

# Identifying Environmental Determinants of Diurnal Distribution in Marine Birds and Mammals

Shandelle M. Henson<sup>a,\*</sup>, James L. Hayward<sup>b</sup>, Smruti P. Damania<sup>b</sup>

<sup>a</sup>Department of Mathematics, Andrews University, Berrien Springs, MI 49104, USA

<sup>b</sup>Biology Department, Andrews University, Berrien Springs, MI 49104, USA

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**Abstract** Marine birds and mammals move between various habitats during the day as they engage in behaviors related to resting, sleeping, preening, feeding, and breeding. The per capita rates of movement between these habitats, and hence the habitat occupancy dynamics, often are functions of environmental variables such as tide height, solar elevation, wind speed, and temperature. If the system recovers rapidly after disturbance, differential equation models of occupancy dynamics can be reduced to algebraic equations on two time scales. Identification of environmental factors that influence movement between habitats requires time series census data collected in both the absence and presence of disturbance.

**Keywords** Akaike information criterion · Animal behavior · Differential equation model · Environmental forcing · Time-scale analysis

## 1. Introduction

### 1.1. General

Animals move from habitat to habitat during the day as they engage in various behaviors related to feeding, resting, and breeding. The timing of the transitions between habitat patches often depends on exogenous conditions. This is particularly true for marine birds and mammals, whose movements typically are influenced by environmental variables such as time of day, tide height, current speed, heat index, and wind speed (e.g., Delius, 1970; Galusha and Amlaner, 1978; Schneider and Payne, 1983; Stewart, 1984; Thompson et al., 1989, 1997; Watts, 1992; Henson et al., 2004; Hayward et al., 2005; Damania et al., 2005).

When temporarily disturbed by predators or humans, the abundance and distribution of marine animals in a system of habitat patches may recover rapidly relative to the rate of change of environmental variables (Henson et al., 2004;

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\*Corresponding author.

E-mail address: henson@andrews.edu (Shandelle M. Henson).

Hayward et al., 2005; Damania et al., 2005). That is, the environment may be assumed to remain constant while the system returns to its predisturbance state. Such a system is said to operate on two time scales, the fast time scale of the recovery, and the slow time scale of the environmental variables. The abundance dynamics during recovery are known as “transient,” and the dynamics after recovery are called “steady state.” Note that steady state dynamics are not necessarily equilibrium dynamics; they can also be periodic or aperiodic.

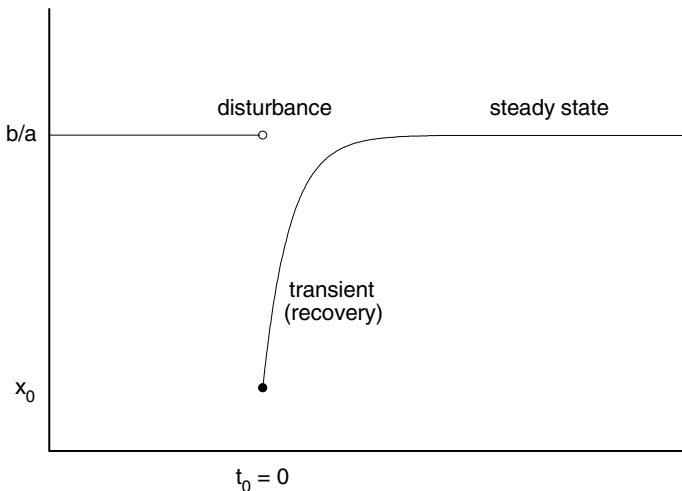
In this paper we show that the identification of environmental correlates for movement between habitat patches requires data collected both in the presence and absence of disturbance. In particular, environmental cues for movement cannot be determined uniquely if data are collected only during steady state dynamics.

### 1.2. Theoretical

Parameter estimation for a mathematical model generally requires data collected during both transient and steady state dynamics. For example, consider an autonomous linear model

$$\frac{dx}{dt} = -ax + b \quad (1)$$

of a single habitat patch, where  $x(t)$  is the occupancy at time  $t$  and the coefficients  $a, b > 0$  are unknown constants to be determined from census data. The steady state is the equilibrium  $x_e = b/a$ . Suppose the habitat suffers a disturbance (after which we set  $t = 0$ ) such that the postdisturbance habitat occupancy is  $x(0) = x_0 \neq b/a$  (Fig. 1). Elementary techniques from differential equations yield the particular solution



**Fig. 1** Dynamics of Eq. (1) with a disturbance at time  $t = 0$ .

$$x(t) = (x_0 - b/a)e^{-at} + b/a. \quad (2)$$

The first term of the solution (2) describes the transient dynamics; the second term describes the steady state (in this case equilibrium) dynamics. As  $t$  increases, the transient dynamics die out and the second term takes over. If the transients die out quickly enough, census intervals may miss most transient effects due to system disturbances, so that data are collected only during steady state dynamics when  $x(t) \approx b/a$ . In this case the ratio  $b/a$  can be estimated from the data, but the individual parameters  $a$  and  $b$  are not uniquely determined. If, on the other hand, data are also collected immediately after disturbance, then the exponential rate  $a$  of return to steady state can be estimated from (2). If both  $b/a$  and  $a$  are known, then the parameter  $b$  can be determined as well. The point is that parameter estimation requires data collected during both transient and steady state dynamics.

