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PREDICTING GULL/HUMAN CONFLICTS WITH MATHEMATICAL MODELS: A TOOL FOR MANAGEMENT

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ABSTRACT. Gulls are highly adaptable animals that thrive in proximity to humans. Although gulls enjoy legal protection in North America, England, and Europe, they often conflict with human interests by spreading disease, transporting contaminants, fouling public areas with droppings, and colliding with aircraft. Of particular concern are aggregates of "loafing" gulls that gather on parking lots, rooftops, and airport runways. Loafing in birds is a general state of immobility that involves behaviors such as sleeping, sitting, standing, resting, preening, and defecating. The ability to predict the incidence of aggregated loafing provides a first step toward the amelioration of bird/human conflicts. We used mathematical models to predict the aggregate loafing behavior of gulls as a function of environmental conditions and tested model portability across years, phase of breeding cycle, loafing location, and species. Because groups of loafing birds quickly reassemble after disturbance, algebraic models for the steady-state dynamics can be obtained from the differential equations using time-scale analysis. The accessible management tool requires

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data collection on an appropriate time scale and information-theoretic model selection from a suite of alternative algebraic models.

KEY WORDS: Airport runways, droppings, environmental variables, gulls, habitat occupancy dynamics, loafing, management, mathematical model, rooftops, *Salmonella*.

1. Introduction. Loafing in birds is defined as a general state of immobility that involves a heterogeneous collection of behaviors such as sleeping, sitting, standing, resting, preening, and defecating (Amlaner and Ball [1983]). Loafing thus serves a variety of functions and cannot be considered as a single behavior. Nevertheless, loafing is a useful term for a class of bird behaviors that often conflict with human interests.

Loafing gulls (Family Laridae) were considered to be a "serious problem" in 23 states of the United States in 1990, and they ranked sixth among all problem species groups among state Animal Damage Control personnel (Packham and Connolly [1992]). Gull droppings contain contaminants and nutrients transferred from landfills (Ganning and Wulff [1969], Fennel et al. [1974], Leonzio et al. [1986], Belant [1997]), accelerate nutrient loading of aquatic systems (Portnoy [1990]), and "whitewash" buildings, boats, piers, and other areas (Fitzwater [1988]). Droppings of roof-nesting gulls erode roofing materials and gull feathers block roof drainage systems (Monaghan and Coulson [1977], Vermeer et al. [1988]). Gulls carry *Salmonella*, *Campylobactor*, and *Listeria* (Quessey and Messier [1992]), and the proportion of gulls carrying *Salmonella* correlates positively with the incidence of salmonellosis among humans (Monaghan et al. [1985]).

Gulls loafing on airport runways pose one of the most serious problems. Gulls and aircraft often collide, resulting in expensive aircraft repairs and loss of avian and human life (Murton and Wright [1968], Stout et al. [1974], Dolbeer et al. [1993], Belant [1997], Cleary and Dolbeer [2005]). In 1912, the first human fatality from a bird/aircraft collision involved a herring gull (*Larus argentatus*). Between 1990 and 2003, 21,684 bird/aircraft strikes involving known species of birds were reported to the United States Federal Aviation Administration. Of these strikes, 5,323 (24.5%) involved gulls and, of these, 891 (16.7%) resulted in damage to aircraft (Cleary and Dolbeer [2005]).

Management of the "gull problem" is complicated by the fact that these indigenous and often migratory species enjoy legal protection in North America, England, and Europe. Moreover, gulls are highly adaptable animals that thrive in proximity to humans. Anthropogenic factors (Kadlec and Drury [1968], Spaans [1971], Patton and Hanners [1984], Belant and Dolbeer [1993]) accounted for dramatic increases in gull populations over the past half century (e.g., Drury and Kadlec [1974], Conover [1983], Dolbeer and Bernhardt [1986], Vermeer [1992]). Gull management requires an integrated, landscape-level approach involving government agencies, businesses, wildlife managers, landscape and building designers, and private citizens (Belant [1997]). An ability to predict the temporal dynamics of aggregate loafing sites would facilitate efforts to lessen the gull/human conflict.

Henson et al. [2004] developed a model that accurately predicted numbers of glaucous-winged gulls (*L. glaucescens*) loafing on a pier near a breeding colony in Washington, USA. The model was validated on an independent data set and successfully field-tested six months later with *a priori* model predictions. Clear dynamic patterns emerged in the abundance of loafing gulls even though individuals moved in and out of the loafing area more or less continuously throughout the day. Dynamics were predicted by three environmental factors: day of the year, height of the tide, and solar elevation. The portability of the model, however, was unknown.

