



Predicting the dynamics of animal behaviour in field populations

SHANDELLE M. HENSON*, BRIAN DENNIS†, JAMES L. HAYWARD‡, J. M. CUSHINGS§
& JOSEPH G. GALUSHA**

*Department of Mathematics, Andrews University

†Department of Fish and Wildlife Resources, Division of Statistics, University of Idaho

‡Biology Department, Andrews University

§Department of Mathematics, Interdisciplinary Program in Applied Mathematics, University of Arizona

**Department of Biological Sciences, Walla Walla College

(Received 9 November 2005; initial acceptance 20 June 2006;
final acceptance 21 November 2006; published online 1 June 2007; MS. number: A10297)

Many species show considerable variation in behaviour among individuals. We show that some behaviours are largely deterministic and predictable with mathematical models. We propose a general differential equation model of behaviour in field populations and use the methodology to explain and predict the dynamics of sleep and colony attendance in seabirds as a function of environmental factors. Our model explained over half the variability in the data to which it was fitted, and it predicted the dynamics of an independent data set. Differential equation models may provide new approaches to the study of behaviour in animals and humans.

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Keywords: colony occupancy; differential equation; dynamic modelling; glaucous-winged gull; habitat ecology; *Larus glaucescens*; mathematical modelling; sleep; territory attendance

Animal behaviour arises from a complicated interaction of internal and external factors. Many species show significant variation in behaviour among individuals (Slater 1978), thus confounding efforts to predict a wide array of important variables, such as social and economic trends, population dynamics, habitat occupancies and the spread of behaviourally driven diseases. Accurate predictions of behavioural dynamics require the construction of mathematical models that operate on scales at which deterministic trends emerge from variability among individuals (Levin 1992).

The dynamics of behaviour typically are modelled with game theory, Markov chains and individual-based models

(Mangel & Clark 1988; Gottman & Roy 1990; Dugatkin & Reeve 1998; Railsback 2001). Historically, ordinary differential equations (ODEs) with 'motivational' dependent variables were developed in the context of control theory as qualitative models of the behaviour of individuals (McFarland 1971; Hazlett & Bach 1977). These ODE models were not tied rigorously to field data because motivational variables are not measurable, and because many 'action patterns' are variable rather than fixed (Slater 1978).

Here we re-examine ODEs as models of animal behaviour, propose a general methodology for the quantitative prediction of behaviour in field populations, and use the methodology to explain and predict the dynamics of sleep and habitat occupancy in a seabird colony.

GENERAL MODEL

The general methodology that we use requires an interdisciplinary paradigm drawn from recent advances in the interface between dynamical systems theory and population biology (Cushing et al. 2003). First, individuals

Correspondence: S. Henson, Department of Mathematics, Andrews University, Berrien Springs, MI 49104, U.S.A. (email: henson@andrews.edu). B. Dennis, Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, U.S.A. J. Hayward, Biology Department, Andrews University, Berrien Springs, MI 49104, U.S.A. J. Cushing, Department of Mathematics, 617 N. Santa Rita, University of Arizona, Tucson, AZ 85721, U.S.A. J. Galusha, Department of Biological Sciences, Walla Walla College, College Place, WA 99324, U.S.A.

are categorized into mutually exclusive 'compartments', each of which represents a specific behavioural state at a specific spatial location. We previously used compartmental models to predict the diurnal movements of animals between habitat patches (Henson et al. 2004, 2005; Damania et al. 2005; Hayward et al. 2005); here we view transitions between behavioural states as conceptually equivalent to transitions between spatial habitats. Second, the state variables (dependent variables) track the numbers of individuals in each compartment. Thus, the state variables are measurable. They are also robust with respect to variability among individuals in the sense that they track patterns in frequencies of behaviour in an aggregate rather than patterns in an individual's behaviour. Data consist of time series of compartment censuses taken at intervals short enough to capture system dynamics. Third, temporal fluctuations in the data are of two types: deterministic fluctuations that are explained by the model, and stochastic fluctuations that make up the variability unexplained by the model (Cushing et al. 2003). Fourth, factors are classified as 'demographic' or 'environmental' rather than internal or external. We define demographic factors as those experienced independently by single individuals or small subsets of individuals, and environmental factors as those experienced by all individuals in a population (Cushing et al. 2003). Finally, both deterministic and stochastic fluctuations can be driven primarily by demographic factors, environmental factors, or a mixture of the two.

