Socially-induced ovulation synchrony and its effect on seabird population dynamics

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Abstract

Spontaneous oscillator synchrony is a form of self-organization in which populations of interacting oscillators ultimately cycle together. This phenomenon occurs in a wide range of physical and biological systems. In rats and humans, estrous/menstrual cycles synchronize through social stimulation with pheromones acting as synchronizing signals. In previous work we showed that glaucous-winged gulls ( ) can lay eggs synchronously on an every-other-day schedule, and that synchrony increases with colony density. We posed a discrete-time mathematical model for reproduction during the breeding season based on the hypothesis that pre-ovulatory luteinizing hormone surges synchronize by means of visual, auditory, and/or olfactory cues. Here we extend the seasonal model in order to investigate the effect of ovulation synchrony on population dynamics across reproductive seasons. We show that socially-stimulated ovulation synchrony can enhance total population size and allow the population to persist at lower birth rates than would otherwise be possible.

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1 Introduction

"Spontaneous oscillator synchrony" is a phenomenon of self-organization in which a population of interacting oscillators ultimately cycles together. Spontaneous oscillator synchrony occurs in a wide range of physical and biological systems, including cardiac pacemaker cells, Malaysian fireflies, pendulum clocks, lasers, and chemical reactions [21],[27]. In Norway rats and humans, ovulation cycles can synchronize through social stimulation with pheromones acting as synchronizing signals [16],[17],[18],[19].

Females of a wide range of taxa experience similar kinds of hormonal fluctuations that drive ovulation cycles. Mammals and birds experience a surge of luteinizing hormone (LH) before each ovulation in a periodic fashion [31]. In women, LH surges approximately every 28 days; in domestic fowl, LH surges every 24 hours during the laying season [15]. For animals that breed or congregate in dense social groups, there is at least the possibility that ovulation synchrony may occur. This has been tested, however, only in Norway rats and humans; currently we are testing for ovulation synchrony in glaucous-winged gulls ( ).

Glaucous-winged gulls lay eggs at approximately two day intervals [30]; this suggests a 48-hour ovulation cycle. We would expect that ovulation synchrony in these birds might be manifest by synchronous every-other-day egg-laying. In previous work [12], we collected egg-laying data for three summers in a glaucous-winged gull colony on Protection Island, Washington, and showed that eggs were laid synchronously on an every-other-day schedule. We also showed that synchrony increased with colony density. The study suggested the possibility of socially-stimulated synchrony of 48-hour ovulation cycles. To probe this hypothesis, we posed a discrete-time mathematical model for population-level ovulation dynamics within the breeding season based on the hypothesis that 48-hour LH surges synchronize by means of olfactory, visual, and/or auditory cues. Model predictions were consistent with the data.

If socially-stimulated ovulation synchrony is found to occur across a wide range of taxa, the question of selective advantage becomes paramount. There are at least three possibilities. First, synchrony could be an epiphenomenon with no selective advantage but could be associated with some other advantageous trait. Second, synchrony might have been advantageous in a common ancestor and may or may not retain selective advantage. Third, synchrony could arise convergently in a number of taxa in which similar mechanisms confer similar selective advantage. For example, in many taxa, including many that experience periodic LH surges such as rats, gulls, and primates, adult animals cannibalize the young of conspecifics in densely-populated environments [13], [22]. If ovulation synchrony, induced by social stimulation in crowded living conditions, were to confer a selective advantage in the presence of cannibalism, then synchrony might arise convergently in a number of such taxa.

The goal of this paper is to investigate the effect of avian ovulation synchrony on population dynamics in the presence of egg cannibalism. We show how socially-stimulated ovulation synchrony can enhance total population size and allow the population to persist at lower birth rates than would otherwise be possible. Section 2 presents an overview of the life history and breeding phenology of glaucous-winged gulls. Section 3 reviews the method by which we measured the level of synchrony in time series data in [12], as well as the within-breeding season model proposed in that study. Section 4 extends the within-breeding season model to track population dynamics across breeding seasons. Section 5 presents a linear stability analysis at the origin and proves the existence of a transcritical bifurcation of nontrivial cycles. Section 6 contains analyses of two limiting models: one with no social stimulation and one with infinitely strong social stimulation. These special cases provide a framework for simulation studies that categorize the dynamic possibilities.

