

ABSTRACT

HOSTETTER, NATHAN JAMES. Data Fusion: Using Multiple Data Sources to Improve Demographic Parameter Estimation in Ecology. (Under the direction of Dr. Beth Gardner and Dr. Theodore R. Simons).

The need to provide science-based recommendations for populations of conservation concern with only limited data has led to new statistical approaches to integrate multiple sources of information. Integrated modeling approaches often provide several benefits, including efficient use of data, more robust inferences, and an ability to overcome major study design impediments such as low detection probability, limited spatial extent, and multiple sources of bias. Although diverse in application, integrated analysis methods share a consistent and unifying theme, whereby a single, unified model is developed to analyze multiple sources of data, and achieve inferences not possible using only a single source. I investigate these topics using three case studies where a lack of data or study design impediment was addressed through the integration of multiple data sources. These challenges motivated the development of several new approaches that provide advances in integrated modeling of environmental data. In the first study, I develop a flexible state-space hierarchical model for mark-recapture-recovery data that incorporates multiple recovery types and state uncertainty to improve survival estimation. Using a simulation study, I found that this model improved parameter precision, reduced sample size requirements, and provided estimation of survival across larger spatial scales relative to separate analyses of mark-recapture data. A case study in the upper Columbia River, OR and WA, of steelhead (*Oncorhynchus mykiss*) found that integrated mark-recapture-recovery methods achieved similar precision with less than half the sample sizes of mark-recapture methods. In a second

study, I describe a multivariate spatial model to integrate multiple sources of spatially overlapping, but misaligned data. Using a simulation study, it was determined that the multivariate spatial model provided lower root mean squared error and reduced bias than distance sampling only when abundances were correlated across surveys. Spatial misalignment was a particular challenge in a case study of loons (*Gavia* spp.) in the North Atlantic Ocean, where the main data source (boat based distance sampling) had a limited spatial extent, while a second data source (aerial high definition videography surveys) collected counts across a much larger spatial extent in the study area. In this study, the improved predictive ability of the integrated model also identified important locations of high loon abundances that were not detected in analysis of the distance sampling data only. Finally, I demonstrate how an integrated model can decompose the components of detection bias and improve density estimation. This approach integrates spatially and temporally replicated distance sampling surveys augmented with time-to-removal data to separate the three primary components of detection. In a case study of Island Scrub-Jays (*Aphelocoma insularis*), median density estimates from the fully integrated hierarchical model were similar to reduced models that used only one or two of the sampling protocols. Reduced models, however, had lower precision and only estimated density for a subset of the potential populations provided by the fully integrated model. The pace and extent of environmental change over the past few decades have given a new urgency and relevance not only to programs that monitor and track population status but also to the demands that come along with continued data collection including methods that integrate across different data types. As conservation and management face new challenges like those presented in my case

studies, the role of data integration will become increasingly important, providing unique and innovative approaches to estimate abundance, demographic parameters, and identify important factors driving population dynamics.

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Data Fusion: Using Multiple Data Sources to Improve Demographic Parameter Estimation in Ecology

by
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DEDICATION

To my family. I would never have achieved this without the support and understanding of my wife, Erin, and son, Wyatt.

BIOGRAPHY

I developed a curiosity for the natural world by spending my childhood exploring the streams, forests, and fields of southeastern Pennsylvania. I completed a B.S. in Biology at Gardner-Webb University and a M.S. in Wildlife Science at Oregon State University.

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CHAPTER 1 INTRODUCTION

Accurate information of population status is fundamental for the management of species of conservation concern (Campbell et al. 2002). Abundance and population size are commonly used as measures of population health and viability (Lack 1954). While abundance estimates may inform the state of a population, it is the underlying vital rates that dictate how a population changes through time (Mills 2012). Information on abundance and vital rates are therefore critical to management and conservation actions.

Rarely, however, are ecologists able to collect complete counts of animals in some specific area. Instead, information on abundance and vital rates are inferred from samples collected over space or time, often using protocols to separate the underlying state process from observed patterns (Thompson 2012, Kéry and Royle 2015). Logistical and financial constraints further limit the quantity, and sometimes quality of data a single study can collect. Recent technological advances, however, have increased the availability of multiple data sources related to a common population, species, or ecosystem (Henry et al. 2008, Banerjee et al. 2014).

The need to provide science-based recommendations in limited data scenarios and the increasing availability of multiple data sources has forced analysts to be creative in using information from multiple data sources (Maunder and Punt 2013). Early methods to combine multiple sources of data often involved ad hoc approaches or multi-stage methods, where results from one analysis are used in subsequent analysis (i.e., “statistics on statistics”, Link et al. 1999). Multi-stage analysis methods provide opportunities to combine data sources, but

are subject to several concerns including: (i) the loss of information when using summarized data, (ii) difficulty in properly estimating variance and fully accounting for uncertainty, (iii) challenges in determining the appropriate likelihood function, and (iv) introduction of bias when using transformed data (Link 1999, Schaub and Abadi 2010, Maunder and Punt 2013).

Recently, substantial progress has been made in approaches that directly integrate multiple sources of data. The goal of integrated analysis is to jointly analyze raw data from multiple sources that inform a shared process of interest (e.g., abundance or survival; Besbeas et al. 2005, Banerjee et al. 2014). Recent advances in the field of integrated analysis are a response to increased availability of multiple and shared data sources (Henry et al. 2008), improvements in computers and computational algorithms (Gelman et al. 2013), and the increasing need for methods to evaluate ecological processes at region- and global-scales that far exceed the scope of any one study (Dickinson et al. 2010).

TYPES OF INTEGRATED ANALYSIS

Integrated analysis methods share a consistent and unifying theme whereby a single, unified model is developed to analyze multiple sources of data and achieve inferences not possible using only a single source. Integrated analysis has become popular across numerous fields, with applications in fisheries, hydrology, medical diagnosis, oceanography, robotics, weather and climate forecasting, and wildlife research (Hall and McMullen 2004, Schaub and Abadi 2010, Banerjee et al. 2014). Across and within these fields integrated analysis goes by multiple names, e.g., data assimilation (Dorigo et al. 2007), data fusion (Banerjee et al.

2014), data integration (Maunder and Punt 2013), or integrated population models (Schaub and Abadi 2010). For instance, integrated analysis methods used for years in fisheries stock assessments are now being adapted for wildlife studies under the popular name of Integrated Population Models (Maunder 2004, Schaub and Abadi 2010).

Given the diversity of applications, integrated analysis methods are sometimes thought to be completely divergent with little shared conceptual framework. However, all integrated analysis involve three basic steps: (1) development of a population dynamics model (i.e., state model), (2) formulating the component likelihoods for all available datasets, and (3) constructing the joint likelihood of all datasets combined, on which inference is based (Besbeas et al. 2003, Schaub and Abadi 2010, Maunder and Punt 2013).

CHAPTER OVERVIEW

Designing integrated analysis methods is important to current real world applications and includes a number of ecological and statistical issues that are interesting from applied and theoretical points of view. In this dissertation, I present three ecological applications of integrated models. These chapters demonstrate the common themes of integrated analysis, and demonstrate similarities in data structure and modeling approaches across a diverse array of datasets. In Chapter 2, I develop a flexible state-space hierarchical model for mark-recapture-recovery data that incorporates multiple recovery types and state uncertainty to improve survival estimation. Chapter 3 describes a multivariate spatial model to integrate multiple sources of spatially overlapping, but misaligned data. Finally, Chapter 4

demonstrates how an integrated model can decompose the components of detection bias and improve density estimation. This approach integrates spatially and temporally replicated distance sampling surveys augmented with time-to-removal data to separate the three primary components of detection. Together, each of these studies addresses a common theme, the ability to overcome impediments in single-source data collection protocols through integrated analysis of multiple datasets.

Motivation for integrated analysis, particularly in these case studies, was due to interest in expanding inference and the need to overcome impediments observed in the single data-source protocols. Integrated analysis also provide several other advantages important to ecological studies. First, integrated analysis methods better capture the true uncertainty in parameter estimates and predictions. Conservation and management actions are increasingly incorporating uncertainty into the decision making process, thus requiring explicit and honest estimation of parameter uncertainty (Clemen and Reilly 2013). Additionally, integrating multiple sources of data often provides improved precision and accuracy of parameter estimates, enhancing statistical power (Schaub and Abadi 2010).

Finally, integrated analysis makes it easier to investigate sensitivity of results to changes in each dataset or assumption (Abadi et al. 2010). I utilize this commonality and develop simulation studies applicable to each of the case studies. Simulation studies are designed to evaluate the results of case study and provide information to guide future research and data collection to improve conservation and management actions.

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CHAPTER 2

**WANTED DEAD OR ALIVE: A STATE-SPACE MARK-RECAPTURE-RECOVERY
MODEL INCORPORATING MULTIPLE RECOVERY TYPES AND STATE
UNCERTAINTY**

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Wanted dead or alive: A state-space mark-recapture-recovery model incorporating multiple recovery types and state uncertainty. *Canadian Journal of Fisheries and Aquatic Sciences*. *In-review*

ABSTRACT

We developed a state-space mark-recapture-recovery model that incorporates multiple recovery types and state uncertainty to estimate survival of an anadromous fish species. We apply the model to a dataset of out-migrating juvenile steelhead trout (*Oncorhynchus mykiss*) tagged with passive integrated transponders, recaptured during outmigration, and recovered on bird colonies in the Columbia River basin (2008-2014). Recoveries on bird colonies are regularly ignored in survival studies because the river reach of mortality is often unknown, which we model as a form of state uncertainty. Median outmigration survival from release to the lower river (river kilometer 729 to 75) ranged from 0.27 to 0.34, depending on year. Recovery probabilities were frequently >0.20 in the first river reach following tagging,

indicating that one out of five fish that died in that reach was recovered on a bird colony. Integrating dead recovery data provided increased parameter precision, estimation of where birds consumed fish, and survival estimates across larger spatial scales. More generally, these modeling approaches provide a flexible framework to integrate multiple sources of tag recovery data into mark-recapture studies.

INTRODUCTION

Survival is one of the fundamental processes governing population dynamics (Morris and Doak 2002). Accurate and precise estimates of survival are vital for evaluating hypotheses about factors influencing population growth rates, forecasting future trajectories, and evaluating conservation and management actions (Williams et al. 2002; Morris and Doak 2002). Mark-recapture methods are widely used to estimate survival in the presence of imperfect detection and encompass some of the most popular statistical models in all of ecology (Pollock 1991; Royle and Dorazio 2008). Relatively high recapture probabilities are key for estimating parameters of interest with satisfactory precision, but the effort required to collect adequate numbers of recaptures is often a critical limitation (Williams et al. 2002).

There is a growing body of literature on the integration of mark-recapture data with supplementary sources of information that may vary in quantity and quality (e.g., Barker 1997; Besbeas et al. 2002; Pradel 2005). One of the most widely used integrated models is the joint analysis of mark-recapture-recovery data (Burnham 1993). Here, mark-recapture studies that rely on detections of uniquely marked live individuals are combined with dead recovery data that can be provided from separate studies or information available from the

public (e.g., fishing and hunting surveys, citizen science, predation studies; Burnham 1993; Barker 1997; Catchpole et al. 1998; Kendall et al. 2006). Joint analysis of mark-recapture-recovery data can improve parameter precision, address broader hypotheses about survival, migration ecology, the distribution of harvest, and possibly reduce sampling costs as similar levels of precision may be achieved with smaller sample sizes (Burnham 1993; Catchpole 1998; Taylor et al. 2005; Martins et al. 2011). This is especially true for studies of species that are difficult to recapture or have large numbers of recoveries (Kendall et al. 2006). Here, we combine a mark-recapture study that used fixed recapture locations with dead recovery data collected at multiple locations across a broader spatial scale to investigate survival of anadromous steelhead trout (*Oncorhynchus mykiss*).

Declines in many salmonid populations have led to widespread protections under the United States Endangered Species Act (ESA; Good et al. 2005). In the Columbia River basin of western North America, 13 evolutionarily significant units (ESUs) of anadromous Pacific salmonids (*Oncorhynchus* spp.) are currently listed as threatened or endangered under the ESA. As part of recovery efforts, tens of thousands of juvenile salmonids from multiple ESUs are tagged annually with passive integrated transponders (PIT tags) and subsequently recaptured to estimate juvenile migration survival (Muir et al. 2001; McClure et al. 2003). These mark-recapture monitoring programs are costly and logistically challenging due to exceptionally low recapture probabilities (generally <0.20) and the consequent large sample sizes of marked smolts required to achieve adequate precision ($>20\ 000$ to $>100\ 000$ individuals tagged annually; Muir et al. 2001; McMichael et al. 2010; Skalski et al. 2012).

Since 1996, independent studies have also recovered thousands of smolt PIT tags on piscivorous waterbird colonies located throughout the Columbia River basin in an effort to estimate avian predation rates (Collis et al. 2001; Ryan et al. 2003; Evans et al. 2012; Hostetter et al. 2015). Recoveries of tags on bird colonies provide important information that an individual smolt died during outmigration, but the river reach where mortality occurred is often unknown (Evans et al. *in-press*). Uncertainty in the mortality occasion violates a basic requirement of mark-recapture-recovery methods, where the mortality occasion for all recovered individuals must be known with certainty (Burnham 1993; although see Catchpole et al. 2001). To date, published PIT tag survival studies in the Columbia River basin have ignored dead recovery data, in part due to the challenges of modeling different levels of state uncertainty in recovery data (i.e. the occasion of mortality for recovered individuals is only partially known).

We use a state-space mark-recapture-recovery model that incorporates recaptures from formal sampling occasions and recoveries that can occur at any time, but may only provide partial information on where an individual died. These methods build upon delayed-recovery mark-recapture-recovery models described by Catchpole et al. (2001) and King et al. (2012). We applied this approach to a seven-year mark-recapture-recovery study of upper Columbia River steelhead, an ESA-listed (threatened) population. Our goal was to utilize live recapture and dead recovery data to (1) investigate river reach and cumulative migration survival through the Columbia River hydrosystem, (2) estimate survival in the unimpounded lower river (hereafter Lower River), a poorly understood river reach that is not estimable

using mark-recapture data alone, and (3) examine where fish were consumed by birds, which can only be addressed by jointly analyzing live recapture and dead recovery data. We then conducted a simulation study to quantify gains in relative efficiency from integrating dead recovery data. That is, we investigated whether mark-recapture-recovery methods could use smaller sample sizes relative to mark-recapture methods, without a loss in precision of survival estimates. We describe the methods relative to the steelhead case study, but the general framework is applicable to any study interested in integrating live and dead recovery data.

METHODS

Tagging, recapture, and recovery

Mark, recapture, and recovery data from more than 49 000 PIT-tagged (hereafter “tagged”) juvenile upper Columbia River steelhead were collected across a seven-year study (2008-2014; Table 1). Each year, juvenile steelhead were captured and tagged at Rock Island Dam (RIS; river kilometer [rkm] 729), Columbia River, Washington, USA, across the peak smolt outmigration season, beginning in mid-April and ending in late-June (Fig. 1; see Evans et al. 2014 for detailed tagging protocols). Tagged steelhead were grouped into weekly cohorts and only weeks when >100 individuals were tagged and released were used for analysis, resulting in 6 - 9 weekly cohorts per year (Table 1). Released steelhead were recaptured alive (passive detections) when passing downstream PIT tag detection facilities at McNary Dam (MCN; rkm 470), John Day Dam (JDA; rkm 347), Bonneville Dam (BON;

rkm 235), and by a net-mounted detector deployed by pair-trawlers in the lower Columbia River (Trawl, rkm 75; Fig. 1; Prentice et al. 1990; Ledgerwood et al. 2004). Most fish were not physically handled when detected at these locations, but we use the term “recapture” to denote live encounters/resightings.

Dead recovery data were collected by scanning for PIT tags on bird colonies located throughout the basin (see Evans et al. 2012 for detailed recovery protocols; Fig. 1). Tags recovered on bird colonies provided information that an individual steelhead died, but for bird colonies located within foraging distance of recapture locations (e.g., dams) it was unknown if the individual steelhead died upstream or downstream of the recapture location (Fig. 1). Conversely, the river reach of mortality was known with certainty for recoveries on bird colonies located beyond the foraging range of the nearest recapture location (Fig. 1). Therefore, the amount of information provided by recovery data depended on the bird colony of recovery, where recoveries on some bird colonies identified the specific river reach of mortality, while recoveries on other colonies indicated the individual died, but the exact river reach of mortality was unknown (Fig. 1). Tag recovery data for this study included 15 bird colonies consisting of five bird species: Caspian terns (*Hydroprogne caspia*), double-crested cormorants (*Phalacrocorax auritus*), Brandt’s cormorant (*P. penicillatus*), California gulls (*Larus californicus*), and ring-billed gulls (*L. delawarensis*). We used estimates reported by

Anderson et al. (2004), Anderson et al. (2007), and Evans et al. (*in-press*) to define foraging ranges and the selection of possible mortality reaches for recovered tags.

State-space mark-recapture-recovery model

Given the mark-recapture-recovery data available, we developed a state-space extension of the mark-recapture-recovery model that allowed for multiple recovery types with varying levels of uncertainty. A schematic of the estimable parameters is provided in Appendix A.

Survival, recapture, and recovery data associated with individual i ($i = 1, 2, \dots, n$) were modeled through a series of Bernoulli random variables. We let z_{iwk} be the state of fish i released as part of weekly cohort w ($w = 1, 2, \dots, W$) at location k ($k = 1, 2, \dots, K$; e.g., dams), where $z_{iwk} = 1$ if the individual was alive and $z_{iwk} = 0$ if dead. Individual i survived from location k to $k + 1$ with survival probability ϕ_{wk} conditional on individual i being alive at location k ; that is we assumed

$$z_{iwk+1} \sim \text{Bernoulli}(\phi_{wk} z_{iwk}).$$

This allowed steelhead survival to vary by week (w) and river reach, following similar methods used in other salmonid survival studies (Muir et al. 2001; Haeseker et al. 2012).