A model of b behaviours in h habitats has at most $m = bh$ compartments, each of which represents a specific behaviour in a specific habitat. The model is the system of ODE balance equations for the inflow and outflow rates for each compartment. For example, a model of seabird preening (two 'behaviours', preening and not preening) without regard to location (one habitat) would have two compartments. The model would be

$$\begin{aligned}\frac{dB}{dt} &= r_{BE}f_{BE} - r_{EB}f_{EB} \\ \frac{dE}{dt} &= r_{EB}f_{EB} - r_{BE}f_{BE},\end{aligned}$$

where B denotes the number of animals preening, E denotes the number not preening, f_{ij} denotes the number of individuals in compartment j that are eligible to move to compartment i , and r_{ij} denotes the per capita rate at which eligible individuals move from compartment j to compartment i .

In general, for m compartments, the model is the system of m equations of the form

$$\frac{dn_i}{dt} = \sum_{\substack{j=1 \\ j \neq i}}^m r_{ij}f_{ij} - \sum_{\substack{j=1 \\ j \neq i}}^m r_{ji}f_{ji}, \quad i = 1, 2, \dots, m \quad (1)$$

where n_i is the number of animals in compartment i . Equation (1) ignores birth and death processes. Thus, the total population size $P = \sum_{i=1}^m n_i$ remains constant, and one of the state variables can be eliminated, for example, by writing $n_m = P - \sum_{i=1}^{m-1} n_i$. The application of equation (1) to a particular system requires modelling the f_{ij} and r_{ij} , which are, in general, functions of time-varying factors and/or compartment densities.

APPLICATION TO COLONY ATTENDANCE AND SLEEP IN SEABIRDS

We applied equation (1) to sleep and colony attendance in a nesting colony of glaucous-winged gulls, *Larus glaucescens*, during the chick-rearing season. Sleep constitutes a common behavioural state in most animals and is defined by Siegel (2005, page 1264) as 'a state of immobility with greatly reduced responsiveness, which can be distinguished from coma or anaesthesia by its rapid reversibility'. The functional significance of sleep, however, remains incompletely understood and may differ for different animals (Siegel 1995, 2005; Hobson 2005). Although sleeping animals are relatively noninteractive with their environments and thus especially vulnerable, the quality and duration of sleep greatly influence the efficiency of wakefulness (Rattenborg et al. 2000).

'Sleep' in gulls is a complex phenomenon that includes both the relatively infrequent 'front sleep' and the much more common 'back sleep' (Amlaner & McFarland 1981; Amlaner & Ball 1983; Shaffery et al. 1985). During front sleep, the head and neck are retracted and the bill faces forward and down. In back sleep, the head is turned back and the bill is tucked under the scapulars. Incidence of both sleep postures is accompanied by heightened thresholds of arousal. Bouts of eye closure are longer for gulls in the back-sleep posture, however, which may suggest that the depth of sleep is deeper for gulls in this posture (Amlaner & McFarland 1981). Sleeping gulls in both postures intermittently monitor the environment by opening one eye or the other, a phenomenon that accompanies uni-hemispherical sleep in these and other birds (Rattenborg et al. 2000). Here, we restrict our use of the term 'sleep' in gulls to the more common 'back sleep', although we recognize the oversimplification of this categorization.

During the chick-rearing season, gulls must divide their time between sleep and alertness on the colony, and activities such as feeding that occur away from colony. Mathematical models that accurately predict the incidence of sleep and colony attendance would help to identify environmental factors that elicit these behaviours and clarify their adaptive functions.

We assumed that each individual was in one of three mutually exclusive compartments: Wake in the colony, Sleep in the colony or Away from the colony, with numbers of animals in each compartment denoted W , S or A , respectively. We assumed that the number of individuals $C = S + W$ attending the colony remained above a minimum threshold $\mu \geq 0$ (at least one mate attends each territory during chick-rearing season) and that no individual moved directly from the S compartment into the A compartment or vice versa without first moving into the W compartment (Fig. 1); that is, $f_{AS} = f_{SA} = 0$. We also assumed that the number of individuals eligible to leave the colony via the W compartment and enter the A compartment was either W or $C - \mu$, whichever was smaller; hence $f_{AW} = \min\{W, C - \mu\}$. We assumed that all individuals in the A and S compartments were eligible to move to the W compartment; thus $f_{WA} = A$ and $f_{WS} = S$. Finally, we assumed that the number of individuals in the W

