



# **Integrated Population Models and Habitat Metrics for Wildlife Management**

**Thèse**

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# RÉSUMÉ

La gestion des espèces est entièrement dépendante de notre capacité à évaluer les décisions de gestion et de les corriger si nécessaire. Dans un monde idéal les gestionnaires auraient une connaissance extensive et mécanistique des systèmes qu'ils gèrent et ces connaissances seraient mises à jour de façon continue. Dans la réalité, les gestionnaires doivent gérer les populations et développer des objectifs de populations en dépit de leur connaissance imparfaites et des manques de données chronique. L'émergence de nouveaux outils statistiques ouvrent toutefois la porte à de nouvelles possibilités ce qui permet une gestion plus proactive de la faune. Dans le Chapitre 1, j'ai évalué l'efficacité de modèles intégrés de populations (MIP) à combler des lacunes dans notre connaissance en présence de données limitées et de modèles de populations mal spécifiés. J'ai démontré que les MIP peuvent maintenir une précision élevée et présenter un biais faible, et ce dans une large gamme de conditions. Dans le chapitre 2, j'ai développé une approche de MIP qui inclut des effets aléatoires entre les différentes populations. J'ai constaté que les effets aléatoires permettent améliorer considérablement les performances des algorithmes d'optimisation, produisent des estimations raisonnables et permettent même d'estimer les paramètres pour les populations avec des données très limitées. J'ai par la suite appliqué le modèle à 51 unités de gestion du Wapiti en Idaho, USA afin de démontrer son application. La viabilité des populations à long terme est généralement réalisé à grâce à des manipulations d'habitat qui sont identifiées grâce à des méthodes de sélection des ressources. Les méthodes basées sur la sélection des ressources assume cependant que l'utilisation disproportionnée d'une partie du paysage reflète la volonté d'un individu de remplir une partie de son cycle biologique. Toutefois, dans le troisième chapitre j'ai démontré que des simples mesures d'habitat sont à mieux de décrire la variation dans la survie des Wapitis. Selon, mes résultats, la variation individuelle dans la sélection des habitats était le modèle qui expliquait le mieux la corrélation entre les habitats et le succès reproducteur et que les coefficients de sélection des ressources n'étaient pas corrélés à la survie.



# ABSTRACT

Successful management of harvested species critically depends on an ability to predict the consequences of corrective actions. Ideally, managers would have comprehensive, quantitative and continuous knowledge of a managed system upon which to base decisions. In reality, wildlife managers rarely have comprehensive system knowledge. Despite imperfect knowledge and data deficiencies, a desire exists to manipulate populations and achieve objectives. To this end, manipulation of harvest regimes and the habitat upon which species rely have become staples of wildlife management. Contemporary statistical tools have potential to enhance both the estimation of population size and vital rates while making possible more proactive management. In chapter 1 we evaluate the efficacy of integrated population models (IPM) to fill knowledge voids under conditions of limited data and model misspecification. We show that IPMs maintain high accuracy and low bias over a wide range of realistic conditions. In recognition of the fact that many monitoring programs have focal data collection areas we then fit a novel form of the IPM that employs random effects to effectively share information through space and time. We find that random effects dramatically improve performance of optimization algorithms, produce reasonable estimates and make it possible to estimate parameters for populations with very limited data. We applied these random effect models to 51 elk management units in Idaho, USA to demonstrate the abilities of the models and information gains. Many of the estimates are the first of their kind. Short-term forecasting is the focus of population models, but managers assess viability on longer time horizons through habitat. Modern approaches to understanding large ungulate habitat requirements largely depend on resource selection. An implicit assumption of the resource selection approach is that disproportionate use of the landscape directly reflects an individual's desire to meet life history goals. However, we show that simple metrics of habitat encountered better describe variations in elk survival. Comparing population level variation through time to individual variation we found that individual variation in habitat used was the most supported model relating habitat to a fitness component. Further, resource selection coefficients did not correlate with survival.



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## General Introduction

Successful management of harvested species critically depends on an ability to predict the consequences of corrective actions. Ideally, managers would have comprehensive, quantitative and continuous knowledge of a managed system upon which to base decisions that seek to meet clearly defined, publicly agreed upon objectives (Lindblom 1959; Bailey 1982). In reality, wildlife managers rarely have comprehensive system knowledge. Limited data and imperfect system knowledge result from several factors. First, wildlife populations are notoriously difficult to count. Second, monitoring programs cannot produce ideal data sets because of constraints imposed by logistical and budgetary realities. Third, wildlife population dynamics are complex, variable and subject to multiple stressors that have complex interacting effects. Despite imperfect knowledge and data deficiencies, a desire, and—in some cases—a legal obligation exists to manipulate populations and achieve objectives. To this end, manipulation of harvest regimes and the habitat upon which species rely have become staples of wildlife management.

Proactive species management depends on an ability to identify a preferred course of action before implementation. Consequently, proactive management suggests defining a model with strong predictive abilities. The objective of the model then is to exemplify the principle of parsimony while making accurate predictions and accounting for uncertainty in biological and observational processes (Nichols & Williams 2006). A desirable secondary objective of the model might include identifying causes of increase or decline, but this goal typically outstrips the data available to many species monitoring programs. Historically, many management programs relied on trend detection to incite action. However, trend detection relegates management to a reactionary posture while proactive management strategies aim to maintain species near management goals in lieu of continually responding to large deviations from objectives.

Big game management in the Rocky Mountain West, USA, has become a contentious topic steeped in litigation and public opinion. Much of the debate surrounds the re-introduction of the gray wolf (*Canis lupus*) and the consequences for socially and economically

important ungulate species, in particular elk (*Cervus elaphus*). Nowhere is this more apparent than in Idaho. Approximately 78,000-84,000 hunters enjoy elk hunting in Idaho each year. Elk hunters generate approximately 150 million dollars in annual revenue, which represents the largest single financial contribution from the exploitation of any one species (Cooper *et al.* 2002). Managers strive to meet management objectives and maintain a harvestable surplus in the face of uncertainty, but the roles of multiple interacting factors in regulating or limiting elk populations remain undefined despite a large body of research.

Having demonstrated a desire to pursue proactive management, chapters 1 and 2 address the feasibility of filling knowledge voids using integrated population models (IPM). IPM's provide a particularly powerful approach to population modeling by piecing together disparate sources of data (Besbeas *et al.* 2002; White & Lubow 2002; Brooks, King & Morgan 2004; Conn *et al.* 2008; Schaub & Abadi 2011). Typical sources of data may include aerial counts, radio-tagging encounter histories, productivity indices, harvest surveys and environmental data. By combining all or several of these sources of data into one analysis, it is possible to obtain more robust (and self-consistent) parameter estimates that fully reflect the information available and the true state of the system (Besbeas *et al.* 2002). A synthetic approach is desirable because analyzing demographic rates in isolation ignores dependencies among rates that produce observed outcomes (Baillie 1991). Other advantages of integrated approaches are the ability to estimate latent or unobserved quantities (Abadi *et al.* 2010b; Schaub *et al.* 2010), increased precision of parameter estimates and so-called honest accounting of error (Besbeas *et al.* 2002; Clark & Bjørnstad 2004). Further IPM's provide a biologically, if not legally, defensible basis for management actions and more efficient allocation of scarce resources. The framework's flexibility accommodates the many complexities inherent to population monitoring and allows for mechanistic linkages between population size and demographic processes. Last, the framework has withstood public scrutiny and proven effective within the context of collaborative structured decision-making (Freddy *et al.* 2004; Thompson 2014).

Short-term forecasting is the focus of population models, but managers assess viability on longer time horizons through habitat. Modern approaches to understanding large ungulate

habitat requirements largely depend on resource selection functions (RSF, (Manly, McDonald & Thomas 1993). An implicit assumption of the RSF approach is that disproportionate use of the landscape directly reflects an individual's desire to meet life history goals. However, recent evidence suggests that animals may not employ the "best" strategy that results in maximized fitness (Arlt & Pärt 2007; DeCesare *et al.* 2013). Several ecological hypotheses suggest the existence of non-ideal habitat selection strategies. Should habitat selection models not remain faithful to individual performance their application to species management could result in misallocation of resources and failure to meet objectives. The third chapter addresses this idea by evaluating estimates of resource selection with survival models.

Harvest and habitat represent two foundational components of species management. Through the combination of modern statistical techniques and ecological knowledge, the following document enhances our understanding of current elk population models and dynamics. The last chapter then tests a critical assumption of habitat models, which illuminates their applicability to long-term assessments of population viability.



# Chapter 1. Evaluating Bias, Accuracy and Precision when Fitting Population Models to Limited Data

## Résumé

Les gestionnaires de la faune doivent définir des objectifs de populations et travailler à la gestion de ces populations, et ce indépendamment de la disponibilité des données. La gestion des espèces est une tâche assujettie à des contraintes de temps et devrait donc bénéficier du développement d'analyses quantitatives et de modèles. Les cadres de modélisation formelles fournissent un moyen de synthétiser les données tout en tenant compte des nuisances caractéristiques des données, ce qui augmente l'accessibilité des données et l'efficacité de la gestion tout en décrivant l'état d'un système et l'état des connaissances du système. Une approche particulièrement puissante pour la modélisation des populations qui consiste à assembler plusieurs sources de données disparates est d'utiliser un modèle de population intégré (PMI). Les données disponibles pour la modélisation des populations sont toutefois généralement perçues comme étant top limité pour les PMI. De plus les données disponibles peuvent avoir un couvrir des espaces ou des séquences de temps disparate. Pour surmonter ces problèmes, nous avons développé une approche nouvelle qui permet le partage d'information à travers le temps et l'espace grâce à l'utilisation d'effets aléatoires dans le modèle. Nous avons utilisé la sélection de modèles afin de comparer différents scénarios qui pourraient expliquer variation des taux démographiques dans le temps ou dans l'espace. Le modèle qui a tenu le recrutement constant et la survie des adultes constante temporellement, mais variable spatialement a reçu le plus de support. À l'échelle de l'état, les modèles qui ont reçu le plus de support suggèrent que la survie des a femelles adultes a oscillé autour de 0.85 (SD = 3.7E-4), la survie des mâles a oscillé autour de 0.61 (SD = 2.0E-3) tandis que le recrutement a été presque constant à 0.33 (SD = 1.3E-3). Compte tenu de nos résultats, la survie des adultes a plus de chances d'affecter la dynamique des populations de Wapiti en Idaho que les variations dans le recrutement. Les variations dans la survie des adultes sont probablement

attribuables aux fluctuations dans la récolte. L'utilisation des PMI s'appuyant sur l'utilisation d'effets aléatoires nous a permis de combiner plusieurs sources de données et nous a permis d'augmenter la précision des estimations, tout en nous permettant de traiter les données manquantes et les nombreuses particularités de notre jeu de données.

## **Abstract**

Estimation of demographic rates and population size is central to the study of ecology and species management. Combining such estimates with matrix projection models allows researchers to simulate population dynamics. However, these problems are better framed as matters of parameters estimation. Inverse matrix models allow estimation of demographics rates and abundance from a time-series of observations. Integrated population models build upon inverse methods to facilitate the use of multiple sources of data while fitting model parameters. Interest in applying these methods to real life scenarios motivated this study in which we used simulation to evaluate the performance of inverse methods under conditions of missing data and model misspecification. To emulate low frequency data collection we simulated data according to five frequencies of data collection, zero to four years between observations. In addition to missing data, we also simulated three scenarios of model misspecification using linear trends and stochastic variation. We then fit inverse matrix models and integrated population models to aerial survey and telemetry data on elk in Idaho, USA. Results from simulations indicated adequate accuracy, precision and bias from inverse matrix methods regardless of data collection frequency or model misspecification. Furthermore, model estimates were most sensitive to misspecification involving adult female survival. Fitting inverse and integrated population models to elk data resulted in similar estimates of demographic rates and abundance. These estimates are the first of their kind for a majority of the administrative units considered. Our results suggest that fitting population models to limited noisy data is not only possible, but under many circumstances will increase the amount and quality of information available for species management.

