Monitoring dynamic spatio-temporal ecological processes optimally

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Abstract

Population dynamics varies in space and time. Survey designs that ignore these dynamics may be inefficient and fail to capture essential spatio-temporal variability of a process. Alternatively, dynamic survey designs explicitly incorporate knowledge of ecological processes, the associated uncertainty in those processes, and can be optimized with respect to monitoring objectives. We describe a cohesive framework for monitoring a spreading population that explicitly links animal movement models with survey design and monitoring objectives. We apply the framework to develop an optimal survey design for sea otters in Glacier Bay. Sea otters were first detected in Glacier Bay in 1988 and have since increased in both abundance and distribution; abundance estimates increased from 5 otters to $>5,000$ otters, and they have spread faster than 2.7 km per year. By explicitly linking animal movement models and survey design, we were able to reduce uncertainty associated with predicted occupancy, abundance, and distribution. The framework we describe is general, and we outline steps to applying it to novel systems and taxa.

Key words abundance, colonization, design criteria, invasion, ecological monitoring, model-based sampling, multiple imputation, objective function, optimal dynamic survey design, sea otters

Introduction

Population spread is a fundamental theme in ecology (Bullock et al. 2002). Applications include reintroductions of endangered species, invasive species management, and the emergence or re-emergence of wildlife or plant disease (Hooten et al. 2007, Williams et al. 2017b, Hefley et al. 2017). The distribution and abundance of a spreading population is a dynamic process that changes in space and time. These dynamics make it challenging to develop efficient monitoring designs that must consider, not only where populations have been in the past, but also, where populations are expected to be in the future. For example, sea otters (Enhydra lutris) in Glacier
Bay have increased rapidly in distribution and abundance through time, making the development of an efficient monitoring design challenging.

During the multi-national commercial maritime fur trade of the 18\textsuperscript{th} and 19\textsuperscript{th} centuries, sea otters were extirpated from southeastern Alaska. Legislation following the maritime fur trade, including the International Fur Seal Treaty (1911), the Marine Mammal Protection Act (1972), and the Endangered Species Act (1977) provided legal protection to sea otters from most harvest \cite{Kenyon1969, Bodkin2015, WilliamsetalInReview}. Legal protection, combined with translocations by wildlife agencies helped sea otters colonize much of their former distribution. By 1988, sea otters were documented at the mouth of Glacier Bay. Since then, sea otter abundance has increased an estimated 21.5\% per year, a rate near their biological maximum reproduction rate. Further, sea otters have spread across Glacier Bay at a rate of at least 2.7 km per year. They are now one of the most abundant marine mammals in Glacier Bay \cite{WilliamsetalInReview}. 

Beginning in 1999, a design-based (probabilistic) survey method was used to monitor the abundance of sea otters in Glacier Bay \cite{BodkinandUdevitz1999}. The survey was conducted eight times between 1999 and 2012, and consisted of systematically selected transects with random starting points \cite{Esslingeretal2015}. Survey effort was stratified based on ocean depth and shoreline features \cite{BodkinandUdevitz1999}. The northern extent of surveys was based on the existing distribution of sea otters. Initially, while sea otter distribution was relatively concentrated, abundance estimates were precise; between 1999 and 2006, the mean of the standard errors equaled 280 otters (mean abundance = 1,496). As sea otters increased in abundance and distribution, distance between transects were increased to accommodate the increasing spatial extent of the sea otter distribution. However, the number of transects remained relatively constant due to logistical and budgetary constraints. As transects became more sparse, and as abundance increased, standard errors of abundance estimates increased, as did coefficients of variation. By 2012, the last year the survey was conducted, the estimated abundance was 8,508.
sea otters, and the standard error was greater than 2,200 sea otters (Esslinger et al. 2015, Williams et al. In Review).

In 2015, sea otters were selected as a vital sign for long-term ecological monitoring by the National Park Service due to their role as a keystone apex predator, and their influence in structuring nearshore marine communities (Estes and Palmisano 1974). The National Park Service is concerned with developing a statistical monitoring framework that maximizes efficiency to estimate sea otter abundance and distribution in Glacier Bay. The monitoring framework will serve as the foundation for understanding sea otters’ role as drivers of the nearshore benthic food web. Thus, a survey design that provides precise, rigorous, and honest estimates of abundance, distribution, and colonization dynamics is required.

Many ecological processes, including population spread, exhibit spatial patterns that change over time in a coherent, dynamic fashion. These dynamics are often ignored when developing spatial survey designs (Wikle and Royle 2005). However, efficient monitoring of such spatio-temporal systems can be achieved by modeling the dynamic system and associated uncertainty, and reducing the uncertainty associated with the effect of sampling locations at future observation times (Hooten et al. 2009). There has been a proliferation of statistical methods for modeling and forecasting the distribution and abundance of a spreading population (e.g., Wikle 2003, Wikle and Hooten 2006, Hooten et al. 2007, Hooten and Wikle 2008, Williams et al. 2017b). Although mathematical and statistical models are ubiquitous for inferring population spread, rarely are data collection and modeling explicitly linked in a unifying framework.

