

# The Mathematics of Animal Behavior: An Interdisciplinary Dialogue

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**M**athematical ecology has attracted a vibrant community of applied mathematicians. Collaborations with biologists are encouraged, and a variety of nonlinear phenomena have been modeled successfully in several laboratory systems [7]. Examples of “hard science” conducted with mathematical models of field populations and ecosystems are still rather uncommon, however, in part because appropriate data sets are hard to obtain. (By “hard science”, we mean a full integration of mathematical models into the scientific method. Models serve as testable hypotheses, providing quantitative descriptions and predictions.) Lacking examples of a rigorous connection between models and data, many biologists remain skeptical that mathematics is a powerful scientific tool in ecology. Certainly the exercise of modeling is useful in its own right—models help clarify definitions and assumptions, illuminate key concepts, and suggest hypotheses—but, in general, ecologists and their students do not become immersed in the problem of doing science with mathematics.

Ecologists of the near future will require mathematical tools. The weight of scientific opinion is that human activity is changing our world at a scale and pace that may lead to irreversible bifurcations in ecological and social systems within this century. Accelerating crises associated with climate change may stimulate increased funding in science, technology, engineering, and mathematics,

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providing significant interdisciplinary opportunities and challenges. There is, however, a cultural separation between mathematics and biology that must be closed if interdisciplinary teams of applied mathematicians and scientists are to make significant advances in understanding the dynamics and tipping points of changing social and ecological systems.

One of us trained as an applied mathematician (SH) and the other as a behavioral ecologist (JH). During eight years of collaborative effort, we have used mathematical models to study the behavior of marine birds and mammals. We have been pleased to find that significant opportunities exist within our research program for training undergraduate and graduate students, and we hope our scientific and educational work will help to close the gap between mathematics and biology.

## **Mathematics and Biology**

**SH:** During a postdoc at the University of Arizona, I studied the applications of bifurcation theory to population biology with the NSF-supported “Beetle Team”,<sup>1</sup> a group of mathematicians, biologists, and statisticians who had set out to test nonlinear theory in laboratory populations of insects. I participated, first with intense skepticism and then with growing surprise, in the documentation of a wide array of nonlinear phenomena—equilibria, cycles, bifurcations, multiple attractors, resonance, basins of attraction, saddle influences, stable and unstable manifolds, transient phenomena, lattice effects, and chaos [3, 4, 6, 11, 17]. The models worked: it was like doing physics, except in biology.

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<sup>1</sup>The original Beetle Team consisted of R. F. Costantino, J. M. Cushing, Brian Dennis, and R. A. Desharnais. Shandelle M. Henson and A. A. King joined later.

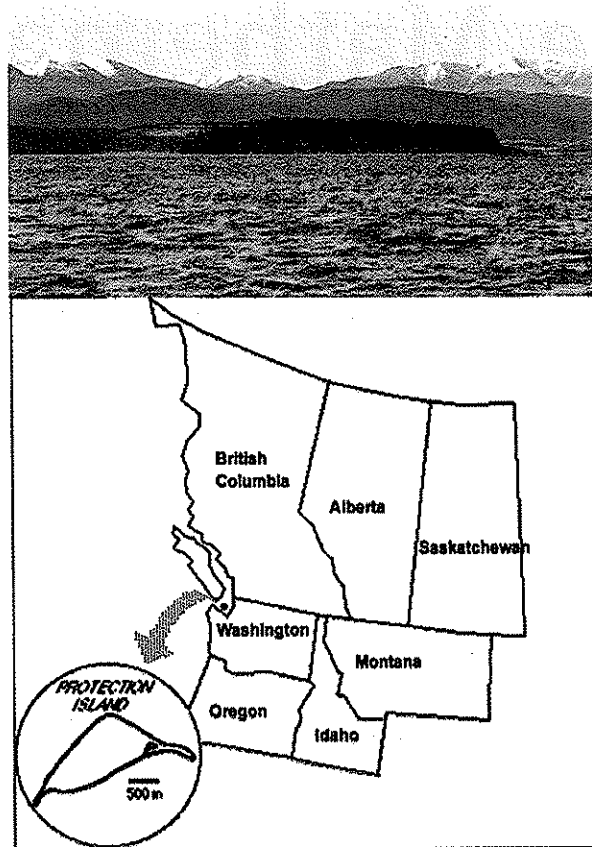
I became convinced that mathematical models can describe, explain, and predict dynamics in ecology just as they do in other branches of science. When I arrived at Andrews University in 2001, I met field ecologist Jim Hayward, and we began applying dynamical systems theory to field data on animal behavior.

**JH:** Early in my professional career, in 1987, ethologist Joe Galusha asked me to join him doing research on a large glaucous-winged gull (*Larus glaucescens*) colony at Protection Island National Wildlife Refuge in the Strait of Juan de Fuca, Washington (Figures 1, 2). Ethology is the study of animal behavior in the natural habitat, and gulls are important animal models in ethology and behavioral ecology. Since then I have spent much of each summer on Protection Island collecting data. Although most behavioral ecologists sample with a view toward statistical analysis, I often have collected long, temporally dense time series because I wanted to understand dynamics. My colleagues were amused; one joked, "Don't you know how to sample?" By the time I met Shandelle, I had many long time series but no satisfactory way to analyze them statistically.

**SH:** Jim's colleagues may have found his methods of data collection excessive, but I was delighted. The long time series were just right for parameterizing dynamic models. We pulled together the interdisciplinary "Seabird Ecology Team",<sup>2</sup> applied for a grant from the National Science Foundation, and set out to try to replicate some of the laboratory successes of the Beetle Team in the field.

**JH:** As a first step in our collaboration, I wanted to model the number of glaucous-winged gulls "loafing" on a pier adjacent to the breeding colony (Figure 3A). Loafing in birds is a general state of immobility involving behaviors such as sleeping, sitting, standing, resting, preening, and defecating. Loafing is of practical importance because it often conflicts with human interests. Gull feces contain landfill contaminants, erode roofing materials, spread *Salmonella*, and foul buildings, boats, and piers. Gulls often loaf on airport runways, from which they fly up and collide with aircraft. Such "bird strikes" result in expensive repairs and loss of human life. An ability to predict the incidence of loafing with a mathematical model would provide a first step toward the amelioration of bird/human conflicts. The first time Shandelle and I discussed the problem, she asked me to name the most important variables influencing the dynamics of loafing in these gulls. I started listing everything that I thought was important, but she cut me off and insisted that I name only the *two* most important variables. I argued vigorously against

<sup>2</sup>James L. Hayward, Shandelle M. Henson, Joseph G. Galusha, and J. M. Cushing: <http://www.andrews.edu/~henson/seabird/>.