In this paper we consider nonautonomous linear models of habitat patch dynamics in which the coefficients are *unknown functions* of environmental variables, to be determined from census data. In particular, we consider a population or other group in which individuals move among  $n$  censused habitat patches during the day, and where the per capita flow rates  $r_{ij}$  from habitat  $j$  to habitat  $i$  ( $i \neq j$ ) are functions of environmental variables. For example, the per capita flow rate from habitat 2 to habitat 1 might be proportional to tide height  $T(t)$  and wind speed  $W(t)$ , that is,  $r_{12}(t) = \alpha_{12}T(t)W(t)$ , where  $\alpha_{12} > 0$  is a constant. If we lump all noncensused locations into an  $(n + 1)^{\text{st}}$  “habitat patch,” then there are  $n(n + 1) = n^2 + n$  per capita flow rate functions  $r_{ij}$  ( $i \neq j$ ). Such models have been used to explain and predict the diurnal abundance dynamics of seabirds and seals (Henson et al., 2004; Hayward et al., 2005; Damania et al., 2005).

By “a set of environmental determinants” we will mean a set of functions of environmental variables that determine the dynamics of the system. For example, the set  $\{r_{ij}\}$  of all per capita flow rate functions is a set of environmental determinants in the sense that if one knows the identity of, and has data for, all the  $r_{ij}$ , then one can predict the diurnal abundance dynamics for each habitat. Note that the logical connection between the environmental determinants and the dynamics is that of mathematical implication rather than scientific causation. That is, environmental determinants are correlative, but may or may not be causative.

The set  $\{r_{ij}\}$  of environmental determinants has  $n^2 + n$  members. Two related questions naturally arise:

1. Is it necessary to know all of the  $n^2 + n$  per capita flow rate functions  $r_{ij}$  in order to predict the census dynamics?
2. Given census data alone, can one recover the  $n^2 + n$  per capita flow rate functions  $r_{ij}$ ?

If one’s primary purpose is prediction, for example with the purpose of management, then one might hope the answer to question 1 is “no,” in which case the answer to question 2 is “no” as well. It might be convenient for the purposes of prediction if there were a set of environmental determinants that was smaller than the set  $\{r_{ij}\}$ . If, however, one’s primary purpose is to test hypotheses regarding environmental cues for animal movement, then one would hope the answer to

question 2 is “yes,” in which case the answer to question 1 is “yes” as well. In this paper we show that the answers to these questions are time scale dependent.

Section 2 describes the modeling assumptions and general model. Section 3 reduces the model on two time scales. We show that steady state dynamics are governed by a set of  $n$  environmental determinants, thus making it impossible to infer uniquely the identity of the  $n^2 + n$  flow rate functions  $r_{ij}$  from steady state census data alone. Section 4 illustrates the theory by reviewing three modeling studies that have been done with field data on marine birds and mammals collected from systems with  $n = 1$  and  $n = 2$  in the absence of disturbance. In Section 5 we revisit one of these studies to show how the  $r_{ij}$  may be identified uniquely if census data are collected in the presence, as well as in the absence, of disturbance.

## 2. Linear model of habitat occupancy dynamics

The model is based on the following assumptions:

- (A1) Animals move between  $n + 1$  different habitat patches during the day in direct response to environmental conditions. Habitats 1 through  $n$  are specific locations that can be censused. Habitat  $n + 1$  consists of everywhere not included in habitats 1 to  $n$ .
- (A2) The total number of animals in the system is given by a known function  $K(t)$  that is relatively constant over short periods of time but varies by season.
- (A3) Animals move from habitat  $j$  to habitat  $i$  ( $i \neq j$ ) at a per capita rate of  $r_{ij}(t) = \alpha_{ij} E_{ij}(t)$ , where  $E_{ij}(t)$  is a function of environmental variables and  $\alpha_{ij} > 0$  is a constant parameter. In particular, the per capita flow rates are density-independent. Animals that leave habitat  $j$  and return directly to habitat  $j$  without stopping in another habitat are assumed to have remained in habitat  $j$  during that time. Thus, although we use  $r_{jj}$  as a formal variable, we set  $r_{jj} = 0$  for each  $j$ .
- (A4) The system returns rapidly to steady state dynamics after perturbation. That is, after a disturbance,  $K(t)$  and all of the  $E_{ij}(t)$  can be considered constant during system recovery.

