CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Monitoring dynamic spatio-temporal ecological processes optimally

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Abstract. Population dynamics vary 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/yr. By explicitly linking animal movement models and survey design, we are able to reduce uncertainty associated with forecasting occupancy, abundance, and distribution compared to other potential random designs. The framework we describe is general, and we outline steps to applying it to novel systems and taxa.

Key words: abundance; colonization; design criteria; ecological monitoring; invasion; 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, Hefley et al. 2017, Williams et al. 2017*b*) 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, requiring surveys to cover larger spatial domains, while operating under the same financial constraints.

During the multi-national commercial maritime fur trade of the 18th and 19th 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 (Kenyon 1969, Bodkin 2015, Williams et al., *in review*). 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 yr, a rate near their biological maximum reproductive rate. Further, sea otters have spread across Glacier Bay at a rate of at least 2.7 km per yr. They are now one of the most abundant marine mammals in Glacier Bay (Williams et al., *in review*).

Beginning in 1999, a design-based survey was used to monitor the abundance of sea otters in Glacier Bay

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(Bodkin and Udevitz 1999). The survey was conducted eight times between 1999 and 2012, and consisted of systematically selected transects with random starting points (Esslinger et al. 2015). Survey effort was stratified based on ocean depth and shoreline features (Bodkin and Udevitz 1999). 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 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 and rigorous estimates of abundance, distribution, and colonization dynamics is required.

Many ecological processes, including population spread, exhibit spatial patterns that change over time in a dynamic, yet predictable fashion. These dynamics are often ignored when developing spatial survey designs (Wikle and Royle 2005). However, efficient monitoring of such spatio-temporal processes can be achieved by modeling the dynamic process and associated uncertainty, and choosing future sampling locations that best help to reduce the uncertainty in the process (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. 2017*b*). Although mathematical and statistical models are widely used 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. We distinguish dynamic survey designs from the traditional statistical notion of *adaptive sampling* (sensu Thompson 1990), although the two concepts are related. 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 designs have been applied to few long-term ecological monitoring programs (e.g., Wikle and Royle 2005, Hooten et al. 2009, 2012, Evangelou and Zhu 2012).

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 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 basis 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, Lindenmayer and Likens 2009). Objectives, or *design criteria*, typically include minimizing average prediction variance, minimizing maximum prediction variance (mini-max), or minimizing variance of parameter estimates (Wikle and Royle 1999, 2005, Hooten et al. 2009), but could also include minimizing multi-model uncertainty (Nichols and Williams 2006),

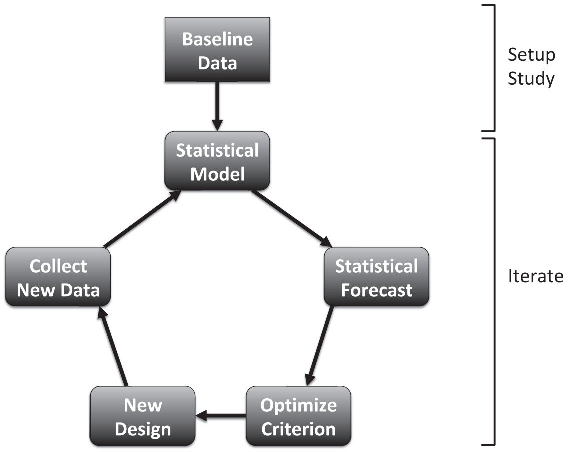

FIG. 1. Schematic of optimal dynamic survey design.

cost (Field et al. 2005, Hauser and McCarthy 2009, Sanderlin et al. 2014), or some combination thereof (Williams and Kendall 2017). Fourth, after a design criterion is selected, a design is chosen that 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, Lindenmayer and Likens 2009).

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 Wikle 2008, Wikle and Hooten 2010, Hooten et al. 2013, Williams et al. 2017*b*). During 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*b*). 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*b*). Assuming no advection or growth, ecological diffusion can be represented by the PDE

$$\frac{\partial u(\mathbf{s},t)}{\partial t}=\left(\frac{\partial^2}{\partial s_1^2}+\frac{\partial^2}{\partial s_2^2}\right)[\mu(\mathbf{s},t)u(\mathbf{s},t)], \qquad (1)$$

where $\frac{\partial u(\mathbf{s},t)}{\partial t}$ represents the instantaneous change in abundance intensity over a continuous spatial domain with coordinates (e.g., latitude and longitude) $\mathbf{s}\equiv(s_1,s_2)'\in\mathcal{S}$ during time t, $(\frac{\partial^2}{\partial s_1^2}+\frac{\partial^2}{\partial s_2^2})$ is the differential (Laplace) operator, and $\mu(\mathbf{s},t)$ 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 such as habitat type (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,

