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Modeling territory attendance and preening behavior in a seabird colony as functions of environmental conditions

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In previous studies we developed a general compartmental methodology for modeling animal behavior and applied the methodology to marine birds and mammals. In this study we used the methodology to construct a system of two differential equations to model the dynamics of territory attendance and preening in a gull colony on Protection Island, Strait of Juan de Fuca, Washington. We found that colony occupancy was driven primarily by abiotic environmental conditions, including tide height, time of day, solar elevation, and wind speed over open water. For birds in the colony, preening behavior was driven to some extent by abiotic environmental conditions (including time of day, solar elevation, humidity, and wind speed on the colony), but apparently was driven primarily by local and/or biotic effects not included in the model. In terms of R^2 values, the model explained 65% and 37% of the variability in colony occupancy and preening data, respectively, as a function of these six abiotic environmental factors.

1. Introduction

A number of 'compartmental' differential equation models have successfully predicted the behavior of marine birds and mammals as functions of abiotic environmental factors. Henson *et al.* [1] and Hayward *et al.* [2] predicted the dynamics of loafing behavior in Glaucous-winged Gulls (*Larus glaucescens*) near a breeding colony on Protection Island, Washington, and Herring Gulls and Great Black-backed Gulls (*L. argentatus* and *L. marinus*, respectively) near a breeding colony on Appledore Island, Maine, as functions of environmental conditions. The models explained up to 83% and 47% of the variability in loafing dynamics on Protection Island and Appledore Island, respectively ($R^2 = 0.83, 0.47$). Hayward *et al.* [3] modeled haul-out behavior in harbor seals (*Phoca vitulina*) on a beach at Protection Island as a function of environmental conditions with $R^2 = 0.40$. Damania *et al.* [4] and Moore *et al.* [5] modeled the

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diurnal occupancy dynamics of a system of habitat patches in and around the Protection Island gull colony as a function of environmental factors with R^2 values up to 0.82. Henson *et al.* [6] modeled the same system on two time scales, and studied recovery from disturbances as a function of environmental conditions. Henson *et al.* [7] used a system of differential equations to predict the dynamics of colony occupancy and sleep in the Protection Island gull colony. In terms of R^2 values, the model explained 65% and 52% of the variability in colony occupancy and sleep data, respectively, as a function of abiotic environmental factors.

In this study we continue the ongoing program of modeling and field observations of the behavior of marine organisms. Specifically, our goal is to explain and predict the dynamics of colony attendance and preening behavior in the Protection Island Glaucous-winged Gull colony during chick-rearing season as a function of environmental conditions.

Colony attendance is constrained by the number of nesting territories within the colony. Each nesting pair of gulls guards a territory ranging in size from 15 to 30 m^2 ([8]; J.G.G. unpublished data). At least one mate remains on the territory at all times, and both mates attend the territory at night. Intruding gulls are driven quickly out of territories; hence only resident birds attend the colony. Gulls leave the colony to loaf, bathe, drink, feed, and acquire food for chicks.

'Preen' is defined as the state in which a sitting or standing gull pulls feathers through its bill and/or moves the head in a smoothing motion over the body [9]. Preening is important for maintenance of feathers for flight and thermoregulation. Gulls have been shown to preen more frequently following return flights to territory than at random times of territory occupancy [10].

We constructed a system of two differential equations to model colony occupancy and preen. In section 2 we derive a general deterministic model of animal behavior. We also provide a stochastic version of the model that is needed for model parameterization. In section 3 we use this general model as a basis on which to derive our Colony–Preen model. Section 4 describes the data collection procedure. In section 5 we connect the Colony–Preen model to the collected data and describe the results. Section 6 provides a discussion of the results and lists a number of important caveats. For an in-depth perspective on the methodology used in this study, see [7].

2. A model of animal behavior

2.1 *Deterministic model*

A compartmental model of b behaviors in h habitats has at most $m = bh$ compartments, each of which represents a specific behavior in a specific habitat. Let $\mathbf{N} = \langle n_1, n_2, \ldots, n_m\rangle^{\mathbf{T}}$ be the vector of numbers of animals in each compartment, $\mathbf{M} = (f_{ij})$ be the matrix of numbers of animals $f_{ij} = f_{ij}(t, \mathbf{N})$ in compartment j that are eligible to move to compartment i, and $\mathbf{R} = (r_{ij})$ be the matrix of per capita rates $r_{ij} = r_{ij}(t, \mathbf{N})$ at which eligible individuals move from compartment j to compartment i. The deterministic model is the ODE balance equation for the inflow and outflow rates for each compartment:

$$\frac{d\mathbf{N}}{dt} = diag(\mathbf{R}\mathbf{M}^{\mathbf{T}} - \mathbf{R}^{\mathbf{T}}\mathbf{M}), \tag{1}$$

where the symbols $^{\mathbf{T}}$ and *diag* denote the matrix transpose and diagonal vector, respectively. For convenience, we take $f_{ii} = r_{ii} = 0$ for each $i \in \{1, 2, \ldots, m\}$. The ODE for the

ith compartment in model (1) is

$$\frac{dn_i}{dt} = \sum_{j=1}^{m} r_{ij} f_{ij} - \sum_{j=1}^{m} r_{ji} f_{ji}.$$

Model (1) ignores birth and death processes. Thus, the total population size

$$K = \sum_{i=1}^{m} n_i$$

remains constant, and we can reduce the dimension of (1) by writing $n_m = K - \sum_{i=1}^{m-1} n_i$.