Let  $x_i(t)$  be the number of animals in habitat  $i$  at time  $t$ . Given (A2), we can eliminate  $x_{n+1}$  by writing

$$x_{n+1}(t) = K(t) - \sum_{j=1}^n x_j(t).$$

The dynamics of the  $i$ th habitat for  $i = 1, 2, \dots, n$  can be described by

$$\begin{aligned} x'_i(t) &= \sum \text{inflow rates} - \sum \text{outflow rates} \\ &= \sum_{j=1}^n r_{ij}(t)x_j + r_{i,n+1}(t) \left( K(t) - \sum_{j=1}^n x_j \right) - \sum_{j=1}^{n+1} r_{ji}(t)x_i. \end{aligned}$$

Our model is therefore a nonautonomous  $n$ -dimensional linear system of the form

$$\mathbf{x}'(t) = \mathbf{A}(t)\mathbf{x} + \mathbf{b}(t), \tag{3}$$

where

$$\mathbf{x} = \begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix}, \quad \mathbf{b} = \begin{pmatrix} r_{1,n+1}K \\ \vdots \\ r_{n,n+1}K \end{pmatrix},$$

and

$$\mathbf{A} = \begin{pmatrix} r_{11} - r_{1,n+1} - \sum_{j=1}^{n+1} r_{j1} & r_{12} - r_{1,n+1} & \cdots & r_{1,n} - r_{1,n+1} \\ r_{21} - r_{2,n+1} & r_{22} - r_{2,n+1} - \sum_{j=1}^{n+1} r_{j2} & r_{23} - r_{2,n+1} & r_{2n} - r_{2,n+1} \\ \vdots & \vdots & \ddots & \vdots \\ r_{n1} - r_{n,n+1} & r_{n2} - r_{n,n+1} & \cdots & r_{nn} - r_{n,n+1} - \sum_{j=1}^{n+1} r_{jn} \end{pmatrix}. \tag{4}$$

Models of this form have been used to predict the diurnal abundance dynamics of seabirds loafing on a pier ( $n = 1$ ) (Henson et al., 2004), explain haul-out dynamics in seals ( $n = 1$ ) (Hayward et al., 2005), and model the diurnal movements of seabirds among four habitats at a Washington colony ( $n = 1, 2, 3$ ) (Damania et al., 2005).

### 3. Two time scales

In general, a solution formula for Eq. (3) cannot be found, since the per capita flow rates  $r_{ij}(t) = \alpha_{ij} E_{ij}(t)$  are functions of environmental variables which themselves may have no closed formula. Given assumption (A4), however, it is possible to construct closed algebraic formulas that approximate both the transient and steady state dynamics of the system. We first derive an equation for the steady state, and then consider the transient dynamics. Because the mathematical techniques are standard, our derivations will be formal; the details of time-scale analysis are made precise elsewhere (e.g. Hoppensteadt, 1974; Tikhonov, 1985). We henceforth assume that model (3) has been nondimensionalized so that the time-scale results will not depend on the units in a particular application. We also assume that the matrix  $\mathbf{A}(t)$  in Eq. (4) is invertible for all  $t$ .

Let  $t = 0$  correspond to a disturbance. Suppose  $t = 1$  corresponds to the time at which system recovery can be considered complete. (This change of variables is accomplished by normalizing the original time variable by the recovery time, producing a dimensionless quantity  $t$ .) Given assumption (A4), there is an  $\varepsilon > 0$  with  $\varepsilon \ll 1$  such that the entries of  $\mathbf{x}'(t)$  are large relative to the entries of  $\mathbf{A}'(t)$

and  $\mathbf{b}'(t)$  for  $0 < t < \varepsilon$ . This “inner boundary layer”  $0 < t < \varepsilon$  characterizes the time of rapid change near the initial condition, that is, the initial part of the system recovery during which the environment can be considered constant.

### 3.1. Steady state: dynamics in the absence of disturbance

Define new state variables and coefficient functions by

$$\mathbf{y}(t) = \mathbf{x}\left(\frac{t}{\varepsilon}\right)$$

$$\bar{\mathbf{A}}(t) = \mathbf{A}\left(\frac{t}{\varepsilon}\right)$$

$$\bar{\mathbf{b}}(t) = \mathbf{b}\left(\frac{t}{\varepsilon}\right).$$

Then

$$\begin{aligned} \mathbf{y}'(t) &= \frac{1}{\varepsilon} \mathbf{x}'\left(\frac{t}{\varepsilon}\right) \\ &= \frac{1}{\varepsilon} \left( \mathbf{A}\left(\frac{t}{\varepsilon}\right) \mathbf{x}\left(\frac{t}{\varepsilon}\right) + \mathbf{b}\left(\frac{t}{\varepsilon}\right) \right), \end{aligned}$$

and so

$$\varepsilon \mathbf{y}'(t) = \bar{\mathbf{A}}(t) \mathbf{y}(t) + \bar{\mathbf{b}}(t).$$

If  $t > \varepsilon$  so that  $\mathbf{y}'(t)$  is not too large, then since  $\varepsilon$  is small we have

$$0 \approx \bar{\mathbf{A}}(t) \mathbf{y}(t) + \bar{\mathbf{b}}(t).$$

The “outer approximation” to the solution of (3) is therefore given by

$$\mathbf{y}_{\text{out}}(t) = -\bar{\mathbf{A}}^{-1}(t) \bar{\mathbf{b}}(t)$$

for  $t > \varepsilon$ . In the original variables, the outer solution is

$$\mathbf{x}_{\text{out}}(t) = -\mathbf{A}^{-1}(t) \mathbf{b}(t) \tag{5}$$

for  $t > 1$ .