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

incorporating Malthusian growth ($f(u(\mathbf{s},t),\mathbf{s},t)=\gamma(\mathbf{s},t)u(\mathbf{s},t)$), or logistic growth ($f(u(\mathbf{s},t),\mathbf{s},t)=\gamma(\mathbf{s},t)(1-u(\mathbf{s},t)/\kappa(\mathbf{s},t))$) where $\gamma(\mathbf{s},t)$ represents the instantaneous growth rate, and $\kappa(\mathbf{s},t)$ represents equilibrium population size. In principle, each of the modeling components, including motility ($\mu(\mathbf{s},t)$), growth ($\gamma(\mathbf{s},t)$), and equilibrium density ($\kappa(\mathbf{s},t)$) 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, $g(\mu(\mathbf{s}_i, t)) = \mathbf{x}'(\mathbf{s}_i)\boldsymbol{\beta}$, and growth, $h(\gamma(\mathbf{s}_i)) = \mathbf{w}'(\mathbf{s}_i)\boldsymbol{\alpha}$, where g and h are link functions (e.g., log and identity, respectively), $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ are vectors of parameters to be estimated, and $\mathbf{x}'(\mathbf{s}_i)$ and $\mathbf{w}'(\mathbf{s}_i)$ are vectors containing spatially referenced covariate values (Williams et al. 2017*b*).

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 $\mathcal{S}$ into a grid $\mathbf{S}(\mathbf{S} \subseteq \mathcal{S})$ with m cells and the temporal domain $\mathcal{T}$ into r bins $\mathbf{T}$ of width Δt $(\mathbf{T} \subseteq \mathcal{T})$. Simple finite-difference discretization results in the vector difference equation

$$\mathbf{u}_t = \mathbf{H}(\boldsymbol{\alpha}, \boldsymbol{\beta})\mathbf{u}_{t-1} + \mathbf{H}(\boldsymbol{\alpha}, \boldsymbol{\beta})^{(\mathrm{b})}\mathbf{u}_{t-1}^{(\mathrm{b})}, \quad t = 2, \ldots, T \qquad (3)$$

where $\mathbf{u}_t \approx u(\mathbf{s}, t)$, $\mathbf{H}(\boldsymbol{\alpha}, \boldsymbol{\beta})$ is a sparse $m \times m$ matrix with five non-zero diagonals accommodating diffusion parameters $(\boldsymbol{\beta})$ and growth parameters $(\boldsymbol{\alpha})$, and the superscript (b) represents conditions at the boundaries. Each row in $\mathbf{H}$ corresponds to a specific cell in the grid $\mathbf{S}$. The five non-zero values in each row correspond to the specific cell in $\mathbf{H}$, and the four nearest (rook) neighbors of that cell. The values of the non-zero cells are determined by the growth and diffusion parameters $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$, respectively, and describe how $\mathbf{u}_{t-1}$ changes in space through time. To simplify notation in what follows, we assume $\mathbf{H}$ depends on diffusion and growth parameters, but omit the notation for $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$ for brevity. We also omit the notation for boundary conditions. The accuracy of the numerical approximation of $u(\mathbf{s}, t)$ increases as the number of cells on the spatial grid increases and Δt becomes small. For additional details on discretization of PDEs and applications of spreading populations, see Wikle and Hooten (2006), Hooten and Wikle (2008), Hefley et al. (2017), and Williams et al. (2017*b*); Wikle and Hooten (2006), Hefley et al. (2017), and Williams et al. (2017*b*) provide R code for implementation (see Hefley et al. 2017, Williams et al. 2017*b*, 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. 2017*b*). Using the discretized form of ecological diffusion in Eq. 3, this framework is written hierarchically as

$$\begin{array}{rll}
\textbf{Data Model:} & y_t(\mathbf{s}_i) \sim [y_t(\mathbf{s}_i) | n_t(\mathbf{s}_i), \phi], & t = 1, \ldots, T, \\
\textbf{Process Models:} & \mathbf{n}_t \sim [\mathbf{n}_t | \mathbf{u}_t, \nu], & \\
 & \mathbf{u}_t = \mathbf{H}\mathbf{u}_{t-1}, & t = 2, \ldots, T, \\
 & \mathbf{u}_1 = f(\boldsymbol{\zeta}) & \\
\textbf{Parameter Models:} & \boldsymbol{\theta} \sim [\phi, \nu, \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\zeta}], &
\end{array} \qquad (4)$$

where $y_t(\mathbf{s}_i)$ represents data collected during discrete time t at spatial location $\mathbf{s}_i$, $[a|b]$ represents the probability density (or mass) function of variable a given variable b (Gelfand and Smith 1990), and $\mathbf{n}_t \equiv (n_t(\mathbf{s}_1), \ldots, n_t(\mathbf{s}_n))'$. The initial condition for $\mathbf{u}_1$ must also be specified, and is represented as a function of (potentially vector valued) parameters $\boldsymbol{\zeta}$. 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., $y_t(\mathbf{s}_i) \sim \text{Binomial}(n_t(\mathbf{s}_i), \phi)$, where $n_t(\mathbf{s}_i)$ is the true latent abundance, and ϕ is the detection probability), and a Poisson process model (i.e., $\mathbf{n}_t \sim \text{Poisson}(\mathbf{u}_t)$, in which case ν is not necessary). Other process models include negative-binomial or Conway-Maxwell Poisson distributions (in which case, ν 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, model uncertainty, and environmental stochasticity. For example, $\mathbf{u}_t = \mathbf{H}\mathbf{u}_{t-1} + \boldsymbol{\epsilon}_t$, where $\boldsymbol{\epsilon}_t \sim \text{Normal}(\mathbf{0}, \boldsymbol{\Sigma})$, and $\boldsymbol{\Sigma}$ is a covariance matrix describing (potentially spatially autocorrelated) error in $\mathbf{u}_t$ (Wikle and Hooten 2010, Thorson et al. 2017).