Dynamic survey designs provide a cohesive framework for coupling models of population spread, and the optimal selection of sampling locations. Dynamic survey designs are common in environmental monitoring, including: monitoring hurricanes via aircraft (Wikle and Royle 1999), ozone monitoring (Wikle and Royle 1999), meteorological forecasting (Berliner et al. 1999), and ground-water-pollution source identification (Mahar and Datta 1997). However, dynamic survey
We have four objectives in this paper: 1) introduce concepts and terminology related to optimal dynamic survey designs, 2) describe a general statistical framework for mechanistically modeling population spread, 3) fuse statistical models of population spread and dynamic survey designs in one coherent framework, and 4) apply the framework to monitoring sea otters in Glacier Bay. Although we motivate this application using monitoring of sea otters in Glacier Bay, we describe the methods in sufficient generality to be applicable to any system or taxa in which investigators are interested in modeling and monitoring the distribution, abundance, and colonization dynamics of a spreading population.

**Optimal dynamic survey design**

In this section, we describe the general methodology to develop an optimal dynamic survey design for a spreading population. Population spread is an ecological process that evolves spatially through time. To improve our understanding in how this process evolves, we first require a baseline understanding of the ecological process, and the associated uncertainty. Thus, a statistical model that incorporates our current understanding of the ecological process is required so that we can predict what the behavior of the population is likely to do in future monitoring periods. If we can predict future behavior, and the associated uncertainty, we can then choose survey locations that help reduce uncertainty in our understanding of the process (Hooten et al. 2009). This is the fundamental notion behind the basic steps of dynamic survey designs that we describe next.

Dynamic survey designs can be broken down into a series of steps that are each conceptually straightforward (Fig. [1]). First, a dynamic spatio-temporal process, such as occupancy or abundance (and the associated uncertainty) is modeled using baseline data. Second,
using the model from the first step, a statistical forecast is made. The forecast provides a base for examining potential survey designs that could be implemented in the future. Third, investigators identify the objectives they wish to achieve with their monitoring (e.g., Nichols and Williams 2006). Objectives, or design criteria, typically include minimizing average prediction variance, minimizing maximum prediction variance (mini-max), or, the minimizing variance of regression parameter estimates (Wikle and Royle 1999, 2005, Hooten et al. 2009), but could also include minimizing multi-model uncertainty (Nichols and Williams 2006), cost (Hauser and McCarthy 2009), or some combination thereof (Williams and Kendall 2017). Fourth, after a design criterion is selected, a design is chosen such that it optimizes the design criterion. Fifth, data are then collected using the optimal design. The original model used to make the forecast is then updated with the new data. This process is iterated through time, increasing the understanding of the underlying ecological process of interest. In this regard, optimal dynamic survey designs are analogous to adaptive resource management, an iterative process of decision making in the face of uncertainty, with an aim to reducing management uncertainty through time by monitoring the system’s response to management (e.g., Johnson et al. 1997).

In what follows, we discuss methods for implementation of these steps generally, such that they may be tailored to other systems and taxa for which investigators seek to model and monitor population spread. We then describe how we tailored these general methods to the specific task of modeling and monitoring sea otters in Glacier Bay.

A general spatio-temporal model for population-level animal movement

Population spread exhibits linear or non-linear dynamics that can be classified as diffusion. Diffusion refers to the process of spreading out over an increasingly larger area through time (Skellam 1951, Wikle and Hooten 2010). Partial differential equations (PDE) are powerful tools for modeling population-level (i.e., Eulerian) animal movement in ecology (e.g., Skellam 1951, Okubo 1980, Andow et al. 1990, Holmes et al. 1994, Turchin 1998, Wikle 2003, Hooten and
diffusion, individual organisms are usually influenced by habitat type. Individuals move slowly through areas that contain necessary resources, and move quickly through areas that do not.

Ecological diffusion is a flexible diffusion model that accommodates this variation in motility by predicting animals will eventually accumulate in desirable habitats, and leave or avoid undesirable ones (Turchin 1998, Garlick et al. 2011, Hefley et al. 2017, Williams et al. 2017). Specifically, ecological diffusion describes the population-level distribution that results from individual random walks, with individual movement probabilities determined by information on local habitat conditions (Garlick et al. 2011, Hefley et al. 2017, Williams et al. 2017). Assuming no advection, ecological diffusion can be represented by the PDE

$$\frac{\partial u(s, t)}{\partial t} = \left( \frac{\partial^2}{\partial s_1^2} + \frac{\partial^2}{\partial s_2^2} \right) \left[ \mu(s, t) u(s, t) \right],$$