The state process, however, was only partially observed and downstream recaptures and recoveries were used to make inference about survival. For recaptures, we let y_{iwk} be the random variable for the recapture of individual i released as part of weekly cohort w at the

k^{th} recapture location, where $y_{iwk} = 1$ if the individual was recaptured alive and $y_{iwk} = 0$ otherwise. We assumed

$$y_{iwk} \sim \text{Bernoulli}(p_{wk}z_{iwk}),$$

where p_{wk} is the detection probability at location k during week w , conditional on individual i being alive at location k . To reduce the number of estimated parameters and improve precision, we modeled detection probabilities on the logit scale as a realization of a random process described by a normal distribution with location-specific means μ_{p_k} and variances $\sigma_{p_k}^2$,

$$\text{logit}(p_{wk}) \sim \text{Normal}(\mu_{p_k}, \sigma_{p_k}^2).$$

Dead recoveries were integrated into the process as another Bernoulli random variable. We let x_{iw} be the random variable for the recovery of individual i released as part of weekly cohort w , where $x_{iw} = 1$ if the individual was recovered dead anywhere in the study and $x_{iw} = 0$ otherwise. Similar to King (2012), we assumed

$$x_{iw} \sim \text{Bernoulli}(\sum_{k=m_i}^{l_i} \lambda_{wk} (z_{iwk} - z_{iw(k+1)})),$$

where λ_{wk} is the probability an individual is recovered given they died in the interval $(k, k + 1]$, with no restriction on where it was recovered (i.e. recovery occasion is no longer indexed; King 2012). We also defined vectors m_i and l_i , denoting the earliest and latest possible mortality occasions for individual i based on information from its recovery location (provided as data). For recovered individuals, m and l varied depending on the colony of recovery, where recoveries on some colonies provided certainty on the mortality occasion and recoveries on other colonies indicated individual i died in one of two possible river

reaches, but the exact river reach of mortality was unknown (Fig. 1). For comparison, setting $m = l$ for all recoveries results in the traditional mark-recapture-recovery model assumption where the mortality occasion of recovered individuals is known with certainty (Burnham 1993). The second term of the recovery formula ($z_{iwk} - z_{iw(k+1)}$) ensures that the recovery probability is only non-zero in the interval of mortality, that is when the individual was alive at location k , but died prior to location $k + 1$ (King 2012). As with recapture probability, we modeled recovery probabilities as a random process on the logit scale with river reach-specific means μ_{λ_k} and variances $\sigma_{\lambda_k}^2$,

$$\text{logit}(\lambda_{wk}) \sim \text{Normal}(\mu_{\lambda_k}, \sigma_{\lambda_k}^2).$$

This allowed recovery probability to vary by week (w) and river reach, but information was shared across weeks to improve precision.

Mark-recapture-recovery models were fitted using a Bayesian state-space framework (King 2012). A useful aspect of Bayesian methods is the ease with which parameters of ecological and management interest can be derived as part of the Markov chain Monte Carlo (MCMC) process. The primary objective of this study was to estimate reach-specific annual survival, estimated as the proportion of individuals alive at location k that survived to $k + 1$ across the entire season. Similarly, annual cumulative survival through the hydrosystem was simply the proportion of individuals released at Rock Island Dam that were alive at each downstream recapture location. The average seven-year survival for each river reach was derived as the median value across all years. A principal objective of estimating river reach, cumulative, and seven-year average survival was to evaluate hypotheses on the spatial scale

of mortality factors. Under the hypothesis that large-scale, basin-wide factors are the primary drivers of survival (e.g., high flow years; Berggren and Filardo 1993), one would expect river reach survival to be above or below average across all reaches within a given year.

Alternatively, a lack of correlation in river reach survival within years supports alternative hypotheses, where survival is primarily affected by local factors that may vary by river reach (e.g., dam operations or predation; Muir et al. 2001; Evans et al. *in-pess*).

The seven-year average survival (2008-2014) is also of particular management interest as it provides a metric for average survival since the 2008 Biological Opinion (BiOp), which linked juvenile salmonid survival to the operation of the Federal Columbia River Power System (NOAA 2008). Finally, we calculated the proportion of dead recoveries assigned to each river reach to investigate where birds likely consumed steelhead (i.e. upstream or downstream of the nearest dam). All values were calculated during each MCMC iteration, providing posterior distributions for each derived parameter that were summarized as medians and 95% credible intervals.

It is important to note that recovery probabilities denote the probability that an individual was recovered given it died in a specific river reach (Brownie et al. 1985). Recovery probabilities are not predation rates, as predation rates generally estimate the probability or rate at which individuals alive at the beginning of the interval are consumed during or after that interval. Predation rates require a slightly different parameterization and adjustments for retrieval rates, reporting rates, and the possibility of scavenging rather than

depredation (Brownie et al. 1985; Evans et al. 2012). These topics are further described in the Discussion.

Finally, following Cormack-Jolly-Seber mark-recapture (CJS) model notation, we use apparent survival ϕ rather than true survival S (Cormack 1964; Jolly 1965; Seber 1965). In this study, steelhead mortality and residualizing (i.e., halting migration) are confounded. Steelhead residualization rates are low (Hausch and Melnychuk 2012) and we found no evidence of residualization across our seven-year study. Apparent and true survival are likely very similar, if not equal, but to be cautious we denote estimates as apparent survival ϕ .

Simulation study

To illustrate anticipated gains in efficiency (i.e. precision of survival estimates) from incorporating dead recovery data, we conducted a simulation study using values similar to those observed in this study and other survival studies of Columbia River basin salmonids (Muir et al. 2001; McMichael et al. 2010; Hostetter et al. 2011; Appendix B). We simulated and analyzed 100 data sets of 7 000 individuals (the average annual sample size in the case study). We then increased the sample sizes to 10 500 and 14 000 individuals (1.5 and 2.0 times larger, respectively) to evaluate the number of additional individuals required for mark-recapture methods to match the precision of the mark-recapture-recovery estimates based on 7 000 individuals. Simulation results were summarized by comparing the average 95% credible interval width of survival estimates. We also evaluated bias and credible interval coverage for all three methods using the same 100 data sets of 7 000 individuals.

Implementation

All models were analyzed in a Bayesian framework using the software JAGS (Plummer 2003) accessed through R version 3.1.2 (R Development Core Team 2014), using the *rjags* (Plummer 2012) and *dclone* (Solymos 2010) packages. We used independent *Uniform*(0, 1) priors for survival, recapture, and recovery parameters and *Gamma*(0.1, 0.1) for the inverse of variance terms. We ran three parallel MCMC simulations. Each chain contained 1 000 adaptation iterations, followed by 25 000 burn-in iterations, and 50 000 posterior iterations thinned by 10. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic (Gelman et al. 2013). We report results as posterior medians along with the 2.5 and 97.5 percentiles, which we refer to as 95% credible intervals (95% CRI). Recapture and recovery hyperparameters (μ_{p_k} and μ_{λ_k} , respectively) were back-transformed and are presented as probabilities (p_k and λ_k , respectively). Variance terms were also back-transformed using the delta method (Powell 2007; Kéry and Schaub 2012) and presented as standard deviations on the probability scale.

RESULTS

Steelhead survival

A total of 49 068 juvenile steelhead were tagged and released at Rock Island Dam during 2008-2014 (Table 1). Annual sample sizes ranged from 5 651 individuals (2013) to 7 687 individuals (2011; Table 1). Numbers of live downstream recaptures varied by year and

location, but were generally <700 individuals annually recaptured at any downstream location (Table 1). Dead recoveries also varied by year and location, with the highest number of recoveries occurring in the first river reach (generally >300 recoveries per year) and in the estuary (generally >250 recoveries per year; Table 1). Numbers of dead recoveries in the estuary were 1.4 to 6.0 times greater than live recaptures at the Lower River trawl (Table 1).

Annual survival estimates varied by year and river reach (Fig. 2). In general, steelhead survival was lower in the McNary and Lower River reaches compared to the John Day and Bonneville reaches (Fig. 2). For instance, annual survival in the McNary reach ranged from 0.58 in 2009 (95% CRI = 0.53-0.64) to 0.69 in 2011 (95% CRI = 0.63-0.77). Comparatively, annual survival estimates in the John Day reach ranged from 0.76 in 2009 (95% CRI = 0.67-0.85) to 0.85 in 2012 (95% CRI = 0.75-0.93). Annual variation in median survival probabilities was not consistent across river reaches (Fig. 2). For example, in 2011, migration survival was above average in the McNary and John Day reaches, but below average in the Bonneville and Lower River reaches (Fig. 2). Unexpectedly, mark-recapture median survival estimates for the Bonneville reach were consistently lower than mark-recapture-recovery results (Fig. 2; see Simulation study below for possible explanation).

Cumulative migration survival from release through the Lower River reach (Rock Island Dam to the Lower River trawl) was remarkably consistent across all seven years, ranging from 0.27 in 2009 (95% CRI = 0.22-0.32) to 0.34 in 2014 (95% CRI = 0.27-0.42; Fig. 3). Mark-recapture-recovery methods improved precision of cumulative survival

estimates and in some cases credible intervals were half the width of those based on mark-recapture methods (Fig. 3).

Steelhead tags recovered on waterbird nesting colonies near McNary Dam were primarily consumed upstream of McNary Dam (Fig. 4). Recoveries on waterbird colonies located near John Day Dam, however, were depredated both upstream and downstream of John Day Dam (Fig. 4). Median recovery probabilities for individuals that died in the McNary reach ranged from 0.14 (2014) to 0.22 in 2008, 2010, and 2011 (Appendix C). The recovery probability for individuals that died in the John Day or Bonneville reaches were all ≤ 0.05 , except for the John Day reach in 2014 (0.13; Appendix C). Recapture probabilities were < 0.20 for 26 of the 28 annual site-specific estimates (Appendix C). Recapture probabilities at the Lower River trawl were ≤ 0.07 in all years (Appendix C).

Simulation study

Integrating dead recoveries reduced bias, increased precision, and improved credible interval coverage for survival estimates relative to mark-recapture methods alone (Table 2; Fig. 5). Mark-recapture-recovery methods greatly improved efficiency, requiring only half the sample size to achieve similar precision as mark-recapture methods (Fig. 5). Mark-recapture credible intervals remained much larger in the third river reach below the release site, even after doubling the sample size (7 000 vs. 14 000 individuals; Fig. 5).

Mark-recapture survival estimates were negatively biased in the second and third river reaches (-0.06 and -0.12, respectively) and did not achieve nominal credible interval

coverage (0.82 – 0.91, depending on river reach; Table 2). Integrating dead recovery data reduced bias in these same parameters (-0.03 and -0.01, respectively) and resulted in nominal credible interval coverage (≥ 0.95 ; Table 2). Recapture and recovery parameters were generally unbiased and achieved nominal credible interval coverage using both methods (Appendix B). Biased and imprecise survival estimates likely resulted from extremely low recapture probabilities (0.05 - 0.15), which were typical of the case study (Tables B1 and C1).

DISCUSSION

We provide a general framework for a state-space mark-recapture-recovery model to estimate survival. These methods increase the flexibility of mark-recapture-recovery models, where mortality is not restricted to the recovery occasion, state uncertainty can vary by the type of dead recovery, and mortality can be constrained to specific intervals depending on the information available from recoveries. Additionally, survival, recapture, and recovery equations are unique to each individual, allowing for individual-based models where survival, recapture, and/or recovery probabilities can be a function of individual level covariates (e.g., length) or random individual level heterogeneity. Similar to other integrated modeling approaches, we found combining mark-recapture-recovery data generated more robust, accurate, and precise parameter estimates (Burnham 1993), while also estimating

ecological processes that are not identifiable using independent approaches (King et al. 2009; Schaub and Abadi 2010).

The results of our simulation study showed that the gain in accuracy and precision from integrating dead recovery data was not trivial when compared to standard mark-recapture methods. Simulation study results also supported the differences observed in the case study, where mark-recapture methods appeared to underestimate survival in certain river reaches. Negatively biased survival estimates are a surprising result. McMichael et al. (2010), however, also observed lower than expected survival probabilities using PIT tag data (survival probability <0.60) compared to acoustic tag data (>0.80) in this same river reach. In both cases, excessively low PIT tag recapture probabilities (<0.20) likely resulted in poor precision and biased survival estimates. Precise parameter estimation in mark-recapture studies requires relatively high recapture probabilities, which is often a limiting constraint (Hewitt et al. 2010). If recapture probabilities cannot be increased, integrating separate sources of information can provide vital information to increase encounter rates and increase precision of survival estimates, while also improving inference, and possibly reduce sample size requirements (Burnham 1993; Kendall et al. 2006; Schaub et al. 2007). The choice of data collection methods (e.g., single- vs multiple sources) is often a balance of benefits and costs. For a practitioner most interested in improving precision, we suggest considering integrated models as one of those options.

We present some of the first salmonid survival estimates for the lower Columbia River that use solely PIT tag data. For decades, salmonid survival in the lower Columbia

River was unknown due to a lack of PIT tag recapture locations in the estuary (Muir et al. 2001; Welch et al. 2008; Clemens et al. 2009). Dead recoveries after the terminal recapture location (Lower River trawl), however, allow estimation of survival in the Lower River (Burnham 1993). Comparisons of our seven-year study to radio and acoustic tag studies in the Lower River suggest that steelhead smolt survival is likely lower than other mid-Columbia river reaches, lower than earlier migrating Chinook salmon (*O. tshawytscha*) smolts, and is characterized by large inter-annual variation (Clemens et al. 2009; McMichael et al. 2010; this study). Additionally, survival estimates in our study (based on PIT tags) and studies based on radio and acoustic tags (Clemens et al. 2009) were often quite similar, with Lower River steelhead survival generally 0.70-0.85 (for run-of-the-river fish) across most years. These multiple lines of evidence suggest that PIT tag survival estimates in the Lower River are reasonable. Nevertheless, comparisons are challenging because studies were conducted in different years, at different release and recapture locations, and using different tag types (radio, acoustic, or PIT tags). Further investigation of Lower River survival and factors influencing survival will be a productive area of future research, especially given the extremely rich source of multi-year, multi-species data from thousands of PIT-tagged individuals (e.g., live recapture and dead recovery data collected annually since 1996; Collis et al. 2001).

We expected survival in all river reaches to be similarly above or below the multi-year average within a given year (e.g., higher flows may result in collectively “good” survival years in all reaches), but we found just the opposite. In our study, above average

survival in one reach often coincided with below average survival in other river reaches within the same year. Disentangling the relative importance of large-scale and local mortality factors is difficult and requires long-term datasets across large spatial scales. Large-scale environmental variables (e.g., river flow) obviously affect juvenile and juvenile-to-adult survival in anadromous salmonids (Petrosky and Schaller 2010; Haesecker et al. 2012); however, mortality factors at local levels (e.g., dam operations, predation) should also be considered when evaluating variation in fish survival. While not an objective of this study, the state-space mark-recapture-recovery model described herein allows tremendous flexibility for incorporating covariates on survival, detection, and recovery probabilities to directly address these hypotheses with improved precision.

In-river, estuarine, and early-ocean migration are critical life stages with particularly profound effects on salmonid population growth rates (Kareiva et al. 2000). In our study, cumulative steelhead survival from release to the Lower River (654 rkm) was remarkably similar across years, with median estimates ranging from 0.27 to 0.34, depending on year. Outmigration survival estimates were also comparable to those of Snake River steelhead and Snake River yearling Chinook salmon, which migrate similar distances of approximately 460 - 687 rkm from Lower Granite Dam to Bonneville Dam and the Columbia River estuary (Welch et al. 2008; McMichael et al. 2010). Steelhead outmigration survival estimates (0.27 to 0.34), however, are noticeably higher than adult return rates (1-3%; Evans et al 2014), indicating substantial mortality still occurs after freshwater migration. Additionally, in the first three years of our study, juvenile outmigration survival did not account for differences in

upper Columbia River steelhead adult return rates, which were two to three times higher for individuals released in 2008 compared to releases in 2009 and 2010 (1% vs 3%; Evans et al. 2014). Although we can speculate on the causes of annual variation between juvenile survival and adult return rates, we do not yet have the multi-species and multi-year data upon which to evaluate those hypotheses.

Dead recovery data are available in many studies across a wide array of taxa (e.g., Barker 1997; Catchpole et al. 2001; Taylor et al. 2005; Kendall et al. 2006; Martins et al. 2011). Dead recovery data may arise from multiple sources, including angler and hunter surveys, designed protocols, opportunistic recoveries, and predation studies. Recoveries of fish tags on piscivorous waterbird colonies are an increasingly, and surprisingly, rich source of information with examples across multiple tag types, fish species, and predator species (e.g., Evans et al. 2011; Frechette et al. 2012; Osterback et al. 2013; Scopettone et al. 2014). It is important to note, however, that recovery probabilities are not predation rates, as recoveries may include scavenging of dead fish and are not adjusted for tag deposition rates (i.e., probability a consumed tag will be deposited on the bird colony). Adjusting tag recoveries on bird colonies for tag deposition probabilities is comparable to ‘reporting rate’ adjustments in fisheries and wildlife studies (Pollock et al. 1991). Regardless of taxa, data on reporting rates for individuals caught by anglers, shot by hunters, or consumed by predators are required to quantify total harvest. State-space models use three equations to separate survival, recapture, and recovery processes. It therefore seems possible to directly integrate reporting rates into the recovery probability equation as additional data or informative priors.

Integrating tag reporting, tag deposition, or even fishing effort will be valuable extensions of this state-space mark-recapture-recovery model and allow investigation of hypotheses on total harvest, exploitation rates, or cause-specific mortality.

The benefits of integrating dead recovery data in a seven-year study of upper Columbia River steelhead included improved precision of survival estimates, estimation of survival across larger spatial scales, information on where fish were consumed by birds, and, based on our simulation study, achieved equal levels of precision with only half the sample size of mark-recapture methods. State-space mark-recapture frameworks offer numerous possibilities for future developments (King 2012). For instance, additional information can be incorporated to discriminate between mortality sources, investigate assumptions about how various parameters may vary with time, age, or other covariates, and are easily incorporated into more extensive Integrated Population Models to estimate multiple demographic parameters and track population dynamics (King 2012; Schaub and Abadi 2010).

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Table 1. Numbers of juvenile steelhead tagged, recaptured (live), and recovered dead on bird colonies (dead). Live and dead encounter columns are ordered by distance from the release site (see Fig. 1).

Year	Released	Weeks	McNary		John Day		Bonneville		Trawl	Estuary
			dead	live	dead ¹	live	dead ¹	live	live	dead
2008	7193	8	354	636	153	821	42	383	78	487
2009	7036	8	475	661	158	428	42	428	112	431
2010	7346	9	405	364	158	307	35	976	104	397
2011	7687	8	354	358	142	1 126	30	147	71	274
2012	6544	7	306	392	75	543	24	337	94	180
2013	5651	6	330	322	144	221	27	390	117	165
2014	7611	8	117	350	288	341	40	524	136	347
Total	49 068	54	2341	3083	1118	3787	240	3185	712	2281

¹ Mortality occasion was unknown

Table 2. Median, bias, and credible interval coverage for estimating survival (ϕ) in the simulation study of 100 datasets with 7 000 individuals. Simulations used data generating values (True value) similar to those observed in the case study. Data were modeled using mark-recapture (CJS) or mark-recapture-recovery (MRR) models. Survival in the last occasion cannot be estimated in the CJS model.

