



## Modeling Animal Behavior in a Changing Environment

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*The following article describes the joint research the three authors have conducted for many years at Protection Island, a federally protected National Wildlife Refuge in the Strait of Juan de Fuca in Washington State, and at Galápagos National Park, Ecuador. Their research, which is sponsored by the National Science Foundation, includes a great number of students. Two of the authors, Shandelle Henson and Jim Cushing, are keynote speakers at the World Conference on Natural Resource Modeling to be held in June 2016 in Flagstaff, Arizona. They will make a joint, two-part presentation on their recent research.*

Planet Earth has entered the Anthropocene Epoch, an era in which humans have earned the dubious distinction of acting both as biologic and geologic forces of environmental change (Waters et al. 2016). The rapid pace and enormous scale of planetary change driven by human activity is leading rapidly to abrupt changes in ecological and social systems, some of which may be irreversible. Mathematical approaches for understanding the dynamics and bifurcations of such systems are imminently important.

For the past 14 years, we have studied the effects of environmental change on the behavior of marine birds, mammals, and reptiles. We have focused primarily on colonial seabirds breeding in the Pacific Northwest. To this end our group engages in three main activities. 1) We collect large sets of temporally-dense behavior data in the field; 2) we construct realistic models, tied rigorously to data, which describe, explain, and predict behavioral dynamics as functions of environmental variables; 3) we construct simplified proof-of-concept models to probe dynamic mechanisms, to clarify ideas and suggest testable hypotheses, and to study population dynamic consequences of environmental perturbations and evolving traits.

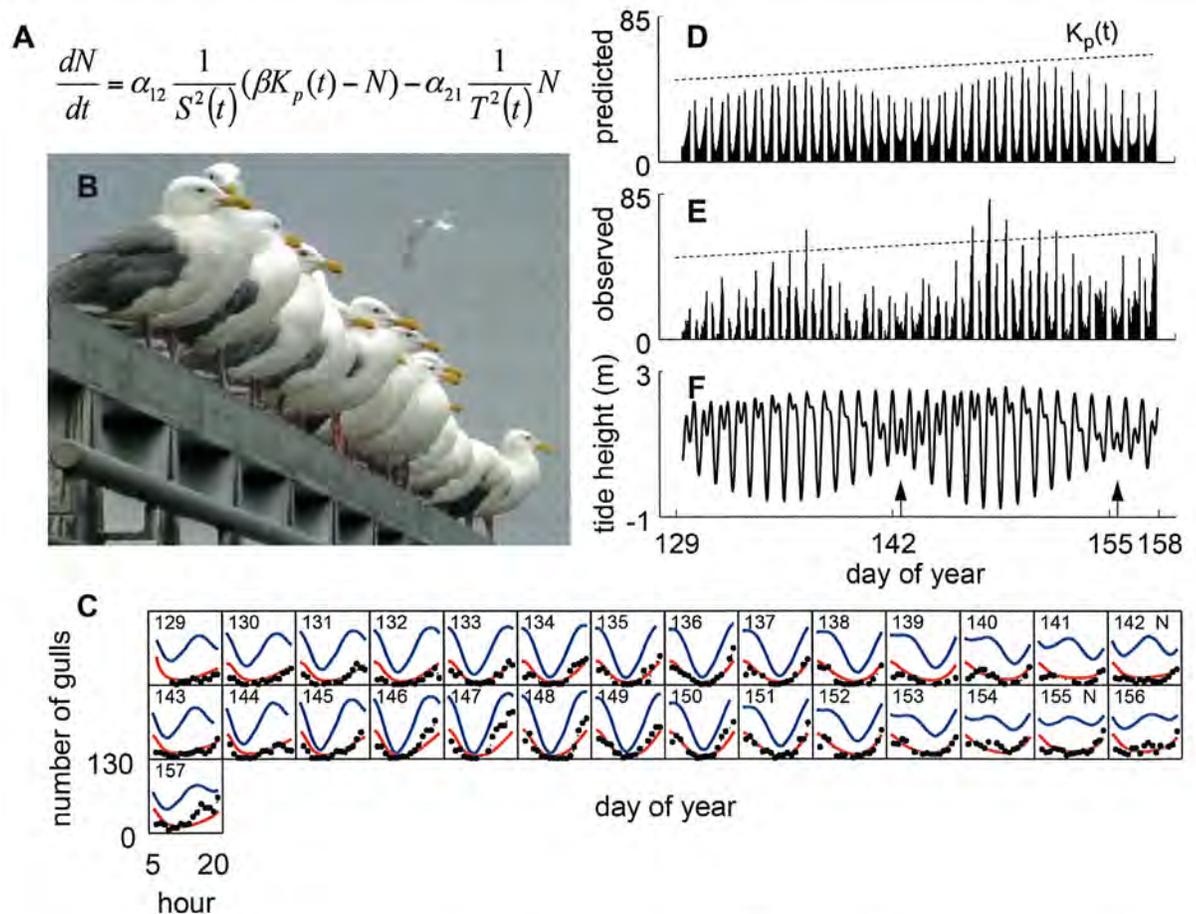
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## Modeling the aggregate: Scale and determinism

