

Optimal GPS tracking for estimating species movements

D.E. Pagendam^a, J.V. Ross^b

^aCSIRO Mathematics, Informatics and Statistics, EcoSciences Precinct, PO Box 2583, Brisbane, QLD 4001

^bOperations Research and Statistics Group, School of Mathematical Sciences, The University of Adelaide, Adelaide, SA 5005, Australia
Email: joshua.ross@adelaide.edu.au

Abstract:

A common approach to learning about species movements is to tag individuals with a GPS transmitter. Here we provide methodology which determines the optimal programming of the times for such a device, and in doing so allow an assessment of the benefit provided over equidistant sampling schedules. We provide an algorithm (and MATLAB code¹) that computes the optimal patch in which to tag an individual, in addition to the optimal timing and number of samples in order to best estimate three parameters describing the species-habitat migration rate (assuming a common form of migration). We use this algorithm to identify some basic conditions of a network that ensure identifiability of model parameters: at least four distinct inter-patch distances. We subsequently apply our algorithm to a number of randomly-generated networks, and demonstrate the efficiency gains from optimising various components of the sampling schedule. Finally, we determine the optimal sampling schedule for a real network: the spotted owl (*Strix occidentalis occidentalis*) in Southern California (Lahaye et al., 1994; Shuford and Gardali (editors), 2008). The comparison of random and real networks demonstrates the improvement in efficiency as the size and heterogeneity of the underlying network increases.

This is believed to be the first methodology to determine the optimal design for monitoring species movements. Our study also differs from previous optimal design methodology for stochastic models in that we evaluate the Fisher Information Matrix exactly (to computational precision) rather than adopting an approximation (Pagendam and Pollett, 2009, 2010b). Furthermore, we provide code to implement *EID*-optimality, which more naturally aligns with the motivation of classical *D*-optimality, but in the situation of prior uncertainties on parameter values as is common to the problems of interest to us here (Walter and Pronzato, 1987).

Keywords: Estimation, GPS transmitters, metapopulation networks, optimal design, stochastic models

¹<http://www.dan.pagendam.com/Code.html> and <http://maths.adelaide.edu.au/joshua.ross/Research/Code.html>

1 INTRODUCTION

The management of endangered species is facilitated by improved understanding of the demographics of those species. This also applies to optimal management of zoonotic diseases in their wild hosts. As an example, in California there have been recommendations for “new demographic monitoring studies...to broaden the sample and determine whether the various subpopulations [of the California Spotted Owl] act as a metapopulation” (Shuford and Gardali (editors), 2008). The particular emphasis in this example is on understanding the migratory behaviour of a spatially-separated species.

As a consequence of habitat fragmentation (generally due to anthropogenic disturbance) many species occupy geographically separated patches. These species are often at risk of extinction, or of concern with uncertainty surrounding their ability to persist in their relatively new habitat network. It is precisely this problem of understanding the migratory behaviour of species occupying metapopulation networks which we consider herein.

A common approach to learning about species movements is to tag individuals with a GPS transmitter. Most modern versions of these transmitters allow a choice between different equidistant sampling schedules, with observations taken, say, each day (Lotek Wireless Inc., 2011). The top-of-the-range devices may permit pre-programming of times (not necessarily equally-spaced in time). Here we provide methodology which determines the optimal programming of the times for such a device, and in doing so allow an assessment of the benefit provided over equidistant sampling schedules.

We provide an algorithm (and MATLAB code) that computes the optimal habitat patch in which to tag an individual, in addition to the optimal timing and number of samples in order to best estimate three parameters describing the species-habitat migration rate (assuming a common form of migration). The user inputs for this algorithm are simply the pairwise distances between habitat patches, characteristics of the power utilisation of the transmitter, and parameters characterising the prior densities for model parameters. We use this algorithm to investigate a number of simple networks, allowing us to identify some basic conditions of a network that ensure identifiability of model parameters. We subsequently apply our algorithm to a number of randomly-generated networks, and demonstrate the efficiency gains from optimising various components of the sampling schedule. Finally, we determine the optimal sampling schedule for a real network: the spotted owl (*Strix occidentalis occidentalis*) in Southern California (Lahaye et al., 1994; Shuford and Gardali (editors), 2008).