Parameter	True value	CJS			MRR		
		Median	Bias	Coverage	Median	Bias	Coverage
ϕ_1	0.65	0.69	0.04	0.91	0.66	0.01	0.97
ϕ_2	0.80	0.74	-0.06	0.87	0.77	0.03	0.95
ϕ_3	0.80	0.68	-0.12	0.82	0.79	0.01	0.99
ϕ_4	0.70	-	-	-	0.68	0.02	0.99

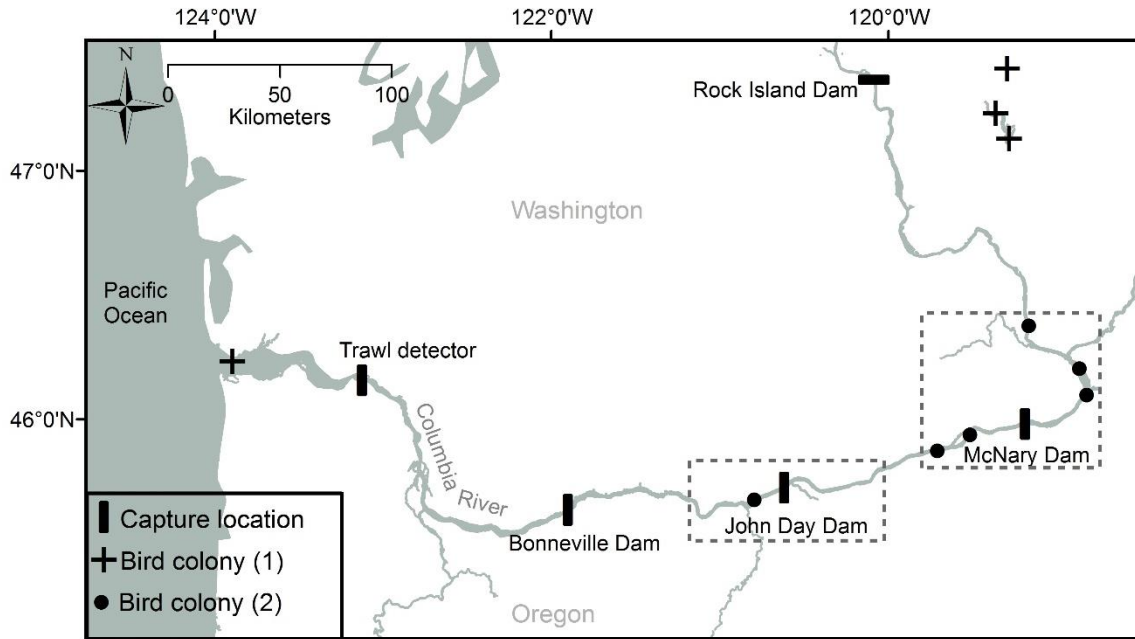


Figure 1. Locations of capture, tagging, and release (Rock Island Dam) and downstream recapture locations for PIT-tagged upper Columbia River steelhead migrating to the Pacific Ocean. Locations of dead recoveries included (1) bird colonies where the river reach of mortality was known (+) or (2) bird colonies where recoveries indicated mortality in one of two river reaches (•; grey boxes indicate the two river reaches where predation may have occurred). See Appendix A for a schematic of the estimable parameters.

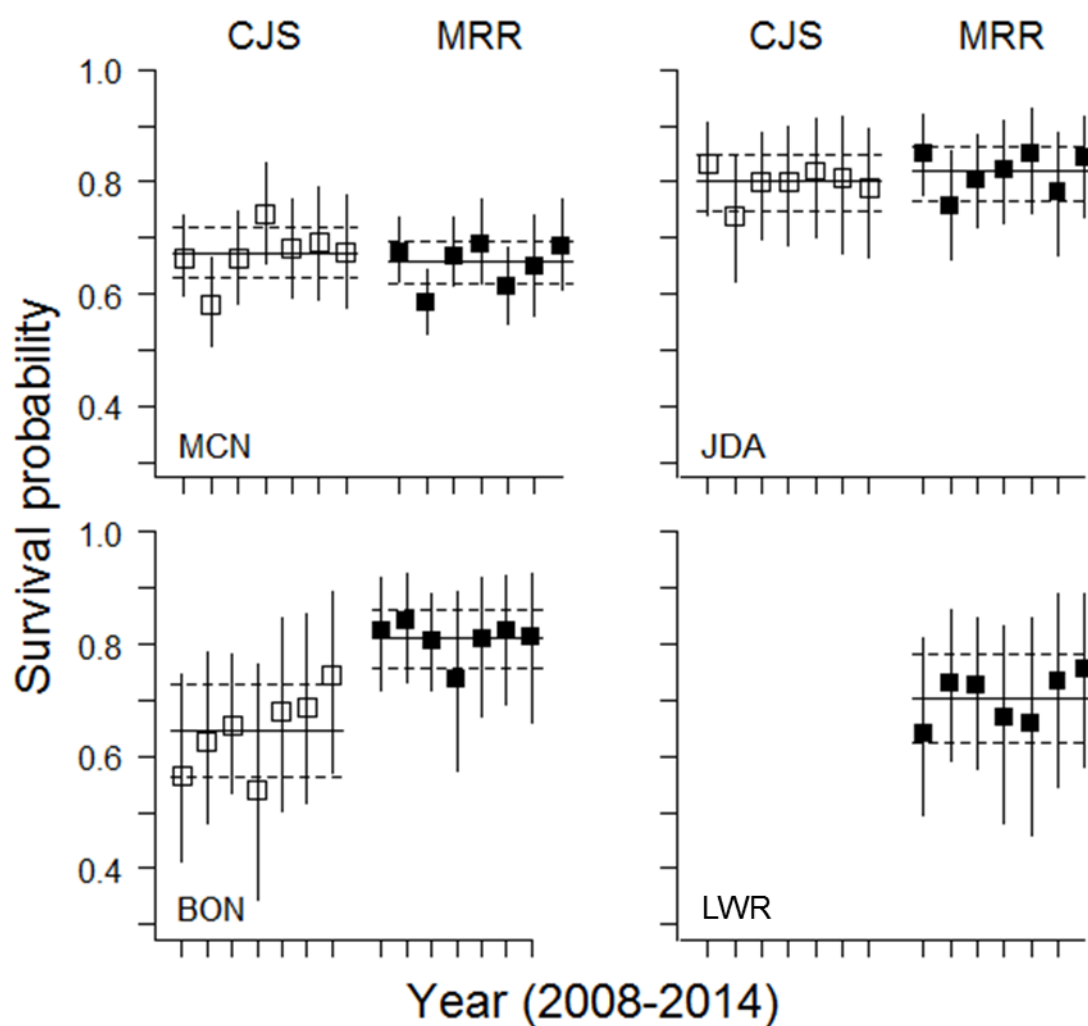


Figure 2. Annual river reach survival probabilities (95% credible interval) for juvenile steelhead using mark-recapture (CJS; open square) or mark-recapture-recovery (MRR; solid square) models. Plots are separated by river reaches: Rock Island Dam to McNary Dam (MCN); McNary Dam to John Day Dam (JDA), John Day Dam to Bonneville Dam (BON), and Bonneville Dam to the Lower River trawl (LWR). Survival estimates are ordered by year from left (2008) to right (2014). Horizontal lines are the median survival probability across the study period (2008 - 2014; 95% credible interval). CJS models cannot estimate survival in the Lower River (LWR).

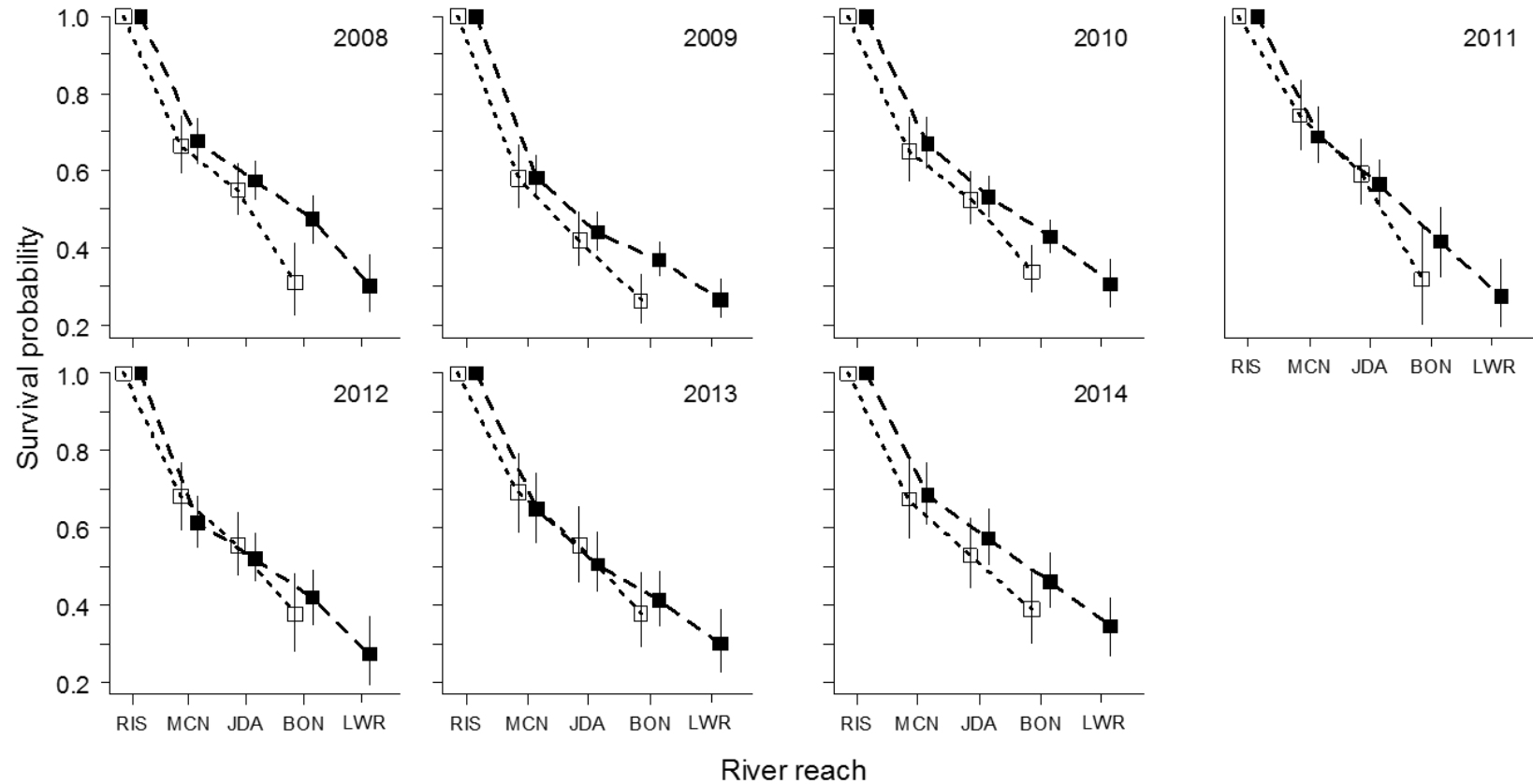


Figure 3. Cumulative migration survival probabilities (95% credible interval) for juvenile steelhead using mark-recapture (CJS; open square) or mark-recapture-recovery (solid square) models. Cumulative survival estimates are from release at Rock Island Dam to McNary Dam (MCN), John Day Dam (JDA), Bonneville Dam (BON), and the Lower River trawl (LWR). CJS models cannot estimate survival to the Lower River trawl.

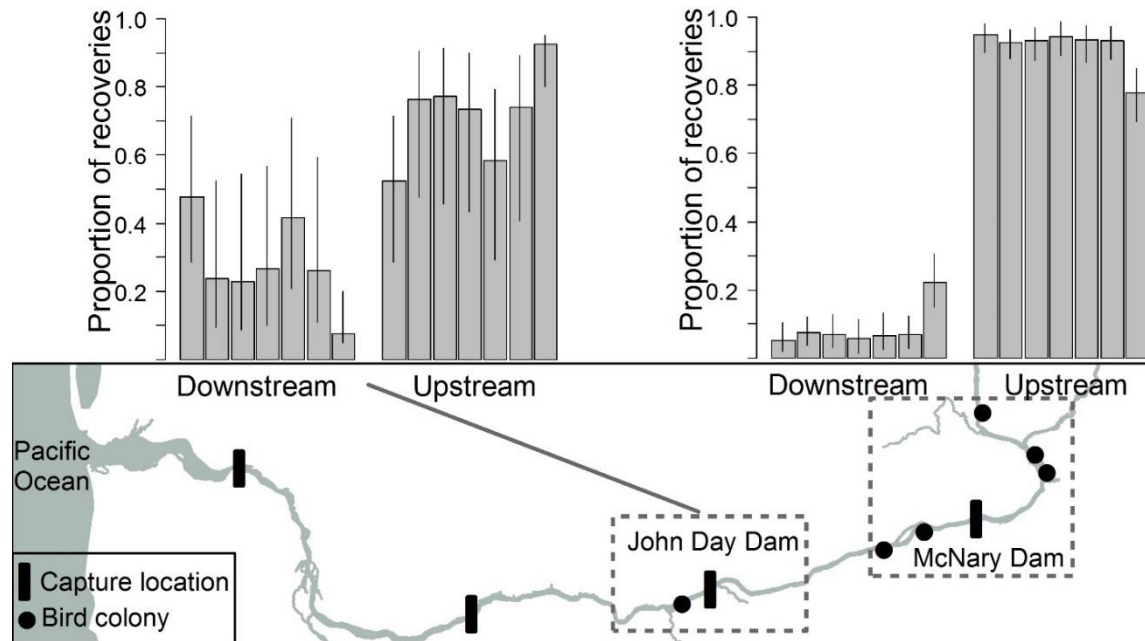


Figure 4. Proportion of recovered smolt PIT tags that were consumed by birds in the river reach upstream or downstream of the nearest recapture location (median and 95% credible interval). Dashed boxes denote the possible river reaches of mortality for each bird colony. Annual proportions are ordered from left (2008) to right (2014).

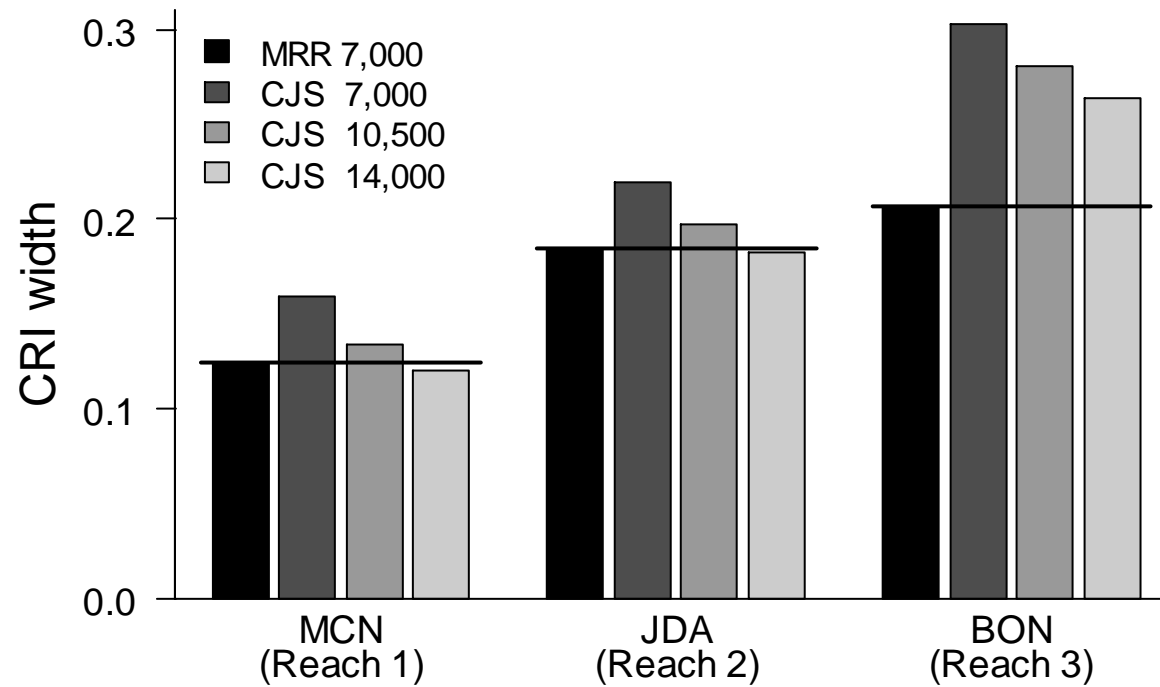


Figure 5. Precision (smaller is better) of mark-recapture (CJS) and mark-recapture-recovery (MRR) survival estimates as measured by their average 95% credible interval width (CRI width) across 100 simulated datasets of varying sample sizes. MRR simulations only included 7 000 individuals, while CJS simulations included analysis of datasets with 7 000, 10 500, or 14 000 individuals. Horizontal bars denote the mean MRR credible interval width. Survival reaches represent: Rock Island Dam to McNary Dam (MCN, Reach 1); McNary Dam to John Day Dam (JDA, Reach 2), John Day Dam to Bonneville Dam (BON, Reach 3).

CHAPTER 3
ESTIMATING ABUNDANCE BY INTEGRATING DIFFERENT SAMPLING
METHODS AND SPATIAL SCALES

ABSTRACT:

1. Large-scale wildlife studies are increasingly in need of integrating multiple data sources to improve spatial and temporal inferences. Combining complementary sources of information, however, faces many challenges including different survey protocols, spatial misalignment of sampling locations, and varying data quality.
2. We describe a multivariate spatial model to estimate animal abundance from multiple sources of spatially overlapping, but misaligned data. The hierarchical approach borrows strength across space and surveys to inform abundance estimates, while also providing a framework to incorporate spatially indexed environmental covariates and imperfect detection.
3. We used the integrated model to combine boat-based distance sampling and digital aerial strip-transect survey data to predict loon (*Gavia* spp.) distribution and abundance off the coast of Virginia, Delaware, and Maryland, USA. We used 10-fold cross validation and a simulation study to compare the integrated model with methods that used only boat data or incorporated aerial data as a constructed covariate.
4. Data integration provided lower root mean squared error and reduced bias when abundances were correlated across surveys. Improved predictive ability of the integrated

model identified areas of high loon abundances that were not detected in analysis of boat data only. Correlation between boat and aerial surveys varied by season, and when the surveys were not correlated a single data source model provided better fit relative to the integrated model.

