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A Compartmental Model of Animal Behavior

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ABSTRACT. - Animal behavior is integral to fitness and arises from complex interactions between internal and external factors. An understanding of how external environmental factors drive animal behavior is important for understanding the way organisms adapt to environmental perturbations such as climate change. Glaucous-winged gulls (*Larus glaucescens*) at Protection Island, Strait of Juan de Fuca, Washington display a variety of behaviors on the colony during the breeding season. The most common gull behaviors are sleeping, preening, and resting. I used a system of four differential equations to predict numbers of sleeping, preening, and resting gulls on the colony as a function of seven environmental factors: hour of day, tide height, solar elevation, heat index, humidity, wind speed on the colony, and wind speed over open water. The model explained 65%, 51%, 44% and 32% of the variability in colony attendance, sleep, preen, and rest dynamics, respectively. Similarly, model validation on an independent data set predicted 70%, 64%, 60% and 47% of the variability in colony attendance, sleep, preen and rest dynamics, respectively.

Key words: Animal behavior, environmental factors, glaucous-winged gulls, colony attendance, sleeping, preening, resting, differential equation model

INTRODUCTION

In biology, the term *fitness* refers to the relative ability of an organism to transmit its genes to the next generation in comparison with other members of the same species. Animal behavior is integral to fitness and arises from complex interactions between internal and external factors. An understanding of how external environmental factors drive animal behavior is important for understanding the way organisms adapt to environmental perturbations such as climate change.

The behaviors of mammals and birds can be quite complicated due to their individual variability (Slater 1978). Glaucous-winged gulls (*Larus glaucescens*) at Protection Island National Wildlife Refuge, Strait of Juan de Fuca, Washington display a variety of behaviors on the colony during the breeding season. The most common gull behaviors in the colony are sleeping, preening, and resting. Other behaviors include upright postures, walking, vocalizations, nest building, courtship, copulation, and tending/feeding chicks (Tinbergen 1961). In addition, glaucous-winged gulls can learn new behaviors in response to their environment (Obozova *et al.* 2011).

I focused on the behaviors of sleeping, preening, and resting. When gulls sleep, their heads are turned 180° and their bills are tucked in under the scapulars. Gulls can sleep while standing or sitting, and with their eyes open. Preening gulls pull their feathers through their beaks and move their head around over their body while standing or sitting. Resting gulls have their head and neck drawn down upon the shoulders and are either sitting or standing. I focused on these three behaviors because they are the most common ones and because they are integral to fitness.

Previous studies have shown that the behavior of marine birds and mammals can be successfully predicted as functions of environmental factors with mathematical models (equations) that are tied rigorously to field data. Henson *et al.* (2004) constructed a differential equation model that accurately predicted the number of gulls occupying a loafing habitat as a function of day of the year, height of the tide and solar elevation. Hayward *et al.* (2005) compared a suite of competing mathematical models that described the haul-out dynamics of harbor seals. The best model was a function of tide height and current direction. Damania *et al*. (2005) used a differential equation model to predict gull occupancy in three loafing habitats as a function of tide height, time of day, solar elevation and temperature. Temperature had the strongest influence on occupancy dynamics. Moore *et al.* (2008) revised the model of Damania *et al.* (2005) to include nesting colony occupancy dynamics as a function of the same environmental factors. Henson *et al.* (2007a) used two differential equations to model the dynamics of sleep and colony attendance in seabirds as functions of environmental factors. Subsequently, Henson *et al.* (2007b) used two differential equations to model territory attendance and preening behavior in seabirds as a function of environmental factors. Other studies have also shown that compartmental models can be used to explain avian influenza transmission and bird migratory dynamics (Hsieh *et al.* 2014 and Knisley *et al.* 2011).

In this project, I used a mathematical model to predict numbers of sleeping, preening and resting gulls in the Protection Island colony as a function of seven environmental factors. My research paper synthesizes the methodologies used by Henson *et al.* (2007a and 2007b) to construct a four-differential-equation model of colony attendance, sleeping, preening, and resting behaviors as a function of seven environmental factors. In particular, I parameterized (fitted) a system of four differential equations to hourly data collected on the Protection Island gull colony during the 2006 and 2007 chick-rearing seasons. The parameterized model is capable of predicting the total number of gulls on the colony as well as the number that are sleeping, preening, and resting at any time, given a set of known environmental conditions. Such predictive models can be useful to wildlife resource managers in helping them to identify how environmental trends, such as long-term climate trends, may place populations at risk, and how to best ameliorate human-bird interference (Henson *et al.* 2004 and Hayward *et al.* 2009).