## Introduction

Estimating demographic rates and population size is central to the study of ecology and species management. Population monitoring seeks to quantify demographic rates, changes in those rates and the resulting population size (Williams, Nichols & Conroy 2002). This information is critical for effective and predictable management of populations. However, logistical and financial constraints typically prohibit the collection of exhaustive data sets. Noisy, incomplete and disparate data are the rule when it comes to population monitoring (Clark & Bjørnstad 2004). Despite data deficiencies, a desire exists to predict future populations, establish current population status and defend management decisions (Freddy *et al.* 2004). To this end, matrix population models have gained immense popularity for their relative simplicity, flexibility and their ability to simultaneously handle noisy, incomplete data while addressing key management questions (Caswell 2006).

The use of a matrix model typically proceeds by first estimating mean demographic rates by age, sex or other delineations (Lefkovich 1965). Future population dynamics are then projected by repeatedly multiplying a population vector by the demographic matrix under the assumption that demographic rates are known without error. The ensuing time-series of population abundances can then be compared to observed abundances (Caswell 2006). Such a simulation-based approach to monitoring is feasible when data describing demographic rates are readily available. However, it is generally only abundances that are commonly estimated by many monitoring programs and simulation-based approaches relegate these hard-earned demographic estimates to the model validation stage. While seemingly attractive, the use of abundance data to validate simulations encourages the modeler to arbitrarily manipulate demographic rates until population projections and abundance data “agree”. As noted by White and Lubow (2002), this problem is better posed as a matter of statistical parameter optimization and methods exist to estimate the parameters of population models from data.

One class of model that uses a time-series of abundance estimates to estimate demographic rates are so-called inverse matrix models (Gross, Craig & Hutchison 2002; Buckland *et al.*



2004; Caswell 2006; Wielgus *et al.* 2008). The term inverse comes from the fact that the models estimate the demographic rates from count data whereas simulation based approaches use demographic rates to produce abundance estimates. Despite differences in how they use data both methods rely on a common demographic projection matrix to specify population transitions through time. The projection matrix describes the biological process of interest. For species where age or stage classification is possible, fitting a model within the inverse framework affords a non-invasive means of estimating demographic rates (Wielgus *et al.* 2008).

Recently developed integrated population models (IPM) offer an opportunity to bolster inverse methods by estimating demographic rates and population size from multiple sources of data (Besbeas *et al.* 2002; Brooks, King & Morgan 2004). Thus, an IPM is nothing more than an inverse matrix model that incorporates auxiliary data on demographic parameters. (Schaub & Abadi 2011) defined integrated population models as any model that “jointly analyses data on population size and data on demographic parameters”. Thus, the primary difference between inverse methods and an IPM is the inclusion of supplementary data on the demographic rates of interest. Typical sources of data may include aerial counts, radio-tagging encounter histories, productivity indices, harvest surveys and environmental data. The flexible and synthetic nature of IPM’s makes them an attractive tool for species management and conservation (e.g Schaub *et al.* 2007; King *et al.* 2008; Johnson *et al.* 2010).

Wildlife monitoring programs often cover large spatial extents comprised of many smaller administrative units with heterogeneity in the quality and quantity of data available. Heterogeneity in data availability challenges our ability to apply a single model to all administrative units. However, progressing from inverse to IPM methods does not necessitate change in the demographic projection matrix. At the complex end of the spectrum, data-rich populations might exploit a full IPM with multiple types of data while data-poor populations will necessarily require simpler inverse methods relying solely on abundance estimates. The key advantage of a consistent approach is that the same demographic projection matrix can be used to model population transitions in any

population across a wide range of data quantities and qualities. Consistency in the modeling approach offers a unifying framework for the analysis of monitoring data while making possible comparative studies, objective optimization of management alternatives and iterative learning from past action all while providing critical information to decision makers.

In this paper, we use simulation to quantify the accuracy, precision and bias of inverse matrix models and then fit inverse models to field data for comparison with an IPM and demographic rate estimates considered in isolation. Having identified at the outset that real data sets are typically far from ideal, we are interested in quantifying model accuracy, precision and bias in the face of missing data and model misspecification. We imagine that in practice supplementary data will only be available for a subset of populations. Models describing data-poor units will unfortunately be bottlenecks for model reality and performance. Past assessments of IPM's demonstrated the capabilities of the methods under data-rich circumstances (Abadi *et al.* 2010a). Here simulations focus on a worst-case scenario where no supplementary data exist (i.e. an inverse model). The first problem addressed by simulation involves missing values in survey data. Missing values are imagined to be the result of only quantifying abundance every 1 to 5 years. We believe an evaluation with missing data to be critical if these methods are to have utility in monitoring programs. Second, we evaluate model performance under three scenarios of misspecification plus one scenario using a correctly specified model. For clarity, the term misspecification is used to describe a situation where data were simulated using a model that did not match the way in which the data were subsequently analyzed.

Specifically, we first consider the effects of misspecification by simulating demographic rates that vary randomly in time, but are modeled as constant parameters. Second, we evaluate linear temporal trends that are present in the data, but not modeled in the survival or recruitment processes. Scenarios of misspecification are important in a management context because limited data will typically dictate the use of reduced parameter models and so misspecification is likely to occur. Quantifying accuracy, precision and bias when models are knowingly misspecified helps to quantify their value when data are limited.

Finally, we conclude the analyses by estimating demographic parameters for 51 populations of elk (*Cervus elaphus*) with inverse methods, an IPM and estimate adult survival in isolation. Through these steps, we highlight information gains, the necessary quantification of uncertainty and time-series complexity. Finally, we discuss accessibility of the models and inferential considerations.

## Methods

To evaluate the feasibility of the inverse methods for sparse data we simulated time-series data for 26 years and then fit models to the simulated time-series using a state-space formulation of an inverse matrix model. Parameter values used in the simulations were chosen to emulate the characteristics of elk demographic rates in Idaho, USA. We then fit models to aerial survey data of 51 elk populations using a state-space inverse matrix model. Following initial model fit, supplementary telemetry data were added to the model structure resulting in an IPM. Finally, telemetry data were used to separately estimate survival for comparison. Fitting multiple models to field data facilitated graphical presentation of comparisons among inverse, IPM and demographic data estimates.

### Field Data

We used data from the research and routine monitoring activities of Idaho Department of Fish and Game (IDFG). We considered data from 51 game management units (GMU) in Idaho. Data span the 26-year period from 1985 to 2011. GMUs were included in the study if they met two criteria. First, we included only those units where the number of aerial surveys conducted between 1985 and 2011 was greater than 1. Second, we considered only GMUs where aerial surveys were designed to produce estimates representative of population size, which eliminated GMUs strictly monitored for trends in the north of the state. Consequently, aerial survey data used here were assumed representative of population size.

Aerial surveys occurred at irregular intervals leading to many missing values and temporal patchiness in data quantities. Surveys occurred in January, February or March. Surveys were generally not flown in the same year for multiple adjacent GMU's, which created spatial patchiness in the sampling protocol and precluded spatial aggregation of units, but created an opportunity for units to inform neighboring non-sampled units. However, some units were flown in aggregate with other GMU's during data collection, which restricted our ability to maintain a common spatial unit of organization. Data collected during full aerial surveys included estimates of female, male and calf elk counts. Periodic composition surveys, which are less onerous than full aerial surveys, were used to estimate age ratios. Raw counts from full surveys were adjusted for visibility bias using the software Aerial Survey 6 (Unsworth *et al.* 1999a). The details of the software and the visibility correction are described in Samuel *et al.* (1987). We used the estimated mean and variance of adjusted count data as observations because raw count data were not available for this study.

Data on elk survival consisted of summaries of 641 telemetry collar deployments, including date of deployment, date of recovery of sensor, sex of the animal and field based age-class estimates. Collars were a mixture of GPS and VHF technologies and manufacturers. Collar deployments spanned a wide geographic range with deployments originating in 21 unique GMU's. Adult elk were captured by helicopter darting or net-gunning, drive nets or corral traps during winter of each year. Animals were fitted with telemetry collars equipped with mortality sensors. IDFG personnel typically monitored the animal's fate by fixed wing aircraft on, at least, a monthly basis.

### Demographic Projection Matrix (Process Model)

We maintained consistency among all populations by using the same demographic projection matrix (i.e. biological process) to fit simulated and field data regardless of the method applied (e.g. IPM, inverse). The demographic projection matrix we used followed a discrete time, two-stage, single sex structure where individual females reproduce for the first time in their second year of life. We set the model anniversary to occur in February to approximate when IDFG conducts aerial counts of elk. We fit models assuming that

demographic rates are constant and the population is closed to immigration and emigration. The model also assumed that males and females were produced in equal proportions. The most general process equations fit to data were as follows:

$$N_t^1 \sim \text{Pois}(N_t^a * \rho)$$

$$N_t^a \sim \text{Bin}(N_{t-1}^1 * 0.5 + N_{t-1}^a, \varphi^a).$$

Where the number of young ( $N_t^1$ ) at annual time step 2 to  $t$  was assumed to be a Poisson distributed variable with mean equal to the product of the number of adult females in the current time step and a recruitment term ( $\rho$ ). The annual number of adult females ( $N_t^a$ ) was considered the outcome of a binomial trial where the sum of half the number of young in the previous time step and the number of adults in the previous time step experience survival at a rate equal to  $\varphi^a$  for time steps 2: $t$ . We assume, therefore, that count data can differentiate young from adults and further that age classification is correct.

The recruitment term ( $\rho$ ) describes the number of young of the year that are born and survive to be counted per adult female. Recruitment was restricted to the range (0, 1) because twinning is rare in elk (Toweill, Thomas & Metz 2002). In wildlife literature this term is commonly called an age ratio. Age ratios can be difficult to interpret because the numerator and denominator both vary according to separate, but likely correlated, biological processes (Caughley 1974). Nevertheless, we suppose that for many populations age ratios will be available whereas specific information about pregnancy rates, fecundity and survival of young may not. Additionally, there is some support that age ratios may be a reliable index of recruitment in elk populations (Harris, Kauffman & Mills 2008).

## Simulations

To evaluate inverse matrix model performance we first simulated population time-series' using the above demographic projection matrix and distributions. The initial population

size of adults and young were 6000 and 2000 respectively for all simulations. These values reflect the estimated abundances in GMU 10 in 1985 and do not conform to a stable-stage distribution (SSD) assumption. Thus, the population simulations begin with transitory dynamics. We simulated 1,000 population time-series for each of four scenarios at five levels of missing data for a total of 20,000 simulations. Model parameters were stochastically drawn for each iteration. We added observation uncertainty to simulations by assuming that population sizes generated by the process models above were observed according to a Poisson process with mean equal to  $N_t^a$  and  $N_t^1$  for adults and young respectively. Our choice of distribution to describe observation uncertainty was one of convenience, but it also ensured that variance increased as the mean increased. All simulations projected population dynamics for 26 years, the length of data available to Idaho Department of Fish and Game. Our four scenarios were constant adult survival and recruitment of young (i.e. correctly specified), random variation in adult survival and recruitment of young, linearly trending adult survival and linearly trending recruitment. All scenarios except the constant scenario reference a type of misspecification because we always fit the same constant parameter model regardless of how the data was generated. In practice, misspecification would occur when simplifying assumptions are made on model complexity by choice or because of limitations imposed by a lack of data.

To simulate the problem of missing data in a time-series of observations, we emulated low frequency data collections by omitting data from the simulated datasets according to the five frequencies of data collection. For example, if we desired a survey every two years, we only extracted observations every other year. We evaluated the effects using the following survey frequencies: once every year, once every other year, every 3, 4 and 5 years. The sampling scheme resulted in 26, 13, 9, 7 and 6 observations of the 26 year simulated time-series, which is approximately 100, 50, 35, 27 and 23 percent coverage of the corresponding time-series.

## *Simulation Scenarios*

### Constant Demographic Rates

In the simplest simulations, we held demographic rates constant through time. For each of 1,000 iterations, a single fixed (i.e., unvarying within the iteration) value of adult survival was randomly drawn with equal probability between 0.80 and 0.95. These values cover the range of annual survival rates observed in North American elk populations (Raithel, Kauffman & Pletscher 2007) and diverse enough to cause rapid population expansion and contraction. Similarly, a single fixed value for recruitment was drawn for each simulation between 0.2 and 0.6 (Raithel, Kauffman & Pletscher 2007). Simulating data in this way served as a control and matched the inverse matrix model used to estimate parameters making it the only scenario free from misspecification.

