

**HABITAT PATCH OCCUPANCY DYNAMICS OF
GLAUCOUS-WINGED GULLS (*LARUS GLAUCESCENS*)
I: A DISCRETE-TIME MODEL**

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ABSTRACT. Diurnal habitat occupancy dynamics of Glaucous-winged Gulls were evaluated in a system of six habitats on and around Protection Island, Washington. Data were collected on the rates of gull movement between habitat patches, and from these data the probabilities of transitions between habitats were estimated as functions of tide height and time of day. A discrete-time matrix model based on the transition probabilities was used to generate habitat occupancy predictions, which were then compared to hourly census data. All model parameters were estimated directly from data rather than through model fitting. The model made reasonable predictions for two of the six habitats and explained 45% of the variability in the data from 2003. The construction and testing of mathematical models that predict occupancies in multiple habitats may play increasingly important roles in the understanding and management of animal populations within complex environments.

KEY WORDS: *Larus glaucescens*, habitat patch dynamics, per capita flow rates, transition probabilities, matrix model.

1. Introduction. A fundamental objective of ecology is to understand how organisms utilize time and space. To what cues do organisms respond in order to effectively carry out their daily activities? Do these activities and movements constitute random asynchronous behavior, or are they triggered by some internal physiological mechanism or external environmental variable? If cues can be identified, can predictions be made of movements based on these cues?

To answer such questions, ecologists are turning to mathematical modeling. Recent applications of mathematics to fluctuations in laboratory systems such as flour beetle (*Tribolium castaneum*) and mite (*Sancassania berlesei*) populations and algal-rotifer communities (*Brachionus spp.*) have demonstrated that dynamics in these systems can be predicted with relatively simple mathematical equations. Dynamic phenomena such as equilibria, cycles, transitions between dynamic regimes (bifurcations), multiple attractors, stable and unstable manifolds, lattice effects, and chaos have been demonstrated in the laboratory; see, for example, Costantino et al. [1995, 1997], Fussmann et al. [2000], Bjørnstad and Grenfell [2001], Dennis et al. [2001], Henson et al. [2001], Benton et al. [2002].

Despite these laboratory successes, few studies have rigorously tied mathematical models to fluctuations in field data. The difficulties involved in experimental manipulation and replication result in a lack of adequate data and validated mathematical models (Cushing et al. [1998, 2003]). Further complexity arises because dynamic patterns typically occur across numerous temporal and spatial scales (Turchin [1998]). The capability of predicting diurnal movements of organisms between habitats, however, may be a prerequisite in some cases for predicting population dynamics (Hayward et al. [2005]).

Henson et al. [2004] developed a mathematical model to predict diurnal habitat occupancy dynamics of glaucous-winged gulls (*Larus glaucescens*) resting on a pier adjacent to a large breeding colony on Protection Island, Washington. A field test of a priori model predictions showed that accurate forecasts of seasonal, biweekly, and daily habitat occupancy fluctuations could be made on the basis of three environmental variables: solar elevation, tide height, and day of year. The model took into consideration only two locations, the pier and elsewhere. How gulls utilized various habitat patches in “elsewhere” was not evaluated.

In this paper a deterministic discrete-time matrix model for the movement of glaucous-winged gulls among six habitat patches on and around Protection Island is constructed. Models of this type, both deterministic and stochastic, have been used successfully in ecology. For example, Markov chains have been used to model succession (Horn [1975], McAuliffe [1988]) and complex community dynamics (Wootton [2001]). In the present study, flow rate observations were used to estimate transition probabilities as functions of tide height and time of day. The resulting deterministic nonautonomous model was used to generate habitat occupancy predictions, which were then compared to hourly census data. The study illustrates some of the considerable challenges faced when connecting mathematical models to field data.

2. Organisms and locality. This study was conducted at Protection Island National Wildlife Refuge, Jefferson County, Washington (48°08'N, 122°55'W), 3.2 km from the mouth of Port Discovery Bay at the southeastern end of the Strait of Juan de Fuca. Protection Island measures 2.9 km by 0.9 km at its widest points. Eighty percent of the island consists of high plateau bordered by 35–76 m cliffs. Low gravel spits extend from the southeastern and southwestern ends of the island (Wilson [1977]). The southeast spit, Violet Point (Figure 1), measures approximately 800 × 200 m and supports 2,441 pairs of nesting glaucous-winged gulls (based on a 2004 nest count; J. Galusha [pers. comm.]). The behavioral ecology of these birds has been extensively characterized, e.g., James-Veich and Booth [1954], Vermeer [1963], Stout and Brass [1969], Stout et al. [1969], Stout [1975], Galusha and Stout [1977], Hayward et al. [1977b], Amlaner and Stout [1978], Galusha and Carter [1987], Reid [1987, 1988a, 1988b, 1988c] and Bell [1997].

3. Data collection. Data were collected from 24 June to 10 July 2002 and 2003. Observations were made using 10x binoculars and a 20–60x spotting scope from an observation point at the top of a 33-m bluff that borders the west end of Violet Point (Figure 1). From this location most of the spit, except for the east beach and portions of the south beach, could be seen. The observation point was located 100 m from the proximal edge of the nearest habitat. The presence