2 Life History and Breeding Phenology of Glaucous-winged Gulls

prey on nests when the incubation activities in neighboring territories are disturbed by eagles or other predators. Parent gulls temporarily flee their territories during these disturbances, leaving eggs exposed and unprotected. Chicks that run into neighboring territories during disturbances are sometimes cannibalized as well. On Protection Island, egg cannibalism was significantly higher during an El Niño year when food was scarce than during other years [8].

A variety of predators take gull eggs, chicks, and adults [10]. On the Protection island colony, however, nearly all predation is due to bald eagles, cannibalism, and the predation of eggs by crows. During the gull incubation period, it is common to find all eggs in entire sections of the colony destroyed after eagles have hopped from nest to nest devouring the contents. Chicks are taken by eagles that swoop down from perch sites and snatch them from the colony surface. Adult gulls are taken while on territory, or, less often, while in flight. Eagle predation and flyovers cause large numbers of gulls to flee their nests, providing opportunity for gull cannibals and crows to snatch unprotected eggs.

The chance that a glaucous-winged gull egg on Protection Island will be fertile, avoid predation, and hatch ranges from 29% to 88%, depending on nest habitat, degree of predation, parent age, and year (unpublished data). Fledging success is difficult to determine, but estimates range from 51% to 55%, depending on time of clutch onset [30]. Survivorship post-fledging ranges from 40% to 87% per year of life, with first year mortality the highest [9].

3 Egg-laying and Ovulation Synchrony

In [12], we collected egg-laying data for three summers in a glaucous-winged gull colony on Protection Island, Washington. We showed that egg-laying occurred synchronously on an every-other-day schedule, and that the level of synchrony increased with colony density. We also posed a mathematical model based on the hypothesis that ovulation cycles synchronize as a result of social stimulation. In order to validate the model, we estimated its parameters on one of 15 data sets and successfully predicted the remaining 14 data sets without re-parameterizing. Model predictions were consistent with the data. In this section we give a brief review of 1) the method used to measure egg-laying synchrony in noisy time series of egg-laying data, 2) the argument used to show that the observed levels of synchrony were significantly different from those that arise by chance, 3) the mathematical model introduced in [12], and 4) the connection between social stimulation and ovulation synchrony in that model. Details are found in [12].

3.1 Measuring egg-laying synchrony in time series

If a group of gulls were perfectly synchronized, the number of eggs laid per day, and the number of clutches initiated per day, would look like the simulation in Fig. 1a. Such a time series would have two distinguishing characteristics. First, it would have a 2-cycle-like oscillation with every-other-day "highs" of (probably) irregular height. Second, the "lows" of the oscillation would equal zero. Because the egg-laying interval of these birds is slightly greater than two days [30], and because there might be days on which no eggs were laid, the time series could have "skips" of two or more zeros in a row (Fig. 1a). Observed time series, of course, are noisy. Figure 1b shows one of the 15 observed time series analyzed in [12]. To measure the level of egg-laying synchrony in noisy time series, we defined a measure of synchrony for time series of the form E_0, E_1, E_2, $E_3, \ldots, E_m$, where E_i is the number of eggs laid on day i, days 1 and m refer to the first and last days on which eggs were laid, and E_0 and E_{m+1} are defined to be zero:

$$= \frac{\sum_{i=0}^{m} |E_{i+1} - E_i|}{2\sum_{i=1}^{m} E_i}. \tag{1}$$

$$x_{t+1} = \mathbf{P}(x_t)\, x_t \qquad (2)$$

where $x_t = (w_t, x_t, y_t)^>$, $x_0 = (w_0, 0, 0)^>$, and

$$\mathbf{P}(x) = \begin{matrix} 1 - fe^{-cx} & 0 & 0 \\ fe^{-cx} & 0 & qe^{-cx} \\ 0 & 1 & q\,(1 - e^{-cx}) \end{matrix}$$

