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Jim M. Cushing · Shandelle M. Henson
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Modeling Behavior and Population Dynamics

Seabirds, Seals, and Marine Iguanas

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Preface

We have entered the Anthropocene, an era of unprecedented, human-induced changes in the biosphere, geosphere, and atmosphere. An understanding and appreciation of the animals with which we share the planet is important for esthetic, ethical, and practical reasons. A significant part of that understanding concerns the behavior of animals and how behavior changes in response to environmental change.

In simplest terms, animal behavior can be defined as muscle movement. Muscle movement occurs in response to internal stimuli such as hormone levels or nervous system activity, and to external stimuli such as predator activity or changes in weather. The study of animal behavior is focused on patterns of animal movement, the internal and external stimuli that elicit these patterns, and the evolution of these patterns. Patterns of movement include things like shifts from one habitat to another, migration, visual signaling, vocalization, courtship, copulation, and predation.

Niko Tinbergen (1907–1988) shaped many of our contemporary concepts of animal behavior. He posited that every behavior should be examined within the context of four questions: How does it develop? How is it physiologically controlled? What is its function? What is its evolutionary origin? [19] Our studies on habitat selection and reproductive behavior in gulls, flightless cormorants, harbor seals, and marine iguanas address the third and fourth of these questions. We study how weather, food supplies, and other environmental variables influence behaviors, and we make predictions about how those behaviors will change in response to changes in environmental parameters and in evolutionary time.

Significant variation in behavior among individuals often thwarts attempts to make predictions about things like population dynamics, habitat occupancies, and the spread of behaviorally driven diseases. An understanding of the dynamics of behavior, however, can be achieved through the application of mathematical modeling, a powerful set of tools that allows not only the perception of how behavioral systems work in the present but also the prediction of how they will function in the future. Since the beginning of our collaboration in 2001, our Seabird Ecology Team has been among the first to use dynamical systems-based models to successfully describe and predict the behavior of vertebrate animals in their natural habitats in response to environmental change. This book summarizes our research and highlights the techniques we used to achieve our goals.

Our research involves three main procedures:

- (1) The collection of large sets of temporally dense behavioral data on natural populations in the field
- (2) The construction of realistic mathematical models rigorously tied to data, which describe, explain, and predict behavioral dynamics in relation to environmental variables
- (3) The construction of simplified, proof-of-concept models to probe dynamic mechanisms, to suggest testable hypotheses, and to study the consequences of environmental change and evolving traits

Purpose and Structure of Book

Results from our work have been published in several dozen papers scattered among diverse mathematical and biological journals. This monograph assembles our main ideas, techniques, and data sets into a coherent whole. By assembling this information within a single volume, we hope to facilitate researchers who wish to apply our modeling approach to their own systems of study, whatever the species. As this volume reveals, we have successfully applied our approach to groups of non-avian reptiles, birds, and mammals, and it could be applied to any group of behaving organisms, from paramecia to humans.

This is not a textbook. Each chapter is self-contained, although we have endeavored to arrange the chapters within each section in a somewhat logical sequence of increasing complexity of techniques. This was not always possible because the same modeling technique might be applied to different organisms in successive chapters, with each chapter describing a unique data gathering process on which the model was predicated.

The book is organized into three parts. The first two parts are empirically based and connect models to data; the third part is theoretical but is motivated by the empirical studies in Part II. Topics are organized by the types of scientific questions being asked rather than by mathematical methods.

Part I deals only with the dynamics of aggregate animal behavior as it occurs locally in time and space, without following population dynamics across generations. We use various methods, including logistic regression, differential equations, and a hybrid of regression and differential equations, to model the behaviors of glaucous-winged gulls, harbor seals, marine iguanas, and flightless cormorants.

Part II focusses on two specific behaviors with major population and evolutionary import in gulls: egg cannibalism and the related adaptation consisting of egg-laying synchrony, which are documented with statistical methods involving logistic regression and discrete-time models of synchrony. These studies are presented as a package because they motivate Part III. Part II also contains a chapter on eagle-gull predator-prey dynamics, which employs a differential equation model of Lotka-Volterra type.