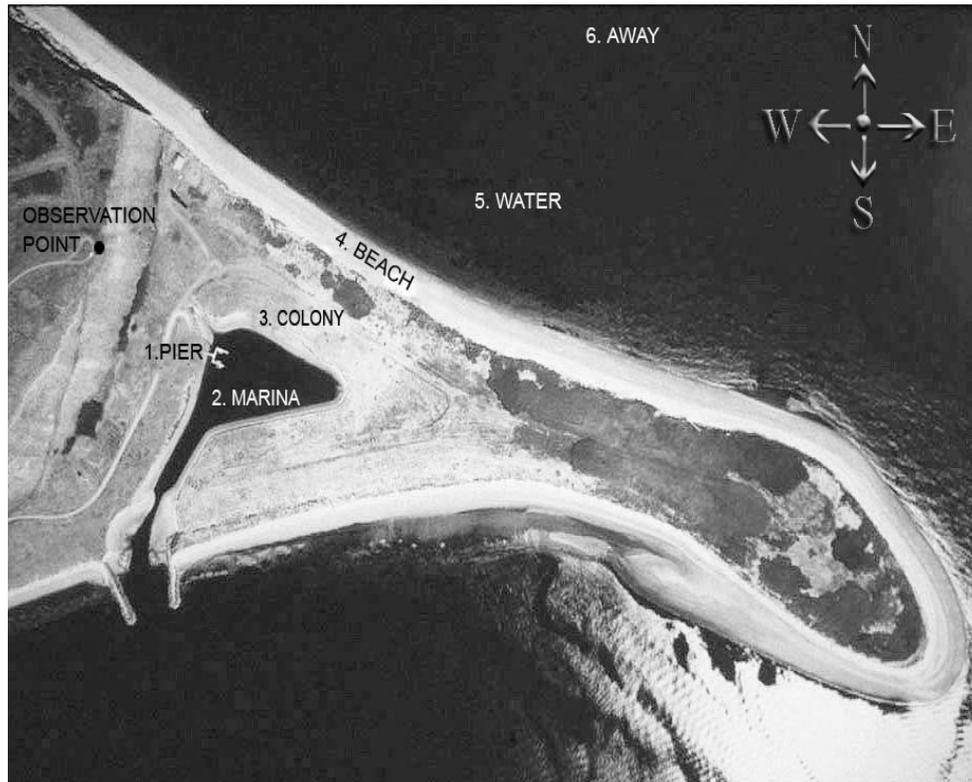


FIGURE 1. Aerial photo of Violet Point, Protection Island, showing the locations of the six designated habitats in relation to the observation point.

of observers did not seem to influence the behavior of the gulls in any way.

We identified five distinct habitats on or around Violet Point, and designated a sixth “Elsewhere” category for all other locations:

i. Pier: This structure consisted of wood pilings, a metal gang plank and railings, and a concrete platform that extended into a small marina which was closed to the public. One to three boats were usually moored to this structure but were not considered part of this habitat.

ii. Marina: This was a small body of water near the proximal end of Violet Point. The Marina was accessible by boat through an artificial inlet on the south side of Violet Point.

iii. Colony: This was the main area used by gulls for nesting and breeding on Violet Point. This area was interspersed with patches of gumweed (*Grindellia integrifolia*), various grasses, and other low vegetation. A 159-m² sample area located just north of the Marina was used for counts. To account for the difference in numbers of birds between the sample colony area and the entire colony, a scaling factor was calculated as the ratio of the sample nest count ($n = 18$) to the whole colony nest count ($n = 2,441$), or $18/2,441 = 1/135.61$.

iv. Beach: This was a 113-m pebble- and cobble-covered sample stretch along the north beach of Violet Point. The sample area appeared to contain a relatively high density of birds compared to some other portions of the beach. To account for the difference in numbers of birds between the sample beach area and the entire beach, a scaling factor was determined in the following way: The total length of visible beach along Violet Point was 1,675 m, whereas the summed lengths of seven sample areas of varying density monitored in 1999 was 541 m. Thus, the total visible beach length was $1,675/541$ times the summed lengths of the seven sample areas. The highest number of gulls occupying the seven sample areas was 625. Under the assumption of an even dispersion pattern, the highest number of gulls using the total visible beach was estimated to be $(1,675/541)(625) = 1,935$. During 2002 and 2003, the highest number of gulls counted in the single 113-m sample stretch of beach was 377. The scaling factor was determined to be the ratio of the maximum observed number of gulls using the sample area to the inferred maximum number using the entire beach, or $377/1,935 = 1/5.13$.

v. Water: This referred to the pelagic regions of the ocean bordering Violet Point extending approximately 200 m out from the beach. The sample area in 2002 was the ocean bordering the north beach. In 2003, however, occupancy observations inadvertently included both north and south water. A scaling factor was determined by comparing the summed north water counts for 2002 to corresponding north-south water counts in 2003. The ratio was 1/2.2. Day 191 in 2003 experienced considerably higher temperatures ($> 25.6^{\circ}\text{C}$) than other days that year ($= 22.8^{\circ}\text{C}$). This may have caused the unusually high numbers of gulls seen in the water on day 191 in 2003; consequently, counts for day 191 in both years were omitted from the calculation of the scaling factor.

vi. Elsewhere: All other locations. Gulls not present within the other five habitats were placed in this category. No observations were made within this "habitat."

At the top of each hour, from 0500-2000 PST (Pacific Standard Time), gull occupancy counts were made for each habitat *i*. Gull movement data were collected during 2-hr observation periods, carried out at 0500-0700, 0900-1100, 1400-1600, and 1800-2000 on most Tuesdays, Wednesdays, and Thursdays, and on other days with less consistency. Observation periods were chosen to represent early morning, late morning, mid-afternoon, and late afternoon/evening gull activity patterns, see Section 5. The 2-hr observation periods were chosen as a compromise between the need for an adequate sample size and a need to minimize observer fatigue. During each observation period, the following data were collected for each non-Elsewhere habitat, with the sequences of habitats observed determined randomly:

a. *Arrival and departure rates*: Each of the five habitats was observed for 5 min, and numbers of all gulls entering and leaving this habitat were recorded.

b. *Destinations of departing gulls*: Gulls departing from each habitat were watched until they reached their destinations. Departing gulls were watched consecutively and one at a time; thus, if more than one gull was flying from the habitat at the same time, only the first to leave was followed and recorded. More gulls departed than could be individually followed. This necessitated use of a 15-min count period per habitat to obtain an adequate sample size, rather than the 5-min period used for arrivals and departures. Gulls flying to any point in

the entire beach or colony were recorded as moving to that habitat. Therefore, flow to these two areas was scaled down by the appropriate scaling factors. The remaining part of the flow to these two areas was considered flow to Elsewhere.

c. Behaviors of gulls in each habitat were sampled for 2–3 min (during 2002 only): Behavior scan counts were recorded by voice on a tape recorder and subsequently transcribed. Behavior designations followed Phillips [2004, Table 1]. Behaviors that accounted for less than 1% of those in a given habitat were combined into an “Other” category. Terrestrial (Pier, Colony, Beach) and aquatic (Marina, Water) habitats were evaluated separately. Chi-square tests were used to determine if distributions of behavior counts differed by habitat. Statistical tests were carried out at the $p < 0.05$ level of significance.