We use ordinary differential equation (ODE) and difference equation models in which state variables measure the density of organisms in a particular behavioral state at a particular time. Thus, our models aggregate individuals under simplifying assumptions and track dynamics at the aggregate or population level. Some researchers feel that this approach is too coarse, that modeling animal 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 dynamics of animal groups (Henson et al. 2007a, Henson and Hayward 2010).

Dynamic patterns depend, of course, on scale (Levin 1992). A seabird colony, for example, 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



**Fig. 1**

Loafing in glaucous-winged gulls (*Larus glaucescens*) depends on the tide height  $T$ , solar elevation  $S$ , and a seasonal envelope  $K_p$ .

**A.** Model equation.

**B.** Gulls loafing on a pier.

**C.** A priori 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.

**D.** Model predictions for the spring of 2002. Oscillations are present on daily, bi-weekly, and yearly time scales. The dotted curve is the seasonal envelope oscillation  $K_p$ .

**E.** Data observations corresponding to the predictions in D.

**F.** Tidal oscillation for the data collection time period in 2002. The tidal nodes are indicated with arrows. See Henson et al. (2004) and Hayward et al. (2009).

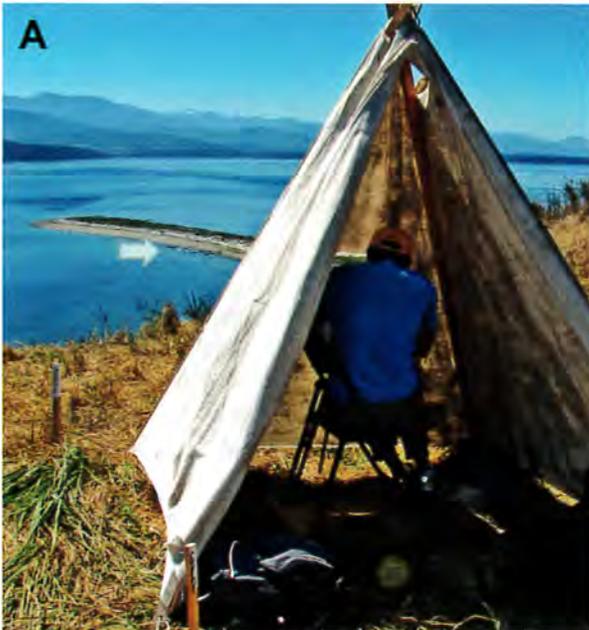
environmental variables. For example, gulls leave colony loafing areas in large numbers to feed when the tide is going out and the sun is high, and they return with an incoming tide in the evening (Fig. 1; Henson et al. 2004, Hayward et al. 2009); harbor seals leave the beach and move into the water with rising tides because the incoming current brings in food (Fig. 2; Hayward et al. 2005, Cowles et al. 2013); Galápagos marine iguanas move from land to feeding sites in the sea primarily in response to changing patterns of solar radiation (Fig. 3; Payne et al. 2015). Some behaviors are more deterministic than others, and it is possible to rank them according to the degree of determinism (Fig. 4).