Part III is a step-wise theoretical investigation of the population and evolutionary consequences of cannibalism and reproductive synchrony from a bifurcation point of view

using discrete-time matrix models for structured populations. We first consider a simple but general two-dimensional discrete-time model of adult-on-juvenile cannibalism and use a Darwinian dynamic extension to consider whether cannibalism can be an evolutionarily stable strategy. We then add a second adult class to the model in order to consider the interplay between cannibalism and reproductive synchrony. A crucial scientific problem is how to model the population dynamic consequences of these behaviors when they occur on a time scale shorter than the generational time scale. We conclude Part III by addressing this issue with a general framework based on nonlinear Leslie models that contain two time scales—daily and yearly—in which reproductive and feeding behaviors occur on a daily basis whereas generations are tracked from year to year.

Data Collection

To capture the dynamic patterns of animal behavior, time-series data must be collected on a finer temporal scale than behavioral and environmental fluctuations. For the marine organisms we study, behaviors often are driven by tidal and diurnal patterns, and we have found that data collected hourly over complete 2-week tidal cycles work best. Depending on the project, we typically collect data at the top of each hour for 16 or 17 hours per day for several weeks. This kind of dense data collection requires either assistants or continuous video or sound recordings from which data are later transcribed.

We work with large aggregations of animals at seabird colonies, seal haul-out sites, and marine iguana haul-out sites. If the number of individuals is not too large, we count every individual in the study area; if the group is very large, we count only individuals within representative sample areas. If we are evaluating fluctuations in behavior, we determine the number of individuals exhibiting the behavior in proportion to the total number of individuals present.

There is no substitute for thorough, temporally dense, long-term observation of the biological system to be modeled. This is time intensive and can be logistically difficult, but it yields two opportunities that cannot be realized in any other way. First, a thorough observation of a system, day in and day out, week after week, year after year, affords a deep understanding of the system that sometimes bears little resemblance to studies based on short-term samples. This is the kind of understanding that allows a scientist to pose realistic models that can be tied rigorously to data. Second, long and temporally dense time series are exactly what are needed to parameterize continuous-time models.

Construction of Realistic Models

Historically, behavior dynamics have been modeled using Markov chain analysis, game theory, and individual-based models [4, 5, 15, 17]. In addition, ordinary differential equations (ODEs) with “motivational” dependent variables were developed in the 1970s as qualitative behavior models of individual animals [8, 14]. These qualitative models, however, were not tied rigorously to empirical data because motivational variables are not measurable [18].

Our research relies on an interdisciplinary paradigm derived from the interface between population ecology and dynamical systems theory [3]. Models designed to quantitatively describe and predict animal behavior in field populations serve as testable scientific hypotheses, with measurable dependent and independent variables operating on scales at which deterministic trends emerge from variability among individuals. We use compartmental models (difference equations and ODEs) in which each compartment represents a specific behavioral state at a specific spatial location, and in which the state variables track the numbers of individuals in each compartment [9]. Applying these models to any particular behavioral system requires specifying the flow rates between compartments by means of modeling assumptions. In general, these flow rates depend on environmental factors. They also can be functions of population densities and/or time, in which case the models are nonlinear and/or nonautonomous. If the system recovers rapidly after disturbance, ODEs can be reduced to algebraic models on two time scales: one for disturbance dynamics and one for steady state dynamics [12].

Dynamic patterns depend, of course, on scale [13]. A seabird colony, for instance, is a complicated place at the scale of the individual. Single birds appear quite autonomous and exhibit a wide variety of complicated behavioral choices; yet we have shown that some behaviors at the aggregate level are highly deterministic and can be predicted as a function of environmental variables. For example, gulls leave colony and loafing areas in large numbers to feed when the tide is going out and the sun is high, and they return with an incoming tide in the evening [7, 10]; harbor seals leave the beach and move into the water with rising tides because the incoming current brings in food [2, 6]; Galápagos marine iguanas move from land to feeding sites in the sea primarily in response to changing patterns of solar radiation [16]. Some behaviors are more deterministic than others, and it is possible to rank them according to the degree of determinism.

Some researchers feel that methods of modeling animal behavior at the aggregate level are too coarse and that modeling behavior must involve individual-based models. Although our approach is not the only way or always the best way to model animal behavior, our results show that ODEs and difference equations can indeed accurately predict the behavior dynamics of animal groups [9, 10, 11].