In the absence of disturbance, the dynamics of system (3) are governed approximately by the algebraic system (5). We can produce formulas for the individual habitats  $x_i(t)$  by writing (5) as

$$\mathbf{A} \mathbf{x}_{\text{out}} = \mathbf{h}K,$$

where

$$\mathbf{h} = -\mathbf{b}/K = \begin{pmatrix} -r_{1,n+1} \\ \vdots \\ -r_{n,n+1} \end{pmatrix}.$$

Then by Cramer’s Rule,

$$x_i(t) = \frac{\det \mathbf{A}_i(t)}{\det \mathbf{A}(t)} K(t) \tag{6}$$

for each  $i$ , where  $\mathbf{A}_i(t)$  is the matrix formed by replacing the  $i$ th column of  $\mathbf{A}(t)$  by the vector  $\mathbf{h}(t)$ .

The function  $\det \mathbf{A}_i(t)/\det \mathbf{A}(t)$  is a function of the per capita flow rates  $r_{ij}$ , which are in turn functions of environmental variables. The set of  $n$  functions of the form  $K(t) \det \mathbf{A}_i(t)/\det \mathbf{A}(t)$  is a set of environmental determinants for the steady state dynamics of the system. More than one set of flow rates  $r_{ij}$  may give rise to the same set of functions  $K \det \mathbf{A}_i/\det \mathbf{A}$ , as we will see in Section 4. Thus, in general it is not necessary to know all of the  $n^2 + n$  per capita flow rate functions  $r_{ij}$  in order to predict the steady state census dynamics; it is sufficient to know the  $n$  functions  $K \det \mathbf{A}_i/\det \mathbf{A}$ . And, in general the identity of the  $n^2 + n$  flow rate functions  $r_{ij}$  cannot be identified uniquely from steady state census data alone.

### 3.2. Transients: post-disturbance dynamics

System (3) can be written as

$$\mathbf{x}'(t) = \bar{\mathbf{A}}(\varepsilon t)\mathbf{x}(t) + \bar{\mathbf{b}}(\varepsilon t).$$

When  $0 < t < \varepsilon$ , we can approximate system (3) with the autonomous equation

$$\begin{aligned} \mathbf{x}'(t) &= \bar{\mathbf{A}}(0)\mathbf{x}(t) + \bar{\mathbf{b}}(0) \\ &= \mathbf{A}(0)\mathbf{x}(t) + \mathbf{b}(0). \end{aligned} \tag{7}$$

The “inner approximation” to the solution of (3) is therefore given by the solution

$$\mathbf{x}_{in}(t) = \Phi(t)\Phi^{-1}(0)[\mathbf{x}(0) + \mathbf{A}(0)^{-1}\mathbf{b}(0)] - \mathbf{A}(0)^{-1}\mathbf{b}(0) \tag{8}$$

of Eq. (7), where  $\Phi(t)$  is the fundamental solution matrix of the associated homogeneous equation  $\mathbf{x}'(t) = \mathbf{A}(0)\mathbf{x}(t)$ .

Immediately after a disturbance, the dynamics of system (3) are governed approximately by the algebraic system (8).

## 4. Steady state examples from field ecology

We now illustrate the theory by reviewing three examples from field data. The first example, taken from Hayward et al. (2005), features a model of steady state seal

haul-out dynamics with  $n = 1$ . The ratio  $r_{21}/r_{12}$  of the two flow rate functions was determined, but the individual  $r_{12}$  and  $r_{21}$  could not be determined uniquely from steady state data alone. The second example, taken from Henson et al. (2004), is a steady state model of seabird loafing behavior with  $n = 1$ . The third example, a steady state seabird model with  $n = 2$  from Damania et al. (2005), is included to illustrate the theory in two dimensions.

#### 4.1. Example 1: harbor seals with $n = 1$

Hayward et al. (2005) modeled the diurnal haul-out dynamics of harbor seals (*Phoca vitulina*) at Protection Island National Wildlife Refuge, Washington. The differential equation model was

$$\frac{dx}{dt} = \alpha_{12} E_{12}(t)(K(t) - x) - \alpha_{21} E_{21}(t)x,$$

where  $x(t)$  is the number of seals hauled out on the north beach of Violet Point at hour  $t$ ,  $r_{12} = \alpha_{12} E_{12}(t)$  is the per capita flow rate of seals to the beach,  $r_{21} = \alpha_{21} E_{21}(t)$  is the per capita flow rate of seals away from the beach, and  $K(t)$  is the total number of seals that may choose to haul out. See Hayward et al. (2005) for the functional form of  $K(t)$ . Under the assumption of two time scales, the outer solution

$$x_{\text{out}}(t) = \frac{K(t)}{1 + \frac{\alpha_{21} E_{21}(t)}{\alpha_{12} E_{12}(t)}} = \frac{K(t)}{1 + \alpha E(t)} \quad (9)$$

of the differential equation was used as the general model for steady state haul-out dynamics, where  $\alpha = \alpha_{21}/\alpha_{12}$  and  $E(t) = E_{21}(t)/E_{12}(t)$ .

