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### A Note on the Onset of Synchronous Egg Laying in a Seabird Behavior Model

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J. N. Andrews Honors Program  
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HONS 497  
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A note on the onset of synchronous egg laying in a seabird behavior model

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Abstract: Protection Island, Washington hosts a large colony of Glaucous-winged gulls (*Larus glaucescens*). These birds are known to exhibit every-other-day egg-laying synchrony in dense areas of the colony in response to egg cannibalism, which is the main source of egg loss. Here we present an equilibrium analysis of a discrete-time animal behavior model for egg laying. We use Jury Conditions to find the stability criteria for the equilibrium as a function of the colony density and show that a 2-cycle bifurcation occurs when the equilibrium loses stability. The 2-cycle pattern in egg laying becomes increasingly synchronous as the colony density increases. We also show that egg-laying synchrony benefits the colony by allowing more eggs to survive cannibalism.

## 1 Introduction

Protection Island, Washington, USA hosts a large colony of Glaucous-winged gulls (*Larus glaucescens*) [5]. The gull hens begin ovulating in the spring, at the beginning of the annual breeding season. An individual's ovulation cycle is approximately two days long [4]. Halfway through the ovulation cycle, a female gull experiences a luteinizing hormone (LH) surge, immediately after which an ovulation occurs. After the next LH surge approximately forty-eight hours later, a new ovulation occurs and the previous egg is laid. On average, a gull hen repeats this cycle three times, resulting in three eggs laid per clutch [5].

During years when sea surface temperature (SST) is high, gulls typically experience low food availability. As SSTs rise, feeder fish, the main source of food for gulls, descend to lower depths to feed on the plankton, which have moved to cooler temperatures in deeper water levels. Since gulls are surface-feeding birds, they cannot dive and thus face a food shortage [3]. A strategy the gulls in the Protection Island colony employ to deal with this food shortage is egg cannibalism since one egg provides half the calories an adult gull needs for one day [2].

Female gulls in the Protection Island colony combat egg cannibalism through an adaptive tactic known as egg-laying synchrony [7]. Egg-laying synchrony is a process in which female gulls in the colony lay eggs together on an every-other-day schedule. This synchrony has been observed to increase with increasing levels of colony density [4] and social interaction [5]. This may occur because of hormone levels affecting the cycles of other birds [4].

Previously, Burton and Henson [1] posed a two-dimensional discrete-time animal behavior model for egg laying, where the "prime" indicates LasSalle's "next iterate" notation and the time step is one day:

$$\begin{aligned}x' &= be^{-cx} + py \\y' &= x.\end{aligned}\tag{1}$$

Here  $x$  is the number of females in the first day of the ovulation cycle,  $y$  is the number in the second day of the ovulation cycle,  $b > 0$  is the inherent number of birds that enter the system each day when  $x$  is small,  $p \in (0, 1)$  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 to begin incubating. Using the parameter  $c > 0$ , which is a "crowding factor" representing colony density, as a bifurcation parameter, they showed the existence and uniqueness of a positive equilibrium that was stable for all  $c$  less than a critical point  $c_{cr}$ . At  $c = c_{cr}$ , the system experiences a two-cycle bifurcation corresponding to the advent of egg-laying synchrony.

However, in that paper the synchronizing mechanism  $e^{-cx}$ , which delays the entry of birds into the system on days when  $x$  is large, depresses the average number of eggs laid per day. Because of this, the authors were not able to show that egg-laying synchrony could provide an advantage in the presence of egg cannibalism.

In this study, we modify the Burton and Henson [1] model so that a constant number of birds enter the system at each time step. We solve for the equilibrium and determine its stability as a function of colony density using the Jury Conditions. We then analyze the properties of the 2-cycle that occurs when the equilibrium loses stability. By extending the model to include egg cannibalism, we also determine whether egg-laying synchrony is beneficial to egg production at the population level in the presence of egg cannibalism.