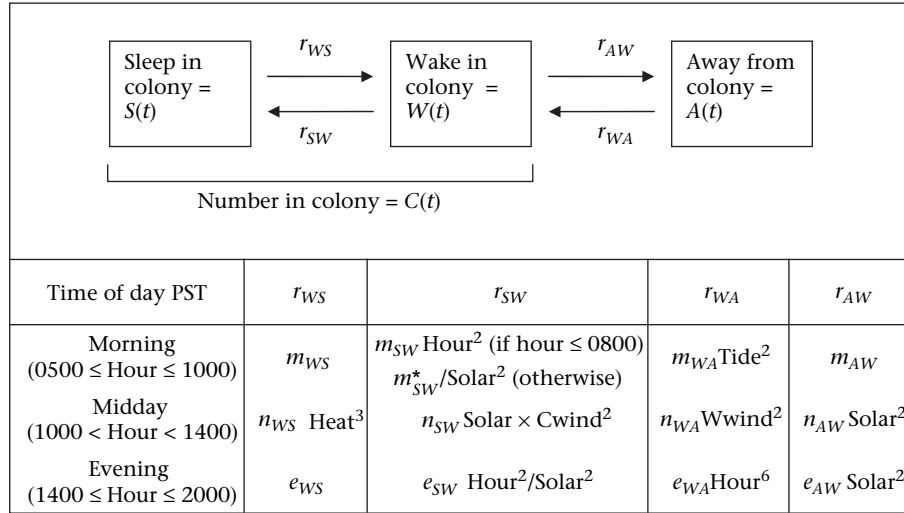


Figure 1. Per capita flow rate submodels as functions of six environmental factors: tide height (Tide), hour of day (Hour) in Pacific Standard Time (PST), solar elevation (Solar), heat index (Heat), wind speed on the colony (Cwind), and wind speed over the open water (Wwind). Assuming $\Psi = 1$, the maximum likelihood parameters as estimated from the calibration data (all data) were $m_{WS} = 1.008$ (1.006), $m_{SW} = 0.08985$ (0.07328), $m_{SW}^* = 0.06299$ (0.07603), $m_{WA} = 0.2465$ (0.1046), $m_{AW} = 0.6115$ (0.3448), $n_{WS} = 4.493$ (4.591), $n_{SW} = 0.3184$ (0.2765), $n_{WA} = 0.1334$ (0.1546), $n_{AW} = 0.05996$ (0.07317), $e_{WS} = 8.759$ (11.77), $e_{SW} = 1.054$ (1.053), $e_{WA} = 0.02029$ (0.02822), $e_{AW} = 0.1198$ (0.1918), $\alpha = 0.6343$ (0.7640). The estimated entries of the variance–covariance matrix Σ were $\sigma_{11} = 0.006279$ (0.006386), $\sigma_{22} = 0.3087$ (0.3955), $\sigma_{12} = \sigma_{21} = 0.009251$ (0.007457).

compartment who were eligible to enter the S compartment was $\alpha C - S$, where $0 < \alpha \leq 1$, as long as $\alpha C - S$ was positive, and zero otherwise; that is, $f_{SW} = \max\{\alpha C - S, 0\}$. We interpret the coefficient α as the fraction of birds in the colony that are either sleeping or engaged in behaviours that can transition directly to sleep, such as the rest posture. The quantity $1 - \alpha$ is the fraction of birds in the colony engaged in behaviours that seldom transition directly to sleep, such as preen (Murdoch 1993). Clearly this fraction changes over time. The model does not track any behaviours except sleep, however, so we assume that α is constant.

Under these assumptions equation (1) becomes

$$\begin{aligned} \frac{dW}{dt} &= r_{WS}S + r_{WA}A - r_{SW} \max\{\alpha C - S, 0\} \\ &\quad - r_{AW} \min\{W, C - \mu\}, \\ \frac{dS}{dt} &= r_{SW} \max\{\alpha C - S, 0\} - r_{WS}S, \\ \frac{dA}{dt} &= r_{AW} \min\{W, C - \mu\} - r_{WA}A. \end{aligned} \quad (2)$$

The identities $W = C - S$ and $A = P - C$ reduce equation (2) to a model for colony occupancy and the number asleep in the colony

$$\begin{aligned} \frac{dC}{dt} &= r_{WA}(P - C) - r_{AW} \min\{C - S, C - \mu\}, \\ \frac{dS}{dt} &= r_{SW} \max\{\alpha C - S, 0\} - r_{WS}S. \end{aligned} \quad (3)$$

Solutions of equation (3) satisfy the inequalities $\mu \leq C(t) \leq P$ and $0 \leq S(t) \leq C(t)$ for all time t provided that the initial conditions do. There were 70 nesting pairs in our sample colony area (see Methods); thus, $P = 140$ and $\mu = 70$. The coefficient α was an unknown parameter, to be estimated from data. We assumed that the four per

capita transition rates r_{ij} were functions of time-varying abiotic environmental conditions.

