

1                   Monitoring dynamic spatio-temporal ecological  
2   processes optimally

3           Perry J. Williams <sup>\*1,2</sup>, Mevin B. Hooten<sup>3,2</sup>, Jamie N. Womble<sup>4,5</sup>, George G.  
4   Esslinger<sup>6</sup> and Michael R. Bower<sup>4</sup>

5           <sup>1</sup>Colorado Cooperative Fish and Wildlife Research Unit, Department of Fish, Wildlife, and Conservation  
6   Biology, Colorado State University, Fort Collins, CO 80523

7   <sup>2</sup>Department of Statistics, Colorado State University, Fort Collins, CO 80523

8           <sup>3</sup>U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Department of Fish,  
9   Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO

10           <sup>4</sup>National Park Service, Southeast Alaska Inventory and Monitoring Network, Juneau, AK

11   <sup>5</sup>National Park Service, Glacier Bay Field Station, Juneau, AK

12           <sup>6</sup>U.S. Geological Survey, Alaska Science Center, Anchorage, AK

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\*Corresponding author: [perry.williams@colostate.edu](mailto:perry.williams@colostate.edu)

## 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 per year. 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, 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. 2017, 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

39 populations are expected to be in the future. For example, sea otters (*Enhydra lutris*) in Glacier  
40 Bay have increased rapidly in distribution and abundance through time, requiring surveys to cover  
41 larger spatial domains, while operating under the same financial constraints.

42 During the multi-national commercial maritime fur trade of the 18<sup>th</sup> and 19<sup>th</sup> centuries, sea  
43 otters were extirpated from southeastern Alaska. Legislation following the maritime fur trade,  
44 including the International Fur Seal Treaty (1911), the Marine Mammal Protection Act (1972),  
45 and the Endangered Species Act (1977) provided legal protection to sea otters from most harvest  
46 (Kenyon 1969, Bodkin 2015, Williams et al. *In Review*). Legal protection, combined with  
47 translocations by wildlife agencies helped sea otters colonize much of their former distribution.  
48 By 1988, sea otters were documented at the mouth of Glacier Bay. Since then, sea otter abundance  
49 has increased an estimated 21.5% per year, a rate near their biological maximum reproductive  
50 rate. Further, sea otters have spread across Glacier Bay at a rate of at least 2.7 km per year. They  
51 are now one of the most abundant marine mammals in Glacier Bay (Williams et al. *In Review*).

52 Beginning in 1999, a design-based survey was used to monitor the abundance of sea otters  
53 in Glacier Bay (Bodkin and Udevitz 1999). The survey was conducted eight times between 1999  
54 and 2012, and consisted of systematically selected transects with random starting points  
55 (Esslinger et al. 2015). Survey effort was stratified based on ocean depth and shoreline features  
56 (Bodkin and Udevitz 1999). The northern extent of surveys was based on the existing distribution  
57 of sea otters. Initially, while sea otter distribution was relatively concentrated, abundance  
58 estimates were precise; between 1999 and 2006, the mean of the standard errors equaled 280  
59 otters (mean abundance = 1,496). As sea otters increased in abundance and distribution, distance  
60 between transects were increased to accommodate the increasing spatial extent of the sea otter  
61 distribution. However, the number of transects remained relatively constant due to logistical and  
62 budgetary constraints. As transects became more sparse, and as abundance increased, standard  
63 errors of abundance estimates increased, as did coefficients of variation. By 2012, the last year the

64 survey was conducted, the estimated abundance was 8,508 sea otters, and the standard error was  
65 greater than 2,200 sea otters (Esslinger et al. 2015, Williams et al. *In Review*).

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

74 Many ecological processes, including population spread, exhibit spatial patterns that change  
75 over time in a dynamic, yet predictable fashion. These dynamics are often ignored when  
76 developing spatial survey designs (Wikle and Royle 2005). However, efficient monitoring of such  
77 spatio-temporal processes can be achieved by modeling the dynamic process and associated  
78 uncertainty, and choosing future sampling locations that best help to reduce the uncertainty in the  
79 process (Hooten et al. 2009). There has been a proliferation of statistical methods for modeling  
80 and forecasting the distribution and abundance of a spreading population (e.g., Wikle 2003, Wikle  
81 and Hooten 2006, Hooten et al. 2007, Hooten and Wikle 2008, Williams et al. 2017). Although  
82 mathematical and statistical models are widely used for inferring population spread, rarely are  
83 data collection and modeling explicitly linked in a unifying framework.

84 Dynamic survey designs provide a cohesive framework for coupling models of population  
85 spread, and the optimal selection of sampling locations. We distinguish dynamic survey designs  
86 from traditional statistical notion of *adaptive sampling* (*sensu* Thompson 1990), although the two  
87 concepts are related. Dynamic survey designs are common in environmental monitoring,  
88 including: monitoring hurricanes via aircraft (Wikle and Royle 1999), ozone monitoring (Wikle

89 and Royle 1999), meteorological forecasting (Berliner et al. 1999), and ground-water-pollution  
90 source identification (Mahar and Datta 1997). However, dynamic survey designs have been  
91 applied to few long-term ecological monitoring programs (e.g., Wikle and Royle 2005, Hooten  
92 et al. 2009, Evangelou and Zhu 2012, Hooten et al. 2012).

93 We have four objectives in this paper: 1) introduce concepts and terminology related to  
94 optimal dynamic survey designs, 2) describe a general statistical framework for mechanistically  
95 modeling population spread, 3) fuse statistical models of population spread and dynamic survey  
96 designs in one coherent framework, and 4) apply the framework to monitoring sea otters in  
97 Glacier Bay. Although we motivate this application using monitoring of sea otters in Glacier Bay,  
98 we describe the methods in sufficient generality to be applicable to any system or taxa in which  
99 investigators are interested in modeling and monitoring the distribution, abundance, and  
100 colonization dynamics of a spreading population.