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 an 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

$$[\mathbf{u}_{T+1}|\mathbf{y}_1,\ldots,\mathbf{y}_T] = \int\ldots\int[\mathbf{u}_{T+1}|\mathbf{u}_T,\boldsymbol{\theta}] \\ [\mathbf{u}_1,\ldots,\mathbf{u}_T,\boldsymbol{\theta}|\mathbf{y}_1,\ldots,\mathbf{y}_T]d\boldsymbol{\theta}d\mathbf{u}_1\ldots d\mathbf{u}_T. \quad (5)$$

The Bayesian hierarchical model described in Eq. 4 provides straightforward calculation of the forecast distribution. Obtaining $[\mathbf{u}_{T+1}|\mathbf{y}_1,\ldots,\mathbf{y}_T]$ is as simple as changing the range of the index for t in Eq. 4 to $t = 2,\ldots,T+1$, and sampling $\mathbf{u}_{T+1}^{(k)}$ 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 $\mathbf{n}_{T+1}^{(k)} \sim [\mathbf{n}_{T+1}|\mathbf{u}_{T+1}^{(k)}, \nu^{(k)}]$. Then sample $\mathbf{y}_{T+1}^{(k)} \sim [\mathbf{y}_{T+1}|\mathbf{n}_{T+1}^{(k)}, \phi^{(k)}]$ for all k to obtain $[\mathbf{y}_{T+1}|\mathbf{y}_1,\ldots,\mathbf{y}_T]$. 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 $[\mathbf{u}_{T+1}|\mathbf{y}_1,\ldots,\mathbf{y}_T]$, or some derived parameter of $\mathbf{u}_{T+1}$. Several authors have discussed specific design criteria (e.g., Berliner et al. 1999, Wikle and Royle 1999, 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 $u_{\text{total},T+1} = \sum_{i=1}^{n} u_{i,T+1}$, the sum of the dynamic spatio-temporal process representing abundance intensity in future years. Specifically, the design criterion we consider is the empirical variance of the future abundance estimate

$$q_d = \frac{1}{K}\sum_{k=1}^{K}\left(u_{\text{total},T+1,d}^{(k)} - \frac{1}{K}\sum_{k=1}^{K}u_{\text{total},T+1,d}^{(k)}\right)^2, \quad (6)$$

where $k = 1,\ldots,K$ corresponds to the kth MCMC iteration, and $u_{\text{total},T+1,d}^{(k)}$ is the sum of the forecasted process at time $T+1$, estimated using real data, $\mathbf{y}_1,\ldots,\mathbf{y}_T$, *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).

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, $\mathbf{y}_1,\ldots,\mathbf{y}_T$. Second, K posterior predictive realizations of future data $\mathbf{y}_{T+1}^{(k)}$ 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, $\mathbf{y}_1,\ldots,\mathbf{y}_T$, on the kth iteration of the MCMC algorithm, we use the fixed data *and* $\mathbf{y}_{T+1}^{(k)}$. 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.

The number of potential designs d that could be considered in most ecological studies is too large (e.g., trillions) to evaluate all of them due to computational constraints, precluding identification of a globally optimal design. Alternatively, investigators could consider, for example, a random subset of designs, exchange algorithms (Cook and Nachtrheim 1980, Fedorov and Atkinson 1988, Nychka and Saltzman 1998), or both. These alternatives sacrifice global optimality for computational efficiency to find a locally optimal solution.

After the optimal design has been identified, the new data, $\mathbf{y}_{T+1,d}$, 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

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 $\mathbf{y}_1, \ldots, \mathbf{y}_T$.
2. Forecast $\mathbf{u}_{T+1}^{(k)}$ for all $k = 1, \ldots, K$ MCMC samples using Eq. 5.
3. Sample $K$ posterior predictive realizations of future data $\mathbf{y}_{T+1}^{(k)}$ for $k = 1, \ldots, K$ MCMC samples.
4. Select a design $d$ that contains a subset of all possible survey locations in study area $\mathcal{D}$.
5. Use multiple imputation to re-fit the model with baseline data $\mathbf{y}_1, \ldots, \mathbf{y}_T$, and imputed data $\mathbf{y}_{T+1,d}^{(k)}$, where $\mathbf{y}_{T+1,d}^{(k)}$ are imputed for locations defined by design $d$.
6. Calculate $u_{\mathrm{total},T+1,d}^{(k)} = \sum_{i=1}^{n} u_{i,T+1,d}^{(k)}$ from the model fit in Step 5.
7. Use $u_{\mathrm{total},T+1,d}^{(k)}$ to calculate Eq. 6 from the text.
8. Repeat Steps 1–7 for all designs under consideration, and identify the design that minimizes $q_d$.
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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 time step. 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-yr 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. (2017*b*). 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. 2017*b*, in review). Pilots did not follow pre-determined routes during distributional surveys. An additional data set was collected during the design-based survey to estimate detection probability (Williams et al. 2017*b*).