4. The model. It was assumed that gulls moved among all six habitats. Per capita flow rates (gull movements) from habitat j to habitat i , denoted by r_{ij} , were assumed to depend on the time of day t and height of tide $T(t)$, that is, $r_{ij} = r_{ij}(t, T(t))$. During a small time step $h > 0$, each gull in habitat j has some probability p_{ij} of moving to habitat i . The p_{ij} depend on the flow rates r_{ij} and thus depend on time of day and tide height: $p_{ij} = p_{ij}(t, T(t))$. If the p_{ij} and the numbers of gulls in each habitat are known at time t and tide T , then occupancy predictions can be generated for time $t + h$ by the matrix equation

$$(1) \quad \begin{pmatrix} N_1(t+h) \\ N_2(t+h) \\ N_3(t+h) \\ N_4(t+h) \\ N_5(t+h) \\ N_6(t+h) \end{pmatrix} = \begin{pmatrix} p_{11} & p_{12} & p_{13} & p_{14} & p_{15} & p_{16} \\ p_{21} & p_{22} & p_{23} & p_{24} & p_{25} & p_{26} \\ p_{31} & p_{32} & p_{33} & p_{34} & p_{35} & p_{36} \\ p_{41} & p_{42} & p_{43} & p_{44} & p_{45} & p_{46} \\ p_{51} & p_{52} & p_{53} & p_{54} & p_{55} & p_{56} \\ p_{61} & p_{62} & p_{63} & p_{64} & p_{65} & p_{66} \end{pmatrix} \begin{pmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ N_4(t) \\ N_5(t) \\ N_6(t) \end{pmatrix},$$

where $N_i(t)$ is the occupancy of habitat i at time t . Each probability must satisfy $0 \leq p_{ij} \leq 1$, and each column of the matrix must sum to one; that is, $\sum_{i=1}^6 p_{ij} = 1$ for each j . The model (1) can be written more succinctly as

$$(2) \quad x(t+h) = M(t, T(t))x(t),$$

where $x(t)$ is the vector of habitat occupancies and $M(t, T(t))$ is the matrix of transition probabilities.

The following two sections explain how the continuous-time per capita flow rates r_{ij} were estimated from the data and how the discrete-time transition probabilities p_{ij} were computed from the r_{ij} .

TABLE 1. Bin categories for glaucous-winged gull movement data by habitat and time of day on Protection Island. Flow-rate data were subdivided into four ranges of time and quarters of tide to form 16 bins. The time categories were extended from the original 2-hour observation periods to account for all daylight hours. M1 through M16 represent transition matrices. Subscripts indicate bin numbers.

Time (PST)	Tide height, m			
	-0.8128-0.0343	0.0344-0.8815	0.8816-1.7287	1.7288-2.5761
0500-0759	M1	M2	M3	M4
0800-1229	M5	M6	M7	M8
1230-1659	M9	M10	M11	M12
1700-2000	M13	M14	M15	M16

5. Estimating flow rates r_{ij} from data. Flow rate data were arranged according to time of day and tide height in the following way: The hours of the day were divided into the unequal ranges 0500-0759, 0800-1229, 1230-1659 and 1700-2000, each of which contained one of the 2 hr observation periods. The ranges were of unequal size because extensive previous experience with these birds suggested that phases of colony activity were of unequal lengths, e.g., Hayward et al. [1977b], Galusha and Hayward [2002], Henson et al. [2004]. For example, in early morning, large numbers of gulls left the colony for distant feeding sites; in mid- to late morning, colony residents engaged in maintenance activities, e.g., preening, tending to chicks, etc.; in early to mid-afternoon, residents tended to be quieter and exhibit more rest posture; and in late afternoon and evening, residents returned in large numbers from distant feeding areas. Tide heights were divided into the quarters -0.8128-0.0343 m, 0.0344-0.8815 m, 0.8816-1.7287 m, and 1.7288-2.5761 m. This procedure yielded 16 possible time-tide combinations or “bins” (Table 1; bin numbers correspond to matrix designations). Flow rate observations that occurred in the same bin for the same habitat were considered replicates. Numbers of replicates per bin per habitat varied from 1 to 9. Six bins did not contain data in 2002 (1, 6, 8, 9, 13, 14), and four bins did not con-

tain data in 2003 (8, 9, 13, 14). These bins either did not contain data for all habitats or the time-tide combinations did not occur during the observation periods. Tide predictions were obtained from the National Oceanic and Atmospheric Administration (NOAA, website [http://140.90.78.170/pred_retrieve.shtml?input_code=100001101ppr&type=pred&station=9444900+Port+Townsend+,+WA]). Port Townsend tide heights were multiplied by a Protection Island correction factor of 0.93 (Anonymous [1998]).

Within each bin, the per minute per capita flow rates r_{ij} from habitat j to habitat i were assumed to be constant and were estimated as follows:

- i. The per minute per capita departure rate from habitat j (dep_j) was estimated by dividing the total number of departures observed during 5 min from habitat j by the total observed occupancy of habitat j at the closest census time, then dividing this value by 5:

$$(3) \quad dep_j = \frac{\sum_{\text{replicates}} (\text{departures from habitat } j \text{ per 5 min})}{5 \sum_{\text{replicates}} (\text{occupancy of habitat } j)}.$$

Disturbances and lack of visibility caused some occupancy counts to be omitted. In such cases the average of the remaining replicate occupancy counts was calculated and substituted.

- ii. The proportion of gulls departing from habitat j that moved to habitat I ($prop_{ij}$) was determined by dividing the total number of gulls followed from habitat j to habitat I by the total number of gulls followed from habitat j during the 15 min observation period:

$$(4) \quad prop_{ij} = \frac{\sum_{\text{replicates}} (\text{no. followed from habitat } j \text{ that went to habitat } i)}{\sum_{\text{replicates}} (\text{total no. followed from habitat } j)}.$$

Note that $prop_{jj}$ is the proportion of departing gulls that returned to habitat j without landing in any other habitat.