Model Parameterization

Estimating model parameters requires a stochastic version of the model that accounts for the noise structure [3]. For example, in many of the systems we have studied, stochastic perturbations are largely uncorrelated in the hourly sample times, and the stochastic model can be written

$$\varphi(N(\tau + 1)) = \varphi(G(\tau, N(\tau))) + E(\tau),$$

where $N = (N_1, N_2, \dots, N_m)$ is the vector of state variables, E is a vector from a multivariate normal random distribution with variance-covariance matrix $\Sigma = (\sigma_{ij})$, and $G(\tau, N(\tau))$ is the deterministic model prediction at hour $\tau + 1$ based on the state of the system at

hour τ . Here φ is a variance-stabilizing transformation; the transformations $\varphi(x) = \ln x$ and $\varphi(x) = \sqrt{x}$ render environmental and demographic stochasticity, respectively, approximately additive [3].

The one-step conditioned residual error vectors are

$$\rho(\tau + 1) = \varphi(n(\tau + 1)) - \varphi(G(\tau, n(\tau))),$$

where n is the vector of observations. The likelihood function, which measures the likelihood that the residuals arose from a joint normal distribution, is a function of the model parameters, and its maximizer is the vector of parameter estimates [3].

Alternative Models and Model Selection

If models serve as testable hypotheses, then we can pose alternative models as a means to test alternative hypotheses. Information theoretic methods of model selection, such as the Akaike Information Criterion (AIC), take into account both the value of the likelihood function and the number of parameters, so that models with more parameters are penalized for over-fitting. This criterion allows one to select the best model from a suite of alternatives [1].

Model Validation

A good model not only describes and explains, but also predicts. Validating a model means testing its predictability on an independent data set that was not used to estimate its parameters. One can validate a model by estimating parameters from a “calibration” data set and computing the goodness-of-fit of the fitted model on that data set, and then comparing that to the goodness-of-fit on an independent “validation” data set without re-estimating parameters. Goodness-of-fit can be computed with a generalized R^2 [3]. For example, when we modeled numbers of gulls loafing on a pier (Chap. 1), we obtained $R^2 = 0.58$ for the calibration data set and $R^2 = 0.61$ for the validation data set [10], which supported model validation. For our model of Galápagos marine iguana haulout (Chap. 3), $R^2 = 0.77$ for the calibration data set and $R^2 = 0.80$ for the validation data set [16], again supporting model validation. Close correspondence in goodness-of-fit between calibration and validation data sets, as in these cases, suggests that a model captures the major dynamics of a system.

The most convincing models are those that make unexpected, a priori predictions that are borne out by new experiments. Most seabird biologists, for example, would have predicted that during high tides gulls, which are intertidal feeders, should be loafing near the breeding colony and not away feeding. Our model predictions, however, counterintuitively suggested that during high tides occurring at midday, gulls should be away feeding—which is exactly what we observed [10].

Proof-of-Concept Models

In addition to models tied rigorously to data, we also construct and analyze “proof-of-concept” models. These are simplified models which focus on a small number of key mechanisms of interest. They are typically of low dimension (involve a small number of state variables) and are amenable to rigorous mathematical analysis. Our goal is to use such models to probe the dynamic consequences of the mechanisms under consideration, thereby not only suggesting hypotheses that can explain the observations we (and others) have made but also guide future observational protocols. In the process, these models also sharpen ideas and clarify definitions.

Given the nature of the phenomena we investigate, we often use discrete-time models (difference equations or maps) of structured populations. This methodology distinguishes different categories of individuals and focuses on interactions among them. The methodology is most appropriate when the stages have strongly discrete characteristics, such as juvenile and adult or larva-pupa-adult stages, and life history events occur at well-defined time intervals. A mathematical advantage of these discrete models is that unlike continuous-time structured models, they pose no difficult problems with regard to basic questions concerning the definition and existence of solutions and their numerical simulation, and the validity of basic analytic methods (such as linearization, bifurcations, etc.). The unit of time in our discrete models is generally determined by either a basic time scale in the modeled population (e.g., a maturation period) or the census time interval.