METHODOLOGY

DATA COLLECTION

The Seabird Ecology team collected hourly data at the Protection Island National Wildlife Refuge, Jefferson County, Washington in a sample plot of the colony during the chick rearing season in 2006 and 2007. The data were collected from plot C of the colony from 0500 to 2000 hr Pacific Standard Time (PST) 13–23 June 2006 and 9–19 July 2007. This plot contained approximately 70 nests in 2006 and 60 nests in 2007 and was in the densest part of the colony with few eagle disturbances. Hourly census counts and behavior scans were made using a spotting scope. The number of gulls on the colony and the number of gulls sleeping, preening and resting were recorded. The census counts of gulls in the colony differed from the total number of birds scanned for behaviors because the observations were not done at exactly the same time. I accounted for this difference by dividing the number of birds exhibiting a particular behavior by the number of birds scanned and multiplying this number by the census count to obtain the number engaged in the behavior. Temperature, humidity, wind speed on the colony, heat index, barometric pressure, rainfall and other environmental data were obtained from an on-site weather station. Other environmental data such as hourly tide heights, solar elevations, and wind speeds over open water were obtained from the National Oceanic and Atmospheric Administration (NOAA) website.

DIVIDING THE DATA SET

I used stratified random sampling to divide the data set into two parts, keeping 75% of the data for parameter estimation and setting aside 25% for model validation. First I grouped the data by morning (0500–1000 hr), midday (1100–1300 hr), and evening (1400–2000 hr). Each group contained days 164–172 and 174 from June 2006, and days 190–194 and 196-200 from July 2007. I then randomly removed 25% of the days from each group for the validation data set. The model validation data set contained days 167, 169, 174, 191, and 196 for the morning, days 169, 192, 194, 197, and 199 for the midday, and days 166, 167, 170, 171, and 193 for the evening time period. The estimation data set contained the remaining 14 days for the morning period and 15 days for the midday and evening time period.

MODELING ASSUMPTIONS

Differential equations measure rates of change for continuous-time processes. The rate of change of a quantity *n* with respect to time *t* is the derivative *dn/dt*. A *compartmental* model is a list of equations that models the dynamics of inflows and outflows between a connected set of "compartments" (in this case, behavioral states) in a population. Each compartment is modeled by the total inflow rate minus the total outflow rate:

$$\frac{dn_i}{dt} = \text{sum of inflow rates} - \text{sum of outflow rates} \tag{1}$$

or

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

where n_i represents the number of individuals in compartment *i*, that is, exhibiting behavior *i*, r_{ij} represents the per capita transition rate from the *j* to the *i* compartment, and f_{ij} represents the number of animals eligible to transition from the *j* to *i* compartment.

Equation (1) is a system of ordinary differential equations that is similar to a deterministic Markov discrete-time model which can be applied to predict the number of gulls exhibiting a particular behavior (Chen *et al.* 2002 and Lusseau 2003). Since there is nothing inherently discrete in the time scale, I used a differential equation model (ODE) instead of a discrete-time Markov model. The ODE can predict gull behavior once the eligibility functions f_{ij} and the per capita transition rates r_{ij} are specified based on underlying biological assumptions observed in the field. The assumptions used to construct the model are based on previous work done by Henson *et al.* (2004, 2007a, and 2007b) and knowledge of gull behavior.

The state variables n_i are defined by categorizing each gull into five mutually exclusive compartments. The compartments are sleeping (S), preening (P), resting (R), every other behavior on the colony (E), and away from the colony (A). The total number of gulls attending the colony is the sum of the number of gulls sleeping, preening, resting, and displaying every other behavior, that is $C = S + P + R + E$. Figure 1 shows these state variables in a conceptual diagram of the compartmental model. The number of gulls in the colony (C) is assumed to satisfy the condition $K/2 \leq C \leq K$, where K represents the total number of nesting gulls in the colony. This assumption is based on the fact that there is always one mate guarding the nesting territory during the chick rearing season. During this season, gulls are quite protective of their nests and drive intruders away from the colony.

The eligibility functions f_{ij} are defined by assumptions that determine whether a gull is eligible to transition between the S, P, R, E and A compartments. I assume that there is no transition between the S and the P compartments ($f_{PS} = f_{SP} = 0$). Gulls are eligible to transition to the A compartment (away from the colony) only through the E compartment (every other behavior) and are ineligible to transition from the S, P and R compartments ($f_{AS} = f_{AP} = f_{AR} = 0$). The number of gulls eligible to leave the colony (C) and go away from the colony (A) is either $C - K/2$, because there is always at least one mate guarding the nesting territory on the colony, or the number of gulls displaying every other behavior (E). Therefore, the number of eligible gulls is the smaller of the two. All gulls are eligible to transition between the S and R, R and E, R and P, P and E, and E and A compartments.