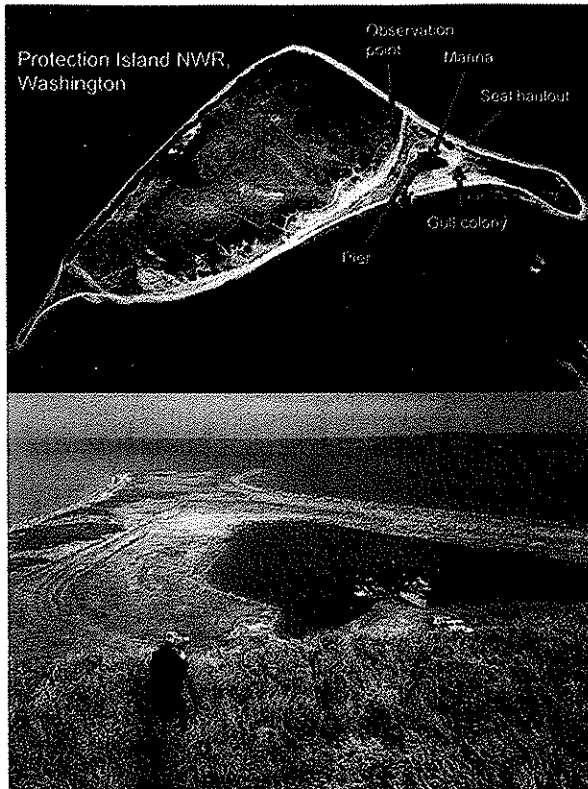
**Figure 1.** Protection Island National Wildlife Refuge lies at the southeast end of the Strait of Juan de Fuca, Washington. Approximately 70 percent of the breeding seabirds in Washington's inland seaways nest here. The refuge is closed to the public.

this but finally named tide height and time of day. I didn't think it was possible that a model based on such limited information could describe or predict the dynamics.

**SH:** In fact, the model based on these two variables didn't quite work, and Jim insisted that we had to include the day of the year. We did so and got a beautiful correspondence between model and data [12]. One should begin with a simple model and add complications only as necessary.

**JH:** We parameterized and validated the model on historical data and then made predictions for the next field season. We took two undergraduate students to Protection Island, and the four of us collected hourly data seventeen hours a day for twenty-nine consecutive days. The correspondence between the *a priori* model predictions and actual fluctuations was remarkable [12] (Figure 3B-D).

**SH:** In a subsequent study [9] we tested the portability of the loafing model. On Protection



**Figure 2.** Protection Island consists of a tall grass prairie on a high plateau bordered by 30m bluffs. The island is in the rainshadow of the Olympic Mountains and receives little precipitation. Violet Point, a gravel spit extending to the southeast, contains a breeding colony of more than 2,400 pairs of nesting glaucous-winged gulls.

Island, the model was portable across years, local loafing location, and phase of the breeding cycle, explaining up to 81% of the variability in hourly census data ( $R^2 = 0.81$ ). With lower sample sizes and more windy conditions on Appledore Island, Maine, the same model structure (but with different environmental variables) explained 48% of the variability in hourly census data of herring and great black-backed gulls (*L. argentatus* and *L. marinus*) loafing on rooftops.

**JH:** An  $R^2$  value of 0.48 may not sound very good to a physicist or laboratory biologist, but it is a fairly strong signal for ecological field data. It means there are definite patterns that can be recognized and predicted.

### Differential Equation Models of Animal Behavior

**JH:** Game theory, Markov chains, and individual-based models have been the most common approaches to modeling animal behavior. In the 1970s, ODE models with "motivational" dependent

variables were developed for the behavior of individuals in the context of control theory [10, 20]. The ODEs were not tied rigorously to data because "motivation" is not well defined and cannot be measured, and many so-called "fixed action patterns" are variable rather than rigidly preprogrammed as once thought. During the last eight years our team has reexamined ODEs as models of animal behavior and proposed a general methodology for the quantitative prediction of animal behavior in field populations [15]. Our models are more than theoretical constructs—they are scientific hypotheses tied to and tested with actual field data.

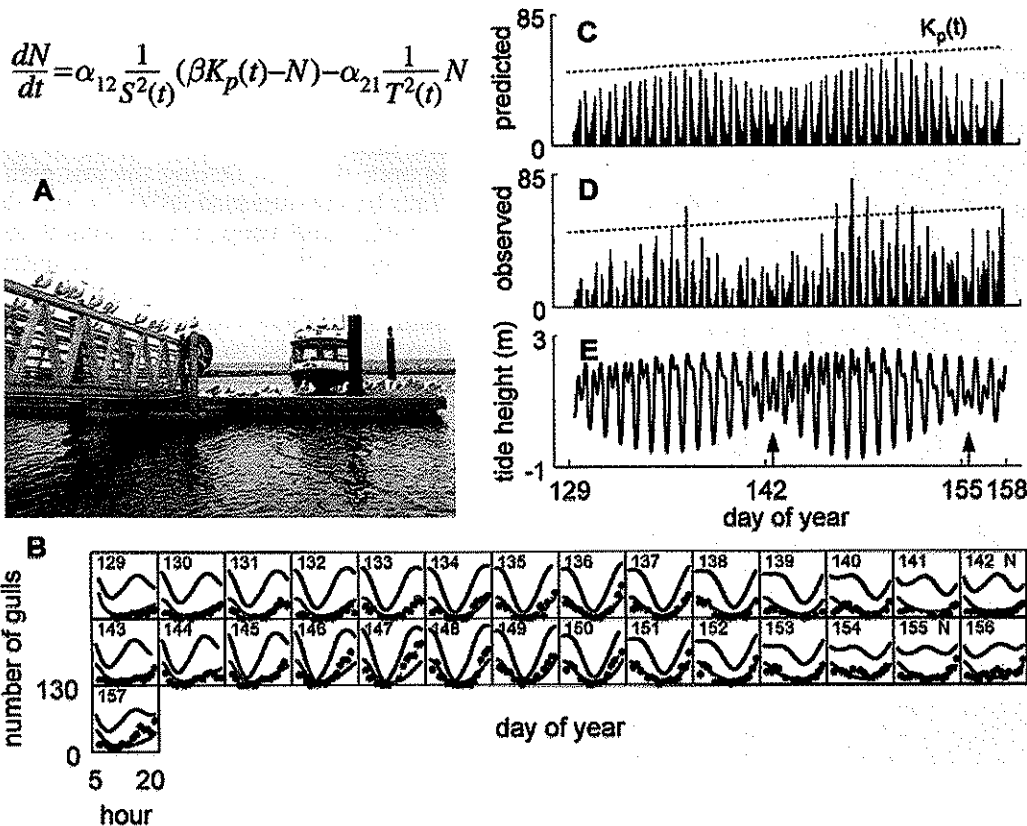
**SH:** We use compartmental ODEs in which each compartment represents a specific behavioral state (perhaps at a specific spatial location) and the state variables track the numbers of individuals in each compartment. For example, to model  $b$  behaviors occurring in  $h$  habitats requires at most  $m = bh$  compartments. If  $\mathbf{N} = \langle n_1, n_2, \dots, n_m \rangle^T$  is the vector of numbers of animals in each compartment,  $\mathbf{M} = (f_{ij})$  is the matrix of numbers of animals  $f_{ij} = f_{ij}(t, \mathbf{N})$  in compartment  $j$  that are eligible to move to compartment  $i$ , and  $\mathbf{R} = (r_{ij})$  is the matrix of per capita rates  $r_{ij} = r_{ij}(t, \mathbf{N})$  at which eligible individuals move from compartment  $j$  to compartment  $i$ , then the ODE balance equation is