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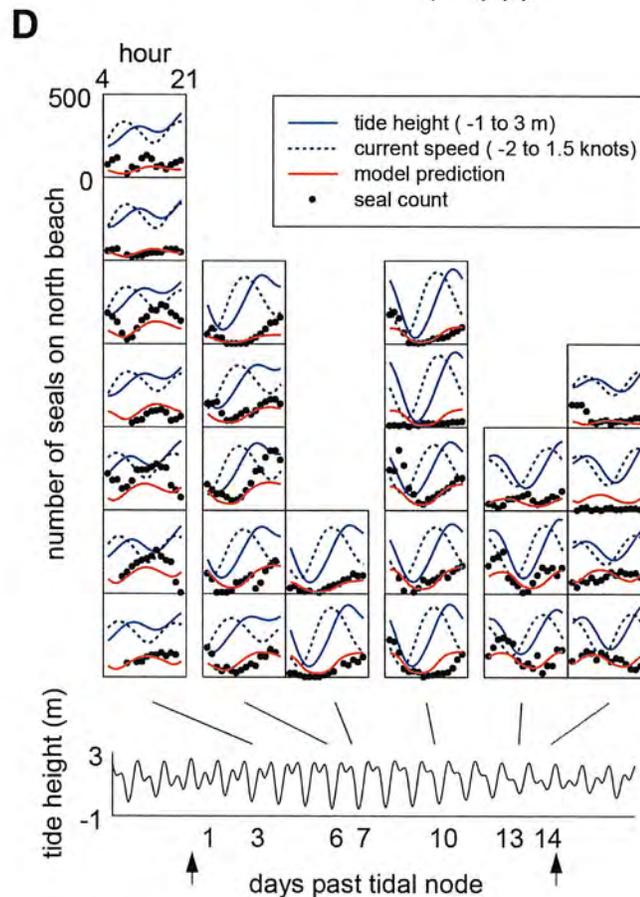
## Fig. 2

Harbor seal (*Phoca vitulina*) haulout depends on current speed  $C_e$  and tide height  $T$ .

- A. Student research assistant uses spotting scope to count seals (arrow) from a blind on Protection Island, Washington.
- B. Harbor seals hauled out on the beach.
- C. Algebraic model for steady state dynamics.
- D. Model prediction (red), seal haul-out 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. See Hayward et al. (2005) and Cowles et al. (2013).



$$N(t) = \frac{\beta e^{-\gamma(\text{day of year} + t/24 - \delta)^2}}{1 + \alpha \frac{(C_e(t))^q}{(T(t))^r}}$$



## ODE and difference equation models of animal behavior

Models designed to quantitatively predict animal behavior in field populations function 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 in which each compartment represents a specific behavioral state at a specific spatial location, and in which the state variables track the densities of individuals in each compartment (Henson et al. 2007a). If all individuals in each compartment are eligible to move to any other compartment, then (ignoring birth and death processes) the dynamics of the  $i^{\text{th}}$  compartment are governed by

$$(1) \quad N_i(t+1) = \sum_{j=1}^m p_{ij} N_j(t)$$

for discrete-time systems and

$$(2) \quad \frac{dN_i}{dt} = \sum_{j=1}^m r_{ij} N_j - \sum_{j=1}^m r_{ji} N_i$$

for continuous-time systems, where  $N_i$  is the density of individuals in the  $i^{\text{th}}$  behavioral state,  $p_{ij}$  is the discrete-time probability that an individual in the  $j^{\text{th}}$  state will move to the  $i^{\text{th}}$  state, and  $r_{ij}$  is the continuous-time per capita rate at which individuals move from compartment  $j$  to compartment  $i$ . If some animals in a compartment are not eligible to make a given transition, then the discrete-time equation for the  $i^{\text{th}}$  compartment is

A

$$N(t) = \frac{\beta(247.7 + 125.2 \sin(0.4481(\text{day of year} + t/24)))}{1 + \alpha \frac{S_e^\zeta H_x^\phi}{H_u^\psi T^\rho}}$$

B



C



**Fig. 3 (left)**

*Marine iguana* (*Amblyrhynchus cristatus*) haulout depends on solar elevation  $S_e$ , heat index  $H_x$ , and tide height  $T$ .

A. Algebraic model for steady state dynamics of hauled out iguanas on a beach at Isla Fernandina, Galápagos, Ecuador.

B. Hauled out marine iguanas.

C. Model predictions (curve) and observations (circles). See Payne et al. (2015).

**Fig. 4 (right)**

Some animal behaviors are highly determined by abiotic environmental variables; others are influenced relatively little.