This is believed to be the first methodology to determine the optimal design for monitoring species movements. Our study also differs from previous optimal design methodology for stochastic models in that we evaluate the Fisher Information Matrix (FIM) exactly (to computational precision) rather than adopting an approximation (Pagendam and Pollett, 2009, 2010b). Furthermore, we provide code which implements *EID*-optimality, which more naturally aligns with the motivation of classical *D*-optimality, but in the situation of prior uncertainties on parameter values as is common to the problems of interest to us here (Walter and Pronzato, 1987).

2 MODEL & PROBLEM STATEMENT

The dynamics are assumed to be governed by a continuous-time Markov chain (CTMC), where the state of the chain at time t is the location of the individual at that time (Norris, 1997; Ross et al., 2008). Markov chains often provide very good models of systems in ecology as these systems typically consist of discrete, interacting entities which exhibit randomness. We have a network of N patches with distance d_{ij} between patch i and patch j , $\forall i, j \in \{1, 2, \dots, N\}$. We assume that an individual migrates between patches i and j at rate $m_{ij} = m_{ji} = \mu \exp(-\delta d_{ij}^\theta) 1_{\{i \leftrightarrow j\}}$, where μ , δ and θ are species and habitat specific parameters, which determine the average rate of movement and how movement decays with distance between patches, and $1_{\{i \leftrightarrow j\}}$ is an indicator variable of whether movement between patches i and j is possible (equal to 1 if possible and 0 otherwise). This form of migration is one commonly adopted in metapopulation modelling (Gilpin and Diamond, 1976; Day and Possingham, 1995; Inchausti and Weimerskirch, 2002; Ross and Pollett, 2010).

We wish to estimate $\phi = (\mu, \delta, \theta)$, under the constraints on battery power of the transmitter. We assume that each recording of position uses p_s units of power per unit of time of searching, and the battery power decays exponentially at rate p_t per unit time; hence, a sampling schedule $\mathbf{t} = (t_1, t_2, \dots, t_n)$

($t_i > t_{i-1}, \forall i$) consisting of n samples is constrained via $\sum_{i=1}^n P_i \leq P$ where $P_i = p_s \alpha_i + (P - \sum_{j=1}^{i-1} P_j)(1 - \exp(-p_i(t_i - t_{i-1})))$, $P(= P_0)$ is the initial total power of the battery, and α_i is the number of seconds to fixation of position on observation i .

In addition to the number and timing of the samples, which are constrained by characteristics of battery utilisation of the GPS transmitter, we assume we have control over the initial location, y_0 , of the tagged individual; we may choose from any of the N patches in the network. Hence, in its most general form, the *design space* for our problem consists of $G = \{y_0, t_1, t_2, \dots, t_n\}$.

3 OPTIMAL EXPERIMENTAL DESIGN

Surprisingly little attention has been paid to the optimal observation, or experimental design, of systems where the underlying system is governed by a Markov chain. There are only a handful of papers in this area (Cook et al., 2008; Pagendam and Pollett, 2009, 2010a,b), most focussing on the simple death (or birth) process. As mentioned earlier, Markov chains often provide nice models of biological systems, and hence the development of methodology appropriate for such systems is beneficial.

We choose to adopt an approach which is very close in spirit to the approach of Pagendam and Pollett (2010b), following the classical experimental design framework of D -optimality. However, in contrast, rather than requiring an approximation for the likelihood, and hence an approximate FIM, we evaluate the FIM exactly (to desired computational tolerances) via EXPOKIT (Sidje, 1998). We also provide code to implement EID -optimality, which seeks to minimise the expected determinant of the inverse of the Fisher Information Matrix (FIM). The mathematical details of how the FIM is computed are presented in the Appendix.

