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Predicting the dynamics of animal behaviour in field populations

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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.

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

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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 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

$$\frac{dB}{dt} = r_{BE}f_{BE} - r_{EB}f_{EB}$$
$$\frac{dE}{dt} = r_{EB}f_{EB} - r_{BE}f_{BE},$$

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

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

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 unihemispheral 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