METHODS

Data Collection

The study was conducted at Protection Island National Wildlife Refuge (48°08'N, 122°55'W), Jefferson County, Washington, U.S.A. The island is at the southeastern end of the Strait of Juan de Fuca and consists mostly of a high plateau bordered by steep bluffs. Violet Point, a gravel spit extending to the southeast, contains a breeding colony of more than 2400 pairs of nesting glaucous-winged gulls.

We selected a 33×100 -m sample colony area containing approximately 70 nests. Observations consisted of hourly census counts and behaviour scans taken during daylight hours in chick-rearing season during 0500–2000 hours Pacific Standard Time (PST) for 14 days on 30 June–2 July and 6–16 July 2004. Observations were made using a 20–60 \times spotting scope from an observation point atop a 33-m bluff that bordered the west end of Violet Point. The observation point was 100 m from the proximal edge of the larger colony and 200 m from the study plot. The presence of observers did not seem to influence the behaviour of the gulls in any way. At the top of each hour, a census and a behaviour scan were taken in that order. Behaviours were recorded by voice and subsequently transcribed. The number of animals in the behaviour scan was typically slightly different from the census, since these observations were not conducted simultaneously. To correct this, we divided the number of birds showing a particular behaviour by the number of birds scanned, and multiplied the result by the census.

A weather station 2 m above site elevation on the north-west end of Violet Point tracked many of the environmental conditions experienced by the colony, including temperature, humidity, wind speed and direction, heat index, barometric pressure, rainfall and solar radiation. Heat index is computed from temperature and relative humidity as a measure of how hot the air feels (Steadman 1979). Hourly tide heights, solar elevations and wind speeds over open water were obtained from the National Oceanic and Atmospheric Administration (NOAA).

Submodels for r_{ij}

Complete specification of equation (3) requires modelling the per capita transition rates r_{ij} as functions of environmental variables. Previous studies found correlations of occupancy and sleep in gulls with time of day, temperature and tide height (Drent 1967; Delius 1970; Galusha & Amlaner 1978). We looked for similar correlations using data from 'Morning' (0500–1000 hours), 'Midday' (1000–1400 hours) and 'Evening' (1400–2000 hours) and a number of other environmental conditions tracked by the on-site weather station. The data were correlated with tide height (Tide), time of day (Hour), solar elevation (Solar), heat index (Heat), wind speed on the colony (Cwind) and wind speed over the open water (Wwind). We assumed that each of the four per capita transition rates r_{WS} , r_{SW} , r_{WA} and r_{AW} in equation (3) could be modelled as

$$\begin{aligned} \text{Morning: } r_{ij} &= m_{ij} \text{Tide}^{b_{1ij}} \text{Hour}^{c_{1ij}} \text{Solar}^{d_{1ij}} \text{Heat}^{f_{1ij}} \text{Cwind}^{g_{1ij}} \\ &\quad \text{Wwind}^{h_{1ij}}, \\ \text{Midday: } r_{ij} &= n_{ij} \text{Tide}^{b_{2ij}} \text{Hour}^{c_{2ij}} \text{Solar}^{d_{2ij}} \text{Heat}^{f_{2ij}} \text{Cwind}^{g_{2ij}} \\ &\quad \text{Wwind}^{h_{2ij}}, \\ \text{Evening: } r_{ij} &= e_{ij} \text{Tide}^{b_{3ij}} \text{Hour}^{c_{3ij}} \text{Solar}^{d_{3ij}} \text{Heat}^{f_{3ij}} \text{Cwind}^{g_{3ij}} \\ &\quad \text{Wwind}^{h_{3ij}}, \end{aligned} \quad (4)$$

where $m_{ij}, n_{ij}, e_{ij} > 0$ are constant coefficients and $b_{ij}, c_{ij}, d_{ij}, f_{ij}, g_{ij}, h_{ij}$ are constant exponents. For numerical convenience, we scaled and nondimensionalized the six environmental variables x so that $1 \leq x \leq 2$ (Henson et al. 2004, 2005; Damania et al. 2005; Hayward et al. 2005). In estimating the parameters for such a model, the scaling is absorbed in the resulting values of the rate coefficients.