Much of optimal experimental design is built on a fundament of maximum likelihood theory. The likelihood of a series of observations $\mathbf{y} = (y_0, y_1, y_2, \dots, y_n)$ at times $\mathbf{t} = (t_0, t_1, t_2, \dots, t_n)$ of a time-homogeneous CTMC, can be exhibited as $L = p(y_0) \prod_{i=1}^n p_{\tau_i}(y_i | y_{i-1})$, where $p_{\tau_i}(y_i | y_{i-1})$ is the conditional probability of transitioning from state y_{i-1} to y_i over the time interval $\tau_i = t_i - t_{i-1}$ and $p_0(y_0)$ is the probability of observing the initial state. For an experimental design, where the initial state of the CTMC is controlled as part of the design, we set $p(y_0) = 1$. Much of maximum likelihood estimation and optimal design in what follows, revolves around the log-likelihood $\ell = \log(L)$.

For CTMC's on a finite state space, the probabilities at the heart of the likelihood are calculated using a matrix \mathbf{Q} of transition rates. For our model, the entries $0 \leq q_{ij} < \infty$ are the rates at which individuals migrate from habitat patch i to j ($i \neq j$), m_{ij} , whilst the diagonal entries $q_{ii} = -q_i$, with $q_i = \sum_{j \neq i} q_{ij}$ being the total rate out of state i . A matrix of transition probabilities can be computed as $\mathbf{P}_\tau = \exp(\mathbf{Q}\tau)$, where τ is the elapsed time between observations and $\exp(\cdot)$ is the matrix exponential evaluated herein using EXPOKIT (Sidje, 1998). The (i, j) th entries of this matrix are the $p_{\tau_i}(j|i)$ present in the likelihood.

D -optimal designs aim to maximise the precision of the maximum likelihood estimator $\hat{\phi} = (\hat{\mu}, \hat{\delta}, \hat{\theta})$ by maximising the determinant of the FIM, denoted herein as \mathcal{I} . The FIM is at the heart of most optimal design criteria and for the model at hand, its (i, j) th element can be calculated from the second derivatives of the log-likelihood function as $\mathcal{I}_{ij} = -\mathbb{E}(\frac{\partial^2 \ell}{\partial \phi_i \partial \phi_j})$, where $\mathbb{E}(\cdot)$ is the expected value. Finding the D -optimal design amounts to solving the problem $g^* = \operatorname{argmax}_{g \in G} \det[\mathcal{I}(\phi, g)]$. Any design, \check{g} , can be compared to g^* by means of the D -efficiency: $D_e = (\det[\mathcal{I}(\check{g})] / \det[\mathcal{I}(g^*)])^{1/p}$. Note, p is the number of parameters being estimated and D_e takes values in $[0, 1]$.

However, a common problem for nonlinear models such as ours, is that \mathcal{I} is dependent on the unknown parameter vector ϕ and therefore so is the optimal design. Such designs are referred to as *locally optimal* and suffer from the complication that, in order to find the D -optimal design, one must already know the values of the parameters being estimated. This conundrum is well documented. Regardless, D -optimal designs provide a useful benchmark against which to compare other designs and to explore the potential pitfalls for the practitioner in collecting data. In practice, one can either: (i) opt to use some 'best guess' at the parameters, ϕ_{guess} , for the purpose of designing the experiment; or (ii) use a design that is robust to a range of possible parameter values. One such robust design is the EID -optimal design (Walter and Pronzato, 1987), which amounts to solving $g^* = \operatorname{argmin}_{g \in G} \int_{\Phi} p(\phi) \det[\mathcal{I}^{-1}(\phi, g)] d\phi$, where $p(\phi)$ is a prior probability density function over the parameter space Φ . This can be thought of as minimising the expected volume of the confidence ellipsoid for the parameters under the prior.