## 101 **Optimal dynamic survey design**

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

111 Dynamic survey designs can be broken down into a series of steps that are each  
112 conceptually straightforward (Fig. 1). First, a dynamic spatio-temporal process, such as

113 occupancy or abundance (and the associated uncertainty) is modeled using baseline data. Second,  
114 using the model from the first step, a statistical forecast is made. The forecast provides a basis for  
115 examining potential survey designs that could be implemented in the future. Third, investigators  
116 identify the objectives they wish to achieve with their monitoring (e.g., Nichols and Williams  
117 2006, Lindenmayer and Likens 2009). Objectives, or *design criteria*, typically include  
118 minimizing average prediction variance, minimizing maximum prediction variance (mini-max),  
119 or minimizing variance of parameter estimates (Wikle and Royle 1999; 2005, Hooten et al. 2009),  
120 but could also include minimizing multi-model uncertainty (Nichols and Williams 2006), cost  
121 (Field et al. 2005, Hauser and McCarthy 2009, Sanderlin et al. 2014), or some combination  
122 thereof (Williams and Kendall 2017). Fourth, after a design criterion is selected, a design is  
123 chosen that optimizes the design criterion. Fifth, data are then collected using the optimal design.  
124 The original model used to make the forecast is then updated with the new data. This process is  
125 iterated through time, increasing the understanding of the underlying ecological process of  
126 interest. In this regard, optimal dynamic survey designs are analogous to adaptive resource  
127 management, an iterative process of decision making in the face of uncertainty, with an aim to  
128 reducing management uncertainty through time by monitoring the system's response to  
129 management (e.g., Lindenmayer and Likens 2009, Johnson et al. 1997).

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

### 134 **A general spatio-temporal model for population-level animal movement**

135 Population spread exhibits linear or non-linear dynamics that can be classified as *diffusion*.  
136 Diffusion refers to the process of spreading out over an increasingly larger area through time  
137 (Skellam 1951, Wikle and Hooten 2010). Partial differential equations (PDE) are powerful tools

138 for modeling population-level (i.e., Eulerian) animal movement in ecology (e.g., Skellam 1951,  
 139 Okubo 1980, Andow et al. 1990, Holmes et al. 1994, Turchin 1998, Wikle 2003, Hooten and  
 140 Wikle 2008, Wikle and Hooten 2010, Hooten et al. 2013, Williams et al. 2017). During diffusion,  
 141 individual organisms are usually influenced by habitat type. Individuals move slowly through  
 142 areas that contain necessary resources, and move quickly through areas that do not. *Ecological*  
 143 *diffusion* is a flexible diffusion model that accommodates this variation in motility by predicting  
 144 animals will eventually accumulate in desirable habitats, and leave or avoid undesirable ones  
 145 (Turchin 1998, Garlick et al. 2011, Hefley et al. 2017, Williams et al. 2017). Specifically,  
 146 ecological diffusion describes the population-level distribution that results from individual  
 147 random walks, with individual movement probabilities determined by information on local  
 148 habitat conditions (Garlick et al. 2011, Hefley et al. 2017, Williams et al. 2017). Assuming no  
 149 advection or growth, ecological diffusion can be represented by the PDE

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

150 where  $\frac{\partial u(\mathbf{s}, t)}{\partial t}$  represents the instantaneous change in abundance intensity over a continuous spatial  
 151 domain with coordinates (e.g., latitude and longitude)  $\mathbf{s} \equiv (s_1, s_2)' \in \mathcal{S}$  during time  $t$ ,  
 152  $\left( \frac{\partial^2}{\partial s_1^2} + \frac{\partial^2}{\partial s_2^2} \right)$  is the differential (Laplace) operator, and  $\mu(\mathbf{s}, t)$  represents the diffusion coefficient  
 153 that could vary in space and time. Ecological diffusion differs from other common  
 154 reaction-diffusion models, in that it allows individual movement to be based on local conditions  
 155 such as habitat type (c.f., Fickian and plain diffusion; Garlick et al. 2011). The mathematical  
 156 driver for this difference is that the diffusion coefficient occurs on the inside of the two spatial  
 157 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:  
 158  $\frac{\partial u}{\partial t} = \mu \frac{\partial^2}{\partial x^2} (u)$ ), resulting in a much less smooth process, and motility-driven congregation to  
 159 differ sharply between neighboring habitat types (Hooten et al. 2013). Hefley et al. (2017)

160 recently described the advantages of ecological diffusion for modeling a spreading population  
 161 including: its ability to connect spatio-temporal processes while providing a mechanism that  
 162 captures transient dynamics, preventing animals from instantaneously accessing all high quality  
 163 habitats; its relative simplicity compared to other mechanistic models; and its flexibility in being  
 164 able to capture a wide range of spatio-temporal dynamics. For example, eq. 1 can be further  
 165 generalized to include growth models,

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

166 incorporating Malthusian growth ( $f(u(\mathbf{s}, t), \mathbf{s}, t) = \gamma(\mathbf{s}, t)u(\mathbf{s}, t)$ ), or logistic growth  
 167 ( $f(u(\mathbf{s}, t), \mathbf{s}, t) = \gamma(\mathbf{s}, t)(1 - u(\mathbf{s}, t)/\kappa(\mathbf{s}, t))$ ) where  $\gamma(\mathbf{s}, t)$  represents the instantaneous growth  
 168 rate, and  $\kappa(\mathbf{s}, t)$  represents equilibrium population size. In principle, each of the modeling  
 169 components, including motility ( $\mu(\mathbf{s}, t)$ ), growth ( $\gamma(\mathbf{s}, t)$ ), and equilibrium density ( $\kappa(\mathbf{s}, t)$ ) can  
 170 depend on covariates that vary over space and time, although standard model-fitting  
 171 considerations apply (i.e., parsimony) when tailoring these models to each system. We consider  
 172 models that incorporate spatial covariates for diffusion,  $g(\mu(\mathbf{s}_i, t)) = \mathbf{x}'(\mathbf{s}_i)\boldsymbol{\beta}$ , and growth,  
 173  $h(\gamma(\mathbf{s}_i)) = \mathbf{w}'(\mathbf{s}_i)\boldsymbol{\alpha}$ , where  $g$  and  $h$  are link functions (e.g., log and identity, respectively),  $\boldsymbol{\beta}$  and  
 174  $\boldsymbol{\alpha}$  are vectors of parameters to be estimated, and  $\mathbf{x}'(\mathbf{s}_i)$  and  $\mathbf{w}'(\mathbf{s}_i)$  are vectors containing spatially  
 175 referenced covariate values (Williams et al. 2017).