Statistical diffusion model and forecast

We tailored Eq. 4 to the sea otter data following Williams et al. (2017*b*, *in review*). Retaining connection to the continuous time, continuous space process model, we assumed

$$
\begin{aligned}
&\textbf{Data Model:}\; y_t(\mathbf{s}_i) \sim \mathrm{Binomial}(n_t(\mathbf{s}_i), \phi),\\
&\textbf{Process Model:}\; n_t(\mathbf{s}_i) \sim \mathrm{Poisson}(u_t(\mathbf{s}_i)),\\
&\qquad \frac{\partial u(\mathbf{s}_i, t)}{\partial t} = \left(\frac{\partial^2}{\partial s_1^2} + \frac{\partial^2}{\partial s_2^2}\right)[\mu(\mathbf{s}, t)u(\mathbf{s}, t)]\\
&\qquad\qquad + \gamma(\mathbf{s}_i)u(\mathbf{s}_i, t), \quad t > 1\\
&\qquad u(\mathbf{s}_i, 1) = \frac{\tau e^{\frac{-|\mathbf{s}_i - \mathbf{d}|^2}{\psi^2}}}{\int_S e^{\frac{-|\mathbf{s}_i - \mathbf{d}|^2}{\psi^2}} d\mathbf{s}}, \qquad t = 1\\
&\qquad \log(\mu(\mathbf{s}_i)) = \beta_0 + \beta_1(\mathrm{depth}(\mathbf{s}_i))\\
&\qquad\quad + \beta_2(\mathrm{dist}(\mathbf{s}_i)) + \beta_3(\mathrm{depth}(\mathbf{s}_i)\\
&\qquad\quad \times \mathrm{slope}(\mathbf{s}_i)) + \beta_4(\mathrm{complexity}(\mathbf{s}_i))\\
&\qquad \gamma(\mathbf{s}_i) = \alpha_0\\
&\textbf{Parameter Models:}\; \phi \sim \mathrm{Beta}(1, 1)\\
&\qquad \boldsymbol{\beta} \sim \mathrm{Normal}(\mathbf{0}, \sigma^2\mathbf{I})\\
&\qquad \alpha \sim \mathrm{Normal}(0, 1.5^2)\\
&\qquad \psi \sim \mathrm{Normal}^{+}(5, 0.001)\\
&\qquad \tau \sim \mathrm{Normal}^{+}(500, 10)
\end{aligned}
\tag{7}
$$

where $y_t(\mathbf{s}_i)$ were sea otter count data within a 400 × 400 m grid cell centered at location $\mathbf{s}_i$ during time t, $n_t(\mathbf{s}_i)$ was the true latent abundance of sea otters, ϕ was the individual sea otter detection probability, and $u_t(\mathbf{s}_i)$ 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 $\boldsymbol{\zeta} \equiv (\tau, \psi)'$, controlling the height and spread of the kernel, respectively, around an epicenter $\mathbf{d}$. The epicenter represents the location of an initial colonization event at the beginning of the time series. 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 for simplicity and because design-based estimates of abundance suggested that Glacier Bay is still in a rapid growth phase (Williams et al., *in review*). However, increasing evidence suggests that density dependence in sea otters occurs at relatively fine spatial scales (Bodkin 2015, Tinker 2015), and it is possible that density dependence may be limiting growth in some areas of Glacier Bay. Further, there is extensive evidence that sea otters alter their own ecosystems through a series of direct and indirect food web impacts. Thus, both diffusion and growth may change through time, and in principle, could be incorporated in our model formulation, provided sufficient data exist to estimate the required parameters. Our approach was to identify a parsimonious model and use a model checking procedure to evaluate our assumptions of exponential growth and static diffusion rates through time.