For finding D -optimal and EID -optimal designs, we use a cross-entropy algorithm, similar to that of Pagendam and Pollett (2009, 2010b), but where the number of allowable observations is constrained by the power available in the GPS battery. Typically, such batteries allow location data to be collected at a relatively large number of times. Furthermore, our investigations have shown that after the first few observations, the optimal observation times tend to be roughly equidistant in time. For computational efficiency, we therefore consider the design space $\{w, t_1, t_2, \dots, t_a, t_a + \tau_e, t_a + 2\tau_e, \dots, t_a + (n-a)\tau_e, \dots\}$, where w is the patch in which to tag the individual, a is the number of non-equidistant observation times, n is the total number of observations and τ_e is the equidistant spacing of the later observations. Our observations suggest that in practice, there is typically little loss of experimental efficiency in choosing $a = 4$, say. MATLAB m-files to find these optimal observation times are available for download².

4 RESULTS & BRIEF DISCUSSION

In this section we present our results. We first report guideline requirements for the type of networks which allow estimation of parameters of our model and in which our methodology will be useful. We then consider ten random networks and by considering optimal schedules under different constraints we demonstrate D -efficiencies which should be typically exhibited and also highlight where the main benefits from optimising GPS scheduling exist. Finally, we apply our methodology to California spotted owl occupying a 22-patch network, and demonstrate improvement in parameter estimates gained by an optimal schedule in comparison to sub-optimal schedules.

4.1 Simple Networks: Identifiability

It was found that sufficient heterogeneity must exist in the network in order to estimate parameters with any reliability, and hence the same requirement exists for the identification of an optimal GPS schedule. This is particularly the case for the general model we consider, with three parameters requiring estimation; if θ , the exponent of distance in the migration rate, is assumed known (as is often the case, typically $\theta = 1/2$) then the level of heterogeneity required is reduced, as one might expect. It is hard to provide specific requirements, but from our investigations we advise the rule-of-thumb that more than four different inter-patch distances are required as a minimum; the methodology becomes more useful with increasing number of distinct inter-patch distances, and with increasing heterogeneity in the distances.

4.2 Random Networks: D -efficiency

We generated ten random networks each consisting of ten patches with X and Y co-ordinates each uniformly distributed over the interval $[0, 150]$. To reflect the situation commonly encountered in practice (for example, as seen in the real example we consider subsequently), we allow a link between two patches to exist with a probability which decreases with distance between the patches; specifically, migration is possible between patches i and j with probability $p_e \exp(-d_{ij}/s)$ where $p_e = 0.925$ and $s = 150^2$. This choice of parameter values means that most links exist in the network. We set other parameters to be equal to those evaluated and assumed in the spotted owl example to follow: battery power decay rate is $p_t = 2.7 \times 10^{-3}$ per day, power usage per second of searching is $p_s = 1.19 \times 10^{-4}$, and we assume, conservatively, that it takes 120s to fixation on each positioning, $\mu = 1/10$, $\delta = 1/3$ and $\theta = 1/2$ (migration rate in units $days^{-1}$) – please see Section 4.3 for further details.

Table 1 presents the results from this investigation. For each of the ten random networks, we first evaluated the impact of choice of patch in which to tag the individual; in the second column we report the average (across designs constrained to tagging the initial individual in each of the possible patches) D -efficiency, and in the third column the minimum D -efficiency. This demonstrates that significant efficiency gains can be made by choice of the patch in which to tag the individual. We then considered the further improvement which could be gained (in addition to the best choice of patch) by also choosing the optimal observation times for a range of a (columns four–eight), over simply adopting the best of equidistant daily, weekly or monthly observations. Small further gains in efficiency can be found by choosing the first few observation times, and then adopting an optimal equidistant sampling schedule, as evidenced by the diminishing performance of the daily, weekly or monthly equidistant designs relative to the optimal.

²<http://www.dan.pagendam.com/Code.html> and <http://maths.adelaide.edu.au/joshua.ross/Research/Code.html>

Table 1. D -efficiencies, D_e , from optimising different schedule components on ten random networks.

