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ABSTRACT. The diurnal distribution and abundance dy-

influences the temporal and spatial distribution of organisms. In addition to intra- and inter-specific factors, abiotic components of the environment can play crucial roles in determining distribution and abundance. Marine animals in particular rely heavily on environmental cues as they move from habitat to habitat to meet their functional needs. Time of day, tide height, solar elevation, and current velocity all play important roles in this regard (Henson et al. [2004], Hayward et al. [2005]). An understanding of these roles is useful to biologists involved in everything from the management of wildlife populations to the control of vector-borne diseases.

Theoretically, deterministic mechanisms that cause fluctuations in animal numbers can be expressed as mathematical equations capable of predicting census dynamics. Mathematical models have been used to predict the dynamics of laboratory systems such as flour beetle (*T. castaneum*) and mite (*D. dentissima*) populations, as well as aquatic microbial communities of rotifers (*B. pectiniferus* spp.; see, for example, Costantino et al. [1995, 1997], Fussmann et al. [2000], Bjørnstad and Grenfell [2001], Henson et al. [2001], Dennis et al. [2001], Benton et al. [2002]). Few mathematical models, however, have been linked rigorously to field data, whether for population dynamics or diurnal movement dynamics. Indeed, the multiple temporal and spatial scales and complexities of ecological interactions in the field make many ecologists skeptical that such models are possible.

Phillips et al. [2005] studied the diurnal habitat occupancy dynamics of Glaucous-winged Gulls (*L. californicus*) at Protection Island National Wildlife Refuge, Washington. By collecting data on rates of gull movement among six designated habitat patches on the southeastern spit of Protection Island, and by estimating probabilities of transition between these habitats, they derived a discrete-time matrix model. The probabilities of transition between habitats were estimated as functions of two environmental variables, tide height and time of day. The habitat occupancy predictions generated by the model were compared with hourly census data using R^2 goodness-of-fit (Dennis et al. [2001]). While the model worked reasonably well for two of the terrestrial habitats, it could not predict the occupancy dynamics of the aquatic habitats. Observations suggested that the dynamics in the aquatic habitats were related not only to tide height and time of day,

but also to ambient temperature, which was not considered in their model.

In this paper continuous-time models are used to revisit the system of habitat patches on Protection Island. In particular, this study focuses on the variations in numbers of gulls present in the three habitats identified by Phillips et al. [2005] which are dedicated to “loafing” behaviors (sleeping, resting, and preening). The remaining habitats are lumped into an “Other” category. Movement among the three loafing habitats (the pier, the marina and the beach) is modeled using differential equations that express flows between habitats as functions of four environmental variables: tide height, time of day, solar elevation, and temperature. A strong association between temperature and the number of gulls present on the aquatic loafing habitat is shown. Parameter estimations for the models in this paper are made indirectly from census data rather than directly from the flow rate data as in Phillips et al. [2005]. Two questions are addressed: What environmental factors influence gull movement among habitats? Is it

[2005]). In the latter two studies, both carried out at Protection Island, Washington, per capita flow rates for animals moving into and out of habitats were found to be functions of deterministic exogenous factors such as tide height, current speed, and solar elevation. Expressing the per capita flow rates r_{12} and r_{21} as functions of the appropriate environmental variables gave rise to non-autonomous differential equation models for the occupancy dynamics of the habitat. Any remaining habitat structure of the system was folded into the “Other” category, possibly confounding environmental factors that influenced movement to and from the modeled habitat. Despite this limitation, two-compartment models can lead to a general understanding of how animals utilize particular habitats.

In this study a sequence of compartmental models is constructed to

1. Pier: This structure consists of wood pilings, concrete pier, metal gangplank and railings that extend into a small marina. One to three boats were usually moored to this structure, but birds on the boats were not counted as being in this habitat. The primary gull behaviors observed here included resting, preening, and sleeping.