with a time step of one day. Figure 2a shows a conceptual diagram of the model. Here w_t is the number of adult gulls that have not yet begun ovulation cycling by day t in the spring, x_t is the number of adults that ovulate on day t, and y_t is the number of adults that are cycling but did not ovulate on day t. The fraction f (0, 1) is the probability that a non-cycling individual is ready to begin ovulation cycling, and $(1 - e^{-cx})$ is the probability that a cycling individual or one ready to cycle will "skip" a day in order to synchronize, where $c \geq 0$ is the strength of social stimulation. The fraction 1 − q, for q (0, 1), is the probability that a bird in the second phase of the cycle (the y class) will stop cycling and incubate.

Remark 1 x t t + 2;

x

x

We presented a stochastic version of model (2) in [12]. Figure 1d shows a stochastic simulation with its -value. Figure 1f shows the estimated distribution of -values arising from the stochastic model, along with the observed value of (arrow) from the observed time series in Fig. 1b.

The model in [12] was nonautonomous; both f and c were expressed with time-dependent submodels in order to model the relationship between temperature-related delays in the onset of ovulation and the fixed endpoints of the reproductive season as set by photoperiod . In this study, however, we disregard the possibility of temperature-related delays in ovulation, and we take f and c to be constant.

Ovulation synchrony is measured in the x component of time series of model (2). The asymptotic dynamics are uninteresting, as the following argument shows.

i

Both the open positive cone R^3_{+w}

is the origin $x = 0$. It follows from LaSalle's invariance principle ([14] Theorem 6.3) that x_t approaches the origin, that is to say, the origin is a global attractor relative to $\bar{R}^3_+$. The origin is also locally asymptotically stable because the eigenvalues $1 - f$ and $\pm\sqrt{q}$ of the Jacobian Þ(0) at the origin are all less than 1 in absolute value. Thus, we have the following theorem:

Theorem 2
$\bar{R}^3_+$

3.4 Connection between social stimulation and ovulation synchrony

In this study our goal is to extend model (2) across breeding seasons and to categorize the effect of socially-stimulated ovulation synchrony on population-level dynamics. We wish to do this by studying the population dynamics as a function of the social stimulation parameter c. First, however, we must mention the connection between the level of ovulation synchrony in transient time series of model (2) and the level of social stimulation c. Model (2) was designed to express the hypothesis that increasing social stimulation c increases ovulation synchrony. The nonlinear mechanism by which this is accomplished is that birds in the w and y classes can "skip" returning to the x class until the x class is large. The relationship between and c is illustrated in Fig. 3a, which shows a graph of as a function of c for deterministic time series of model (2). The three arrows indicate pairs of (c,) for which time series (for x) are shown in Fig. 3b-d. In Fig. 3b, social stimulation is zero and the synchrony level is low. In Fig. 3c, social stimulation is moderately high and the synchrony level is near 0.5. In Fig. 3c, social stimulation is very high and the time series is almost perfectly synchronous.

In the next section we extend model (2) to include births and deaths across breeding seasons. We then study the effect of socially-stimulated ovulation synchrony on population dynamics by studying the effect of the parameter c.

4 Across-season Population Model

Extending model (2) across breeding seasons requires tracking births and deaths from year to year. Figure 2b shows a conceptual diagram of the extended model, in which we make a number of simplifying assumptions in order to reduce dimensionality.