Application of model (1) to a particular biological system requires specifying the functions $f_{ij} = f_{ij}(t, \mathbf{N})$ and $r_{ij} = r_{ij}(t, \mathbf{N})$ by means of modeling assumptions and/or model selection techniques. In general, model (1) is nonautonomous and nonlinear.

Suppose data are collected at discrete times with constant time step Δt. Without loss of generality, choose the time units so that $\Delta t = 1$. Consider the Poincaré map that takes stroboscopic snapshots of the continuous-time model at these discrete times of data sampling:

$$\mathbf{N}_{\tau+1} = F(\tau, \mathbf{N}_\tau)\ \tau = 0, 1, 2, \ldots \tag{2}$$

where $\mathbf{N}_\tau = \mathbf{N}(\tau)$ and F is defined by

$$F(\tau, \mathbf{N}_\tau) = \mathbf{N}_\tau + \int_{\tau}^{\tau+1} diag(\mathbf{R}\mathbf{M}^{\mathbf{T}} - \mathbf{R}^{\mathbf{T}}\mathbf{M})dt.$$

We will use model (2) to connect model (1) to the discrete-time data.

2.2 *Stochastic model*

A stochastic version of a deterministic model is necessary in order to connect it to data through parameter estimation. A stochastic counterpart of model (2) is

$$\phi(\mathbf{N}_{\tau+1}) = \phi(F(\tau, \mathbf{N}_\tau)) + E_\tau, \qquad \tau = 0, 1, 2, \ldots \tag{3}$$

where ϕ is a variance-stabilizing transformation that renders noise additive on the ϕ-scale, and E_τ is a vector from a multivariate normal random distribution with variance–covariance matrix $\mathbf{\Sigma} = (\sigma_{ij})$. A transformation for ecological data [7] is

$$\phi(x) = \frac{2\ln\left(\frac{1}{2}\sqrt{\psi x} + \frac{1}{2}\sqrt{\psi x + 4(1-\psi)}\right)}{\sqrt{\psi}}, \tag{4}$$

where $\psi \in (0, 1]$ is a parameter that measures the relative amount of environmental noise in the data. The value $\psi = 1$ corresponds to environmental stochasticity with transformation $\phi(x) = \ln x$, and $\psi \to 0^+$ corresponds to demographic stochasticity with transformation $\phi(x) = \sqrt{x}$ [11].

Note that model (3) assumes stochastic perturbations of the system are uncorrelated in the sample times $\tau = 0, 1, 2, \ldots$.

3. Colony–Preen model

The Colony–Preen model that we use for our field study is based on the following assumptions:

(A1) Each individual gull is categorized as belonging to one of three mutually exclusive compartments: in the colony and preening (P), in the colony but not preening (E, for 'everything else'), or away from the colony (A). The numbers of animals in each compartment are denoted P, E, and A, respectively. Animals away from the colony could not be observed and hence could not be categorized as preening or not preening. Thus, the dimension of the system is $m = 3$ and $\mathbf{N} = \langle P, E, A\rangle^{\mathbf{T}}$. For readability, we use letters instead of numbers for subscripts; for example, the number of individuals eligible to move from P to E will be denoted f_{EP} instead of f_{21}.

(A2) The number of individuals $C = P + E$ attending the colony at any time t must satisfy $K/2 \leq C(t) \leq K$, where $K/2 > 0$ is the number of nests/territories and K is the number of territory owners. This assumption is based on the fact that at least one mate attends each territory during chick-rearing season, and that intruding gulls are promptly driven from the colony.

(A3) No individual moves directly from the P compartment to the A compartment; that is, we assume that undisturbed gulls do not leave the colony during or immediately after a bout of preening. Hence,

$$f_{AP} = 0.$$

(A4) The number of individuals eligible to leave the colony via the E compartment and enter the A compartment is typically E. However, given assumption A2, the number of gulls in the colony that are eligible to leave cannot exceed $C - K/2$. Thus, the number of individuals eligible to move from the E compartment to the A compartment is

$$f_{AE} = \min\{E, C - K/2\}.$$

(A5) All individuals in the A and P compartments are eligible to move to the E compartment and all individuals in the A compartment are eligible to move to the P compartment. Indeed, Forseyth [10] showed that preening is the most common behavior used by Glaucous-winged Gulls within the first five minutes after they return to territory. Thus,

$$f_{EA} = f_{PA} = A, \text{ and } f_{EP} = P.$$

(A6) The number of individuals in the E compartment that are eligible to enter the P compartment is $\alpha C - P$, where $0 < \alpha \leq 1$, as long as $\alpha C - P$ is positive, and zero otherwise; that is,

$$f_{PE} = \max\{\alpha C - P, 0\}, \text{ where } 0 < \alpha \leq 1.$$

We interpret the coefficient α as the fraction of birds in the colony that are either preening or engaged in behaviors that can transition directly to preen, such as rest or upright postures. The quantity $1 - \alpha$ is the fraction of birds in the colony engaged in behaviors that seldom transition directly to preen, such as sleep [12]. Clearly this fraction changes over time. Because the model does not track any behaviors except preen, however, we assume α is constant.