Equation (3) thus contained 13 coefficients $\alpha, m_{ij}, n_{ij}, e_{ij} > 0$ and 72 constant exponents. Numerical estimation of a total of 85 parameters would have required a very large data set. Thus, we restricted the model parameters to the 13 coefficients and treated the 72 exponents as follows.

Each of the 72 exponents $b_{ij}, c_{ij}, d_{ij}, f_{ij}, g_{ij}, h_{ij}$ was assumed to have the value $-1, 0, \text{ or } 1$. This assumption created a very large number of possible models in the form of equation (3). We chose a relatively small subset of these based on (1) the biologists' knowledge of what was likely to be most biologically reasonable for the system, (2) statistical investigations comparing the data and the environmental variables and (3) the experience gained by weeks of trial-and-error searches for models that could fit the data. Of the remaining alternative models, we took

the best to be the one with the lowest (fitted) sum of squared residuals, and discarded the others. Each of the alternative models had 13 parameters, so it was not necessary to use information-theoretic model selection indexes such as the Akaike information criterion (AIC), which penalize models having more parameters (Hayward et al. 2005).

Once the best model was determined from the list of alternatives, the exponents with value -1 (or 1) were decreased (or increased) by integer units until the best integer exponents were obtained.

Parameter Estimation

We randomly divided the 14 days of data into two sets of 7 days each, one for parameter estimation (the 'calibration data') and the other for an independent evaluation of the parameterized model (the 'validation data'). The calibration data set contained five days of 16 consecutive hourly records (30 June, 2 July, 6 July, 8 July and 11 July 2004), one day of two and 12 consecutive hourly records (14 July 2004) and one day of 11 consecutive hourly records (15 July 2004). The validation data set contained six days of 16 consecutive hourly records (7 July, 9–10 July, 12–13 July, 16 July 2004) and one day of four and seven consecutive hourly records (1 July 2004).

We used the method of maximum likelihood to estimate the parameters for equation (3). Numerical integration of equation (3) with the r_{ij} given in Fig. 1 yields a 'one-step' prediction (C_{t+1}, S_{t+1}) at hour $t+1$, given the observation (c_t, s_t) at hour t as the initial condition. We produced one-step model predictions with the MatLab ODE integrator (MathWorks, Natick, Massachusetts, U.S.A.).

Before calculating the maximum likelihood parameter estimates, we transformed the data and the predictions to stabilize the variances of the one-step departures of data from model. The likelihood estimation procedure assumes, for each state variable, that the variances of such residual prediction errors do not depend on the sizes of the state variables. If the (one-step, conditional) variance $\text{Var}(x_t)$ of a state variable x_t is a function $v(x_{t-1})$ of the size of the system at time $t-1$, then a transformed state variable $w_t = \phi(x_t)$ that has an approximately constant variance can be found as the solution of the equation $v(x)[\phi'(x)]^2 = c$, where c is an arbitrary constant (Cushing et al. 2003). Ecologists have recognized two principal types of variance scaling in ecological systems, 'demographic' and 'environmental' (Engen & Sæther 1998). Demographic scaling is often modelled by $v(x) = \gamma x$, while environmental scaling is given by $v(x) = \delta x^2$, where γ and δ are positive constants. A model of both demographic and environmental stochasticity is $v(x) = \gamma x + \delta x^2$. The variance stabilizing transformation for both is

$$\phi(x) = \frac{2 \ln \left(\frac{1}{2} \sqrt{\psi x} + \frac{1}{2} \sqrt{\psi x + 4(1 - \psi)} \right)}{\sqrt{\psi}},$$

where $\psi = \delta / (\delta + (\gamma/4))$ is a measure of the relative amount of environmental noise in the data. The value $\psi = 1$ corresponds to environmental stochasticity with

transformation $\phi(x) = \ln x$, and $\psi \rightarrow 0^+$ corresponds to demographic stochasticity with transformation $\phi(x) = \sqrt{x}$ (Cushing et al. 2003).

For a given value of ψ , the parameter estimation procedure assumes that the vectors $(\phi(c_t) - \phi(C_t), \phi(s_t) - \phi(S_t))$ of transformed one-step residual errors come from a joint normal distribution with variance–covariance matrix Σ , and that they are uncorrelated in time. Under these assumptions, the parameters are estimated by maximizing the log likelihood as a function of the model parameters (Cushing et al. 2003). We maximized the log-likelihood function numerically with the Nelder–Mead algorithm (Press et al. 1986) under three types of stochasticity: mostly demographic ($\psi = 0.01$), a mixture of demographic and environmental ($\psi = 0.5$) and purely environmental ($\psi = 1$).