- iii. The per capita flow rate for birds flying from habitat j to habitat i was calculated by multiplying the per capita departure rate from habitat j , given in equation (3), by the proportion of departing gulls that move to habitat i , given in equation (4):

$$r_{ij} = (dep_j)(prop_{ij}).$$

Note that r_{jj} is the per capita flow rate of birds leaving habitat j that return to habitat j without landing in another habitat.

Some of the departing gulls that were followed landed outside the designated habitats or flew out of sight. These gulls were counted as flying to Elsewhere, which enabled calculation of r_{6j} for each habitat j . The per capita flow rates r_{i6} from Elsewhere to other habitats could not be observed directly and were computed in the following way:

a. Let K denote the total number of birds that utilized the sample areas of all habitats. The value of K changes during the season; however, K was assumed constant during the data collection period. The value of K was estimated by summing the occupancies across the five non-Elsewhere habitats for each hourly census made during 2002 and 2003. K was designated as the largest of these summed occupancies (616 at 2000 hours on 28 June 2002, and 596 at 2000 hours on 10 July 2003). At 2000 hours it was assumed that gulls were no longer away feeding, so that the occupancy of Elsewhere was zero and all birds were accounted for in the non-Elsewhere censuses.

b. At each time t , the occupancy for Elsewhere was taken to be the difference between K and the sum of the observed occupancies of the five censused habitats:

$$n_6(t) = K - \sum_{j=1}^5 n_j(t),$$

where $n_j(t)$ is the observed occupancy of the j th habitat at time t .

c. The per capita flow rate r_{ij} from habitat j to habitat i multiplied by the observed habitat occupancy n_j of habitat j is the total number of birds leaving habitat j for habitat i per minute. Thus, the product $r_{ij}n_j$ can also be interpreted as the number of arrivals per minute in habitat i from habitat j . In each non-Elsewhere habitat i , the number of arrivals per minute from all habitats except Elsewhere can therefore be expressed as $\sum_{j=1}^5 r_{ij}n_j$. The difference between this sum and the observed arrivals would be due to arrivals from Elsewhere. For each bin, the observed number of arrivals per 5 min and the occupancies were averaged over the replicates. For each habitat i , the number $\overline{\text{arrivals}}_i$ represented the mean number of arrivals per 5 min, and \bar{n}_i represented the mean occupancy count. The value $\overline{\text{arrivals}}_i$ was divided by 5 and then compared to the sum $\sum_{j=1}^5 r_{ij}\bar{n}_j$. In each case the number

of averaged observed arrivals was larger than the calculated arrivals $\sum_{j=1}^5 r_{ij}\bar{n}_j$ for the corresponding habitat and bin. The discrepancy between these two values was attributed to arrivals from Elsewhere $r_{i6}\bar{n}_6$. The per minute per capita flow rate from Elsewhere to habitat i was therefore calculated as:

$$r_{i6} = \frac{1}{\bar{n}_6} \left(\frac{\overline{\text{arrivals}}_i}{5} - \sum_{j=1}^5 r_{ij}\bar{n}_j \right).$$

6. Estimating transition probabilities p_{ij} from flow rates r_{ij} .

The transition matrix $M(t, T(t))$ in equation (2) was estimated from the data under the assumption that its entries remained constant within each bin. This gave rise to 16 constant matrices, which were designated M_1 through M_{16} , Table 1. The entries p_{ij} of the 16 transition matrices were computed in the following way:

a. Let Δt be a small unit of time. The probability that a gull in habitat j will depart for habitat i during Δt units of time is $r_{ij}\Delta t$, and the probability that a bird in habitat j will not depart to habitat i during Δt is $1 - r_{ij}\Delta t$.

b. The probability that a gull in habitat j will depart during Δt is $\sum_{i=1}^6 r_{ij}\Delta t$. The probability that a bird in habitat j will not depart is $1 - \sum_{i=1}^6 r_{ij}\Delta t$.

c. Assuming that “not departing during Δt time units” is an independent event, the probability of not departing habitat j during m time intervals of length Δt is $(1 - \sum_{i=1}^6 r_{ij}\Delta t)^m$. Hence, the probability of not departing during h minutes (one model time step) is $(1 - \sum_{i=1}^6 r_{ij}\Delta t)^{h/\Delta t}$.

d. Because Δt is vanishingly small, the probability of not departing habitat j during h minutes is actually

$$\begin{aligned} \lim_{\Delta t \rightarrow 0} \left(1 - \sum_{i=1}^6 r_{ij}\Delta t \right)^{h/\Delta t} &= \lim_{\Delta t \rightarrow 0} \exp \left[\ln \left(1 - \sum_{i=1}^6 r_{ij}\Delta t \right)^{h/\Delta t} \right] \\ &= \lim_{\Delta t \rightarrow 0} \exp \left[\frac{h}{\Delta t} \ln \left(1 - \sum_{i=1}^6 r_{ij}\Delta t \right) \right] \end{aligned}$$

$$\begin{aligned}
&= \lim_{\Delta t \rightarrow 0} \exp \left[h \frac{-\sum_{i=1}^6 r_{ij}}{1 - \sum_{i=1}^6 r_{ij} \Delta t} \right] \\
&= \exp \left[-h \sum_{i=1}^6 r_{ij} \right],
\end{aligned}$$

by L'Hopital's rule. Thus, the probability of departing habitat j during h minutes is

$$(5) \quad 1 - \exp \left[-h \sum_{i=1}^6 r_{ij} \right].$$

e. The probability p_{ij} of departing habitat j for habitat $i \neq j$ during h minutes is therefore the product of the probability of departing, given in equation (5), and the probability that a gull moves to habitat i given that it departs habitat j , given in equation (4):

$$p_{ij} = \left(1 - \exp \left[-h \sum_{k=1}^6 r_{kj} \right] \right) (\text{prop}_{ij}).$$

It is straightforward to verify that for $i \neq j$,

$$p_{ij} = \left(1 - \exp \left[-h \sum_{k=1}^6 r_{kj} \right] \right) \left(\frac{r_{ij}}{\sum_{k=1}^6 r_{kj}} \right).$$

f. The probability p_{jj} is the probability that a bird in habitat j either does not depart, or else departs and returns directly to habitat j . Thus,

$$p_{jj} = \exp \left[-h \sum_{i=1}^6 r_{ij} \right] + \left(1 - \exp \left[-h \sum_{i=1}^6 r_{ij} \right] \right) \left(\frac{r_{jj}}{\sum_{k=1}^6 r_{kj}} \right).$$

Note that for each j the probability of either departing to one of the six habitats or not departing is one: $\sum_{i=1}^6 p_{ij} = 1$.