## 2 The Model

In this note we modify model (1) by adding a third compartment:

$$\begin{aligned}w' &= b + (1 - e^{-cx}) w \\x' &= py + we^{-cx} \\y' &= x.\end{aligned}\tag{2}$$

Here  $w$  is the number of females not yet ovulating. We assume that  $b$  new birds enter the  $w$  class each day. We also assume that, each day, birds in the  $w$  class move to the  $x$  class with a probability  $e^{-cx}$ . The other parameters and variables retain their meaning from [1]. A diagram incorporating these assumptions is shown in Figure 1.

## 3 Equilibrium stability

Our goal is to study the equilibrium of model (2) as a function of the crowding factor parameter  $c$ . From model (2) we obtain the unique equilibrium

$$\begin{aligned}w &= be^{\frac{bc}{1-p}} \\x &= \frac{b}{1-p} \\y &= \frac{b}{1-p}.\end{aligned}\tag{3}$$

The Jacobian at the equilibrium is

$$\begin{pmatrix}1 - e^{-\frac{bc}{1-p}} & bc & 0 \\e^{-\frac{bc}{1-p}} & -bc & p \\0 & 1 & 0\end{pmatrix}$$



and the characteristic equation is

$$\lambda^3 - \lambda^2(q - bc) - \lambda(p + bc) + pq = 0 \quad (4)$$

where  $q$  is defined to be

$$q \doteq 1 - e^{-\frac{bc}{1-p}}. \quad (5)$$

Note that  $0 < q < 1$  and that  $q$  monotonically increases on  $[0, 1)$  as a function of  $c$ , with  $\lim_{c \rightarrow \infty} q = 1$ .

Using the Jury Conditions in Lewis [6], we obtain four conditions for the stability of the equilibrium:

$$(1 - p)(1 - q) > 0 \quad (6)$$

$$(1 - p)(1 + q) - 2bc > 0 \quad (7)$$

$$pq < 1 \quad (8)$$

$$|1 - p^2q^2| > |(p + bc) + pq(bc - q)|. \quad (9)$$

Conditions (6) and (8) are clearly true for all values of  $c > 0$ . We now show that conditions (7) and (9) fail at unique values  $c = c_1$  and  $c = c_2$ , respectively.

**Lemma 1** *There is a unique  $c_1 > 0$  satisfying  $(1 - p)(1 + q) - 2bc_1 = 0$ . Furthermore,  $(1 - p)(1 + q) - 2bc > 0$  for all  $c < c_1$  and  $(1 - p)(1 + q) - 2bc < 0$  for all  $c > c_1$ .*

**Proof.** Define  $F(c) \doteq (1 - p)(1 + q) - 2bc$ . Then  $F(0) = 1 - p > 0$  and by (5) we have  $\lim_{c \rightarrow \infty} F(c) = -\infty$ . Also,

$$\begin{aligned} \frac{dF}{dc} &= (1 - p) \frac{dq}{dc} - 2b \\ &= (1 - p) \frac{b(1 - q)}{1 - p} - 2b \\ &= b(1 - q - 2) \\ &= -b(1 + q) \\ &< 0. \end{aligned}$$

Thus, there exists a unique  $c_1 > 0$  such that  $F(c_1) = 0$ . Also,  $F(c) > 0$  for  $c < c_1$  and  $F(c) < 0$  for  $c > c_1$ . ■

**Lemma 2** *There is a unique  $c_2 > 0$  satisfying  $|1 - p^2q^2| = |(p + bc_2) + pq(bc_2 - q)|$ . Furthermore,  $|1 - p^2q^2| > |(p + bc) + pq(bc - q)|$  for all  $c < c_2$  and  $|1 - p^2q^2| < |(p + bc) + pq(bc - q)|$  for all  $c > c_2$ .*

**Proof.** First we show that the absolute value signs can be eliminated on both sides of (9). Clearly  $1 - p^2q^2$  is positive. In order to show that  $(p + bc) + pq(bc - q)$  is positive, we consider the sign of  $(bc - q)$ . The derivative of  $bc - q = bc - \left(1 - e^{-\frac{bc}{1-p}}\right)$  with respect to  $c$  is

$$b - \frac{b}{1-p} e^{-\frac{bc}{1-p}}.$$

It is easy to show that the zeros of the derivative occur when  $p = q$ . The second derivative of  $cb - q$  at this point is

$$\frac{b^2}{(1-p)^2} e^{-\frac{bc}{1-p}} > 0.$$

Thus,  $bc - q$  is concave up as a function of  $c$ , and so it has a local minimum when  $q = p$ . Thus  $bc - q \geq bc - p$ , and so

$$\begin{aligned} (p + bc) + pq(bc - q) &\geq p + bc + pq(bc - p) \\ &= p(1 - pq) + bc(1 + pq) \\ &> 0. \end{aligned}$$