From left to right: seabird rest (unpublished data), seabird preen (Henson et al. 2007), seal haulout (Hayward et al. 2005), seabird sleep (Henson et al. 2007), seabird colony attendance (Henson et al. 2007), seabird loafing (Hayward et al. 2009). After Henson and Hayward (2010).

$$(3) \quad N_i(t+1) = N_i(t) + \sum_{j=1}^m p_{ij} f_{ij} - \sum_{j=1}^m p_{ji} f_{ji}$$

$$= \sum_{j=1}^m p_{ij} f_{ij} + N_i(t) \left( 1 - \sum_{j=1}^m p_{ji} \frac{f_{ji}}{N_i(t)} \right)$$

and the continuous-time equation is

$$(4) \quad \frac{dN_i}{dt} = \sum_{j=1}^m r_{ij} f_{ij} - \sum_{j=1}^m r_{ji} f_{ji}$$

where  $f_{ij} \leq N_j$  is the density of individuals in compartment  $j$  that are eligible to move to compartment

$i$ . If the total population size  $K = \sum_{i=1}^m N_i$  remains constant on the time scale of the model, we can eliminate one of

the state variables by setting  $N_m = K - \sum_{i=1}^{m-1} N_i$ .

Applying these models to any particular biological

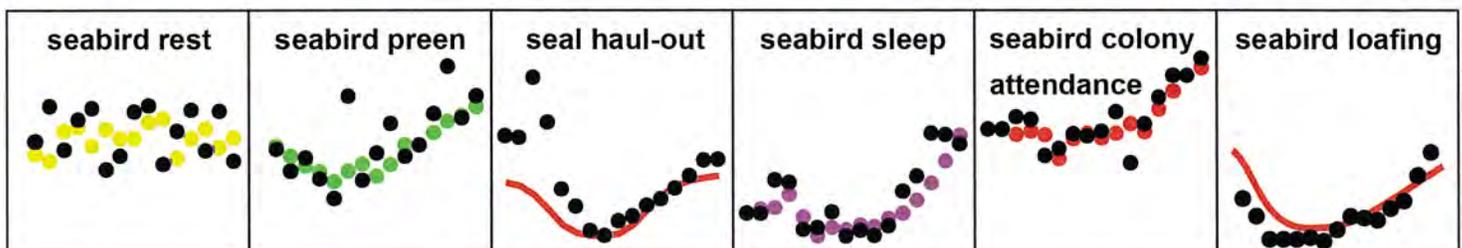
system requires specifying  $f_{ij}$ ,  $p_{ij}$ ,  $r_{ij}$  by means of modeling assumptions. In general, these coefficients are functions of population densities and time, which renders the models nonlinear and nonautonomous.