There were 360 transition probabilities for 2002 (36 entries in each of 10 6×6 transition matrices corresponding to the 10 bins containing data), and 432 transition probabilities estimated for 2003 (36 entries

in 12 matrices/bins). All transition probabilities are given in Phillips [2004].

7. One-step model predictions. Since all model parameters were estimated directly from data, no model fitting procedures were carried out. To evaluate model performance, hourly predictions of habitat occupancies were generated using a mathematical programming language called GNU Octave (<http://www.octave.org>). Given an observed census vector $\mathbf{y}(t)$ at hour t as an initial condition, the model was iterated $60/h$ times to produce a prediction vector $\mathbf{x}(t + 1)$ for the next hour $t + 1$. Predictions thus generated are known as “conditioned one-step predictions,” because each prediction is conditional given the observation at the previous hour. In this usage, “one-step” refers to one hour, and not one model time step h . The residual error at hour $t + 1$ is $\rho(t + 1) = \mathbf{y}(t + 1) - \mathbf{x}(t + 1)$, that is, the difference between the observed and predicted occupancies at hour $t + 1$. For an observed hourly time series of length q , the residual sum of squares (RSS) for a single habitat is therefore

$$\text{RSS} = \sum_{t=2}^q (\rho(t))^2.$$

For the system of habitat patches, the overall RSS was taken to be the sum of the RSS for the individual habitats.

Goodness-of-fit as measured by

$$(6) \quad R^2 = 1 - \frac{\text{RSS}}{\sum_{t=2}^q (\text{observation} - \text{mean})^2}$$

was computed for each habitat, where “mean” denotes the mean of the observations for that habitat. For the entire set of habitats, R^2 was computed as

$$R^2 = 1 - \frac{\text{overall RSS}}{\sum_{\text{habitats}} [\sum_{t=2}^q (\text{observation} - \text{mean})^2]},$$

where “mean” denotes the mean of the observations for the appropriate habitat. R^2 estimates the proportion of the observed variability that is explained by the model and provides a measure of the accuracy of model predictions.

Since the occupancies for Elsewhere were computed rather than observed, they were not included in the calculations of RSS and R^2 .

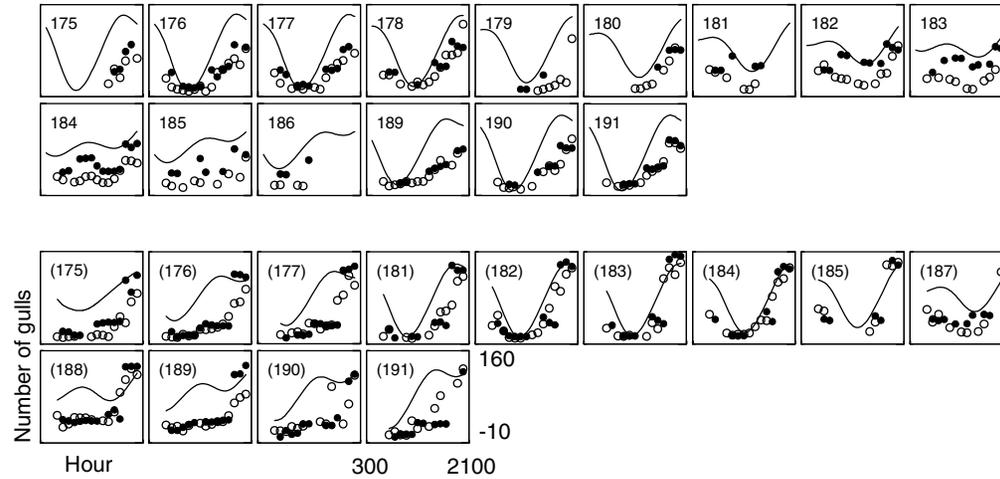
8. Results. A model time step of $h = 4$ min yielded the best goodness-of-fit. Table 2 compares the R^2 goodness-of-fit estimates between hourly counts and predictions for 2002 and 2003. Pier and Beach R^2 values for 2003, with 25% of bins empty, exceeded those for 2002, with 37.5% of bins empty. The model explained a large part of the variability of census data for the Pier and Beach. Predictions and counts for the Pier tended to decrease in the morning, rise in the afternoon, and then peak toward 2000 hours (Figure 2A). A general increase toward the end of the day was seen in predictions and counts for the beach (Figure 2D).

R^2 values for the remaining habitats were negative; this means that the model did worse than a horizontal line would have done for predicting data. Although model predictions were of the right order of magnitude, the model did not successfully predict the diurnal fluctuations within the Marina, Colony, or Water. Numbers of gulls in the Marina were usually fairly constant during the day, although often with some increase late in the day (Figure 2B). Peak counts were made

TABLE 2. R^2 goodness-of-fit values for comparisons between glaucous-winged gull habitat occupancy observations and predictions on Protection Island during the 2002 and 2003 breeding seasons. A model time step of $h = 4$ min gave the best R^2 values. Negative R^2 values reflect the fact that the mean of the observations fit the data better than the model did, i.e., there was little variability in the observed data.

Habitat	R^2 (2002)	R^2 (2003)
1. Pier	0.2460	0.6320
2. Marina	-0.0289	-0.0775
3. Colony	-0.2977	-1.6043
4. Beach	0.2749	0.4442
5. Water	-0.0262	-0.0012
Overall	0.2238	0.4522

A. PIER



FIGURES 2A-2F. One-step model predictions (black circles) of gull habitat occupancies, on and around Protection Island, point matched against the observations (open circles) in relation to tide (line). Each panel represents one day of observation. Day of the year is noted at the top lefthand corner of each panel, with days in 2003 shown in parentheses. The horizontal axis is the hour of the day, and the vertical axis is the number of birds in the habitat. Some observations in the Water on days 176, 179, (177), and (191), exceeded the y -axis and are represented by crossed out circles. The vertical scale for the tide curve is -1 to 3 m.