$$(1) \quad \frac{d\mathbf{N}}{dt} = \text{diag}(\mathbf{R}\mathbf{M}^T - \mathbf{R}^T\mathbf{M}),$$

where the symbols  $^T$  and  $\text{diag}$  denote the matrix transpose and diagonal vector, respectively, and where we define  $f_{ii} = r_{ii} = 0$  for each  $i \in \{1, 2, \dots, m\}$  [15]. The ODE for the  $i$ th compartment in model (1) is the sum of its inflow rates minus the sum of its outflow rates. Since birth and death processes are not included, the total population size  $K$  remains constant, and we can reduce the dimension by writing  $n_m = K - \sum_{i=1}^{m-1} n_i$ . Model (1) is in general nonautonomous and nonlinear. Application to a particular system requires specifying the functions  $f_{ij} = f_{ij}(t, \mathbf{N})$  and  $r_{ij} = r_{ij}(t, \mathbf{N})$  by means of modeling assumptions and/or model selection techniques.

### Data Collection

**JH:** The use of models such as (1) as testable hypotheses requires rigorous connection to data, which in turn requires the right kinds of data. In order to capture the dynamic patterns of animal behavior and other ecological processes, the researcher must collect data on an appropriate time scale, one with a finer mesh than the scale of the behavioral or environmental fluctuations themselves. To model the diurnal behaviors of aggregates of marine birds and mammals, for example, we commonly collect hourly data for sixteen or seventeen hours each day for several



**Figure 3.** The loading model depends on the (nondimensionalized and scaled) tide height  $T(t)$ , solar elevation  $S(t)$ , and a seasonal envelope  $K_p(t)$  that depends on day of year. **A.** Gulls loading on the pier. **B.** Model prediction (red), data from spring 2002 (circles), and tide height (blue). Each daily panel is identified with the day of the year. Each row of 14 panels corresponds to one 2-week tidal cycle. Tidal nodes (N) occur on or near days 142 and 155. Each column of panels contains similar patterns in data. **C.** Model predictions for the spring of 2002. Oscillations are present on daily, biweekly, and yearly time scales. The dotted curve is the yearly envelope oscillation  $K_p(t)$ . **D.** Data observations corresponding to the predictions in **C.** **E.** Tidal oscillation for the data collection time period in 2002. The tidal nodes are indicated with arrows.

weeks at a time, since the aggregate dynamics and environmental conditions do not change much during one hour. Student research assistants make such dense data collection possible. Furthermore, it is best to collect enough data so that some can be set aside for the purposes of model validation. Animal behavior is an excellent candidate for rigorous dynamic modeling. Obviously it could take months or years to collect long time series at the population level. For example, the generation time of the flour beetle *Tribolium castaneum* studied by the Beetle Team is about four weeks, and the chaotic *Tribolium* time series reported in *Science* spanned eighty weeks [2].<sup>3</sup> To collect an analogous data set for a

population of glaucous-winged gulls (generation time about four years) would require eighty years.

### Connecting Models to Data

**SH:** Parameterization requires a stochastic version of the model that properly accounts for the noise structure of the particular system. For example, in the systems we discuss in this article, stochastic perturbations are largely uncorrelated in hourly sample times. We take stroboscopic snapshots

$$(2) \quad N_{\tau+1} = F(\tau, N_{\tau})$$

of the continuous-time system at the hourly sample times  $\tau = 0, 1, 2, \dots$ , where  $N_{\tau} = N(\tau)$  and

$$(3) \quad F(\tau, N_{\tau}) = N_{\tau} + \int_{\tau}^{\tau+1} \text{diag}(\mathbf{R}\mathbf{M}^T - \mathbf{R}^T\mathbf{M}) dt.$$

The stochastic model is

$$(4) \quad \phi(N_{\tau+1}) = \phi(F(\tau, N_{\tau})) + E_{\tau}.$$

<sup>3</sup>Experimental/mathematical ecologist Bob Costantino continued the study for nearly eight years (ninety-seven generations), producing one of the longest population time series in ecology.

Here  $\phi$  is a variance-stabilizing transformation that renders noise approximately additive on the  $\phi$ -scale, and  $E_\tau$  is a vector from a multivariate normal random distribution with variance-covariance matrix  $\Sigma$ .

Given an observed sequence  $\{n_\tau\}_{\tau=0}^q$  of data vectors, the "conditioned one-step" model prediction for the next observation at time  $\tau + 1$  is  $N_{\tau+1} = F(\tau, n_\tau)$ . The (transformed) residual error is

$$(5) \quad \phi(n_{\tau+1}) - \phi(N_{\tau+1}) = \phi(n_{\tau+1}) - \phi(F(\tau, n_\tau)).$$

Model (4) assumes the residuals come from a joint normal distribution and are uncorrelated in sample time. The likelihood that the residuals arose from such a distribution can be expressed as a function of the model parameters. The maximizer of the likelihood function is the vector of parameter estimates [4].