Now we can drop the absolute value signs from the right hand side of (9) and the Jury condition becomes

$$(1 - p^2q^2) > (p + bc) + pq(bc - q).$$

Define  $G(c) \doteq (1 - p^2q^2) - (p + bc) - pq(bc - q)$ . Then  $\lim_{c \rightarrow 0^+} G(c) = 1 - p$  and  $\lim_{c \rightarrow \infty} G(c) = -\infty$ . Also,

$$\begin{aligned} \frac{dG}{dc} &= -2p^2q \frac{dq}{dc} - b - p \frac{dq}{dc} (bc - q) - pq \left( b - \frac{dq}{dc} \right) \\ &= -2p^2qb \frac{1-q}{1-p} - b - pb \frac{1-q}{1-p} (bc - q) - pq \left( b - b \frac{1-q}{1-p} \right) \end{aligned}$$

and so

$$\begin{aligned} \frac{(1-p)}{b} \frac{dG}{dc} &= -2p^2q(1-q) - (1-p) - p(1-q)(bc-q) - pq((1-p) - (1-q)) \\ &= -2p^2q(1-q) - (1-p) - p(1-q)(bc-q) - pq(q-p) \\ &= p + pq - bcp + bcpq - 2pq^2 - p^2q + 2p^2q^2 - 1 \\ &= -2pq^2(1-p) - bcp(1-q) - p^2q - 1 + p + pq \\ &= -2pq^2(1-p) - bcp(1-q) - (1-pq)(1-p) \\ &< 0. \end{aligned}$$

Thus, since  $dG/dc < 0$ , there exists a unique  $c_2 > 0$  such that  $G(c_2) = 0$ . Also,  $G(c) > 0$  for  $c < c_2$  and  $G(c) < 0$  for  $c > c_2$ .

■

In the next Lemma we show that condition (7) fails first:

**Lemma 3**  $c_1 < c_2$ .

**Proof.** It is sufficient to show that  $G(c) > F(c)$  for all  $c > 0$ . To this end, we note that

$$\begin{aligned}
 G(c) - F(c) &= (1 - p^2q^2) - (p + bc) - pq(bc - q) - (1 - p)(1 + q) + 2bc \\
 &= 1 - p^2q^2 - p - cb - bcpq + pq^2 - 1 - q + p + pq + 2bc \\
 &= bc - q + pq - bcpq + pq^2 - p^2q^2 \\
 &= -q(1 - p) + bc(1 - pq) + pq^2(1 - p) \\
 &= (-q + pq^2)(1 - p) + bc(1 - pq) \\
 &= -q(1 - pq)(1 - p) + bc(1 - pq) \\
 &= (1 - pq)(bc - q(1 - p)).
 \end{aligned}$$

We know that  $1 - pq > 0$  is positive; it suffices to show that  $bc - q(1 - p) > 0$ . Note that when  $c = 0$ , we have  $bc = q(1 - p) = 0$ . As  $c$  increases from zero, the functions  $bc$  and  $q(1 - p)$  both increase from zero. To determine which function increases faster, we compare their derivatives for  $c > 0$ :

$$\frac{d}{dc}(bc) = b > be^{-\frac{cb}{1-p}} = \frac{d}{dc}(q(1 - p)).$$

Therefore  $bc - q(1 - p) > 0$  and hence

$$G(c) - F(c) = (1 - pq)(bc - q(1 - p)) > 0.$$

■

The above lemmas lead to the stability theorem for the equilibria:

**Theorem 4** *The equilibrium (3) is locally asymptotically stable for  $c < c_1$  and unstable for  $c > c_1$ , where  $c_1$  satisfies  $(1 - p)(1 + q) = 2bc_1$ .*