First, in this model we assume that the total number of "births" (eggs laid) on day $t + 1$ is the number of ovulations x on day t reduced by a factor b $(0, 1]$ to account for unfertilized/addled eggs and also reduced by a factor $e^{-d(x+y)}$ with $d \geq 0$ to account for the cannibalism of eggs by neighboring nesting gulls. (Note, however, that in the biological system the number of eggs laid on day $t + 1$ is the number of ovulations on day $t - 1$, and that an egg is subject to cannibalism every day before hatching, instead of just the day it is laid). Thus, b is the "birth rate per ovulation" in the absence of cannibalism. The parameter b plays an important role in the analysis that follows. In particular, we will use b as a bifurcation parameter in proving the existence of periodic solutions of the across-season model.

Second, in this model we place eggs and chicks, along with adults that are incubating and chick-rearing, into a single class (z) with a common death rate (per day) of μ $(0, 1)$ due to predation by eagles. We assume no other source of mortality during the breeding season other than egg cannibalism. In particular, the model does not include the cannibalism of chicks by neighboring adults.

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Third, we track the dynamics of the breeding season using a time step of one day as in model (2), and at the end of the breeding season we assess (in one time step) an over-winter mortality $\nu \quad (0,1)$ on all birds and return the survivors to the w class to begin the next breeding season. In this model, therefore, juveniles are assumed to mature in one year. This is a major simplification, given that in the biological system juveniles require four years to mature.

Mathematically, we pose the model in the following way.

Let $k \quad\ ^{+} \backslash \{1, 2, 3\}$ be the number of days in the breeding season. The periodically-forced population-level model is

$$x_{t+1} = M\,(t, x_t)\,x_t \tag{3}$$

where $x = (w, x, y, z)^{>}$. The time step is one day, and the k-periodic projection matrix is defined by

$$M\,(t, x) = \begin{cases} P\,(x) & \text{for } t = 0, 1, \cdots, k-2 \\ Q & \text{for } t = k-1 \end{cases},$$

and extendedr=i4(5.7(s)2(ystem)-331.5(jTf70.994aa9r)81≥Tf0.63470TD53Tj43o(i1.2391Tf15.f5.08980.5868TD/TT554≥Tj/T where

$$\begin{aligned} \mathbf{1} &\circeq (1,0,0,0)^{>} \\ x_{nk} &= \mathbf{1}w_{nk} = (w_{nk},0,0,0)^{>}. \end{aligned}$$

The composite map is therefore equivalent to an autonomous scalar map of the form

$$w_{t+1} = g(w_t)\, w_t \tag{6}$$

where the time unit is equal to k time units in the original model.

Remark 3

x

c.

x

$c = 0$

$c = 0.7$

Our first goal will be to study the asymptotic dynamics of the across-season population model (3). Using bifurcation theoretic methods, we will study the existence and stability of (annual) periodic solutions of this nonautonomous, periodically forced matrix model. We will then obtain results on how these attractors (or more specifically, how bifurcating branches of periodic solutions) depend on the social stimulation coefficient c. According to Remark 3, this will permit us to determine the relationship between socially-stimulated ovulation synchrony and characteristics of the population dynamics (e.g., total population size).

5 Existence and Stability of Periodic Solutions of Model (3)

In this section our goal is to prove the existence of nontrivial k-periodic solutions of model (3). We do this by proving the existence of nontrivial equilibria of the scalar map (6), and hence the composite map (5), using a bifurcation theoretic approach. Specifically, we use b as a bifurcation parameter and show that the trivial equilibrium destabilizes as b increases through a critical value b_k. This destabilization results in the bifurcati

b k
$b = b_k$ $g^0(0) < 0,$ g
k b b_k $g^0(0) > 0,$
k b b_k

We begin by posing a slightly different model and proving several technical lemmas that will be useful in this section as well as Section 6.