Two main sources of noise in ecological systems are "demographic" and "environmental". Demographic stochasticity is experienced independently by single individuals or small subsets of individuals, whereas environmental stochasticity is experienced by all individuals in a population [4]. Noise in a given system can be primarily demographic, primarily environmental, or a mixture of the two. The transformations  $\phi(x) = \ln x$  and  $\phi(x) = \sqrt{x}$  render environmental and demographic noise, respectively, approximately additive [4]. Another transformation,  $\phi(x, \psi)$ , constructed by statistician Brian Dennis and dynamicist J. M. Cushing, parses out the relative effects of environmental and demographic noise through the estimation of a parameter  $\psi \in (0, 1]$  that yields  $\phi(x, 1) = \ln x$  and  $\lim_{\psi \rightarrow 0^+} \phi(x, \psi) = \sqrt{x}$  [15].

### Model Validation

**JH:** A good model not only describes and explains, but also predicts; otherwise modeling is merely a curve-fitting exercise. Model validation is about testing model predictability on a data set not used to estimate the parameters.

**SH:** One way to validate a model is to randomly divide a data set into "estimation data" and "validation data". First, estimate the model parameters using the estimation data. The goodness-of-fit (to the estimation data) can be computed with a generalized  $R^2$

$$(6) \quad R^2 = 1 - \frac{\sum_{\tau=1}^q (\phi(n_\tau) - \phi(N_\tau))^2}{\sum_{\tau=1}^q (\phi(n_\tau) - \bar{\phi}(n))^2}$$

where  $n_\tau$  and  $N_\tau$  are, respectively, the observed and predicted values at time  $\tau$  and  $\bar{\phi}(n)$  is the sample mean of the transformed observations [4]. Second, compute the goodness-of-fit for the validation data without reestimating parameters and compare this with the goodness-of-fit for the estimation data.

**JH:** The most convincing models are those further tested by making *a priori* predictions that are then borne out by new experiments. Unexpected predictions are ideal opportunities for testing a model. For example, the loafing model predicted, successfully, that the lowest numbers of gulls would occur at high tide on days corresponding to tidal nodes (Figure 3B, days 142 and 155). This is contrary to previously published assertions, based on data averaging, that the lowest numbers occur near low tide. While it is true that gulls tend to be away foraging at low tide, it is also true that gulls tend to return to loafing sites in the morning and evening. In the previous studies, data averaging masked the effect of time of day, whereas the modeling approach made it possible to predict low loafing numbers at high tides that occurred in the middle of the day.

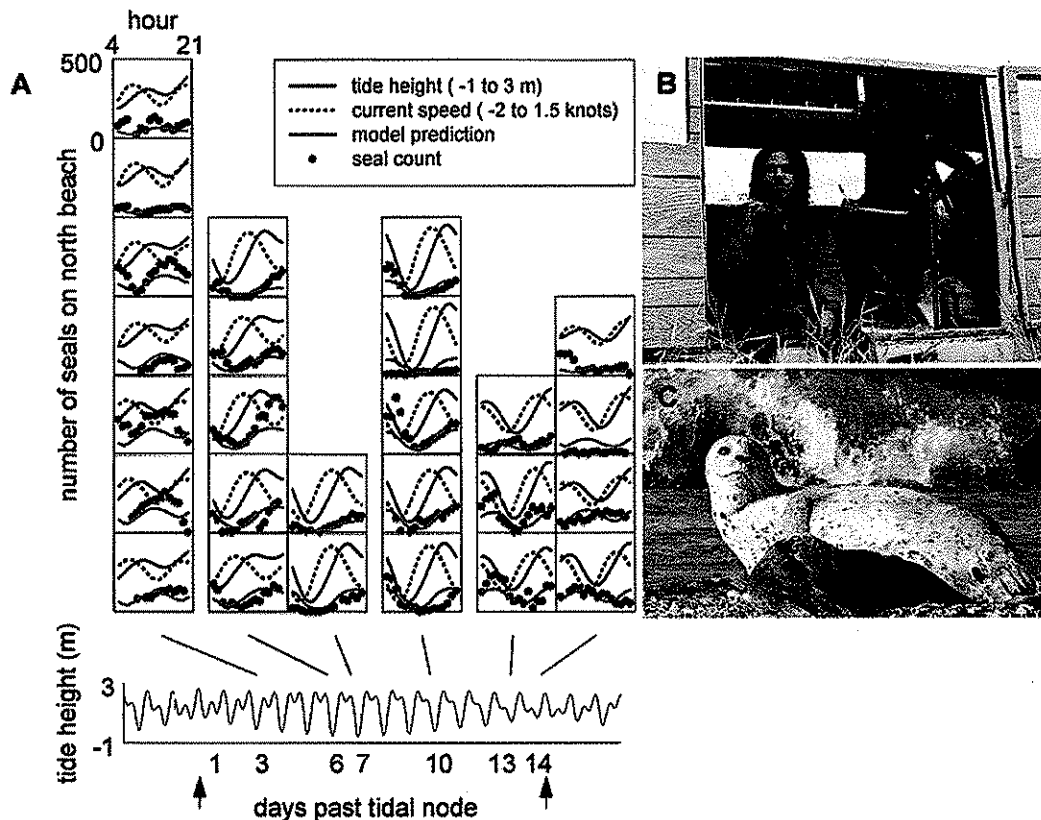
### Model Selection

**SH:** If mathematical models are to serve as testable hypotheses, there must be a way to test *alternative* hypotheses. Information theoretic methods such as the Akaike information criterion (AIC) are ideally suited for choosing the best model from a suite of alternatives [1]. The AIC takes into account both the value of the likelihood function and the number of parameters, penalizing models for overfitting:

$$(7) \quad \text{AIC} = -2 \ln L + 2\kappa,$$

where  $L$  is the likelihood value for the (fitted) model and  $\kappa$  is the number of model parameters (including the variance of the likelihood function as estimated from the residuals) [1]. Model comparison is based on the rank of AIC values for each model, with the smallest AIC indicating the best model.