2. Marina: This small body of water is located toward the southwest end of Violet Point and surrounds the pier. The marina is accessible by boat through an artificial inlet on the south side of Violet Point.

rates were assumed to be density independent. The procedures for determining the environmental variables and their exponents, and for estimating the parameters β_{ij} , are given in Sections 9 and 10.

(A3) The flow rates between the Pier and Beach, and from the Beach to the Marina, were assumed to be zero. Flow from Other to the Pier in the three- and four-compartment models was also assumed to be zero. These assumptions were based on flow rate observations collected by Phillips [2004]. Per capita flow rates were noted to be particularly small in the above-mentioned instances, and thus were eliminated to reduce the total number of parameters in the models.

(A4) The system was assumed to recover rapidly after disturbance. In particular, it was assumed that after a perturbation, all habitat occupancies changed much faster than the environmental variables, so that the environmental conditions could be considered constant during recovery. This assumption was suggested by the results of Henson et al. [2004], as well as by seven years of extensive observations, during which time it has become clear that the habitat occupancies recover within approximately 20 minutes after most disturbances.

(A5) The main source of noise in the census data was assumed to be demographic stochasticity, due to a stochastic “arrival-and-departure” process (Hayward et al. [2005]), rather than environmental stochasticity. This assumption was motivated by three considerations. First, an inspection of model residuals showed that the variance of the residual model errors was stabilized by a square root transformation (Rao [1973], Dennis et al. [2001], Hayward et al. [2005]). Second, all major environmental correlates were incorporated explicitly into the models. Third, data collected within 30 minutes after a disturbance (such as an eagle flyover or person walking onto the pier) were eliminated from the data set.

(A6) The hourly residual model errors were assumed to be uncorrelated in time. That is, it was assumed that a stochastic event affecting the census at one hour would not affect the census an hour later, due to the rapid recovery of the system post-perturbation, assumption (A4). Furthermore, at any given census time t the covariances of the residuals between habitats were assumed small relative to the variances. That is, it was assumed that stochastic events mainly affected single habitats.

6. Three two-compartment models of the form

$$(1) \quad \frac{dx}{dt} = r_{12}(K - x) - r_{21}x$$

were constructed, one for each of the Pier, Marina and Beach. Here x is the number of birds in the censused habitat, K is the total number of birds in the system, $K - x$ is the number of birds in Other, i.e., not in the censused habitat, r_{12} is the per capita flow rate from Other to the censused habitat and r_{21} is the per capita flow rate from the censused habitat to Other.

Using assumption A4 and multiple time scale analysis, the steady state dynamics of the differential equation (1) can be approximated by the algebraic equation

$$(2) \quad x(t) = \frac{r_{12}K}{r_{12} + r_{21}}$$

were constructed for the Pier/Marina system and the Marina/Beach system. Due to negligible flow between the Pier and the Beach, the Pier/Beach system was not modeled. Here x_1 and x_2 are the occupancies of the censused habitats, K is the total number of birds in the system, and $K - x_1 - x_2$ is the occupancy of Other. The four positive terms indicate inflow rates into the censused habitats, while the four negative terms indicate outflow rates.

In this case, multiple time scale analysis yields the algebraic steady state model

$$(3) \quad x_1(t) = \frac{\det A_1(t)}{\det A(t)} K, \quad x_2(t) = \frac{\det A_2(t)}{\det A(t)} K,$$

where

$$A = \begin{pmatrix} -r_{13} - r_{21} - r_{31} & r_{12} - r_{13} \\ r_{21} - r_{23} & -r_{23} - r_{12} - r_{32} \end{pmatrix},$$

$$A_1 = \begin{pmatrix} -r_{13} & r_{12} - r_{13} \\ -r_{23} & -r_{23} - r_{12} - r_{32} \end{pmatrix},$$

$$A_2 = \begin{pmatrix} -r_{13} - r_{21} - r_{31} & -r_{13} \\ r_{21} - r_{23} & -r_{23} \end{pmatrix}$$