Network	Avg. D_e (patch)	Min. D_e (patch)	$a = 0$	$a = 1$	$a = 2$	$a = 3$	$a = 4$
1	0.9590	0.9158	0.9700	0.9554	0.9532	0.9511	0.9496
2	0.9292	0.8287	1.0000	0.9817	0.9765	0.9724	0.9686
3	0.9253	0.8761	1.0000	0.9823	0.9774	0.9732	0.9700
4	0.9848	0.9631	0.9880	0.9850	0.9829	0.9814	0.9801
5	0.9667	0.9399	0.9344	0.9262	0.9247	0.9231	0.9220
6	0.9538	0.9107	0.9630	0.9557	0.9537	0.9522	0.9507
7	0.9530	0.9175	0.9805	0.9686	0.9647	0.9620	0.9591
8	0.9647	0.9349	1.0000	0.9837	0.9806	0.9783	0.9765
9	0.9769	0.9604	1.0000	0.9834	0.9804	0.9785	0.9769
10	0.9314	0.8865	0.9912	0.9816	0.9748	0.9702	0.9664
Avg.	0.9545	0.9133	0.9827	0.9704	0.9669	0.9642	0.9620

4.3 Real Networks: Power Parameterisation & Estimation

GPS Tag Power Parameterisation. Data for the ‘‘GPS Bug Tag’’TM produced by *Lotek Wireless*, provides the number of samples possible at three different equidistant sampling schedules, each with two different times to fixation (25s and 70s). Using this information, we estimate the battery power decay rate per second p_t and power usage per second of searching, p_s , to be $p_t = 3.08 \times 10^{-8}$ and $p_s = 1.19 \times 10^{-4}$ (Lotek Wireless Inc., 2011). These estimates were derived by choosing p_s and p_t to minimise the maximum absolute error between the power used by each design and the battery power of the GPS tag; the optimisation was performed using MATLAB’s `fminsearchbnd` routine. Whilst we believe these values to be close to the true values, some error will exist; however, the precise values are not overly important to optimal schedule design.

Spotted Owl in California. As a real example of our methodology, we consider the spotted owl (*Strix occidentalis occidentalis*) in Southern California (Lahaye et al., 1994; Shuford and Gardali (editors), 2008). The details of the network can be found in Fig. 1 of (Lahaye et al., 1994), where we evaluated inter-patch distances between patches where dispersal was indicated as possible using the scale provided and edge-to-edge distances. The assumed migration rate parameters were motivated by those assumed in (Lahaye et al., 1994) and the obvious slow rate of migration which warrants investigation of possible metapopulation structure (Shuford and Gardali (editors), 2008): $\mu = 1/10$, $\delta = 1/3$ and $\theta = 1/2$ (migration rate in units $days^{-1}$).

As for random networks, we first evaluated the impact of choosing the patch in which to tag the owl. The average (across all possible choices of patch) D -efficiency was 0.6266, which demonstrated the importance of the optimal choice of patch. The minimum D -efficiency was 0.2839, which clearly highlights the potentially catastrophic loss of experimental efficiency one may encounter when failing to consider the patch in which to tag the owl.

We then considered the further improvement which could be gained (in addition to the best choice of patch) by also choosing the optimal observation times ($a = 4$), over simply adopting the best of equidistant daily, weekly or monthly observations. The average D -efficiency was 0.882, which shows that further, significant improvements in experimental efficiency can be gained by optimising choice of the first few initial times and equidistant gap.

Parameter Estimates under the Optimal Design. Under the assumption that tagged individuals behave independently of one another, the optimal design for a single individual applies to all tagged individuals. Table 2 shows the statistical properties of the maximum likelihood estimator, under the optimal design, for various numbers of tagged spotted owls in our 22 patch network. The table is populated using data from 100 simulations of the experiment. In general, the precision in estimating μ is very high for just a single tagged individual, however, the precision and bias in estimating δ and θ were large for small numbers of tagged individuals. With roughly 20 tagged owls, estimates of μ and δ were reasonably good, but θ was still estimated with considerable bias and low precision. Comparison of the median and mean of the maximum likelihood estimates for θ shows that this estimator exhibits a noticeable right skew. This highlights that often a large number of individuals will need to be tagged in order to accurately estimate

Table 2. Statistical properties of the maximum likelihood estimator $\hat{\phi} = (\hat{\mu}, \hat{\delta}, \hat{\theta})$ under the D -optimal design for the 22 patch network with different numbers of tagged individuals.