5. *Synthesis and applications.* We demonstrate an approach to combine different sampling methods and spatial scales into a single composite estimate of abundance. Multivariate spatial models provide flexible frameworks to combine data across different spatial scales, improve accuracy and inference, and are applicable to a wide variety of data collection protocols.

INTRODUCTION

The recent explosion in spatial data collection has led to increased availability of complementary data sources collected across different spatial scales (Banerjee et al. 2014). For example, a standardized protocol may collect data on abundance at one set of locations, while synchronous surveys using different protocols collect data across broader spatial scales (e.g., citizen science [Dickinson et al. 2010]; digital aerial surveys [Buckland et al. 2012]; remote technologies [Diehl et al. 2003, Desholm et al. 2006]). Situations like this are becoming increasingly common as resources and budgets often limit the spatial extent of standardized protocols, while new technologies or less intensive data collection methods provide information across larger areas (Dickinson et al. 2010, Giraud et al. 2015). These situations present new challenges and opportunities for efficient study designs and data

analyses. Formal inferential frameworks to integrate different survey methods, spatial scales, and data quality are sparse, and their efficacy may vary due to data availability and study objectives (Dickinson et al. 2010, Giraud et al. 2015, Pacifici et al. *in-review*).

A common challenge to integrating different study protocols is the spatial misalignment of sampling locations. Sampling points may vary across surveys, but are often nested within similar regions (e.g., Zimmerman et al. 2012, Karanth et al. 2013, Winiarski et al. 2014). One would anticipate a correlation in observed counts across different survey types nested in the same region. It therefore seems intuitive that methods to utilize correlations between survey types may improve abundance estimation (Giraud et al. 2015).

Herein, we describe a hierarchical model to estimate abundance by integrating data from multiple survey methods collected across overlapping spatial areas. These methods build upon integrated species distribution modeling in Pacifici et al. (*in-review*), which we extend to estimate abundance for spatially mismatched data. We develop a multivariate spatial model that allows dependence between surveys, thus borrowing strength across space and survey type to inform abundance estimates (hereafter termed “Integrated model”). We demonstrate these methods on a dataset of boat-based distance sampling surveys and digital aerial strip-transect surveys focused on loon (*Gavia* spp.) abundance off the coast of Virginia, Delaware, and Maryland, USA. This study included several complexities common to wildlife studies, including varying spatial coverage, spatially misaligned sampling units, important habitat covariates, and survey specific protocols and detection probabilities.

Integrated modeling approaches may not always provide improvements over analyses of single data sources (Giraud et al. 2015, Pacifici et al. *in-review*). We therefore explored the utility of the fully Integrated model by comparing it to two other approaches (1) a hierarchical distance sampling (HDS) model (Royle et al. 2004) using only the boat-based data and (2) an approach that allows aerial data to indirectly contribute to abundance estimation as a constructed covariate in the HDS model. We compared models using 10-fold cross validation in the case study and used a simulation study to evaluate the bias and accuracy of abundance estimates.

METHODS

Integrated model development

We consider a study design where multiple survey types $s = 1, \dots, S$, collect abundance data at $i = 1, \dots, m$ sites (e.g., points, plots, transects) within study area D . We assume that the number of individuals at site i in survey type s , N_{is} , follows some probability mass function f (e.g., Poisson, Negative binomial) with λ_{is} denoting the mean abundance in the i th sample unit in survey type s , which may also be a function of site- and survey-specific covariates. We anticipate correlations between surveys that occur in close proximity, but differences in protocols and spatial misalignment of points prevent simple aggregation of all data. Instead, correlations across survey types are modeled using a multivariate conditional autoregressive (*MCAR*) prior that partitions variation into shared spatial components (Θ) and survey specific random effects (ϵ_s). The spatial misalignment of sites across survey types is

addressed by dividing the study area into $j = 1, \dots, J$ non-overlapping areal units (hereafter “blocks”). Each site i is assigned to block j which it is contained within, thus linking sites nested within the same block. We will use the notation $j(i)$ to indicate site $i \in$ block j .

Together,

$$\begin{aligned}
 N_{is} &\sim f(\lambda_{is}) \\
 \log(\lambda_{is}) &= \beta_{0s} + \mathbf{X}_i^T \boldsymbol{\beta}_s + \varepsilon_{is} + \theta_{j(i)s} \\
 \varepsilon_{is} &\sim \text{Normal}(0, \sigma_s^2) \\
 \boldsymbol{\theta}_{j_s} &\sim \text{MCAR}(1, \boldsymbol{\Sigma})
 \end{aligned}$$

where β_{0s} is the survey specific intercept, $\boldsymbol{\beta}_s$ is a vector of survey specific regression parameters for covariates \mathbf{X} , ε_{is} are random effects at the site level, and $\boldsymbol{\theta}_{j_s}$ are mean zero spatially structured random effects that are assigned a $\text{MCAR}(1, \boldsymbol{\Sigma})$ prior (following notation of Gelfand, and Vounatsou [2003]) smoothed at the block level. Specifically,

$$\boldsymbol{\theta}_j | \boldsymbol{\theta}_{-j} \sim \text{Normal}\left(\bar{\boldsymbol{\theta}}_j, \frac{1}{m_j} \boldsymbol{\Sigma}\right)$$

where $\boldsymbol{\theta}_j = (\theta_{j1}, \dots, \theta_{jS})$, $\bar{\boldsymbol{\theta}}_j$ is the average of the adjacent to $\boldsymbol{\theta}_j$ (i.e., of $\boldsymbol{\theta}_{-j}$), m_j is the number of these adjacencies, and $\boldsymbol{\Sigma}$ is a $S \times S$ variance-covariance matrix. The diagonal elements Σ_{ss} represent the conditional variances for each survey type and the off diagonals represent the conditional within-block covariance between survey types. For instance, for two survey types the conditional correlation is $\Sigma_{12} / \sqrt{\Sigma_{11}\Sigma_{22}}$, where correlation values >0 indicate similar geographical patterns in expected abundances. The $\boldsymbol{\Sigma}$ matrix is key to the

Integrated model as it allows information to be shared across survey types, thus utilizing cross-survey and spatial correlations to inform abundance estimates.

The multivariate spatial model also provides a method to incorporate different spatial sampling protocols, as there is no requirement that each survey type occur in every block. Using the MCAR prior, unsampled blocks are informed by the correlation among survey types and the spatial dependence observed within the sampled blocks. The ability to integrate spatially mismatched data can be especially informative when surveys collect data across different areas, but include overlapping areas.

Case study

We demonstrated these approaches in a study investigating loon abundance off the coast of Virginia, Delaware, and Maryland, USA (Figure 1). This study was motivated by proposed offshore wind energy development on the Atlantic Outer Continental Shelf and the need for accurate estimates of marine bird distributions and abundances in this region (Goyert et al. 2016). Marine animal data were collected using two different methods: (i) boat-based distance sampling and (ii) high-definition video aerial strip-transect surveys (hereafter “boat surveys” and “aerial surveys”, respectively). Boat surveys primarily occurred in the northern and southern regions of the study area (Figure 1). Aerial surveys used a sawtooth pattern to survey the entire north-south length of the study area and included high density transects near proposed wind energy development sites (Figure 1; Williams et al. 2015). Both survey types were carried out in December 2012 and March 2013. Our case study focuses on

common loons (*G. immer*) and red-throated loons (*G. stellate*) as a group due to large numbers of observations identified to genus, but not species.

Data collection

The study area consisted of a 15,760 km² area off the coast of Delaware, Maryland, and Virginia, USA (Figure 1). Boat-based distance sampling data were collected along a combined transect length of approximately 643 km. Boat surveys were conducted on five days between mid-December 2012 and early-January 2013 and five days in late March 2013. Protocols were designed to follow standard line transect distance sampling methods of Buckland et al. (2001) and are described in Goyert et al. (2016). In brief, an observer recorded all observations of animals to an unlimited distance on one side of the boat, including species, radial distance, and the angle of observed individuals. Survey speed was maintained at approximately 18.5 km hr⁻¹ and sampling only occurred when Beaufort sea states were ≤ 6 , however, only Beaufort sea states ≤ 4 were observed in this dataset.

Aerial survey methods are described in detail in Hatch et al. (2013). Data were collected along approximately 3,003 km transect length during three days in mid-December 2012 and two days in late March 2013 (Figure 1). Surveys were conducted from a twin-engine Cessna flying at approximately 250 km hr⁻¹ at 610 m above the water surface. Four super high-definition (2 cm ground spatial resolution) video cameras angled at 30-45° from vertical each captured a 50 m strip width, resulting in a combined strip width of 200 meters. Recorded images were subsequently reviewed by two teams of reviewers to locate objects

and identify animals to the lowest possible taxonomic group (see Hatch et al. [2013] for complete details).

Data preparation

For boat surveys, we set the maximum observable distance at 600 m binned into 100-m distance categories based on observed distances. We used a hierarchical distance sampling approach to analyze boat-based data (Royle et al. 2004). Methods to estimate detection probability in digital aerial surveys are generally lacking and we therefore assumed all individuals within the 200 m strip width were counted (Buckland et al. 2012). Boat and aerial transects were split into segments of approximately 4 km and hereafter referred to as “sites”. The resulting datasets included 161 and 803 boat and aerial sites in December 2012 and 166 and 1003 boat and aerial sites in March 2013, respectively.

We divided the study into 985 16-km² non-overlapping blocks with each survey site assigned to its associated block. In December 2012, boat surveys observed 472 individual loons, while aerial surveys counted 703 individuals (Table 1; Figure 1). Counts in March 2013 were 348 individuals during the boat surveys, and 477 individuals in aerial surveys.

Environmental covariates

We incorporated three covariates to explain spatial variation in loon abundance: distance to shore (*DTS*), sea surface temperature (*SST*), and salinity (*SAL*). Distance to shore was calculated in ArcGIS 10.2 (ESRI, Redlands, CA). Marine Geospatial Ecology Tools in

ArcGIS (Roberts et al. 2010) were used to download remotely-sensed sea surface temperature ($^{\circ}\text{C}$, 1-km GHRSSST L4) and salinity (Practical Salinity Units, 9-km HYCOM GLBa0.08 Equatorial 4D). We additionally included a binary value of Beaufort sea state as a covariate on detection in boat surveys, where Beaufort states 0 - 2 were assigned a 0 (i.e., calm seas), and Beaufort states 3 and 4 were assigned a 1 (rough seas).

Parameterization of the case study

In addition to spatially indexed covariates, we included survey specific intercepts (β_{0s}) and survey-specific random effects to allow mean abundances, λ_{is} , to vary spatially and between survey types. Specifically,

$$N_{is} \sim \text{Poisson}(\lambda_{is})$$

$$\log(\lambda_{is}) = \beta_{0s} + \text{offset}(\text{length}_{is}) + \beta_1 \text{DTS}_i + \beta_2 \text{SST}_i + \beta_3 \text{SAL}_i + \varepsilon_{is} + \theta_{j(i)s}$$

$$\varepsilon_{is} \sim \text{Normal}(0, \sigma_s^2)$$

$$\theta_{js} \sim \text{MCAR}(1, \Sigma)$$

where β_{0s} is the survey specific intercept, $\text{offset}(\text{length}_{is})$ is the log of transect length, $(\beta_1, \beta_2, \beta_3)$ are the regression parameters for the previously described environmental covariates, ε_{is} are site level random effects, and θ_{js} are spatially structured random effects at the block level assigned an $\text{MCAR}(1, \Sigma)$ prior smoothed at the block level. Fixed effects $(\beta_1, \beta_2, \beta_3)$ were jointly estimated using both data types as preliminary analysis found boat and aerial surveys identified similar habitat relationships. For convention, we assigned boat surveys as data source 1 and aerial surveys as data source 2.

Boat-based distance sampling data were modeled using a HDS model to account for imperfect detection (Royle et al. 2004). We used a half-normal detection function to describe the decline in detection probability with distance from the trackline. The detection scale parameter σ was allowed to vary by Beaufort sea state, where σ_{clam} and σ_{rough} are the scale parameters when Beaufort states were 0 – 2 (i.e., calm seas) or 3 - 4 (rough seas), respectively. The observed number of individuals at boat site i (n_{i1}) was modeled as a binomial random variable, where N_{i1} is the abundance at boat site i and $p \cdot t_{i1}$ is the total detection probability at boat site i (i.e., the integral over the detection function; Buckland et al. 2001),

$$n_{i1} \sim \text{Binomial}(N_{i1}, p \cdot t_{i1}).$$

As previously noted, detection probability cannot be estimated in digital aerial surveys and was assumed to be 1.0 (Buckland et al. 2012).

Abundances were predicted for each 4x4 km block using covariate values (DTS , SST , SAL) from the midpoint of each block. Temporally varying covariate values (SST and SAL) were from the midpoint of the survey dates (December 25, 2012 and March 25, 2013).

Model comparison

We considered two other modeling approaches. The first method used only boat data in the HDS model hereafter termed “Boat model”). This approach allowed estimation of detection probability and abundance but ignored information available in the aerial data. The

second method used aerial survey data as a constructed covariate to inform the boat-based HDS model. Here, a conditional autoregressive model was used to smooth aerial abundance estimates at the block level across the study area. Smoothed estimates from the aerial analysis were then used as a constructed explanatory variable on abundance in the boat-based HDS model (hereafter termed “Combined model”). In this approach, aerial data provide extra information on abundance to the boat only model, but a direct link between aerial and boat data was not required (i.e., the parameter estimate could be non-significant). All models included the previously described environmental covariates.

We used 10-fold cross validation to compare the predicative ability of each model. Specifically, posterior median parameter estimates from training folds were used to predict boat observations in held-out folds. Predictive performance was assessed by root mean squared error (RMSE) and average relative bias, where smaller values indicated better model fit.

Simulation study

In addition to the case study, we evaluated the performance of the Integrated, Combined, and Boat models through a simulation study. We considered three scenarios with varying levels of spatial and cross-survey correlations. We simulated abundance data for two survey types across a 25 x 25 grid ($m = 625$ sites). Similar to the case study, Poisson means, λ_{iS} , included survey specific intercepts $\beta_{0S} = (1.0, 0.5)$, one site level covariate

$X \sim \text{Normal}(0,1)$, its associated coefficient $\beta_1 = 1.0$, and survey specific variances, $\Sigma_{SS} = (1.0, 1.5)$.

For the first scenario, we simulated data using an $MCAR(1, \Sigma)$ prior, with a strong correlation across surveys $\frac{\Sigma_{12}}{\sqrt{\Sigma_{11}\Sigma_{22}}} = 0.75$. In the second scenario, we simulated data using the $MCAR(1, \Sigma)$ prior and a weak correlation across surveys of 0.25. For the third scenario, we generated data with no spatial dependence and zero correlation between surveys. To reflect the case study, survey type #1 sampled 25% of the sites, while survey type #2 sampled 75% of the study area. We simulated and analyzed 100 datasets for each scenario.

Analyses followed the model descriptions above, but without the observation/detection component described for the case study boat surveys. RMSE and relative bias were used to evaluate predictions, then averaged values across all 100 simulations.

Implementation

All models were fit using Markov-chain Monte Carlo (MCMC) methods implemented in a Bayesian framework using the package R2WinBUGS (Sturtz et al. 2005) to run the software WinBUGS (Lunn et al. 2000) in R version 3.1.2 (R Development Core Team 2015). We ran three parallel Markov chains with 10,000 burn-in iterations and 100,000 post burn-in iterations. Chains were thinned by 10 to reduce the size of model output. The number of iterations for the simulation study was reduced to 5,000 burn-in and 15,000 post burn-in iterations to reduce run time. Convergence was assessed using diagnostic plots and

the Gelman-Rubin statistic (\hat{R} ; Gelman et al. 2013). We used vague priors, where β_{0s} were independent flat priors, the remaining β were independent $Normal(0,100)$; $\log(\sigma_{calm})$, $\log(\sigma_{rough})$, and σ_ε were independent $Uniform(0,10)$; and Σ^{-1} was $Wishart(2, \mathbf{\Omega})$, where $\mathbf{\Omega}$ was a 2 x 2 identity matrix. Model fit was evaluated using Freeman-Tukey fit statistics and Bayesian p-values (Brooks et al. 2000). The abundance and observation components were evaluated and results indicated adequate model fit. We report results as posteriors medians as well as 2.5 and 97.5 percentiles (95% CRI). Abundance estimates are reported as posterior modes due to skewed distributions at some locations.

RESULTS

Case study

The Integrated and Combined models provided lower RMSE and relative bias compared to the Boat model in December 2012 surveys (Table 2). The Integrated model identified a statistically significant positive cross-survey correlation in abundances (0.75; 95% CRI 0.23-0.93; Sup 1A). In the Combined model, the constructed covariate explained much of the spatial variation in loon abundance (Figure 2), further supporting the strong correlation between boat and aerial survey data.

In March 2013, we found no statistically significant correlation between boat and aerial surveys (Sup 1B). Similarly, the constructed aerial covariate explained very little of the spatial variation in loon abundance in the Combined model (Figure 2). In March 2013, the

Combined model had the lowest relative bias, while the Combined and Boat models had the lowest RMSE (Table 2).

A negative relationship between loon abundance and distance to shore was observed in both surveys (Figure 2). Parameter estimates for sea surface temperature and salinity were generally closer to zero and relationships sometimes varied between surveys (Figure 2). The Combined model did not support a negative relationship with distance to shore in December 2012 primarily due to the strong effect of the constructed aerial covariate (Figure 2).

The Integrated model predicted increased spatial aggregation of abundances compared to the Boat model in December 2012 (Figure 3). Loon abundances were highest near the mouths of the two large bays, especially the southwestern section of the study area (Figure 3). The Integrated and Combined models also predicted very low loon abundances in along the coast of Maryland, while the Boat model predicted relatively higher abundances in that region (Figure 3). Overall, the Integrated and Combined models predicted similar patterns in December 2012, coinciding with their similarly lower RMSE relative to the Boat model.

Loon abundances in March 2013 were more dispersed relative to December 2012. The Integrated model predicted higher abundances near the same two bays in March as was predicted in the December results. The Combined and Boat models predicted a more homogeneous distribution with a slight decrease with distance to shore (Figure 3). Coefficient of variation maps indicated increased uncertainty near the edges of the study area (Figure 4).

Simulation study

The Integrated model provided the lowest RMSE and bias in both the high and low correlation scenarios (Table 3). Improvements were largest when the correlation between surveys was high (0.75), but also substantial when correlations were low (0.25; Table 3). The Single data source and Combined model provided lower RMSE and bias in the scenario of zero correlation with no spatial dependence (Table 3). The requirement of spatial dependence in the Integrated model also resulted in higher than expected relative bias in the scenario of zero correlation with no spatial dependence (relative bias = 0.12; Table 3).

