_0}(2e^{2c(b-y_0)} - 2 + (b - y_0)ce^{-cy_0}).
\end{aligned}$$

Note that if $y_0 \in (0, b)$ then $V(y_0) > 0$.

When $c < c_1$, $\frac{dV}{dy}\Big|_{y=b} > 0$. Thus the root of $\frac{dV}{dy}\Big|_{y=b} = y_0 < b$. Therefore when $c < c_1$, the minimum of $V(y)$ occurs at $y_0 < b$. Then since $V(y_0) > 0$ for all $y_0 \in (0, b)$, $V(y) > 0$ for all y . Therefore, when $c < c_1$, we have $\frac{dB}{dy} > 0$. \square

Lemma 3.3. *$B(y)$ has exactly one root when $c \in [0, c_1]$, and exactly three roots when $c \in (c_1, \infty)$.*

Proof. Observe that

$$B(0) = -\frac{b}{e^{2bc}} < 0 \tag{22}$$

$$B(b) = 0$$

$$B(2b) = b > 0. \tag{23}$$

- (1) When $c < c_1$, Lemma 3.2 implies $\frac{dB}{dy}$ is strictly positive, thus $B(y)$ has exactly one root.
- (2) When $c = c_1$, Lemma 3.1 implies $\frac{dB}{dy}\Big|_{y=b} = 0$. $\frac{dB}{dy}$ is positive for all $y \neq b$, thus $B(y)$ has exactly one root.
- (3) When $c > c_1$, Lemma 3.1 implies $\frac{dB}{dy}\Big|_{y=b} < 0$. $\frac{dB}{dy}$ as a function of y is first positive then negative then positive again, thus $B(y)$ has exactly three roots.

\square

Thus we have shown that (see Fig. 1):

Theorem 3.4. *The first composite map of model (3) has exactly one equilibrium for all $c \in [0, c_1]$ and exactly three equilibria for all $c \in (c_1, \infty)$.*

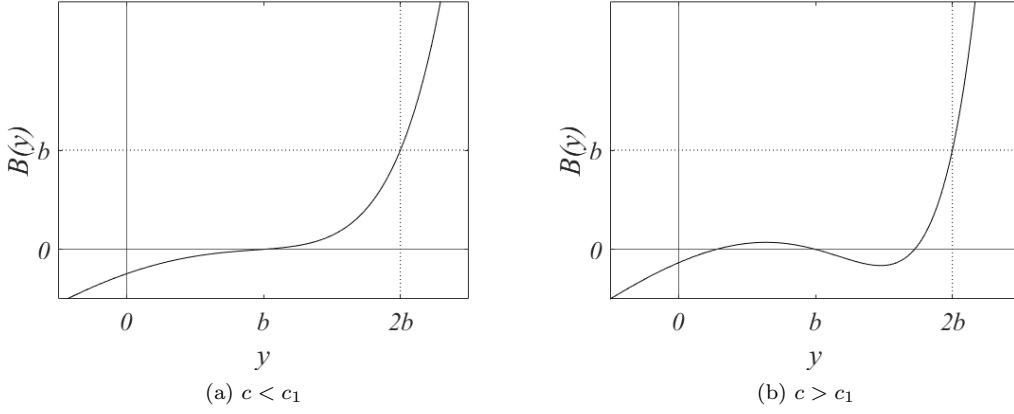


Figure 1. Graph of $B(y)$ showing how one root splits into three as c increases through c_1

In the latter case, when $c > c_1$, the upper and lower equilibria of the composite map correspond to the values of the two-cycle in model (3), and the middle equilibrium of the composite map corresponds to the (now unstable) equilibrium of model (3). We now consider the behavior of the two-cycle branches as a function of c (see Fig. 2).