### Random Temporal Variation

The random temporal variation scenario evaluated demographic rates that changed through time. We simulated random annual fluctuations around fixed mean values in both adult survival and the recruitment of young. A mean value for the demographic rate was selected on the real scale and then annual fluctuations were added according to a Normal distribution with a mean of 0 and standard deviation drawn from a Uniform distribution with a minimum of 0.2 and maximum of 0.6. The mean value plus the random noise was transformed using a logit function to map the values between 0 and 1 and formed the linear predictor for a given demographic rate. These simulated data were analyzed using the constant parameter demographic projection matrix described above. Thus, this scenario is equivalent to modeling a time varying parameter with a model that assumes the parameter constant. Real world analogs for this scenario include weather and harvest that fluctuates annually about a mean.

## Trending Survival and Recruitment Rates

For scenarios where demographic rates experienced linear trends through time we followed a similar procedure for projecting and observing the population as described for the constant demographic rate models. The difference was in the creation of the demographic rates. Mean values of survival ( $\alpha_0$ ) and recruitment ( $\beta_0$ ) were drawn as before, but in the trending simulations, they were the intercept of a linear predictor (Brooks, King & Morgan 2004). The effect of time was included as a covariate that was randomly selected from a uniform distribution with bounds at negative one and one. This procedure resulted in the linear predictors,

$$\text{logit}(\varphi_t^a) = \alpha_0 + \alpha_1 * yr_t$$

$$\text{logit}(\rho_t) = \beta_0 + \beta_1 * yr_t.$$

Where  $yr$  represents year scaled from zero to one. An inverse logit link was used on the predictor to ensure that all values of recruitment and survival fell in a reasonable range. Trends in survival and recruitment were considered separately and treated as two different scenarios. Similar to the random temporal variation scenario, this scenario created data in a manner different from how it was analyzed. However, unlike the random variation scenario, when demographic rates change linearly with time the consequences of the constant assumption is likely to be more severe. Real world analogs for this scenario include directional habitat change, climate change or a trending predation rate.

### *Analysis of Simulated Data*

The state-space formulation of the inverse methods we chose required a process model to describe the biological process of interest and an observation model to describe error in the observation process (Buckland *et al.* 2004; Clark & Bjørnstad 2004; Knape, Jonzén & Sköld 2011). We used the demographic projection matrix presented above for the process



model. All demographic rates were always assumed constant despite how the data might have been simulated. For the observation process, we used a Poisson distribution with mean equal to the latent stage specific population size in year  $t$ .

$$y_t^1 \sim \text{Pois}(N_t^1)$$

$$y_t^a \sim \text{Pois}(N_t^a),$$

Where  $y_t^1$  is the number of calves and  $y_t^a$  the number of adult females observed at time  $t$ . That is, the mean of the observation process is the outcome of the biological process. An implicit assumption of the Poisson distribution is that the variance is equal to the mean of the count. This assumption is convenient from the modeler's perspective as it restricts the error to a finite range and eliminates a parameter from the model.

### *Model Evaluations*

Upon completion of each of 1,000 iterations, we compared estimates to the true values of demographic rates, geometric mean growth rate and annual estimates of adult female and young of the year population size. To evaluate model performance, we calculated the accuracy (root mean squared error, RMSE), precision (standard error, SE) and relative bias for each parameter.

### *Analysis of Field Data*

#### *Inverse Methods*

We fit aerial survey data to the same process model as that used to fit simulated data. The observation model used to fit aerial survey data collected in the field differed from the simulation observation model. Aerial survey data collected by IDFG during routine surveys of elk populations consisted of counts of calves (young of the year) and cows (adult

females greater than one and a half years of age). Counts were conducted at highly irregular intervals and are always adjusted for visibility bias. Because data collection procedures followed a statistically rigorous design, the visibility bias correction model produces variance estimates during the adjustment process. A desire to incorporate this information motivated us to choose a Normal distribution for the observation process when using count data. We could then use the estimated variances as the variance of the observation process when modeling survey data. If ignored, observation error could bias results (Calder *et al.* 2003). The choice to include estimates of observation error as data reduced the number of parameters in the model. The choice of a Normal distribution assumes that observations above and below the true value are possible. We believe this to be reasonable if the assumptions of the visibility bias correction model hold because adjustments are as likely to over- as underestimate the true size of the population. It is also important to note that data storage protocols lead to a minimum of information that only provided the mean and confidence interval for each estimate.

### *IPM Methods*

Transitioning from inverse methods to an IPM model allowed the incorporation of an extra observation model for telemetry data describing survival. However, telemetry data lacked complete spatial coverage and only occurred in 20 of 51 GMUs. We modeled those 20 units in an IPM framework by combining the telemetry data and aerial survey data. We modeled telemetry data using a known-fate binomial model. The size parameter of the binomial distribution to be the total number of adult females collared ( $C_m^a$ ) and at risk in month  $m$  while the response was the number of collared adult females alive ( $A_m^a$ ) month  $m$ . Therefore, we estimated the probability of survival using,  $A_m^a \sim Bin(C_m^a, \tau^a)$ , where we estimate  $\tau^a$  as the probability of surviving from month  $m$  to month  $m+1$  from the number of animals collared and at risk and the number of animals alive. A monthly time interval allowed handling of animals that entered and exited the study at different times. Annual survival was derived by raising monthly survival estimates to the twelfth power  $\varphi^a = \tau^{a12}$ .

## *Telemetry Only Estimates*

For comparison, telemetry data were analyzed independent of aerial survey data to estimate adult female survival. The likelihood was the same as the telemetry observation model presented in the IPM Methods section. Unlike inverse and IPM methods, the estimates of survival calculated independently were not informed by the time-series of abundance estimates and thus independent of the time-series.

## MCMC

We fit all models using program R and package rjags to call JAGS 3.0.0 (Plummer 2003; R Development Core Team 2013). The process model remained the same for all analyses despite changes in simulation procedures and field data. Model specification required formulation of priors and initial values. Prior distributions for mean recruitment and survival rates were given as  $N(0, 1000)$  for both parameters, where  $N(x,y)$  indicates a normal distribution with a mean,  $x$  and a standard deviation,  $y$ . Demographic rate priors operated on the real scale and went through a logit link function. The prior for population size in the first year was given as  $N(6000, 100000)$  and  $N(2000, 100000)$  for adults and young respectively. Population size priors were truncated at 0 to exclude negative values. Markov Chain Monte Carlo (MCMC) sampling algorithms require specification of initial values. For the time-series of population abundances we drew values from a Poisson distribution with mean equal to the mean of the observed time-series. Initial values of demographic rates took randomly drawn values between the minimum and maximum values used to simulate data.

An adaptive phase of 50,000 iterations was followed by 25,000 simulated draws from the posterior distributions. At this point we assessed convergence using the Brooks-Gelman (BG) scale reduction statistic (Brooks & Gelman 1998). If the upper confidence interval of any of the BG statistics was deemed greater than 1.1 the model was updated 25,000 more iterations. Upon completion of each iterative update convergence was reassessed. This iterative process continued for a maximum of 10 repetitions.

## Results

### Analysis of Simulated Data

As expected, models fit using the same demographic projection matrix for data creation and analysis resulted in estimates of survival and recruitment that were least biased, most accurate and precise (Column 1 of Figures 1,2 and 3 relative to other columns). Across all scenarios, missing observations decreased precision and to a lesser degree accuracy (across x-axis of Figures 1, 2 and 3). Few generalizations can be made across the scenarios, except that precision of demographic rate estimates was similar across all scenarios (row 2 of Figures 1 and 2). Random temporal variation and trending survival scenarios had similar effects on bias, precision and accuracy (Columns 2 and 3, Figures 1, 2 and 3), which were larger effects than trending recruitment (Columns 4, Figures 1, 2 and 3). Recruitment trend scenarios showed the second highest degree of accuracy and second least amount of bias after the constant parameter scenario (column 4 of Figure 1, 2 and 3).

Estimates of mean population growth rate were consistently unbiased and accurate to two decimal places (Figure 3). The random variation and trending survival scenarios had the largest potential to influence mean growth rate as evidenced by the extended error bars in Figure 3. However, the ability to negatively influence the mean decreased at the extremes of 0 and 4 years of missing data (Figure 3).

Increasing numbers of years between surveys consistently decreased accuracy and precision of population estimates (pink diamonds, Figures 4 and 5). Standard error and RMSE correctly reflect the implicit time scale of error structures whereby error increases the further the distance from an observation (e.g. pink diamonds of Figure 5, rows 2 and 3). The tendency of standard error and RMSE to increase with time implies the accumulation of error through time due to auto-correlation in the time-series (Figure 4, Figure 5). Estimates of adult female population sizes were relatively unbiased. The most biased abundance estimates were the trending survival scenario, which deviates in the last 5 years

of the analysis, but note the relatively restricted range of the y-axis, in an absolute sense (row 1, Figure 4). All models considering misspecification produced less precise and more biased estimates of calf population size in years without data as evidenced by differences among mean performance metrics in years with and without aerial survey data (Figure 5).

### Analysis of Field Data

Inverse matrix method estimates of adult survival ranged from a low of 0.73 (SD =  $2.0 \times 10^{-2}$ ) to a high of 0.94 (SD =  $1.0 \times 10^{-2}$ , Appendix 1-1, Figure 1), while estimates of recruitment spanned a range from 0.13 (SD =  $9.7 \times 10^{-3}$ ) to 0.65 (SD =  $7.0 \times 10^{-2}$ , Appendix 1-1, Figure 2). Standard deviations of posterior distributions ranged from  $4.4 \times 10^{-3}$  to  $7.2 \times 10^{-2}$  for recruitment and from  $2.0 \times 10^{-3}$  to  $2.7 \times 10^{-2}$  for adult survival (Appendix 1-1, Figure 2).

IPM methods closely agreed with the inverse methods (Figure 6) producing mean adult survival estimates that ranging from 0.73 (SD =  $2.0 \times 10^{-2}$ ) to 0.94 (SD =  $1.0 \times 10^{-2}$ ). Similarly recruitment estimates between the two methods agreed in the range of recruitment estimates (0.13-0.64, SD =  $9.2 \times 10^{-3}$  and  $7.2 \times 10^{-2}$  respectively). Precision of estimates, as measured by the standard deviation of the posterior distributions, ranged from  $2.0 \times 10^{-3}$  to  $2.8 \times 10^{-2}$ .

Analysis of adult survival using only telemetry data produced a minimum estimate of 0.25 (SD =  $8 \times 10^{-2}$ ) and a maximum of 0.96 (SD =  $2 \times 10^{-2}$ ). Estimates from isolated telemetry data analysis were generally less precise than combined analyses (range minSD =  $2.2 \times 10^{-2}$ , maxSD =  $9.6 \times 10^{-2}$ , Figure 6).

In the case of GMU 48 telemetry data strongly disagreed with survival estimates from the inverse analysis (Figure 6). Consequently, recruitment estimates obtained using IPM methods compensated for a lowered survival rate (GMU 48, Figure 6, Figure 7). Independent age ratio observations were highly variable covering a much larger range than posterior estimates (Figure 7).

## Discussion

Overcoming data limitations is a primary difficulty of species management and conservation that challenges the relevance of science in management decisions. We have illustrated a non-invasive procedure for the simultaneous estimation of population size and demographic rates from minimal data that scales seamlessly from small-localized areas to larger spatial scales. Estimates of survival and recruitment from field data are the first of their kind for 31 of the 51 administrative units considered. In addition to novel estimates, the quantity of information available in all units increased, which made available estimates of survival, recruitment and abundance, which also makes possible the calculation of annual and mean growth rates. Considering survival data in combination with aerial surveys dramatically increased precision of estimates, which increased utility. Finally, we note that by incorporating aerial survey and telemetry data into the same analysis the model ensured more self-consistent estimates as evidenced by adjustments to the recruitment and survival estimates obtained in GMU 48.

Through simulation, we showed that missing data of up to 4 years did not create an unreasonable amount of bias for real life conditions like climate change, introduced predators, or changes in harvest. Our results also suggest that mean growth rate maintains high fidelity to the true value despite misspecification. In sum, these results encourage us to recommend the use of inverse and IPM methods for management applications.