DISCUSSION

We demonstrate an approach to estimate abundance by integrating data collected across different spatial scales and sampling methods. This integrated model holds promise for improving parameter estimates, which is highlighted in the case study combining distance sampling surveys and strip-transect surveys to estimate marine bird abundance. More generally, this modeling approach is applicable to a variety of abundance protocols and studies interested in combining datasets of different quality and spatial scales (e.g., mark-recapture [Otis et al. 1978], repeated counts [Royle 2004], double observer [Nichols et al. 2000]).

In this study, we used boat-based distance sampling protocols to estimate abundance adjusted for detection probability to leverage the large scale count data provided by digital aerial surveys. Integrating data collected by different protocols provided several advantages

compared to a single survey method. For instance, boat-based distance sampling surveys are generally not suitable for large spatial scales, but likely provided better estimates of true abundance by accounting for imperfect detection (Buckland et al. 2001). Aerial surveys, conversely, cover a much larger area in a shorter time window, but in our case study strip width was limited and assumptions of perfect detection were required (Buckland et al. 2012). We see similar challenges in other studies where well-structured protocols may be limited by accessibility, logistical constraints, funding, or the speed at which surveys can be conducted (Karanth et al. 2003, Bouché, et al. 2012, Zimmerman et al. 2012). In these instances, an alternative and possibly efficient study design may include a second survey type that can offset these challenges (e.g., double sampling; Thompson 2012). As noted in our simulation study, incorporating a second source of data via an Integrated model noticeably improved model performance, even when correlations across surveys were low.

Another advantage of data integration is that secondary data sources may be available as ‘free’ information. For instance, large-scale citizen science programs can contribute information to studies focused on local or regional animal abundances (Hochachka et al. 2012). The increasing quality and expanding diversity of citizen science programs provide opportunities to utilize larger scale, but possibly lesser quality data sources (e.g., breeding bird surveys [Peterjohn 1994], ebird [Sullivan et al. 2009], eMammal [McShea et al. 2016], North American Amphibian Monitoring Program [Weir and Mossman 2005]). Integrating these multiple sources of information, however, requires methods to address challenges such as differing data quality, spatial mismatch, and uncertainty in correlations among surveys.

Approaches to address these challenges are active areas of research and provide tremendous potential to improve large-scale wildlife studies (Dickinson et al. 2010, Giraud et al. 2015, Pacifici et al. *in-review*; this study).

While Integrated model performed well, even when correlations across surveys were low, the Combined and Single data source models provided better fit when surveys were uncorrelated. In most situations, there will be little motivation to combine completely uncorrelated survey methods. Correlations among different protocols, however, are often unknown, imperfect, and may vary across space or time. Although not exhaustively explored here, numerous extensions and restrictions to the Integrated model are easily incorporated to investigate these challenges. On one end, connections between survey types can be removed by forcing a correlation of zero in the covariance matrix and introducing survey specific covariate relationships. Additionally, variable spatial dependence may be addressed by introducing a parameter, ρ , into the mean of the MCAR prior (i.e. $MCAR(\rho, \Sigma)$; Gelfand and Vounatsou 2003). Here, ρ can be interpreted as a coefficient measuring the strength of spatial dependence, where $\rho = 0$ implies that residuals are independent, but variances still depend on the number of neighbors (Banerjee et al. 2014).

Parsimonious approaches to integrate multiple survey types are recommended for a second reason: advancing technologies may require a calibration factor to compare historical and new datasets (Buckland et al. 2012). New technologies create the possibility of confounding changes in the ecological process (e.g., abundance) with changes in technology (Buckland et al. 2012). Joint analysis of synchronous surveys provides an approach to

calibrate surveys and verify different protocols identify similar patterns in abundance and distribution. Although not the focus of this study, joint analysis – particularly the Integrated model– provides an approach to evaluate the correlation between survey methods and possibly develop correction factors where appropriate. The topic of cross-survey calibration was beyond the scope of this study, but warrants further investigation.

Incorporating aerial survey data as a constructed covariate (Combined model) also provided improved fit relative to modeling only the boat data. An advantage of the Combined model is that it makes no assumptions about the quality of the second data source. This approach may be particularly useful when the secondary data sources are of lesser quality or may identify different patterns in abundance (Pacifci et al. *in-review*). A particular challenge with the Combined model, however, is the subsequent interpretation of other parameters. For instance, when cross-survey correlations are high, the constructed covariate will explain a large portion of spatial variation in abundance and likely mute relationships with other important ecological variables. Overall, we expect that the Integrated and Combined model to improve accuracy of abundance estimates when surveys identify similar geographical patterns. When both data sources provide high quality data, however, the Integrated model will likely outperform the Combined model by utilizing correlations across both space and survey type, while also providing better inference to ecological variables of interest.

SUMMARY

The overall goal of integrated modeling approaches is to synthesize multiple data sources by utilizing complementary information, dependencies across surveys, and the strengths of each data set (Schaub and Abadi 2012, Banerjee et al. 2014, Giraud et al. 2015). The anticipated benefits from integrated approaches include improved parameter estimation, broader inferences over spatial or temporal scales, and enhanced understanding of multiple ecological processes. Our results establish that information from different sampling methods and spatial scales can be combined into a composite estimate of abundance. Our integrated approaches address several common challenges in animal studies by (i) allowing the inclusion of survey specific covariates and survey specific detection processes, (ii) retaining the capability to have separate variance components for each survey type, and (iii) flexible hierarchical structure to integrate data collected across different spatial scales. We expect these approaches to be applicable to an increasing number of studies due to increased data availability and interest in integrating multiple sources of data.

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Table 1. Counts of loons during boat and aerial surveys in December 2012 and March 2013.

Survey	Boat	Aerial
December	472	703
March	348	477

Table 2. Relative bias and root mean squared error from ten-fold cross validation comparing abundance estimates from three estimation methods. Modeling approaches integrated boat and aerial data (Integrated), incorporated aerial data as a constructed covariate (Combined), or used only boat data (Single source). Values closest to zero indicate better model fit.

	December 2012			March 2013		
	Integrated	Combined	Boat	Integrated	Combined	Boat
Bias	0.34	0.18	0.75	1.06	0.59	0.69
RMSE	3.25	3.17	3.48	1.75	1.49	1.49

Table 3. Relative bias and root mean squared error for estimating abundance in the simulation study. Modeling approaches integrated boat and aerial data (Integrated), incorporated aerial data as a constructed covariate (Combined), or used only boat data (Boat). Data generating scenarios varied by spatial dependence and correlation between surveys. Values closest to zero indicate better model fit.

Simulated Correlation	Relative bias			Root mean squared error		
	Integrated	Combined	Single	Integrated	Combined	Single
0.75	0.01	0.01	0.02	4.03	4.90	5.15
0.25	0.00	0.01	0.01	4.75	5.59	5.65
0.00	0.12	0.05	0.06	15.61	14.11	14.11

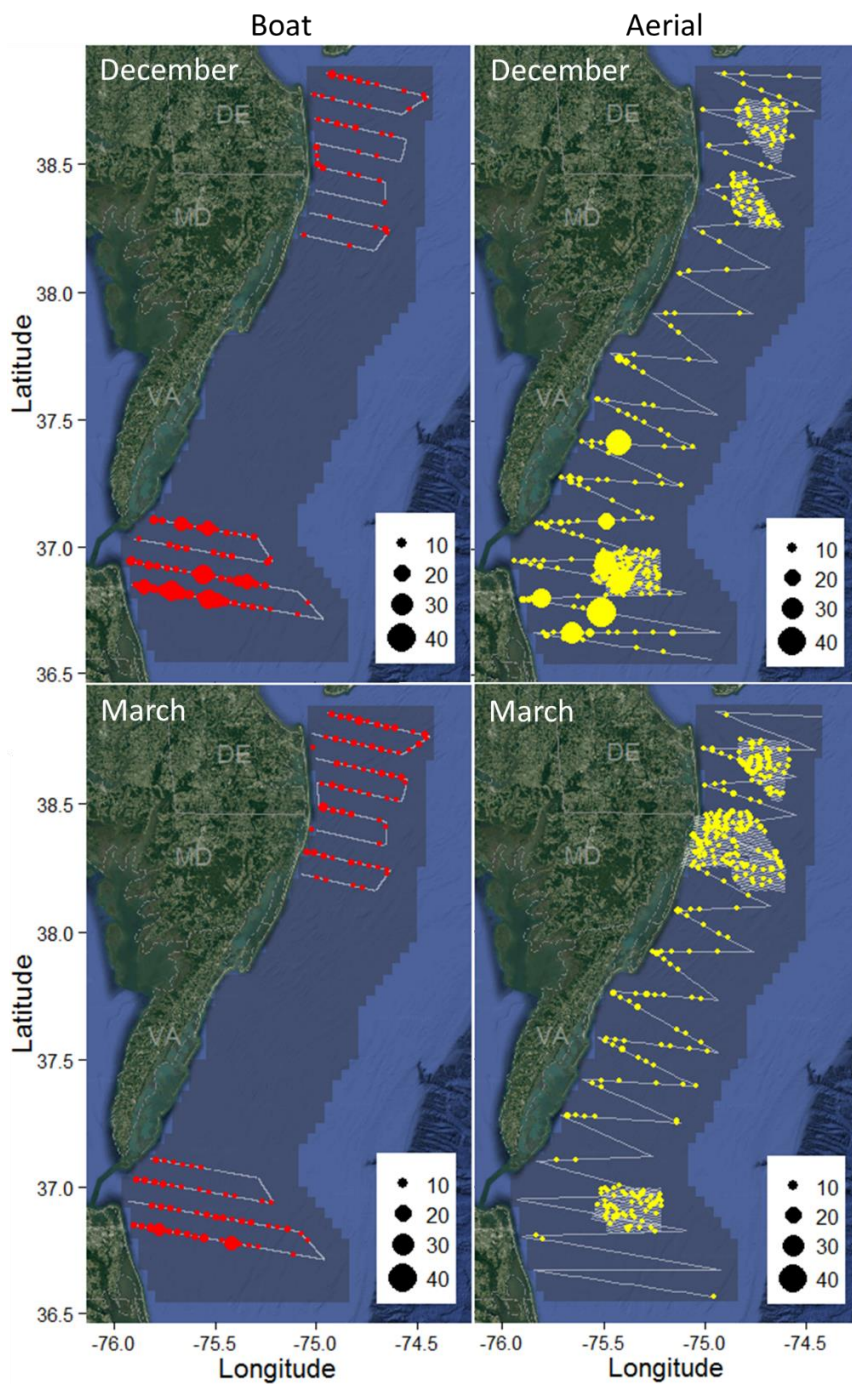


Figure 1. Counts of loons within 4-km segments during boat (left) and digital aerial (right) surveys in December 2012 and March 2013. Survey routes are shown in white and the study area is shaded.

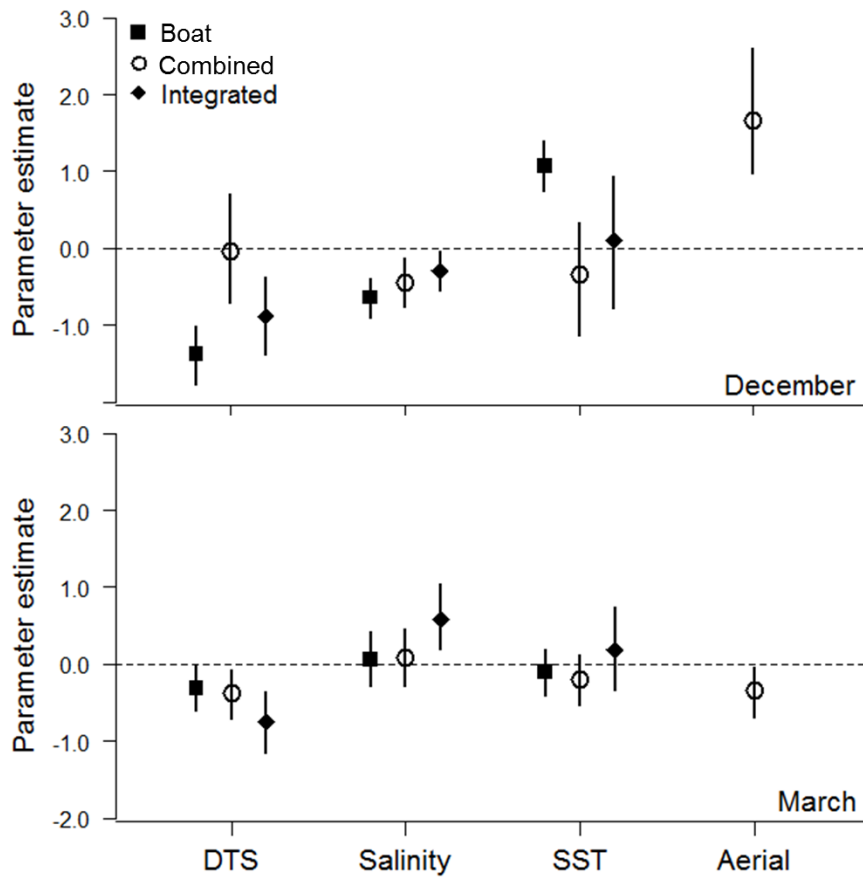


Figure 2. Covariate effects on loon abundance in December 2012 and March 2013. Modeling approaches integrated boat and aerial data (Integrated), incorporated aerial data as a constructed covariate (Combined), or used only boat data (Boat). Habitat covariates included distance to shore (DTS), salinity, and sea surface temperature (SST). The Combined model included an additional constructed covariate (Aerial). Values are posterior medians and 95% credible intervals.

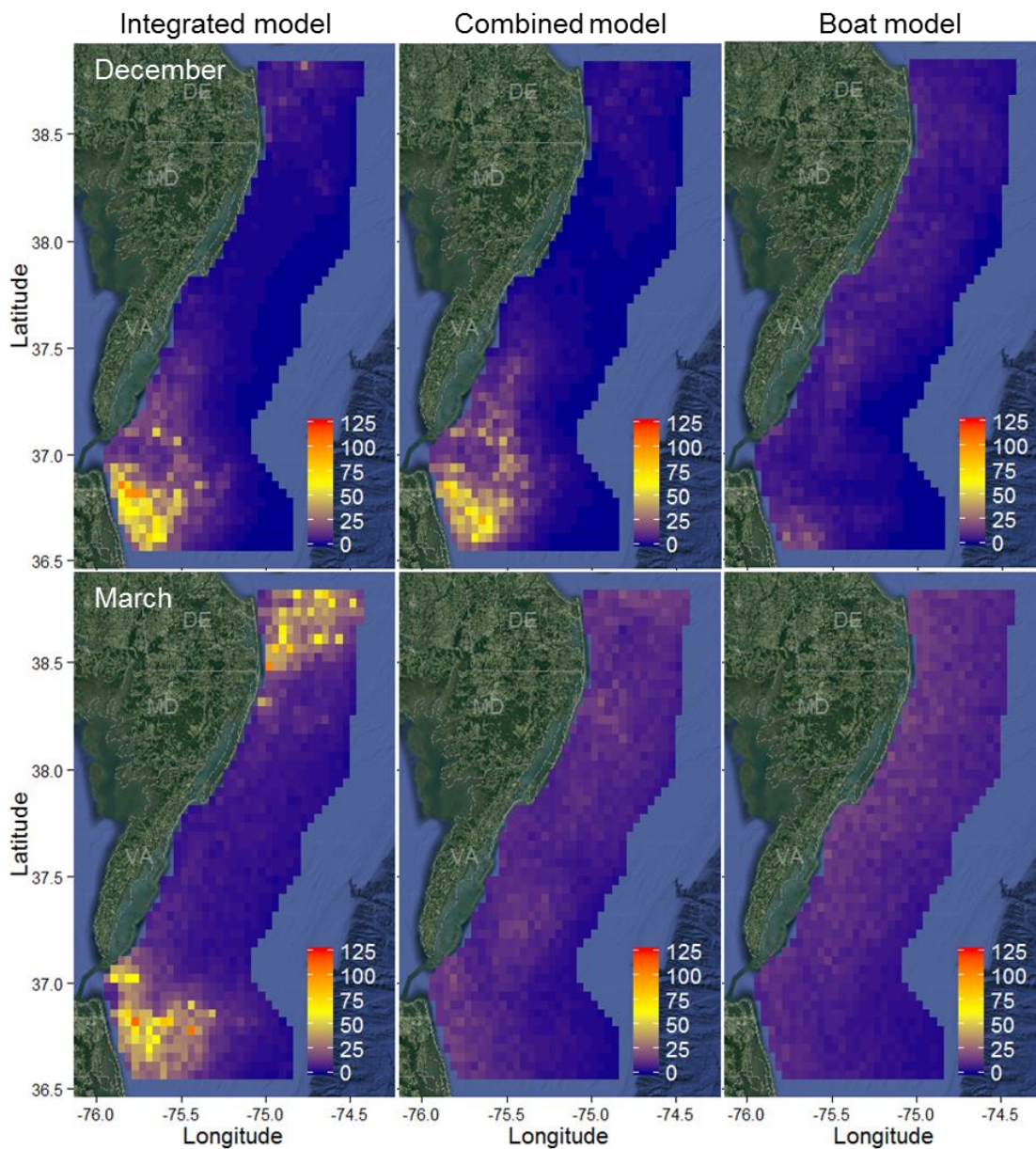


Figure 3. Predicted loon abundances in December 2012 (top) and March 2013 (bottom). Modeling approaches integrated boat and aerial data (Integrated), incorporated aerial data as a constructed covariate (Combined), or used only boat data (Boat). Values are posterior modes.