Number of Tags	Mean($\hat{\phi}$)	Median($\hat{\phi}$)	s.d.($\hat{\phi}$)
1	(3.40 E-2, 0.765, 16.8)	(3.44 E-2, 0.232, 0.917)	(6.80 E-3, 1.47, 37.3)
5	(3.33 E-2, 0.297, 8.26)	(3.31 E-2, 0.0560, 0.766)	(3.11 E-3, 0.407, 15.7)
10	(3.37 E-2, 0.415, 3.43)	(3.38 E-2, 0.214, 0.432)	(2.34 E-3, 0.589, 8.96)
20	(3.34 E-2, 0.361, 1.01)	(3.32 E-2, 0.253, 0.416)	(1.51E-3, 0.360, 2.30)

individual parameter values.

Figure 1 shows the gain in experimental efficiency when using the optimal observation times over an arbitrary weekly observation schedule. Using 100 simulations of 20 tagged individuals migrating between the patches of the 22 patch metapopulation, we estimated the three model parameters under both designs. Our figure plots the estimated migration functions obtained from these 100 simulations (solid grey) along with the true dispersal function (dashed red) as a function of distance. We see that, in general, the dispersal function is estimated with much greater accuracy and precision under our optimal design. Many more of the estimated functions under the weekly observation scheme seem to result in a highly exaggerated, plateau-like function.

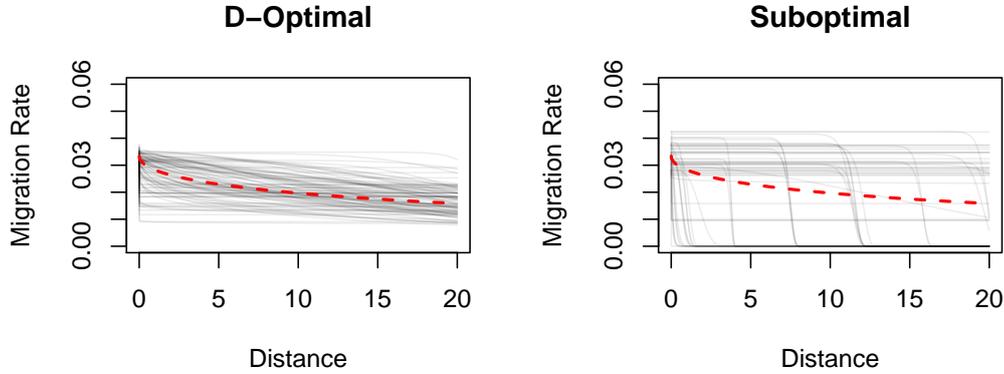


Figure 1. Estimated migration functions from 100 simulations (solid grey) along with the true dispersal function (dashed red) as a function of distance for (left) D -optimal design and (right) weekly suboptimal design.

Acknowledgement. This research was supported by the Australian Research Council's Discovery Projects funding scheme (project number DPI10101929).