Here we use the Henson et al. [2004] study as a basis to develop an accessible tool for managers. We test the tool's portability across years, local loafing location, breeding cycle phase, species, and continent. In particular, we test the procedure in four circumstances, each involving loafing by gulls on human-made structures adjacent to breeding colonies: (a) glaucous-winged gulls loafing on the same pier during the same reproductive phase (nest-building/egg-laying) as in the original Henson et al. [2004] study but two years later; (b) glaucous-winged gulls loafing during the same reproductive phase as in the original study but on a rock jetty approximately 200 m from the pier; (c) glaucous-winged gulls occupying the same jetty during a different reproductive phase (chick-rearing) than in the original study; and (d) herring and great black-backed gulls (*L. argentatus* and *L. marinus*, respectively) loafing on roof tops on Appledore Island, Maine, USA, during the incubation/chick-hatching phase.

2. Methods

2.1 Data collection. Data must be collected sufficiently densely in time to capture system dynamics. In this study, we collected data hourly because the abundance of loafing gulls depends primarily on environmental conditions that tend to change over a period of several hours.

At the top of each hour, from 0500 to 2000 Pacific Standard Time (PST) on May 9, 2002 to June 6, 2002 (original study) and June 3–16, 2004, numbers of glaucous-winged gulls loafing on a pier in the marina adjacent to the Protection Island National Wildlife Refuge nesting colony (48°7″N, 122°55″W), Strait of Juan de Fuca, Washington, were monitored. Counts were made using a 20–60× spotting scope from a 33-m-high bluff (Henson et al. [2004]). Also on June 3–16, 2004 and additionally on June 28, 2004 to July 16, 2004, counts were made of gulls loafing on a jetty at the entrance of the marina, 200 m south of the pier. Both the pier and jetty were protected from prevailing westerly winds by a steep bluff.

At the top each hour, from 0500 to 2000 Eastern Standard Time (EST) on May 14, 2005 to May 21, 2005 and May 27, 2005 to June 10, 2005, loafing herring and great black-backed gulls were counted on seven roofs of buildings at the Shoals Marine Laboratory, Appledore Island, Maine (42°59″N, 70°37″W). The seven sites were directly adjacent to a large breeding colony of these birds. The colony and roofs were somewhat protected from prevailing easterly winds by island topography. Counts were made through binoculars by on-foot observers without visible disturbance to the birds.

Solar elevations and tide height predictions were obtained from the National Oceanographic and Atmospheric Administration (NOAA). Weather data for Protection Island were obtained from the NOAA weather station located on Smith Island, 22 km to the north. Weather data for Appledore Island were obtained from the NOAA Isle of Shoals weather station located on Appledore Island. In each case, weather data included wind speed, barometric pressure, temperature, and wind direction. Table 1 summarizes the variables used to designate the environmental factors.

2.2 Modeling assumptions. A primary principle of mathematical modeling is to identify a parsimonious set of simplifying

TABLE 1. Environmental variables.

Environmental factor	Variable
Solar elevation	$S(t)$
Tide height	$T(t)$
Wind speed	$W(t)$
Barometric pressure	$B(t)$
Air temperature	$H(t)$
Wind direction	$D(t)$

Note: Each environmental variable x was nondimensionalized and scaled so that $1 \leq x(t) \leq 2$.

assumptions that captures the main dynamics of a system. The model proposed in this study is formulated from six assumptions:

(i) The number of gulls in the loafing site can be described with a two-compartment model consisting of the loafing site and a remote location (places other than the loafing site).

(ii) Fluctuations in numbers of gulls at the loafing site occur in direct response to environmental variables that vary in time t. In particular, gulls arrive at the site at a per capita rate proportional to a function of environmental variables $E_1(t)$, and leave at a per capita rate proportional to a function of environmental variables $E_2(t)$.

(iii) The rate functions $E_1(t)$ and $E_2(t)$ are multiplicative functions of powers of environmental variables (Damania et al. [2005], Henson et al. [2007a, b], Moore et al. [2008]). This is equivalent to the assumption of log-linear, or Poisson, regression of rates on environmental factors (McCullagh and Nelder [1989]).

(iv) The total number of gulls in the two-compartment system—that is, the total number of gulls that are either occupying the loafing site or may choose to occupy the loafing site—is constant. This assumption holds for short-term studies during times of the season in which gull numbers are relatively stable.

(v) The system recovers sufficiently rapidly after a disturbance that the abiotic environment can be considered constant during the recovery. That is, the values $E_1(t)$ and $E_2(t)$ remain approximately constant during the time it takes the system to return to "steady state" dynamics. This assumption is based on our observations over many years at the Protection Island colony that occupancies (and behaviors) essentially recover within 15 minutes after short-term "point disturbances" by eagles and humans (Henson et al. [2004, 2006], Damania et al. [2005]).

(vi) The main source of noise in the census data is assumed to be demographic rather than environmental stochasticity. This assumption is motivated by the fact that all major environmental correlates are incorporated explicitly into the model. Demographic stochasticity in this context arises from independent random binary choices of individual gulls as they arrive in or depart from a habitat. This is analogous to a stochastic birth–death model at the population level (Henson et al. [2007b]).