5.1 Some lemmas

Let $\{s_t\}$ be a real-valued k-periodic sequence satisfying $s_0 > 0$ and $0 \le s_t \le 1$ for all $t \ge 0$. Consider the k-periodic map

$$x_{t+1} = N(t, x_t)x_t \tag{7}$$

with initial condition (4), where

$$N(t, x) = \begin{cases} R(t, x) & \text{for } t = 0, 1, \cdots, k-2 \\ Q & \text{for } t = k-1 \end{cases}$$

and

$$R(t, x) = \begin{matrix} 1 - fs_t & 0 & 0 & 0 \\ fs_t & 0 & qs_t & 0 \\ 0 & 1 & q(1 - s_t) & 0 \\ 0 & be^{-d(x+y)} & 1 - q & 1 - \mu \end{matrix} .$$

Because of the structure of matrix Q, the Jacobian

$$J \overset{\circ}{=} QR(k-2, 0)\, R(k-3, 0) \cdots R(0, 0) \tag{8}$$

of the $(k-1)^{th}$ composite of (7) evaluated at the origin has zero entries in all but the first row. The eigenvalues of J are therefore 0 (multiplicity three) and the upper left hand entry of J, which we denote by $\lambda(k)$. Note that $\lambda(k)$ is the product of $1 - \nu$ and the sum of the entries of the first column of $R(k-2, 0)\, R(k-3, 0) \cdots R(0, 0)$. The first column of $R(k-2, 0)\, R(k-3, 0) \cdots R(0, 0)$ is generated by applying the map

$$\begin{aligned} p_1(t+1) &= (1 - fs_{t+1})\, p_1(t) && \text{(9a)} \\ p_2(t+1) &= fs_{t+1} p_1(t) + qs_{t+1} p_3(t) && \text{(9b)} \\ p_3(t+1) &= p_2(t) + q(1 - s_{t+1})\, p_3(t) && \text{(9c)} \\ p_4(t+1) &= bp_2(t) + (1 - q)\, p_3(t) + (1 - \mu)\, p_4(t) && \text{(9d)} \end{aligned}$$ μ

Remark 5

$$u_{t+1} = QP^{k-1}u_t$$

$$P \doteq P(0) = \begin{matrix} 1-f & 0 & 0 & 0 \\ f & 0 & q & 0 \\ 0 & 1 & 0 & 0 \\ 0 & b & 1-q & 1-\mu \end{matrix} \quad .$$

$s_t = 1$ $t \geq 0$ $J = QP^{k-1}$ $\lambda(k)$ $\lambda(k)$

Lemma 6 $t \geq 0$ $p_1(t)$, $p_2(t)$, $p_3(t)$ b. $t \geq 1$ $p_4(t)$ b $b = 0$ $m(t) > 0$

Proof. It is obvious that $p_i(t) \geq 0$ for all t

We proceed by induction on k to show that the intercepts β(k) are less than 11

Proof. Given initial condition (4), it is straightforward to calculate

$$x_2 = \begin{matrix} (1 - f s_1)(1 - f s_0) \\ f s_1 (1 - f s_0) \\ f s_0 \\ b e^{-d f s_0 w_0} f s_0 \end{matrix} \quad w_0 .$$

Here the constants $\omega_2 = (1 - f s_1)(1 - f s_0)$, $\xi_2 = f s_1 (1 - f s_0)$, $\theta_2 = f s_0$, and $\zeta_2 = 0$ satisfy (11) and $\gamma_2 (w_0) \circeq b e^{-d f s_0 w_0} f s_0$ satisfies (12).

Suppose, for purposes of induction, that

$$x_{t-1} = \begin{matrix} \omega_{t-1} \\ \xi_{t-1} \\ \theta_{t-1} \\ \gamma_{t-1}(w_0) + \zeta_{t-1} \end{matrix} \quad w_0$$

where the scalar sequences $\omega_{t-1}, \xi_{t-1}, \theta_{t-1}, \zeta_{t-1}$ are independent of w_0 and satisfy (11) and where $\gamma_{t-1}(\cdot)$ satisfies (12). Then

$$\begin{aligned} x_t &= R(t-1, x_{t-1}) x_{t-1} \\ &= \begin{matrix} (1 - f s_{t-1}) \omega_{t-1} \\ f s_{t-1} \omega_{t-1} + q s_{t-1} \theta_{t-1} \\ \xi_{t-1} + q(1 - s_{t-1}) \theta_{t-1} \\ b e^{-d(\xi_{\mu-1} + \theta_{\mu-1}) w_0} \xi_{t-1} + (1-q)\theta_{t-1} + (1-\mu) \left[\gamma_{t-1}(w_0) + \zeta_{t-1} \right] \end{matrix} \quad w_0 . \end{aligned}$$