Model Validation

We compared the (fitted) goodness of fit on the calibration data set to the goodness of fit on the validation data set without re-estimating parameters. The goodness of fit for the colony was computed as

$$R_C^2 = 1 - \frac{\sum_{t=1}^T (\phi(c_t) - \phi(C_t))^2}{\sum_{t=1}^T (\phi(c_t) - \overline{\phi(c)})^2}$$

where $\overline{\phi(c)}$ denotes the sample mean of the transformed observations. The R_S^2 for sleep was computed similarly.

There are presently no good statistical hypothesis tests of goodness of fit for dynamic models. Indeed, it is not clear that such tests would be useful if they existed. More informative, in our opinion, is to evaluate the predictive performance of a model under as wide a variety of conditions as possible. Therefore, we use this generalized R^2 to quantify goodness of fit, and we use model validation analysis to probe the predictions of the model under environmental conditions encountered postestimation.

RESULTS

Best Model

The per capita transition rates r_{ij} for the best model are shown in Fig. 1. These rates are for the chick-rearing season; dynamics can be markedly different during other times of year.

Parameter Estimates

Fixed values of $\Psi = 0.01, 0.5$ and 1 for the best model yielded log-likelihood values of $-138, -3$ and 30 , respectively, for the calibration data set, and $-287, -22$ and 32 , respectively, for the entire data set. Thus, we took $\psi = 1$ as the appropriate transformation. The maximum likelihood parameter estimates for equation (3) with $\psi = 1$ are given in the legend for Fig. 1.

Model Validation

For the calibration data set, the goodness of fits were $R_C^2 = 0.60$ and $R_S^2 = 0.57$; for the validation data set, they were $R_C^2 = 0.63$ and $R_S^2 = 0.46$. The goodness of fits obtained by fitting the model to the entire data set were $R_C^2 = 0.65$ and $R_S^2 = 0.52$.

Figure 2 compares the data with one-step model predictions based on parameters estimated from the entire data set.

DISCUSSION

The Model

An alternative modelling formulation for behavioural data is the integer-valued Markov chain (e.g. Chen et al. 2002; Lusseau 2003), which accommodates the discrete nature of behaviour compartment membership. The Markov behaviour model casts animal behaviour as transitions among discrete behaviour types; the associated transition probabilities are collected into a projection matrix. Quite generally, the mean compartment sizes in such models are solutions to linear differential equations of the same form as our model. To focus on the effect of the six environmental covariates, we chose to build a ‘deterministic skeleton’ for the means and add ‘noise’ in a way that would potentially accommodate the ordinary variability of such Markov models as well as the variability arising from environmentally caused fluctuations in the transition probabilities. We used (continuous-time) differential equations as the deterministic skeleton rather than (discrete-time) difference equations because there was nothing inherently discrete in the timescale of the process other than our observations.

Demographic and Environmental Variability

The terms ‘demographic’ and ‘environmental’ variability can potentially cause confusion. In ecology, the terms refer to types of variability in population growth models. Mathematically, what ecologists refer to as demographic variability arises as the variability in the sum of a fixed number of independent random variables: the net birth and death contributions of n individuals in a time interval. Mathematically, environmental variability as used by ecologists refers to random changes through time in the rate constants (average per individual births and deaths) themselves, which characteristically induces a covariation of births and deaths among individuals.

These concepts directly describe the types of variability we are concerned with in the behaviour model. A ‘population’ is the number of animals in a behavioural state at time t ; this population increases or decreases based on arrivals (animals choosing the behaviour) and departures (animals changing to some other behaviour). If the number of animals engaged in a behaviour is the sum of independent random binary choices (1 or 0) of n individuals, then variability will be scaled in proportion to n , just as it is in a population growth model with demographic