2.3 Deterministic model. The general model is derived from a standard "compartmental" ordinary differential equation. The net rate of change of the number N of animals at the loafing site is the inflow rate minus the outflow rate:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = [\text{inflow rate}] - [\text{outflow rate}]. \tag{1}$$

Let $M(t)$ denote the total number of gulls in the two-compartment system at time t. The inflow rate is the per capita flow rate $aE_1(t)$ into the loafing site multiplied by the number of animals $M(t)-N(t)$ outside the site, and the outflow rate is the per capita flow rate $bE_2(t)$ away from the site multiplied by the number of animals $N(t)$ in the site, where $a,b > 0$ are constants of proportionality (assumptions (i) and (ii)). Model (1) thus becomes

$$\frac{\mathrm{d}N}{\mathrm{d}t} = aE_1(t)(M(t) - N) - bE_2(t)N. \tag{2}$$

Note that $M(t)$ is not in general a population size but rather is the total number of animals that are either already at the loafing site or are eligible to choose to enter the loafing site.

Given assumption (v), the dynamics of equation (2) occur on two time scales. Time-scale analysis introduces a small parameter in front of the derivative in equation (2), and the undisturbed "steady state" dynamics of equation (2) are well-approximated by the algebraic equation $0 = aE_1(t)(M(t) - N) - bE_2(t)N$, that is

$$N(t) = \frac{M(t)}{1 + bE_2(t)/(aE_1(t))} \tag{3}$$

(Henson et al. [2006]). Over short time periods such as a few weeks, the value of $M(t)$, which is seasonally variable, often can be approximated by a constant β (assumption (iv)). Substitution of $M(t) = \beta$, $E(t) = E_2(t)/E_1(t)$, and $\alpha = b/a$ into equation (3) yields the algebraic model

$$N(t) = \frac{\beta}{1 + \alpha E(t)}, \tag{4}$$

where $N(t)$ is the number of animals occupying the loafing site at time t in the absence of disturbance, the variable $E(t)$ is a multiplicative function of powers of environmental variables, and $\alpha,\ \beta > 0$ are constant parameters to be determined from data.

Model (4) is the model used in the management tool. When applied to a specific loafing site, the function $E(t)$ must be identified and the parameters α and β must be estimated from data.

2.4 Stochastic model. Observations nearly always deviate from model predictions; these model errors are called "residuals." In a model that captures the main trends of the dynamics, the residuals can be considered "noise" in the system. That is, the residuals can be thought of as realizations of a random variable having some hypothesized distribution. The process of "model fitting"—the connection of a deterministic mathematical model to data through parameter estimation—requires assumptions regarding the distribution of residuals. A stochastic model provides these assumptions and hence forms the basis for parameter estimation.

Demographic noise—in this context meaning the variability due to independent choices resulting in arrivals and departures—is approximately additive on the square root scale (Dennis et al. [2001], Hayward et al. [2005], Henson et al. [2007b]). Thus, given assumption (vi), a stochastic model is

$$\sqrt{N(t)} = \sqrt{\frac{\beta}{1+\alpha E(t)}} + \sigma\omega(t), \tag{5}$$

or equivalently,

$$N(t) = \left(\sqrt{\frac{\beta}{1+\alpha E(t)}} + \sigma\omega(t)\right)^2, \tag{6}$$

where $\omega(t)$ is a standard normal random variable (mean zero and standard deviation one) uncorrelated in time and $\sigma > 0$ is a constant. In the event that the quantity inside the parentheses in equation (6) becomes negative, it is taken to be zero.

The stochastic model (5) is the basis of parameter estimation; the (square root-transformed) residuals are modeled by the random variable $\sigma\omega(t)$. Model (6) can be used by a manager to produce realistically noisy simulations once α, β, σ, and E are known.

2.5 Environmental variables. By assumption (iii), we can write

$$E = S^\gamma T^\delta W^\varepsilon B^\zeta H^\eta D^\theta, \tag{7}$$

where γ, δ, ε, ζ, η, θ are constant parameters that can be positive, zero, or negative, and where S, T, W, B, H, D are the solar elevation, tide height, wind speed, barometric pressure, air temperature, and wind direction, respectively (Table 1).

We nondimensionalized and scaled variables S, T, W, B, H so that their values always lay between one and two (Damania et al. [2005], Henson et al. [2007a, b], Moore et al. [2008]). This is accomplished by subtracting off the minimum value, dividing by the new maximum value, and adding one. For example,

$$S_{\text{scaled}} = \frac{S_{\text{unscaled}} - \min(S_{\text{unscaled}})}{\max(S_{\text{unscaled}} - \min(S_{\text{unscaled}}))} + 1. \tag{8}$$

Input variables are nondimensionalized so that their units of measurement are irrelevant, and they are scaled to be greater than one to avoid numerical instability if exponents are negative.