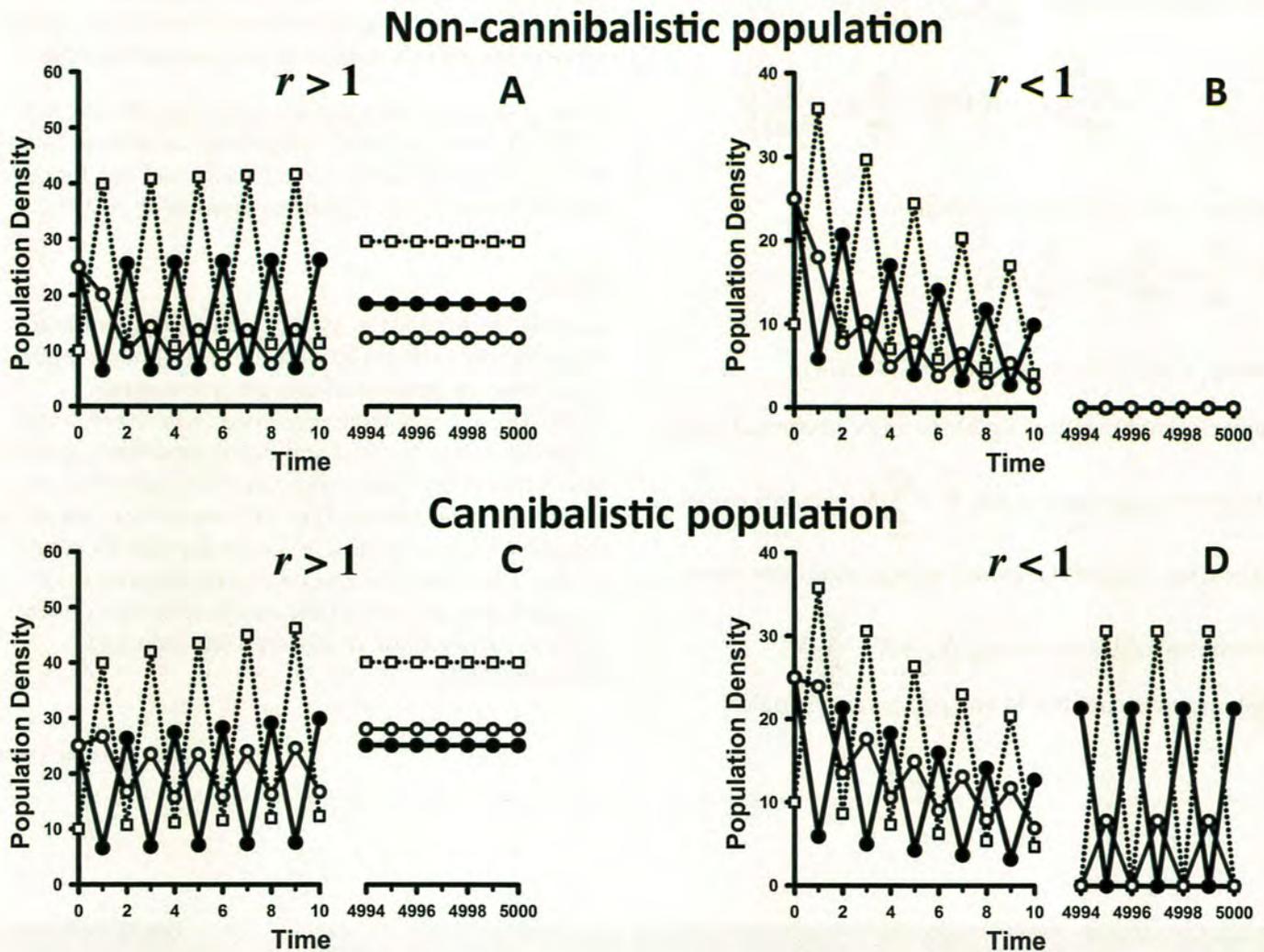
If the system recovers rapidly after disturbance, the ODEs (4) can be reduced to algebraic models on two time scales, one for disturbance dynamics and one for steady state dynamics (Figs. 2c and 3a; Henson et al. 2006).

## Data

In order to capture the dynamic patterns of animal behavior, data should be collected on a finer temporal scale than the behavioral and environmental fluctuations. For marine organisms whose behaviors often are driven by tidal and diurnal patterns, we have found that hourly data collected over a complete two-week tidal cycle is best. Typically we 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 student assistants and offers many opportunities for student participation in research (Henson and Hayward 2010).

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**Fig. 5**

Sample trajectories of a three stage, discrete time structured population model whose state variables are juveniles (open squares), reproductively active adults (solid circles), and reproductively inactive adults (open circles). Juveniles are victims of cannibalism by both adult classes. The first row of graphs is for a population without cannibalism and placed in two different environments: **A.** healthy ( $r > 1$ ) and **B.** degraded ( $r < 1$ ). Each graph shows a plot of initial transients for 10 time steps separated by a plot of the final attractor for the last 7 of 5,000 time steps. Note in **B** that this non-cannibalistic population goes extinct in the degraded environment. The second row of graphs shows the trajectories that result when

cannibalism is introduced into this population with a sufficient positive benefit to adult survival. Note in **D** that this cannibalistic population does not go extinct in the degraded environment. Also note that the cannibals' attractor is a cycle of period 2 in which the two adult classes are out-of-phase (reproductive synchrony). The explanation for this is that a backward bifurcation at  $r = 1$  has created a strong Allee effect, i.e. the existence of two attractors: a survival 2-cycle and the extinction equilibrium. Initial conditions other than those used in **D** can result in extinction. Graphs taken from Veprauskas and Cushing (2016b).