(1)

where $\frac{\partial u(s, t)}{\partial t}$ represents the instantaneous change in abundance intensity over a continuous spatial domain with coordinates (e.g., latitude and longitude) $s \equiv (s_1, s_2)' \in S$ during time $t$, $\left( \frac{\partial^2}{\partial s_1^2} + \frac{\partial^2}{\partial s_2^2} \right)$ is the differential (Laplace) operator, and $\mu(s, t)$ represents the diffusion coefficient that could vary in space and time. Ecological diffusion differs from other common reaction-diffusion models, in that it allows individual movement to be based on local conditions, rather than non-local conditions (c.f., Fickian and plain diffusion; Garlick et al. 2011). The mathematical driver for this difference is that the diffusion coefficient occurs on the inside of the two spatial derivatives rather than between them (e.g., Fickian: $\frac{\partial u}{\partial t} = \frac{\partial}{\partial x} \mu \frac{\partial}{\partial x} (u)$) or on the outside (e.g., plain: $\frac{\partial u}{\partial t} = \mu \frac{\partial^2}{\partial x^2} (u)$), resulting in a much less smooth process, and motility-driven congregation to differ sharply between neighboring habitat types (Hooten et al. 2013, Hefley et al. 2017) recently described the advantages of ecological diffusion for modeling a spreading population including: its ability to connect spatio-temporal processes while providing a
mechanism that captures transient dynamics, preventing animals from instantaneously accessing 
all high quality habitats; its relative simplicity compared to other mechanistic models; and its 
flexibility in being able to capture a wide range of spatio-temporal dynamics. For example, eq. [1] 
can be further generalized to include growth models,

\[
\frac{\partial u(s, t)}{\partial t} = \left(\frac{\partial^2}{\partial s^2_1} + \frac{\partial^2}{\partial s^2_2}\right)[\mu(s, t)u(s, t)] + f(u(s, t), s, t),
\]

incorporating Malthusian growth \(f(u(s, t), s, t) = \gamma(s, t)u(s, t)\), or logistic growth

\(f(u(s, t), s, t) = \gamma(s, t)(1 - u(s, t)/\kappa(s, t))\)

where \(\gamma(s, t)\) represents the instantaneous growth rate, and \(\kappa(s, t)\) represents equilibrium population size. In principle, each of the modeling 
components, including motility \(\mu(s, t)\), growth \(\gamma(s, t)\), and equilibrium density \(\kappa(s, t)\) can 
depend on covariates that vary over space and time, although standard model-fitting 
considerations apply (i.e., parsimony) when tailoring these models to each system. We consider 
models that incorporate spatial covariates for diffusion, \(g(\mu(s, t)) = X\beta\), and growth,

\(h(\gamma(s, t)) = W\alpha\),

where \(g\) and \(h\) are link functions, \(\beta\) and \(\alpha\) are parameters to be estimated, and \(X\) 
and \(W\) are matrices containing spatially referenced covariate values.

Implementation of eqs. [1] and [2] require numerical methods to solve the PDE. Finite 
differencing is a common method for solving PDEs, and is often used when PDEs are 
implemented within a Bayesian hierarchical framework [Wikle and Hooten 2010]. Solving a PDE 
using finite differencing involves partitioning the spatial domain \(S\) into a grid \(S (S \subseteq S)\) with \(q\) 
cells and the temporal domain \(T\) into \(r\) bins \(T (T \subseteq T)\). Simple finite-difference 
discretization results in the vector difference equation

\[
\mathbf{u}_t = \mathbf{H}(\alpha, \beta)\mathbf{u}_{t-1} + \mathbf{H}(\alpha, \beta)^{(b)} \mathbf{u}_{t-1}^{(b)}, \quad t = 2, ..., T
\]

where \(\mathbf{u}_t \approx u(s, t)\), \(\mathbf{H}(\alpha, \beta)\) is a sparse \(q \times q\) matrix with five non-zero diagonals accommodating
diffusion parameters ($\beta$) and growth parameters ($\alpha$), and the superscript (b) represents conditions at the boundaries. To simplify notation in what follows, we assume $H$ depends on diffusion and growth parameters, but drop the notation for $\alpha$, $\beta$. We also drop the notation for boundary conditions. The accuracy of the numerical approximation of $u(s, t)$ increases as the number of cells on the spatial grid increases and $\Delta t$ becomes small. For additional details on discretization of PDEs and applications of spreading populations, see Wikle and Hooten (2006), Hooten and Wikle (2008), and Williams et al. (2017b); both Wikle and Hooten (2006) and Williams et al. (2017b) provide R code for implementation (see Williams et al. 2017b for ecological diffusion).