Raw wind direction data are on a circular scale with 0 and 360 at true north. We transformed wind direction to a linear scale by

$$D_{\text{linear}} = \begin{cases} D_{\text{circular}} & \text{if } D_{\text{circular}} \leq 180, \\ 360 - D_{\text{circular}} & \text{if } D_{\text{circular}} > 180, \end{cases} \tag{9}$$

and then nondimensionalized and scaled the result as in equation (8).

A set of alternative models of the form (4) is generated by taking combinations of the environmental variables in equation (7); for example, $E = S^{\gamma} T^{\delta}$ and $E = S^{\gamma} B^{\zeta} H^{\eta}$ yield two possible alternatives.

2.6 Parameter estimation. Parameters were estimated using the method of nonlinear least squares (LS) on the square root scale. That is, the sum of squared residuals

$$RSS(\Omega) = \sum_{data} (\sqrt{observation} - \sqrt{prediction})^2 \tag{10}$$

was minimized as a function of the vector Ω of model parameter values. The minimizer $\hat{\Omega}$ gives the LS parameter estimates. Minimization was carried out numerically in Matlab using the Nelder–Mead downhill method (Press et al. [1986]).

2.7 Model selection. When comparing models, one should use a selection criterion that takes into account the number of parameters as well as the goodness of fit; models having more parameters should be penalized. The Akaike Information Criterion (AIC) is an information-theoretic model selection index designed to select the best model from a suite of alternative models. For LS parameters, the criterion is equivalent to

$$AIC = n \ln \hat{\sigma}^2 + 2\kappa, \tag{11}$$

where n is the number of observations, $\hat{\sigma}^2 = RSS(\hat{\Omega})/n$ is the variance of the likelihood function as estimated from the residuals, and κ is the number of model parameters, including σ^2 (Burnham and Anderson [2002]). The actual value of AIC, which can be positive or negative, does not give any information about model selection; rather, model comparison is based on the rank of the AIC values. The smallest AIC value indicates the best model.

2.8 Test of model portability. This study considers whether the model that was rigorously developed and validated in Henson et al. [2004] is portable across years, local loafing sites, breeding-cycle phase, species, and continental coasts as a management tool. The most rigorous procedure for model testing involves validating the parameterized model on independent data without re-estimating parameters (see, e.g., Hayward et al. [2005]). Although rigorous model validation in this sense should be carried out for data obtained at the same location in the same season by randomly dividing the data into "estimation" and "validation" sets, such validation attempts typically fail when applied across seasons, habitats, and species. For example, the total number of gulls β is expected to vary across habitats with differing occupancy capacities and across seasons due to migration. Thus, in testing model portability, we re-estimated parameters for each new data set.

In the initial Henson et al. [2004] study, the function $E(t)$ was determined to be $E(t) = S(t)^2\, T(t)^{-2}$, where $S(t)$ and $T(t)$ denote the solar elevation and tide height, respectively. To test the portability of the model in Henson et al. [2004], we parameterized model (4) with $E = S^{\gamma}\, T^{\delta}$ on each data set.

To test the portability of the general model structure, we parameterized the suite of alternative models on each data set and used the AIC to choose the best model for each.

2.9 Goodness of fit. We used goodness of fit as measured by the generalized R^2

$$R^2 = 1 - \frac{\sum\limits_{data} (\sqrt{observation} - \sqrt{prediction})^2}{\sum\limits_{data} (\sqrt{observation} - mean)^2}, \tag{12}$$

where *mean* denotes the sample mean of the square roots of the observations. R^2 estimates the proportion of the observed variability that

TABLE 2. Least squares parameter estimates and goodness of fit R^2 values for model (4) with $E(t) = S(t)^{\gamma}\, T(t)^{\delta}$.

Location	α	β	γ	δ	R^2
Protection Island Pier—June 2002	19.29	40.22	1.987	−7.034	0.66
Protection Island Pier—June 2004	8.170	118.8	2.773	−3.678	0.60
Protection Island Jetty—June 2004	98.99	706.9	2.051	−4.145	0.81
Protection Island Jetty—July 2004	3.612	171.6	7.086	−7.483	0.75
Appledore Island Roofs—June 2005	Model did not parameterize				

Note: Parameter estimates for the 2002 data (from Henson et al. [2004]) are shown for comparative purposes. Protection Island birds were glaucous-winged gulls. Appledore Island birds were mixed groups of herring gulls and great black-backed gulls.

is explained by the model and thus gives a measure of the accuracy of the model predictions.