The predictions of a model, for example its equilibrium states and stability properties, are determined by the model coefficients or parameters which represent various vital rates (birth, survival, resource consumption, etc.). A significant change in a model prediction caused by a change in a model parameter is called a bifurcation. By “significant change” one typically means a change in the stability properties of an equilibrium (or some other attractor, such as a periodic state). A destabilization of equilibrium generally signals the creation of a new attractor. Such bifurcations can be of significant interest because the old and new attractors generally predict very different dynamic and long-term consequences for a population. For example, the most basic difference concerns survival versus extinction. Others include changes from equilibrium to cyclic fluctuations (crash and boom outbreaks) or other dramatic states such as chaos. The parameter values at which a bifurcation occurs is called a bifurcation point (or sometimes a tipping point).

One compelling reason we are interested in bifurcation points in our models is that the location of most of our field studies, Protection Island, Washington in the Salish Sea, is experiencing significant climate change (specifically, increased mean sea surface temperature in surrounding waters) which, in turn, effects certain vital rates of the populations we are modeling. Thus, climate change is represented in our models by a change in model parameters, which can cause bifurcations to occur. A basic question to ask of a model is, then, where are the bifurcation points that indicate a threat to the survival of the population? Which vital rates are involved and are most important? We can also inquire as to what counter changes in other parameters might mitigate the threat of extinction. We can use

a model to investigate whether observed behavioral changes in the population that highly correlate with climate change are likely to be adaptive in the long run. Using Darwinian dynamic (evolutionary game theory) modeling methodology, we also investigate conditions under which these adaptive changes can be attained by means of natural selection.

Conclusion

A burgeoning human population, propped up by synthetic fertilizers and energy from fossil fuels, is taking a decided toll on resource availability, climate, and biodiversity. Each of these ecosystem components plays a role in how animals and humans behave and thrive. There has never been a more opportune time for mathematicians and biologists to collaborate to create a better understanding of the behavior of animals—from the honeybees that pollinate our crops, to the birds that bring us pleasure but interfere with jet engines, to the vast herds of wildlife that provide esthetic enjoyment and crucial ecosystem services. We believe the techniques highlighted in the following chapters will play a positive role in the understanding and health of the animal components of our planet.

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Part I

**Modeling Behavior in Space and
Time**

The timing, spacing, and location of animal behaviors, along with transitions from one behavioral state to another, occupy the attention of biologists for both theoretical and practical reasons. Theoretically, information regarding these phenomena allows for interpretations concerning origin and function. Practically, this information can lead to better resource management, as well as to improved health and safety for humans with whom animals share Earth's resources.

The following six chapters describe how we applied principles of mathematical modeling and statistics toward a better understanding of the three groups of marine animals: birds, mammals, and non-avian reptiles. Previous attempts to relate mathematics to changes in behavior states in animals often have been purely theoretical, without direct connections to actual data. In contrast, we tie mathematical models of behavior directly to data obtained from free-living animals in their natural habitats.

Chapters 1–3 use differential equation models to test predictions concerning specific behaviors engaged in by groups of glaucous-winged gulls, harbor seals, and marine iguanas, respectively. Chapter 4 illustrates how techniques developed in the previous three chapters can be used to make predictions concerning systems of multiple behaviors. In Chap. 5 we use generalized linear models and multi-model inference to examine the responses of flightless cormorants to environmental variables. Chapter 6 applies logistic regression and Darwinian dynamics to explore how a behavior used for one function might evolve to perform an additional function.



Chapter 1

Predicting the Dynamics of Aggregate Loafing Behavior in Gulls

*Research reported in this chapter was the initial project carried out by the Seabird Ecology Team. It provided one of the first rigorous demonstrations that a differential equation model using environmental variables can be used to describe, explain, and accurately predict the aggregate behavior of marine vertebrates. It also served as the impetus and conceptual basis for much of the work in the remaining chapters of this volume. Hypothesis formation, data collection, and analysis were carried out by senior researchers Shandelle Henson, James Hayward, and Joseph Galusha, with the assistance of undergraduate students Christina Burden and Clara Logan. The initial report of this work was published in *The Auk* in 2004 [20].*

1.1 Introduction

Many animals enhance their fitness by moving selectively from habitat to habitat [5, 9, 22, 38], and habitat selection is a central concern of ecologists, evolutionary biologists, and resource managers [36]. Ecologists examine relations between habitat and an animal's morphology, physiological requirements, and behavior in an effort to understand the role of the animal in an ecological community; evolutionary biologists are concerned with these same variables, except that they are viewed in the context of fitness and adaptive processes; and resource managers attempt to identify and create optimal habitat features to provide attractive settings within which animals of interest can thrive and multiply.