(Henson et al. [2005]). Expansion of the determinants in (3) yields the model equations

$$x_1 = \frac{K}{1 + \frac{(r_{21}r_{13} + r_{21}r_{23} + r_{31}r_{23}) + (r_{12}r_{31} + r_{21}r_{32} + r_{31}r_{32})}{(r_{13}r_{21} + r_{23}r_{31} + r_{31}r_{32})}},$$

$$x_2 = \frac{K}{1 + \frac{(r_{12}r_{13} + r_{12}r_{23} + r_{31}r_{23}) + (r_{13}r_{21} + r_{21}r_{32} + r_{31}r_{32})}{(r_{13}r_{21} + r_{23}r_{31} + r_{31}r_{32})}}.$$

The stochastic version of the three-compartment model was taken to be

$$x_1(t) = \left(\sqrt{\frac{\det A_1(t)}{\det A}} \right)$$

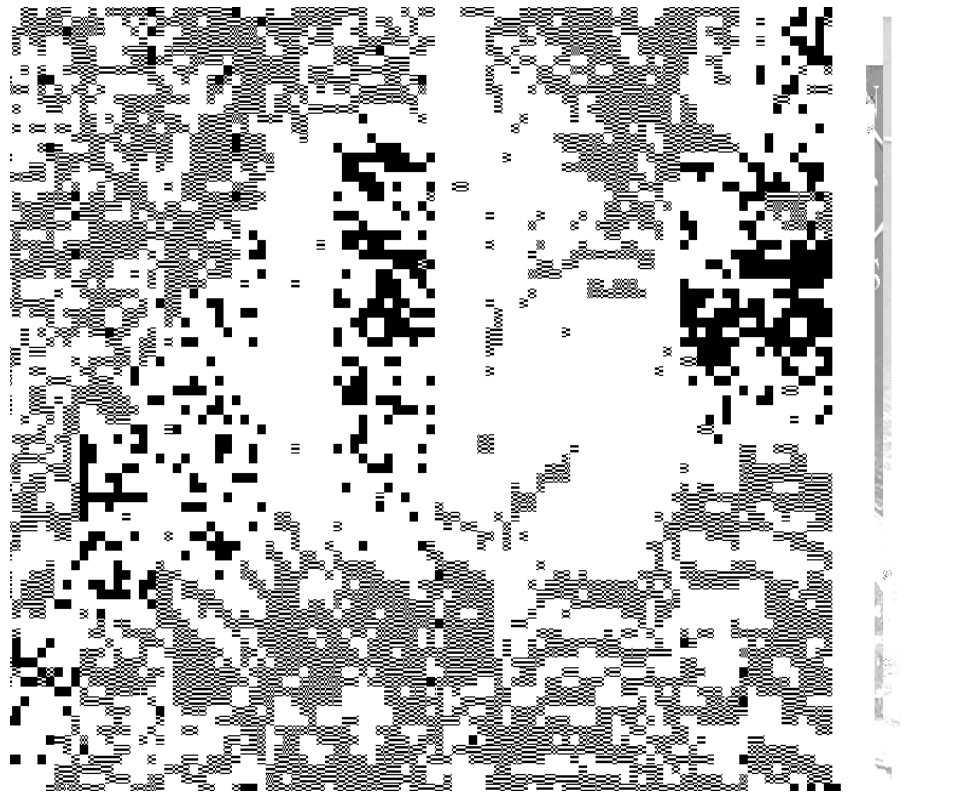
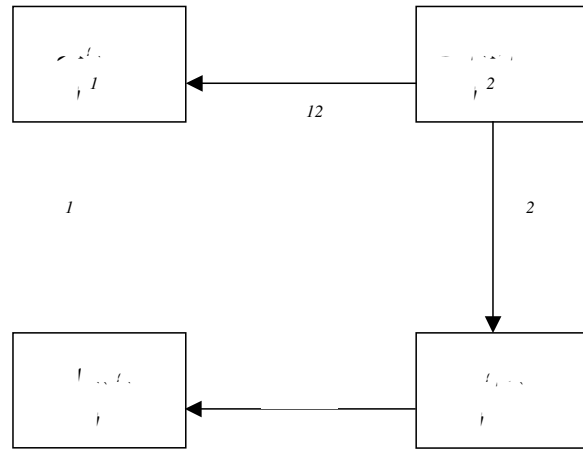