Theorem 3.5. *The lower branch of equilibria of the first composite map approaches 0 and the upper branch approaches $2b$ as $c \rightarrow \infty$.*

Proof. From equation (22) it is easy to see that

$$\lim_{c \rightarrow \infty} B(0) = 0,$$

and hence the lower equilibrium must approach 0 as $c \rightarrow \infty$. For the upper branch, consider the behavior of $\left. \frac{dB}{dy} \right|_{y=2b}$ as $c \rightarrow \infty$. From equation (17), we have

$$\left. \frac{dB}{dy} \right|_{y=2b} = e^{2bc} - bc.$$

Taking the limit as $c \rightarrow \infty$ shows that $\left. \frac{dB}{dy} \right|_{y=2b}$ tends to infinity. Note also that for $y \in (b, 2b)$,

$$\begin{aligned} \lim_{c \rightarrow \infty} B(y) &= \lim_{c \rightarrow \infty} \left[y - \frac{b(2e^{cy} - 1) + y(1 - e^{cy})}{e^{2bc - cy}} \right] \\ &= \lim_{c \rightarrow \infty} \left[y - \frac{2b - be^{-cy} + ye^{-cy} - y}{e^{2c(b-y)}} \right] \\ &= -\infty. \end{aligned}$$

From equation (23), $B(2b) = b$. Since $B(2b)$ is a fixed value and $\left. \frac{dB}{dy} \right|_{y=2b}$ tends to infinity as $c \rightarrow \infty$ and $\forall y \in (b, 2b)$, $\lim_{c \rightarrow \infty} B(y) = -\infty$, we can conclude that the largest root of $B(y)$, and hence the upper branch of equilibria of the composite map, approaches $y = 2b$ as $c \rightarrow \infty$. \square

In summary, the equilibrium of model (3) splits into a two-cycle at $c = c_1$. The

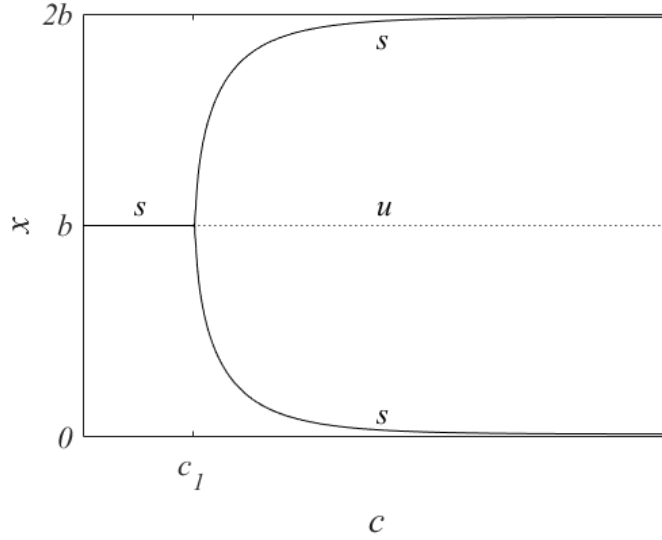


Figure 2. The equilibrium branch splits into two two-cycle branches at $c = c_1$. Stable is indicated by "s", and unstable is indicated by "u".

lower branch of the two-cycle approaches 0 and the upper branch approaches $2b$ as $c \rightarrow \infty$ (Fig. 2). This corresponds to increasing synchrony as $c \rightarrow \infty$.

4. Effect of Egg Cannibalism

We now incorporate cannibalism of first-laid eggs into model (3):

$$\begin{aligned}
 w_{t+1} &= b + (1 - e^{-cx_t})w_t \\
 x_{t+1} &= w_t e^{-cx_t} \\
 y_{t+1} &= x_t \\
 z_{t+1} &= p_0 y_t \\
 r_{t+1} &= z_t \\
 s_{t+1} &= p_1 r_t \\
 u_{t+1} &= s_t \\
 E_{t+1} &= E_t + (x_t + z_t + s_t) - \min(x_t, aG).
 \end{aligned} \tag{24}$$

Here $G > 0$ is the number of gull cannibals present in the population and $a > 0$ corresponds to the number of first eggs that can be cannibalized per day by each cannibal. For simplicity, we assume that the numbers of first, second, and third eggs laid in a clutch are x_t , z_t , and s_t , respectively. Thus, $\min(x_t, aG)$ represents the number of eggs lost on day t due to cannibalization of the first eggs. Hence, E_t represents the total number of eggs that have escaped cannibalization by day t . Note that the inclusion of state variable E does not change the dynamics of the other state variables.