By the induction hypotheses, the quantities

$$\begin{aligned} \omega_t &\circeq (1 - f s_{t-1}) \omega_{t-1} \\ \xi_t &\circeq f s_{t-1} \omega_{t-1} + q s_{t-1} \theta_{t-1} \\ \theta_t &\circeq \xi_{t-1} + q(1 - s_{t-1}) \theta_{t-1} \\ \zeta_t &\circeq (1 - q) \theta_{t-1} + \zeta_t \end{aligned}$$

conditions for scalar maps from more general versions, which can be found, for example, in [2], [3], and [11].

Proof of Theorem 4. (a) Let $s_t = 1 \quad t \geq 0$. By Remark 5, $\lambda(k)$ is the eigenvalue of the linearization of scalar map (6) at the origin. By Lemma 7, we know that $\lambda(k)$ is a linear, increasing function of b that is less than 1 for $b = 0$. Clearly there exists a unique $b_k > 0$ such that

$$\lambda(k)\big|_{b=b_\neg} = 1, \tag{13}$$

and

$$\frac{d}{db}\lambda(k)\Big|_{b=b_\neg} = \alpha(k) > 0. \tag{14}$$

Thus, the origin is stable if $0 < b < b_k$ and unstable for $b > b_k$.

(b) Given (13)-(14), the bifurcation theory of nonlinear scalar maps implies the bifurcation of a branch of positive equilibria at $b = b_k$ for the scalar map (6). Since

$$\frac{d^2}{dw^2}[g(w)w]\Big|_{w=0} = 2g^0(0), \tag{15}$$

it follows that the bifurcation is supercritical if $g^0(0) <$ ɲ ض

Theorem 9 $c = 0$

Proof. By Theorem 4, it is sufficient to show that $g'(0) < 0$ when $c = 0$. We determine the function g by a direct calculation of the map $g(w_0)w_0$ in (6). Let $\|\cdot\|_1$ denote the L^1 norm. An application of Lemma 8 with $d > 0$ and $s_t = 1 \quad t \geq 0$ implies

$$\begin{aligned}
g(w_0)w_0 &= \|x_k\|_1 \\
&= \|QP(x_{k-2})P(x_{k-3})\cdots P(x_0)x_0\|_1 \\
&= (1-\nu)\|P(x_{k-2})P(x_{k-3})\cdots P(x_0)x_0\|_1 && (16) \\
&= (1-\nu)\|x_{k-1}\|_1 && (17) \\
&= (1-\nu)\left(\omega_{k-1} + \xi_{k-1} + \theta_{k-1} + \zeta_{k-1} + \gamma_{k-1}(w_0)\right) w_0 \\
&= (1-\nu)\left(1 + \gamma_{k-1}(w_0)\right) w_0.
\end{aligned}$$

Thus, $g(w) = (1-\nu)\left(1 + \gamma_{k-1}(w)\right)$. Since $\gamma_{k-1}(\cdot)$ satisfies where

$$C(t,x) = \begin{matrix} A(x) & \text{for } t \text{ even, } t < k-1 \\ B(x) & \text{for } t \text{ odd, } t < k-1 \\ Q & \text{for } t = k-1 \end{matrix} .$$

An application of Lemmas 7-8 with

$$s_t = \begin{matrix} 1 & \text{for } t \text{ even, } t < k-1 \\ 0 & \text{for } t \text{ odd, } t < k-1 \\ 0 & \text{for } t = k-1 \end{matrix}$$

yields the following result.