**JH:** We used information theoretic model selection techniques to determine the environmental drivers of harbor seal (*Phoca vitulina*) haulout during the pupping season on Protection Island [8] (Figure 4C). Seals "haul out" on the beaches of Protection Island by the hundreds, where they remain safe from killer whales, rest from feeding, and give birth to offspring. Harbor seal numbers are monitored closely by governmental authorities in both Europe and North America, and optimal census times occur when they are hauled out. A list of alternative hypotheses for environmental haulout cues gave rise to a suite of twenty-three alternative models. The best model (with lowest AIC) was a function of tide height and direction of the current and explained 40% of the variability in hourly census data ( $R^2 = 40$ ; Figure 4A). The model showed that, at this pupping site, managers can expect maximal daily haulouts to occur during receding tides, approximately midway between high and low tides. This may be because food availability is lowest when the current is strongest during receding tides and peaks during the maximal current during incoming tides, which corresponds with



**Figure 4. Seal haulout dynamics. A. Model prediction (red), seal haulout data (circles), tidal curve (blue solid curve), and current velocity (blue dashed curve). Each panel corresponds to one day. A typical 14-day tidal period for Protection Island is shown at the bottom; tidal nodes are indicated with arrows. B. Students Michael Scott and Brianna Payne collect data from the blind at the observation point. C. Harbor seal (*Phoca vitulina*) with pup.**

low haulout numbers. The modeling procedure should be carried out separately for each haulout location, because tides and currents depend on the geometry of local river discharges, basin shapes, and coastal geometries.

### Behavior on Multiple Time Scales

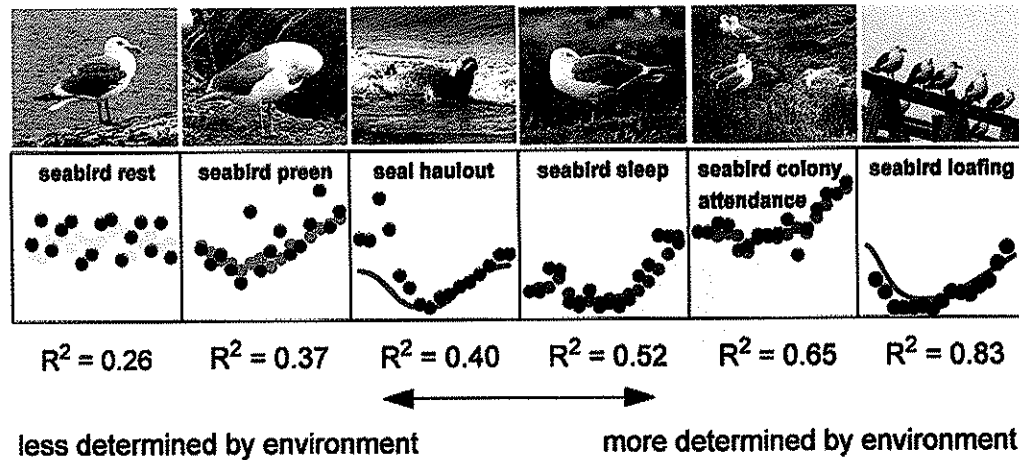
**JH:** Animals experience life on multiple time scales much like a combat platoon: long periods of boredom punctuated by short periods of terror. Some behaviors recover rather quickly from “point disturbances”; aggregates of loafing gulls, for example, reassemble within about five to fifteen minutes after a bald eagle flyover.

**SH:** In such systems, we can use multiple time scale analysis to reduce the differential equations to algebraic equations by assuming the environmental drivers are essentially constant during system recovery. The time scale is changed to  $\tau = t/\varepsilon$ , where  $\varepsilon > 0$  is a small parameter related to the recovery time. Differentiation of the state variables with respect to  $\tau$  introduces an  $\varepsilon$  in front of the derivatives with respect to  $t$ ; the latter can

then be set to zero to obtain an approximation to the steady state dynamics [13].

**JH:** The reduced models are much easier for wildlife managers to use than the original differential equations. But there is loss of information, because the same steady state dynamics could be maintained by more than one set of parameters and environmental drivers; that is, the inverse problem is not well defined. For example, a room with two people per hour entering and two per hour leaving can have the same steady state as a room with ten people per hour entering and ten per hour leaving.

**SH:** In one study we showed how data collected during system recovery can be used to identify uniquely the parameters and environmental drivers of the steady state dynamics [13]. We tested the theoretical results by creating “point disturbances” for loafing gulls. From the observation point (Figure 2), I videotaped the pier as Jim walked on, dispersed the loafing gulls, and walked back off. From the videos, we recorded each time during the recovery at which a bird arrived at or departed



**Figure 5.** Some animal behaviors are highly determined by abiotic environmental variables; others are influenced relatively little. Model predictions are in color; observations are black circles. The  $R^2$  value can be interpreted as the proportion of variability in the data that is explained by abiotic environmental variables.

from the pier. These data were then used to construct “recovery time series” for the numbers of birds on the pier at each minute for five minutes following the disturbances. To these data we fitted alternative versions of the fast time scale model, in which various environmental drivers were posed for system inflow and outflow rates. Using the AIC to identify the best model, we were able to infer that, in the absence of disturbance, birds on the pier leave when the tide is low, whereas those away from the pier return when the sun is low (Figure 3, differential equation). The experiments demonstrated how short bursts of very dense data collection (during disturbances) coupled with periods of less dense data collection can make the inverse problem well defined.

### Determinism and Scale

**JH:** A gull colony is a busy and complicated place. Individual birds appear quite autonomous. They have a wide range of complex behaviors, and they come and go asynchronously in a heterogeneous system of habitat patches adjacent to the nesting colony. It is fascinating that systems of differential equations can predict their movement and behaviors [5, 14, 15, 21]. Even though individual animals make independent choices, a clear deterministic signal can exist at the aggregate level [18].

**SH:** A few colleagues have protested that animal behavior must be modeled with individual-based models, that ODEs are too coarse to predict animal behavior because they lump individuals into aggregates under simplifying assumptions. Certainly we are not suggesting that ODEs are the only way, or always the best way, to model animal behavior. But our work makes it clear that individual-based

models are not always necessary to study the dynamics of aggregates. You wouldn’t use quantum models to study the classical dynamics of a falling apple. Similarly, you don’t always need to use a collection of individual-based simulations to study the mean-field dynamics of an aggregate.

**JH:** One interesting outcome of our work is the ranking of behaviors by the degree to which they are determined by the abiotic environment (Figure 5). For example, in glaucous-winged gulls, the incidence of territory attendance, sleep, and preening can be predicted to a large extent by knowing the tide height, hour of the day, solar elevation, ambient temperature, humidity, and wind speed [14, 15] (Figure 6). Territory attendance is highly determined by the environment, sleep somewhat less so, and preening still less so (Figure 5).