176 Implementation of eqs. 1 and 2 require numerical methods to solve the PDE. Finite  
 177 differencing is a common method for solving PDEs, and is often used when PDEs are  
 178 implemented within a Bayesian hierarchical framework (Wikle and Hooten 2010). Solving a PDE  
 179 using finite differencing involves partitioning the spatial domain  $\mathcal{S}$  into a grid  $\mathbf{S}$  ( $\mathbf{S} \subseteq \mathcal{S}$ ) with  $m$   
 180 cells and the temporal domain  $\mathcal{T}$  into  $r$  bins  $\mathbf{T}$  of width  $\Delta t$  ( $\mathbf{T} \subseteq \mathcal{T}$ ). Simple finite-difference



181 discretization results in the vector difference equation

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

182 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  
 183 accommodating diffusion parameters ( $\boldsymbol{\beta}$ ) and growth parameters ( $\boldsymbol{\alpha}$ ), and the superscript (b)  
 184 represents conditions at the boundaries. Each row in  $\mathbf{H}$  corresponds to a specific cell in the grid  $\mathbf{S}$ .  
 185 The five non-zero values in each row correspond to the specific cell in  $\mathbf{H}$ , and the four nearest  
 186 (rook) neighbors of that cell. The values of the non-zero cells are determined by the growth and  
 187 diffusion parameters  $\boldsymbol{\alpha}$  and  $\boldsymbol{\beta}$ , respectively, and describe the how  $\mathbf{u}_{t-1}$  changes in space through  
 188 time. To simplify notation in what follows, we assume  $\mathbf{H}$  depends on diffusion and growth  
 189 parameters, but omit the notation for  $\boldsymbol{\alpha}$ ,  $\boldsymbol{\beta}$  for brevity. We also omit the notation for boundary  
 190 conditions. The accuracy of the numerical approximation of  $u(\mathbf{s}, t)$  increases as the number of  
 191 cells on the spatial grid increases and  $\Delta t$  becomes small. For additional details on discretization  
 192 of PDEs and applications of spreading populations, see Wikle and Hooten (2006), Hooten and  
 193 Wikle (2008), Hefley et al. (2017), and Williams et al. (2017); Wikle and Hooten (2006), Hefley  
 194 et al. (2017), and Williams et al. (2017) provide R code for implementation (see Hefley et al.  
 195 2017, Williams et al. 2017, for ecological diffusion).

## 196 **Models of ecological diffusion and statistical uncertainty**

197 Bayesian hierarchical models can be described in terms of three levels (Berliner 1996). At the top  
 198 level, a data model links the observed data and associated variation to latent ecological processes.  
 199 Next, a process model describes the underlying ecological processes (i.e., spatio-temporal  
 200 colonization dynamics). Finally, parameter models represent prior knowledge about the parameter  
 201 inputs in the ecological process model and data model. This framework allows us to incorporate  
 202 mathematical models that characterize spreading populations, such as the PDEs in eqs. 1 or 2, as

203 process models within a statistical framework, permitting appropriate estimation of uncertainty at  
 204 multiple levels (Wikle 2003, Hooten and Wikle 2008, Wikle and Hooten 2010, Cressie and Wikle  
 205 2011, Hooten et al. 2013, Hefley et al. 2017, Williams et al. 2017). Using the discretized form of  
 206 ecological diffusion in eq. 3, this framework is written hierarchically as

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

207 where  $y_t(\mathbf{s}_i)$  represents data collected during discrete time  $t$  at spatial location  $\mathbf{s}_i$ ,  $[a|b]$  represents  
 208 the probability density (or mass) function of variable  $a$  given variable  $b$  (Gelfand and Smith  
 209 1990), and  $\mathbf{n}_t \equiv (n_t(\mathbf{s}_1), \dots, n_t(\mathbf{s}_n))'$ . The initial condition for  $\mathbf{u}_1$  must also be specified, and is  
 210 represented as a function of (potentially vector valued) parameters  $\boldsymbol{\zeta}$ . Bayesian hierarchical  
 211 models that incorporate PDE processes are flexible and can be modified to address the specifics of  
 212 the study (Hefley et al. 2017). For example, a common specification of eq. 4 for discrete data  
 213 (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  
 214  $n_t(\mathbf{s}_i)$  is the true latent abundance, and  $\phi$  is the detection probability), and a Poisson process  
 215 model (i.e.,  $\mathbf{n}_t \sim \text{Poisson}(\mathbf{u}_t)$ , in which case  $\nu$  is not necessary). Other process models include  
 216 negative-binomial or Conway-Maxwell Poisson distributions (in which case,  $\nu$  is a parameter that  
 217 controls either overdispersion or underdispersion, respectively; Wu et al. 2013). Equation 4 can  
 218 be further generalized to address error in discretization, model uncertainty, and environmental  
 219 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  
 220 matrix describing (potentially spatially autocorrelated) error in  $\mathbf{u}_t$  (Wikle and Hooten 2010,

221 Thorson et al. 2017).

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

### 230 **Forecast distribution**

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

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

236 The Bayesian hierarchical model described in eq. 4 provides straightforward calculation of the  
 237 forecast distribution. Obtaining  $[\mathbf{u}_{T+1} | \mathbf{y}_1, \dots, \mathbf{y}_T]$  is as simple as changing the range of the index  
 238 for  $t$  in eq. 4 to  $t = 2, \dots, T + 1$ , and sampling  $\mathbf{u}_{T+1}^{(k)}$  on each  $k = 1, \dots, K$  iteration of an MCMC  
 239 algorithm (Tanner 1996, Hobbs and Hooten 2015). The posterior predictive distribution can then  
 240 be easily obtained from the forecast distribution using two additional steps; first sample  
 241  $\mathbf{n}_{T+1}^{(k)} \sim [\mathbf{n}_{T+1} | \mathbf{u}_{T+1}^{(k)}, \nu^{(k)}]$ . Then sample  $\mathbf{y}_{T+1}^{(k)} \sim [\mathbf{y}_{T+1} | \mathbf{n}_{T+1}^{(k)}, \phi^{(k)}]$  for all  $k$  to obtain  
 242  $[\mathbf{y}_{T+1} | \mathbf{y}_1, \dots, \mathbf{y}_T]$ . The forecast distribution and posterior predictive distribution can then be used

243 to select a survey design that is optimal with respect to a design criterion.

## 244 **Design criteria**

245 Design criteria are mathematical representations of the objectives investigators seek to achieve by  
 246 collecting data (Williams and Hooten 2016). As such, design criteria are specific to each study.  
 247 However, a common objective of collecting data for many studies is to reduce the uncertainty  
 248 associated with ecological forecasts/predictions. That is, choose a survey design  $d$  that allows us  
 249 to minimize the uncertainty associated with  $[\mathbf{u}_{T+1} | \mathbf{y}_1, \dots, \mathbf{y}_T]$ , or some derived parameter of  
 250  $\mathbf{u}_{T+1}$ . Several authors have discussed specific design criteria (e.g., Wikle and Royle 1999,  
 251 Berliner et al. 1999, Wikle and Royle 2005, Le and Zidek 2006, Hooten et al. 2009), as well as  
 252 efficient methods for estimating them (e.g., Kalman filters). Here, we consider choosing a design  
 253 that minimizes the uncertainty of  $u_{\text{total},T+1} = \sum_{i=1}^n u_{i,T+1}$ , the sum of the dynamic  
 254 spatio-temporal process representing abundance intensity in future years. Specifically, the design  
 255 criterion we consider is the empirical variance of the future abundance estimate

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

256 where  $k = 1, \dots, K$  corresponds to the  $k^{\text{th}}$  MCMC iteration, and  $u_{\text{total},T+1,d}^{(k)}$  is the sum of the  
 257 forecasted process at time  $T + 1$ , estimated using real data,  $\mathbf{y}_1, \dots, \mathbf{y}_T$ , and future data,  $y_{T+1,d}$ .  
 258 Obviously, future data are unavailable prior to the survey. Lacking such data, one approach is to  
 259 use the mean of the posterior predictive distribution as a surrogate for future data, and assume it  
 260 represents the true data that remain to be collected. This technique, known as *imputation*, may not  
 261 accommodate the proper uncertainty associated with data collection. Another technique, known  
 262 as *multiple imputation*, helps to account for the uncertainty associated with the modeled data that  
 263 we intend to use for identifying optimal survey designs (Rubin 1996, Hooten et al. 2017, Scharf  
 264 et al. 2017).