The per capita transition rates are defined as functions of the environmental factors. The flow rates are proportional to powers of seven environmental variables: hour of day (t), tide height (T), solar elevation (S), heat index (I), humidity (H), wind speed on the colony (W_c), and wind speed over open water (W_w). The per capita rate can vary depending on the time period of the day. The flowrates are different in the morning ($5 \le t < 10$), midday ($10 \le t < 14$), and evening ($14 \le t \le 20$):

$$r_{ij}(t) = \begin{cases} m_{ij} t^{a_{ij1}} T^{b_{ij1}} S^{c_{ij1}} I^{d_{ij1}} H^{f_{ij1}} W_c^{g_{ij1}} W_w^{h_{ij1}} & \text{if } 5 \le t < 10 \\ n_{ij} t^{a_{ij2}} T^{b_{ij2}} S^{c_{ij2}} I^{d_{ij2}} H^{f_{ij2}} W_c^{g_{ij2}} W_w^{h_{ij2}} & \text{if } 10 \le t < 14 \\ e_{ij} t^{a_{ij3}} T^{b_{ij3}} S^{c_{ij3}} I^{d_{ij3}} H^{f_{ij3}} W_c^{g_{ij3}} W_w^{h_{ij3}} & \text{if } 14 \le t \le 20 \end{cases} \tag{2}$$

Here m_{ij}, n_{ij}, and $e_{ij} > 0$, and $a_{ijk}, b_{ijk}, c_{ijk}, d_{ijk}, f_{ijk}, g_{ijk}, h_{ijk} \in \Re$ are parameters. The per capita transition rates used in the model, based on previous studies (Henson *et al.* 2004, 2007a and 2007b, and Damania *et al.* 2005), are shown in Table 1. Figure 1 shows these flowrates between the compartments.

The compartmental model is a system of five differential equations:

$$
\begin{aligned}
\frac{dS}{dt} &= r_{SR}R - r_{RS}S, \\
\frac{dP}{dt} &= r_{PE}E + r_{PA}A + r_{PR}R - (r_{EP} + r_{RP})P \\
\frac{dR}{dt} &= r_{RE}E + r_{RP}P + r_{RS}S - (r_{ER} + r_{PR} + r_{SR})R \\
\frac{dE}{dt} &= r_{ES}S + r_{EP}P + r_{ER}R + r_{EA}A - \left(r_{SE} + r_{PE} + r_{RE} + r_{AE}\right)E \\
\frac{dA}{dt} &= r_{AE}\min\left\{E, C - K/2\right\} - \left(r_{PA} + r_{EA}\right)A
\end{aligned}
\tag{3}
$$

Given that $E = C - S - P - R$ and $A = K - C$, the model can be reduced to a system of four differential equations

$$
\begin{aligned}
\frac{dC}{dt} &= (r_{PA} + r_{EA})(K - C) - r_{AE}\min\left\{C - S - P - R, C - K/2\right\} \\
\frac{dS}{dt} &= r_{SR}R - r_{RS}S \\
\frac{dP}{dt} &= r_{PE}(C - S - P - R) + r_{PA}(K - C) + r_{PR}R - (r_{EP} + r_{RP})P \\
\frac{dR}{dt} &= r_{RE}(C - S - P - R) + r_{RP}P + r_{RS}S - (r_{ER} + r_{PR} + r_{SR})R
\end{aligned}
\tag{4}
$$

where *C*, *S*, *P* and *R* represent the number of gulls in the colony, the number in the colony that are sleeping, the number in the colony that are preening, and the number in the colony that are resting, respectively. The model is visually represented in Fig. 2.

PARAMETER ESTIMATION

I used Matlab to estimate the 37 parameters for the CSPR model from the estimation data using the least-square method (LS) on the square-root scale, which renders demographic noise additive (Cushing *et al.* 2003). The LS method relaxes the assumptions about the distribution of the residual errors (Hayward *et al.* 2005) and minimizes the residual sum of squares (*RSS*) as a function of the vector θ of parameters:

$$RSS(\theta) = \sum \left(\sqrt{observations} - \sqrt{predictions} \right)^2 \tag{5}$$

MODEL VALIDATION

Model validation is the process by which a model that has been parameterized on one data set is then used to predict another data set without re-parameterizing. In order to measure how well the model fit the data, I used a generalized R^2 for goodness-of-fit:

$$R^2 = 1 - \frac{RSS(\theta)}{\sum (\sqrt{observation} - mean)^2} \tag{6}$$

The 'mean' here denotes the mean of the square roots of the observations, and $RSS(\theta)$ denotes the fitted value of the *RSS*. The R^2 value estimates the proportion of observed variability explained by the model. The closer R^2 is to 1, the better the model fit. R^2 values were computed for the estimation data set and were compared to those computed for the validation data set.