Note from the characteristic equation (4) that  $\lambda = -1$  corresponds to  $(1 - p)(1 + q) = 2bc$ . Thus, from the Jury Conditions and previous lemmas it is clear that an eigenvalue exits the unit circle in the complex plane at the value  $\lambda = -1$  when  $c = c_1$ . This suggests that a 2-cycle bifurcates from the equilibrium at  $c = c_1$ . To verify this, we must check



that  $\lambda$  exits the unit circle with non-zero speed. Differentiating (4) with respect to  $c$  and evaluating at  $\lambda = -1$  and  $2bc = (1-p)(1+q)$  gives

$$3\frac{d\lambda}{dc} + 2\frac{d\lambda}{dc}(q-bc) - \left(\frac{dq}{dc} - b\right) - \frac{d\lambda}{dc}(p+bc) + b + p\frac{dq}{dc} = 0$$

$$\frac{d\lambda}{dc}(3+2q-3bc-p) + b + bq = 0,$$

but  $d\lambda/dc = 0$  leads to a contradiction. Thus,

$$\left.\frac{d\lambda}{dc}\right|_{\lambda=-1} \neq 0.$$

This shows that

**Theorem 5** *The equilibrium branch undergoes a 2-cycle bifurcation at  $c = c_1$ . The 2-cycle is locally asymptotically stable for  $c > c_1$  where  $c$  is sufficiently close to  $c_1$ .*

Figure 2 illustrates the destabilization of the equilibrium.

#### 4 Existence of the 2-cycle for $c > c_1$

The values of the 2-cycle are equilibria of the first composite of model (2). The equilibrium equations of the first composite map are

$$w = b + \left(1 - e^{-c(py+we^{-cx})}\right) (b + (1 - e^{-cx}) w)$$

$$x = px + (b + (1 - e^{-cx}) w) e^{-c(py+we^{-cx})}$$

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

which are equivalent to

$$w = b + (1 - e^{-cy}) (b + (1 - e^{-cx}) w) \quad (10)$$

$$(1-p)x = (b + (1 - e^{-cx}) w) e^{-cy} \quad (11)$$

$$(1-p)y = we^{-cx}. \quad (12)$$

From (10) we can solve for  $w$  in terms of  $x$  and  $y$ :

$$w = \frac{b(2 - e^{-cy})}{e^{-cx} + e^{-cy} - e^{-cx}e^{-cy}}, \quad (13)$$

and from (13) and (12), we can eliminate  $w$  to obtain

$$(1-p)y = \frac{b(2 - e^{-cy}) e^{-cx}}{e^{-cx} + e^{-cy} - e^{-cx}e^{-cy}} \quad (14)$$

$$= \frac{b(2 - e^{-cy})}{1 + e^{-cy}e^{cx} - e^{-cy}}.$$

From (14) we can write

$$e^{-cx} = \frac{(1-p)y}{(1-p)y(1-e^{cy}) + b(2e^{cy} - 1)}. \quad (15)$$

From (11), (15), and (13), we obtain

$$(1-p)x = be^{-cy} + \left( 1 - \left[ \frac{(1-p)y}{(1-p)y(1-e^{cy}) + b(2e^{cy} - 1)} \right] \right) \left[ \frac{b(2 - e^{-cy})}{e^{-cx} + e^{-cy} - e^{-cx}e^{-cy}} \right] e^{-cy}.$$

Application of (15) leads to

$$\begin{aligned} & -\frac{(1-p)}{c} \ln \left( \frac{(1-p)y}{(1-p)y(1-e^{cy}) + b(2e^{cy} - 1)} \right) \\ & = be^{-cy} + \left( 1 - \left[ \frac{(1-p)y}{(1-p)y(1-e^{cy}) + b(2e^{cy} - 1)} \right] \left[ \frac{b(2 - e^{-cy})}{\left( \frac{(1-p)y(1-e^{-cy})}{(1-p)y(1-e^{cy}) + b(2e^{cy} - 1)} \right) + e^{-cy}} \right] \right) e^{-cy}. \end{aligned}$$

After considerable algebra, this leads to an equation for  $y$ :

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

The roots of  $H$  are the equilibria of the first composite map. It is easy to check that the equilibrium  $y = b/(1-p)$  of model (2) is a root for all values of  $c$ . It is also easy to check that

$$H(0) = -e^{\frac{-2bc}{1-p}} < 0 \quad \forall c \geq 0, \quad (16)$$

that

$$H(2b/(1-p)) = e^{\frac{-2bc}{1-p}} > 0, \quad (17)$$

and that  $H$  has a vertical asymptote at  $y = y_v$ , where  $y_v > 2b/(1-p)$ .