Models of ecological diffusion and statistical uncertainty

Bayesian hierarchical models can be described in terms of three levels (Berliner 1996). At the top level, a data model links the observed data and associated variation to latent ecological processes. Next, a process model describes the underlying ecological processes (i.e., spatio-temporal colonization dynamics). Finally, parameter models represent prior knowledge about the parameter inputs in the ecological process model and data model. This framework allows us to incorporate mathematical models that characterize spreading populations, such as the PDEs in eqs. 1 or 2, as process models within a statistical framework, permitting appropriate estimation of uncertainty at multiple levels (Wikle 2003, Hooten and Wikle 2008, Wikle and Hooten 2010, Cressie and Wikle 2011, Hooten et al. 2013, Hefley et al. 2017, Williams et al. 2017b). Using the discretized form of
ecological diffusion in eq. 3, this framework is written hierarchically as

Data Model: \[ y_t(s_i) \sim [y_t(s_i) | n_t(s_i), \phi], \quad t = 1, \ldots, T, \]

Process Models: \[ n_t \sim [n_t | u_t, \nu], \]
[4] \[ u_t = H\epsilon_{t-1}, \quad t = 2, \ldots, T, \]
[4] \[ u_1 = f(\zeta) \]

Parameter Models: \[ \theta \sim [\phi, \nu, \alpha, \beta, \zeta], \]

where \( y_t(s_i) \) represents data collected during discrete time \( t \) at spatial location \( s_i \), \([a | b]\) represents the probability density (or mass) function of variable \( a \) given variable \( b \) ([Gelfand and Smith 1990]), and \( n_t \equiv (n_t(s_1), \ldots, n_t(s_n))^\prime \). The initial condition for \( u_1 \) must also be specified, and is represented as a function of (potentially vector valued) parameters \( \zeta \). Bayesian hierarchical models that incorporate PDE processes are flexible and can be modified to address the specifics of the study ([Hefley et al. 2017]). For example, a common specification of eq. 4 for discrete data (e.g., count data), consists of a binomial data model (i.e., \( y_t(s_i) \sim \text{Binomial}(n_t(s_i), \phi) \)), where \( n_t(s_i) \) is the true latent abundance, and \( \phi \) is the detection probability), and a Poisson process model (i.e., \( n_t \sim \text{Poisson}(u_t) \), in which case \( \nu \) is not necessary). Other process models include negative-binomial or Conway-Maxwell Poisson distributions (in which case, \( \nu \) is a parameter that controls either overdispersion or underdispersion, respectively; [Wu et al. 2013]). Equation 4 can be further generalized to address error in discretization, or model uncertainty. For example, \[ u_t = H\epsilon_{t-1} + \epsilon_t, \quad \text{where} \quad \epsilon_t \sim \text{Normal}(0, \sigma^2 I), \quad \text{and} \quad I \text{ is the identity matrix} \] ([Wikle and Hooten 2010]).

Although discretization of the PDE (i.e., eq. 3) provides a convenient form that results in a series of matrix equations, it is important to note that the theoretical foundations for this model are based in continuous time and space, and discretization provides only an approximate solution.
that may contain error. Coarser discretizations are more likely to contain larger error. Further, maintaining the connection to the PDE defined in continuous time and space (as we do in our specific application to sea otters, below; eq. [7) is advantageous for development and facilitation of numerical techniques for efficient implementation (e.g., homogenization: Garlick et al. 2011, Hooten et al. 2013, Hefley et al. 2017).

**Forecast distribution**

Forecasting the ecological process and associated uncertainty is necessary for optimal dynamic survey design. That is, we seek the probability distribution of the true state at the future point in time when data will be collected, conditional on the data we collected in the past (i.e., the forecast distribution, or the predictive process distribution, sensu Hobbs and Hooten 2015). The forecast distribution is defined as

\[
[u_{T+1}|y_1, \ldots, y_T] = \int \cdots \int [u_{T+1}|u_T, \theta][u_1, \ldots, u_T, \theta|y_1, \ldots, y_T]d\theta du_1 \cdots du_T.
\]

The Bayesian hierarchical model described in eq. [4] provides straightforward calculation of the forecast distribution. Obtaining \([u_{T+1}|y_1, \ldots, y_T]\) is as simple as changing the range of the index for \(t\) in eq. [4] to \(t = 2, \ldots, T + 1\), and sampling \(u_{T+1}^{(k)}\) on each \(k = 1, \ldots, K\) iteration of an MCMC algorithm (Tanner 1996, Hobbs and Hooten 2015). The posterior predictive distribution can then be easily obtained from the forecast distribution using two additional steps; first sample \(n_{T+1}^{(k)} \sim [n_{T+1}|u_{T+1}^{(k)}, \nu^{(k)}]\). Then sample \(y_{T+1}^{(k)} \sim [y_{T+1}|n_{T+1}^{(k)}, \phi^{(k)}]\) for all \(k\) in \(K\) to obtain \([y_{T+1}|y_1, \ldots, y_T]\). The forecast distribution and posterior predictive distribution can then be used to select a survey design that is optimal with respect to a design criterion.