265 **Multiple imputation**

266 Implementing multiple imputation within a Bayesian model using MCMC is straightforward  
 267 (Hooten et al. 2017). First, the model is fit using the original data,  $\mathbf{y}_1, \dots, \mathbf{y}_T$ . Second,  $K$   
 268 posterior predictive realizations of future data  $\mathbf{y}_{T+1}^{(k)}$  are sampled for MCMC samples  
 269  $k = 1, \dots, K$ , using the methods described in *Forecast distribution*, above. Third, the model is  
 270 re-fit using a modified MCMC algorithm. Instead of conditioning only on the fixed data,  
 271  $\mathbf{y}_1, \dots, \mathbf{y}_T$ , on the  $k^{\text{th}}$  iteration of the MCMC algorithm, we use the fixed data *and*  $\mathbf{y}_{T+1}^{(k)}$ . Finally,  
 272 we obtain posterior summaries for model parameters, and derived parameters including  $u_{\text{total}, T+1}$ .  
 273 The modified MCMC algorithm will integrate over the uncertainty in the true future data, and  
 274 incorporate the uncertainty in the inference for the model parameters (Hooten et al. 2017).

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

279

**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  $\mathbf{y}_1, \dots, \mathbf{y}_T$ .
2. Forecast  $\mathbf{u}_{T+1}^{(k)}$  for all  $k = 1, \dots, K$  MCMC samples using eq. 5.
3. Sample  $K$  posterior predictive realizations of future data  $\mathbf{y}_{T+1}^{(k)}$  for  $k = 1, \dots, K$  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  $\mathbf{y}_1, \dots, \mathbf{y}_T$ , 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  $u_{\text{total},T+1,d}^{(k)} = \sum_{i=1}^n u_{i,T+1,d}^{(k)}$  from the model fit in step 5.
7. Use  $u_{\text{total},T+1,d}^{(k)}$  to calculate eq. 6 from the text.
8. Repeat steps 1-7 for all designs under consideration, and identify the design that minimizes  $q_d$ .

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

286 After the optimal design has been identified, the new data,  $\mathbf{y}_{T+1,d}$ , can be collected, the  
 287 model can be subsequently re-fit using the new data, ecological learning can be assessed by

288 comparing the previous model fit to the new model fit, and the procedure can be repeated to  
289 identify the optimal design for time  $T + 2$ . In the next section, we apply this general procedure to  
290 identify optimal transects to survey for estimating the distribution, abundance, and colonization  
291 dynamics of sea otters in Glacier Bay.

## 292 **Application: sea otters in Glacier Bay**

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

## 299 **Baseline data**

300 Sea otter occupancy and abundance data have been collected over a 20-year period between 1993  
301 and 2012. A detailed description of the methods that were used for collecting data are provided in  
302 Bodkin and Udevitz (1999) and Williams et al. (2017). Briefly, a *design-based survey* was  
303 conducted eight times (1999–2004, 2006, 2012), and a *distributional survey* was conducted eight  
304 times (1993, 1995–1998, 2005, 2009, 2010). The design-based survey consisted of observers  
305 flying in aircraft piloted along transects. The transects were systematically placed across Glacier  
306 Bay, with a random starting point. Observers flew along transects and recorded the number of sea  
307 otters observed within 400 m of the transect, and mapped the location of sea otters during  
308 observations. The distributional surveys consisted of observers flying in aircrafts that were piloted  
309 in close proximity to shorelines and islands, the preferred habitat of sea otters (Williams et al.  
310 2017, Williams et al. *In Review*). Pilots did not follow pre-determined routes during distributional  
311 surveys. An additional data set was collected during the design-based survey to estimate detection

312 probability (Williams et al. 2017).

313 **Statistical diffusion model and forecast**

314 We tailored eq. 4 to the sea otter data following Williams et al. (2017) and Williams et al. (*In*  
 315 *Review*). Retaining connection to the continuous time, continuous space process model, we  
 316 assumed

**Data Model:**  $y_t(\mathbf{s}_i) \sim \text{Binomial}(n_t(\mathbf{s}_i), \phi),$

**Process Model:**  $n_t(\mathbf{s}_i) \sim \text{Poisson}(u_t(\mathbf{s}_i)),$

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

$$u(\mathbf{s}_i, 1) = \frac{\tau e^{-\frac{|\mathbf{s}_i - \mathbf{d}|^2}{\psi^2}}}{\int_S e^{-\frac{|\mathbf{s}_i - \mathbf{d}|^2}{\psi^2}} d\mathbf{s}}, \quad t = 1$$

$$\log(\mu(\mathbf{s}_i)) = \beta_0 + \beta_1(\text{depth}(\mathbf{s}_i)) + \beta_2(\text{dist}(\mathbf{s}_i)) + \beta_3(\text{depth}(\mathbf{s}_i) \times \text{slope}(\mathbf{s}_i)) \\ + \beta_4(\text{complexity}(\mathbf{s}_i))$$

$$\gamma(\mathbf{s}_i) = \alpha_0$$

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

$$\boldsymbol{\beta} \sim \text{Normal}(\mathbf{0}, \sigma^2 \mathbf{I})$$

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

$$\psi \sim \text{Normal}^+(5, 0.001)$$

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

(7)

317 where  $y_t(\mathbf{s}_i)$  were sea otter count data within a  $400 \times 400$  m grid cell centered at location  $\mathbf{s}_i$  during  
 318 time  $t$ ,  $n_t(\mathbf{s}_i)$  was the true latent abundance of sea otters,  $\phi$  was the individual sea otter detection  
 319 probability, and  $u_t(\mathbf{s}_i)$  was the dynamic spatio-temporal process (abundance intensity) when data



320 were collected during time  $t$ . We used a scaled Gaussian kernel for our initial condition for  
321 abundance intensity, with two parameters  $\zeta \equiv (\tau, \psi)'$ , controlling the height and spread of the  
322 kernel, respectively, around an epicenter  $\mathbf{d}$ . The epicenter represents the location of an initial  
323 colonization event at the beginning of the time series. We used a log-linear relationship between  
324 motility and four spatial habitat covariates that we hypothesized affect sea otter motility. The  
325 covariates were ocean depth (an indicator of depth < 40 m), distance to shore, slope of the ocean  
326 floor, and an index for shoreline complexity that was calculated by summing the number of  
327 shoreline grid cells that were within 1,000 m of each grid cell. We used the interaction between  
328 depth and slope because the slope of the ocean floor may only be important if it is shallow enough  
329 for sea otters to reach it during feeding dives.