RESULTS

Table 1 shows the LS parameters. The R^2 values for the estimation data set and the validation data set are recorded in Table 2. The model explained 65%, 51%, 44% and 32% of the variability in colony attendance, sleep, preen, and rest dynamics, respectively, in the estimation data set. Model predictions for colony attendance from the estimation data set are shown in Fig. 3A-B. Model predictions for the validation data set explained 70%, 64%, 60% and 47% of the variability in colony attendance, sleep, preen and rest dynamics, respectively, indicating successful model validation. Model predictions for colony attendance from the validation data set are shown in Fig. 4A-B.

DISCUSSION

Model (4) with the flow rates in Table 1 poses hypotheses about how environmental factors affect gull behavior. These factors influence gull behavior differently in the morning, midday and the evening time periods (Table 1).

In the morning, gulls tend to enter the colony when tide height is elevated; otherwise they would leave the colony at a constant per capita rate. When humidity goes up, the gulls tend to preen. However, as the morning progresses, this tendency decreases. Gulls also tend to preen less when the sun rises and if the weather is hot or if it is windy on the colony. Gulls tend to sleep as time approaches around 0800 hr but this tendency decreases afterwards.

During the midday time period, gulls tend to leave the colony when the sun is high; but, they come back into the colony if it is windy over the open water and in this case preen as soon as they arrive on the colony. If the sun is high and it feels hot, gulls lose their tendency to preen. As the time approaches 1300 hr, when solar elevation is at its highest point, gulls tend to sleep; but, the tendency decreases after 1300 hr. If it is windy on the colony, gulls tend to sleep. However, this tendency dissipates as soon as it feels hot, likely because gulls must extend their necks to pant when it is hot.

In the evening, gulls tend to return to the colony and do not tend to leave. If heat index or barometric pressure is high, the gulls tend to stop preening. Gulls also tend to preen if it is quite humid and when the colony starts filling up in the evening. As the day comes closer to an end, the gulls’ tendency to preen and sleep increases.

The initial goal of my project was to parameterize the model on the 2006 data set and validate it on the 2007 data set. However, while compiling the two data sets for analysis, I could not include all of the available behavioral data because the NOAA website did not have some of the corresponding environmental data. As a result, the data sets were small and I was not able to parameterize the model on the 2006 data. In order to resolve this challenge, I combined the 2006 and the 2007 data, used 75% of the combined data set for parameter estimation, and reserved 25% for model validation. This yielded stable parameter estimates and good R^2 values (Table 2), and the parameterized model gave good predictions on the independent data set (Table 2; Fig. 4A-B). Based on these results, I was able to conclude that glaucous-winged gulls' behaviors are largely deterministic and are driven by environmental variables. Particular behaviors such as colony attendance and sleeping are more deterministic than other behaviors such as preening and resting (Table 2).

In summary, it is clear that the most common behaviors of some colonial marine birds are largely deterministic, and that compartmental mathematical models can be used successfully to predict the behavioral dynamics as a function of environmental variables.

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FIGURE CAPTIONS

FIGURE 1. A diagrammatical representation of the CSPR model showing the state variables and the flow rates in between the compartments.

FIGURE 2. A visual representation of the CSPR model with pictures of the gulls exhibiting the behavioral state of the compartment.

FIGURE 3. Model predictions (orange) and estimation data (blue) for colony occupancy. A. Days 164–174. B. Close-up view for days 164–166.

FIGURE 4. Model predictions (red) and validation data (blue) for colony occupancy. A. Days 164–174. B. Close-up view for 169–172.