FIGURE 1. Aerial photograph of Violet Point, Protection Island, showing the locations of the six designated habitats including the three study loafing habitats in relation to the observation point.



Determination of the best E_{ij} for the two-compartment models greatly reduced the number of alternative three-compartment models. This, in turn, reduced the number of alternative four-compartment models. The E_{ij} that were found to give the best fit for each model are listed in Table 1.

10. The method of maximum likelihood (ML) was used to estimate the parameters θ_{ij} from the hourly census data. Let q be the number of observations for each habitat, n be the number of censused habitats, and

t_i

TABLE 1. Best flow rate structures for each compartmental model along with corresponding R^2 values for habitat occupancies by Glaucous-winged Gulls on Protection Island. In each case, "Other" refers to all locations other than those being modeled. Note that r_{ij} refers to the per capita flow rate from habitat j to habitat i . Maximum likelihood (ML) parameter estimates are given for each model structure.

	r_{ij}	ML parameter estimates	R^2
Pier (1) / Other (2)	$r_{21} = \alpha_{21}(\text{sun})/(\text{tide}*\text{temp})$ $r_{12} = \alpha_{12}(\text{tide}*\text{hour})/(\text{temp}*\text{sun})$	$\alpha_{21} = 0.0007$ $\alpha_{12} = 405.94$	$R^2_{\text{Pier}} = 0.76$
Marina (1) / Other (2)	$r_{21} = \alpha_{21}1/(\text{temp}^2)$ $r_{12} = \alpha_{12}\text{hour}*\text{tide}*\text{temp}^3$	$\alpha_{21} = 0.0090$ $\alpha_{12} = 57.677$	$R^2_{\text{Marina}} = 0.43$
Beach (1) / Other (2)	$r_{21} = \alpha_{21}1/\text{tide}$ $r_{12} = \alpha_{12}\text{hour}$	$\alpha_{21} = 0.2070$ $\alpha_{12} = 3.9285$	$R^2_{\text{Beach}} = 0.34$
Pier (1) / Marina (2) / Other (3)	$r_{12} = \alpha_{12}\text{hour} / \text{temp}^2$ $r_{21} = \alpha_{21}\text{temp}^3$ $r_{13} = 0$ $r_{31} = \alpha_{31}\text{sun}^3 / \text{tide}^3$ $r_{23} = \alpha_{23}\text{temp}^2*\text{hour}$ $r_{32} = \alpha_{32}1 / (\text{temp}^2*\text{tide})$	$\alpha_{12} = 11.01073$ $\alpha_{21} = 0.96406$ $\alpha_{31} = 1.58887$ $\alpha_{23} = 0.00529$ $\alpha_{32} = 14.8330$	$R^2_{\text{Pier}} = 0.76$ $R^2_{\text{Marina}} = 0.42$ $R^2_{\text{Overall}} = 0.64$
Marina (1) / Beach (2) / Other (3)	$r_{21} = \alpha_{21}1 / (\text{temp}^2*\text{tide})$ $r_{12} = 0$ $r_{31} = \alpha_{31}1 / (\text{temp}^2*\text{tide})$ $r_{13} = \alpha_{13}\text{temp}^2*\text{hour}$ $r_{23} = \alpha_{23}\text{hour}$ $r_{32} = \alpha_{32}1 / \text{tide}$	$\alpha_{21} = 8.70382$ $\alpha_{31} = 22.19711$ $\alpha_{13} = 0.00800$ $\alpha_{23} = 0.01803$ $\alpha_{32} = 0.42291$	$R^2_{\text{Marina}} = 0.41$ $R^2_{\text{Beach}} = 0.35$ $R^2_{\text{Overall}} = 0.35$
Pier (1) / Marina (2) / Beach (3) / Other (4)	$r_{12} = \alpha_{12}\text{hour} / \text{temp}^2$ $r_{21} = \alpha_{21}\text{temp}^3$ $r_{24} = \alpha_{24}\text{hour}*\text{temp}^3$ $r_{32} = \alpha_{32}1/(\text{tide}*\text{temp})$ $r_{23} = 0$ $r_{34} = \alpha_{34}\text{hour}$ $r_{41} = \alpha_{41}\text{sun}^3/\text{tide}^3$ $r_{14} = 0$	$\alpha_{12} = 41.8047$ $\alpha_{21} = 3.30940$ $\alpha_{24} = 0.01886$ $\alpha_{32} = 46.4665$ $\alpha_{34} = 0.26589$ $\alpha_{41} = 6.80682$ $\alpha_{42} = 2.55731\text{e-}05$ $\alpha_{43} = 5.59700$	$R^2_{\text{Pier}} = 0.76$ $R^2_{\text{Marina}} = 0.43$ $R^2_{\text{Beach}} = 0.35$ $R^2_{\text{Overall}} = 0.41$