In ecology, the analysis of spatial distribution patterns of organisms is an important subdiscipline [34]. Many studies of spatial distribution involve statistical or stochastic analyses, as well as regression models. Moreover, theoretical studies commonly incorporate deterministic dynamic models (e.g., continuous-time differential equations or discrete-time difference equations), although typically these models have not been tested in the field nor are they well connected to data. Ideally, deterministic mathematical models function as testable hypotheses. Statistical techniques connect models with data, and laboratory or field experiments test model predictions. This ideal set of circumstances is often difficult to achieve given a paucity of data, difficulty of experimentation, or mobility of research subjects [6, 7].

A major challenge in modeling ecological dynamics is the determination of scales at which the asynchronous behavior of individuals forms patterns and the identification of mechanisms leading to these patterns [22, 23, 30]. Quantum-level randomness in matter self-assembles into deterministic rules for the properties and behavior of larger objects. Similarly, although individual animals may move relatively independently due to individual differences and social interactions, patterns in habitat utilization may emerge for animal groups [30].

In [20] we constructed and tested a differential equation model for the prediction of numbers of animals occupying a single habitat in relation to environmental variables. We used glaucous-winged gulls (*Larus glaucescens*, Fig. 1.1) as our model organisms. Gulls are among the most widespread and thoroughly studied birds on the planet. They make excellent field study subjects because they are large, active during the day, and feed, nest, and “loaf” together in large aggregations [1, 11, 15, 28, 31, 33]. “Loaf” is a behavior category that refers to preening, defecating, standing, resting, sitting, or sleeping in nonfeeding and nonbreeding locations. Gulls typically favor loafing habitats with good visibility [5, 38], a propensity that often puts them at odds with human cleanliness, health, and safety [2, 32, 39].

Loafing behavior by gulls is correlated with tide height, most likely due to changes in food availability and/or time of day [10, 13, 26, 38]. Typically, the number of loafing gulls in a habitat rises with rising tides and decreases around midday. These correlations led us to pose four hypotheses upon which our mathematical model is based:

(H1) Numbers of loafing gulls fluctuate in direct response to an environmental variable $E(t)$, selected from the following set of alternative sub-hypotheses:

(H1A) $E(t)$ = tide height

(H1B) $E(t)$ = 1/solar elevation

(H1C) $E(t)$ = tide height/solar elevation

(H2) Numbers of loafing gulls during daytime can be described with a two-compartment model, with one compartment being the loafing area and the other compartment encompassing everywhere else.



Figure 1.1: Male (background) and female (foreground) glaucous-winged gulls on their breeding territory at Protection Island National Wildlife Refuge, Washington. Note the different head shapes of the two birds and the larger body size of the male (Photo by J. L. Hayward.)

(H3) Gulls enter the loafing site at a per capita rate proportional to $E(t)$ and exit the site at a per capita rate inversely proportional to $E(t)$.

(H4) The total number of gulls in the system is proportional to the weekly maximum number occupying the loafing site, which varies during the course of the year.

Hypotheses H1–H4 are biological hypotheses. They are also modeling assumptions which we converted into mathematical equations in order to test them with empirical data. In the following sections, we describe how to rigorously connect this mathematical model to hourly time series data for numbers of gulls at a loafing site where individual birds enter and leave the site asynchronously throughout the day. We show how we validated the model on an independent data set and then predicted future numbers of loafing gulls during each daylight hour for 29 consecutive days during the next nesting season.

1.2 Methods

Our study was carried out with glaucous-winged gulls loafing on a pier (Fig. 1.2) adjacent to a breeding colony at Protection Island National Wildlife Refuge ($48^{\circ}7'N$, $122^{\circ}55'W$) in the Salish Sea, Strait of Juan de Fuca, Washington, USA. During this study, the breeding colony contained more than 3,000 gulls.