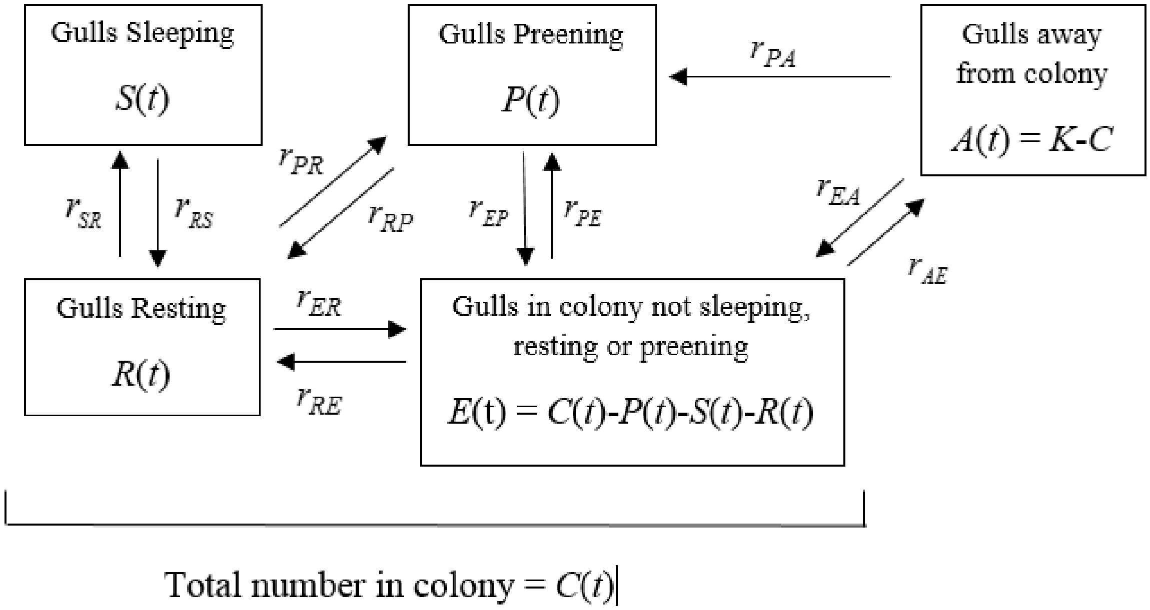
Gulls Sleeping
S(t)
Gulls Preening
P(t)
Gulls away from colony
A(t) = K-C
r_PA
r_PR
r_RP
r_SR
r_RS
r_EP
r_PE
r_EA
r_AE
Gulls Resting
R(t)
r_ER
r_RE
Gulls in colony not sleeping, resting or preening
E(t) = C(t)-P(t)-S(t)-R(t)
Total number in colony = C(t)

Figure 1

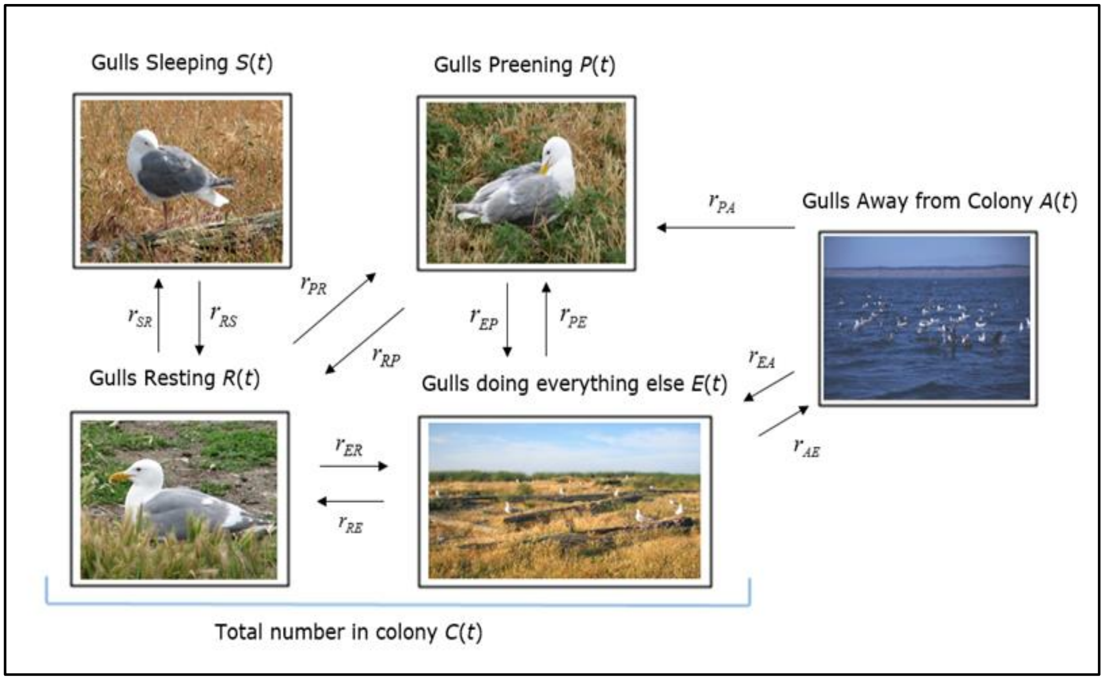
Gulls Sleeping $S(t)$
Gulls Preening $P(t)$
Gulls Away from Colony $A(t)$
r_{PA}
r_{SR}
r_{RS}
r_{PR}
r_{RP}
r_{EP}
r_{PE}
r_{EA}
r_{AE}
Gulls Resting $R(t)$
Gulls doing everything else $E(t)$
r_{ER}
r_{RE}
Total number in colony $C(t)$