We are aware of no other studies that used simulation to describe accuracy and precision of model estimates of inverse or IPM based models using stage-structured data. These characterizations help us form realistic expectations when applying such methods in real life circumstances. Several authors used simulation to characterize the influence of assumptions (Abadi *et al.* 2010a), feasibility of estimating populations from age-at-harvest data (Conn, White & Laake 2009; Fieberg *et al.* 2010) and the effect of choice of observation distribution for abundance estimates (Knape, Jonzén & Sköld 2011). Our simulations add an assessment of model misspecification and missing data to existing literature. Understanding the influence of these is critical to successful implementation of

the IPM framework for species conservation because observational datasets are frequently characterized by these challenges.

Where model misspecification is likely large, fidelity of geometric mean growth rate suggests that at a minimum the method could be used to identify areas or species of concern. A useful derived metric of growth is the cumulative distribution of the mean growth rate, which describes the probability of being above or below some objective. We omitted this step because our study did not focus on a specific management application and objective. More focused questions that strive to delve deeper than a mere growth rate will necessarily require more data. We considered a simple representation of population growth, but more data facilitates more realistic biological structures and complexities. Examples include environmental variation (King *et al.* 2008; Johnson *et al.* 2010b), density dependence and multiple age classes. Implementations of added complexities are straightforward in practice. The incorporation of environmental data, for instance, would require specifying a covariate in the linear predictor of the demographic rate of interest (e.g. survival, recruitment). Such representations force mechanistic and biologically meaningful consideration and analysis of relationships. Despite these potential additions, the basic form of the statistical machinery required to conduct analyses does not change.

A potential shortcoming of our approach was the use of a Poisson distribution to describe observation error associated with count data. The Poisson distribution is a statistically reasonable choice for count data. It was also convenient when coding simulations and ensured that the variance of the population increased as the mean increased. This relationship exists because the mean of a Poisson distributed variable is equal to its variance. In practice, the variance of count data is often several times larger than the estimated mean. Because of this, readers working with average datasets (variance  $\gg$  mean) are encouraged to view our results as optimistic, which is to say that we evaluated the models under the favorable condition of high quality abundance data. However, for those researchers working with exceptional datasets (variance = mean) our results can be considered sufficiently realistic. In the context of monitoring wild populations, the Poisson distribution provides a useful benchmark. Poisson data represent the highest quality of data

likely obtainable from field methods such as aerial surveys. Using such a benchmark to describe the best possible outcome is useful because it enables one to quantify losses in accuracy and precision as deviations from the benchmark increase.

Statistical analyses require a compromise between generality and complexity. Differences in model complexity derive in part from data availability. Similarly, the feasibility of using stage-structured counts to estimate demographic rates is limited by data availability because limited amounts of data restrict model complexity, which in turn holds consequences for the accuracy and precision of estimates. However, when compared to more pointed means of investigation (e.g. intensive telemetry studies), using IPMs allowed us to simultaneously estimate population size, growth rate and various derived products. This appears efficient from a sampling perspective. Furthermore, circumvention of legal and ethical difficulties may motivate the use of non-invasive methods in some circumstances while risk to personnel and individual animals may outweigh advantages of individual based methods in other settings. When desired model complexity outstrips data availability, random effects parameterizations that effectively share information through space or time (see Chapter 2) may provide a means of improving model estimates.

Working with limited data implies a certain amount of risk. The analyses presented here leverage statistical tools and compromised biological complexity to provide information for the management of elk. We note that the easy option at the end of an ecological study of saying that we need more data does not appear to be true under many conditions. For instance, increasing the frequency of aerial surveys from once every 5 years to once every 4 years does not change the bias. So, while we acknowledge that more data could allow for better estimates and do not promote prolonged reliance on limited data, decisions are being made today.



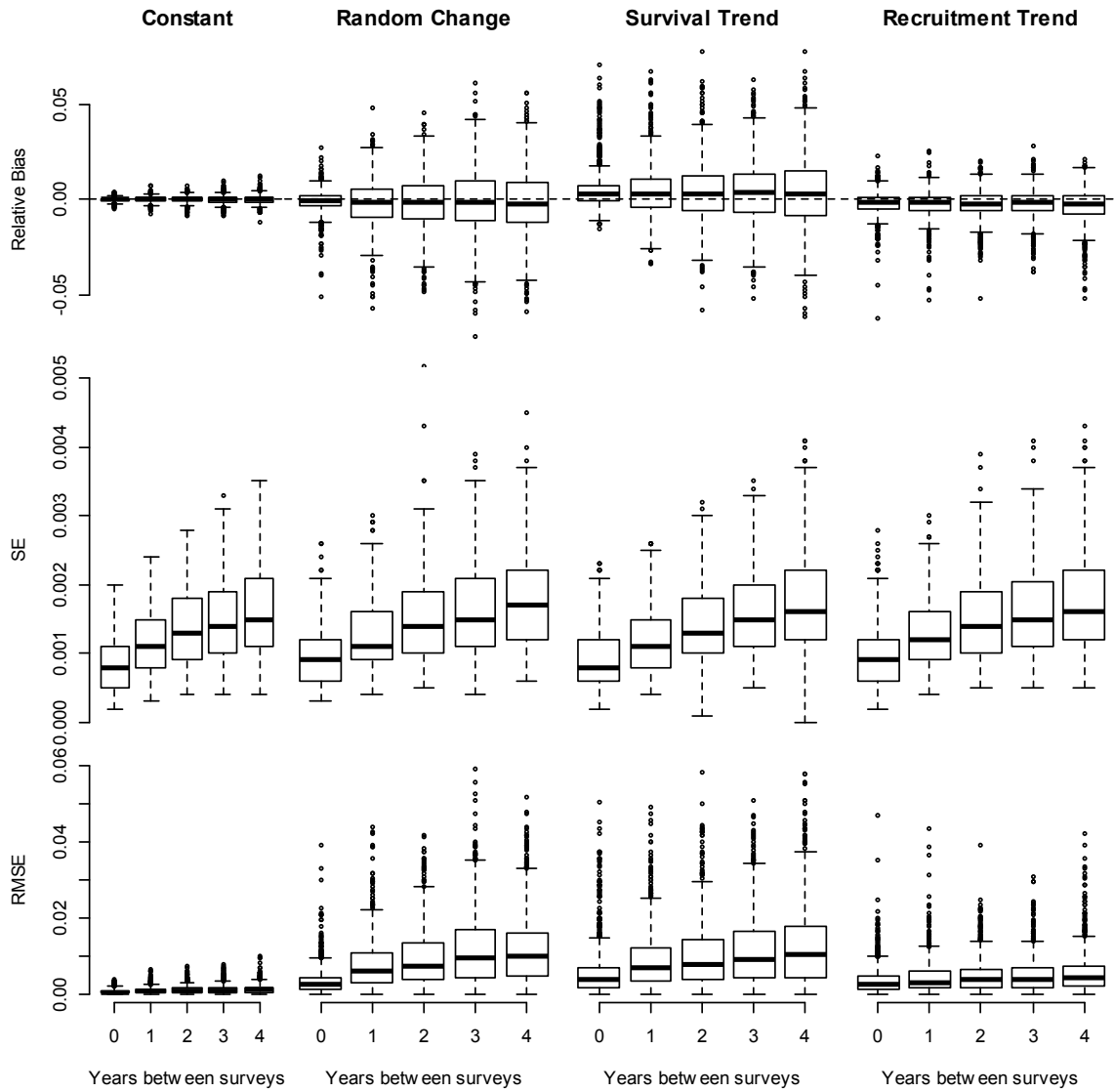


Figure 1-1 Simulation study survival estimates. Vertically boxplots are arranged by simulation scenario (constant, random temporal variability, survival trend and recruitment trend). Within each scenario five levels of missing data are compared. On the y-axis we present bias, precision (SE) and accuracy (RMSE) of estimates.

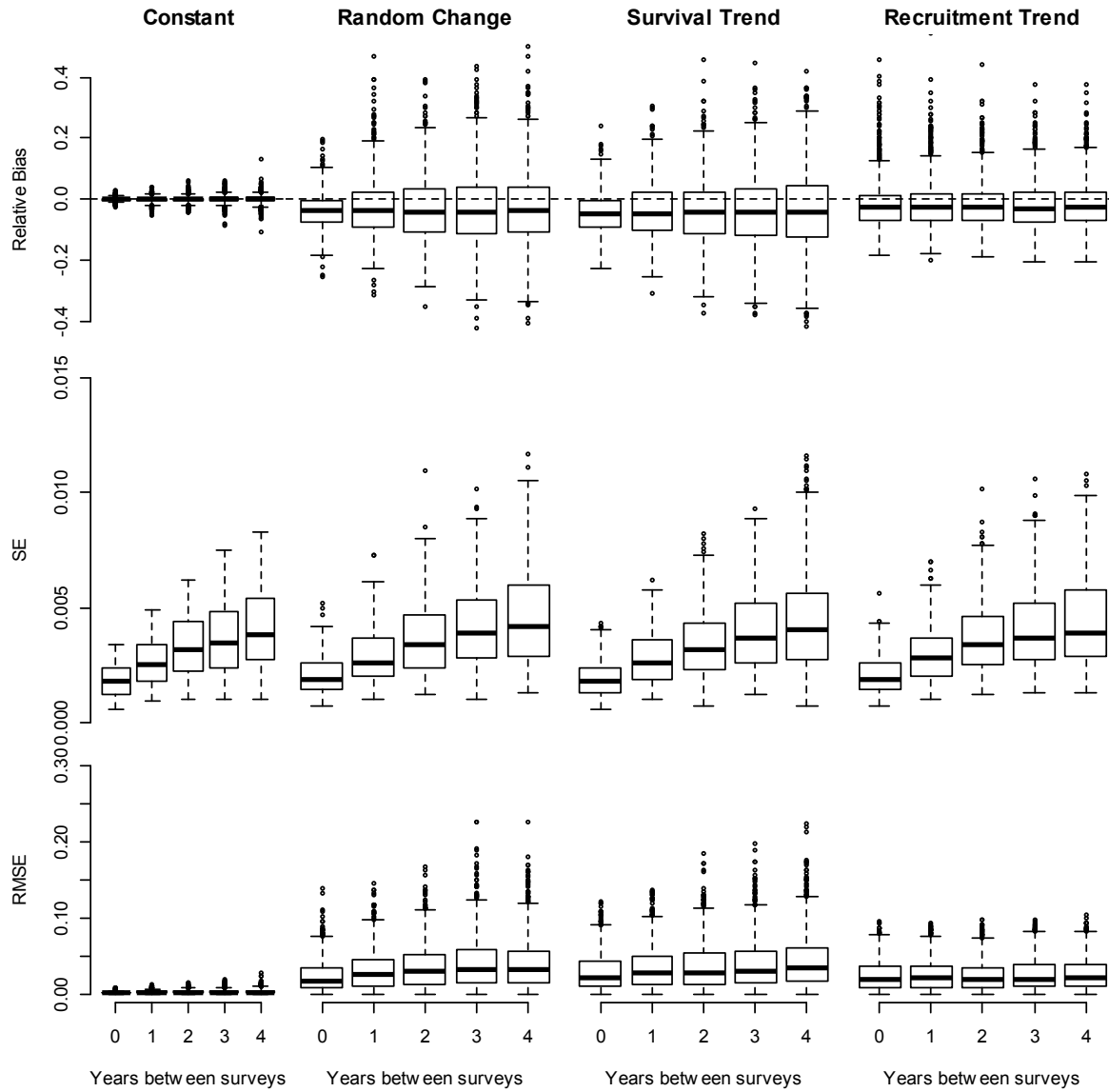


Figure 1-2 Simulation study recruitment estimates. Vertically boxplots are arranged by simulation scenario (constant, random temporal variability, survival trend and recruitment trend). Within each scenario, five levels of missing data are compared. On the y-axis we present bias, precision (SE) and accuracy (RMSE) of estimates.