It is straightforward to show that

$$\left. \frac{dH}{dy} \right|_{y=b/(1-p)} = \frac{(1-p) \left( 2 - e^{\frac{-bc}{1-p}} \right) - 2bc}{be^{\frac{2cb}{1-p}}}. \quad (18)$$

The sign of (18) is determined by

$$(1-p) \left( 2 - e^{\frac{-bc}{1-p}} \right) - 2bc = (1-p)(1+q) - 2bc.$$

Thus by Lemma 1,

$$\left. \frac{dH}{dy} \right|_{y=b/(1-p)} > 0 \text{ for all } c < c_1, \quad (19)$$

and

$$\left. \frac{dH}{dy} \right|_{y=b/(1-p)} < 0 \text{ for all } c > c_1. \quad (20)$$

Thus, it follows that, locally, the root at  $y = b/(1-p)$  splits into three roots of  $H$  as  $c$  increases through  $c_1$ . In order to establish that these are the only roots of  $H$ , we now consider the derivative of  $H$ .

**Lemma 6**  $H(y)$  has exactly one root if  $c \leq c_1$  and exactly three roots if  $c > c_1$ .

**Proof.** First we note that

$$\frac{dH}{dy} = \frac{(1-p)(y^2c(1-p)(2-e^{-cy}) - ybc(4-e^{-cy}) + b(2-e^{-cy}))}{(b(2e^{cy}-1) + y(1-p)(1-e^{cy}))^2}.$$

The numerator of this expression excluding the factor  $(1-p)$  determines the sign of the derivative of  $H$ . We call this expression  $K$ :

$$K \doteq y^2c(1-p)(2-e^{-cy}) - ybc(4-e^{-cy}) + b(2-e^{-cy}).$$

We then take the derivative of  $K$  with respect to  $y$ :

$$\begin{aligned} \frac{dK}{dy} &= 2yc(1-p)(2-e^{-cy}) + y^2c^2(1-p)e^{-cy} - bc(4-e^{-cy}) - ybc^2e^{-cy} + bce^{-cy} \\ &= 2yc(1-p)(2-e^{-cy}) + y^2c^2(1-p)e^{-cy} - bc(4-2e^{-cy}) - ybc^2e^{-cy} \\ &= 2yc(1-p)(2-e^{-cy}) + y^2c^2(1-p)e^{-cy} - 2bc(2-e^{-cy}) - ybc^2e^{-cy} \\ &= 2c(2-e^{-cy})(y(1-p)-b) + c^2ye^{-cy}(y(1-p)-b) \\ &= (y(1-p)-b)(2c(2-e^{-cy}) + c^2ye^{-cy}). \end{aligned}$$

The only value of  $y$  for which  $K'$  can change sign is when  $y(1-p)-b=0$ . If  $y < \frac{b}{1-p}$  then  $K' < 0$ , and if  $y > \frac{b}{1-p}$  then  $K' > 0$ . Therefore,  $K$  is decreasing for  $y < \frac{b}{1-p}$  and increasing for  $y > \frac{b}{1-p}$ , with a minimum at  $y = \frac{b}{1-p}$ . By (19), we know that  $\frac{dH}{dy}$ , and hence  $K$ , is positive at  $y = \frac{b}{1-p}$  for  $c < c_1$ . Thus  $K$ , and hence  $\frac{dH}{dy}$ , is positive for all  $y$  when  $c < c_1$ . Therefore, by (16) and (17),  $H$  has exactly one root when  $c < c_1$ . By (20), we see that  $K$  is negative at  $y = \frac{b}{1-p}$  for  $c > c_1$ . For a neighborhood around  $y = \frac{b}{1-p}$ ,  $K$  is negative, but for greater or smaller  $y$ ,  $K$  is positive. Thus, the derivative of  $H$  is first positive, then negative, then positive again, and so by (16) and (17),  $H$  has exactly three roots for  $c > c_1$ . ■