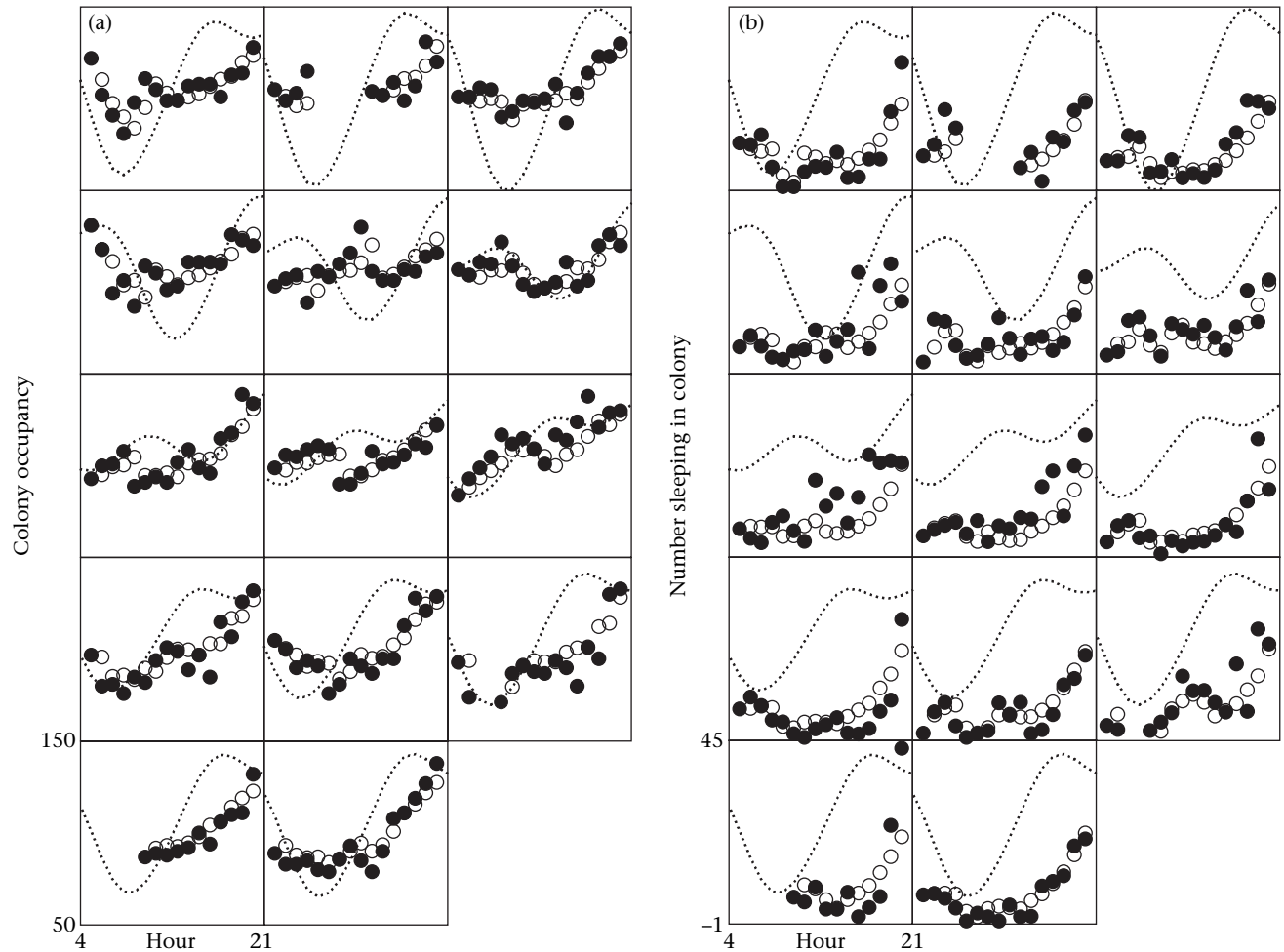


Figure 2. Hourly observations (solid circles), one-step model predictions (open circles), and tide height (dotted curve) as a function of time (PST). (a) Number of birds in the colony. (b) Number of birds asleep in the colony. In (a) and (b), 14 days of data are shown in chronological order from left to right, top to bottom.

variability. If the choice probability itself varies randomly through time, then the number of animals engaged in a behaviour has an additional component of variability whose scale is proportional to n^2 , as in the scaling of environmental noise in an ecological model.

The type of stochasticity implicit in a Markov chain is demographic; that is, individual animals in a particular behaviour state independently face fixed and identical probabilities of making a behaviour transition. Demographic stochasticity becomes essentially deterministic if large numbers of animals are governed by such a model, in that the relative variability (coefficient of variation) of the animal numbers displaying a behaviour becomes small.

Deterministic and Stochastic Fluctuations in the Colony Sleep System

In our application of the methodology outlined in this paper, we were able to show that the majority of the temporal fluctuations in colony occupancy and sleep incidence were deterministic. Furthermore, we were able

to identify six abiotic environmental factors that determined the dynamics of these variables. Note that the logical connection here between ‘environmental determinants’ and behavioural dynamics is that of mathematical implication rather than scientific causation. That is, environmental determinants are correlative, and may or may not be causative (Henson et al. 2005). Nevertheless, the identification of environmental determinants narrows the search for cues that elicit behaviour.