An array of specific hypotheses was posed regarding the identity of  $E(t)$ , giving rise to a suite of alternative models of the form (9). Hourly census data collected in the absence of disturbance were used to parameterize each of the competing models, and the Akaike Information Criterion (AIC) (Burnham and Anderson, 2002) was invoked to choose the best one. The best model was the one with

$$E(t) = \frac{E_{21}(t)}{E_{12}(t)} = \frac{[C(t)]^a}{[T(t)]^b}, \quad (10)$$

where  $T(t)$  and  $C(t)$  are the nondimensionalized tide height and current, respectively, with  $1 \leq T(t)$ ,  $C(t) \leq 2$ , and  $\alpha = 2.607$ ,  $a = 2.737$ , and  $b = 4.014$ . Of course, Eq. (10) does not imply that  $E_{21} = C^a$  and  $E_{12} = T^b$ .

Hayward et al. (2005) did not have census data representing recovery after disturbance. Hence, the identity of the individual functions  $E_{21}$  and  $E_{12}$  could not be inferred from the census data alone. Hayward et al. posed three possibilities

$$(H1) \quad E_{21} = \frac{1}{T^b} \quad \text{and} \quad E_{12} = \frac{1}{C^a}$$



$$(H2) E_{21} = \sqrt{\frac{C^a}{T^b}} \quad \text{and} \quad E_{12} = \sqrt{\frac{T^b}{C^a}}$$

$$(H3) E_{21} = C^a \quad \text{and} \quad E_{12} = T^b,$$

and proposed to collect census data at small time intervals following disturbances in order to test which possibility was correct.

4.2. Example 2: seabirds with  $n = 1$

Henson et al. (2004) modeled the diurnal abundance dynamics of loafing Glaucous-winged Gulls (*Larus glaucescens*) on a pier at Protection Island National Wildlife Refuge, Washington. They found that the number of gulls  $x(t)$  on the pier at time  $t$  could be modeled by the differential equation

$$\frac{dx}{dt} = \alpha \frac{T(t)}{S(t)}(K(t) - x) - \frac{1}{\alpha} \frac{S(t)}{T(t)}x, \tag{11}$$

where  $T(t)$  and  $S(t)$  were the nondimensionalized tide height and solar elevation,  $K(t)$  was the total number of birds in the system, and  $\alpha > 0$  was a parameter. See Henson et al. (2004) for the functional form of  $K(t)$ .

The data used to parameterize and validate model (11) were collected hourly; counts occurring less than 30 min after a disturbance were eliminated from the data set (Henson et al., 2004). Henson et al. noted that recovery after disturbance was rapid (less than 30 min), and that the steady state dynamics of both model (11) and data were well approximated by the outer solution

$$x_{\text{out}}(t) = \frac{K(t)}{1 + \frac{1/\alpha}{\alpha} \frac{S(t)/T(t)}{T(t)/S(t)}} = \frac{K(t)}{1 + \frac{1}{\alpha^2} \left(\frac{S(t)}{T(t)}\right)^2}. \tag{12}$$

In fact, however, any differential equation of the form

$$\frac{dx}{dt} = \alpha_{12} E_{12}(t)(K(t) - x) - \alpha_{21} E_{21}(t)x \tag{13}$$

on two time scales with

$$\frac{E_{21}(t)}{E_{12}(t)} = \left(\frac{S(t)}{T(t)}\right)^2 \tag{14}$$

and

$$\frac{\alpha_{21}}{\alpha_{12}} = \frac{1}{\alpha^2} \tag{15}$$

would have produced the same steady state Eq. (12). This begs the question of whether the particular structure of differential equation model (11) as given in

Henson et al. (2004) was functionally correct. Were the per capita flow rates really proportional to  $E_{12} = T/S$  and  $E_{21} = S/T$ , or might they have been some other combination yielding the same ratio (14), for example  $E_{12} = T^2$  and  $E_{21} = S^2$ ? According to the theory, disturbance data are required in order to answer this question. We will return to this example in Section 5.