3. Results. Table 2 summarizes the results of applying model (4) with $E = S^{\gamma}\, T^{\delta}$ to each of the data sets. Application of the model to the 2002 data (from Henson et al. [2004]) is shown for comparative purposes. Note that because E is in the denominator of model (4), positive (negative) exponents are associated with decreasing (increasing) numbers of loafing gulls. The same model parameterized with a relatively high R^2 value for each of the Protection Island data sets. The model originally was developed on the basis of data from the pier; however, R^2 values for the jetty were considerably higher than those for the pier. The model suggests that gulls move to the respective loafing sites when the solar elevation is low and the tide is high; they exit the sites when solar elevation is high and tide height is low. This model did not parameterize when applied to the Appledore Island data, however.

Table 3 summarizes the best models of the form $E = S^{\gamma}\,T^{\delta}\,W^{\varepsilon}\,B^{\zeta}\,H^{\eta}\,D^{\theta}$ for each 2004 data set from Protection Island and for the 2005 data set from Appledore Island. Values of R^2 were modestly higher for each Protection Island model of this form when compared with results for $E = S^{\gamma}\,T^{\delta}$ in Table 2. Decreases in solar elevation and increases in tide height and temperature were associated with increases in numbers of loafing gulls in all three Protection Island data sets. Increases in barometric pressure were associated with decreases in numbers of loafing birds on the pier in June and on the jetty in July. Increases in wind speed and in deviation of wind direction from the north were associated with decreases in loafing gulls on the jetty in July. Wind speed and direction were not predictors for the pier or jetty in June, nor was barometric pressure a predictor for the jetty in June.

The models did not fit the Appledore Island data as well as the Protection Island data but still predicted a sizable proportion of the dynamic variability ($R^2 = 0.48$). Just as for the Protection Island models, decreases in solar elevation and increases in tide height were associated with increased numbers of loafing gulls, and increases in wind speed were associated with decreases in numbers of loafing gulls. Unlike models for Protection Island, however, increases in barometric pressure were associated with predicted increases in loafing gull numbers, and decreases in temperature were associated with predicted increases in loafing gull numbers. Deviation of wind direction from the north, most often from the northeast, east, or southeast, resulted in increased numbers of loafing gulls.

Figures 1A–C shows a close correspondence between predictions and data for Protection Island. Predictions and data for Appledore Island are shown in Figure 2. In both systems, counts toward the end of the day often exceeded predictions.

4. Discussion

4.1 Scale, determinism, and individual variability. The identification of scales at which random individual-level behaviors form patterns and the mechanisms behind the pattern formation is of key

TABLE 3. Best model selected (lowest AIC) from the suite of alternatives of the form (4) generated by all combinations of $E = S^{\gamma}\, T^{\delta}\, W^{\varepsilon}\, B^{\zeta}\, H^{\eta}\, D^{\theta}$.

Data set	α	β	Solar γ	Tide δ	Wind speed ε	Bar ζ	Temperature η	Wind direction θ	R^2
Protection Island Pier—June 2004	6.427	88.82	2.775	−3.863	*	0.7593	−1.380	*	0.62
Protection Island Jetty—June 2004	54.26	333.5	2.010	−4.299	*	*	−0.4581	*	0.82
Protection Island Jetty—July 2004	6.643	249.0	4.788	−6.544	0.3574	0.8773	−1.743	1.229	0.81
Appledore Island Roofs—June 2005	0.4153	107.8	2.224	−0.5217	0.4469	−0.5192	1.410	−0.4545	0.48

Note: Because E is in the denominator of model (4), positive (negative) exponents are associated with decreasing (increasing) numbers of loafing gulls. Protection Island birds were glaucous-winged gulls. Appledore Island birds were mixed groups of herring gulls and great black-backed gulls. An asterisk (*) indicates that the best model did not include the associated variables.