(A7) The per capita transition rates r_{ij} are proportional to powers of six abiotic nondimensionalized environmental variables: time of day $\Theta(t)$, tide height $T(t)$, solar elevation $S(t)$, humidity $H(t)$, wind speed on the colony $W_c(t)$, and wind speed over open water $W_w(t)$, where $1 \leq \Theta, T, S, H, W_c, W_w \leq 2$. The r_{ij} functions can be different in the time periods we designate as 'Morning' ($5 \leq t \leq 10$), 'Midday' ($10 < t < 14$) and 'Evening' ($14 \leq t \leq 20$) [7]. Thus,

$$r_{ij}(t) = \begin{cases} m_{ij}\Theta^{a_{ij1}} T^{b_{ij1}} S^{c_{ij1}} H^{d_{ij1}} W_c^{f_{ij1}} W_w^{g_{ij1}} & \text{if } 5 \leq t < 10 \\ n_{ij}\Theta^{a_{ij2}} T^{b_{ij2}} S^{c_{ij2}} H^{d_{ij2}} W_c^{f_{ij2}} W_w^{g_{ij2}} & \text{if } 10 \leq t < 14 \\ e_{ij}\Theta^{a_{ij3}} T^{b_{ij3}} S^{c_{ij3}} H^{d_{ij3}} W_c^{f_{ij3}} W_w^{g_{ij3}} & \text{if } 14 \leq t \leq 20, \end{cases} \tag{5}$$

where $m_{ij}, n_{ij}, e_{ij} > 0$ and $a_{ijk}, b_{ijk}, c_{ijk}, d_{ijk}, f_{ijk}, g_{ijk} \in \mathbf{R}$ are constant parameters.

Given assumptions A1–A7 and the identities $E = C - P$ and $A = K - C$, it is straightforward to show that model (1) is equivalent to the two-dimensional system

$$\begin{aligned} \frac{dC}{dt} &= r_{PA}(K - C) + r_{EA}(K - C) - r_{AE}\min\{C - P, C - K/2\}, \\ \frac{dP}{dt} &= r_{PE}\max\{\alpha C - P, 0\} + r_{PA}(K - C) - r_{EP}P, \end{aligned} \tag{6}$$

which we refer to as the Colony–Preen model. It is also straightforward to show that solutions of model (6) satisfy the inequalities $K/2 \leq C(t) \leq K$ and $0 \leq P(t) \leq C(t)$ for all time t provided the initial conditions do.[†]

4. Hourly data

We collected data on colony occupancy and preen behavior at Protection Island National Wildlife Refuge (48°08′N, 122°55′W), Jefferson County, Washington. The island lies at the southeastern end of the Strait of Juan de Fuca, and consists mostly of a high plateau bordered by steep bluffs. Violet Point, a gravel spit extending to the southeast, contains a breeding colony of more than 2400 pairs of nesting Glaucous-winged Gulls. We selected a 33 × 100 m sample colony area containing approximately 70 nests.

Observations consisted of hourly census counts and behavior scans taken during daylight hours in chick-rearing season from 0500–2000 Pacific Standard Time (PST) for 14 days on 30 June–2 July and 6 July–16 July 2004. Observations were made using a 20–60× spotting scope from an observation point atop a 33 m bluff that borders the west end of Violet Point. The observation point was located 100 m from the proximal edge of the colony, and 200 m from the study plot. The presence of observers did not seem to influence the behavior of the gulls in any way. At the top of each hour, a census and a behavior scan were taken, in that order. Behaviors were recorded by voice and subsequently transcribed. The number of animals in the behavior scan was typically slightly different from the census, since these observations were not conducted simultaneously. To correct for this, we divided the number of birds exhibiting a particular behavior by the number of birds scanned, and multiplied the result by the census.