Figure 2

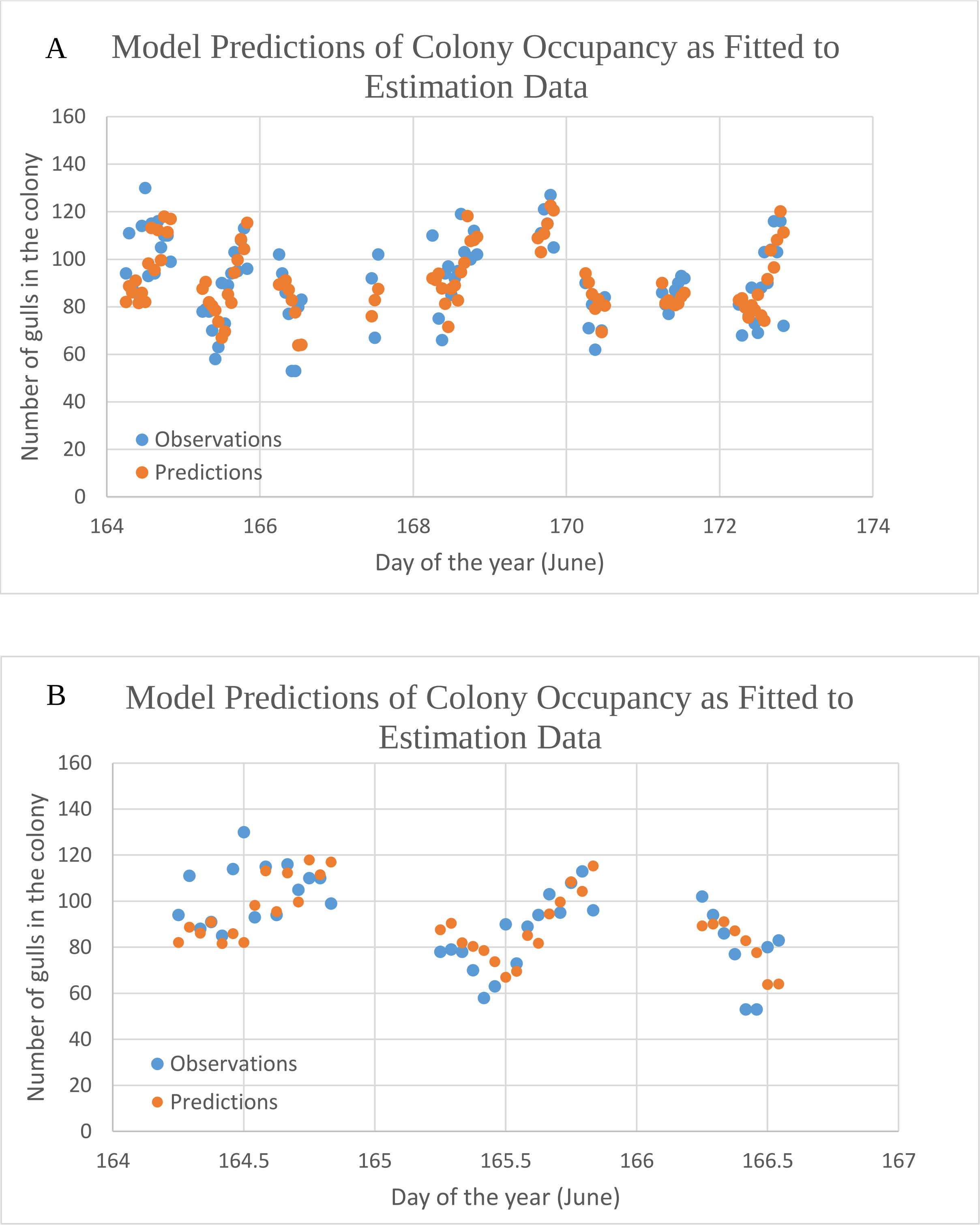
A
Model Predictions of Colony Occupancy as Fitted to Estimation Data
Number of gulls in the colony
160
140
120
100
80
60
40
20
0
164
166
168
170
172
174
Day of the year (June)
● Observations
● Predictions
B
Model Predictions of Colony Occupancy as Fitted to Estimation Data
Number of gulls in the colony
160
140
120
100
80
60
40
20
0
164
164.5
165
165.5
166
166.5
167
Day of the year (June)
● Observations
● Predictions