## Parameterization

Estimating parameters requires a stochastic version of the model that accounts for the noise structure (Cushing et al. 2002). 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

$$(5) \quad \varphi(\mathbf{N}(\tau+1)) = \varphi(G(\tau, \mathbf{N}(\tau))) + \mathbf{E}(\tau)$$

where  $\mathbf{N} = (N_1, N_2, \dots, N_m)$  is the vector of state variables,  $\mathbf{E}$  is a vector from a multivariate normal random distribution with variance-covariance matrix  $\Sigma = (\sigma_{ij})$ , and  $G(\tau, \mathbf{N}(\tau))$  is the deterministic prediction at hour  $\tau+1$  based on the state of the system at hour  $\tau$ . Here  $\varphi$  is a variance-stabilizing transformation; the transformations  $\varphi(x) = \ln x$  and  $\varphi(x) = \sqrt{x}$  render environmental and demographic stochasticity, respectively, approximately additive (Cushing et al. 2002).

The one-step conditioned residual error vectors are

$$(6) \quad \rho(\tau+1) = \varphi(\mathbf{n}(\tau+1)) - \varphi(G(\tau, \mathbf{n}(\tau)))$$

where  $\mathbf{n}$  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 (Cushing et al. 2002).

## 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 (Burnham and Anderson 2010).

## 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 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 the parameters. Goodness-of-fit can be computed with a generalized  $R^2$  (Cushing et al. 2002). For example, when we developed a model to predict numbers of gulls loafing on a pier,  $R^2 = 0.58$  for the calibration data set and  $R^2 = 0.61$  for the validation data set (Henson et al. 2004); for Galápagos marine iguana haul-out numbers,  $R^2 = 0.77$  for the calibration data set and  $R^2 = 0.80$  for the validation data set (Payne et al. 2015). 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, of course, 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 colony and not away feeding. Our model predictions, however, counterintuitively suggested that during high tides close to tidal nodes (when high tide occurs at midday) gulls should be away feeding — which is exactly what we observed (Fig. 1c, days 142 and 155).

## Proof-of-concept models and evolutionary game theory models

In addition to realistic models that are tied rigorously to data, we also use simplified proof-of-concept models to probe dynamic consequences, sharpen ideas and definitions, and suggest hypotheses.

Currently we are using discrete-time proof-of-concept models to study the effects of rising sea surface temperatures and concomitant resource paucity on

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the feeding and reproductive strategies of colonial seabirds. The phenomena of interest involve interactions of individuals from different lifecycle stages and behavioral categories (eggs, juveniles, reproductively active and inactive adults, etc.) and therefore require that we build structured matrix models of the form (Caswell 2001)

$$(7) \mathbf{N}(t+1) = \mathbf{P}(\mathbf{N}(t)) \mathbf{N}(t)$$

where the (density-dependent) entries of the  $m \times m$  projection matrix  $\mathbf{P}$  describe the reproductive, survival, and category transition rates. This matrix is nonnegative (i.e. its entries are nonnegative) and is assumed to be irreducible so that each category of individuals is reachable (through birth or transition processes) from any other category. With regard to population survival, the extinction equilibrium  $\mathbf{N}(t) \equiv \mathbf{0}$

and its stability are of fundamental interest. The Linearization Principles says that its stability can be determined by the eigenvalues of the Jacobian at  $\mathbf{0}$ , which is the (inherent or density-free) projection matrix  $\mathbf{P}(\mathbf{0})$ . Perron-Frobenius theory implies the existence of a positive dominant eigenvalue  $r$ , the inherent population growth rate. The extinction equilibrium loses stability as  $r$  increases through 1, which introduces survival (positive) equilibria through a transcritical bifurcation (Cushing 1998). (Other bifurcation parameters are usually more convenient to use, such as the inherent net reproduction number  $R_0$  or other model-specific parameters.) Our modeling efforts so far have concentrated on the nature of this bifurcation and how it is related to specific biological mechanisms, in particular to adult-on-juvenile cannibalism, reproductive timing, and environmental resource degradation (due to climate and environmental change).