$$(1/q) \sum_{t=1}^q \binom{2}{ti}.$$

$$\begin{aligned} F(\cdot) &= -\frac{nq}{2} \ln(2) - \frac{q}{2} \ln \left(\prod_{i=1}^n \left[\frac{1}{q} \sum_{t=1}^q \binom{2}{ti} \right] \right) - \frac{nq}{2} \\ &= -\frac{nq}{2} \ln(2) - \frac{q}{2} \ln \left(\frac{1}{q^n} \prod_{i=1}^n \left[\sum_{t=1}^q \binom{2}{ti} \right] \right) - \frac{nq}{2} \\ &= -\frac{nq}{2} \ln(2) - \frac{q}{2} \ln \left(\frac{1}{q^n} \right) - \frac{q}{2} \ln \left(\prod_{i=1}^n \left[\sum_{t=1}^q \binom{2}{ti} \right] \right) - \frac{nq}{2} \\ &= \frac{nq}{2} (\ln q - \ln(2)) - 1 - \frac{q}{2} \sum_{i=1}^n \ln \left(\sum_{t=1}^q \binom{2}{ti} \right). \end{aligned}$$

The first term in

$$F(\cdot) = \frac{nq}{2} (\ln q - \ln(2)) - 1 - \frac{q}{2} \sum_{i=1}^n \ln \left(\sum_{t=1}^q \binom{2}{ti} \right)$$

11. The goodness-of-fit as measured by R^2 was used to choose the best model from each suite of competing models. For models of a single censused habitat, R^2 is given by

$$R^2 = 1 - \frac{\text{RSS}(\hat{\cdot})}{\sum_{t=1}^q (\sqrt{\text{observation}_t} - \text{mean})^2}$$

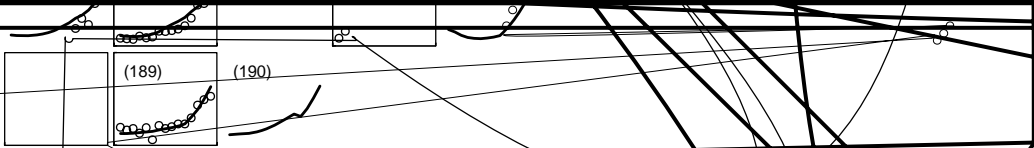
where $\hat{\cdot}$ denotes the mean of the square roots of the observations for the habitat. In the multivariate case there is no standard way of computing an overall R^2 (Agresti [1990]). In this paper

$$R^2 = 1 - \frac{\sum_{i=1}^n \sum_{t=1}^q \hat{t}_i^2}{\sum_{i=1}^n \sum_{t=1}^q (\sqrt{\text{observation}_{ti}} - \text{mean}_i)^2}$$