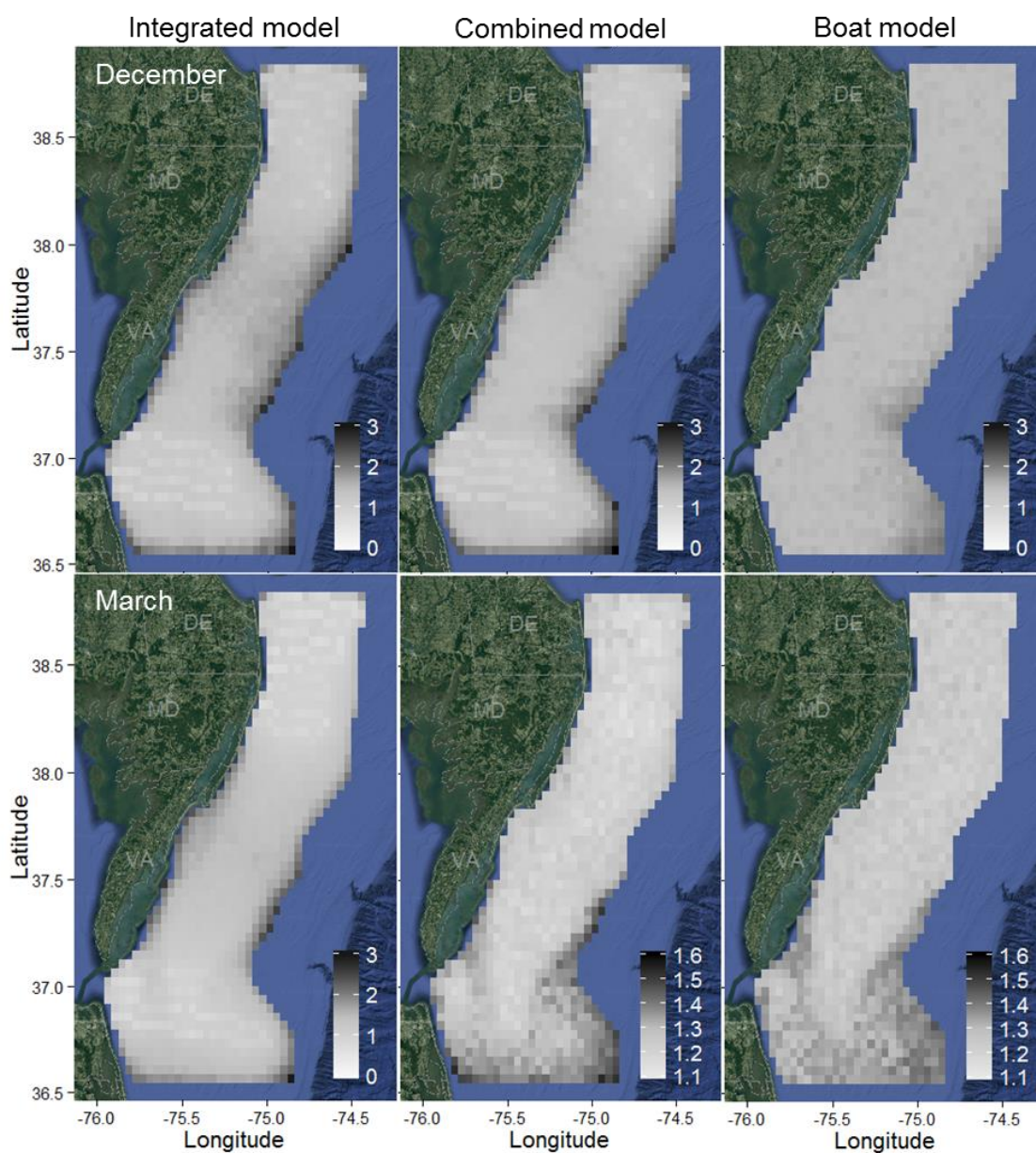


Figure 4. Coefficient of variation for predicted loon abundances in December 2012 (top) and March 2013 (bottom). Modeling approaches integrated boat and aerial data (Integrated), incorporated aerial data as a constructed covariate (Combined), or used only boat data (Boat). Scale range for Boat and Combined models in March 2013 was resized to better display variation.

CHAPTER 4

**COMBINING MODELING APPROACHES TO DECOMPOSE DETECTION AND
IMPROVE DEMOGRAPHIC PARAMETER ESTIMATION**

ABSTRACT

Accurate estimates of abundance and density are essential to both theoretical and applied ecology. Rarely, however, are all animals detected during a survey and many models for estimating abundance incorporate some form of imperfect detection. There are generally considered to be three components of detection probability: probability of presence during a survey, probability of availability given presence, and probability of detection given availability and presence. We present a hierarchical model to separate these three components of detection using spatially and temporally replicated distance sampling surveys augmented with time-to-removal data. Separating detection components provides density estimates of the number of individuals available for detection, the number of individuals present in the sampling plot, and the superpopulation of individuals that use the plot. We conducted a simulation study to test the validity of the model and apply the model to a case study of Island Scrub-Jays (*Aphelocoma insularis*). Simulation results indicated <4% relative bias of density estimates for the present and available populations when availability, presence, and detection were as low as 0.75, 0.75, 0.25, respectively (combined detection probability of 0.14). Relative bias of superpopulation density estimates were >9% when detection probability was ≤ 0.50 . In the case study on Island Scrub-Jays, the resulting median

probabilities of presence, availability, and detection were 0.75, 0.92, and 0.26, respectively. Density estimates for available and present individuals were relatively similar (0.85-0.95 individuals/ha) due to high probability of birds being available. Superpopulation density was noticeably higher (1.09 individuals/ha), indicating a lack of geographical closure (i.e., animals moving in and out of surveyed area) between surveys. Reduced models that used data from only one or two of the sampling protocols provided similar density estimates as the fully integrated model, but only estimated a subset of densities and detection components.

INTRODUCTION

Accurate estimates of abundance and density are essential for answering many ecological questions. A principle challenge in estimating abundance is that observations can be biased by several sources of measurement error. Imperfect detection probability is a well-studied source of bias and numerous protocols are available to account for imperfect detection such as mark-capture (Otis et al. 1978), distance sampling (Buckland et al. 2001), double sampling (Pollock et al. 2002), repeated counts (Royle 2004), multiple observer (Nichols et al. 2000), removal sampling (Farnsworth et al. 2002), and time-of-detection (Allredge et al. 2007). Each of these methods addresses issues of imperfect detection and help to improve the accuracy or abundance estimates for populations, particularly those that may be elusive or rare.

However, one less commonly discussed topic in the literature is that detection probability (p) consists of multiple components in itself (see reviews in Pollock et al. 2004

and Nichols et al. 2009). The combined probability of detecting an individual can be thought of as a product of three primary components: (i) the probability an individual that is associated with the sampling area is present during a survey (p_p), (ii) the probability an individual is available for detection given it is present ($p_a|p_p$; e.g., vocalizes during a point count), and (iii) the probability an individual is detected by an observer given it is present and available ($p_d|p_p, p_a$; e.g., the observer hears and records the individual that is present during a point count). Various sampling protocols can account for a subset of these detection components, however, they also require different assumptions for the unmodeled components (McCallum 2005). For instance, distance sampling methods estimate the probability of detection p_d , but require probability of availability (p_a) and presence (p_p) to be perfect or constant over space and time to properly compare densities across study areas or years (Buckland et al. 2001). Alternatively, removal and time-of-detection protocols estimate the combined probability of detection and availability ($p_a p_d$; Farnsworth et al. 2002, Alldredge et al. 2007). Similarly, repeated count protocols provide the product of all detection probability components, $p_d p_a p_p$ (Royle 2004). When used alone, none of these methods provides separate estimates for all three components of p (Nichols et al. 2009, Riddle et al. 2010). Several analytical approaches are now available to integrate multiple protocols and separate multiple detection components (e.g., Alpizar-Jara and Pollock 1996, Laake et al. 2008, Stanislav et al. 2010, Amundson et al. 2014). However, no current method is available to jointly estimate all three components of detection.

Practitioners must also be aware that different approaches to estimate p affect conclusions on population size and density (Reidy et al. 2011). For instance, protocols that solely adjust for p_d provide density or abundance of individuals available for detection within the sampled area (Nichols et al. 2000, Buckland et al. 2001, Nichols et al. 2009). Conversely, repeated count protocols estimate the product of $p_d p_a p_p$ and provide information on the superpopulation of individuals that use the sample area, but may have home range centers outside of the surveyed area (Royle 2004, Kéry et al. 2005, Chandler et al. 2011). Abundance and density estimates are not directly comparable across these protocols and careful consideration of species behavior, study design, and assumptions are required to prevent the confounding of changes in population densities and changes in the detection processes.

To decompose the components of detection, we develop a novel framework that integrates three commonly used sampling protocols. The model is based on spatially and temporally replicated distance sampling surveys augmented with time-to-removal data. These methods provide a flexible analytical framework that can incorporate multiple survey protocols (e.g., multiple observer [Nichols et al. 2000], time-of-detection [Allredge et al. 2007]) and have application to a variety of sampling situations. Our approach builds upon methods described in Chandler et al. (2011) and Amundson et al. (2014), where inferences on density, temporary emigration, and detection components are derived from unmarked populations. Model development was motivated by the need to improve our understanding of

the types of detections probabilities and how that may impact the validity of density comparisons across different survey types and years.

We first describe the data collection methods and sampling scenario required for our approach. Next, we describe an integrated analysis to estimate the components of detection probability and density using a Bayesian framework. Using simulations, we then investigate the impacts of different levels of detection, availability, and presence on density estimates. Application of the methods is demonstrated in a study of Island Scrub-Jays (*Aphelocoma insularis*), which are a species of management concern endemic to Santa Cruz Island, off the coast of southern California, USA (Curry and Delaney 2002). Finally, we compare density estimates from the full model developed herein to reduced models that only fit one or two of the data sources.

METHODS

Model development

We consider a study design where individuals are counted at $s = 1, 2, \dots, S$ plots on $t = 1, 2, \dots, T$ sampling occasions. Plot specific counts are conducted within a short, standardized period (e.g., 10-minutes) and divided into $k = 1, 2, \dots, K$ sub-intervals (e.g., four 2.5-minute intervals). Survey duration and plot size generally reflect the behavior of the study species so one can assume demographic closure during the entire study (i.e., no births or deaths) and geographic closure within a survey (e.g., individuals do not move in or out of the plot during a 10-minute count). A full list of assumptions is provided in Appendix A. For

simplicity, we suppose that sample units are circular, fixed-radius plots commonly used in avian survey protocols. Wherever possible, we attempt to use notation similar to Chandler et al. (2011) and Amundson et al. (2014).

At each plot we assume a superpopulation of individuals, N_{super_s} , denoting the total number of individuals that could possibly be detected at plot s during the entire study period. We assume N_{super_s} to follow a probability mass function f (e.g., Poisson or negative binomial) with mean λ (denoted $f(N_{super_s}|\lambda)$), which could also be a function of covariates.

During a particular survey, t , only a proportion of individuals from the superpopulation will be present within the plot, which we denote as $N_{pres_{st}}$. Under the classical random temporary emigration model of Kendall et al. (1997), each member of the superpopulation will be present during survey t with probability $p_{p_{st}}$. We assume $N_{pres_{st}}$ follows a binomial probability mass function $h(N_{pres_{st}}|p_{p_{st}}, M_s)$, where $p_{p_{st}}$ could be modeled as a function of site- and survey-specific covariates.

Finally, only a proportion of individuals present at site s during survey t will be available for detection (e.g., produce a cue such as singing). The number of individuals that are available for detection, $N_{avail_{st}}$, then follows a binomial probability mass function $h(N_{avail_{st}}|p_{a_{st}}, N_{pres_{st}})$, where $p_{a_{st}}$ is the probability of availability. Again, $p_{a_{st}}$ can be a function of site and survey specific covariates.

Data structure and observation model

During each sampling occasion a single observer records the distance to a detected individual, r_i , $i = 1, 2, \dots, n$, following distance sampling protocols described in Buckland et al. (2001). Observers also record the sub-interval of first detection for each individual x_i , at which time the individual is removed from further counting during that sampling occasion (i.e., removal sampling; Farnsworth et al. 2002). The observed data are then counts of individuals at each site and sampling occasion, n_{st} , the distance of each individual from the observer, r_i , and the sub-interval of initial detection for each individual, x_i . Under this protocol, distance data provide information on p_d , time-to-removal data provide information on p_a , and repeated spatial and temporal surveys provide information on p_p .

To estimate p_a and p_d , we generally follow the integrated time-to-removal and distance sampling model described in Amundson et al. (2014). For time-to-removal data, let $\mathbf{m} = (m_1, m_2, \dots, m_K)$ be the vector of the number of initial detections in sub-interval k . Conditional on n , the vector \mathbf{m} has a multinomial distribution with conditional cell probabilities $\pi_{a_k}^+ = \pi_{a_k}/p_a$, where π_{a_k} is the probability of removal in sub-interval k , and $p_a = \sum_k \pi_{a_k}$ is the probability of being available in at least one sub-interval. Using the removal model, the probability of removal in sub-interval k is calculated as $\pi_{a_k} = a(1 - a)^{k-1}$, where a is the probability of availability during each sub-interval. For instance, the probability of first detection in occasion three is $a(1 - a)^2$, as the individual was not available on two occasions and detected on the third.

Similar to availability, detection probability is modeled conditional on detection. Here, detection probability, p_d , is assumed to be a declining function of distance to the observer. For example, the half-normal detection function for distance data is:

$$g(r) = \exp\left(-\frac{r^2}{2\sigma^2}\right)$$

where r is the radial distance and σ is the scale parameter of the half-normal function, which can be modeled as function of covariates on the log scale (Marques et al. 2007).

Although the model can be fit using continuous distance data, we develop our methods using $j = 1, 2, \dots, J$ discrete distance categories or bins. Discrete distance bins are commonly used to smooth inaccuracies in distance estimation and reduce the effects of animal movement in response to observers (Buckland et al. 2001). Let $\mathbf{b} = J + 1$ break points of the J distance bins. Then, detection probabilities can be derived by integrating $g(r)$ over j ,

$$\pi_{d_j} = \frac{2\pi \int_{b_j}^{b_{j+1}} g(r) r x}{A_j}$$

Where π_{d_j} is the probability of detecting an individual that is in distance bin j and A_j is the area of the area of distance bin j .

Assuming individuals are distributed uniformly around the sampling point (Appendix A), the probability of an individual occurring in distance bin j , ψ_j , is simply the proportion of the sample area within the j -th distance bin. Let y_j be the number of individuals detected in distance bin j and $\mathbf{y} = (y_1, y_2, \dots, y_J)$ denote the vector be the number of individuals

observed in each of the J distance bins. Conditional on n , the vector \mathbf{y} has a multinomial distribution with conditional cell probabilities $\pi_{d_j}^+ = \pi_{d_j}\psi_j/p_d$, where $\pi_{d_j}\psi_j$ is the probability of detecting an individual in distance bin d , and $p_d = \sum_j \pi_{d_j}\psi_j$ is the probability of detection in any distance bin.

Letting $f(N_{super_s}|\lambda)$ be Poisson, the full model can now be described as:

$$\begin{aligned}
 N_{super_s} &\sim \text{Poisson}(\lambda) \\
 N_{pres_{st}} &\sim \text{Binomial}(N_{super_s}, p_{p_{st}}) \\
 N_{avail_{st}} &\sim \text{Binomial}(N_{pres_{st}}, p_{a_{st}}) \\
 n_{st} &\sim \text{Binomial}(N_{avail_{st}}, p_{d_{st}}) \\
 \mathbf{m} &\sim \text{Multinomial}(\boldsymbol{\pi}_a^+) \\
 \mathbf{y} &\sim \text{Multinomial}(\boldsymbol{\pi}_d^+)
 \end{aligned}$$

With so many components and survey methods, this model has a number of assumptions, the primary assumptions are provided in Appendix A.

Density estimation

Density (D) can be estimated for the available-, present- and super-populations by dividing expected abundances by the plot area. The actual spatial extent of the superpopulation is unknown as some individuals will have activity centers outside of the plot (Chandler et al. 2011). Density estimates for the superpopulation are still provided for reference. Density for the populations of available, present, and superpopulation are denoted as D_{super} , D_{pres} , D_{avail} , respectively.

SIMULATION STUDY

Overview of simulation study

We developed a simulation study to evaluate model performance and the effects of variation in detection, availability, and presence probabilities on density estimates. The simulations mimicked a study design similar to our case study and other line-transect point counts.

We used the following specifications for all simulation scenarios, $S = 100$ 150-m radius plots divided into 15 10-m bins, $K = 4$, $T = 3$, and $M_s \sim \text{Poisson}(\lambda = 10.6)$, which corresponds to an expected superpopulation density of 1.5 individuals/ha. Presence probabilities, p_p , varied by two levels, high = 0.90 and low = 0.75. Availability probabilities, p_a , also varied by two levels, high = 0.90 and low = 0.75, with subsequent sub-interval probability of availability was approximately 0.29 and 0.54, respectively. We used a half-normal detection function with scale parameter $\sigma = 53.5$ or 84.0, resulting in detection probabilities (p_d) of approximately 0.25 and 0.50, respectively. All eight possible combinations of values were evaluated. We simulated and analyzed 100 datasets under each scenario. Mean relative bias and credible interval coverage were calculated for each parameter and density estimate.

Scenarios where the probability of presence or availability were 0.50 were also investigated. Estimates for p_p and superpopulation density were rarely identifiable, however, and results are not shown but examined further in the Discussion.

Models were fit using Markov-chain Monte Carlo (MCMC) methods implemented in a Bayesian framework using the software JAGS (Plummer 2003) accessed through R version 3.1.2 (R Development Core Team 2014), using the *rjags* (Plummer 2012) and *dclone* (Solymos 2010) packages. We ran three parallel Markov chains with 20,000 burn-in iterations and 200,000 post burn-in iterations. Chains were thinned by 50 to reduce the size of model output. Convergence was assessed using diagnostic plots and the Gelman-Rubin statistic (\hat{R} ; Gelman et al. 2013). We used vague priors, $\log(\lambda) \sim Normal(0,100)$, $\log(\sigma) \sim Uniform(0,10)$, and a and p_p independent $Uniform(0,1)$. We summarize posteriors of parameter estimates using the median and 2.5 and 97.5 percentiles (95% CRI). Density estimates are presented as posterior modes due to skewed posterior distributions for superpopulation estimates.

Simulation results

Relative bias of density estimates was low for all scenarios and never exceeded 11% (Figure 1). Superpopulation density estimates were relatively unbiased when the probability of detection was high, but showed either positive or negative bias when detection was low (Figure 1). Low detection probability also resulted in several extreme superpopulation density estimates, which were primarily a result of poorly estimated probability of presence (Figure 1; Table 1).

Median parameter estimates were generally unbiased and achieved nominal credible interval coverage (Table 1). Probability of presence was negatively biased, which was often a

result of left skewed posteriors and some simulated datasets with nearly non-identifiable probabilities (Table 1). Simulations with poorly identifiable probabilities were often obvious as densities estimates were abnormally high (Figure 1).