### Ongoing Work: Oscillator Synchrony

**JH:** After four years of collecting reproductive success data, we recently documented an exciting nonlinear dynamic on the gull colony: the synchronization of egg-laying. Female glaucous-winged gulls typically lay three eggs total, at two-day intervals. We have shown that birds within sufficiently large social groups in sufficiently dense areas of the colony lay eggs synchronously on an every-other-day schedule [16]. This is similar to the phenomenon of menstrual synchrony in women [19, 22].

**SH:** We are using a discrete-time dynamic model to pose the hypothesis that preovulatory luteinizing hormone surges synchronize through social stimulation (Figure 7A). Model analysis has yielded two or three mathematical papers currently

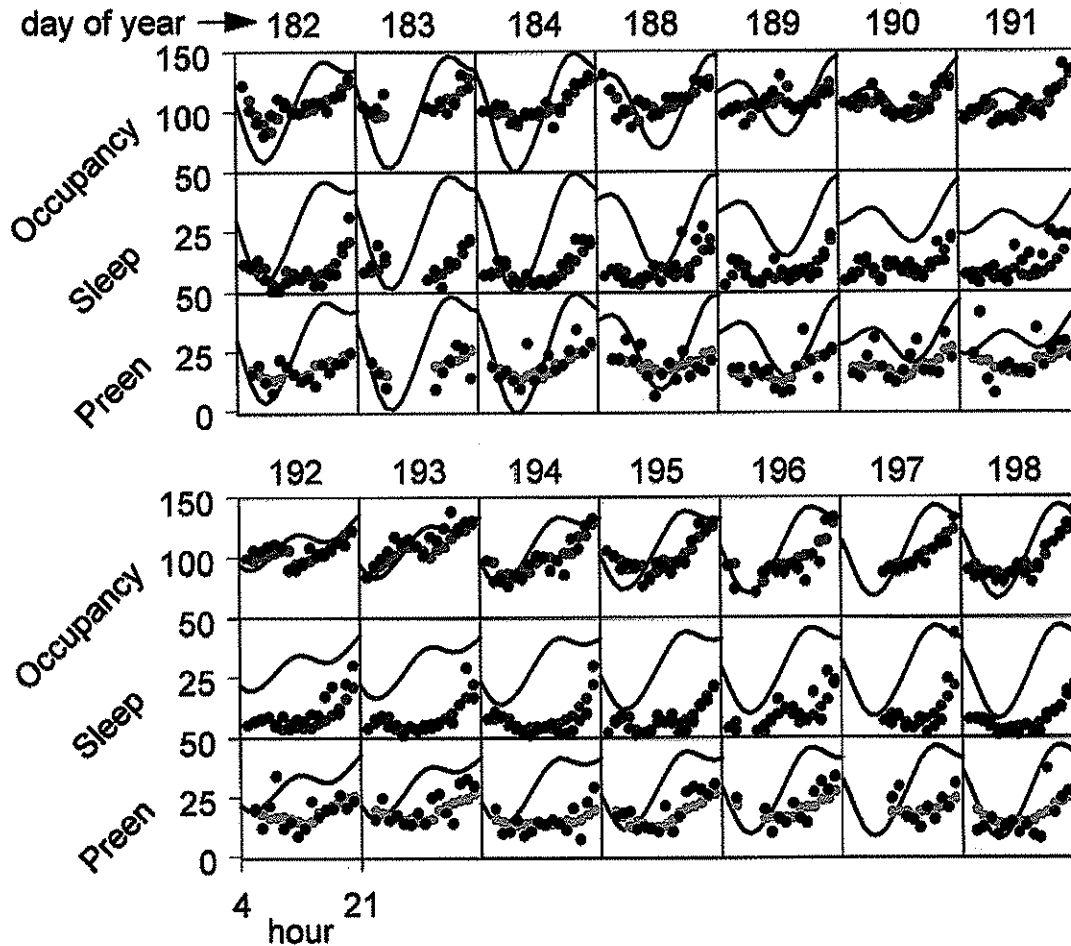
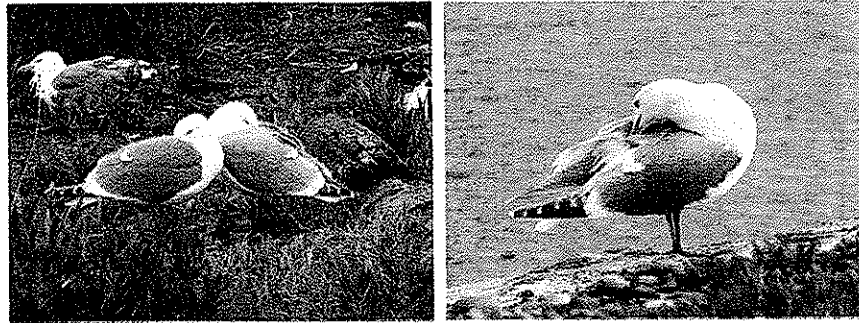


Figure 6. Colony occupancy, numbers of birds asleep in the colony, and numbers of birds preening in the colony. Each panel corresponds to one day. One-step model predictions are shown in red, magenta, and green; observations are shown as black circles; tide height is in blue. Model predictions are from a system of three coupled differential equations.

in progress, and I look forward to exploring this class of models more fully with the team.

