Predicting the dynamics of animal behaviour in field populations

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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

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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 compartment who were eligible to enter the S compartment was $\alpha C \quad S$, where $0 < \alpha \quad 1$, as long as $\alpha C \quad S$ was positive, and zero otherwise; that is, $f_{SW} \quad \max\{\alpha C \quad S, 0\}$. We interpret the coefficient α as the fraction of birds in the colony

A weather station 2 m above site elevation on the northwest 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).

S b r_{ij}

Complete specification of equation (3)

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 $\langle \phi(c_t) - \phi(C_t), \phi(s_t) - \phi(S_t) \rangle$ of transformed one-step residual errors come from a joint normal distribution with variance−covariance matrix $\sum$,

with our observations of the system. In our application, we observed many environmental stochastic events such as

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