CASE STUDY

Overview and estimation

The Island Scrub-Jay is a species of management concern endemic to Santa Cruz Island, off the coast of southern California, USA (Curry and Delaney 2002). Recent work to estimate Island Scrub-Jay abundance and track population growth rates have focused on point transect distance sampling methods. Island-wide surveys are logistically challenging and involve single visit surveys to >300 points across the island (Sillett et al. 2012). In November 2011, a smaller scale but more concentrated study was conducted to evaluate the underlying assumptions regarding the components detection probability and subsequent effects on density estimates. In this study, data on Island Scrub-Jay density were collected using distance sampling methods, augmented with time-to-removal data, repeated at 97 sites on three occasions during a two-week period in November 2011. Surveys consisted of 10-minute point counts divided into four 2.5-minute intervals with a fixed distance radius of 150 m. For all counts, observers recorded the distance and first sub-interval of detection for observed individuals (removal sampling; Farnsworth et al. 2002). Distance data were discretized into 15 10-meter bins to the maximum distance of 150 m. In total, 467 Island Scrub-Jay observations were recorded during the survey period.

We fit our hierarchical modeling approach to estimate the three components of detection probability and Island Scrub-Jay density. Several reduced models were fit to compare density estimates across different sampling protocols, however reduced models only estimated a subset of densities (D_{super} , D_{pres} , D_{avail} , see Table 2). Specifically, we compared reduced models that analyzed (i) distance sampling data only, (ii) combined distance sampling and time-to-removal data, (iii) repeated count data, and (iv) combined distance sampling and repeated count data (Table 2).

MCMC methods for analysis of the case study were the same as those in the simulation study. Additionally, we evaluated model fit for the abundance, removal, and detection components of the model using Freeman-Tukey fit statistics and Bayesian P -values (Brooks et al. 2000).

Case study results

Bayesian P -values indicated adequate fit for abundance ($P = 0.88$) and removal components of the model ($P = 0.49$). The distance sampling detection component indicated a lack of fit ($P = 0.99$), primarily due to too many observations in the first two distance bins, 0-10 m and 10-20 m. Alternate detection functions and binning distances were investigated, however, model fit was not improved or results were unreasonably extreme (e.g., density estimates of >10 individuals per ha).

The combined detection probability for an individual in the superpopulation during a 10-minute survey was 0.18 (0.10 – 0.24; Figure 2). Median probability of presence was 0.75

(0.40 – 0.98; Figure 2). Availability probability in the 2.5-minute sub-interval was 0.47 (0.42 – 0.52), resulting in a 0.92 probability of being available at least once during the 10-minute survey given the individual was present (0.89 – 0.95; Figure 2). The probability of detection given availability and detection was 0.26 (0.24 – 0.29; Figure 2).

The superpopulation density estimate was 1.09 (0.94 – 2.33). Median density estimates for the available and present populations were similar across all surveys, ranging from 0.85 – 0.94, all of which were noticeably higher than the density of observed individuals (Figure 3).

Reduced models that estimated only one or two detection components provided similar density estimates as the full model (Table 3). In all scenarios, however, the reduced models estimated a subset of detection components and densities (Tables 2 and 3). Credible intervals were often smaller in the full model, which was likely due to information from a shared superpopulation (Table 3). The full model and repeated count model (i.e., *N*-mixture model) provided similar superpopulation density estimates, but credible intervals in the full model were slightly smaller (Table 3).

DISCUSSION

We presented a flexible approach to separate the components of detection probability and estimate density adjusted for each type of detection probability using spatially and temporally replicated distance sampling and time-to-removal data. Our model builds upon previous methods to estimate density, temporary emigration, and components of detection in

unmarked populations (Alldredge et al. 2007, Stanislav et al. 2010, Chandler et al. 2011, Amundson et al. 2014, Kéry and Royle 2015). Our approach unifies these models and accounts for sources of bias including temporary emigration (i.e., probability of presence), changes in availability, and imperfect detection.

In the context of distance sampling, the probability of availability and presence are often combined into a joint estimate of temporary emigration (Chandler et al. 2011, Kéry and Royle 2015). Definitions of these two processes, however, are noticeably different. First, individuals associated with a plot may move in and out of the plot between survey occasions (Chandler et al. 2011). Kéry and Royle (2015) call this process “spatial temporary emigration”, while our study followed the terminology in the detection probability literature and denoted this as p_p , the probability of presence. Second, individuals present in the plot may be hidden or unavailable available for detection, which Kéry and Royle (2015) call “random temporary emigration” and we denote as p_a , the probability of availability. These two types of temporary emigration cannot be separated using distance sampling alone.

Our integrated analyses uniquely identified these two processes and the simulation study demonstrated that the full model works well when detection probability components are relatively high. Unbiased estimates of superpopulation densities were, at times, poorly estimated and were non-identifiable when availability or presence probabilities were ≤ 0.50 . These results provide important study design considerations regarding the trade-offs of different sampling protocols and field methods (e.g., duration of survey versus number of repeated visits) and would be a useful area of further research.

In analyzing the Island Scrub-Jay data, we found density estimates of 0.85 – 0.95 individuals/ha, which are much higher than estimates of approximately 0.25 to 0.56 for a similar portion of the island in Sillett et al. (2012). One possible explanation for this disparity is that survey points in our study were in a small portion of the island known to have high Jay densities. Additionally, our results also highlight possible biases due to imperfect availability. The probability a Scrub-jay was available during a 10-minute survey was >0.90 , however, the median probability of availability in any 2.5-minute sub-interval was 0.47. Comparing surveys of different durations may therefore result in different density estimates, not because of changes in the population, but changes in the sampling protocol. For instance, deriving a per-minute availability indicates a 6-minute and 10-minute point count would estimate approximately 0.78 and 0.92 of the individuals present within the plot, respectively, if the probability of availability was not included.

The large, loud, and conspicuous behavior of Scrub-jays, and the fact that these birds may be attracted to humans, likely contributed to the high availability probability (>0.90) observed in this study. Species specific traits, such as behavior, size, vocalizations, and territory size can particularly influence availability probabilities and may confound changes true changes in density when not addressed. Overall, most studies will not regularly require the full suite of sampling methods as described herein. However, a single season dedicated to identifying the important components of detection can provide practitioners with valuable information for study design and comparisons of density estimates across years and species.

Separating these detection probability components in our hierarchical model also required the assumption of geographic closure during a survey (e.g., 10-minute point count). Severe violation of a geographical closure assumption will lead to large differences in density estimates of the available and present populations, as new birds moving into the plot during later sub-intervals are incorrectly interpreted as always present plot, but unavailable in the earlier intervals (i.e., low availability). Instead, our case study supported spatial temporary emigration across surveys, but geographical closure within a survey. An interesting extension to evaluate these assumptions would be to create a capture history with the explicit location (bearing and distance) and sub-interval of detection for each individual (e.g., time-of-detection; Alldredge et al. 2002). This spatial capture history would be similar to that required for a spatial-capture-recapture model (Royle et al. 2013), where the location of an individual is observed on multiple occasions allowing estimation of animal movement and home range centers.

Data collection protocols to separate all components of detection are often labor intensive and require additional expenses. We encourage researchers to identify the population and detection probabilities of primary interest *a priori* and consider the use of integrated methods to best address those objectives. Our results indicated that reduced models provided similar density estimates as the full model, but only estimated a subset of population components. Findings thus far are limited to a single species using a single data collection protocol. We therefore encourage future work with the fully integrated model that

investigates site-, survey-, and individual-level covariates, possible Markovian temporary emigration or availability, and comparisons across multiple species.

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Table 1. Simulation results showing the relative bias and credible interval coverage of median parameter estimates from 100 simulated datasets. Simulations included combinations of presence (high = 0.90, low = 0.75), availability (high = 0.90, low = 0.75), and detection (high = 0.50, low = 0.25). Probability of detection given availability and presence p_d is a function of the distance sampling scale parameter, σ . Detection probabilities of 0.50 and 0.25 are $\sigma = 84.0$ and 53.5, respectively.

Simulation values			Relative bias (coverage)			
Detection p_d (σ)	Availability p_{avail}	Presence p_{pres}	σ	p_{avail}	p_{pres}	$\log(\lambda)^a$
0.50 (84.0)	0.90	0.90	0.01 (0.92)	0.00 (0.90)	-0.06 (0.97)	0.03 (0.98)
0.50 (84.0)	0.90	0.75	0.01 (0.98)	0.00 (0.94)	0.00 (0.97)	0.01 (0.97)
0.50 (84.0)	0.75	0.90	0.01 (0.97)	0.01 (0.98)	-0.09 (0.93)	0.04 (0.92)
0.50 (84.0)	0.75	0.75	0.01 (0.95)	0.00 (0.94)	-0.06 (0.94)	0.03 (0.96)
0.25 (53.5)	0.90	0.90	0.00 (0.93)	0.00 (0.92)	-0.20 (0.95)	0.11 (0.88)
0.25 (53.5)	0.90	0.75	0.01 (0.97)	0.00 (0.94)	-0.09 (0.97)	0.06 (0.96)
0.25 (53.5)	0.75	0.90	0.01 (0.95)	0.00 (0.97)	-0.22 (0.96)	0.11 (0.92)
0.25 (53.5)	0.75	0.75	0.01 (0.92)	0.00 (0.94)	-0.19 (0.96)	0.10 (0.97)

^a λ was set at 10.6, which is a superpopulation density of 1.5 individuals per hectare.

Table 2 Comparison of identifiable densities (X) using distance sampling (DS), time-to-removal (TTR), repeated counts (RC), and integrated methods. Estimable densities include individuals available for detection (Available), individuals present during a survey (Present), and individuals that used the plot across the entire season (Super-pop).

Population	Method				
	DS	DS & TTR	RC	DS & RC	DS & TTR & RC
Available	X	X		X	X
Present		X			X
Super-pop.			X	X	X

Table 3. Mode and 95% credible intervals for Island Scrub-Jay density estimates (individuals per hectare). Data were modeled using distance sampling (DS), time-to-removal (TTR), repeated counts (RC), and integrated methods. Density inferences vary by method and include individuals available for detection (Available), individuals present during a survey (Present), and all individuals that used the plot across the entire season (Super-pop). Density estimates are survey specific (three surveys) with one overall superpopulation. Confounded density estimates are denoted by (-).

Population (survey num.)	DS	DS & TTR	RC	DS & RC	DS & TTR & RC
Available (1)	0.94 (0.76-1.18)	0.90 (0.77-1.08)	(-)	0.86 (0.76-0.99)	0.87 (0.76-0.99)
Available (2)	0.75 (0.59-0.97)	0.71 (0.60-0.86)	(-)	0.84 (0.74-0.97)	0.85 (0.74-0.97)
Available (3)	0.84 (0.69-1.06)	0.95 (0.80-1.12)	(-)	0.87 (0.77-0.99)	0.87 (0.76-0.99)
Present (1)	(-)	0.98 (0.84-1.17)	(-)	(-)	0.94 (0.82-1.07)
Present (2)	(-)	0.77 (0.65-0.94)	(-)	(-)	0.93 (0.80-1.06)
Present (3)	(-)	1.03 (0.87-1.22)	(-)	(-)	0.94 (0.83-1.07)
Super-pop.	(-)	(-)	1.08 (0.83-2.38)	1.07 (0.91-2.47)	1.09 (0.94-2.33)

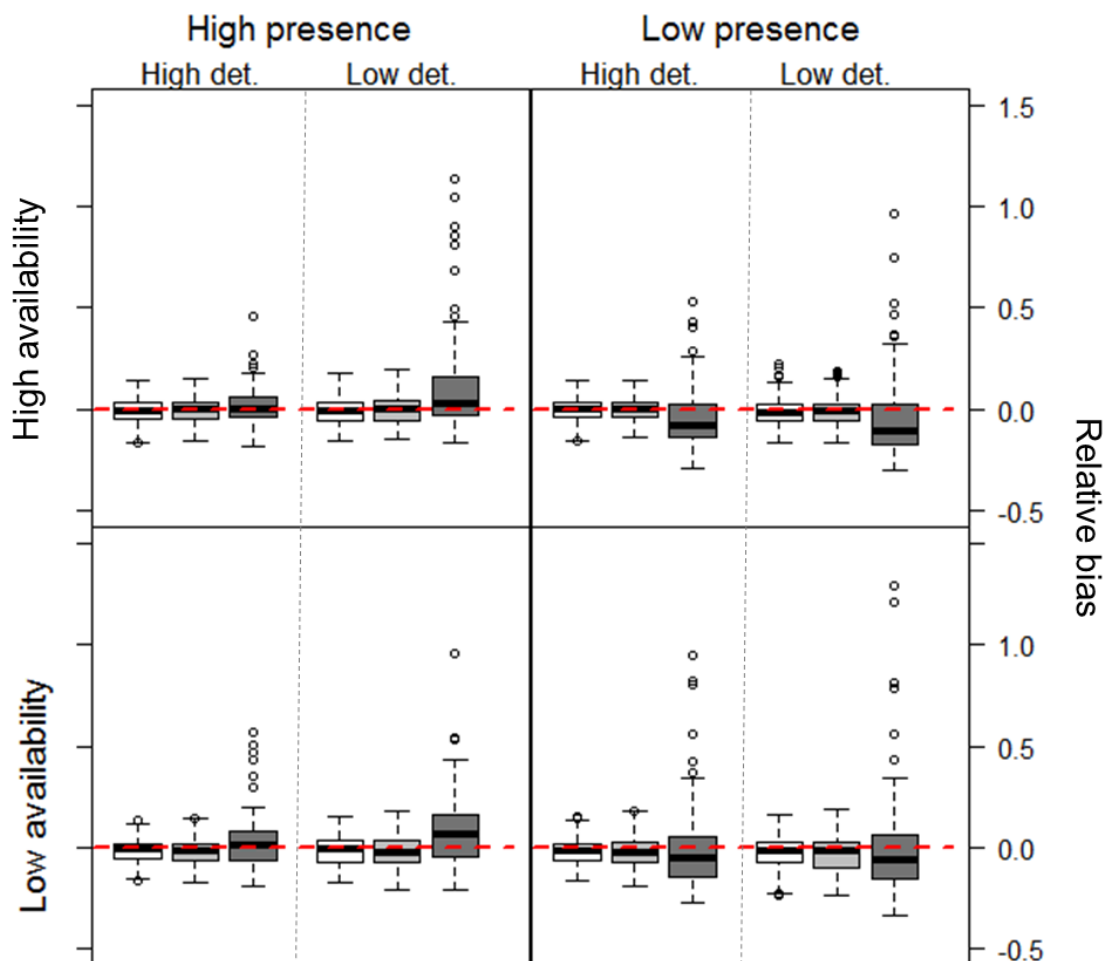


Figure 1. Simulation results showing the relative bias of mode density estimates (\hat{D}) from 100 simulated datasets. Density estimates include individuals available for detection (white), individuals present during a survey (light grey), and individuals that used the area across the entire season (i.e., superpopulation; dark grey). Simulations included combinations of presence (high = 0.90, low = 0.75), availability (high = 0.90, low = 0.75), and detection (high = 0.50, low = 0.25) probabilities. The black line in the middle of the box is the median value, the outlines are the interquartile range, whiskers are values within ± 1.5 times the interquartile range, and outliers are beyond that range. Relative bias = $((\hat{D} - D)/D) \times 100$.

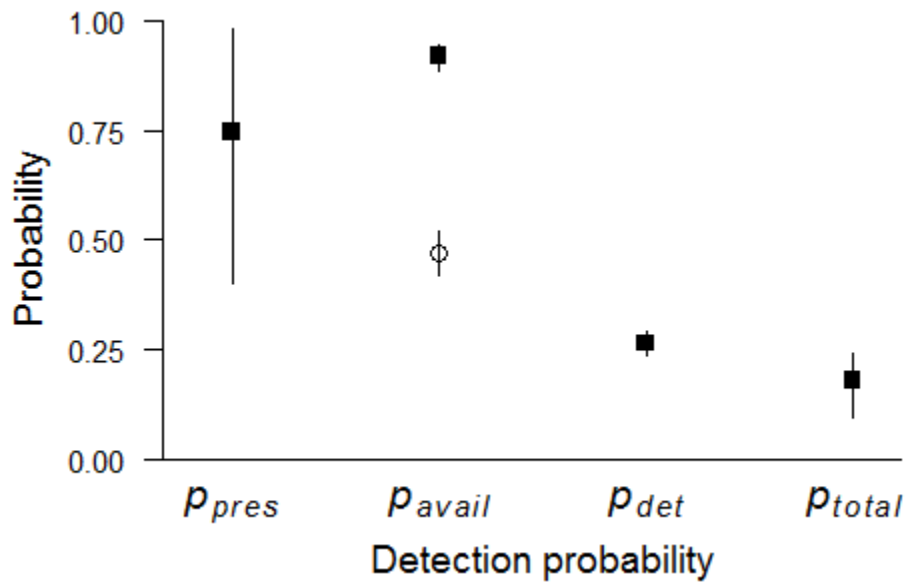


Figure 2. Components of detection probability from surveys of Island Scrub Jays. Detection probability includes the probability of presence during a survey p_{pres} , availability during the 10-minute survey given presence p_{avail} , and detection given availability and presence p_{det} . The total probability of detection, p_{total} , is the product of the three components. The hollow circle denotes availability probability for a single 2.5-minute sub-interval. Error bars are 95% credible intervals.

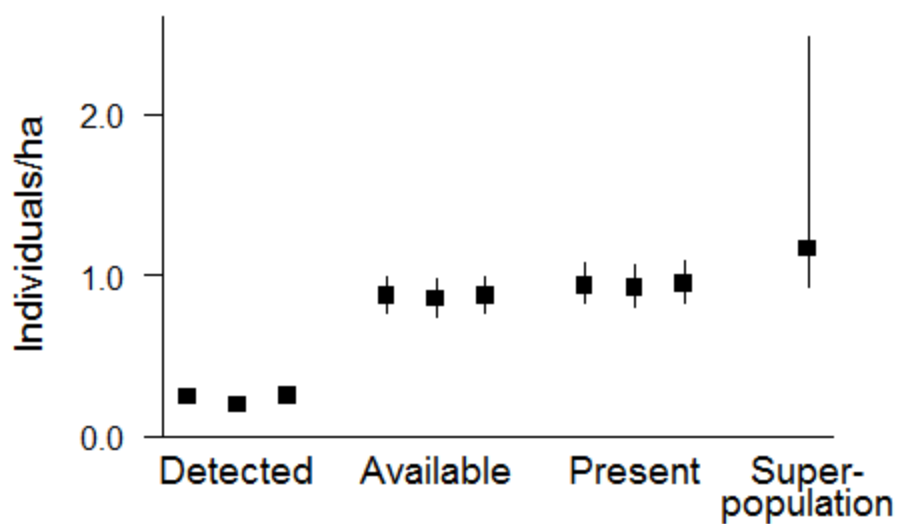


Figure 3. Island Scrub Jay number of individuals per ha observed (Detected) and density estimates (mode and 95% credible intervals). Density estimates include individuals available for detection (Available), individuals present during a survey (Present), and individuals that used the area across the entire season (Super-population). Density estimates are survey specific (three surveys) with one overall superpopulation.