Thus we have proved:

**Theorem 7** *The composite map has exactly one equilibrium if  $c \leq c_1$  and exactly three equilibria if  $c > c_1$ .*

## 5 Effect of egg cannibalization

Consider the following model, which is an extension of model (2):

$$\begin{aligned} w' &= b + (1 - e^{-cx}) w \\ x' &= py + we^{-cx} \\ y' &= x \\ E' &= E + x - \min \{x, aP\} \end{aligned} \tag{21}$$

where  $E$  represents the total number of eggs laid that have escaped cannibalization,  $P$  represents the number of gull cannibals present, and  $a > 0$  represents the number of eggs taken by a cannibal in one day. The expression  $x - \min \{x, aP\}$  denotes the number of eggs laid in the current day which were not cannibalized. This construction is based on the field observation that eggs tend to be cannibalized on the day they are laid [7].

Note that in model (21), the first three equations are decoupled from the fourth equation, meaning that  $w$ ,  $x$ , and  $y$  have the same dynamics as in model (2).

We define

$$M \doteq \frac{b}{1-p} - \min \left( \frac{b}{1-p}, aP \right) \tag{22}$$

and

$$L \doteq \frac{2b}{1-p} - \min \left( \frac{2b}{1-p}, aP \right). \tag{23}$$

In equation (22), the value  $\frac{b}{1-p}$  is the equilibrium number of eggs laid per day in model (2) if  $c < c_1$ . The value  $\min \left( \frac{b}{1-p}, aP \right)$  represents the number of eggs cannibalized per day at equilibrium in model (2). Thus  $M$  is the number of eggs that escape cannibalization per day when  $c < c_1$ . Similarly, in equation (23), the value  $\frac{2b}{1-p}$  is the number of eggs laid every other day in model (2) for arbitrarily large  $c$ , and  $\min \left( \frac{2b}{1-p}, aP \right)$  represents the number of eggs cannibalized every other day in that case. Thus  $L$  is the number of eggs that survive cannibalization every other day when  $c > c_1$ . Note that on the "in-between days", zero eggs are laid, resulting in no eggs lost to cannibalism.

Consider the solution of the  $E$  equation in the extended model (21) as it depends on a fixed value of  $c$ . Denote the solution by  $E_t^c$ , and define  $E_t^\infty$  to be the limiting solution for arbitrarily large  $c$ . We want to compare  $E_t^c$  and  $E_t^\infty$  for  $c < c_1$ . To this end we assume that the initial values  $E_0^c = E_0$  are the same for all  $c \geq 0$ .



It is easy to check that, for  $c \leq c_1$ , and when model (2) is at equilibrium, the solution for the  $E$  equation is

$$E_t^c = E_0 + tM.$$

It is also easy to check that if  $c$  is arbitrarily large, and model (2) is on the 2-cycle, with  $x$  starting on the lower branch ( $x_0 = 0$ ), the limiting solution for the  $E$  equation is given on even and odd days by

$$E_{2\tau}^\infty = E_{2\tau+1}^\infty = E_0 + \tau L.$$

If  $aP > \frac{2b}{1-p}$ , then  $L = M = 0$ ; that is, no eggs survive cannibalism. Hence, for  $c \leq c_1$ , we have  $E_t^c = E_0 = E_t^\infty$  for all  $t \geq 0$ .

If  $\frac{b}{1-p} < aP < \frac{2b}{1-p}$ , then  $M = 0$  and  $L > 0$ . Thus, for  $c \leq c_1$ , we have  $E_t^c = E_0 < E_t^\infty$  for all  $t \geq 2$ .