A weather station located 2 m above site elevation on the northwest end of Violet Point recorded hourly values of a large number of environmental conditions on the colony, including temperature, humidity, wind speed and direction, heat index, barometric pressure, rainfall, and solar radiation. Hourly tide heights and solar elevations, as well as wind speeds in the Strait (measured at Smith Island), were obtained from the National Oceanic and Atmospheric

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[†] The trapezoid $\{(C, P)|0 \leq P \leq C \text{ and } K/2 \leq C \leq K\}$ is forward invariant under model (6). This is because along the lines $C = K/2$, $C = K$, and $P = 0$, we have the inequalities $\mathrm{d}C/\mathrm{d}t > 0$, $\mathrm{d}C/\mathrm{d}t \leq 0$, and $\mathrm{d}P/\mathrm{d}t > 0$, respectively. Suppose $P = C$. Then $\mathrm{d}C/\mathrm{d}t \geq 0$ and $\mathrm{d}P/\mathrm{d}t < \mathrm{d}C/\mathrm{d}t$. Thus, $\mathrm{d}P/\mathrm{d}t < 0$ if $\mathrm{d}C/\mathrm{d}t = 0$, and $\mathrm{d}P/\mathrm{d}C < 1$ if $\mathrm{d}C/\mathrm{d}t > 0$.

Administration (NOAA). We nondimensionalized all environmental variables x so that $1 \leq x \leq 2$ [1,3,4,6,7].

5. Connecting model and data

Models are connected to data through the determination of parameter values. In general, parameters can be (a) determined directly from data, (b) selected from a discrete number of alternative values by means of model selection techniques, or (c) estimated from data through statistical model fitting procedures. In this study we use all three methods in concert.

Model (6) contains 107 parameters: the two parameters K and α shown explicitly in equation (6), and three coefficients and 18 exponents as shown in equation (5) for each of five per capita flow rates shown in equation (6). The stochastic model (3)–(4) further contains the parameter ψ (as well as three variance–covariance parameters, but these can be computed from the fitted sum of squared residuals). Numerical estimation of this many parameters through model fitting would require a very large data set. Thus, we utilized all three methods of parameter determination in the following way. (a) We set $K = 140$, since our sample colony area contained 70 nesting pairs. (b) We selected the values of the 90 exponents and ψ from the alternatives $a_{ijk}, b_{ijk}, c_{ijk}, d_{ijk}, f_{ijk}, g_{ijk} \in \{-1, 0, 1\}$ and $\psi \in \{0.01, 0.5, 1\}$ by means of model selection techniques as explained below. (c) We estimated the 16 parameters $\alpha, m_{ij}, n_{ij}, e_{ij}$ from data using the maximum likelihood (ML) method as explained below.

5.1 *Model selection*

Each of the 90 exponent parameters was assumed to have the value -1, 0, or 1, and ψ was assumed to have the value 0.01, 0.5, or 1. This created a very large number of possible models in the form of model (6). We chose a relatively small subset of these based on (a) the biologists' knowledge of what was likely to be most biologically reasonable for the system, (b) statistical investigations comparing the data and the environmental variables, and (c) the experience gained by weeks of trial and error searches for models that could fit the data. Of these alternative models, we took the best to be the one with the smallest (fitted) sum of squared residuals after ML parameterization, and we discarded the others. Because each of the alternative models had the same number of ML parameters, it was not necessary to use information-theoretic model selection indices such as the Akaike Information Criterion (AIC), which penalize models having more parameters [13].

Once the best model was determined from the list of alternatives, the exponents with value -1 (or 1) were decreased (or increased) by integer units until the best integer exponents were obtained.

The per capita transition rates r_{ij} for the best model are shown in figure 1.

5.2 *Parameter estimation*

In order to compare the alternative models, each had to be fitted to the data through parameter estimation. We used the method of maximum likelihood (ML) to estimate the 16 parameters $\alpha, m_{ij}, n_{ij}, e_{ij}$. Let $\{\mathbf{n}_\tau\}_{\tau=0}^{q}$ be the sequence of data vectors observed at times $\tau = 0, 1, 2, \ldots, q$. Given the observation $\mathbf{n}_\tau$ at time τ, the 'one-step' model prediction for the next census at time $\tau + 1$ is