Results of our maximum likelihood analysis revealed that the fluctuations left unexplained by the model were largely due to environmental stochasticity rather than to demographic stochasticity or a mixture of the two. (This conclusion was based on our finding that $\psi = 1$ yielded higher log-likelihood values than did $\psi = 0.5$ or $\psi = 0.01$.) In a Markov chain formulation, this would mean that the transition probabilities themselves were undergoing stochastic fluctuations. Our approach of using a deterministic system of differential equations upholstered with a stochastic noise component allowed model fitting and evaluation under different hypothesized types of stochastic variability. The conclusion of environmental variability was consistent

with our observations of the system. In our application, we observed many environmental stochastic events such as disturbances by bald eagle, *Haliaeetus leucocephalus*, flyovers (Galusha & Hayward 2002). Demographic stochastic events such as between-individual differences in gull behaviour, the timings of arrivals and departures in the habitat and localized conspecific intrusions also occurred, but our analysis showed that these events contributed relatively little to the variability in the data. In theory, the large number of animals observed suggests that demographic variability should indeed be negligible.

Function

Predictive mathematical models can clarify the functions of behaviour and generate new hypotheses. We mention two examples from our current application. (1) The Midday per capita tendency to enter sleep increased with solar elevation and wind speed on the colony, and the tendency to leave sleep increased with heat index (Midday r_{SW} and r_{WS} in Fig. 1). This is consistent with a previous report of increased colony sleep at midday among herring gulls, *Larus argentatus*, in England (Galusha & Amlaner 1978) and also suggests a thermoregulatory function of the sleep posture. (2) The Morning per capita rate at which birds left the colony was constant, while the per capita rate of return increased with tide height (Morning r_{AW} and r_{WA} in Fig. 1). This is consistent with previous reports of decreased/increased habitat occupancy in gulls at low/high tide, presumably because of increased/decreased food availability at low/high water levels (Drent 1967; Galusha & Amlaner 1978; Henson et al. 2004). In another report, however, a mathematical model suggested more specifically that gulls left loafing habitats (near a colony) in response to low tide height and returned in response to low solar elevation (Henson et al. 2005). It is unclear, however, whether the contradiction with the current study is due to differences in behaviour of gulls in the colony versus away from the colony, or whether it is an artefact of insufficient data. These two examples illustrate that each of the per capita flow rates shown in Fig. 1 generates new hypotheses and suggests further study.

Mathematical Models as Hypotheses

A mathematical model is the precise formulation of 'modelling assumptions'. In our application, these included the assumptions regarding the three compartments W , S and A , the specific form of the f_{ij} as given in equation (2) and the general form of r_{ij} as given in equation (4). Modelling assumptions, and therefore mathematical models, are actually scientific hypotheses. These hypotheses can be tested rigorously with data, not in the sense of statistical hypothesis testing, but in the sense of applied dynamical systems theory, through parameter estimation, comparison of alternative models, model selection and model validation (Cushing et al. 2003; Hayward et al. 2005). To be taken seriously as scientific hypotheses, mathematical models must transcend mere

curve fitting. That is, the models should be motivated by a mechanistic understanding of the system in question and have predictive capability. Model validation, performed on data not used to estimate parameters, is therefore of particular importance, since it tests the predictive capability of the model.

Summary

Mathematical models can identify, explain and predict deterministic trends in behaviour, and parse out the contributions of environmental and demographic stochasticity. Such models are powerful tools for detecting factors that elicit behaviour, for clarifying functions of behaviour and for generating new hypotheses. Although compartmental models are standard tools in the physical sciences, pharmacology, epidemiology and population biology (Anderson 1983), they have been considered too coarse to predict animal behaviour, because they lump individuals into aggregates under simplifying assumptions (Railsback 2001). Using compartmental modelling techniques, however, we have shown that some behaviours of gulls are determined largely by environmental factors and are mathematically predictable at the aggregate level despite variability among individuals. We suggest that compartmental models may provide a new approach to the study of deterministic trends in the behaviour of animals and humans.

Acknowledgments

We thank K. Ryan, U.S. Department of the Interior Fish and Wildlife Service, for permission to work on Protection Island National Wildlife Refuge, Walla Walla College Marine Station for logistical support, and S. P. Damania and K. W. Phillips for field assistance. This research was supported by Andrews University faculty grants and U. S. National Science Foundation grant DMS 0314512 (S.M.H. and J.L.H.).

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