We used vague prior distributions for all parameters except for the shrinkage parameter σ, and the initial condition parameters, τ and ψ. We parameterized the initial condition parameters 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 50,000 MCMC draws and discarded the first 10,000. 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*b*). Homogenization is a multi-scale technique that allowed us to optimally up-scale (decrease) the resolution of our spatial domain for computation, and then optimally downscale (increase) the resoultion of the spatial domain to make fine-scale inference. We used regularization combined with *k*-fold cross-validation to conduct model selection. Specifically, we first randomly partitioned the data into eight folds. Second, we selected a diffuse value of σ and fit the model using seven of the eight groups of data. Third, we used the remaining group of data to calculate the log-posterior predictive distribution score function (Hooten and Hobbs 2015). Fourth, we repeated the procedure for the remaining seven combinations of data and summed the log-posterior predictive distribution score function for all eight hold-out samples. Fifth, we decreased σ (a mechanism to induce regularization) and repeated this procedure. That is, we calculated the sum of the log-posterior predictive distribution score function for each σ over a range of values and identified which value of σ resulted in the best (lowest) score. We used the resulting value of σ in our final model for prediction and inference. We assessed goodness of fit of our final model using Bayesian *p*-values (see Williams et al., *in review* for more 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 (23,800 total 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. We chose East-West transects to simplify navigation, computation, and to align with the previous design-based surveys that used East-West transects in the past.

Selecting an optimal design.—We selected a sample size of $n = 20$ transects to be used for our monitoring design. Twenty transects were approximately the maximum number of transects 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 10 h to obtain 50,000 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

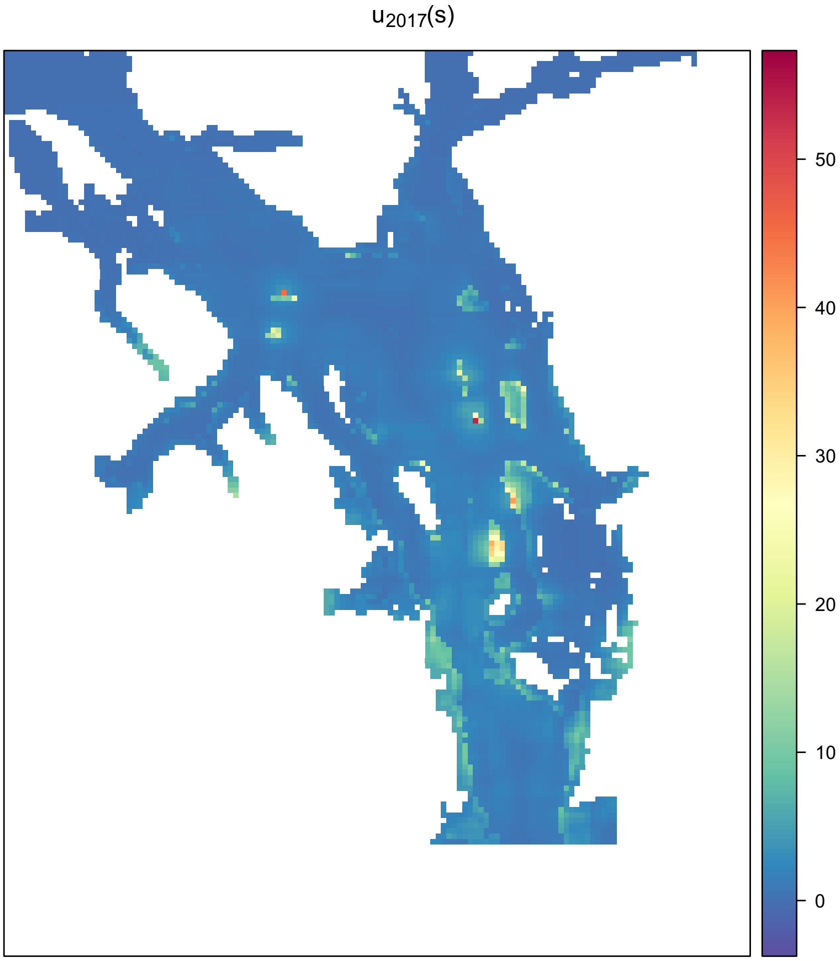

FIG. 2. Forecasted mean of dynamic spatio-temporal process ($u_{2017}(\mathbf{s})$) representing abundance intensity of sea otters in Glacier Bay National Park, Alaska. Units are mean sea otters per 400 m^2.

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 occurs 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

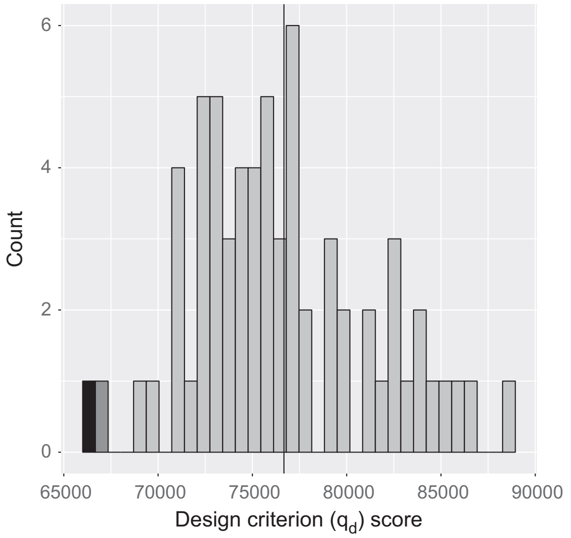

FIG. 3. Histogram of q_d values from 64 randomly selected designs (gray) and the optimal design (black), each design containing 20 randomly selected transects to be flown over Glacier Bay National Park in the upcoming survey year. The design criterion q_d was calculated using Eq. 6 from the text, and corresponds to reducing uncertainty in the forecast distribution of mean total abundance of sea otters in the future year. The best random design had $q_d = 66,685$ (dark gray), and was improved to $q_d = 65,764$ (black) using an exchange algorithm. The mean value of q_d for the 64 random transects equaled 76,680 (vertical line).