330 We assumed the growth rate was constant across space and time for simplicity and because  
331 design-based estimates of abundance suggested that Glacier Bay is still in a rapid growth phase  
332 (Williams et al. In Review). However, increasing evidence suggests that density dependence in  
333 sea otters occurs at relatively fine spatial scales (Bodkin 2015, Tinker 2015), and it is possible that  
334 density dependence may be limiting growth in some areas of Glacier Bay. Further, there is  
335 extensive evidence that sea otters alter their own ecosystems through a series of direct and  
336 indirect food web impacts. Thus, both diffusion and growth may change through time, and in  
337 principle, could be incorporated in our model formulation, provided sufficient data exist to  
338 estimate the required parameters. Our approach was to identify a parsimonious model and use a  
339 model checking procedure to evaluate our assumptions of exponential growth and static diffusion  
340 rates through time.

341 We used vague prior distributions for all parameters except for the shrinkage parameter  $\sigma$ ,  
342 and the initial condition parameters,  $\tau$  and  $\psi$ . We parameterized the initial condition parameters  
343 based on observations of sea otters during the first year of monitoring, where Normal<sup>+</sup> represents  
344 the zero-truncated normal distribution.

345 We fit the model described in eq. 7 to the baseline data using a custom MCMC algorithm  
346 written in R version 3.3.2 (R Core Team 2013) and C++. For each model fit, we obtained two  
347 chains of 50,000 MCMC draws and discarded the first 10,000. We examined convergence using  
348 trace plots and Gelman-Rubin diagnostics. To facilitate computation, we used homogenization to  
349 implement the model (Garlick et al. 2011, Hooten et al. 2013, Hefley et al. 2017, Williams et al.  
350 2017). Homogenization is a multi-scale technique that allowed us to optimally up-scale  
351 (decrease) the resolution of our spatial domain for computation, and then optimally downscale  
352 (increase) the resolution of the spatial domain to make fine-scale inference. We used  
353 regularization combined with k-fold cross-validation to conduct model selection. Specifically, we  
354 first randomly partitioned the data into 8 folds. Second, we selected a diffuse value of  $\sigma$  and fit the  
355 model using seven of the eight groups of data. Third, we used the remaining group of data to  
356 calculate the log-posterior predictive distribution score function (Hooten and Hobbs 2015).  
357 Fourth, we repeated the procedure for the remaining seven combinations of data and summed the  
358 log-posterior predictive distribution score function for all eight hold-out samples. Fifth, we  
359 decreased  $\sigma$  (a mechanism to induce regularization) and repeated this procedure. That is, we  
360 calculated the sum of the log-posterior predictive distribution score function for each  $\sigma$  over a  
361 range of values and identified which value of  $\sigma$  resulted in the best (lowest) score. We used the  
362 resulting value of  $\sigma$  in our final model for prediction and inference. We assessed goodness of fit  
363 of our final model using Bayesian p-values (see Williams et al. *In Review* for more details). We  
364 then estimated the forecast distribution for  $T + 5 = 2017$ , because the last time sea otter data  
365 were collected was  $T = 2012$  (Fig. 2).

## 366 **Optimal design**

### 367 **Potential survey transects**

368 To identify the set of all potential transects that could be surveyed, we partitioned Glacier Bay  
369 into a regular grid of  $400 \times 400$  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,  $400 \times 400$  m represented the scale at which the baseline data were collected. After partitioning Glacier Bay into  $400 \times 400$  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 hours 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<sup>®</sup>, 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

395 recalculated  $q_d$  after the exchange. This required re-fitting the model with the inclusion of a  
396 neighboring transect and the exclusion of the original transect. If the exchange improved  $q_d$ , we  
397 retained the new transect in place of the old transect. Then, the next transect on the list was  
398 exchanged. The process repeated until the design criterion could not be improved through  
399 exchange. Because each exchange requires re-fitting the model, and it must occur sequentially  
400 (except for examining the two immediate neighbors, which can occur in parallel), this required a  
401 sequence of several model fits. However, in practice, convergence to the optimal survey design  
402 occurs with relatively few exchanges using this approach. The sea otter survey required six  
403 exchanges before  $q_d$  could no longer be improved through exchange.

## 404 **Results**

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

## 411 **Discussion**

412 How to best use available resources to monitor ecological processes for conservation,  
413 management, and ecological insight remains a critical area of scientific investigation (Nichols and  
414 Williams 2006). Probabilistic (i.e., design-based) surveys have been used widely in ecology, and  
415 can provide data that result in objective, unbiased estimates of abundance (Cochran 2007,  
416 Thompson 2012). However, when financial resources limit the effort that can be devoted to  
417 collecting data, classical design-based inference may result in estimates that are insufficiently  
418 precise for management or conservation (e.g., sea otters in Glacier Bay). The situation becomes

419 more acute for populations that are spreading in space through time. Alternatively, optimal  
420 dynamic survey designs allow managers and scientists the ability to extract the most information  
421 out of the data they can afford to collect. Further, dynamic survey designs better allow for the  
422 observation of dynamically evolving spatio-temporal processes, and ultimately result in higher  
423 quality data (Wikle and Royle 1999; 2005, Hooten et al. 2009).