Figure 3

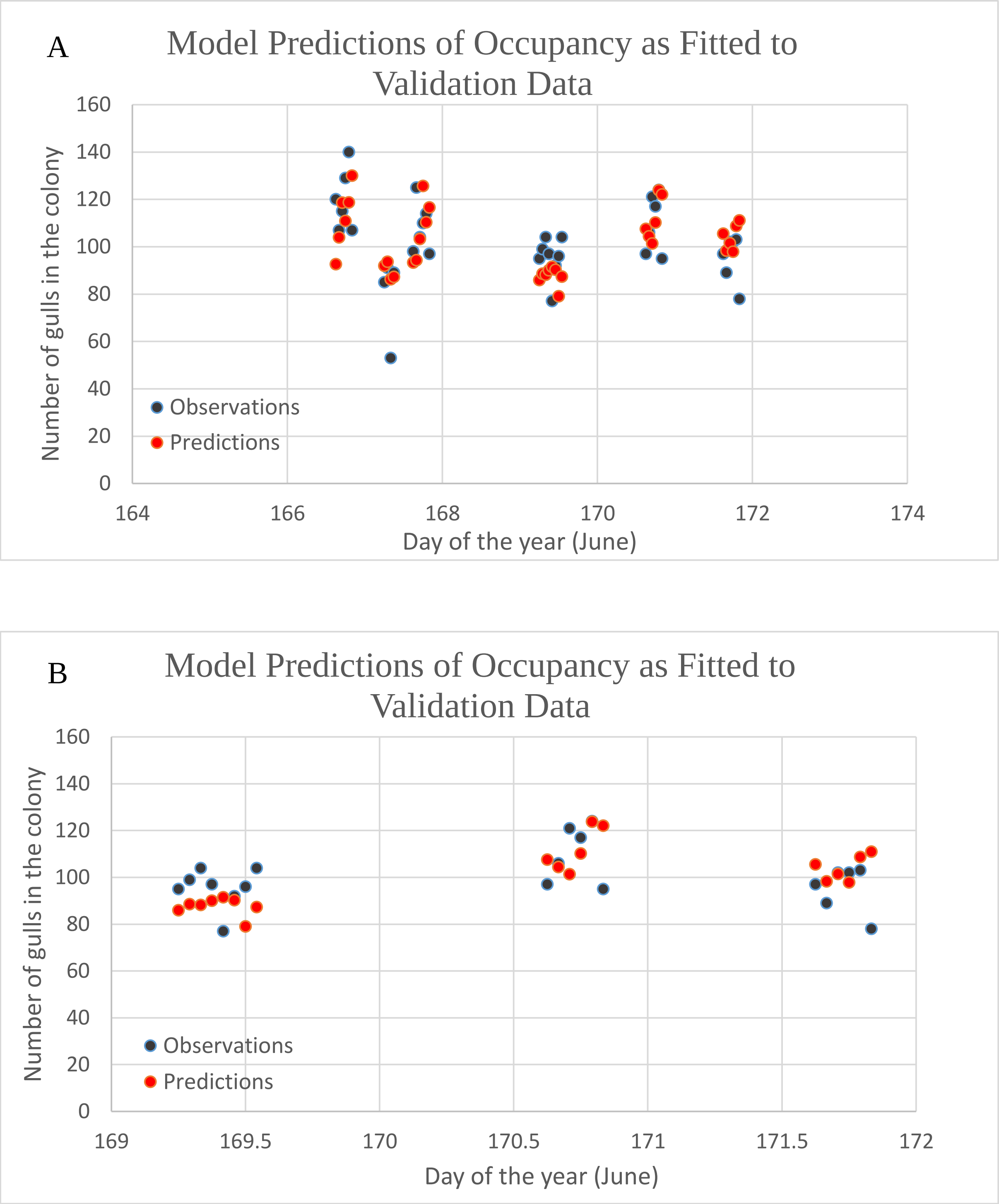
A
Model Predictions of Occupancy as Fitted to Validation Data
Number of gulls in the colony
160
140
120
100
80
60
40
20
0
164
166
168
170
172
174
Day of the year (June)
● Observations
● Predictions
B
Model Predictions of Occupancy as Fitted to Validation Data
Number of gulls in the colony
160
140
120
100
80
60
40
20
0
169
169.5
170
170.5
171
171.5
172
Day of the year (June)
● Observations
● Predictions

Figure 4

TABLE 1. Per capita transition rates r_{ij} and Least Square (LS) parameter estimates.