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 studies (Hooten et al. 2009). 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 and rigorous 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 otter 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. 2017*a*).

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).

Monitoring dynamic processes optimally is a growing subject in ecology. There is much more to learn about the choice of design criterion for estimating and predicting

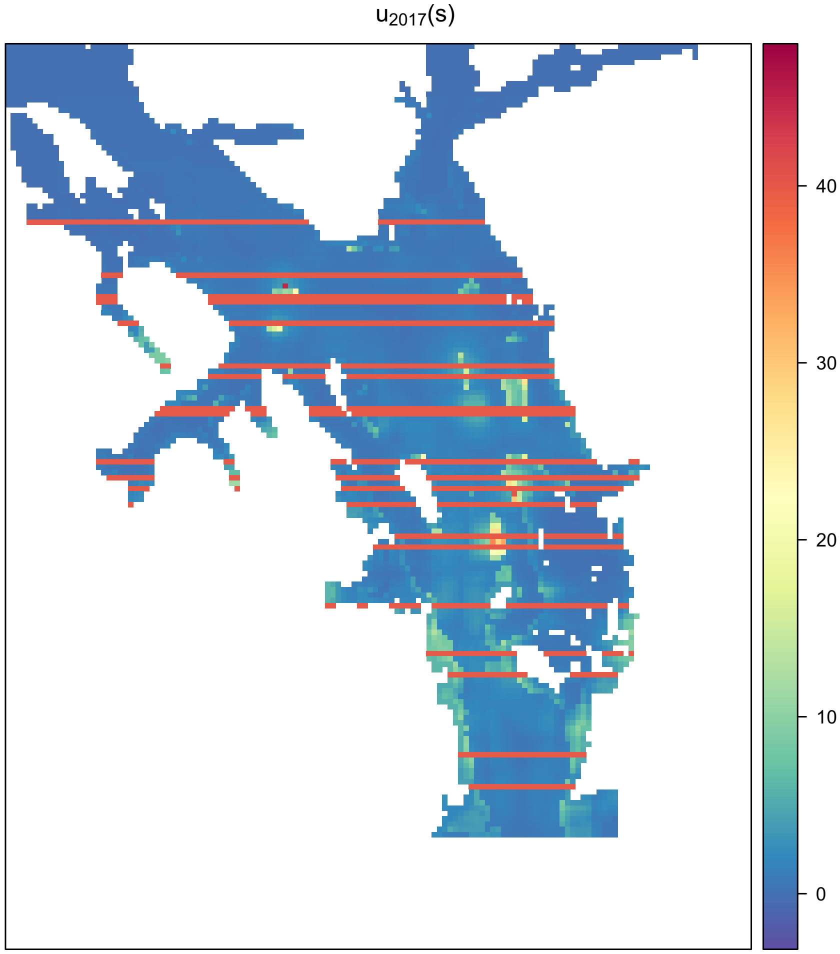

FIG. 4. Optimal dynamic survey design for sea otters in Glacier Bay National Park, 2017.

count data (Wikle and Royle 2005). In the sea otter example presented, minimizing prediction uncertainty was a logical choice for a design criterion. Establishing the theoretical optimality properties of this, and other design criteria, remains an area of active research. Other subjects of future research include the impact of alternative design criteria on selecting monitoring locations, the sensitivity and robustness of inference and predictions to recurrent surveys and model (mis)specification, and confronting potential bias due to preference sampling (sensu Diggle et al. 2010, Conn et al. 2017).

Extentions 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 be used alone to obtain design-based estimates of abundance, and may provide desirable statistical characteristics (e.g., unbiased estimation; Cochran 2007, Thompson 2012, although at a cost in precision). When using a hybrid approach, investigators can evaluate the efficacy of each sampling type to examine the potential trade-off in bias vs. variance.

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. 2017*b*). 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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LITERATURE CITED

Andow, D., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. Landscape Ecology 4: 177–188.

Berliner, L. M. 1996. Hierarchical Bayesian time series models. Pages 15–22 *in* K. M. Hanson, and R. N. Silver, editors. Maximum entropy and Bayesian methods. Springer Science & Business Media, Dordrecht, The Netherlands.

Berliner, L. M., Z.-Q. Lu, and C. Snyder. 1999. Statistical design for adaptive weather observations. Journal of the Atmospheric Sciences 56:2536–2552.

Bodkin, J. L. 2015. Historic and contemporary status of sea otters. Pages 44–59 *in* S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom, editors. Sea otter conservation. Academic Press, Cambridge, Massachusetts, USA.