$$\mathbf{N}_{\tau+1} = F(\tau, \mathbf{n}_\tau).$$

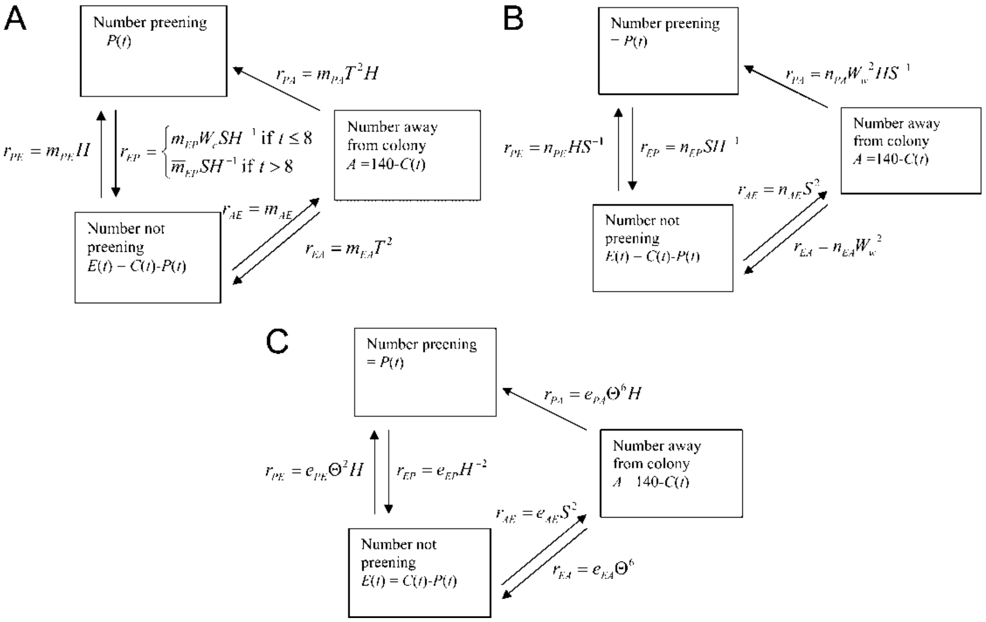

Figure 1. Per capita flow rates for best model, as a function of nondimensionalized time of day Θ, tide height T, solar elevation S, humidity H, wind speed on the colony W_c, and wind speed over open water W_w. A. Morning (0500–1000 PST). B. Midday (1000–1400 PST). C. Evening (1400–2000 PST). The ML parameters with $\psi = 1$ were $\alpha = 0.234$, $m_{EA} = 0.00297$, $m_{AE} = 0.393$, $m_{PA} = 0.0709$, $m_{EP} = 1.19$, $\bar{m}_{EP} = 1.29$, $m_{PE} = 0.797$, $n_{EA} = 0.0123$, $n_{AE} = 0.0502$, $n_{PA} = 0.127$, $n_{EP} = 0.834$, $n_{PE} = 1.36$, $e_{EA} = 0.0217$, $e_{AE} = 0.171$, $e_{PA} = 0.00277$, $e_{EP} = 7.61$, $e_{PE} = 2.92$. The estimated entries of $\mathbf{\Sigma}$ were $\sigma_{11} = 0.00644$, $\sigma_{22} = 0.0957$, $\sigma_{12} = \sigma_{21} = 0.00635$.

The (transformed) residual error vector for this prediction is given by

$$\boldsymbol{\rho}_{\tau+1} = \phi(\mathbf{n}_{\tau+1}) - \phi(\mathbf{N}_{\tau+1}) = \phi(\mathbf{n}_{\tau+1}) - \phi(F(\tau, \mathbf{n}_\tau)).$$

According to the assumptions implicit in the stochastic model (3), these one-step residual model errors come from a joint normal distribution with variance-covariance matrix $\mathbf{\Sigma}$, and they are uncorrelated in the sample times $\tau = 0, 1, 2, \ldots$. Let $\boldsymbol{\theta}$ be the vector of model parameters to be estimated. Then the maximizer $\hat{\boldsymbol{\theta}}$ of the log-likelihood function

$$\ln L(\boldsymbol{\theta}, \mathbf{\Sigma}) = -q \ln(2\pi) - \frac{q}{2} \ln |\mathbf{\Sigma}| - \frac{1}{2} \sum_{\tau=1}^{q} \boldsymbol{\rho}_\tau^{\mathrm{T}} \mathbf{\Sigma}^{-1} \boldsymbol{\rho}_\tau$$

is the vector of ML parameter estimates [11]. We maximized the log-likelihood function numerically by minimizing its negative with the Nelder–Mead algorithm [14] under three different types of stochasticity: mostly demographic ($\psi = 0.01$), a mixture of demographic and environmental ($\psi = 0.5$), and purely environmental ($\psi = 1$) [7].

Fixed values of $\Psi = 0.01$, 0.5, and 1 for the best model yielded log-likelihood values of -260, 65.0, and 175, respectively. Thus, we took $\psi = 1$ as the appropriate transformation and concluded that the stochasticity in the system was largely environmental. The ML parameter estimates assuming $\psi = 1$ are given in the caption of figure 1.

5.3 *Goodness-of-fit*

The goodness-of-fit for the colony attendance was computed as

$$R_C^2 = 1 - \frac{\sum_{\tau=1}^{q}(\phi(c_\tau) - \phi(C_\tau))^2}{\sum_{\tau=1}^{q}(\phi(c_\tau) - \overline{\phi(c)})^2}$$

where c_τ and C_τ are, respectively, the observed and predicted colony occupancy at time τ, and $\overline{\phi(c)}$ is the sample mean of the transformed observations. The R_P^2 for preen was computed similarly.

The goodness-of-fits were $R_C^2 = 0.65$ and $R_P^2 = 0.37$. Figure 2 compares the data with the one-step model predictions.

5.4 *Model orbits in the C–P plane*

In order to simulate trajectories of model (6) that span more than one day, the behavioral transition rates must be specified for nighttime hours. In the absence of data on the behavior of gulls after dark, we assume all transition rates are zero, so that the system remains constant between 2000 and 0500 hours.