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

430 We described a general, cohesive framework for modeling and monitoring population-level  
431 animal movement that explicitly links survey design, data collection, and monitoring objectives.  
432 The generality of this framework stems from the flexibility of hierarchical statistical models to  
433 draw conclusions from data that arise from complex ecological processes, the flexibility of PDEs  
434 (specifically, ecological diffusion) to capture a wide range of spatio-temporal dynamics, and the  
435 ability to tailor design criteria to meet the objectives of each unique study. We applied the  
436 framework to identify an optimal dynamic survey design for sea otters in Glacier Bay. Sea otters  
437 have been identified as a vital sign for Glacier Bay. Vital-sign monitoring is used to track specific  
438 ecosystem processes that are selected to represent the overall health or condition of park  
439 resources, known or hypothesized effects of stressors, or elements that have important human  
440 values. Inference that results from monitoring is then used by employees and partners to support  
441 management decision-making, park planning, research, education, and public understanding of  
442 park resources. Thus, a survey design that results in precise and rigorous estimates of abundance,  
443 distribution, and colonization dynamics is required. We examined a monitoring scenario in which

444 available funding permitted surveying 20 of the 170 potential transects that partition Glacier Bay.  
445 Generally, posterior mean estimates of sea otter expected abundance were similar among the  
446 designs we considered; all designs predicted approximately 9,500 sea otters in 2017. However,  
447 the uncertainty associated with these predictions varied widely among designs. The optimal  
448 design reduced prediction uncertainty by 13% compared to the mean of all the random designs  
449 that were considered (Fig. 3). The dynamic survey designs employed for sea otter surveys here,  
450 are applicable to any type of aerial survey method used for sea otters, including aerial  
451 observations where observers count sea otters from an aircraft (Bodkin and Udevitz 1999), or  
452 aerial photographs (Williams et al. In Press).

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

469 information needs in the conservation process, and therefore, the effectiveness of conservation  
470 can be greatly increased (Nichols and Williams 2006).

471 Monitoring dynamic processes optimally is a growing subject in ecology. There is much  
472 more to learn about the choice of design criterion for estimating and predicting count data (Wikle  
473 and Royle 2005). In the sea otter example presented, minimizing prediction uncertainty was a  
474 logical choice for a design criterion. Establishing the theoretical optimality properties of this, and  
475 other design criteria, remains an area of active research. Other subjects of future research include  
476 the impact of alternative design criteria on selecting monitoring locations, the sensitivity and  
477 robustness of inference and predictions to recurrent surveys and model (mis)specification, and  
478 confronting potential bias due to preference sampling (*sensu* Diggle et al. 2010, Conn et al. In  
479 Press).

480 Extensions of dynamic survey designs include hybrid survey designs. Hybrid survey designs  
481 combine classical survey techniques (e.g., random sampling) with dynamic survey designs to  
482 identify an optimal dynamic survey design (Hooten et al. 2009; 2012). Hybrid survey designs are  
483 advantageous because they leverage the benefits of traditional survey techniques (e.g., generally  
484 more convenient, economically feasible, and computationally inexpensive), with the benefits of  
485 dynamic survey designs (e.g., optimal efficiency, capture spatio-temporal evolution in a process,  
486 flexibility to add or remove monitoring locations as budgets change; Hooten et al. 2009). When  
487 hybrid survey designs contain a design-based sampling component, the design-based data can be  
488 used alone to obtain design-based estimates of abundance, and may provide desirable statistical  
489 characteristics (e.g., unbiased estimation; Cochran 2007, Thompson 2012, although at a cost in  
490 precision). When using a hybrid approach, investigators can evaluate the efficacy of each  
491 sampling type to examine the potential trade-off in bias vs. variance.

492 Finally, spreading populations are ideal candidates for dynamic survey designs because  
493 spreading populations have significant spatio-temporal interactions that are difficult to observe

494 using traditional survey designs. The spatio-temporal processes that regulate population spread  
495 are often of ecological interest (e.g., processes that influence species invasions, mesopredator  
496 release, (re)establishment of apex predators; Williams et al. 2017). When baseline data exist to  
497 develop appropriate models of population spread, implementing dynamic survey designs for  
498 future data collection provide an opportunity to maximize efficiency in learning about these  
499 spatio-temporal processes (Wikle and Royle 1999). When resources are limited, as they always  
500 are, the efficient use of monitoring is vital to successful conservation (Nichols and Williams  
501 2006).

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652 **Figure 1** Schematic of optimal dynamic survey design.

653 **Figure 2** Forecasted mean of dynamic spatio-temporal process ( $u_{2017}(\mathbf{s})$ ) representing  
654 abundance intensity of sea otters in Glacier Bay National Park, Alaska. Units are mean sea otters  
655 per 400 m<sup>2</sup>

656 **Figure 3** Histogram of  $q_d$  values from 64 randomly selected designs (gray) and the optimal  
657 design (black), each design containing 20 randomly selected transects to be flown over Glacier  
658 Bay National Park in the upcoming survey year. The design criterion  $q_d$  was calculated using eq.  
659 6 from the text, and corresponds to reducing uncertainty in the forecast distribution of mean total  
660 abundance of sea otters in the future year. The best random design had  $q_d = 57,439$  (dark gray),  
661 and was improved to  $q_d = 55,261$  (black) using an exchange algorithm. The mean value of  $q_d$  for  
662 the 64 random transects equaled 62,804 (vertical line).

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

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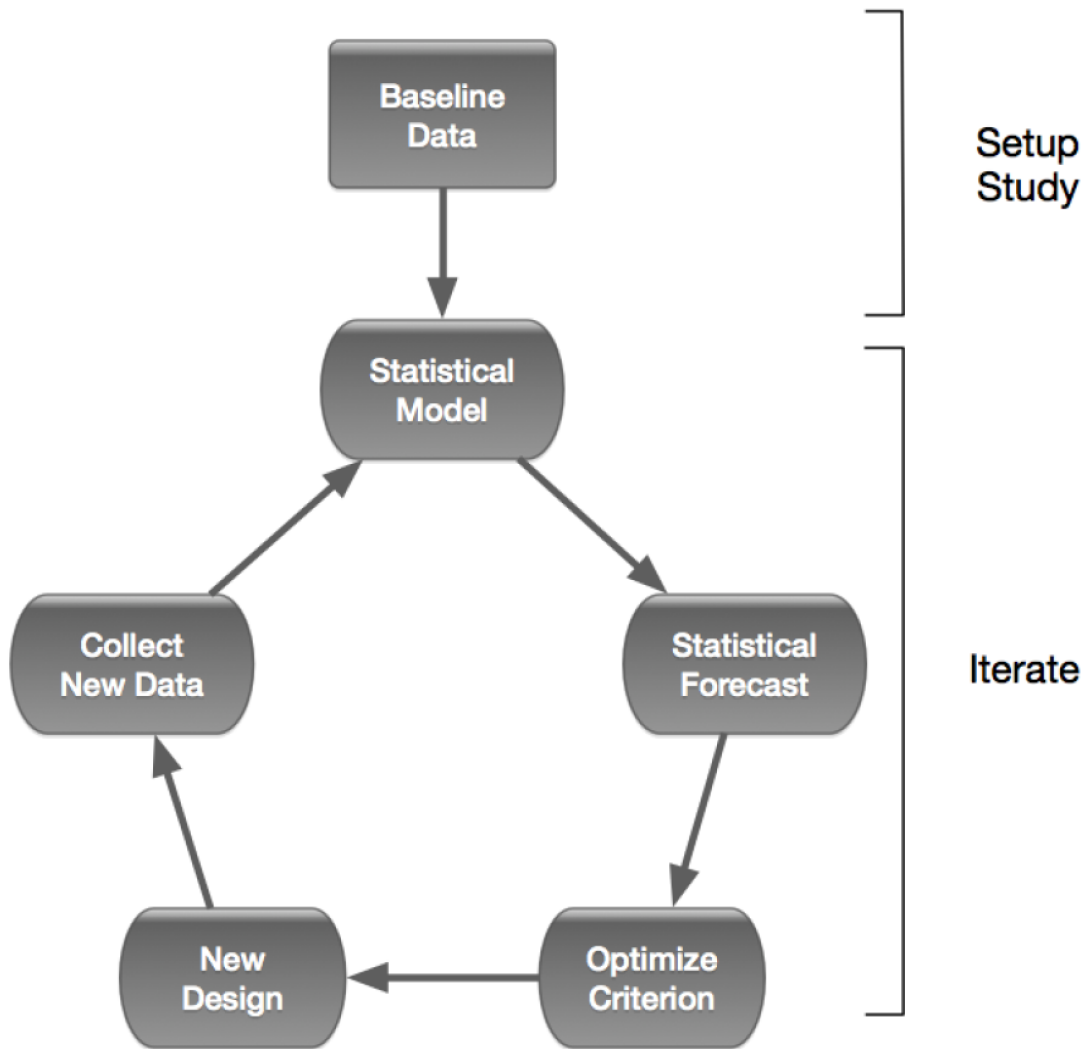