APPENDIX

Let Q be the matrix of transition rates as described in Section 3. We compute the second derivatives of the likelihood with respect to the parameters, following an approach adopted earlier for extended Poisson process models (Podlich et al., 1999), and then evaluate the transition probabilities using EXPOKIT (Sidje, 1998) in order to compute the expected values, resulting in the entries of \mathcal{I} . To achieve this, begin by constructing the augmented matrix Q^* below. The vector of observation times is $\mathbf{t} = (t_1, t_2, \dots, t_n)$ and each observation yields a vector \mathbf{y}_i of length N , consisting of zeros everywhere except the entry corresponding to the location of the organism at t_i (entry equals 1). Let \mathbf{y}_0 denote the initial location of the organism at $t = 0$. For any time, t , it is then a simple task to calculate $(\mathbf{p}_t, \frac{\partial \mathbf{p}_t}{\partial \mu}, \frac{\partial \mathbf{p}_t}{\partial \delta}, \frac{\partial \mathbf{p}_t}{\partial \theta}, \frac{\partial^2 \mathbf{p}_t}{\partial \mu^2}, \frac{\partial^2 \mathbf{p}_t}{\partial \delta^2}, \frac{\partial^2 \mathbf{p}_t}{\partial \theta^2}, \frac{\partial^2 \mathbf{p}_t}{\partial \mu \partial \delta}, \frac{\partial^2 \mathbf{p}_t}{\partial \theta \partial \mu}, \frac{\partial^2 \mathbf{p}_t}{\partial \theta \partial \delta}) = \mathbf{w}^* \exp(Q^* t)$, where $\mathbf{w}^* = (\mathbf{y}_0, \mathbf{0}_{1 \times 9N})$ is a row vector of length $10N$ corresponding to the initial conditions. Here, $\mathbf{0}_{1 \times 9N}$ is a row vector of zeros having length $9N$. Let $\mathbf{M}_\tau = (\mathbf{I}_{N \times N}, \mathbf{0}_{N \times 9N}) \exp(Q^* \tau)$ be a matrix whose i th row is the vector $(\mathbf{p}_\tau(\cdot|i), \frac{\partial \mathbf{p}_\tau(\cdot|i)}{\partial \mu}, \frac{\partial \mathbf{p}_\tau(\cdot|i)}{\partial \delta}, \frac{\partial \mathbf{p}_\tau(\cdot|i)}{\partial \theta}, \frac{\partial^2 \mathbf{p}_\tau(\cdot|i)}{\partial \mu^2}, \frac{\partial^2 \mathbf{p}_\tau(\cdot|i)}{\partial \delta^2}, \frac{\partial^2 \mathbf{p}_\tau(\cdot|i)}{\partial \theta^2}, \frac{\partial^2 \mathbf{p}_\tau(\cdot|i)}{\partial \mu \partial \delta}, \frac{\partial^2 \mathbf{p}_\tau(\cdot|i)}{\partial \theta \partial \mu}, \frac{\partial^2 \mathbf{p}_\tau(\cdot|i)}{\partial \theta \partial \delta})$ where $\mathbf{p}_\tau(\cdot|i)$ denotes the probability distribution of an individual after time τ given that it was last observed in patch i . Straight-forward manipulation of the log-likelihood presented in Section 3 yields:

$$\mathcal{I}_{i,j} = \sum_{k=1}^n \mathbb{E} \left([\mathbf{p}_{\tau_k}(\mathbf{y}_k | \mathbf{y}_{k-1})]^{-2} \frac{\partial \mathbf{p}_{\tau_k}(\mathbf{y}_k | \mathbf{y}_{k-1})}{\partial \phi_i} \frac{\partial \mathbf{p}_{\tau_k}(\mathbf{y}_k | \mathbf{y}_{k-1})}{\partial \phi_j} \right) - \sum_{k=1}^n \mathbb{E} \left([\mathbf{p}_{\tau_k}(\mathbf{y}_k | \mathbf{y}_{k-1})]^{-1} \frac{\partial^2 \mathbf{p}_{\tau_k}(\mathbf{y}_k | \mathbf{y}_{k-1})}{\partial \phi_i \partial \phi_j} \right)$$

$$= \sum_{k=1}^n \sum_{x=1}^N p_{t_{k-1}}(x) \sum_{z=1}^N [p_{\tau_k}(z|x)]^{-1} \frac{\partial p_{\tau_k}(z|x)}{\partial \phi_i} \frac{\partial p_{\tau_k}(z|x)}{\partial \phi_j} - \sum_{k=1}^n \sum_{x=1}^N p_{t_{k-1}}(x) \sum_{z=1}^N \frac{\partial^2 p_{\tau_k}(z|x)}{\partial \phi_i \partial \phi_j},$$

where $p_{t_k}(x)$ is the x th element of \mathbf{p}_{t_k} and similarly $p_{\tau_k}(z|x)$ is the z th element of $\mathbf{p}_{\tau_k}(\cdot|x)$.