Theorem 10 $d > 0.$ $b_k^\infty > 0$
$0 < b < b_k^\infty$ $b > b_k^\infty$
k b
k b b_k^∞

As we illustrate in the next section, the relative positions of b_k (as defined in Theorem 4) and b_k^∞ (as defined in Theorem 10) provide the framework for understanding the effect of social stimulation c, and hence of ovulation synchrony, on the behavior of model (3).

6.3 Direction of bifurcation for $< c < \infty$

and hence

$$g(w_0) = (1 - \nu)\|x_{k-1}\|_1 = (1 - \nu)(w_{k-1} + x_{k-1} + y_{k-1} + z_{k-1})\} \nu$$

Our numerical explorations suggest that the pri recruitment from the w class (Fig. 4a,f) into the x class (Fig. 4b,g). This is related to Jensen's Inequality and the fact that the nonlinearity e^{-cx} is concave up. This reduces $x + y$ (Fig. 4c,h), which in turn increases egg survivorship from cannibalism $e^{-d(x+y)}$ (Fig. 4d,i). Also, the slower progression of birds through the series of classes decreases the average amount of time an adult spends in class z (Fig. 4e,j), which decreases its exposure to the mortality rate μ by eagles.

Biologically speaking, the model suggests that total population size can be enhanced by socially-stimulated ovulation synchrony through the following mechanisms. On average over time, ovulation synchrony can slightly delay the onset of ovulation in enough birds to 1) decrease the risk that a given egg is cannibalized by neighbors, and 2) decrease the average amount of time an adult spends incubating and chick-rearing (which decreases its risk of predation by eagles).

Several caveats and comments deserve mention.

First, the two mechanisms (stated above) for enhancing total population size rest on two model assumptions: 1) only birds experiencing ovulation cycles (classes x and y) cannibalize eggs, and 2) adults not yet incubating or chick-rearing (w, x, y classes) do not suffer eagle predation. The first of these assumptions is plausible: adult birds that have not yet laid eggs (w class) leave their territories unattended much of the day while loafing and foraging off the colony; hence they are not as likely to cannibalize conspecifics on the colony. Similarly, an adult that is incubating or tending chicks (z class) is less likely to leave its territory to predate neighboring nests. The second assumption also is plausible: adult birds that are incubating or rearing chicks (z class) likely exhibit greater aggression and territory tenacity and are more likely to be taken by eagles, whereas adult birds with less reproductive investment in their territories (w, x, y classes) may be more likely to flee and escape. Note, however, that birds that delay ovulation and spend less time chick rearing at the end of the season may have to abandon their unfledged chicks when the adults leave the colony in the fall, hence reducing their fitness; this type of chick mortality is not accounted for in our model.

Second, the ovulation synchrony hypothesis remains to be verified by observations and experiments. At the present we are certain only that egg-laying events can be synchronized. We currently are doing experiments to test whether this corresponds to ovulation synchrony. We also are doing experiments to test whether the means of oscillator “communication” is olfactory, auditory, and/or visual.

investigators to support at least some aspects of Darling’s conjecture, while other investigators have doubted the value of the concept. Gochfeld concluded that “in certain cases synchrony is occurring

FIGURE CAPTIONS

Figure 1. Clutch initiation data, simulations, and distributions of -values. (a) Simulation of perfect synchrony. (b) Data from 2006. (c) Monte Carlo simulation of null hypothesis. (d) Simulation of stochastic version of egg-laying model in [12]. (e) Distribution of -values generated from Monte Carlo simulations of null hypothesis. Vertical bar indicates distribution mean; arrow indicates observed -value. The null hypothesis is rejected ($p = 0.0006$). (f) Distribution of -values generated from stochastic version of egg-laying model. Vertical bar indicates distribution mean; arrow indicates observed -value. The egg-laying model is not rejected.

Figure 2. Conceptual diagrams for models. (a) Within-season dynamics, model (2). Here w_t is the number of adult gulls that have not yet begun ovulation cycling by day t in the spring, x_t is the number o91.8fnthevndithe oc[(46o)-24-336(the)30d4(y)]TwJ/TT9ng

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