#### 4.3. Example 3: seabirds with $n = 2$

Damania et al. (2005) modeled the diurnal distribution of loafing Glaucous-winged Gulls as they moved between a pier, a marina, and elsewhere. The differential equation model was

$$\begin{aligned}\frac{dx_1}{dt} &= \alpha_{12} E_{12} x_2 + \alpha_{13} E_{13} (K - x_1 - x_2) - \alpha_{21} E_{21} x_1 - \alpha_{31} E_{31} x_1 \\ \frac{dx_2}{dt} &= \alpha_{21} E_{21} x_1 + \alpha_{23} E_{23} (K - x_1 - x_2) - \alpha_{12} E_{12} x_2 - \alpha_{32} E_{32} x_2,\end{aligned}$$

where  $x_1(t)$  and  $x_2(t)$  represent the number of gulls on the pier and in the marina, respectively, at hour  $t$ . The value of  $K$  was assumed constant. Here

$$\mathbf{A} = \begin{pmatrix} -r_{13} - r_{21} - r_{31} & r_{12} - r_{13} \\ r_{21} - r_{23} & -r_{23} - r_{12} - r_{32} \end{pmatrix},$$

where  $r_{ij} = \alpha_{ij} E_{ij}(t)$ . The outer solution  $\mathbf{x}_{\text{out}}$  is given by

$$\begin{aligned}x_1 &= \frac{K}{1 + \left[ \frac{(r_{21}r_{13} + r_{21}r_{23} + r_{31}r_{23}) + (r_{12}r_{31} + r_{21}r_{32} + r_{31}r_{32})}{r_{12}r_{13} + r_{12}r_{23} + r_{13}r_{32}} \right]} \\ x_2 &= \frac{K}{1 + \left[ \frac{(r_{12}r_{13} + r_{12}r_{23} + r_{13}r_{32}) + (r_{12}r_{31} + r_{21}r_{32} + r_{31}r_{32})}{r_{21}r_{13} + r_{21}r_{23} + r_{31}r_{23}} \right]}.\end{aligned}\tag{16}$$

The best model selected from a suite of biologically reasonable alternatives had per capita flow rates

$$\begin{aligned}r_{12} &= \alpha_{12} \frac{\text{hour}}{\text{temp}^2}; \quad r_{13} = 0; \quad r_{21} = \alpha_{21} \text{temp}^3; \quad r_{23} = \alpha_{23} \text{temp}^2 \cdot \text{hour} \\ r_{31} &= \alpha_{31} \frac{\text{sun}^3}{\text{tide}^3}; \quad r_{32} = \alpha_{32} \frac{1}{\text{temp}^2 \cdot \text{tide}},\end{aligned}\tag{17}$$

where *hour*, *temp*, *sun*, and *tide* were the nondimensionalized hour of the day, temperature, solar elevation, and tide height, respectively.

During model selection and parameterization, it was obvious that the inverse problem was not well-posed; that is, many sets of parameters (and various combinations of environmental variables) could give rise to similar model predictions.

**5. Identifying environmental determinants with disturbance data**

In this section we tentatively extend the analysis of Henson et al. (2004) as described in Example 2 by attempting to identify uniquely the flow rate functions of seabirds to and from the pier. To do this, we collected data from eight controlled pier disturbances during the summer of 2004.

The disturbances were conducted at a variety of combinations of solar elevations and tide heights. Each disturbance involved two researchers, a “disturber” and an “observer.” The observer filmed the disturbances with a digital video camera from a blind atop a 33-m bluff at least 100 m from the pier. Before each disturbance, the observer started the video recorder, counted the number of birds on the pier, and signaled to the disturber below. The disturber then walked onto the pier, causing some, but not necessarily all, of the birds to take flight. The disturber remained on the pier until the disturbed birds, many of which initially circled overhead, had dispersed to other locations. The disturber then walked off the pier, and at this instant the observer noted the number of birds remaining on the pier. The time at which the disturber left the pier was taken to be  $t = 0$ , the initial time for the recovery, and the number of birds on the pier at time  $t = 0$  was taken to be the initial condition  $x_0$  for the recovery. The observer continued to videotape the pier until the occupancy had recovered to at least 75% of the original occupancy prior to the disturbance (this typically required less than 20 min). The beginning of the recoveries ( $t = 0$ ) occurred at 19:44:40 on 6 June, 18:30:00 on 28 June, 13:05:05 on 11 July, 07:01:24 on 13 July, 15:02:11 on 14 July, 14:01:26 on 15 July, 17:02:40 on 15 July, and 09:59:10 on 16 July, 2004, Pacific Standard Time (PST).

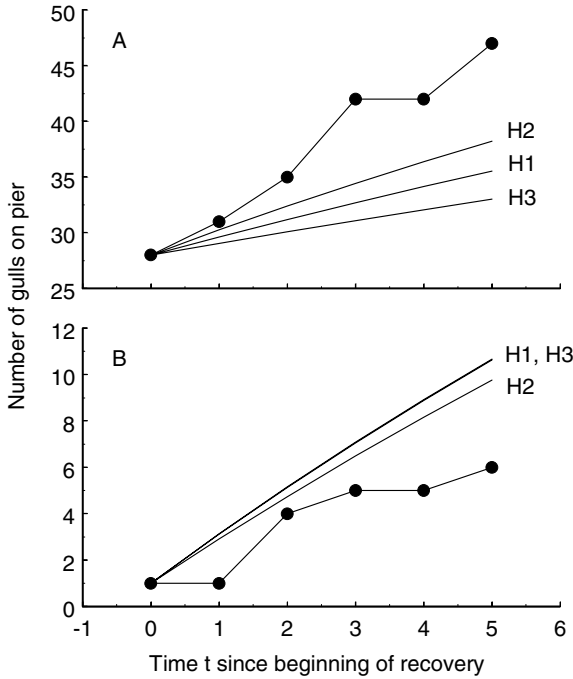
The videos were used to identify each time during the recovery at which a bird arrived at or departed from the pier. These data were then used to construct “recovery time series” for the numbers of birds on the pier at each minute for 5 min following the disturbances (Fig. 2). We used the following procedure to identify  $E_{12}(t)$  and  $E_{21}(t)$  from the collection of recovery time series, given that  $E_{21}/E_{12} = S^2/T^2$  (see Example 2):