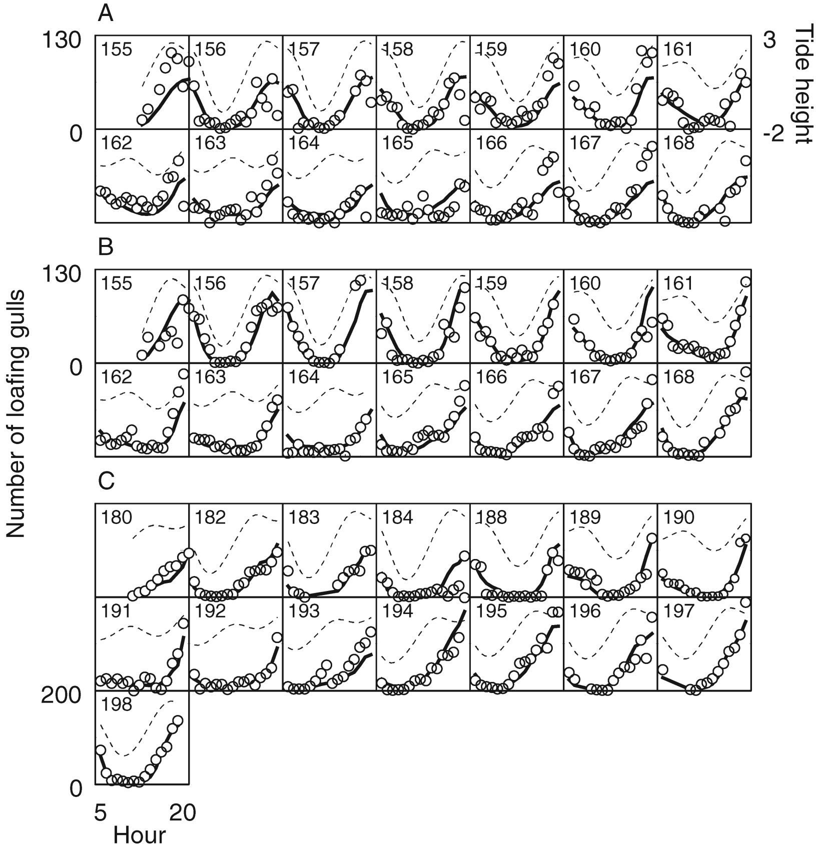

FIGURE 1. Protection Island model prediction (solid curve), observed number of glaucous-winged gulls (circles), and tide height (dashed curve) versus hour of day. Each panel is identified with the day of the year. Tide heights are in meters. (A) For gulls on the pier during the June 2004 data collection. (B) For gulls on the jetty during the June 2004 data collection period. (C) For gulls on the jetty during the July 2004 data collection period.

importance (Hunt and Schneider [1987], Levin [1992], Silverman et al. [2001]). Dynamic patterns emerge for assemblages of birds even though individual birds move more or less independently or in small groups due to individual differences and histories as well as to social interactions (Silverman et al. [2001]). The ability to predict the dynamics of

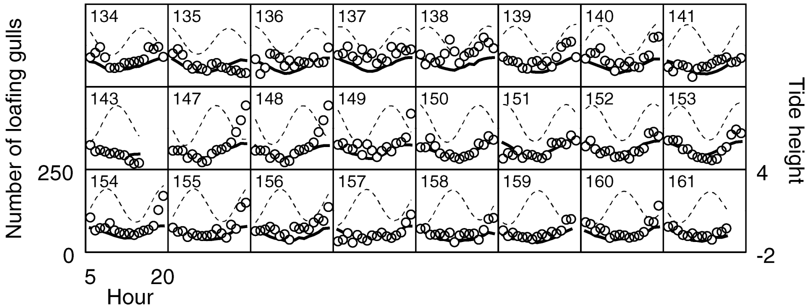

FIGURE 2. Appledore Island model prediction (solid curve), observed number of herring and great black-backed gulls on the roofs (circles), and tide height (dashed curve) versus hour of day. Each panel is identified with the day of the year. Tide heights are in meters.

loafing assemblages of gulls suggests that individual variability is less important than deterministic forces at our scale of observation and enumeration.

4.2 Application to the management of loafing gulls. The timing of animal behavior, including loafing, is influenced by a variety of demographic and environmental variables; thus, accurate prediction based on a single variable is rarely possible (Henson et al. [2007b]). Our results suggest that the modeling methodology detailed works best for relatively predictable environments. Under these circumstances, a good model may be locally portable both spatially and temporally. Indeed, the Protection Island model was portable across years for the pier, across location from the pier to the jetty, and across seasons for the jetty.

The considerably higher R^2 values for the Protection Island system compared with the Appledore Island system deserve comment. Protection Island is situated in Washington's inland waters, which are somewhat shielded from high winds. By contrast, Appledore Island occurs in the open ocean and is subject to almost continuous winds. Wind clearly alters the behavior and movement patterns of gulls (Henson et al. [2007a, b]). Although wind direction was included as a variable in the Appledore model, its highly variable nature and relative unpredictability seemed responsible for much higher levels of stochasticity for the loafing patterns there. Moreover, concentrations of loafing gulls on Appledore Island typically were smaller than those on Protection Island (perhaps in part due to the wind), leading to increased demographic stochasticity.

4.3 Summary of management tool. The management tool for predicting aggregates of loafing gulls can be summarized as follows:

1. Census data should be collected at regularly spaced, discrete time intervals much shorter that the periods of environmental oscillations and should be collected throughout the entire cycle of environmental change.
2. The deterministic loafing model is

$$N(t) = \frac{\beta}{1 + \alpha E_1^{\gamma_1} E_2^{\gamma_2} \dots E_k^{\gamma_k}}, \tag{13}$$

   where the E_i are the environmental variables, nondimensionalized and scaled to be greater than one, that are hypothesized to drive the dynamics. If the model is used over time spans during which local numbers of gulls are changing rapidly (e.g., during migration), then the constant β should be replaced by a function $M(t)$ that describes the total number of gulls in the two-compartment system. Such a function can be estimated from seasonal maximal counts (e.g., see Henson et al. [2004]).
3. A collection of candidate models results from various combinations of the environmental variables. If the candidate models do not share the same number of parameters, the best model should be selected using an information-theoretic criterion such as the AIC. Otherwise, the model with the largest R^2 can be deemed best.
4. Parameters $\alpha, \beta, \gamma_1, \gamma_2, \dots$ for the deterministic model can be estimated by LS on the basis of a stochastic model that accounts for the main type of noise in the system.
5. The stochastic model can be used to simulate noisy time series.
6. Ideally, the fitted model should be tested against an independent data set from the same location and time period. Sufficiently large data sets can be divided into "estimation" and "validation" sets by random sampling that is stratified so that both sets include a variety of environmental conditions (Henson et al. [2004]).