Figure 3 shows an orbit of model (6) for 26 June–16 July 2004 as a continuous curve in the *C–P* plane. The discrete-time orbit of model (2) lies at hourly intervals along this curve and

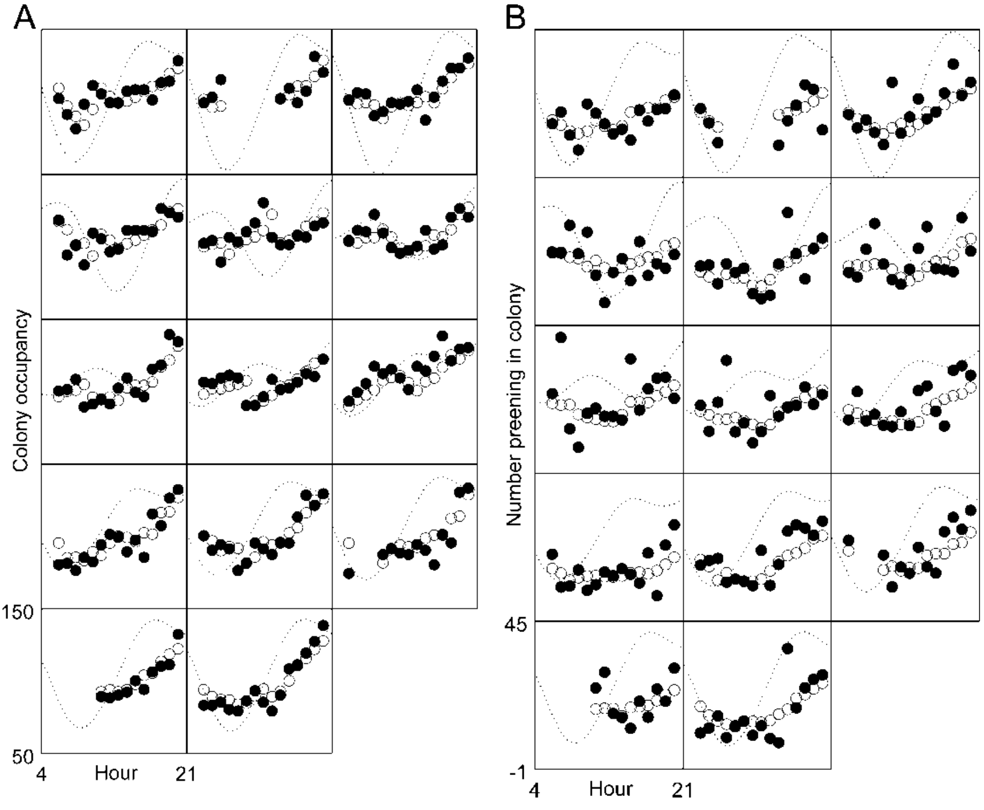

Figure 2. Hourly observations (solid circles), conditioned one-step model predictions (open circles), and tide height (dotted curve) as a function of time (PST). Figures 2A and 2B both show 14 days of data in chronological order from left to right, top to bottom. A. Number of birds in the colony. B. Number of birds preening in the colony.