Bodkin, J. L., and M. S. Udevitz. 1999. An aerial survey method to estimate sea otter abundance. Pages 13–26 *in* G. W. Garner, S. C. Amstrup, J. L. Laake, B. F. J. Manly, L. L. McDonald, and D. G. Robertson, editors. Marine mammal survey and assessment methods. CRC Press, Boca Raton, Florida, USA.

Bullock, J. M., R. E. Kenward, and R. S. Hails. 2002. Dispersal ecology: 42nd symposium of the British Ecological Society. Cambridge University Press, Cambridge, UK.

Cochran, W. G. 2007. Sampling techniques. John Wiley & Sons, Hoboken, New Jersey, USA.

Conn, P. B., J. T. Thorson, and D. S. Johnson. 2017. Confronting preferential sampling when analysing population distributions: diagnosis and model-based triage. Methods in Ecology and Evolution 8:1535–1546.

Cook, R. D., and C. J. Nachtrheim. 1980. A comparison of algorithms for constructing exact D-optimal designs. Technometrics 22:315–324.

Cressie, N., and C. K. Wikle. 2011. Statistics for spatio-temporal data. John Wiley & Sons, Hoboken, New Jersey, USA.

Diggle, P. J., R. Menezes, and T.-L. Su. 2010. Geostatistical inference under preferential sampling. Journal of the Royal Statistical Society: Series C (Applied Statistics) 59:191–232.

Esslinger, G. G., D. Esler, S. Howlin, and L. A. Starcevich. 2015. Monitoring population status of sea otters (*Enhydra lutris*) in Glacier Bay National Park and Preserve, Alaska–Options and considerations. Technical report, US Geologial Survey open-file report 2015–1119, 42 p.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

Evangelou, E., and Z. Zhu. 2012. Optimal predictive design augmentation for spatial generalised linear mixed models. Journal of Statistical Planning and Inference 142:3242–3253.

Fedorov, V., and A. Atkinson. 1988. The optimum design of experiments in the presence of uncontrolled variability and prior information. Pages 327–344 *in* Y. Dodge, V. V. Fedorov, and H. Wynn, editors. Optimal design and analysis of experiments. North-Holland, Amsterdam, The Netherlands.

Field, S. A., A. J. Tyre, and H. P. Possingham. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. Journal of Wildlife Management 69: 473–482.

Garlick, M. J., J. A. Powell, M. B. Hooten, and L. R. McFarlane. 2011. Homogenization of large-scale movement models in ecology. Bulletin of Mathematical Biology 73:2088–2108.

Gelfand, A. E., and A. F. Smith. 1990. Sampling-based approaches to calculating marginal densities. Journal of the American Statistical Association 85:398–409.

Hauser, C. E., and M. A. McCarthy. 2009. Streamlining ‘search and destroy’: cost-effective surveillance for invasive species management. Ecology Letters 12:683–692.

Hefley, T. J., M. B. Hooten, R. E. Russell, D. P. Walsh, and J. A. Powell. 2017. When mechanism matters: Bayesian forecasting using models of ecological diffusion. Ecology Letters 20: 640–650.

Hobbs, N. T., and M. B. Hooten. 2015. Bayesian models: a statistical primer for ecologists. Princeton University Press, Princeton, New Jersey, USA.

Holmes, E. E., M. A. Lewis, J. Banks, and R. Veit. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. Ecology 75:17–29.

Hooten, M. B., M. J. Garlick, and J. A. Powell. 2013. Computationally efficient statistical differential equation modeling using homogenization. Journal of Agricultural, Biological, and Environmental Statistics 18:405–428.

Hooten, M. B., and N. Hobbs. 2015. A guide to Bayesian model selection for ecologists. Ecological Monographs 85:3–28.

Hooten, M. B., D. S. Johnson, B. T. McClintock, and J. M. Morales. 2017. Animal movement: statistical models for telemetry data. CRC Press, Boca Raton, Florida, USA.

Hooten, M. B., B. E. Ross, and C. K. Wikle. 2012. Optimal spatio-temporal monitoring designs for characterizing population trends. Pages 443–459 *in* R. A. Gitzen, J. J. Millspaugh, A. B. Cooper, and D. S. Licht, editors. Design and analysis of long-term ecological monitoring studies. Cambridge University Press, Cambridge, Massachusetts, USA.

Hooten, M. B., and C. K. Wikle. 2008. A hierarchical Bayesian non-linear spatio-temporal model for the spread of invasive species with application to the Eurasian Collared-Dove. Environmental and Ecological Statistics 15:59–70.

Hooten, M. B., C. K. Wikle, R. M. Dorazio, and J. A. Royle. 2007. Hierarchical spatiotemporal matrix models for characterizing invasions. Biometrics 63:558–567.

Hooten, M. B., C. K. Wikle, S. L. Sheriff, and J. W. Rushin. 2009. Optimal spatio-temporal hybrid sampling designs for ecological monitoring. Journal of Vegetation Science 20:639–649.