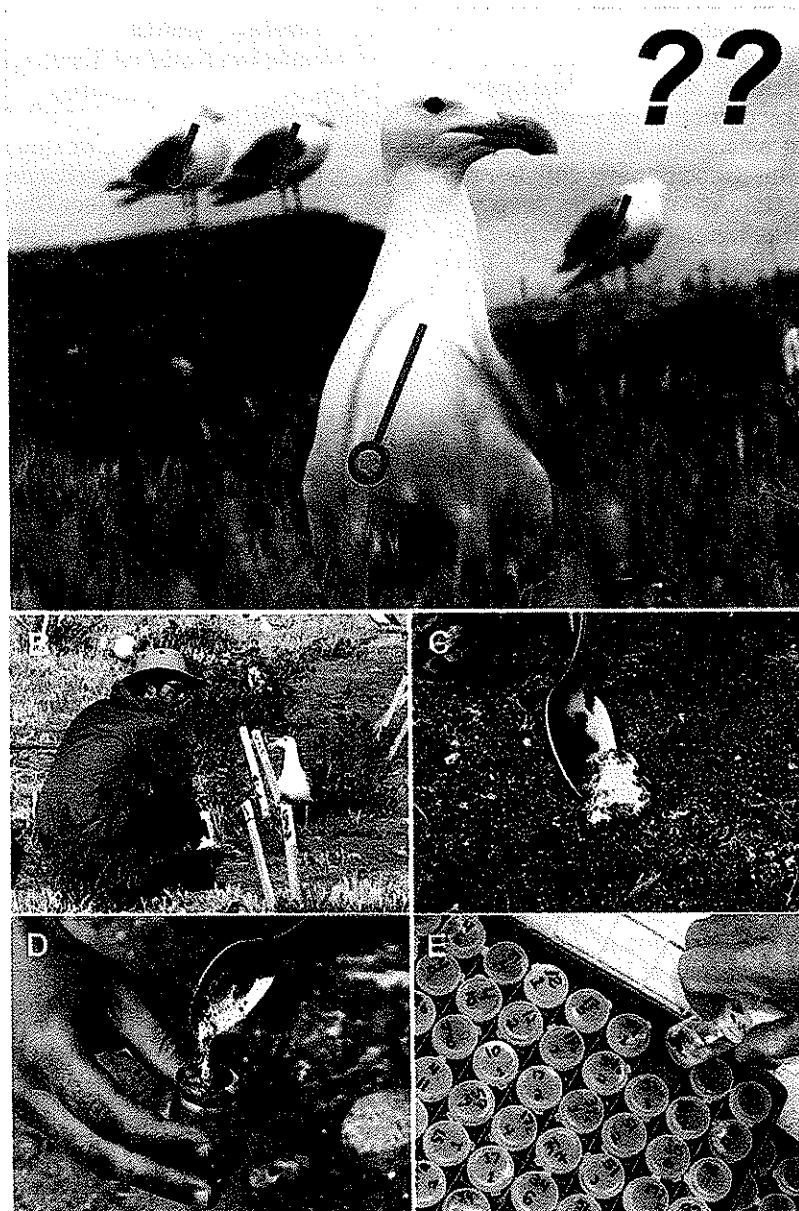
**JH:** The field work involved in testing the hypothesis noninvasively will keep our team busy for several years to come. It involves collecting gull droppings from particular territories and analyzing them for hormone metabolites (Figure 7B-E). We carried out pilot studies during the 2009 field

season and now have results upon which to base our work over the next several seasons.

#### Recommendations for Mathematicians

**JH:** Biologists and biology students may be timid about approaching mathematicians, whom they may perceive as rigid and detached from the "real world". I recommend that mathematicians





**Figure 7. Synchrony in every-other-day egg-laying. A. We hypothesize that each female acts as an oscillator with an every-other-day surge of luteinizing hormone and that dense collections of oscillators synchronize. B. Student André Moncrieff waits patiently for a gull to produce a sample. C-E. The dropping is collected and placed in a portable freezer that runs on solar panels.**

drop in to visit biologists in their offices, attend their seminars, and ask good questions. Offer suggestions as to how mathematics might benefit their research projects. Relate your symbols and equations to the biology through words and diagrams. Explain that mathematical models are hypotheses to be tested. Biology students have had the “scientific method” drilled into them since high school, but most never understand how that “method” can incorporate a mathematical equation (except in the form of statistical analysis).

**SH:** As a research mathematician, don’t be afraid to be a beginner. Immerse yourself in the intricacies of the biological problem. Spend time in the lab or the field, observing the system. Be willing to use whatever mathematical techniques turn out to be most appropriate for the scientific problem. I don’t mean that an algebraist should become a dynamicist, but that a person who specializes in, say, almost-periodically-forced ODEs might need to use discrete-time matrix modeling instead. Biologists are understandably annoyed and insulted when a mathematician supposedly

"collaborates" but is really only looking for the perfect application of his or her pet theorems. While you are becoming a scientist, always remain a mathematician; keep publishing your own work in mathematics journals. Projects that involve real data and intense interdisciplinary collaborative effort take a long time to mature, so keep your own independent work going in the meantime.

**JH:** Be patient with your biologist colleagues. It will take time for them to enter your world of symbolic language and precise deduction. You may be frustrated by a field ecologist's global thinking about a problem, but he or she may think you naive when you want to reduce the problem to a handful of variables.

**SH:** Drop any feelings of superiority you might have as a mathematician. Remember, mathematics is a simplification of the "real world", not vice versa. The universe is a complex place, and there are plenty of scientific problems that will give you a vigorous intellectual workout if you are willing to engage them.

### Postscript

It is not our purpose here to list all of the research groups, institutes, meeting venues, or journals involved in the rigorous connection of mathematical models to ecological field data. The interested reader might begin, however, with the bark beetle collaboration of James Powell of Utah State University and Jesse Logan of the USDA-Forest Service,<sup>4</sup> the green tree frog collaboration of Azmy Ackleh of the University of Louisiana at Lafayette with the USGS National Wetlands Research Center,<sup>5</sup> and the various projects of Mark Lewis's group at the University of Alberta.<sup>6</sup> NSF-funded institutes such as the National Institute for Mathematical and Biological Synthesis (NIMBioS),<sup>7</sup> located at the University of Tennessee, and the Mathematical Biosciences Institute (MBI),<sup>8</sup> located at Ohio State University, bring mathematicians and biologists together in interdisciplinary collaboration and training of students. The Joint Mathematics Meetings have hosted special sessions in this area for several years, and a number of journals are specifically interested in this type of work, including *Natural Resource Modeling*, the *Journal of Biological Dynamics*, and the *Bulletin of Mathematical Biology*. An expanded version of this article that includes information on pedagogy and research training of undergraduate and master's students is online.<sup>9</sup>

<sup>4</sup><http://www.math.usu.edu/~powell/>.

<sup>5</sup><http://www.ucs.louisiana.edu/~asa5773/ubm/index.html>.

<sup>6</sup><http://www.math.ualberta.ca/~mlewis/>.

<sup>7</sup><http://www.nimbios.org/>.

<sup>8</sup><http://mbi.osu.edu/>.

<sup>9</sup><http://www.andrews.edu/~henson/HensonHayward2010.pdf>.