Figure 1



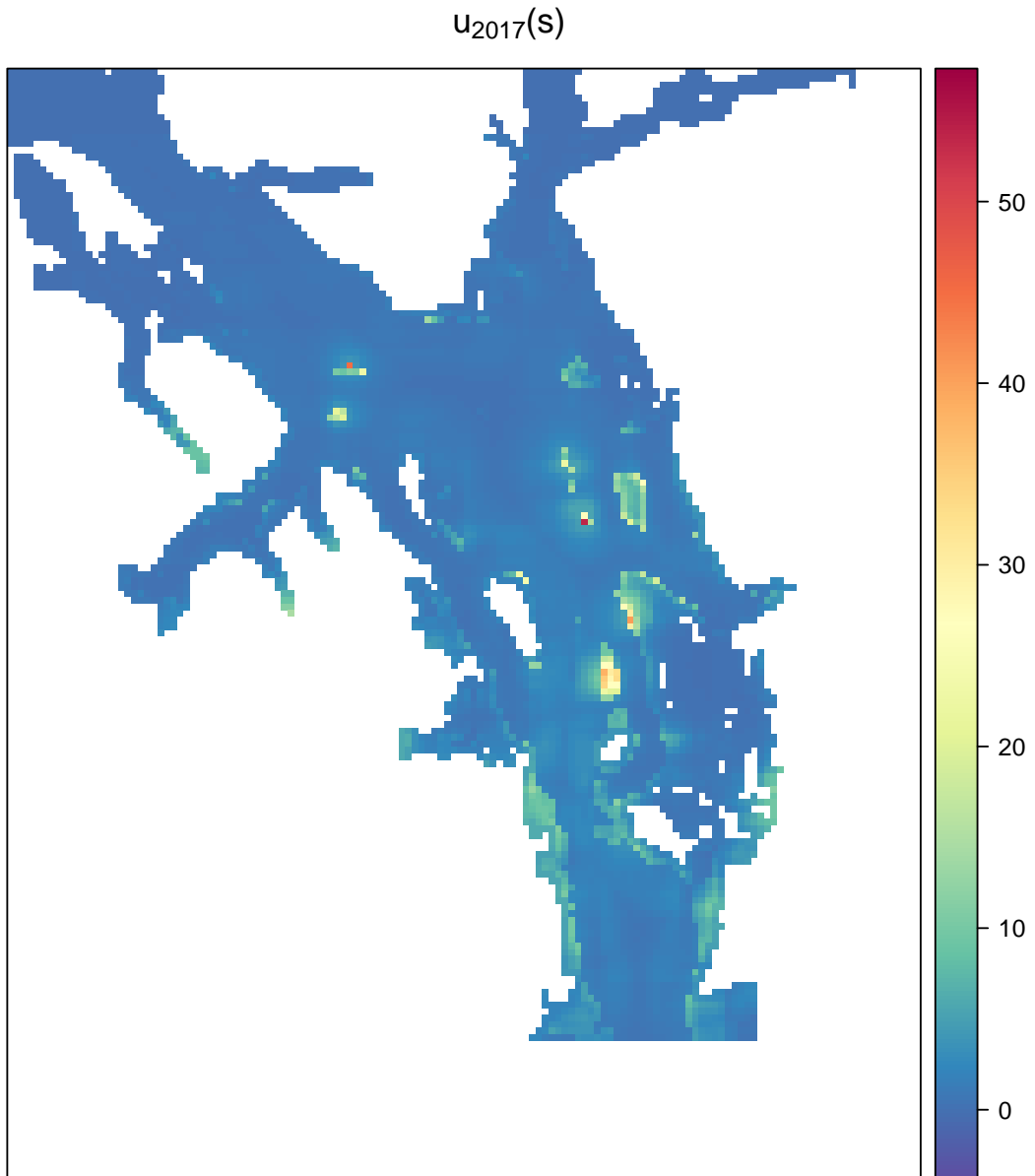


Figure 2