B. MARINA

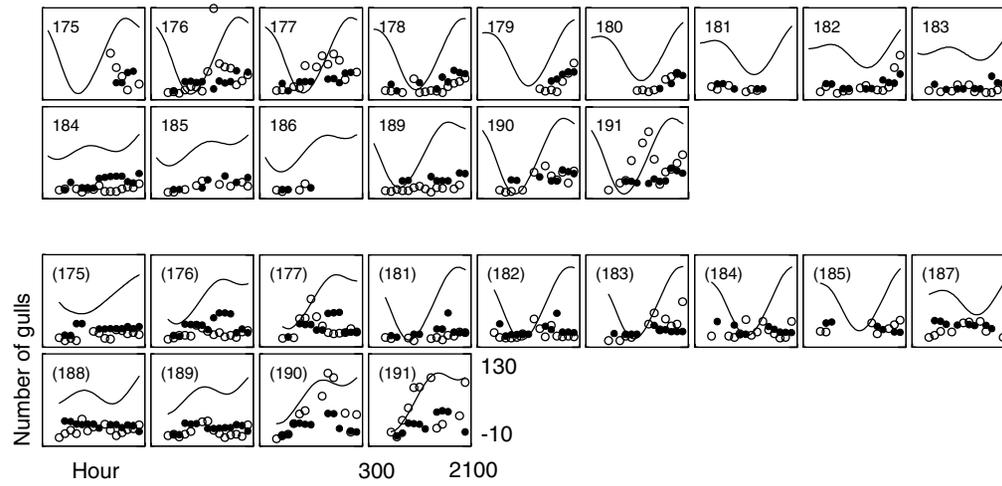


FIGURE 2B.

C. COLONY

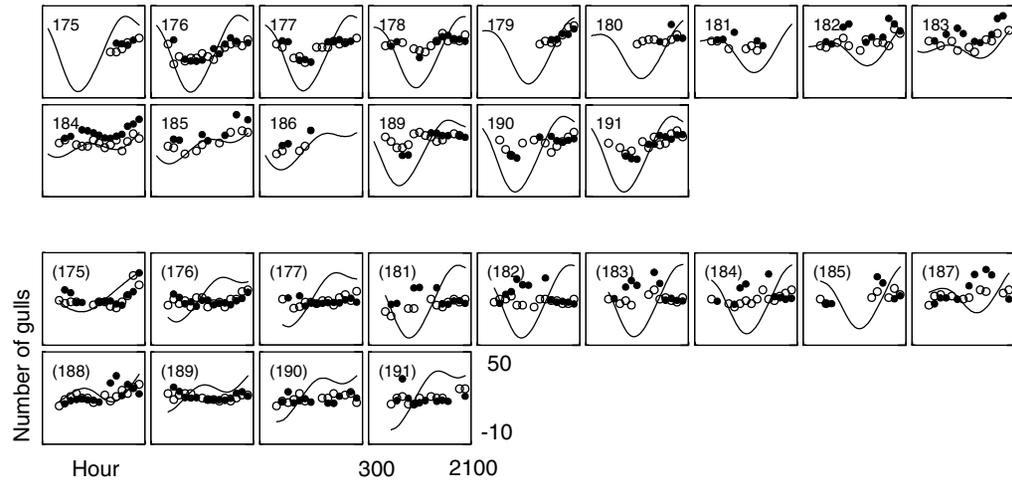


FIGURE 2C.

D. BEACH

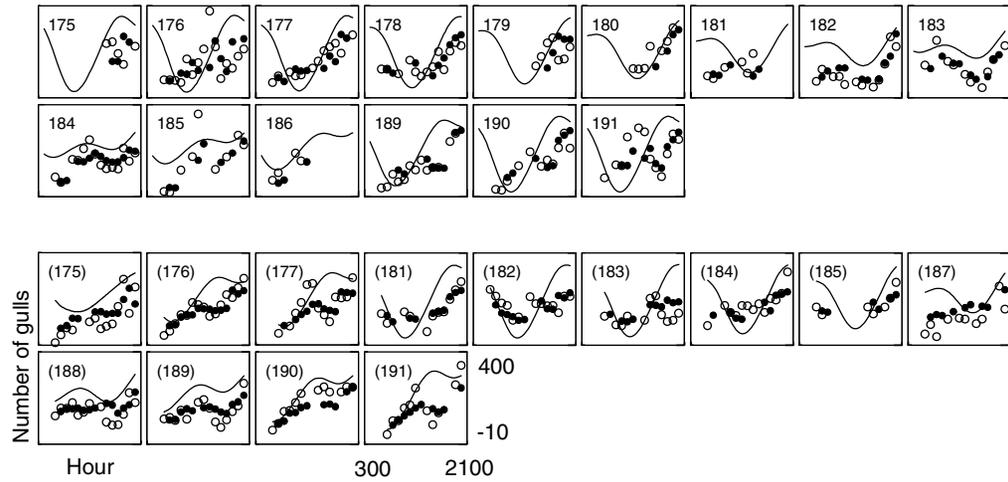


FIGURE 2D.