### Acknowledgments

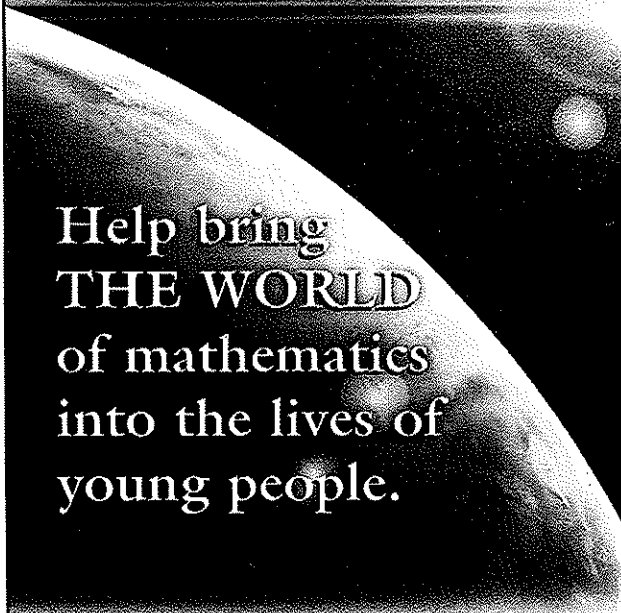
We thank the National Science Foundation (DMS 0314512 and DMS 0613899) and Andrews University (faculty grants 2002-2010); fellow Seabird and Beetle Team members J. M. Cushing, J. G. Galusha, R. F. Costantino, R. A. Desharnais, B. Dennis, and A. A. King; K. Ryan, Project Director of the Washington Maritime National Wildlife Refuge Complex, U.S. Fish and Wildlife Service, for permission to work on Protection Island; Rosario Beach Marine Laboratory for logistical support; and our many student field assistants.

### References

- [1] K. P. BURNHAM and D. R. ANDERSON, *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*, Second Edition, Springer, New York, 2002.
- [2] R. F. COSTANTINO, R. A. DESHARNAIS, J. M. CUSHING, and B. DENNIS, Chaotic dynamics in an insect population, *Science* 275 (1997), 389-391.
- [3] R. F. COSTANTINO, R. A. DESHARNAIS, J. M. CUSHING, B. DENNIS, S. M. HENSON, and A. A. KING, Nonlinear stochastic population dynamics: The flour beetle *Tribolium* as an effective tool of discovery. In R. A. Desharnais (ed.), *Population Dynamics and Laboratory Ecology*, Academic Press, New York, 2005, pp. 101-141.
- [4] J. M. CUSHING, R. F. COSTANTINO, B. DENNIS, R. A. DESHARNAIS, and S. M. HENSON, *Chaos in Ecology: Experimental Nonlinear Dynamics*, Academic Press, San Diego, 2003.
- [5] S. P. DAMANIA, K. W. PHILLIPS, S. M. HENSON, and J. L. HAYWARD, Habitat patch occupancy dynamics of glaucous-winged gulls (*Larus glaucescens*) II: A continuous-time model, *Nat. Resource Modeling* 18 (2005), 469-499.
- [6] B. DENNIS, R. A. DESHARNAIS, J. M. CUSHING, S. M. HENSON, and R. F. COSTANTINO, Estimating chaos and complex dynamics in an insect population, *Ecol. Monogr.* 71 (2001), 277-303.
- [7] R. A. DESHARNAIS, ed., *Population Dynamics and Laboratory Ecology*, Academic Press, New York, 2005.
- [8] J. L. HAYWARD, S. M. HENSON, C. J. LOGAN, C. R. PARRIS, M. W. MEYER, and B. DENNIS, Predicting numbers of hauled-out harbour seals: A mathematical model, *J. Appl. Ecol.* 42 (2005), 108-117.
- [9] J. L. HAYWARD, S. M. HENSON, R. D. TKACHUCK, C. M. TKACHUCK, B. G. PAYNE, and C. K. BOOTHBY, Predicting gull/human conflicts with mathematical models: A tool for management, *Nat. Resource Modeling* 22 (2009), 544-563.
- [10] B. A. HAZLETT and C. E. BACH, Predicting behavioral relationships. In B. A. Hazlett, (ed.), *Quantitative Methods in the Study of Animal Behavior*, Academic Press, New York, 1977, pp. 121-144.
- [11] S. M. HENSON, R. F. COSTANTINO, J. M. CUSHING, R. F. DESHARNAIS, B. DENNIS, and A. A. KING, Lattice effects observed in chaotic dynamics of experimental populations, *Science* 294 (2001), 602-605.
- [12] S. M. HENSON, J. L. HAYWARD, C. M. BURDEN, C. J. LOGAN, and J. G. GALUSHA, Predicting dynamics of aggregate loafing behavior in glaucous-winged gulls



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- (*Larus glaucescens*) at a Washington colony, *Auk* 121 (2004), 380-390.
- [13] S. M. HENSON, J. L. HAYWARD, and S. P. DAMANIA, Identifying environmental determinants of diurnal distribution in marine birds and mammals, *Bull. Math. Biol.* 68 (2006), 467-482.
- [14] S. M. HENSON, J. G. GALUSHA, J. L. HAYWARD, and J. M. CUSHING, Modeling territory attendance and preening behavior in a seabird colony as functions of environmental conditions, *J. Biol. Dynamics* 1 (2007), 95-107.
- [15] S. M. HENSON, B. DENNIS, J. L. HAYWARD, J. M. CUSHING, and J. G. GALUSHA, Predicting the dynamics of animal behaviour in field populations, *Anim. Behav.* 74 (2007), 103-110.
- [16] S. M. HENSON, J. L. HAYWARD, J. M. CUSHING, and J. G. GALUSHA, Socially-induced synchronization of every-other-day egg laying in a seabird colony, *Auk* 127 (2010), 571-580.
- [17] A. A. KING, R. F. COSTANTINO, J. M. CUSHING, S. M. HENSON, R. A. DESHARNAIS, and B. DENNIS, Anatomy of a chaotic attractor: Subtle model-predicted patterns revealed in population data, *Proc. Nat. Acad. Sci.* 101 (2004), 408-413.
- [18] S. A. LEVIN, The problem of pattern and scale in ecology, *Ecology* 73 (1992), 1943-1947.
- [19] M. K. MCCLINTOCK, Menstrual synchrony and suppression, *Nature* 229 (1971), 244-245.
- [20] D. J. MCFARLAND, *Feedback Mechanisms in Animal Behaviour*, Academic Press, London, 1971.
- [21] A. L. MOORE, S. P. DAMANIA, S. M. HENSON, and J. L. HAYWARD, Modeling the daily activities of breeding colonial seabirds: Dynamic occupancy patterns in multiple habitat patches, *Math. Biosci. Eng.* 5 (2008), 831-842.
- [22] S. STROGATZ, *Sync: The Emerging Science of Spontaneous Order*, Hyperion, New York, 2003.

**Note:** The aerial image at the top of Figure 2 is courtesy of the Washington Department of Transportation. All the other figures are collaborative efforts of the authors.