**Design criteria**

Design criteria are mathematical representations of the objectives investigators seek to achieve by collecting data (Williams and Hooten 2016). As such, design criteria are specific to each study.
However, a common objective of collecting data for many studies is to reduce the uncertainty associated with ecological forecasts/predictions. That is, choose a survey design $d$ that allows us to minimize the uncertainty associated with $[u_{T+1} | y_1, \ldots, y_T]$, or some derived parameter of $u_{T+1}$ (e.g., $\sum_{i=1}^n u_{i,T+1}$, the expected total abundance during time $T + 1$). Several authors have discussed specific design criteria (e.g., Wikle and Royle 1999, Berliner et al. 1999, Wikle and Royle 2005, Le and Zidek 2006, Hooten et al. 2009), as well as efficient methods for estimating them (e.g., Kalman filters). Here, we consider choosing a design that minimizes the uncertainty of $u_{total,T+1} = \sum_{i=1}^n u_{i,T+1}$, the sum of the dynamic spatio-temporal process representing abundance intensity in future years. Specifically, the design criterion we consider is

$$q_d = \frac{1}{K} \sum_{k=1}^K \left( u_{total,T+1,d}^{(k)} - \frac{1}{K} \sum_{k=1}^K u_{total,T+1,d}^{(k)} \right)^2,$$

where $k = 1, \ldots, K$ corresponds to the $k^{th}$ MCMC iteration, and $u_{total,T+1,d}^{(k)}$ is the sum of the forecasted process in time $T + 1$, estimated using real data, $y_1, \ldots, y_T$, and future data, $y_{T+1,d}$.

Obviously, future data are unavailable prior to the survey. Lacking such data, one approach is to use the mean of the posterior predictive distribution as a surrogate for future data, and assume it represents the true data that remain to be collected. This technique, known as imputation, may not accommodate the proper uncertainty associated with data collection. Another technique, known as multiple imputation, helps to account for the uncertainty associated with the modeled data that we intend to use for identifying optimal survey designs (Rubin 1996, Hooten et al. 2017, Scharf et al. 2017 In Review).

Multiple imputation

Implementing multiple imputation within a Bayesian model using MCMC is straightforward (Hooten et al. 2017). First, the model is fit using the original data, $y_1, \ldots, y_T$. Second, $K$ posterior predictive realizations of future data $y_{T+1}^{(k)}$ are sampled for MCMC samples.
\( k = 1, \ldots, K \), using the methods described in *Forecast distribution*, above. Third, the model is re-fit using a modified MCMC algorithm. Instead of conditioning only on the fixed data, \( y_1, \ldots, y_T \), on the \( k \)th iteration of the MCMC algorithm, we use the fixed data *and* \( y_{T+1}^{(k)} \). Finally, we obtain posterior summaries for model parameters, and derived parameters including \( u_{\text{total}, T+1} \).

The modified MCMC algorithm will integrate over the uncertainty in the true future data, and incorporate the uncertainty in the inference for the model parameters (Hooten et al. 2017).

Given the Bayesian hierarchical model described in eq. 4, the forecast distribution described in eq. 5 (and the associated posterior predictive distribution), and a design criterion described in eq. 6 pseudo-code for combining animal movement models and survey design to identify the optimal monitoring of a spreading population is provided in Box 1.
Box 1. Pseudo-code for combining animal movement models and survey design to identify the optimal monitoring of a spreading population.

1. Fit a model (i.e., eq. 4) with baseline data $y_1, \ldots, y_T$.

2. Forecast $u_{T+1}^{(k)}$ for all $k = 1, \ldots, K$ MCMC samples using eq. 5.

3. Sample $K$ posterior predictive realizations of future data $y_{T+1}^{(k)}$ for $k = 1, \ldots, K$ MCMC samples.

4. Select a design $d$ that contains a subset of all possible survey locations in study area $D$.

5. Use multiple imputation to re-fit the model with baseline data $y_1, \ldots, y_T$, and imputed data $y_{T+1,d}^{(k)}$, where $y_{T+1,d}^{(k)}$ are imputed for locations defined by design $d$.

6. Calculate $u_{T+1,d}^{(k)} = \sum_{i=1}^{n} u_{i,T+1,d}^{(k)}$ from the model fit in step 5.

7. Use $u_{T+1,d}^{(k)}$ to calculate eq. 6 from the text.

8. Repeat steps 1-7 for all designs under consideration, and identify the design that minimizes $q_d$.

After the optimal design has been identified, the new data, $y_{T+1,d}$, can be collected, the model can be subsequently re-fit using the new data, ecological learning can be assessed by comparing the previous model fit to the new model fit, and the procedure can be repeated to identify the optimal design for time $T + 2$. In the next section, we apply this general procedure to identify optimal transects to survey for estimating the distribution, abundance, and colonization dynamics of sea otters in Glacier Bay.
Application: sea otters in Glacier Bay

We used the general framework described above to identify an optimal dynamic survey design for sea otters in Glacier Bay. We used baseline data to develop a Bayesian hierarchical model of population spread, with a process model tailored from the general ecological diffusion PDE described in eq. 2. We then use our model to forecast abundance and distribution to a future monitoring period. Finally, we select a design that is optimal with respect to the forecast distribution, and a design criterion motivated by minimizing process prediction uncertainty.