	Per capita transition rates	**Parameters**	**LS estimates**
Morning $(5 \le t < 10)$	$r_{\mathrm{PA}} = m_{\mathrm{PA}} * T^2 * H$	m_{PA}	0.0051307952365960
	$r_{\mathrm{EA}} = m_{\mathrm{EA}} * T^2$	m_{EA}	0.0755457449515250
	$r_{\mathrm{AE}} = m_{\mathrm{AE}}$	m_{AE}	0.8589807639988070
	$r_{\mathrm{PE}} = m_{\mathrm{PE}} * H$	m_{PE}	0.2307122039416090
	$r_{\mathrm{RP}} = m_{\mathrm{RP}} * W_{\mathrm{c}}$	m_{RP}	1.9144540780549200
	$r_{\mathrm{PR}} = m_{\mathrm{PR}} * H$	m_{PR}	1.2654782372738300
	$r_{\mathrm{RS}} = m_{\mathrm{RS}}$	m_{RS}	1.5698610500445800
$(5 \le t \le 7)$	$r_{\mathrm{SR}} = m_{\mathrm{SR}} * t^2$	m_{SR}	0.2306201564791630
	$r_{\mathrm{RE}} = m_{\mathrm{RE}} * W_{\mathrm{c}}$	m_{RE}	0.9999801907515030
	$r_{\mathrm{EP}} = m_{\mathrm{EP}} * W_{\mathrm{c}} * S / H$	m_{EP}	0.5867791239196410
	$r_{\mathrm{ER}} = m_{\mathrm{ER}} * t^2$	m_{ER}	0.0038028474598140
$(8 \le t < 10)$	$r_{\mathrm{SR}} = m_{\mathrm{SR\ star}} / S^2$	$m_{\mathrm{SR\ star}}$	1.3421735189812800
	$r_{\mathrm{RE}} = m_{\mathrm{RE\ star}} * W_{\mathrm{c}} * t^2$	$m_{\mathrm{RE\ star}}$	1.3512578879955100
	$r_{\mathrm{EP}} = m_{\mathrm{EP\ star}} * S / H$	$m_{\mathrm{EP\ star}}$	0.8906520131670580
	$r_{\mathrm{ER}} = m_{\mathrm{ER\ star}}$	$m_{\mathrm{ER\ star}}$	0.4154008765133420
Midday $(10 \le t < 14)$	$r_{\mathrm{PA}} = n_{\mathrm{PA}} * W_{\mathrm{w}}^{\ 2} * H / S$	n_{PA}	0.0001422609055870
	$r_{\mathrm{EA}} = n_{\mathrm{EA}} * W_{\mathrm{w}}^{\ 2}$	n_{EA}	0.0358512660642240
	$r_{\mathrm{AE}} = n_{\mathrm{AE}} * S^2$	n_{AE}	0.1303916958061210
	$r_{\mathrm{PE}} = n_{\mathrm{PE}} * H / S$	n_{PE}	0.2646100129552590
	$r_{\mathrm{RP}} = n_{\mathrm{RP}}$	n_{RP}	5.7867114259226600
	$r_{\mathrm{PR}} = n_{\mathrm{PR}} * H$	n_{PR}	2.2045160173868500
	$r_{\mathrm{RS}} = n_{\mathrm{RS}} * I^3$	n_{RS}	0.2934296892158480
	$r_{\mathrm{SR}} = n_{\mathrm{SR}} * S * W_{\mathrm{c}}^{\ 2}$	n_{SR}	0.0600168184548500
	$r_{\mathrm{RE}} = n_{\mathrm{RE}} * I$	n_{RE}	0.0007591547888090
	$r_{\mathrm{EP}} = n_{\mathrm{EP}} * S / H$	n_{EP}	0.7528607680934700
	$r_{\mathrm{ER}} = n_{\mathrm{ER}}$	n_{ER}	0.0679325585750790
Evening $(14 \le t \le 20)$	$r_{\mathrm{PA}} = e_{\mathrm{PA}} * t^6 * H$	e_{PA}	0.0028200510184460

	$r_{\mathrm{EA}} = e_{\mathrm{EA}} * t^6$	e_{EA}	0.0044865700879940
	$r_{\mathrm{AE}} = e_{\mathrm{AE}} * S^2$	e_{AE}	0.0649957341330130
	$r_{\mathrm{PE}} = e_{\mathrm{PE}} * H * t^2$	e_{PE}	0.0443309322517170
	$r_{\mathrm{RP}} = e_{\mathrm{RP}}$	e_{RP}	2.1384652277039100
	$r_{\mathrm{PR}} = e_{\mathrm{PR}} * H * t$	e_{PR}	0.6460955992277160
	$r_{\mathrm{RS}} = e_{\mathrm{RS}}$	e_{RS}	0.4012585815045750
	$r_{\mathrm{SR}} = e_{\mathrm{SR}} * t^2 / S^2$	e_{SR}	0.2124387360578280
	$r_{\mathrm{RE}} = e_{\mathrm{RE}} * S$	e_{RE}	0.0017779882827390
	$r_{\mathrm{EP}} = e_{\mathrm{EP}} / H^2$	e_{EP}	1.1920917115915200
	$r_{\mathrm{ER}} = e_{\mathrm{ER}} * t * H^2$	e_{ER}	0.0361886118883590

TABLE 2. Goodness-of-fit of CSPR model for estimation data and validation data.

Goodness of fit (R^2)	**Colony**	**Sleep**	**Preen**	**Rest**
Estimation Data	0.65	0.51	0.44	0.32
Validation Data	0.70	0.64	0.60	0.47