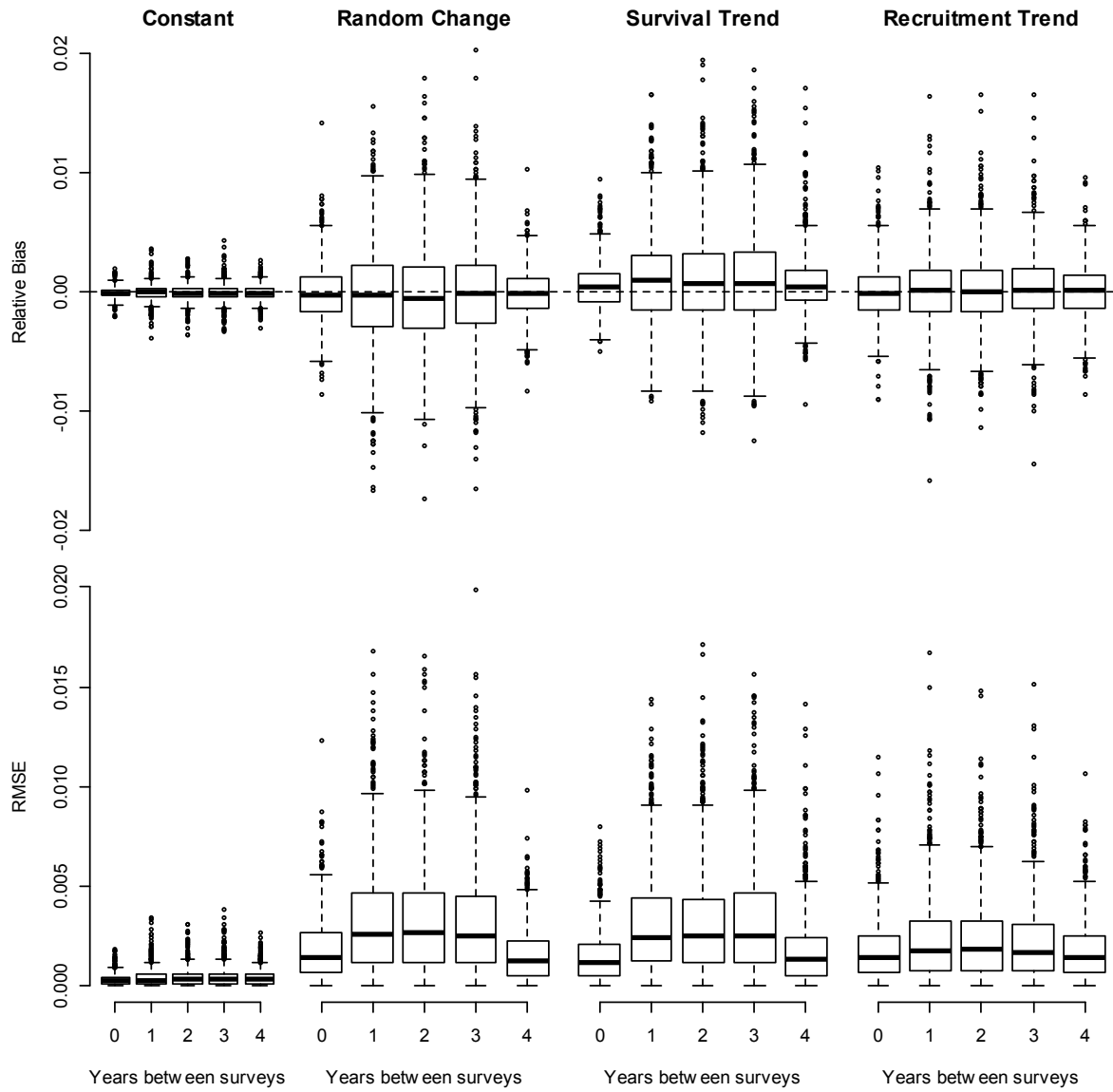


Figure 1-3 Boxplots of relative bias and root mean squared error of geometric mean growth rates from 1,000 simulations. The number of years between aerial surveys is depicted on the x-axis. Simulation scenarios, from left to right, include correct/constant model specification, extra random variation, linear trend in adult survival and a linear trend in recruitment.

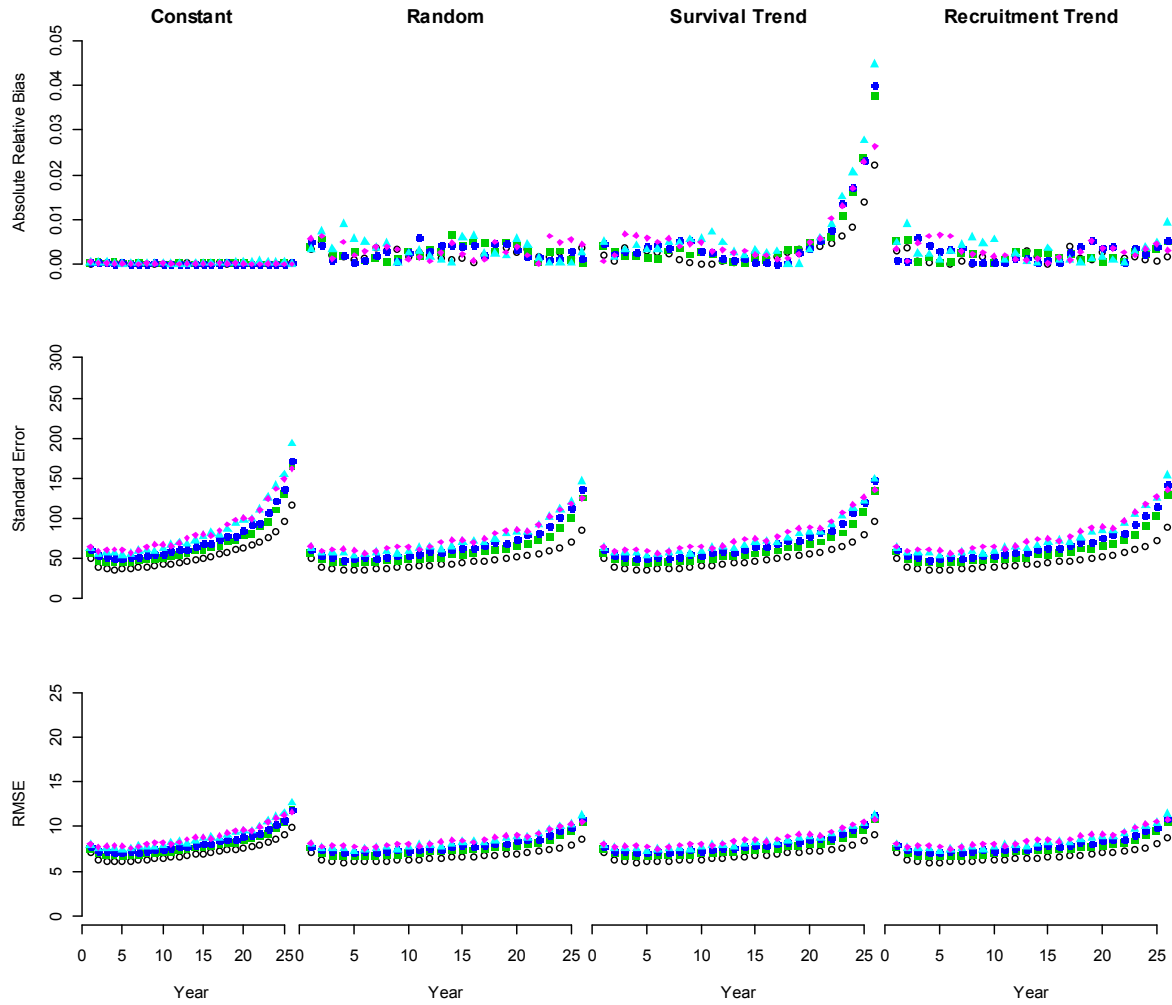


Figure 1-4 Plots display mean absolute relative bias, standard error and root mean squared error (RMSE) of adult female population size estimates over the 26 step time-series. Black open circles represent mean estimates without missing data. The remaining color shape combinations represent the number of years of missing data where filled green squares, filled dark blue circles, filled light blue triangles and filled pink diamonds represent one through four years of missing data between surveys.

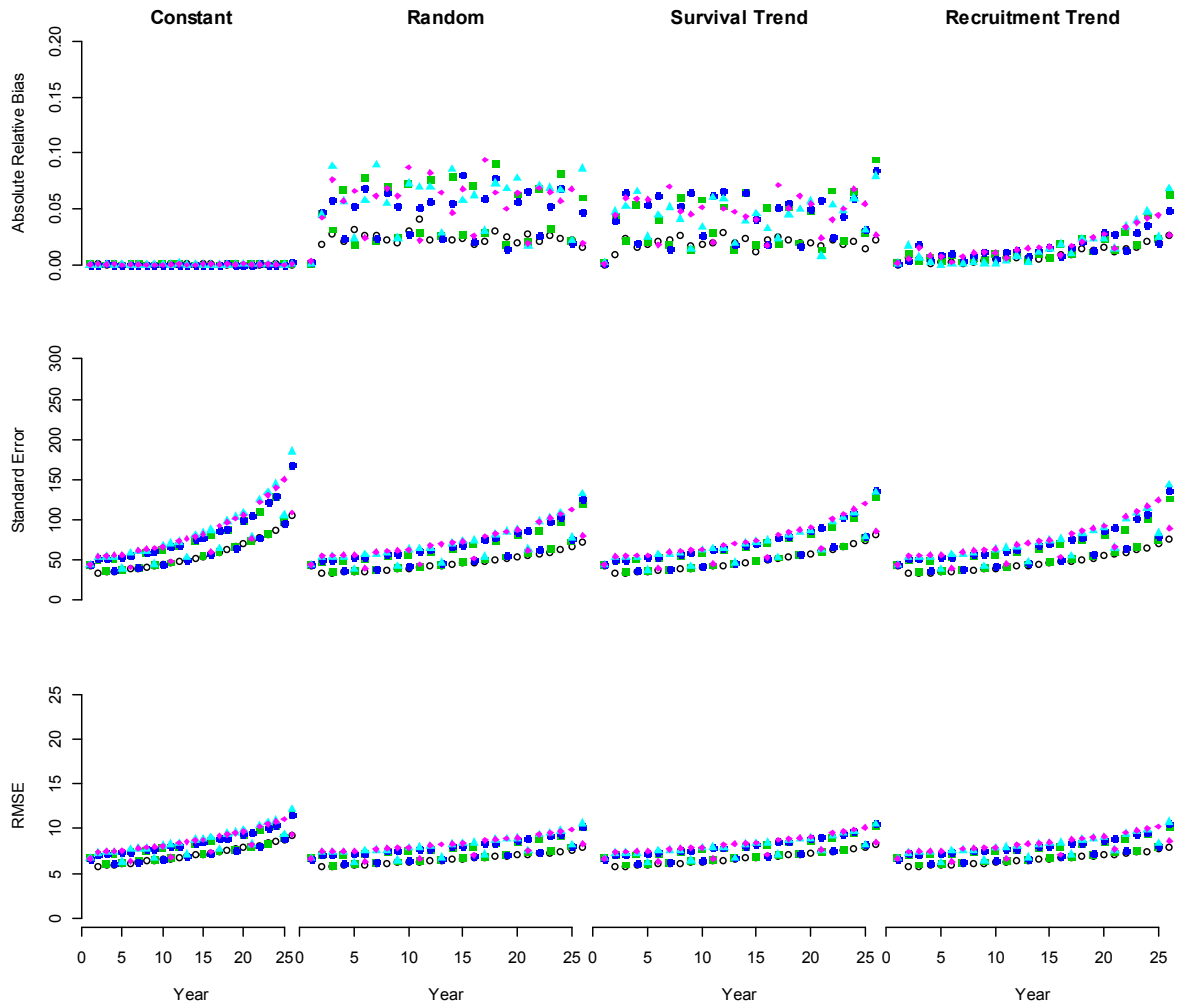


Figure 1-5 Plots display mean absolute relative bias, standard error and root mean squared error (RMSE) of young of year population size estimates over the 26 step time-series. Black open circles represent mean estimates without missing data. The remaining color shape combinations represent the number of years of missing data where filled green squares, filled dark blue circles, filled light blue triangles and filled pink diamonds represent one through four years of missing data between surveys.