For example, a low dimensional cannibalism model that includes the negative and positive effects on juvenile (victim) and adult (cannibal) survival rates, respectively, and a trade-off between environmental resource availability and cannibalism activity shows that cannibalism can result in a stable survival equilibrium in circumstances under which the absence of cannibalism would lead to extinction (namely, when

environmental resource is low and the positive effect of cannibalism on adult survival is significant enough). Mathematically, this is due to a backward bifurcation at  $r = 1$ , which in turn creates a strong Allee effect and its corresponding survival equilibrium when  $r < 1$  (Cushing et al. 2015). In the absence of cannibalism the bifurcation is forward and  $r < 1$  (a degraded environment) implies extinction.



Another model, designed to explore the effects of reproductive synchrony by adults, has a more complicated bifurcation. Mathematically, this is caused by the imprimitivity of  $\mathbf{P}(\mathbf{0})$  ( $r$  is not a *strictly* dominant eigenvalue). The result is the simultaneous bifurcation of periodic cycles at  $r = 1$ , cycles whose adult components are out-of-phase and represent reproductive synchrony. The stability of these cycles is promoted by environmental degradation, the resulting

increase in cannibalism, and an assumed victim (prey) saturation effect of cannibals (predators) (Veprauskas and Cushing 2016b).

These findings support our hypotheses concerning the observed correlations between cannibalism, reproductive synchrony, and climate change (for which mean sea surface temperature is a surrogate) in seabird colonies (Henson et al. 2010, Henson et al. 2011, Hayward et al. 2014).

To explore whether the traits that produce these conclusions are adaptive in an evolutionary sense, we have begun investigations of evolutionary versions of the models using the methodology of evolutionary game theory. This methodology assumes the individual vital rates modeled by the entries in the projection matrix are functions of a vector  $\mathbf{v}$  of phenotypic traits of the individual, subject to Darwinian evolution, as well as the traits of other individuals (which is why “game” appears in the name of this methodology) as represented by the population mean trait vector  $\mathbf{u}$ . Thus,  $\mathbf{P} = \mathbf{P}(\mathbf{N}, \mathbf{v}, \mathbf{u})$ . Evolutionary game theory models population dynamics by

$$(8) \mathbf{N}(t+1) = \mathbf{P}(\mathbf{N}(t), \mathbf{v}, \mathbf{u}(t))|_{\mathbf{v}=\mathbf{u}(t)} \mathbf{N}(t)$$



The canonical assumption of Darwinian evolution states that the change in the mean trait  $\mathbf{u}$  is proportional to the fitness gradient (with respect to  $\mathbf{v}$ ). In the multi-trait context this assumption is expressed by the equation

$$(9) \quad \mathbf{u}(t+1) = \mathbf{u}(t) + \mathbf{C} \nabla_{\mathbf{v}} \mathbf{F}(\mathbf{N}(t), \mathbf{v}, \mathbf{u}(t))|_{\mathbf{v}=\mathbf{u}(t)}$$

where  $\mathbf{C}$  is a variance-covariance matrix among the traits. This is often called the Breeder's or Fisher's or Lande's equation. The connection between the population and trait dynamics (together called Darwinian dynamics) is made by relating fitness  $\mathbf{F}$  to the projection matrix  $\mathbf{P}$ . The most commonly adopted definition of fitness is  $\mathbf{F}(\mathbf{N}, \mathbf{v}, \mathbf{u}) = \ln \mathbf{r}(\mathbf{N}, \mathbf{v}, \mathbf{u})$ . For these Darwinian dynamic models we have established extensions of the fundamental bifurcation theorems that occur as the extinction equilibrium destabilizes (Veprauskas and Cushing 2016a) and used them (and numerical simulation explorations) to study evolutionary versions of our cannibalism and reproductive synchrony models. For example, by use of this methodology we have shown that cannibalism rates that produce population survival in degraded environments can be

an evolutionary adaptive strategy (evolutionary stability strategy or ESS) (Veprauskas and Cushing 2016b).

### Closing thoughts

The role of the burgeoning human populace as a major planet changer provides a rich field of opportunities for applied mathematicians and ecologists. As we look to the future, a serious problem is the lack of quantitative training for biologists; in many universities, biology majors are no longer required to take calculus. As a consequence, biologists sometimes do not have enough basic mathematical training to collaborate effectively with mathematicians. Mathematicians, on the other hand, often are more interested in finding applications of a particular theorem than in actually addressing a scientific problem with its attendant messiness of data and stochasticity. Never has there been a more opportune time, however, for mathematicians and biologists to work together to solve pressing scientific problems.

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