Consider the E state variable in model (24) as it depends on a fixed value of c . We denote the solution by E_t^c and define E_t^∞ as the limiting solution when c is arbitrarily large. We want to compare E_t^c for $c < c_1$ and E_t^∞ in order to compare the total number of eggs that escape cannibalization in non-synchronous ($c < c_1$) vs. synchronous ($c \rightarrow$

∞) colonies.

For model (3) and (24) at equilibrium, when $c < c_1$, the expected number of eggs laid per day is $b + bp_0 + bp_0p_1$. In this case, the number of first eggs cannibalized per day is $\min(b, aG)$.

For model (3) and (24) on the two-cycle when c is large, the expected number of eggs laid per day oscillates approximately between $(0, 0, 0)$ and $(2b, 2bp_0, 2bp_0p_1)$. In this case, the number of first eggs cannibalized per day alternates between 0 and $\min(2b, aG)$.

Thus, we can compare the total number of eggs that survive cannibalism every *two* days by comparing

$$\begin{aligned} N &\equiv 2b(1 + p_0 + p_0p_1) - 2\min(b, aG) \\ &= 2b(1 + p_0 + p_0p_1) - \min(2b, 2aG) \end{aligned} \tag{25}$$

in the non-synchronous case ($c < c_1$) with

$$S \equiv 2b(1 + p_0 + p_0p_1) - \min(2b, aG)$$

in the synchronous case ($c \rightarrow \infty$).

If $aG < 2b$, that is, if the number of eggs that can be cannibalized per day is less than the number of first eggs laid every two days, then $S > N$. Thus, on the model attractors, the synchronous colony produces more eggs. In general,

Theorem 4.1. *Fix an initial condition vector for model (24) that is independent of c . If $aG < 2b$ and $c < c_1$, then $E_t^c < E_t^\infty$ for all $t > 0$.*

The proof follows Gallos et al. [2] sufficiently closely that we need not repeat it here.

5. Discussion

In this paper, we created a model that simulates gull egg-laying habits while tracking the egg-laying order. We showed that when the colony density exceeds a certain value c_1 , the system bifurcates and egg-laying synchrony occurs. Furthermore, the system becomes increasingly synchronous as the colony density continues to increase. We implemented the empirical observation that only the first-laid eggs are cannibalized and showed that egg-laying synchrony leads to an advantage in the overall survival of the gull eggs in the presence of cannibalism.

Interestingly, although model (3) is more biologically accurate and has more state variables than model (2), the stability criterion which comes from the Jury Conditions is simpler in model (3) than in model (2). In particular, the stability criterion for model (3) has three non-trivial conditions in comparison to four non-trivial conditions for model (2). This is noteworthy because in mathematical modeling an increase in realism usually corresponds to a decrease in tractability. The extra condition for model (2) is due to the " p term" that feeds a percent of the y class back into the x class, where p is set so that the expected number of loops through x and y is 3, which is the expected number of ovulation cycles for a given female. If this "loop" is eliminated in model (2) by setting $p = 0$, so that all gulls exit the system after class y , the rank of the Jacobian matrix of model (2) is reduced to 2. If two more ovulation cycles (4 classes) are appended to the end of the system, with no loops, to account explicitly

for all 3 ovulation cycles as in model (3), the rank remains 2 and the dimension of the nullspace increases by 4. In general, in a model such as model (3), the stability criterion is independent of the number of ovulation cycles. It is therefore not only more realistic, but also more tractable, to model the number of ovulation cycles explicitly rather than via an expected number of circuits through a single loop.

This study is a theoretical proof-of-concept investigation and is not meant to be connected to data, although it is heavily motivated by field data. Biological simplifications include the assumption that the number of birds entering the system has no limit and that the breeding season is infinitely long; these assumptions allow analysis of asymptotic dynamics.

In summary, in years of high SST, female gulls start to lay eggs synchronously when the population density increases through a critical value. The egg-laying becomes increasingly synchronous as density increases further. In the context of a prolonged increase in SST and the resulting cannibalism behavior, specifically first-egg cannibalism, model (24) shows that synchronous colonies produce more eggs than non-synchronous colonies. This suggests that egg-laying synchrony is beneficial not only at the level of individual fitness, but also at the population level, and may decrease the chance of colony extirpation in the face of climate change.

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Disclosure statement

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