If  $aP < \frac{b}{1-p}$ , then  $M > 0$  and  $L > 0$ , and it is easy to check that

$$L = 2M + aP.$$

That is, the number of eggs surviving every other day in a completely synchronous colony is more than twice the number that would survive every day in a completely nonsynchronous colony, and it exceeds that value by  $aP$ . If we wish for the cumulative number of surviving eggs to satisfy  $E_t^\infty > E_t^c$  for each day  $t$ , we must look far enough down the trajectory so that the extra  $aP$  surviving eggs that are added every two days in the synchronous situation accumulate sufficiently to offset the extra  $M$  surviving eggs that are added every second day in the nonsynchronous situation.

If we consider the number of surviving eggs for  $\tau > M/(aP)$ , we see that, at even time steps,

$$\begin{aligned} E_{2\tau}^\infty &= E_0 + \tau L \\ &= E_0 + 2\tau M + \tau aP \\ &> E_{2\tau}^c + \left(\frac{M}{aP}\right) aP \\ &= E_{2\tau}^c + M \\ &> E_{2\tau}^c \end{aligned}$$

and that, at odd time steps,

$$\begin{aligned} E_{2\tau+1}^\infty &= E_0 + \tau L \\ &= E_0 + 2\tau M + \tau aP \\ &> E_0 + 2\tau M + \left(\frac{M}{aP}\right) aP \\ &= E_0 + (2\tau + 1)M \\ &= E_{2\tau+1}^c. \end{aligned}$$



The condition  $\tau > M/(aP)$  can be fulfilled by requiring the regular time step  $t$  to satisfy  $t > 2M/(aP) + 1$ .

Thus we have proved:

**Theorem 8** *If  $aP < \frac{2b}{1-p}$  and  $c < c_1$ , we have  $E_t^c < E_t^\infty$  for all  $t > 2M/(aP) + 1$ .*

Thus in the presence of egg cannibalism, synchronous egg-laying can be advantageous due to ‘predator satiation.’ Since only new eggs are cannibalized, if twice the equilibrium number of eggs are laid one day and no eggs the next, fewer eggs are cannibalized overall than if no synchrony exists.

## 6 Discussion

In this study we determined the stability criteria of the equilibrium as a function of the crowding factor  $c$  by using the Jury Conditions. We showed the equilibrium destabilizes when the crowding factor exceeds a critical value  $c_1$ . This loss of stability coincides with a 2-cycle bifurcation and results in the onset of egg-laying synchrony. We also showed that egg-laying synchrony leads to an increase in the number of eggs that survive cannibalism. Thus synchrony is beneficial at the population level in the presence of egg cannibalism.

Model (2) is a proof-of-concept model rather than a biologically accurate model. Two simplifying mathematical assumptions are that the number of birds entering the system has no limit and that the breeding season is infinitely long. Also, the results of this study pertain to one breeding season only as opposed to multiple seasons. That is, model (2) is an animal behavior model for egg laying rather than a population model.

In summary, increasing nest density leads to a 2-cycle oscillation in egg laying. As the nest density continues to increase, egg laying becomes more and more synchronized, resulting in twice the equilibrium number of eggs laid one day and no eggs laid the next day, with this pattern being repeated during the breeding season. Egg-laying synchrony can be advantageous due to predator satiation since fewer eggs are cannibalized overall when they are laid synchronously.

## 7 Acknowledgments

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## FIGURE CAPTIONS

Figure 1. Discrete-time model for egg laying.

Figure 2. Bifurcation diagram. The equilibrium branch bifurcates into a 2-cycle at the critical value  $c_1$ . Each branch of the 2-cycle represents the number of eggs laid at every other time step, that is, every other day.

Figure 1.

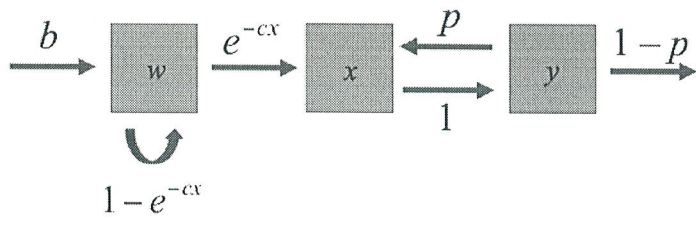


Figure 2.