E. WATER

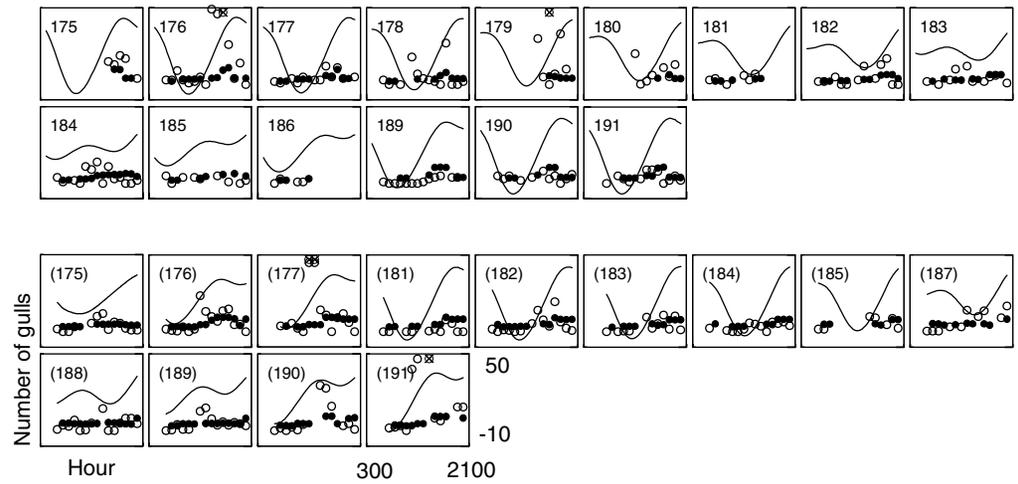


FIGURE 2E.

F. ELSEWHERE

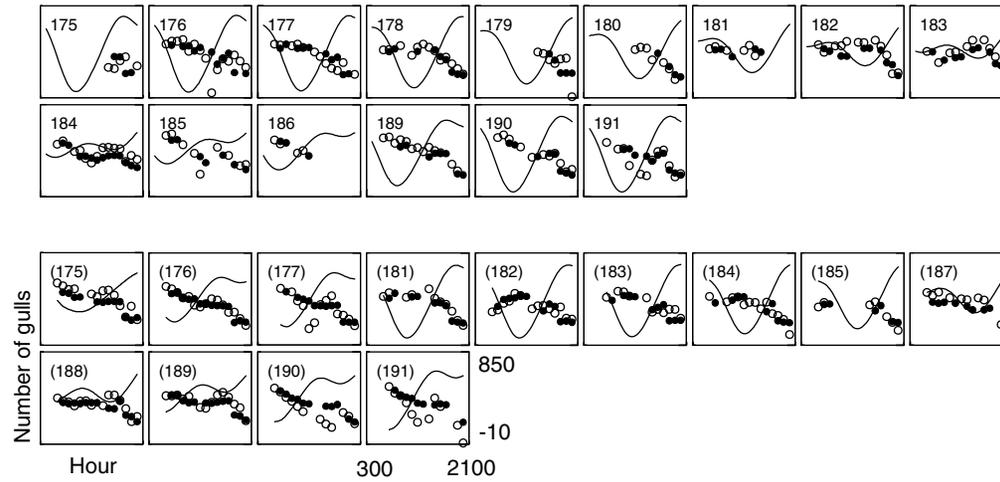


FIGURE 2F.

during some midday hours when temperatures were highest. Numbers of gulls in the Colony showed little variability; generally there was a slight decrease in numbers during the middle of the day followed by an increase during the evening (Figure 2C). Except for peaks in the midday hours, predictions and counts for the Water were also rather constant (Figure 2E).

Model predictions and estimated “counts” for Elsewhere showed a peak in mid- to late morning, followed by a general decrease in the evening hours, an inverse relationship compared with other habitats (Figure 2F). Since the occupancies for Elsewhere were computed rather than observed, they were not included in the calculations of RSS and R^2 .

Statistical tests for behaviors (Phillips [2004]) showed that behavior frequencies differed significantly by habitat in both terrestrial and aquatic environments (Figure 3). The following behaviors were more common than expected: Pier – Stand Rest, Stand Sleep and Stand Preen; Colony – Sit Upright, Sit Rest, Stand Upright, Stand Rest, Walk and Other; Beach – Sit Sleep, Stand Preen, Walk and Other; Marina – Float; Water – Bathe, Drink and Preen.

9. Discussion. Short-term fluctuations in habitat occupancies are likely to be driven by the functional needs of birds (DeWoskin [1980], Cody [1985], Walsberg [1985]). To carry out various behaviors such as preening, feeding, and resting, etc., gulls need to be in appropriate environments (Cooke and Ross [1972], Wondolowski [2002]). For example, gulls tended to congregate in the Marina or Water on very warm days to float, bathe, and preen, and presumably unload heat (Damania et al. [2005]). Gulls used the terrestrial habitats primarily for sleeping, sitting, standing, resting and/or preening behaviors, generally referred to as loafing (Henson et al. [2004]). Behaviors on the colony also included those associated with territorialism.

The Pier and Beach yielded the best goodness-of-fit R^2 values, partly because these two habitats experienced large fluctuations in gull occupancies. A habitat with large fluctuations around its mean occupancy will have a higher R^2 than a habitat with an equal model error RSS but relatively constant occupancies. This is because a larger denominator in equation (6) leads to a higher R^2 value. The Marina, Colony, and

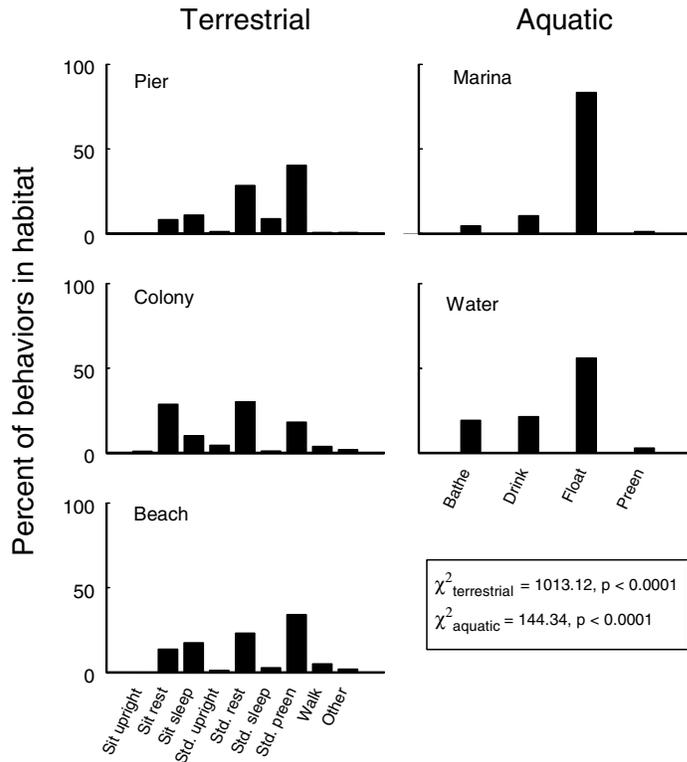


FIGURE 3. Percentages of behaviors exhibited most frequently by glaucous-winged gulls in each habitat on and around Protection Island. The category “Other” included behaviors which accounted for less than 1% of those counted within that habitat. Chi-square analysis was used to test the hypothesis that distributions of behaviors differed among habitats; expected values were determined under the assumption of identical distributions across habitats. Habitats in terrestrial and aquatic environments were analyzed separately. Behavior designations follow Phillips [2004, Table 1].