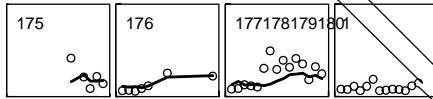
counts and predictions, on the other hand, remained fairly constant during most parts of the day, Figure 3b. Occasional large fluctuations in gull numbers in the Marina often corresponded with fluctuations in temperature. An increased occupancy was commonly observed in the Marina at the end of the day; however, the predictions do not show this increase. Beach occupancies fluctuated more than those in the Marina, and showed a general increase in both predicted and observed occupancies toward evening, Figure 3c. There occurred a general decrease in both the observed and predicted occupancies for

A. PIER

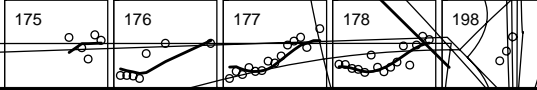
175	176	177	178	179	180	181	182	183
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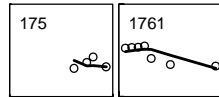
B. MARINA



C. BEACH



D. OTHER



rather than by high tide. Flow data collected by Phillips [2004] show negligible flow from the nesting colony to the Beach. Thus, flow from Other to the Beach probably originates primarily from the water and o -island feeding locations and presumably consists of gulls returning from feeding. This model structure therefore suggests that the return of gulls to the island from feeding is driven by hour of day rather than tide height and occurs at the end of the day. This is consistent with the increase in observed occupancies at the end of the day.

During data collection, it was observed that birds returning from feeding in o -island locations almost always landed on the beach before dispersing into the other habitats interior to Violet Point. This led to the formulation of the hypothesis that gulls returning from feeding in remote locations land first on the Beach, survey the spit for danger, then move to the nesting colony, and finally disperse to the other habitats (the Pier and the Marina). Even though the four-compartment model structure shows flow from the Other habitat to the Marina, the

flow data in Phillips [2004] show that the flow originates at the Beach, rather than from the Other habitat to the Marina. This suggests that the flow from the Other habitat to the Marina is likely due to gulls returning from feeding in o -island locations and landing on the beach before dispersing into the other habitats.

The per capita flow rate from the Marina to the Pier (r_{12}) in the model is proportional to the ratio N_1 / N_2^2 . Since this four-compartment model structure eliminates flow from Other to the Pier, the return of gulls to the Pier, presumably from feeding, occurs via the Marina. This is consistent with the increase in Pier occupancies noted at the end of the day.

While the observed data generally matched trends predicted by the model, there existed considerable departure of data from model predictions. This variability may be explained by several factors:

1. N_1 : Count errors can occur due to marginal light conditions or fog.
2. r_{12} : The model assumes that per capita flow rates between habitats occur in direct response to external environmental factors only. It does not take into account density dependent factors such as Allee effects, social facilitation, or crowding.
3. B : Boats were usually moored to the Pier, which increased the local area available to the birds for loafing. Although occupancy counts for the Pier did not include birds loafing on the boats, the presence of boats may have resulted in an under-representation of the total number of birds using the Pier habitat.
4. t : Data collected within 30 min of an observed disturbance (e.g., Pier being cleaned, boat approaching the Pier, Bald Eagle flying over the island) were discarded for that time period, but unobserved disturbances may have influenced habitat occupancies.
5. K :

6. R^2 values for the Pier and Marina yielded higher R^2 values than the Beach. This may be partly

values. The Pier and the Beach R^2 values dropped very little (from 0.76 and 0.36 to 0.75 and 0.34, respectively). The Marina R^2 , however, was drastically affected, dropping from the previous 0.43 to 0.13. This once

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