7. Model (13) can be used to make long-range predictions if the total number of birds in the two-compartment system is fairly stable (β is constant) or if $M(t)$ is known, and if the environmental variables that account for most of the variability are largely deterministic (e.g., solar elevation, tide height). Otherwise, the model can make short-range predictions based on weather forecasts, and it can suggest a range of predicted outcomes based on a range of possible weather changes.

The management tool outlined in this study has been used to predict haul-out patterns of harbor seals (*Phoca vitulina* L.; Hayward et al. [2005]) and most likely could be adapted to predict the behavioral dynamics of a variety of marine organisms.

5. Conclusion. We wish to highlight the difference between our approach and other management tools for predicting site occupancies. First, rather than using traditional hypothesis testing, we use an information-theoretic criterion for model selection. This powerful approach requires a mechanistic understanding of the system, works nicely with mathematical modeling, and penalizes models for overfitting. Second, our mathematical approach differs significantly from more commonly used statistics-based analyses, techniques that often entail data averaging, which masks important relationships among variables (Hayward et al. [2005]).

For personnel who make management decisions about loafing birds, we believe the mathematical methodology presented in this study, in tandem with preliminary statistical exploration, can offer a distinct advantage over purely statistics-based decisions.

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REFERENCES

C.J. Amlaner and N.J. Ball [1983], *A Synthesis of Sleep in Wild Birds*, Behaviour **87**, 85–119.

J.L. Belant [1997], *Gulls in Urban Environments: Landscape-level Management to Reduce Conflict*, Landsc. Urban Plann. **38**, 245–258.

J.L. Belant and R.A. Dolbeer [1993], *Population Status of Nesting Laughing Gulls in the United States 1977–1991*, Am. Birds **47**, 220–224.

K.P. Burnham and D.R. Anderson [2002], *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*, 2nd ed., Springer, New York.

E.C. Cleary and R.A. Dolbeer [2005], *Wildlife Hazard Management at Airports: A Manual for Airport Personnel*, *2nd ed.*, U.S. Federal Aviation Administration, Washington, DC.

M.R. Conover [1983], *Recent Changes in Ring-billed and California Gull Populations in the Western United States*, Wilson Bull. **95**, 362–383.

S.P. Damania, K.W. Phillips, S.M. Henson, and J.L. Hayward [2005], *Habitat Patch Occupancy Dynamics in Glaucous-winged Gulls* (Larus glaucescens) *II: A Continuous-time Model*, Nat. Resour. Model. **18**, 469–499.

B. Dennis, R.A. Desharnais, J.J. Cushing, S.M. Henson, and R.F. Costantino [2001], *Estimating Chaos and Complex Dynamics in an Insect Population*, Ecol. Monogr. **71**, 277–303.

R.A. Dolbeer, J.L. Belant, and J.L. Sillings [1993], *Shooting Gulls Reduces Strikes with Aircraft at John F. Kennedy International Airport*, Wildl. Soc. Bull. **21**, 442–450.

R.A. Dolbeer and G.E. Bernhardt [1986], *Early-Winter Population Trends of Gulls on Western Lake Erie, 1950–1984*, Am. Birds **40**, 1097–1102.

W.H. Drury and J.A. Kadlec [1974], *The Current Status of the Herring Gull Population in the Northeastern United States*, Bird-Banding **45**, 297–306.

H. Fennel, D.B. James, and J. Morris [1974], *Pollution of a Storage Reservoir by Roosting Gulls*, Water Treat. Exam. **23**, 5–24.

W.D. Fitzwater [1988], *Solutions to Urban Bird Problems*, in (A.C. Crabb and R.E. Marsh, eds.) *Proceedings of the Thirteenth Vertebrate Pest Conference*, University of California, Davis, pp. 254–259.

B. Ganning and F. Wulff [1969], *The Effects of Bird Droppings on Chemical and Biological Dynamics in Brackish Water Rockpools*, Oikos **20**, 274–286.

J.L. Hayward, S.M. Henson, C.J. Logan, C.R. Parris, M.W. Meyer, and B. Dennis [2005], *Predicting Numbers of Hauled-out Harbour Seals: A Mathematical Model*, J. Appl. Ecol. **42**, 108–117.