Johnson, F. A., C. T. Moore, W. L. Kendall, J. A. Dubovsky, D. F. Caithamer, J. R. Jr Kelley, and B. K. Williams. 1997. Uncertainty and the management of mallard harvests. The Journal of Wildlife Management 61:202–216.

Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. Technical report, US Fish and Wildlife Service.

Le, N. D., and J. V. Zidek. 2006. Statistical analysis of environmental space-time processes. Springer Science & Business Media, Dordrecht, The Netherlands.

Lindenmayer, D. B., and G. E. Likens. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology & Evolution 24:482–486.

Mahar, P. S., and B. Datta. 1997. Optimal monitoring network and ground-water–pollution source identification. Journal of Water Resources Planning and Management 123: 199–207.

Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. Trends in Ecology & Evolution 21:668–673.

Nychka, D., and N. Saltzman. 1998. Design of air quality monitoring networks. Case studies in environmental statistics 132:51–76.

Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, Berlin, Germany.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Royle, J. A., and D. Nychka. 1998. An algorithm for the construction of spatial coverage designs with implementation in SPLUS. Computers & Geosciences 24:479–488.

Rubin, D. B. 1996. Multiple imputation after 18 + years. Journal of the American statistical Association 91:473–489.

Sanderlin, J. S., W. M. Block, and J. L. Ganey. 2014. Optimizing study design for multi-species avian monitoring programmes. Journal of Applied Ecology 51:860–870.

Savage, L. J. 1954. The foundations of statistics. Wiley, New York, New York, USA.

Scharf, H. R., M. B. Hooten, and D. S. Johnson. 2017. Imputation approaches for animal movement modeling. Journal of Agricultural, Biological and Environmental Statistics 22:335–352.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika 38:196–218.

Tanner, M. A. 1996. Tools for statistical inference: methods for the exploration of posterior distributions and likelihood functions. Springer, New York, New York, USA.

Thompson, S. K. 1990. Adaptive cluster sampling. Journal of the American Statistical Association 85:1050–1059.

Thompson, S. K. 2012. Sampling, Third edition.. Wiley, Hoboken, New Jersey, USA.

Thorson, J. T., J. Jannot, and K. Somers. 2017. Using spatiotemporal models of population growth and movement to monitor overlap between human impacts and fish populations. Journal of Applied Ecology 54:577–587.

Tinker, M. T. 2015. The use of quantitative models in sea otter conservation. Pages 257–300 *in* S. E. Larson, J. L. Bodkin, and G. R. VanBlaricom, editors. Sea otter conservation. Academic Press, Cambridge, Massachusetts, USA.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Massachusetts, USA.

Wald, A. 1950. Statistical decision functions. Wiley, New York, New York, USA.

Wikle, C. K. 2003. Hierarchical Bayesian models for predicting the spread of ecological processes. Ecology 84:1382–1394.

Wikle, C. K., and M. B. Hooten. 2006. Hierarchical Bayesian spatio-temporal models for population spread. Pages 145–169 *in* J. S. Clark, and A. Gelfand, editors. Hierarchical modelling for the environmental sciences. Oxford University Press, Oxford, UK.

Wikle, C. K., and M. B. Hooten. 2010. A general science-based framework for dynamical spatio-temporal models. Test 19:417–451.

Wikle, C. K., and J. A. Royle. 1999. Space: time dynamic design of environmental monitoring networks. Journal of Agricultural, Biological and Environmental Statistics 4:489–507.

Wikle, C. K., and J. A. Royle. 2005. Dynamic design of ecological monitoring networks for non-Gaussian spatio-temporal data. Environmetrics 16:507–522.

Williams, P. J., and M. B. Hooten. 2016. Combining statistical inference and decisions in ecology. Ecological Applications 26:1930–1942.

Williams, P. J., M. B. Hooten, J. N. Womble, and M. R. Bower. 2017*a*. Estimating occupancy and abundance using aerial images with imperfect detection. Methods in Ecology and Evolution 8:1679–1689.

Williams, P. J., M. B. Hooten, J. N. Womble, G. G. Esslinger, M. R. Bower, and T. J. Hefley. 2017*b*. An integrated data model to estimate spatiotemporal occupancy, abundance, and colonization dynamics. Ecology 98:328–336.

Williams, P. J., M. B. Hooten, G. G. Esslinger, J. N. Womble, J. L. Bodkin, and M. R. Bower. *in review*. The rise of an apex predator following deglaciation. Diversity and Distributions.

Williams, P. J., and W. L. Kendall. 2017. A guide to multi-objective optimization for ecological problems with an application to cackling goose management. Ecological Modelling 343: 54–67.

Wu, G., S. H. Holan, and C. K. Wikle. 2013. Hierarchical Bayesian spatio-temporal Conway-Maxwell Poisson models with dynamic dispersion. Journal of Agricultural, Biological and Environmental Statistics 18:335–356.