(1) The inner solution of Eq. (13) was written as

$$\begin{aligned}
 x_{in}(t) &= \left( x_0 - \frac{K(0)}{1 + \frac{\alpha_{21} E_{21}(0)}{\alpha_{12} E_{12}(0)}} \right) e^{-[\alpha_{12} E_{12}(0) + \alpha_{21} E_{21}(0)]t} + \frac{K(0)}{1 + \frac{\alpha_{21} E_{21}(0)}{\alpha_{12} E_{12}(0)}} \\
 &= (x_0 - x_{out}(0)) e^{-\alpha_{12} [E_{12}(0) + (1/\alpha^2) E_{21}(0)]t} + x_{out}(0), \tag{18}
 \end{aligned}$$

where

$$x_{out}(0) = \frac{K(0)}{1 + \frac{1}{\alpha^2} \left( \frac{S(0)}{T(0)} \right)^2},$$



**Fig. 2** Two of the recovery time series from the pier disturbances. The *circles* are census counts at each minute during the first 5 min of recovery after disturbance. The *curves* show the fitted model predictions. A. Time series from 6 June 2004 at 19:44:40 PST. The nondimensionalized tide and solar elevation were 1.97 and 1.05, respectively (a high tide at sundown). B. Time series from 14 July 2004 at 15:02:11 PST. The nondimensionalized tide and solar elevation were 1.85 and 1.74, respectively (a fairly high tide in mid-afternoon).

$x_0$  is the initial number of animals (at  $t = 0$ , the beginning of the recovery), and  $1/\alpha^2 = \alpha_{21}/\alpha_{12}$  (see Example 2).

- (2) The value of  $\alpha$  estimated in Henson et al. (2004) was substituted into Eq. (18). The values of  $x_0$ ,  $T(0)$ ,  $S(0)$ , and  $K(0)$  were known (and different) for each recovery time series. The unknown quantities in Eq. (18) were therefore  $\alpha_{12}$ ,  $E_{12}(0)$ , and  $E_{21}(0)$ .
- (3) We made three a priori hypotheses regarding the identity of  $E_{12}(t)$  and  $E_{21}(t)$ :

$$(H1) \ E_{12} = \frac{T}{S} \left( \text{and hence } E_{21} = \frac{S}{T} \right)$$

$$(H2) \ E_{12} = \frac{1}{S^2} \left( \text{and hence } E_{21} = \frac{1}{T^2} \right)$$

$$(H3) \ E_{12} = T^2 \left( \text{and hence } E_{21} = S^2 \right).$$

The first hypothesis implies that the gulls responded to both tide height and solar elevation (or correlates thereof), whether on the pier or away. The second

**Table 1** Goodness-of-fit and model selection.

	AIC	$\Delta_{AIC}$	$R^2$
(H1)	149	12	0.91
(H2)	137	0	0.93
(H3)	159	22	0.89

implies that birds on the pier responded to tide height, while those away from the pier responded to solar elevation. The third implies that birds on the pier responded to solar elevation, while those away responded to tide height.

- (4) From the three hypotheses (H1)–(H3), we formed three alternative models, also designated (H1)–(H3):

$$(H1) \ x_{in}(t) = (x_0 - x_{out}(0)) e^{-\alpha_{12}[T(0)/S(0)+(1/\alpha^2)S(0)/T(0)]t} + x_{out}(0)$$

$$(H2) \ x_{in}(t) = (x_0 - x_{out}(0)) e^{-\alpha_{12}[1/S^2(0)+(1/\alpha^2)1/T^2(0)]t} + x_{out}(0)$$

$$(H3) \ x_{in}(t) = (x_0 - x_{out}(0)) e^{-\alpha_{12}[T^2(0)+(1/\alpha^2)S^2(0)]t} + x_{out}(0),$$

where

$$x_{out}(0) = \frac{K(0)}{1 + \frac{1}{\alpha^2} \left( \frac{S(0)}{T(0)} \right)^2}.$$

- (5) Model (H1) was fitted to the entire collection of recovery time series by estimating the free parameter  $\alpha_{12}$  via the method of nonlinear least squares. The appropriate experimental values of  $x_0$ ,  $T(0)$ ,  $S(0)$ , and  $K(0)$  were used for each time series. Note that the fitted (H1) predictions in Fig. 2 do not pass through the data of the two recovery time series shown. This is because we did not fit each time series separately, but rather required model (H1) to fit all of the recovery time series (with their variety of initial habitat occupancies and environmental conditions) using the same value of  $\alpha_{12}$ . This fitting procedure was carried out for models (H2) and (H3) as well.