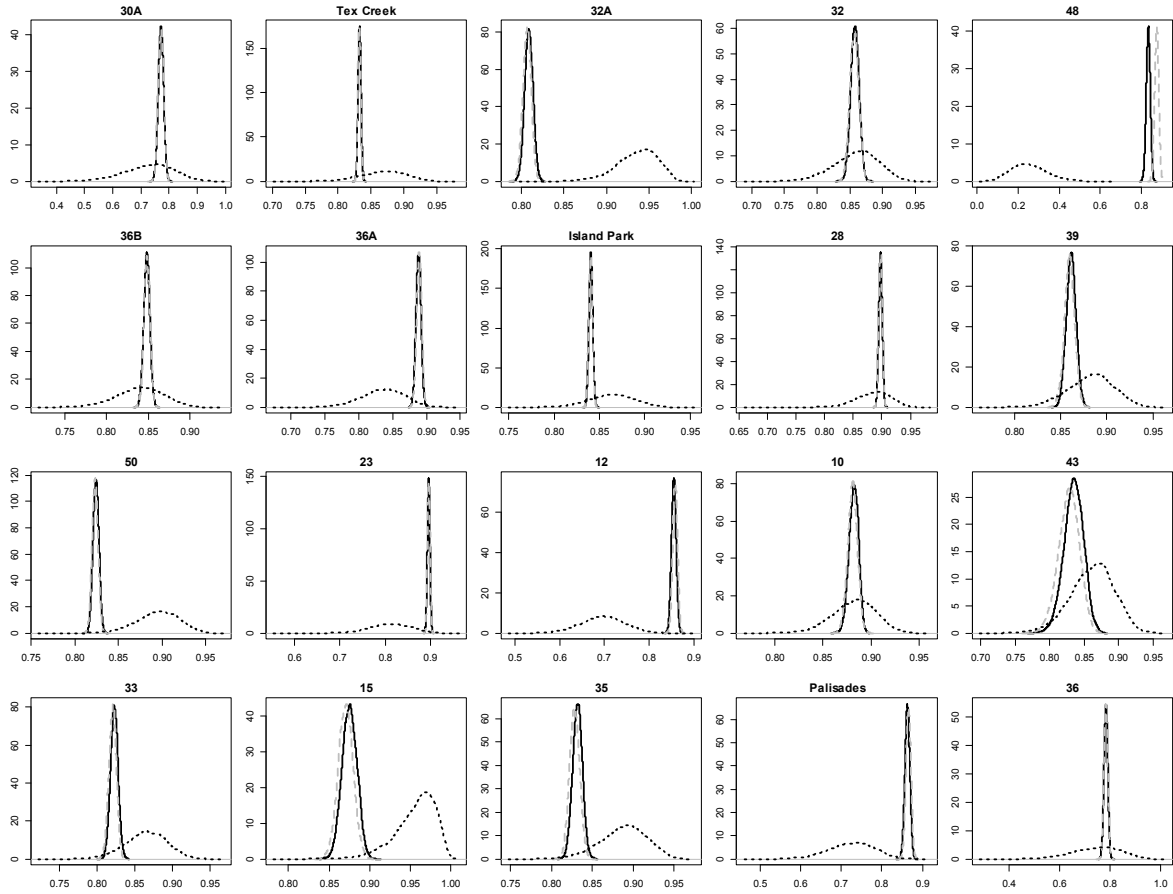
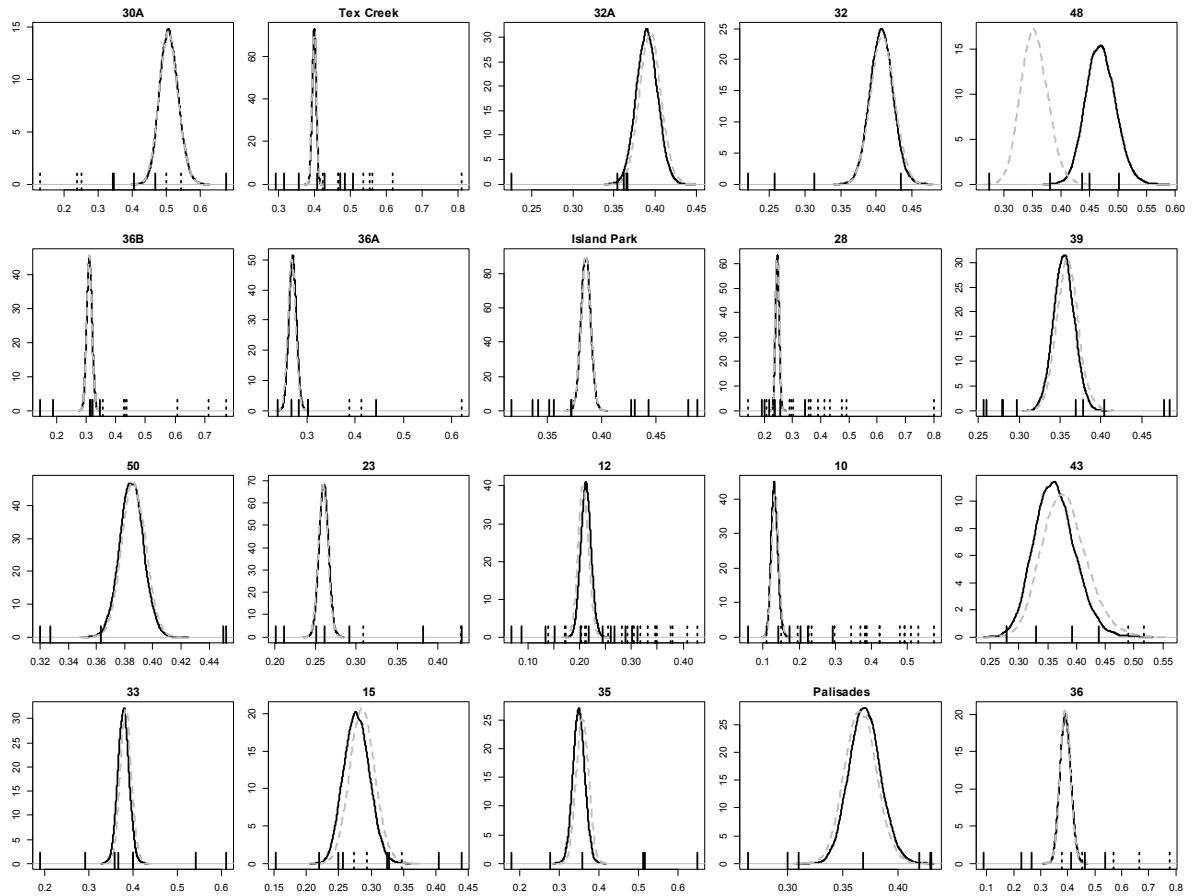
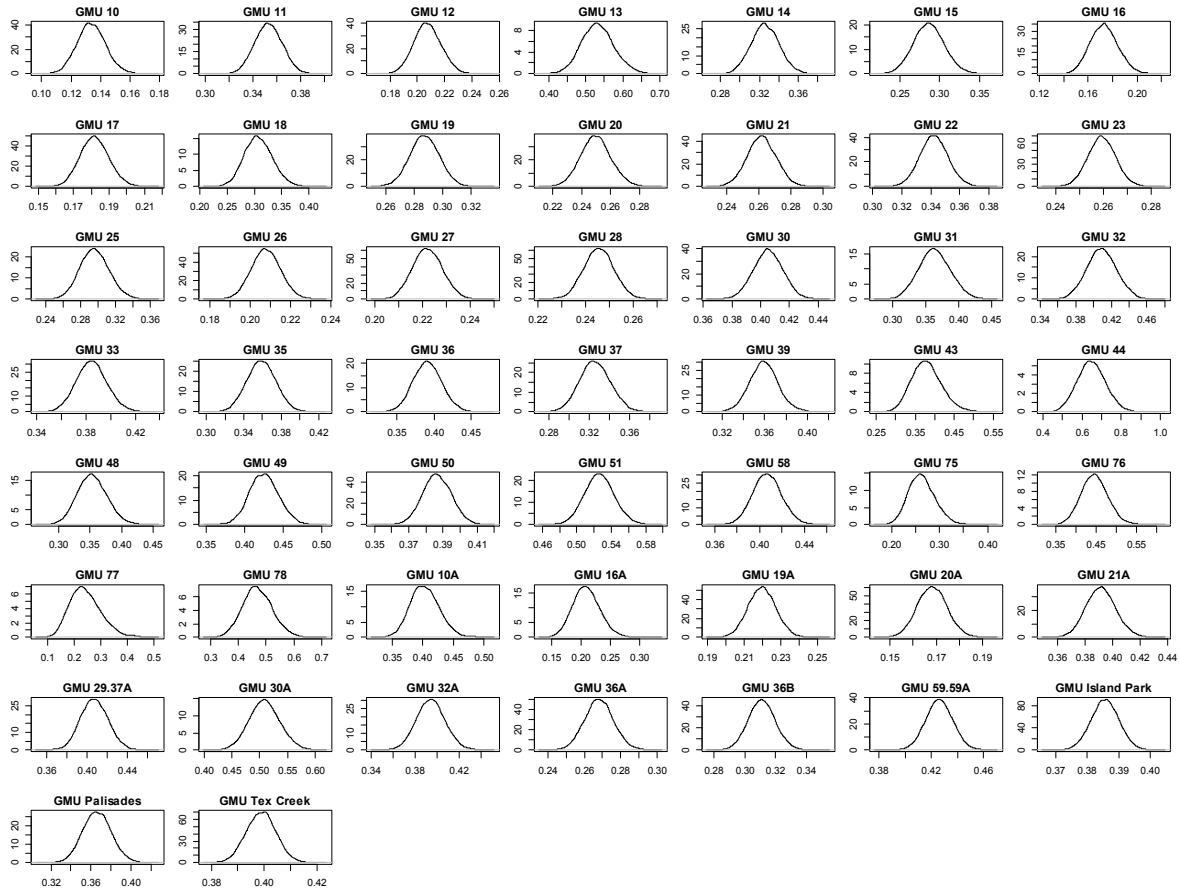


Figure 1-6 Comparison of adult survival estimates. Dashed gray lines represent posterior density estimates derived from an inverse matrix model using only stage structured aerial survey data of elk in Idaho, USA. Solid black lines depict posterior densities from an IPM considering aerial survey and telemetry data. Dotted black lines characterize estimates obtained from analysis of telemetry data in isolation of aerial survey data.



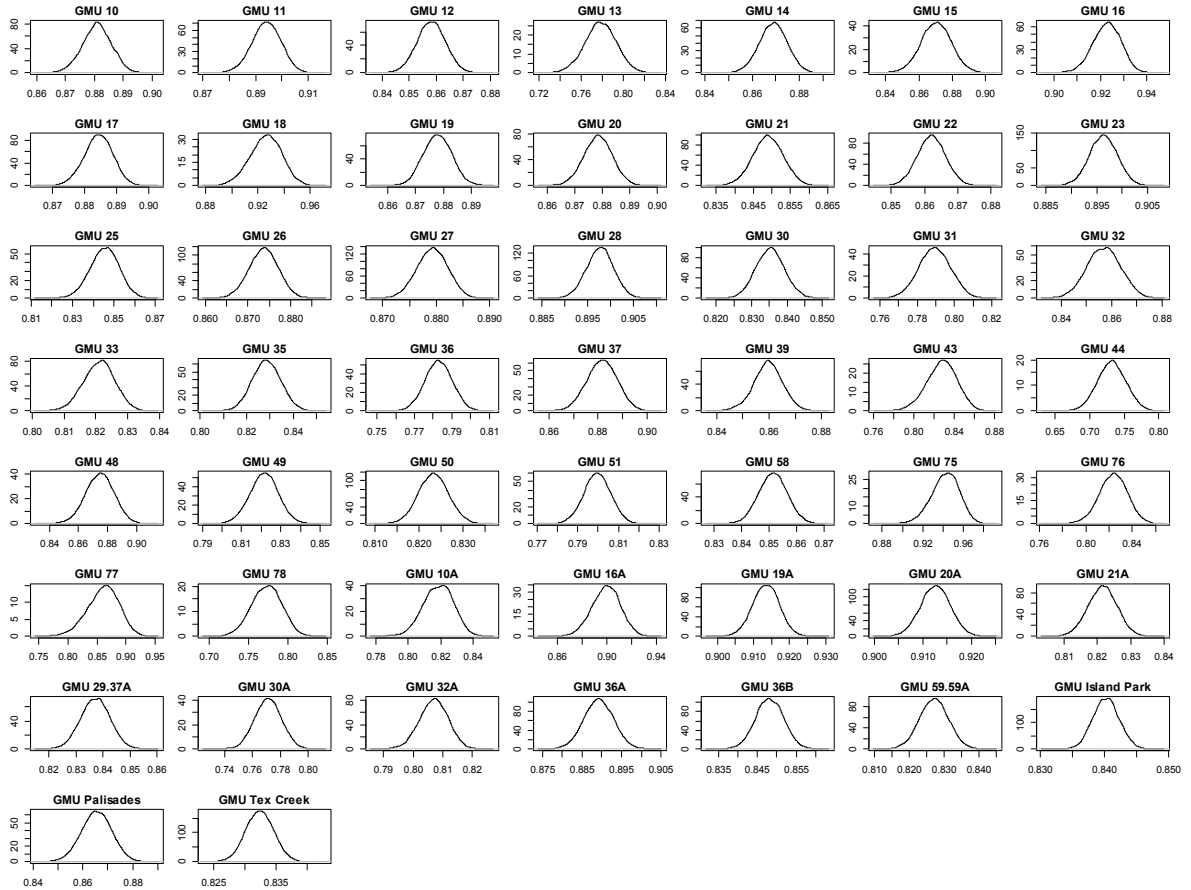
**Figure 1-7** Posterior density plots of recruitment estimates. Dashed gray lines represent posterior density estimates derived from inverse-matrix model using only stage structured aerial survey data. Solid black lines show recruitment estimates derived from IPM with aerial survey and telemetry data. Tick marks at the bottom of each plot portray age ratio estimates obtained during aerial surveys. Dotted tick marks depict estimates from independent data collected during composition surveys.