Baseline data

Sea otter occupancy and abundance data have been collected over a 20-year period between 1993 and 2012. A detailed description of the methods that were used for collecting data are provided in Bodkin and Udevitz (1999) and Williams et al. (2017b). Briefly, a design-based survey was conducted eight times (1999–2004, 2006, 2012), and a distributional survey was conducted eight times (1993, 1995–1998, 2005, 2009, 2010). The design-based survey consisted of observers flying in aircraft piloted along transects. The transects were systematically placed across Glacier Bay, with a random starting point. Observers flew along transects and recorded the number of sea otters observed within 400 m of the transect, and mapped the location of sea otters during observations. The distributional surveys consisted of observers flying in aircrafts that were piloted in close proximity to shorelines and islands, the preferred habitat of sea otters (Williams et al. 2017b, Williams et al. In Review). Pilots did not follow pre-determined routes during distributional surveys. An additional data set was collected during the design-based survey to facilitate estimating detection probability (Williams et al. 2017b).

Statistical diffusion model and forecast

We tailored eq. 4 to the sea otter data following Williams et al. (2017b) and Williams et al. (In Review). Retaining connection to the continuous time, continuous space process model, we
Perry J. Williams et al. · Optimal dynamic survey designs

assumed

**Data Model:** \[ y_t(s_i) \sim \text{Binomial}(n_t(s_i), \phi), \]

**Process Model:** \[ n_t(s_i) \sim \text{Poisson}(u_t(s_i)), \]

\[
\frac{\partial u(s_i, t)}{\partial t} = \left( \frac{\partial^2}{\partial s_1^2} + \frac{\partial^2}{\partial s_2^2} \right) [\mu(s, t)u(s, t)] + \gamma(s_i)u(s_i, t), \quad t > 1
\]

\[
u(s_i, 1) = \frac{\tau e^{-\frac{|s_i-d|^2}{\kappa^2}}}{\int_S e^{-\frac{|s-d|^2}{\kappa^2}} ds}, \quad t = 1
\]

\log(\mu(s_i)) = \beta_0 + \beta_1(\text{depth}(s_i)) + \beta_2(\text{dist}(s_i)) + \beta_3(\text{depth}(s_i) \times \text{slope}(s_i)) + \beta_4(\text{complexity}(s_i)) \]

\[ \gamma(s_i) = \alpha_0 \]

**Parameter Models:** \[ \phi \sim \text{Beta}(1, 1) \]

\[ \beta \sim \text{Normal}(0, 1.5^2I) \]

\[ \alpha \sim \text{Normal}(0, 1.5^2) \]

\[ \kappa \sim \text{Normal}^+(5, 0.001) \]

\[ \tau \sim \text{Normal}^+(500, 10) \]

(7)

where \( y_t(s_i) \) were sea otter count data within a 400×400 m grid cell centered at location \( s_i \) during time \( t \), \( n_t(s_i) \) was the true latent abundance, \( \phi \) was the individual sea otter detection probability, and \( u_t(s_i) \) was the dynamic spatio-temporal process (abundance intensity) when data were collected during time \( t \). We used a scaled Gaussian kernel for our initial condition for abundance intensity, with two parameters \( \zeta \equiv (\tau, \kappa)' \), controlling the height and spread of the kernel, respectively, around an epicenter \( d \). We used a log-linear relationship between motility and four spatial habitat covariates that we hypothesized affect sea otter motility. The covariates were ocean depth (an indicator of depth<40 m), distance to shore, slope of the ocean floor, and an index for
shoreline complexity that was calculated by summing the number of shoreline grid cells that were within 1,000 m of each grid cell. We used the interaction between depth and slope because the slope of the ocean floor may only be important if it is shallow enough for sea otters to reach it during feeding dives. We assumed the growth rate was constant across space and time. We used vague prior distributions for all parameters except for the initial condition parameters, $\tau$ and $\kappa$, which we parameterized based on observations of sea otters during the first year of monitoring, where Normal$^+$ represents the zero-truncated normal distribution.

We fit the model described in eq. 7 to the baseline data using a custom MCMC algorithm written in R version 3.3.2 (R Core Team 2013) and C++. For each model fit, we obtained two chains of 20,000 MCMC draws and discarded the first 5,000. We examined convergence using trace plots and Gelman-Rubin diagnostics. To facilitate computation, we used homogenization to implement the model (Garlick et al. 2011, Hooten et al. 2013, Hefley et al. 2017, Williams et al. 2017). We used regularization combined with k-fold cross-validation to conduct model selection, and assessed goodness of fit using Bayesian p-values (see Williams et al. In Review for details). We then estimated the forecast distribution for $T + 5 = 2017$, because the last time sea otter data were collected was $T = 2012$ (Fig. 2).