- (6) We used the AIC to select the best model from the suite of three alternatives (Table 1; Fig. 2).

Model (H2) had the highest  $R^2 = 0.93$  and lowest  $AIC = 137$ . Since the difference between the AIC for this model and the next best model was  $\Delta_{AIC} = 12 > 10$ , hypothesis (H2) can be considered significantly better than (H1) (Burnham and Anderson, 2002).

This result supports the functional hypothesis that birds on the pier leave in response to low tide height, while those away from the pier return in response to low solar elevation. The result is consistent with a pier-marina-beach-elsewhere model ( $n = 3$ ) presented by Damania et al. (2005), in which flows from all three loafing habitats into the elsewhere category were driven primarily by a low tide. It is also consistent with other studies that suggest gulls leave loafing habitats at low

tide, probably as a result of increased food availability (Patterson, 1965; Drent, 1967; Delius, 1970; Galusha and Amlaner, 1978; Wondolowski, 2002).

More than eight recovery time series are needed to make a convincing case that hypothesis H2 identifies the correct per capita flow rates. We plan to record at least 12 more disturbances in the summer of 2006.

## 6. Discussion

Abiotic components of the environment can play crucial roles in determining the distribution and abundance of organisms. An understanding of these roles is useful to biologists involved in everything from the management of wildlife populations to the control of vector-borne diseases.

Marine animals rely heavily on environmental cues such as time of day, tide height, solar elevation, and current velocity as they move from habitat to habitat to meet their functional needs (Henson et al., 2004; Hayward et al., 2005). There are two types of environmental variables. Some, such as tide height and solar elevation, are largely deterministic, and can be obtained as long-range predictions. Others, such as wind speed and temperature, can be obtained only as historical measurements or as short-range predictions. The predictability of the system depends on how much of the data variability can be explained by using only deterministic  $E_{ij}$ .

Some aggregations of marine birds and mammals recover quickly following disturbance. This introduces two time scales, the time scale of recovery and the time scale of environmental variables. Such a system depends only on the current condition of the environment; it is not necessary to integrate over the past in order to compute the solution at time  $t$ . Ecologically, this implies that, at least at the scale of a group of animals occupying the same habitat, behavior change occurs simply and directly in response to environmental change, irrespective of historical contingencies. This is not true, however, at the scale of the individual. For example, preceding conditions demonstrably alter the probabilities of succeeding behaviors in individual Glaucous-winged Gulls (Hayward et al., 1977; Amlaner et al., 1978). From a modeling perspective, the algebraic equations generated by the time scale analysis allow a large number of hypotheses to be tested quickly, since parameter estimation reduces to nonlinear curve fitting. An important outcome of this type of analysis is that wildlife managers can use algebraic equations instead of differential equations to predict system dynamics. In a system that operates on two time scales, however, both transient and steady state data are required to identify uniquely the environmental determinants and parameters.

Several caveats are in order. The first is that a model cannot be expected to predict recovery from disturbance if the main factors influencing recovery are not included in the model. Animal behavior can be complicated, and recovery dynamics might depend on factors (such as social facilitation or Allee effects) that play little role in the steady state dynamics. That is, recovery may involve more than the “normal” ebb and flow of animals between habitats. Indeed, we observed such a phenomenon in our experiments. When we first began recording disturbances, the disturber left the pier immediately after the birds flew. Some of the disturbed birds

flew away to other areas of the colony, but others simply circled overhead until the disturber had gone, and then quickly dropped back onto the pier. This created a very fast initial recovery, followed by a relatively slower recovery that was due to the normal coming and going of birds. Because the model did not incorporate the mechanism of disturbed animals waiting to reenter the habitat, it could not predict the fast initial recovery. Thus, we revised the experimental protocol so that the disturber remained on the pier until the birds circling overhead had dispersed to other locations. In this way we tried to ensure that the recovery was due to the environmentally-driven flux between habitats.

A second caveat is that the experimental procedure for one habitat as outlined in Section 5 may not be feasible for a system of habitats, or for some types of habitats. Furthermore, we have found that recording and analyzing natural disturbances is difficult. For example, the times of the disturbances are not known in advance, and it is often unclear when the disturbance is over.

A final caution is that the inner solution  $x_{in}(t)$  only describes dynamics immediately after a disturbance, that is, for the inner boundary layer  $0 < t < \varepsilon \ll 1$ . For transient times outside of the inner boundary layer, both time scales become important, and the solution of (3) is approximated by the sum of the inner and outer solutions, corrected by a “matching term” (Lin and Segel, 1988) to eliminate overlap.

Human alteration of natural systems has exerted increasing pressures on animal populations. Resource managers must respond to these pressures with ever more sophisticated tools. The modeling technique developed here could allow managers to identify more precisely the environmental factors influencing animal habitat occupancies, which could lead, in turn, to more effective management strategies.

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