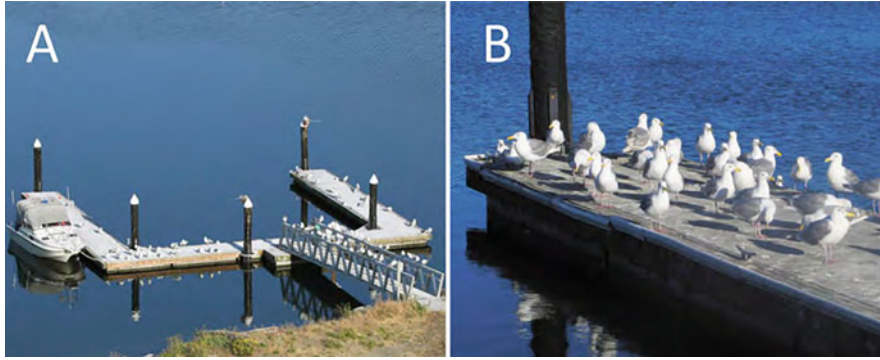


Figure 1.2: Glaucous-winged gulls used this pier in a small marina at Protection Island National Wildlife Refuge, Washington, for “loafing”. (a) Pier structure. (b) Close-up of gulls loafing on the pier (Photos by J. L. Hayward.)

For an initial application of mathematical modeling to this field system, we chose to restrict our study area to the pier, a well-defined site that was easy to census. The pier was located at the west side of a small marina closed to the public, with limited use by humans. It was used during most daylight hours for loafing by both breeding and nonbreeding gulls.

1.2.1 Historical Data

Counts of loafing gulls on the pier were made each hour, from 05:00 to 20:00 hours (LST, here and below), May to August 1997, 1998, 1999, and 2001. Hourly sampling allowed us to track tidal and diurnal periodicities [22]. Tides in the water surrounding Protection Island are semidiurnal with strong diurnal inequalities in the lows. Approximately every 14 days, tidal “nodes” with minimal amplitudes occur.

We partitioned the historical data using stratified random sampling by dividing each 14-day tidal period into approximately four quarters and, from each quarter, randomly selecting half the data for model calibration and the other half for independent model validation (Fig. 1.3).

1.2.2 A General Mathematical Model

At each point in time we classified individual gulls in the system into two compartments: those on the pier and those not on the pier. We used a rate balance equation,

$$\frac{dN}{dt} = [\text{inflow rate}] - [\text{outflow rate}],$$

to account for the net rate of change of the number of gulls on the pier as the inflow rate minus the outflow rate. Here $N(t)$ is the number of birds on the pier at time t , and t is the

day of the year, including the decimal fraction of the specific time of day. The inflow rate is the per capita flow rate to the pier multiplied by the number of gulls elsewhere in the system. The outflow rate is the per capita flow rate away from the pier times the number of gulls loafing on the pier. The mathematical model incorporating hypotheses H1–H4 is

$$\frac{dN}{dt} = \alpha E(t)(\beta K_p(t) - N) - \frac{1}{\alpha E(t)}N \quad (1.1)$$

$$0 < \alpha < \infty, \quad 1 \leq \beta \leq 80.$$

The expression $\beta K_p(t)$ is the total number of gulls in this two compartment system at time t , where $K_p(t)$ is an estimate of the maximal historical numbers of gulls at the pier throughout the year (hypothesis H4). The difference $\beta K_p(t) - N(t)$ is the number of birds elsewhere in the system at time t . The proportionality constants $\alpha, \beta > 0$ are parameters to be estimated from the historical data. The maximal number of gulls nesting in the adjacent breeding colony was approximately 60 times the maximal value of $K_p(t)$, so we chose 80 as an ample upper bound for β . Similar compartmental models have been used for waterfowl [29].

We estimated $K_p(t)$ from historical data sampled from January 1 to March 21 and May 23 to December 31, 1997–1999 and 2001 [19]. Using these data we estimated seasonal maxima for the fluctuating pier counts by fitting a modified lognormal curve through the averages, for each week of the year, of the maximal pier counts (Fig. 1.4):

$$K_p(t) = 76.36 \exp \left[\frac{[\ln(40.29 - t/7) - 2.504]^2}{-0.7225} \right].$$

After October 2 and before March 6, the average maximal pier counts were zeros or ones, so we set $K_p(t) = 0$ for those intervals (Fig. 1.4).