$$Q^* = \begin{pmatrix} Q & \frac{\partial Q}{\partial \mu} & \frac{\partial Q}{\partial \delta} & \frac{\partial Q}{\partial \theta} & \frac{\partial^2 Q}{\partial \mu^2} & \frac{\partial^2 Q}{\partial \delta^2} & \frac{\partial^2 Q}{\partial \theta^2} & \frac{\partial^2 Q}{\partial \mu \partial \delta} & \frac{\partial^2 Q}{\partial \theta \partial \mu} & \frac{\partial^2 Q}{\partial \theta \partial \delta} \\ 0 & Q & 0 & 0 & 2 \frac{\partial Q}{\partial \mu} & 0 & 0 & \frac{\partial Q}{\partial \delta} & \frac{\partial Q}{\partial \theta} & 0 \\ 0 & 0 & Q & 0 & 0 & 2 \frac{\partial Q}{\partial \delta} & 0 & \frac{\partial Q}{\partial \mu} & 0 & \frac{\partial Q}{\partial \theta} \\ 0 & 0 & 0 & Q & 0 & 0 & 2 \frac{\partial Q}{\partial \theta} & 0 & \frac{\partial Q}{\partial \mu} & \frac{\partial Q}{\partial \delta} \\ 0 & 0 & 0 & 0 & Q & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & Q & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & Q & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & Q \end{pmatrix}.$$

REFERENCES

Chernoff, H. (1953). Locally optimal designs for estimating parameters. *The Annals of Mathematical Statistics* 24(4), 586–602.

Cook, A., G. Gibson, and C. Gilligan (2008). Optimal observation times in experimental epidemic processes. *Biometrics* 64, 860–868.

Day, J. and H. Possingham (1995). A stochastic metapopulation model with variability in patch size and position. *Theoretical Population Biology* 48, 333–360.

Gilpin, M. and J. Diamond (1976). Calculation of immigration and extinction curves from the species-area-distance relation. *Proceedings of the National Academy of Sciences USA* 73, 4130–4134.

Inchausti, P. and H. Weimerskirch (2002). Dispersal and metapopulation dynamics of an oceanic seabird, the wandering albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology* 71, 765–770.

Lahaye, W., R. Gutierrez, and H. Akcakaya (1994). Spotted owl metapopulation dynamics in Southern California. *Journal of Animal Ecology* 63, 775–785.

Lotek Wireless Inc., . (2011). Fish & wildlife monitoring, <http://www.lotek.com/>.

Norris, J. (1997). *Markov chains*. Cambridge: Cambridge University Press.

Pagendam, D. and P. Pollett (2009). Optimal sampling and problematic likelihood functions in a simple population model. *Environmental Modeling & Assessment* 14, 759–767.

Pagendam, D. and P. Pollett (2010a). Locally optimal designs for the simple death process. *Journal of Statistical Planning and Inference* 140, 3096–3105.

Pagendam, D. and P. Pollett (2010b). Robust optimal observation of a metapopulation. *Ecological Modelling* 221, 2521–2525.

Podlich, H., M. Faddy, and G. Smyth (1999). Likelihood computations for extended poisson process models. *Interstat September no.1*.

Ross, J. and P. Pollett (2010). Simple rules for ranking and optimally managing metapopulations. *Ecological Modelling* 221, 2515–2520.

Ross, J., D. Sirl, P. Pollett, and H. Possingham (2008). Metapopulation persistence in a dynamic landscape: more habitat or better stewardship? *Ecological Applications* 18, 590–598.

Shuford, W. and T. Gardali (editors) (2008). California bird species of special concern: A ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California. studies of western birds 1. western field ornithologists, Camarillo, California, and California Department of Fish and Game, Sacramento.

Sidje, R. (1998). EXPOKIT. A software package for computing matrix exponentials. *ACM Transactions on Mathematical Software* 24, 130–156.

Walter, E. and L. Pronzato (1987). Optimal experiment design for nonlinear models subject to large prior uncertainties. *The American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 243, R530–R534.