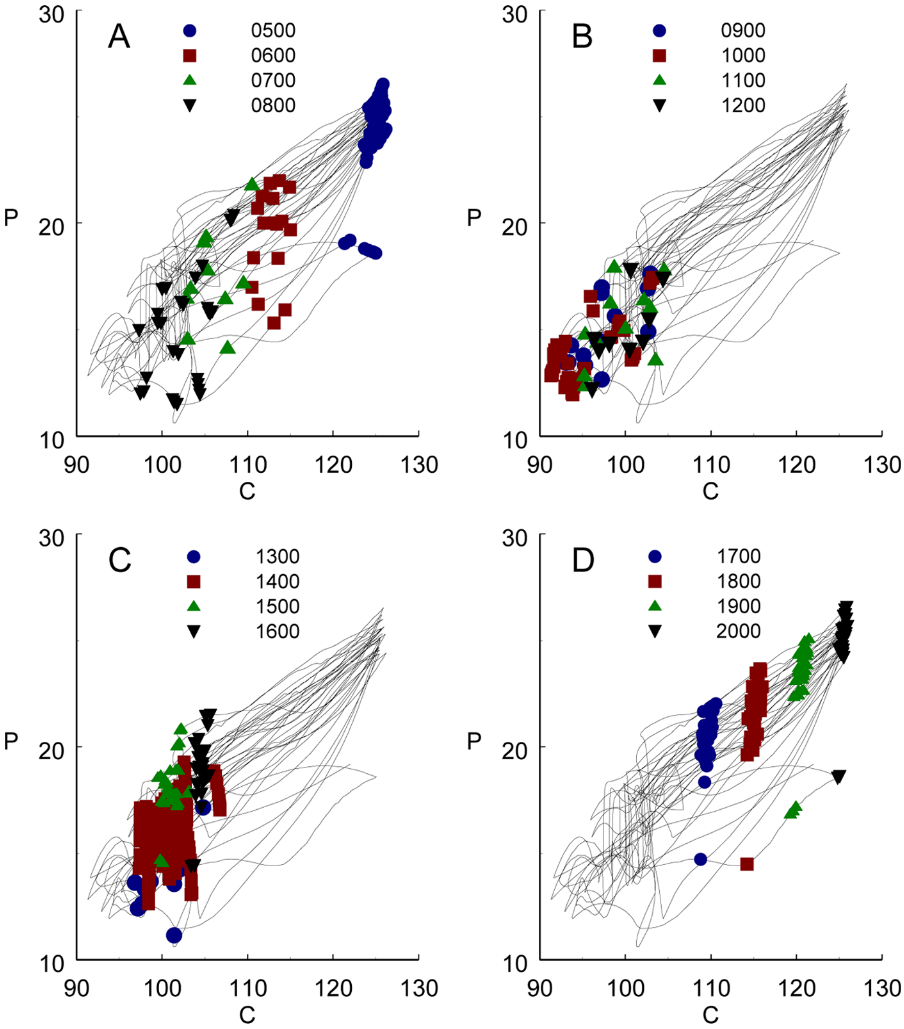

Figure 3. Model orbit for 26 June 26–16 July 2004 in *C*–*P* plane. The 24-h Poincaré sections are shown for each hour. A. 0500–0800 PST. B. 0900–1200 PST. C. 1300–1600 PST. D. 1700–2000 PST.

is marked by symbols at each data collection hour (0500–2000). Symbols 24 h apart have the same geometric shape, generating 24-h Poincaré sections.

6. Discussion

6.1 *Model predicted environmental cues for behavior*

The connection between the ‘driving’ environmental factors in the model and the behavioral dynamics is that of mathematical implication rather than scientific causation. That is, the environmental ‘determinants’ isolated in this study are correlative and may or may not be causative [6]. Nevertheless, the identification of environmental determinants may narrow the search for cues that elicit behavior. Model (6), with the per capita flow rates shown in figure 1, suggests specific environmental cues for behavior.

Morning (0500–1000 PST). The model suggests that in the Morning, gulls tend to leave the colony at a constant per capita rate (figure 1A, r_{AE}) but return to the colony if the tide is high (figure 1A, r_{EA}). Returning birds tend to preen immediately upon arrival if it is also humid (figure 1A, r_{PA}). In the colony, birds tend to begin preening if the humidity is high (figure 1A, r_{PE}). Preening birds tend to stop preening as the sun rises in the sky, or if the humidity is low. In the early morning birds stop preening if it is windy on the colony (figure 1A, r_{EP}).

Midday (1000–1400 PST). During Midday, gulls tend to leave the colony when the sun is high (figure 1B, r_{AE}), but tend to return if it is windy over the open water (figure 1B, r_{EA}). Returning birds tend to preen immediately upon arrival if it is also humid, but this tendency is reduced when the sun is high (figure 1B, r_{PA}). Birds in the colony tend to stop preening when the sun is high (figure 1B, r_{EP}) and start preening if it is humid (figure 1B, r_{PE}).

Evening (1400–2000 PST). As the evening progresses, gulls tend to return to the colony (figure 1C, r_{EA}), and the tendency to leave the colony is reduced (figure 1C, r_{AE}). There is an increased tendency to preen in humid conditions and also toward the end of the day (figure 1C, r_{PE} and r_{PA}).

This model suggests that relative humidity is an important cue for preening behavior. Previous data show that preening is more likely to occur after rain than at other times (J.L.H. unpublished data). It should be noted, however, that there was no measurable precipitation during the data collection period in this study.

6.2 *Other factors influencing preen*

Our analysis suggests that a majority (65%) of the temporal fluctuations in colony occupancy were driven by, or at least correlated with, abiotic environmental factors. However, only 37% of the variability in incidence of preen was explained by abiotic environmental factors; the majority of preen dynamics apparently was due to other factors. For instance, preening activity is known to function in maintenance of feathers after they become damp or water soaked [15, 16]. The regularity and duration of preening bouts varies dramatically after different lengths of bathing activities in Herring Gulls [17]. It is hypothesized that preening may also be a displacement activity involved in soothing or quieting gulls after extended periods of disturbance or flight back to the breeding colony [16, 18].

Another reason preen may be hard to predict from abiotic environmental factors is social facilitation. Palestis and Burger [19] and Wilson [20] showed an increase in preening in the presence of preening mates or nearby neighbors. Specific factors driving these and other social interactions in gulls are complicated and poorly understood. When the per capita transition rates r_{PE} from other behaviors to preen were made proportional to the number preening $P(t)$, the goodness-of-fit for preen rose only slightly, from $R_P^2 = 0.365$ to $R_P^2 = 0.368$. We therefore hypothesize that the effects of social facilitation on preening are localized and not necessarily operative at the aggregate level.