# Appendix 1-1



Appendix 1-1 Posterior density plots of estimated elk recruitment rates for 51 administrative units in Idaho, USA (1985 – 2011). Estimates were computed using inverse methods that considered only age-structured abundance estimates collected at irregular intervals.





Appendix 1-2 Posterior density plots of estimated adult elk survival rates for 51 administrative units in Idaho, USA (1985-2011). Estimates were computed using inverse methods that considered only age-structured abundance estimates collected at irregular intervals.



# Chapter 2. Big Insights from Little Data: Managing Populations when Data are Scarce

## Résumé

Estimer les paramètres démographiques d'une population et la taille de celle-ci joue un rôle central en écologie et pour la gestion des espèces. La combinaison des estimations avec des matrices de projection de population permet aux chercheurs de simuler la dynamique des populations. Toutefois, ces problèmes peuvent être plus facilement formulés comme un problème d'estimation de paramètres. Les matrices inversées de population permettent l'estimation de paramètres démographiques et de l'abondance à partir de séries chronologiques d'observations. Les modèles de populations intégrés s'appuient sur les méthodes de matrices inversées pour faciliter l'utilisation de multiples sources de données pour estimer les paramètres du modèle. L'intérêt pour l'application de ces méthodes à des scénarios réalistes a motivé cette étude dans laquelle nous avons utilisé des simulations pour évaluer la performance des méthodes inverses dans des conditions de données manquantes et spécification du modèle. Pour simuler la collection de données à faible fréquence nous avons simulé des données en à des fréquences qui variaient de zéro à quatre ans entre les observations. En plus des données manquantes, nous avons aussi simulé trois scénarios de spécification du modèle en utilisant des tendances temporelles linéaires dans la population et de la variation stochastique. Nous avons par la suite utilisé des modèles de matrices inversées de population et des modèles de population intégrés à des inventaires aériens et des suivis télémétriques de wapiti dans l'Idaho, É.-U.. Les résultats de simulations ont indiqué que les modèles de matrices inverses ont fourni des résultats qui avaient une précision adéquate, indépendamment de la fréquence de collecte des données ou de la spécification du modèle. Les estimations du modèle sont cependant les plus sensibles aux erreurs de spécification concernant la survie des femelles adultes. L'utilisation de matrices de populations inversées et de modèles de population intégrée a donné des résultats similaires pour les taux démographiques et l'abondance. Les estimations de nos modèles sont les premiers de leur genre pour la majorité des unités administratives considérées. Nos résultats suggèrent que l'ajustement des modèles de

population de données limitée qui contiennent du bruit est non seulement possible, mais dans de nombreuses circonstances permettront d'accroître la quantité et la qualité de l'information disponible pour la gestion des espèces.

## **Abstract**

Wildlife managers have to define population objectives and manipulate wildlife populations regardless of data availability. Species management is a time sensitive iterative task that should benefit from quantitative analyses and models. Formal modeling frameworks provide a means of synthesizing data while accounting for characteristic nuisances, thereby increasing accessibility of data and efficiency of management while describing the state of a system and the state of system knowledge. A particularly powerful approach to population modeling consists of piecing together disparate sources of data using an integrated population model (IPM). However, data may regularly be perceived too sparse to fit an IPM. Moreover, monitoring data may not align in time or space. To overcome these issues we consider a novel parameterization of an IPM that permits sharing of information through time and space using random effects. We used model selection to compare a suite of models considering variation in demographic rates through time or space. A model that held recruitment constant while characterizing adult survival as constant in time and variable in space received overwhelming support. Statewide mean estimates from the most supported model suggested survival of adult females hovered near 0.85 (SD = 3.7E-4), while adult male survival was lower at 0.61 (SD = 2.0E-3) and recruitment held nearly constant at 0.33 (SD = 1.3E-3). Given our models, assumptions and results, we found that adult survival is the more likely to drive Idaho elk population dynamics than recruitment. Variation in adult survival likely results from fluctuating levels of harvest. As a method of synthesizing monitoring data, IPMs leveraging random effects increased precision of estimates, dealt with missing data, combined multiple sources of data and accommodated the many idiosyncrasies of our data.

## Introduction

Wildlife managers have to define population objectives and manipulate wildlife populations regardless of data availability. Ideally, managers would have comprehensive, quantitative and continuous knowledge of a managed system upon which to base decisions that seek to meet clearly defined, publicly agreed upon objectives (Lindblom 1959; Bailey 1982). In reality, wildlife managers rarely have comprehensive system knowledge. Limited data and imperfect system knowledge result from several factors. First, wildlife populations are notoriously difficult and expensive to quantify. Second, monitoring programs cannot produce ideal data sets because of constraints imposed by logistical and budgetary realities. Third, wildlife population dynamics are complex, variable and subject to multiple stressors that have complex interacting effects. Despite imperfect knowledge and data deficiencies, a desire, and—in some cases—a legal obligation exists to manage populations and achieve objectives.

Species conservation and management are time sensitive iterative tasks that should benefit from quantitative analyses and models. Quantifying uncertainty is a primary benefit of fitting population models (Buckland *et al.* 2004; Schaub & Abadi 2011); when uncertainty is unknown, data tend to convey an overly optimistic assessment of system knowledge. Raw data contain high levels of uncertainty due to observational biases, missing values, disparate scales and multiple sources of stochasticity (Clark & Bjørnstad 2004; Cressie *et al.* 2009). Because of uncertainty, direct comparisons and mental syntheses of raw data contain limited information. To further complicate the usefulness of existing data, many monitoring programs experience methodological changes over time. Methodological changes do not render data useless, but such changes impose a need for careful handling and flexible modeling approaches (e.g. Johnson *et al.* 2010). Ultimately, some types of models facilitate prediction with uncertainty. Formal modeling frameworks provide a means of synthesizing data while accounting for characteristic nuisances, thereby increasing accessibility of data and efficiency of management while describing the state of a system *and* the state of system knowledge (Schaub & Abadi 2011). Thus, managers gain

the ability to play “what if” games to evaluate potential management scenarios. Proposed policies can then be evaluated relative to well-defined objectives (Williams, Nichols & Conroy 2002; Nichols & Williams 2006). In this way, a predictive model allows for the identification of optimal policies, given the available data and knowledge of the system.

Whether or not continuous long-term data sets on demographic rates and population counts exist, a particularly powerful approach to population modeling consists of piecing together disparate sources of data using an integrated population model (IPM, (Besbeas *et al.* 2002; White & Lubow 2002; Brooks, King & Morgan 2004; Conn *et al.* 2008; Schaub & Abadi 2011). Typical sources of data may include aerial counts, radio-tagging encounter histories, productivity indices, harvest surveys and environmental data. By combining all or several of these sources of data into one analysis, it is possible to obtain more robust and self-consistent parameter estimates that fully reflect the information available and the true state of the system (Besbeas *et al.* 2002). A synthetic approach is desirable because analyzing demographic rates in isolation ignores dependencies among rates that produce observed outcomes (Baillie 1991). Other advantages of integrated approaches are the ability to estimate latent or unobserved quantities (Abadi *et al.* 2010b; Schaub *et al.* 2010), increased precision of parameter estimates (Besbeas *et al.* 2002; Tavecchia *et al.* 2009; Abadi *et al.* 2010b) and so-called honest accounting of error (Besbeas *et al.* 2002; Clark & Bjørnstad 2004). Further, IPM’s provide a biologically, if not legally, defensible basis for management actions and more efficient allocation of scarce resources. At the core of an IPM is a demographic projection matrix model. The matrix model is used to link demographic parameters to population size and subsequently describes population transitions through time according to species’ biology (Brooks *et al.* 2004). Ideally, the demographic rates that populate the matrix model would be estimated from independent data alongside the matrix model (Abadi *et al.* 2010a). IPMs are a uniquely unified framework for the analysis of population count and demographic data. Their flexibility accommodates the many complexities inherent to population monitoring and allows for mechanistic linkages between population size and demographic processes.

However, when sparse data do not align in space or time, a means of sharing information among analysis units is highly desirable (Lukacs *et al.* 2009). Further, sharing information bolsters sample sizes to permit inclusion of more complex model structures that may better capture the underlying biological processes. For instance, elk (*Cervus elaphus*) populations are a routinely monitored species in North America due to their value as a game species (Toweill, Thomas & Metz 2002). Long-term and large-scale studies have contributed greatly to our understanding of elk population dynamics (Toweill, Thomas & Metz 2002; Garrott, White & Watson 2009; Griffin *et al.* 2011; Brodie *et al.* 2013). However, aerial survey data in the state of Idaho consist of stage structured aerial counts every 3-5 years (Figure 1). Certain data poor units are characterized by as few as 3 aerial surveys in 27 years. Over the last decade Idaho Department of Fish and Game (IDFG) also affixed telemetry collars to animals. Telemetry studies occurred sporadically in time and space resulting in far from continuous and complete coverage of the state in time and space, but have contributed greatly to localized understanding of vital rates. Despite imperfect knowledge and data deficiencies, elk harvest continues across the state. Thus, managers seek knowledge of the annual population size and an ability to forecast in order to evaluate management options.

We imagine that data may regularly be perceived too sparse to fit a model. In an effort to overcome data limitations, we consider a novel approach to the IPM wherein demographic rates are shared across monitored populations via random effects. Perception of large-scale data deficiencies may be intimidating, but some monitoring units are likely better described than others. A consistent population-modeling framework provides an opportunity to share demographic rate information across units wherein data rich units may inform data poor units in a defensible manner. To this end, our objectives were 1) to provide a framework for modeling multiple populations simultaneously and 2) to demonstrate the ability of models to produce estimates in data deficient populations. We respond to these objectives by developing a hierarchical IPM of elk populations in Idaho where we combine routine monitoring data with various supplementary data (e.g. GPS and VHF collars) from punctuated and opportunistic research activities to inform state-wide management



scenarios. Finally, we report model selection results to compare models with different forms of varying demographic rates through space and time.

## Methods

### Data Collection

Data for this study come from the research and routine monitoring activities of IDFG 1985-2011. We considered data from 51 game management units (GMU). We chose to include GMUs meeting two criteria: 1) at least one aerial survey was conducted since 1985 2) aerial surveys were thought to produce estimates representative of population size. Historical data collection efforts focused on the GMU as the spatial resolution of interest. A recent shift in focus has IDFG considering management at the elk zone level. An elk zone is comprised of multiple GMUs.