Water showed much less variability in counts, which led to correspondingly smaller R^2 values.

Because the model made reasonable predictions for the censused habitats with large fluctuations in counts, the predictions for Elsewhere also should have been reasonable. Indeed, the results show distinct “occu-

pancy” patterns for Elsewhere (Figure 2F) that make biological sense, even though occupancy data were not collected for that habitat. The maximum “occupancy” in Elsewhere always coincided with the lowest tides, possibly as a result of increased food availability at low water levels in other locations, as demonstrated in other studies (Patterson [1965], Drent [1967], Galusha and Amlaner [1978], Wondolowski [2002], Henson et al. [2004]). At higher tides gulls were expected to be distributed throughout the five non-Elsewhere habitats. Model predictions suggested such a trend.

Although counts showed a general relationship with trends in model predictions, considerable deviation occurred between the two. This deviation might have been due to several factors:

i. *Disturbance*: Human disturbances occurred mainly on the Pier and Colony, whereas flyovers by Bald Eagles (*Haliaeetus leucocephalus*) commonly influenced all the habitats (Galusha and Hayward [2002]). Gulls often responded to eagle disturbances with cyclonic “panic flights” (Hayward et al. [1977a]).

ii. *Environmental variables*: Whereas time of day and tide apparently functioned as the primary driving forces for count fluctuations in some habitats (Henson et al. [2004]), no doubt other factors also were involved. Additional weather variables, including temperature, wind speed and direction, rain, and humidity also could have influenced habitat selection. Flow to the Marina, for example, seemed to be driven more by temperature than by time or tide (Damanian et al. [2005]); hence, observations for this habitat showed considerable deviation from model predictions. Thus, studies of additional environmental factors beyond tide height and time of day are needed to more accurately predict gull habitat occupancies. Variables such as temperature, however, cannot be used to develop long-range predictions.

iii. *Visibility*: The number of boats moored at the Pier not only altered visibility but also affected the area available for loafing. Although gulls on boats were excluded, higher numbers of gulls on the Pier would be expected if boats were not present. Count inaccuracies also may have occurred due to limited visibility during poor lighting conditions such as during fog and low solar elevation.

iv. *Sampling and binning*: Sample times may not have been representative of movement patterns across habitats. Calculated flow rates may have been biased due to greater or lesser flow during non-observation hours. Although data were collected at discrete time intervals much shorter than the periods of the tidal and diurnal cycles (Hunt and Schneider [1987], Levin [1992], Silverman et al. [2001]), the scale on which flow rates were binned and averaged was nonetheless rather coarse. Binning at a finer scale may have produced better predictions, but would have required considerably more data.

v. *Low counts*: Small numbers of departures during some observation periods and small occupancies in some habitats undoubtedly gave rise to considerable error in estimates of many of the per capita flow rates. In particular, the Water generally showed the lowest occupancies (Figure 2E), making reasonable predictions for this habitat difficult.

vi. *Density-dependence and nesting behavior*: Although some per capita flow rates may have depended on the density of gulls in the origin or destination habitats, the model did not take this into account. Unlike the other habitats, the Colony consisted of defended territories. Colony dynamics were probably tied to breeding behaviors that may have been driven by aggressive encounters or other factors beyond simply time of day and tide height.

vii. *Social facilitation*: Gulls appeared to move to and from other habitats independently of other gulls, except during disturbances and when assembling into feeding groups. This possibility, however, remains unconfirmed. Other studies have found that social facilitation does play a role in at least some movement patterns of gulls (Evans [1982], Wittenberger and Hunt [1985], Götmark et al. [1986]).

Studies that closely tie mathematical models of diurnal distribution to field data are rare in the literature. Exceptions include the study by Henson et al. [2004] described in the introduction, and a study by Hayward et al. [2005] who developed a deterministic model to predict seal haul-out patterns at Protection Island. Hayward et al.'s best model explained 40% of the variability in hourly haul-out censuses. Silverman et al. [2001] developed a stochastic model for the dynamics of mixed species waterfowl aggregations that described migration between two "Colonies" in a closed system. Finally, Damania et al. [2005], in a continuous-time companion paper to this study, used differential

equations based on environmental variables to model the dynamics of gulls in the Protection Island system of habitats. The Damania et al. [2005] model greatly increased accuracy by including the effects of temperature and solar elevation.

Mathematical models typically are tied to data using free constants called “parameters.” Parameters are estimated by fitting the model to data using statistical procedures appropriate for the kind of noise in the system. All of the related studies mentioned above utilized model parameterization techniques such as sequential least squares. It should be emphasized that the model developed in this paper involved no free parameters and no model fitting. Instead, the parameters were estimated directly from observations of flow rates.

In this paper the matrix model could not be iterated indefinitely into the future because some bins contained missing data. Data collection plans for the future include provisions for filling in the “missing bins,” which will allow the model to be run for longer periods of time. A future paper will address the asymptotic dynamics as well as stochastic versions of the matrix model.

10. Conclusion. Results from this study suggest that gull movements on and around Protection Island are correlated with a variety of environmental cues, especially time of day and tide height. This suggests that in some cases complicated fluctuations of animal abundance in the field are influenced by deterministic forces and can be mathematically modeled. Successful development of models that predict animal movements could lead, among other benefits, to safer scheduling at airports to reduce the chance of bird/aircraft collisions, improvements in public health measures to control the spread of animal vector-borne diseases, and better resource management policies.

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