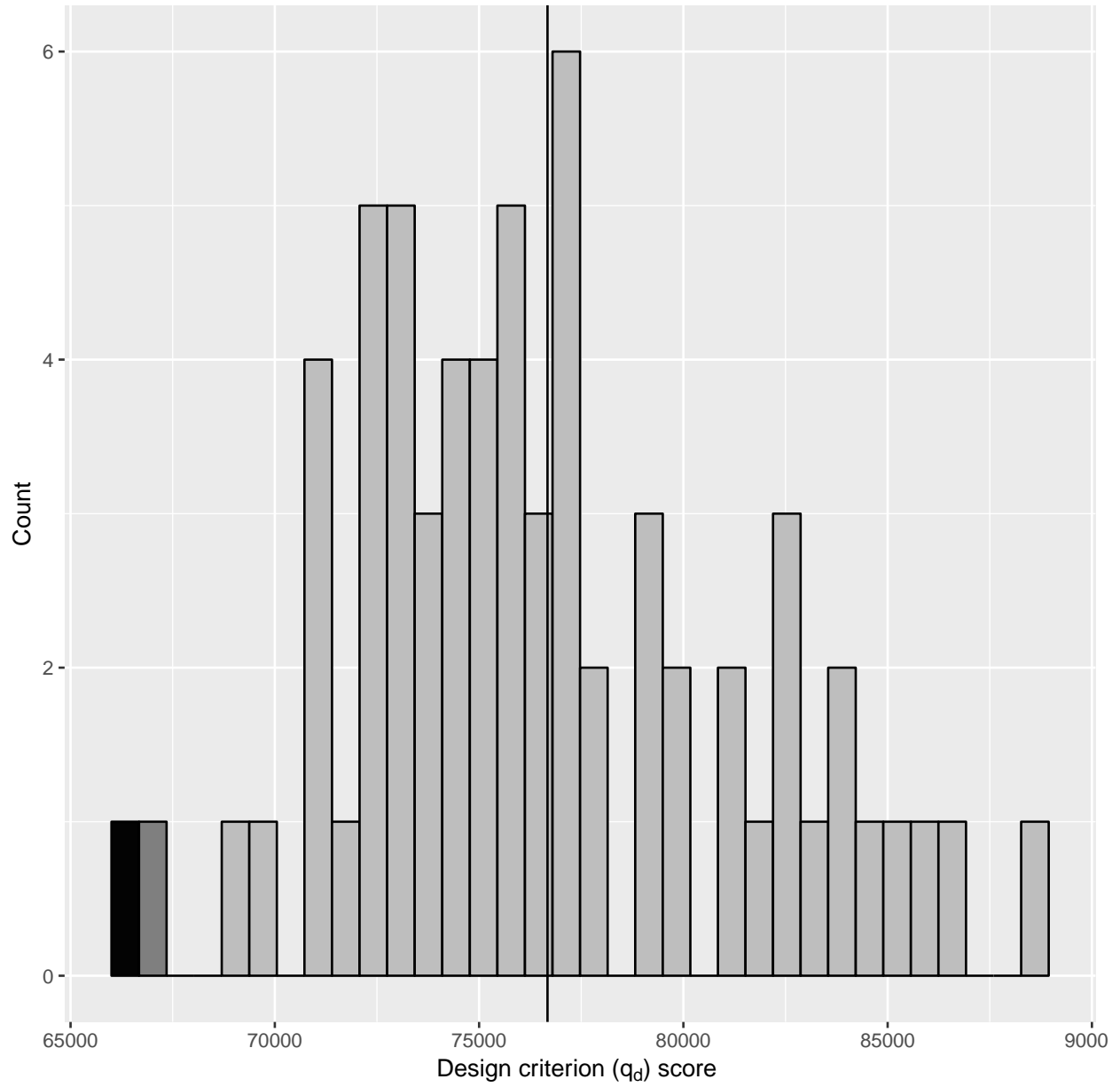


Figure 3

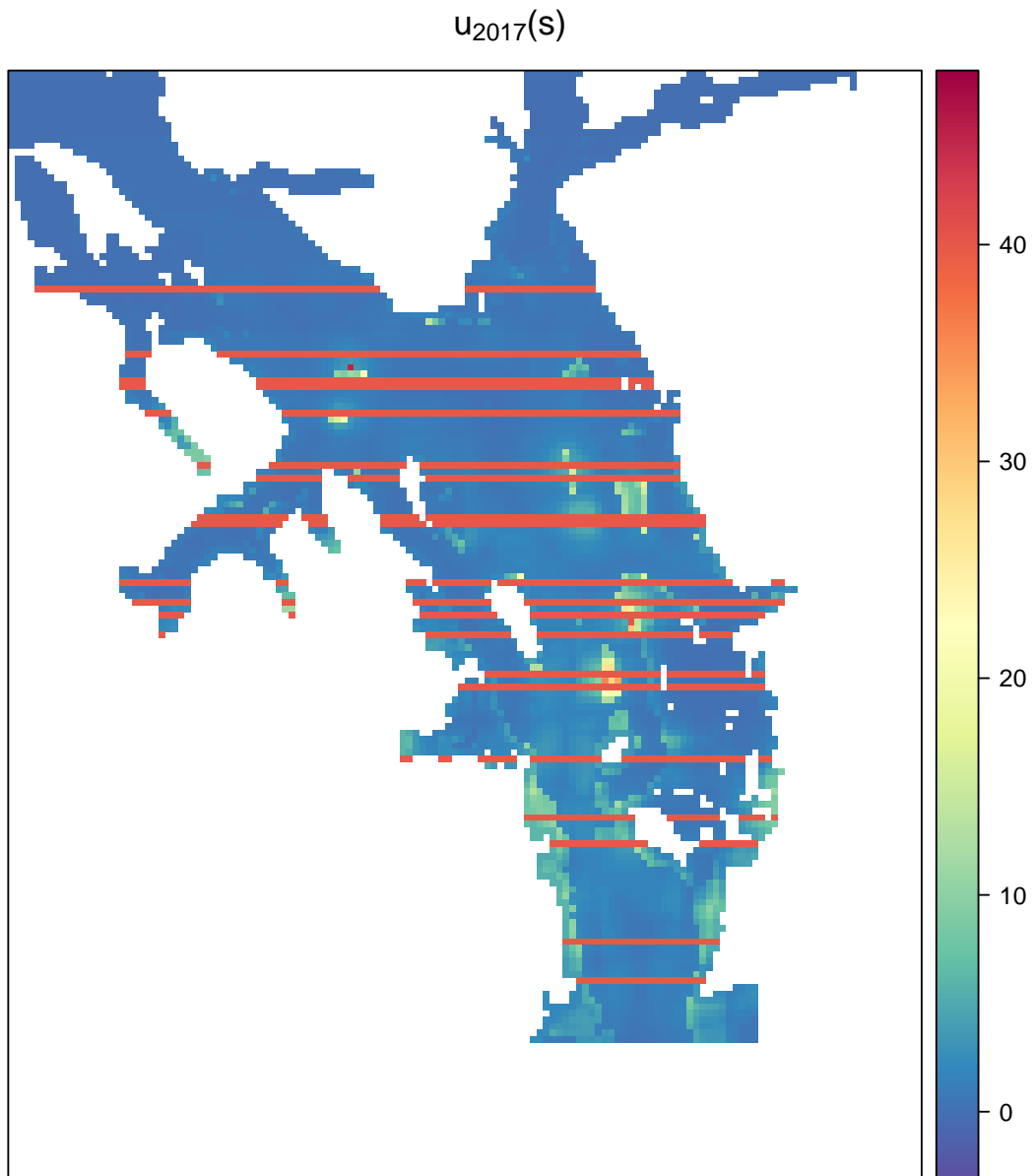


Figure 4