6.3 *Model error*

Because $\psi = 1$ yielded higher log-likelihood values than did $\psi = 0.01$ or $\psi = 0.5$, our analysis suggested that the fluctuations left unexplained by the model were due largely to environmental stochasticity rather than demographic stochasticity or a mixture of the two. This is consistent with our observations of increased preening after eagle disturbances, which constitute one of the most frequent environmental stochastic perturbations of the system [21].

Much of the model error in preen dynamics was due to approximately 7% of the data: when all data points with preen residual ≥ 10 were removed (14 data points out of 196 total), the fit rose to $R_P^2 = 0.47$ (R_C^2 remained approximately the same at 0.68).

6.4 *Diurnal periodicity in model system*

From the Poincaré sections in figure 3A,C,D, one can see that the model system predicts an approximate 24-h return time during 0500–0600 and 1500–2000 PST. During 0700–1400 PST, however, model dynamics are more complicated (figure 3A–C). That is to say, the observer who studies the system as a function only of time of day will find it relatively predictable for 0500–0600 and 1500–2000 as compared to other times. This is because tide height, humidity, and wind speeds at Protection Island are least variable at these times: summer tides are high in the afternoon and evening, humidity is generally highest in the morning and evening, and winds tend to be calm in the morning and evening.

6.5 *Caveats in modeling process*

The model identification process used in this study is more ad hoc than it appears in the explanation of the methodology. Parameterization of systems of ODEs with more than a few parameters is computationally intensive. One circumvents exhaustive model selection (such as that employed in [3]) by gaining experience with the system both through long periods of direct observation in the field and through many hours spent at the computer trying to parameterize hypothesized models.

One quickly realizes that the 'best' flow rate functions, although quite robust, are not unique; other, similar, flow rate functions can give similar model fits. This is true for several reasons. First, some of the environmental factors may be correlated. For example, hour of day Θ and solar elevation S or its reciprocal $1/S$ are in some cases interchangeable. Second, it is often difficult to determine from census data alone which variables drive inflow versus outflow rates. For example, it is not clear whether birds leave the colony in response to low tide ($r_{AE} \propto T^{-1}$), or return in response to high tide ($r_{EA} \propto T$), or both. Henson *et al.* [6] show how inflow and outflow rates can be determined separately when census data are collected on a finer time scale immediately after a disturbance of the system. Third, after the best values of the exponents $a_{ijk}, b_{ijk}, c_{ijk}, d_{ijk}, f_{ijk}, g_{ijk}$ are determined from the set $\{-1, 0, 1\}$, it is too computationally time-consuming to try many combinations of higher or lower integer exponents. A number of combinations might work equally well. Thus, for example, the specific power 6 in the Evening flow rate $r_{EA} = e_{EA}\Theta^6$ into the colony should not necessarily be viewed as significant.

A further caveat is that the set of ML parameters often is not unique—the ML function typically has multiple local maxima—and sometimes the multiple parameterizations have fairly similar ML values. This is because various magnitudes of inflows and outflows, if properly balanced, can give rise to the same net rate of change. A detailed mathematical discussion of this is given in [6].

6.6 *Summary*

Using the Colony–Preen model derived and parameterized in this study, we found that territory attendance by gulls in an observed breeding colony was driven largely by abiotic environmental conditions (namely time of day, solar elevation, tide height, and wind speed over nearby open water), whereas only 37% of the variability in preening behavior was driven by abiotic environmental conditions (time of day, solar elevation, humidity, and wind speed on the colony). We conclude that local and/or biotic effects not included in the aggregate-level model played an important role in preening behavior.

Mathematical models can identify, explain and predict deterministic trends in behavior, and parse out the contributions of environmental and demographic stochasticity. Such models are powerful tools for detecting factors that elicit behavior, for clarifying functions of behavior, and for generating new hypotheses. Although compartmental models are standard tools in the physical sciences, pharmacology, epidemiology, and population biology [22], they have been considered too coarse to predict animal behavior because they lump individuals into aggregates under simplifying assumptions [23]. Using compartmental modeling techniques, however, we have shown that some behaviors of gulls (such as loafing, territory attendance, and sleeping) are determined largely by environmental factors and are mathematically predictable at the aggregate level despite variability among individuals. We have shown that other behaviors (such as preening) are more complicated. We suggest that compartmental models may provide a new approach to the study of deterministic trends in the behavior of animals and humans.

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Appendix. List of variables

f_{ij}	number of individuals in j eligible to move to i
r_{ij}	per capita rate at which eligible individuals move from j to i
K	total number of colony residents = twice the number of nesting territories
P	number in colony preening
E	number in colony not preening
C	number in colony $= P + E$
A	number away from colony $= K - C$
t	time of day, in hours
Θ	time of day, nondimensionalized
T	tide height, nondimensionalized
S	solar elevation, nondimensionalized
H	humidity, nondimensionalized
W_c	wind speed on colony, nondimensionalized
W_w	wind speed over open water, nondimensionalized
Ψ	parameter measuring environmental noise