GENERAL CONCLUSIONS

Estimating abundance and density are critical to many areas of fundamental and applied ecology. Rapid environmental change over the past few decades has given a new urgency and relevance not only to programs that monitor and track population status but also to the demands of continued data collection. As conservation and management face new challenges, the role of data integration will become increasingly important, providing unique and innovative approaches to estimate abundance, demographic parameters, and identify important factors driving population dynamics.

The goal of integrated modeling approaches is to synthesize multiple data sources by utilizing complementary information, dependencies across surveys, and the strengths of each data set (Schaub and Abadi 2012, Banerjee et al. 2014, Giraud et al. 2015). Anticipated benefits include improved parameter estimation, broader inferences over spatial or temporal scales, and enhanced understanding of multiple ecological processes (Besbeas et al. 2005). Integrated analysis methods developed and applied in this dissertation demonstrate how data integration can be used to address several common challenges in ecological studies, including low detection probability, data collection using different protocols and spatial extents, and multiple sources of bias.

In Chapter 2, integrating live recapture and dead recovery data in a study of upper Columbia River steelhead provided improved precision of survival estimates, survival estimates across larger spatial scales, information on where fish were consumed by birds,

and, based on our simulation study, achieved equal levels of precision with only half the sample size of mark-recapture methods. Additionally, the integrated framework developed therein can easily be expanded to investigate covariates effects, incorporate additional sources of data, and extended to other mark-recapture studies interested in integrating auxiliary information.

Chapter 3 described a multivariate spatial model to estimate animal abundance from multiple sources of spatially overlapping, but misaligned data. I applied these methods to combine distance sampling surveys and strip-transect surveys to estimate marine bird abundance. General methods, however, are applicable to a variety of abundance protocols and studies interested in combining datasets of different quality and spatial scales (e.g., mark-recapture [Otis et al. 1978], repeated counts [Royle 2004], double observer [Nichols et al. 2000]).

In chapter 4, I presented a flexible approach to separate the components of detection probability and estimate density adjusted for each type of detection probability using spatially and temporally replicated distance sampling and time-to-removal data. Separation of detection components allowed density estimation for multiple population levels, including the densities of individuals available for detection, individuals present in the sampling plot, and the superpopulation of individuals that use the plot. This approach unifies previous methods to estimate density, temporary emigration, and components of detection in unmarked populations (Chandler et al. 2011, Amundson et al. 2014, Kéry and Royle 2015).

Findings from these chapters provide several common observations regarding the use of integrated analysis methods in ecological applications. First, integrated analysis improved parameter precision and accuracy relative to single source analysis. Increased precision was particularly noticeable when specific impediments in single source data (e.g., low detection probability, reduced spatial coverage) were supplemented by the inclusion of additional data directly addressing those deficiencies.

Second, simulation studies provided a flexible approach to verify results and evaluate sensitivity of analysis to changes in data quality and quantity (Abadi et al. 2010). For instance, the efficacy of different sampling protocols can be evaluated by simulating the expected types of data each protocol may contribute. For instance, simulation studies in Chapter 2 indicated that increasing the number of tagged and release fish would not provide the same benefits as efforts to increase encounter rates after release. Similarly, simulation studies in Chapter 4 demonstrated the need to achieve relatively high rates of detection to estimate unbiased superpopulation abundance, however, there were numerous trade-offs for simpler study designs if monitoring superpopulation abundance was not the study objective.

Third, parameter confounding becomes an increasing problem as integrated models become more complex (Abadi et al. 2010). In principle, analysts are free to specify any number of large models to address ecological hypotheses, however, there is no guarantee that parameters will be identifiable (Gimenez et al. 2004, Gimenez et al. 2009). Two types of parameter confounding often arise in integrated analysis: intrinsic and extrinsic identifiability (Kéry and Schaub 2012). Intrinsic identifiability occurs in parameter redundant models,

where at least one parameter is unidentifiable in the model (Catchpole et al. 2001). For instance, in the fully time-dependent Cormack-Jolly-Seber mark-recapture model, the last survival and detection probability cannot be separately estimated without some constraint on the model. Alternatively, extrinsic non-identifiability occurs when two or more parameters are highly correlated and there is insufficient information in the data to separate the effects of each parameter (Schaub et al. 2007, Abadi et al. 2010). Here, the model can algebraically estimate the parameters, but insufficient data are available to separate components of the model (Bailey et al. 2010). For instance, simulation studies in Chapter 4 indicated that high probabilities of availability or presence (e.g., >0.75) are required to estimate superpopulation abundances.

Finally, although applications of integrated analyses are diverse, methods are unified through a basic three step approach: (1) development of a state model, (2) formulating the component likelihoods for all available datasets, and (3) constructing the joint likelihood of all datasets combined (Besbeas et al. 2003, Schaub and Abadi 2010, Maunder and Punt 2013).

Integrated analyses are intuitively superior to single-source or multi-step analyses. Nevertheless, practitioners should consider and even question whether the use of integrated analyses is justified. Findings from this dissertation support previous suggestions, whereby the use of integrated analysis may be particularly beneficial when (i) information on a single state process is available in multiple data sources, (ii) accurate estimates of uncertainty are important for management decisions, and (iii) the spatial or temporal scales of interest are

beyond the scope of any one study (Besbeas et al. 2005, Schaub and Abadi 2010, Maunder and Punt 2013). Ultimately, the optimal study design will depend on numerous factors. However, the integration of innovative field methods coupled with analytical approaches that utilize complementary data sources, provide numerous opportunities to improve estimation of important vital rates and monitor population status.

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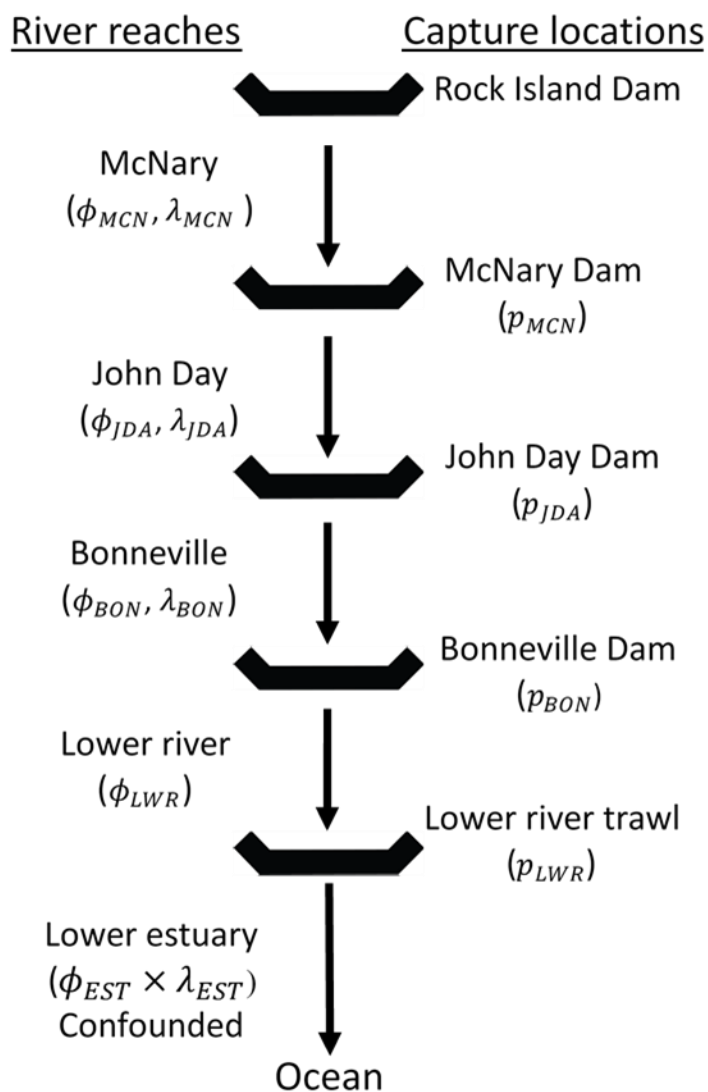
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Parameter	True value	CJS			MRR		
		Median	Bias	Coverage	Median	Bias	Coverage
ϕ_1	0.65	0.69	0.04	0.91	0.66	0.01	0.97
ϕ_2	0.80	0.74	-0.06	0.87	0.77	0.03	0.95
ϕ_3	0.80	0.68	-0.12	0.82	0.79	0.01	0.99
ϕ_4	0.70	-	-	-	0.68	0.02	0.99
p_1	0.15	0.14	-0.01	0.99	0.15	0.00	0.96
p_2	0.15	0.16	0.01	0.99	0.16	0.01	0.96
p_3	0.15	0.19	0.04	0.86	0.16	0.01	0.99
p_4	0.05	-	-	-	0.06	0.01	0.99
λ_1	0.20	-	-	-	0.22	0.02	0.97
λ_2	0.05	-	-	-	0.07	0.02	0.97
λ_3	0.05	-	-	-	0.03	0.02	0.97
σ_{p_1}	0.04	0.05	0.01	0.98	0.04	0.00	0.99
σ_{p_2}	0.04	0.05	0.01	0.96	0.04	0.00	0.98
σ_{p_3}	0.04	0.05	0.01	0.99	0.04	0.00	1.00
σ_{p_4}	0.01	-	-	-	0.02	0.01	1.00
σ_{λ_1}	0.05	-	-	-	0.06	0.01	1.00
σ_{λ_2}	0.01	-	-	-	0.03	0.02	0.92
σ_{λ_3}	0.01	-	-	-	0.02	0.01	1.00

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Parameter ¹	Year						
	2008	2009	2010	2011	2012	2013	2014
Recapture							
p_{MCN}	0.14 (0.10-0.19)	0.17 (0.11-0.25)	0.08 (0.06-0.10)	0.08 (0.05-0.14)	0.11 (0.07-0.16)	0.10 (0.07-0.19)	0.08 (0.06-0.13)
p_{JDA}	0.19 (0.14-0.24)	0.15 (0.09-0.25)	0.08 (0.05-0.14)	0.24 (0.18-0.30)	0.15 (0.11-0.21)	0.08 (0.06-0.10)	0.07 (0.04-0.11)
p_{BON}	0.14 (0.09-0.22)	0.17 (0.13-0.23)	0.30 (0.23-0.37)	0.06 (0.03-0.11)	0.14 (0.09-0.23)	0.18 (0.12-0.27)	0.17 (0.12-0.25)
p_{LWR}	0.04 (0.02-0.08)	0.06 (0.04-0.09)	0.05 (0.03-0.07)	0.04 (0.02-0.06)	0.06 (0.03-0.10)	0.07 (0.04-0.11)	0.06 (0.04-0.12)
σ_{MCN}	0.05 (0.03-0.11)	0.07 (0.04-0.18)	0.02 (0.01-0.06)	0.05 (0.03-0.12)	0.03 (0.01-0.10)	0.05 (0.02-0.15)	0.04 (0.02-0.10)
σ_{JDA}	0.05 (0.03-0.11)	0.09 (0.05-0.23)	0.05 (0.03-0.14)	0.06 (0.03-0.13)	0.04 (0.01-0.10)	0.01 (0.00-0.04)	0.03 (0.01-0.09)
σ_{BON}	0.06 (0.03-0.17)	0.03 (0.00-0.09)	0.07 (0.01-0.15)	0.04 (0.02-0.11)	0.07 (0.02-0.19)	0.06 (0.01-0.19)	0.06 (0.02-0.15)
σ_{LWR}	0.02 (0.01-0.09)	0.01 (0.00-0.04)	0.01 (0.00-0.03)	0.01 (0.00-0.03)	0.01 (0.00-0.05)	0.01 (0.00-0.07)	0.02 (0.00-0.10)

CHAPTER 2 - Appendix C (continued)

Recovery

λ_{MCN}	0.22 (0.15-0.35)	0.21 (0.16-0.28)	0.22 (0.16-0.32)	0.22 (0.16-0.35)	0.16 (0.11-0.24)	0.21 (0.10-0.42)	0.14 (0.09-0.23)
λ_{JDA}	0.04 (0.02-0.12)	0.05 (0.02-0.12)	0.04 (0.01-0.09)	0.04 (0.01-0.11)	0.04 (0.01-0.17)	0.04 (0.01-0.16)	0.13 (0.05-0.30)
λ_{BON}	0.03 (0.01-0.13)	0.02 (0.00-0.28)	0.01 (0.00-0.22)	0.01 (0.00-0.11)	0.02 (0.00-0.11)	0.02 (0.00-0.07)	0.01 (0.00-0.04)
σ_{MCN}	0.09 (0.04-0.24)	0.05 (0.01-0.13)	0.02 (0.00-0.12)	0.03 (0.00-0.16)	0.04 (0.00-0.13)	0.12 (0.03-0.39)	0.04 (0.00-0.16)
σ_{JDA}	0.02 (0.01-0.13)	0.02 (0.00-0.12)	0.01 (0.00-0.08)	0.01 (0.00-0.12)	0.01 (0.00-0.12)	0.02 (0.00-0.30)	0.05 (0.00-0.27)
σ_{BON}	0.02 (0.00-0.23)	0.01 (0.00-0.15)	0.00 (0.00-0.05)	0.00 (0.00-0.06)	0.01 (0.00-0.12)	0.01 (0.00-0.10)	0.00 (0.00-0.07)

CHAPTER 3 - Appendix A. Median parameter estimates (95% credible interval) predicting loon abundance and detection during December 2012 surveys. Modeling approaches integrated boat and aerial data (Integrated), incorporated aerial data as a constructed covariate (Combined), or used only boat data (Boat). Habitat covariates included distance to shore (DTS), salinity, and sea surface temperature (SST). The Combined model included an additional constructed covariate (Aerial). See Methods for complete model description.

Parameter	Integrated	Combined	Boat
Cluster abundance (log scale)			
β_{01} (<i>Boat intercept</i>)	-0.31 (-0.86 - 0.17)	-0.30 (-0.74 - 0.08)	-0.11 (-0.42 - 0.16)
β_{02} (<i>Aerial intercept</i>)	-1.23 (-1.89 - -0.54)	-1.00 (-1.25 - -0.79)	-
β_1 (<i>DTS</i>)	-0.89 (-1.39 - -0.38)	-0.05 (-0.71 - 0.71)	-1.39 (-1.77 - -1.02)
β_2 (<i>SST</i>)	-0.29 (-0.55 - -0.03)	-0.45 (-0.76 - -0.12)	-0.64 (-0.91 - -0.40)
β_3 (<i>SAL</i>)	0.10 (-0.78 - 0.94)	-0.34 (-1.14 - 0.34)	1.07 (0.75 - 1.40)
β_4 (<i>Aerial</i>)	-	1.67 (0.97 - 2.60)	-
σ_1 (<i>Boat overdispersion SD</i>)	0.58 (0.06 - 0.95)	0.65 (0.16 - 1.02)	1.10 (0.89 - 1.38)
σ_2 (<i>Aerial overdispersion SD</i>)	1.11 (0.97 - 1.27)	1.11 (0.97 - 1.27)	-
Σ_{11} (<i>Boat spatial residual SD</i>)	1.75 (1.10 - 2.45)	-	-
Σ_{22} (<i>Aerial spatial residual SD</i>)	0.99 (0.67 - 1.39)	1.07 (0.77 - 1.45)	-
$\frac{\Sigma_{12}}{\sqrt{\Sigma_{11}\Sigma_{22}}}$ (<i>Spatial correlation</i>)	0.75 (0. -23 - 0.93)	-	-
Detection (distance sampling)			
σ_{calm}	230 (212 - 252)	230 (211 - 252)	232 (213 - 253)
σ_{rough}	276 (232 - 351)	280 (233 - 357)	270 (227 - 335)

CHAPTER 3 - Appendix B. Median parameter estimates (95% credible interval) predicting loon abundance and detection during March 2013 surveys. Modeling approaches integrated boat and aerial data (Integrated), incorporated aerial data as a constructed covariate (Combined), or used only boat data (Boat). Habitat covariates included distance to shore (DTS), salinity, and sea surface temperature (SST). The Combined model included an additional constructed covariate (Aerial). See Methods for complete model description.

Parameter	Integrated	Combined	Boat
Cluster abundance (log scale)			
β_{01} (Boat intercept)	-0.04 (-0.62 - 0.46)	0.38 (0.10 - 0.62)	0.39 (0.14 - 0.63)
β_{02} (Aerial intercept)	-1.47 (-1.78 - -1.18)	-1.31 (-1.59 - -1.06)	-
β_1 (DTS)	-0.74 (-1.15 - -0.35)	-0.38 (-0.71 - -0.07)	-0.31 (-0.61 - -0.02)
β_2 (SST)	0.58 (0.19 - 1.04)	0.08 (-0.29 - 0.46)	0.06 (-0.29 - 0.42)
β_3 (SAL)	0.18 (-0.35 - 0.73)	-0.20 (-0.53 - 0.12)	-0.11 (-0.41 - 0.19)
β_4 (Aerial)	-	-0.34 (-0.70 - -0.04)	-
σ_1 (Boat overdispersion SD)	0.43 (0.05 - 0.77)	0.91 (0.69 - 1.14)	0.97 (0.78 - 1.20)
σ_2 (Aerial overdispersion SD)	0.74 (0.56 - 0.92)	0.72 (0.53 - 0.91)	-
Σ_{11} (Boat spatial residual SD)	1.64 (1.07 - 2.17)	-	-
Σ_{22} (Aerial spatial residual SD)	1.38 (0.99 - 1.81)	1.65 (1.28 - 2.07)	-
$\frac{\Sigma_{12}}{\sqrt{\Sigma_{11}\Sigma_{22}}}$ (Spatial correlation)	0.02 (-0.45 - 0.49)	-	-
Detection (distance sampling)			
σ_{calm}	174 (155 - 197)	174 (155 - 196)	173 (155 - 195)
σ_{rough}	174 (157 - 195)	174 (158 - 194)	174 (158 - 194)

CHAPTER 4 – Appendix A. List of primary assumptions for the fully integrated distance sampling, time-to-removal, and repeated count model.

Assumption
1. Animals on the point are detected with certainty (i.e., $g(r) = 1.0$)
2. Animals are detected at their initial location prior to any movement
3. Animals are distributed independently of the points
4. Distances are measured accurately
5. Individuals are identified without error (i.e., no double-counting)
6. Observations are independent
7. There is no movement in or out of the plots during a survey (i.e., geographical closure during a survey)
8. p_p , p_a , and p_d are independent
9. The distribution of N_{super_s} is adequately described by the chosen parametric form (e.g., Poisson)