We numerically integrated the differential equation model (1.1) using tidal and solar data obtained from the National Oceanic and Atmospheric Administration (NOAA) as described below.

1.2.3 Alternative Models

We normalized hourly tide data as follows: We first subtracted the minimal tide value from each tide height in order to set the minimum equal to zero, then divided each by the resulting maximum to set the new maximum equal to one, and finally added one to the quotient so that the result was between one and two:

$$T(t) = \frac{\text{tide} - \min(\text{tide})}{\max(\text{tide} - \min(\text{tide}))} + 1.$$

This resulted in a nondimensional tide height function with $1 \leq T(t) \leq 2$. For solar elevation, we set negative elevations to zero and then normalized solar elevation data as

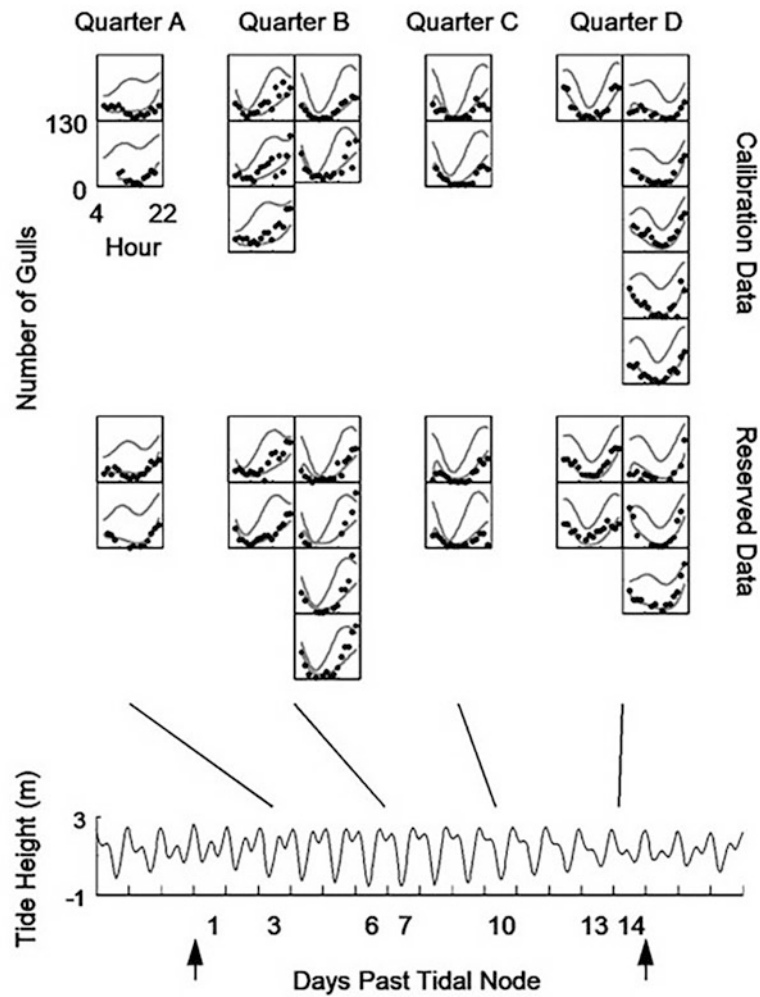


Figure 1.3: Tidal-solar model prediction (lower curve), historical data (circles), and tidal curve (upper curve). Each panel corresponds to 1 day. Tide height is graphed on a vertical scale of -1 to 3 m. Initial condition for each day's model prediction was taken to be the first data point collected that day. A typical tidal sequence for Protection Island is shown at the bottom; tidal nodes are indicated with arrows. Data from days occurring during the same quarter of the tidal sequence are stacked vertically. Data in a given column show similar diurnal patterns. Conditioned least-squares (CLS) parameters were estimated from the “calibration data.” The “reserved data” were used to independently validate model performance without re-estimated parameters. The CLS parameter estimates appear in Table 1.1. Following are dates for days in each of the six columns, left to right, top to bottom: first column, July 21, 1999; August 18, 1999; July 7, 1999; August 4, 1999; second column, July 2, 1997; July 16, 1997; August 13, 1997; July 30, 1997; August 5, 1998;