**Optimal design**

**Potential survey transects**

To identify the set of all potential transects that could be surveyed, we partitioned Glacier Bay into a regular grid of 400×400 m cells. We selected 400 m as the unit of length for two reasons. First, this partitioning assisted with computation, because computation at a finer resolution became prohibitive. Second, 400×400 m represented the scale at which the baseline data were collected. After partitioning Glacier Bay into 400×400 m grid cells, there were 170 potential transects (running West to East) from which we could select a sampling design. This resulted in $\binom{170}{n}$ unique possible designs that could be considered, where $n$ is the number of transects that
could be flown during a survey.

Selecting an optimal design

We considered a sample size of \( n = 20 \) transects to be observed for our monitoring design, which is approximately the maximum number that can be flown in one day. This resulted in a total number of possible designs that was much larger than one trillion. It is not feasible to calculate the design criterion \( q_d \) for all possible unique designs, thus we considered an approach based on improving efficiency relative to a random selection of transects. First, we selected a large number of different designs, \( d \), uniformly at random and calculated the design criterion \( q_d \) for each design using eq. 6. Fitting the sea otter model described in eq. 7 to the baseline data described above, and calculating \( q_d \) for one design required approximately 5.4 hours to obtain 20,000 MCMC samples. To facilitate fitting a large number of different random designs, we used the Amazon Elastic Compute Cloud (Amazon EC2®, instance: Linux m4.16xlarge; with 64 vCPUs) to calculate \( q_d \) for 64 different random designs in parallel. We then compared \( q_d \) among all 64 designs, and selected the design that minimized \( q_d \). A histogram of the \( q_d \) values for all 64 random designs we examined is shown in Fig. 3.

After we identified the optimal set of random transects, we further improved the design using an exchange algorithm (Royle and Nychka 1998). That is, we sequentially exchanged each of the 20 transects with their neighbors (one transect above it, and one transect below it), and recalculated \( q_d \) after the exchange. This required re-fitting the model with the inclusion of a neighboring transect and the exclusion of the original transect. If the exchange improved \( q_d \), we retained the new transect in place of the old transect. Then, the next transect on the list was exchanged. The process repeated until the design criterion could not be improved through exchange. Because each exchange requires re-fitting the model, and it must occur sequentially (except for examining the two immediate neighbors, which can occur in parallel), this required a sequence of several model fits. However, in practice, convergence to the optimal survey design
optimal dynamic survey designs occur with relatively few exchanges using this approach. The sea otter survey required six exchanges before \( q_d \) could no longer be improved through exchange.

**Results**

The posterior mean abundance estimates of sea otters in 2017 were similar among all designs (mean = 9,430; range = 9,250–9,770), suggesting mean abundance estimates were not sensitive to the choice of designs we considered. However \( q_d \) values ranged from 66,685 (best) to 88,948 (worst) and averaged 76,680 (Fig. 3). Thus, the \( q_d \) value of the optimal design improved by 13% when compared to the average \( q_d \) value of all other designs we considered. The optimal survey design is shown in Fig. 4.

**Discussion**

How to best use available resources to monitor ecological processes for conservation, management, and ecological insight remains a critical area of scientific investigation (Nichols and Williams 2006). Probabalistic (i.e., design-based) surveys have been used widely in ecology, and can provide data that result in objective, unbiased estimates of abundance (Cochran 2007, Thompson 2012). However, when financial resources limit the effort that can be devoted to collecting data, classical design-based inference may result in estimates that are insufficiently precise for management or conservation (e.g., sea otters in Glacier Bay). The situation becomes more accute for populations that are spreading in space through time. Alternatively, optimal dynamic survey designs allow managers and scientists the ability to extract the most information out of the data they can afford to collect. Further, dynamic survey designs better allow for the observation of dynamically evolving spatio-temporal processes, and ultimately result in higher quality data (Wikle and Royle 1999, 2005, Hooten et al. 2009).

Optimal dynamic survey designs are becoming widespread in atmospheric and environmental studies. However, they have been used in relatively few long-term ecological
While model-based inference has become ubiquitous in ecology, survey design and modeling are usually developed independently of each other. By explicitly linking survey design, and the models that will be fit to future data, we gain the ability to employ more sophisticated ecological models that ultimately contain less uncertainty (Hooten et al. 2009).