S.M. Henson, J.G. Galusha, J.L. Hayward, and J.M. Cushing [2007a], *Modeling Territory Attendance and Preening Behavior in a Seabird Colony as Functions of Environmental Conditions*, J. Biol. Dynamics **1**, 95–107.

S.M. Henson, B. Dennis, J.L. Hayward, J.M. Cushing, and J.G. Galusha [2007b], *Predicting the Dynamics of Animal Behaviour in Field Populations*, Anim. Behav. **74**, 103–110.

S.M. Henson, J.L. Hayward, C.M. Burden, C.J. Logan, and J.G. Galusha [2004], *Predicting Dynamics of Aggregate Loafing Behavior in Gulls at a Washington Colony*, Auk **121**, 380–390.

S.M. Henson, J.L. Hayward, and S.P. Damania [2006], *Identifying Environmental Determinants of Diurnal Distribution in Marine Birds and Mammals*, Bull. Math. Biol. **68**, 467–482.

G.L. Hunt, Jr. and D.C. Schneider [1987], *Scale-dependent Processes in the Physical and Biological Environment of Marine Birds*, in (J.P. Croxall, ed.) *Seabirds: Feeding, Ecology and Role in Marine Ecosystems*, Cambridge University Press, Cambridge, pp. 7–41.

J.A. Kadlec and W.H. Drury [1968], *Structure of the New England Herring Gull Population*, Ecology **49**, 644–676.

C. Leonzio, C. Fossi, and S. Focardi [1986], *Lead, Mercury, Cadmium and Selenium in Two Species of Gulls Feeding on Inland Dumps and in Marine Areas*, Sci. Total Environ. **57**, 121–127.

S.A. Levin [1992], *The Problem of Pattern and Scale in Ecology*, Ecology **73**, 1943–1967.

P. McCullagh and J.A. Nelder [1989], *Generalized Linear Models*, 2nd ed. Chapman and Hall, London.

P. Monaghan and J.C. Coulson [1977], *Status of Large Gulls Nesting on Buildings*, Bird Study **24**, 89–104.

P. Monaghan, C.B. Shedden, C.R. Fricker, and R.W.A. Girdwood [1985], *Salmonella Carriage by Herring Gulls in the Clyde Area of Scotland in Relation to Their Feeding Ecology*, J. Appl. Ecol. **22**, 669–680.

A.L. Moore, S.P. Damania, S.M. Henson, and J.L. Hayward [2008], *Modeling the Daily Activities of Breeding Colonial Seabirds: Dynamic Occupancy Patterns in Multiple Habitat Patches*, Math. Biosci. Eng. **5**, 831–842.

R.K. Murton and E.N. Wright (eds.) [1968], *The Problems of Birds as Pests*, Academic Press, New York.

C.J. Packham and G. Connolly [1992], *Control Methods Research Priorities for Animal Damage Control*, Proc. Vetebr. Pest Conf. **15**, 12–16.

S.R. Patton and L.A. Hanners [1984], *The History of the Laughing Gull Population in Tampa Bay, Florida*, Fla. Field Nat. **12**, 49–57.

J.W. Portnoy [1990], *Gull Contributions of Phosphorus and Nitrogen to a Cape Cod Kettle Pond*, Hydrobiologia **202**, 61–69.

W.H. Press, B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling [1986], *Numerical Recipes: The Art of Scientific Computing*, Cambridge University Press, Cambridge.

S. Quessey and S. Messier [1992], *Prevalence of* Salmonella *spp., Campylobacter spp. and* Listeria *spp. in Ring-billed Gulls* (Larus delawarensis), J. Wildl. Dis. **28**, 526–531.

E.D. Silverman, M. Kot, and E. Thompson [2001], *Testing a Simple Stochastic Model for the Dynamics of Waterfowl Aggregations*, Oecologia **128**, 608–617.

A.L. Spaans [1971], *On the Feeding Ecology of the Herring Gull* Larus argentatus *Pont. in the Northern Part of the Netherlands*, Ardea **59**, 75–188.

J.F. Stout, J.L. Hayward, and W.H. Gillett [1974], *Aggregations of Gulls (Laridae) on Aerodromes and Behavioral Techniques for Dispersal*, in (J.P. Croxall, ed.) *Proceedings of the Conference on the Biological Aspects of the Bird/Aircraft Collision Problem*, Clemson University, Clemson, NC, pp. 125–148.

K. Vermeer [1992], *Population Growth Rate of the Glaucous-winged Gull Larus glaucescens in the Strait of Georgia, British Columbia, Canada*, Ardea **80**, 181–185.

K. Vermeer, D. Power, and G.E.J. Smith [1988], *Habitat Selection and Nesting Biology of Roof-nesting Glaucous-winged Gulls*, Coln. Waterbirds **11**, 189–201.