We described a general, cohesive framework for modeling and monitoring population-level animal movement that explicitly links survey design, data collection, and monitoring objectives. The generality of this framework stems from the flexibility of hierarchical statistical models to draw conclusions from data that arise from complex ecological processes, the flexibility of PDEs (specifically, ecological diffusion) to capture a wide range of spatio-temporal dynamics, and the ability to tailor design criteria to meet the objectives of each unique study. We applied the framework to identify an optimal dynamic survey design for sea otters in Glacier Bay. Sea otters have been identified as a vital sign for Glacier Bay. Vital-sign monitoring is used to track specific ecosystem processes that are selected to represent the overall health or condition of park resources, known or hypothesized effects of stressors, or elements that have important human values. Inference that results from monitoring is then used by employees and partners to support management decision-making, park planning, research, education, and public understanding of park resources. Thus, a survey design that results in precise, rigorous, and honest estimates of abundance, distribution, and colonization dynamics is required. We examined a monitoring scenario in which available funding permitted surveying 20 of the 170 potential transects that partition Glacier Bay. Generally, posterior mean estimates of sea otter expected abundance were similar among the designs we considered; all designs predicted approximately 9,500 sea otters in 2017. However, the uncertainty associated with these predictions varied widely among designs. The optimal design reduced prediction uncertainty by 13% compared to the mean of all the random designs that were considered (Fig. 3). The dynamic survey designs employed for sea otters surveys here, are applicable to any type of aerial survey method used for sea otters,
including aerial observations where observers count sea otters from an aircraft (Bodkin and Udevitz 1999), or aerial photographs (Williams et al. 2017a).

The design criterion we employed, chosen by the National Park Service, is a measure of the prediction uncertainty of the expected abundance of sea otters in Glacier Bay (i.e., how many sea otters are there next year). Many choices of design criteria are possible, and depend on the objectives of the study. The explicit choice of a design criterion pairs survey design with the motives of a decision maker in a decision theoretic framework (Wald 1950, Savage 1954, Williams and Hooten 2016). This pairing is natural in monitoring for ecology because data are often collected with the explicit purpose to inform both models and decisions. Nichols and Williams (2006, p. 668) state “targeted monitoring is defined by its integration into conservation practice, with monitoring design and implementation based on a priori hypotheses and associated models of system responses to management.” Thus, the framework we present is directly amenable to targeted monitoring, sensu Nichols and Williams (2006), due to the explicit incorporation of a design criterion. Further, by selecting a design criteria focused on minimizing structural (i.e., multi model) uncertainty, or the uncertainty associated with management actions, the framework becomes amenable to adaptive resource management (e.g., Johnson et al. 1997), and our framework provides an efficient method for achieving targeted monitoring for conservation. That is, it is a method for explicitly focusing monitoring efforts on crucial information needs in the conservation process, and therefore, the effectiveness of conservation can be greatly increased (Nichols and Williams 2006).

Extensions of dynamic survey designs include hybrid survey designs. Hybrid survey designs combine classical survey techniques (e.g., random sampling) with dynamic survey designs to identify an optimal dynamic survey design (Hooten et al. 2009, 2012). Hybrid survey designs are advantageous because they leverage the benefits of traditional survey techniques (e.g., generally more convenient, economically feasible, and computationally inexpensive), with the benefits of
dynamic survey designs (e.g., optimal efficiency, capture spatio-temporal evolution in a process, flexibility to add or remove monitoring locations as budgets change; Hooten et al. 2009). When hybrid survey designs contain a design-based sampling component, the design-based data can stand alone to obtain design-based estimates of abundance, which provides desirable operating characteristics (e.g., unbiased estimation; Cochran 2007, Thompson 2012 although at a cost in precision).

Finally, spreading populations are ideal candidates for dynamic survey designs because spreading populations have significant spatio-temporal interactions that are difficult to observe using traditional survey designs. The spatio-temporal processes that regulate population spread are often of ecological interest (e.g., processes that influence species invasions, mesopredator release, (re)establishment of apex predators; Williams et al. 2017b). When baseline data exist to develop appropriate models of population spread, implementing dynamic survey designs for future data collection provide an opportunity to maximize efficiency in learning about these spatio-temporal processes (Wikle and Royle 1999). When resources are limited, as they always are, the efficient use of monitoring is vital to successful conservation (Nichols and Williams 2006).

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Figure 1  Schematic of optimal dynamic survey design.

Figure 2  Forecasted mean of dynamic spatio-temporal process \( u_{2017}(s) \) representing abundance intensity of sea otters in Glacier Bay National Park, Alaska. Units are mean sea otters per 400 m\(^2\).

Figure 3  Histogram of \( q_d \) values from 64 randomly selected designs (gray) and the optimal design (black), each design containing 20 randomly selected transects to be flown over Glacier Bay National Park in the upcoming survey year. The design criterion \( q_d \) was calculated using eq. 6 from the text, and corresponds to reducing uncertainty in the forecast distribution of mean total abundance of sea otters in the future year. The best random design had \( q_d = 57,439 \) (dark gray), and was improved to \( q_d = 55,261 \) (black) using an exchange algorithm. The mean value of \( q_d \) for the 64 random transects equaled 62,804 (vertical line).

Figure 4  Optimal dynamic survey design for sea otters in Glacier Bay National Park, 2017.
Figure 1
Figure 2
Figure 3
Figure 4

$u_{2017}(s)$