Aerial surveys occurred at irregular intervals leading to many missing values and disparate spatial extents (Figure 1 & Figure 2). Surveys were generally not flown in the same year for multiple neighboring GMU's or those that comprise an elk zone. Some units were flown in aggregate with other GMU's during data collection and in a few cases an entire elk zone made up the sampling unit. Data collected during full aerial surveys minimally consisted of stage-structured counts of the number of female elk, bull elk and calf elk. Raw counts were adjusted for visibility bias using the software Aerial Survey 6 (Unsworth *et al.* 1999a). The details of the software and the visibility bias correction model are described in (Unsworth *et al.* 1999b). For several unit-year combinations, only partial aerial surveys provided herd composition metrics including calf:female ratios and bull:female ratios. Surveys occurred in January, February or March.

Data on elk survival consisted of summaries of 641 telemetry collar deployments, including date of deployment, date of recovery or censor, sex of the animal and field-based age-class estimates supplemented by cementum annuli analysis of extracted teeth. Collars were a

mixture of GPS and VHF technologies and manufacturers. Collar deployments spanned a wide geographic range with deployments originating in 21 unique GMU's (Figure 3). Adult elk were captured by helicopter darting or net-gunning, drive nets or corral traps during winter of each year. Animals were fitted with telemetry collars equipped with mortality sensors. IDFG personnel typically monitored the animal's fate by fixed wing aircraft.

## Population Growth

We used a Bayesian IPM to estimate survival, recruitment, population size and derived parameters from the previously described sources of data. Model development begins with the state process likelihood. The model is a pre-birth pulse matrix model with two age classes, two sexes, reproduction beginning at age two and an assumption that birth sex ratio is equal.

$$N_{g,t}^f \sim \text{Bin}(N_{g,t-1}^f + \frac{1}{2} N_{g,t-1}^1, \varphi_{g,t-1}^f)$$

$$N_{g,t}^m \sim \text{Bin}(N_{g,t-1}^m + \frac{1}{2} N_{g,t-1}^1, \varphi_{g,t-1}^m)$$

$$N_{g,t}^1 \sim \text{Pois}(N_{g,t}^f * \rho_{g,t}),$$

where the expected number of adult female ( $N_{g,t}^f$ ) elk in GMU  $g$ , at time  $t$  is equal to the number of female elk in the previous year plus half the number of recruited calf elk ( $N_{g,t-1}^1$ ) from the previous year. Process error is represented by a binomial distribution with, in the case of female elk, size parameter equal to the expected number of female elk and probability of success equal to annual female elk survival ( $\varphi_{g,t-1}^f$ ) at the previous time step  $t-1$  in GMU  $g$ . Male populations transitioned through time in the same manner as the female populations. We followed (White & Lubow 2002) and defined recruitment as

equivalent to the calf:female ratio in the current year ( $\rho_{g,t}$ ) times the number of female elk in the current year ( $N_{g,t}^f$ ). This formulation was desirable because we lacked information on the number of calves born and on survival in the first six months. It also reduced the number of parameters to be estimated. This definition of recruitment further facilitated use of observed calf:female ratios collected during herd composition surveys.

### Aerial Counts Likelihood

Aerial counts were adjusted for visibility bias, which suggested that estimates of population size could be smaller or larger than the actual population size. Visibility correction models output a point estimate of abundance and standard deviation for each aerial survey. For this reason, we assumed a Normal error distribution for these aerial counts. Again using female elk, the number of females in a given year was assumed to come from a Normal distribution with a mean equal to  $N_{g,i}^f$  and standard deviation (SD) equal to the standard error estimated by the sightability model applied to the count data in that spatial location and year ( $\sigma_{g,t}^f$ ). Thus, we assumed that the calculated error about the count data was a reasonable estimate. This assumption allowed the observation error to change in space and time relative to effort and sighting conditions while keeping the number of parameters in the model as small as possible given data uncertainty.

### Recruitment Likelihood

Calf:female ratios were calculated during full aerial surveys and herd composition flights. We only included calf:female estimates from herd composition surveys to maintain independence between the recruitment likelihood and aerial count likelihood. Explicit accounting of covariance in the model was not possible due to loss of information when the data were stored. Ratio estimates were also adjusted for sightability and storage protocols dictated that the mean and SE alone were recorded in the database. The counts that gave rise to the ratios were rarely recorded in the data, which suggested a Normal distribution

would best describe the available data. We used a truncated (0-1) Normal distribution with mean equal to  $\rho_{g,t}$  and SD equal to the SE output by Aerial Survey 6,

$$Y_{g,t}^{age.ratio} \sim N(\rho_{g,t}, \sigma_{g,t}^{age.ratio}), Y \in (0, 1).$$

### Sex Ratio Likelihood

Sex ratio data were collected and stored in the same manner as recruitment data. For this reason we again chose a truncated (0-1) Normal distribution, but the mean of the distribution was  $\frac{N_{g,t}^m}{N_{g,t}^f}$ . The SD was assumed equal to the SE calculated by the sightability model,

$$Y_{g,t}^{sex.ratio} \sim N\left(\frac{N_{g,t}^m}{N_{g,t}^f}, \sigma_{g,t}^{sex.ratio}\right), Y \in (0, 1).$$

### Survival Likelihood

To address survival, we incorporated VHF and GPS telemetry data using a known-fate product binomial model. The size parameter of the binomial distribution was set equal to the number of at risk collared animals ( $C_{g,m}^s$ ) of sex  $s$  in month  $m$  in GMU  $g$ , while the response ( $A_{g,m}^s$ ) was the number of sex  $s$  collared animals alive in month  $m$  in GMU  $g$ . Therefore, in the most general case possible the probability of monthly survival ( $\tau_{g,t}^s$ ) followed  $A_{g,m}^s \sim \text{Bin}(C_{g,m}^s, \tau_{g,t}^s)$ . A monthly time interval was used to allow for individual animals entering and exiting the study at different times. Monthly probability of survival was assumed equal for all months of the year, but in time varying models monthly survival was indexed by year  $t$ . Annual survival was calculated by raising the monthly survival estimate to the twelfth power,  $\phi_{g,t}^s = \tau_{g,t}^s{}^{12}$ .

## Random Effects

One way to fit a model to sparse data is to reduce the number of parameters. The simplest approach would involve fixing parameters to a single value in space and time. A single fixed value would be useful if the population of interest was the entire study area, but elk are managed at a much smaller scale and elk demographic rates are thought to vary in space and time (e.g. (Raithel, Kauffman & Pletscher 2007)). The novelty of our model is the sharing of information to overcome data scarcity. This is accomplished via modeling demographic rates with random effects. From the perspective of data scarcity this two level approach is attractive because data poor administrative units will borrow information from the global distribution when searching for an optimal parameter value. When units vary distinctly from the global mean, and enough data is available to describe this deviation, the local estimate may deviate from the global mean. Random effects can be placed on the survival, recruitment or both parameters to allow variation in time and space. We incorporated random effects by adding a random error term to the mean demographic rate and indexing by spatial or temporal unit as appropriate for the candidate model structure,

$$\text{logit}(\varphi_{g,i}^f) = \mu + \varepsilon_g^f,$$

$$\text{logit}(\varphi_{t,i}^f) = \mu + \varepsilon_t^f.$$

Where  $\varepsilon_g^f$  and  $\varepsilon_t^f$  are random effects distributed as  $N(0, \sigma^2)$ . The global mean survival rate is represented by  $\mu$ . As a result, the annually and spatially indexed survival parameter  $\varphi_{g,t}^f$  is the sum of the global mean and the random effect. The inverse logit link was used to ensure appropriate values of demographics (0, 1) were available to the process distributions. Although omitted for brevity, random effects placed on the recruitment terms followed the same form as survival and used the same link function because twinning is rare in elk (Toweill, Thomas & Metz 2002). For models where survival or recruitment was held constant, the linear predictor was modified to take the form:

$$\text{logit}(\varphi_{g,i}^f) = \mu.$$

## Candidate Models and Prior Distributions

Our interest centers on variation in demographic rates. Long-lived ungulate populations are generally regarded as being most sensitive to changes in adult female survival (Gaillard, Festa-Bianchet & Yoccoz 1998). However, because adult survival can be very stable through time, recent literature has focused more attention on the highly variable recruitment process (e.g. (Raithel, Kauffman & Pletscher 2007)). Then again, harvested populations may experience elevated variation in adult female survival because of changing hunting season structures, weather and hunter participation.

We considered combinations of spatial and temporal variation among recruitment and survival allowing each demographic rate to vary in space or time, but never both (Table 1). This was accomplished by specifying a time or space varying random effect on the relevant demographic rate(s) as described under subheading random effects in the methods section. Our approach produced 7 candidate models, which we ranked according to deviance information criterion (DIC). Similar to AIC, DIC attempts to quantify the tradeoff between model complexity and model fit. This is done using the deviance and a penalty term according to

$$\text{DIC} = -2\log L(\theta) - 2p_D,$$

where  $-2\log L(\theta)$  quantifies how well the model fits the data and  $2p_D$  is a penalty term accounting for the effective number of parameters in the model (Spiegelhalter *et al.* 2002). Bayesian models require prior specification for all parameters. Because one objective of our work was to evaluate the strength of a random effects approach to IPMs, we chose vague priors for all parameters. We hierarchically centered all random effect terms on the global estimate. Global and constant demographic parameters were given a  $N(0, 10000)$  prior, while the standard deviations of random effects were specified as  $U(0, 50)$ . Because

the time-series is conditioned on the first year, a prior is needed for the initial population size. We specified initial population size using a normal distribution with a mean equal to the first full aerial survey in that GMU, a standard deviation of 100 and truncated the distribution so that only positive values were possible.

Bayesian estimation was performed using Markov Chain Monte Carlo (MCMC) simulations as implemented in JAGS called from R using package rjags (Plummer 2003; R Core Team 2013). Model runs consisted of 3 chains run for 200,000 iterations with the first 90,000 iterations discarded. Models were thinned such that every tenth value of the MCMC chain was retained. We evaluated convergence based on the Brooks-Gelman ( $\hat{R}$ ) statistic and visual inspection of the MCMC time-series and posterior distributions (Brooks & Gelman 1998).

### *Derived Parameters*

We calculated derived parameters to enhance our descriptions of populations. Annual population growth rate was calculated using only females following:  $(N_{g,t}^f + N_{g,t}^1/2) / (N_{g,t-1}^f + N_{g,t-1}^1/2)$ . We used a geometric mean growth rate to describe long-term population growth and derived the probability that the geometric growth rate was greater than 1 by calculating the proportion of the total iterations that MCMC chains estimated the rate above 1.

### *Single Unit Comparison*

To illustrate the sharing of data, we selected one data poor unit for which we fit a single GMU model with constant demographic rates. The data used for fitting the illustrative model was restricted to data collected in the unit over the course of the study. Specifically we chose GMU 43, which had survey data for just four years between 1985 and 2011. There was no telemetry, composition flight or other supplementary data available for this unit. With such limited data, fitting a model to GMU 43 in isolation should result in very

diffuse posterior distributions and so the comparison is included to illustrate the influence of the random effects approach for facilitating estimation in data poor units.

## Results

Diagnostics of model runs revealed adequate chain mixing, smooth univariate posteriors and  $\hat{R}$  estimates less than 1.1 for all parameters, which suggests convergence. Convergence was achieved quickly for simpler models, with diagnostics reporting convergence within the first 10,000 iterations. Moderate amounts of within-chain autocorrelation were present when complex models were considered and when data was limited for a given GMU.

Model selection ranked the model with spatial variation in adult survival and constant recruitment well above the other models (Table 1). The difference in DIC between the top model and the second most supported alternative was greater than 1000. The simplest model, which had constant parameters, received the least support ( $\Delta\text{DIC} = -4464.84$ ). Full details of model selection results and demographic rate estimates can be found in Tables 1 and 2 respectively.

Mean adult female survival fluctuated modestly according to model structure with values ranging from 0.82 (SD = 0.11) to 0.89 (SD = 0.03). Temporal and spatial variation, as measured by the random effects, was consistently less in recruitment than variation in adult survival. There did appear to be some relevant spatial autocorrelation, with a large area of high female survival (white and light greys) in the west and center-west, and low female survival being in the north-north-east (dark grey to black; Figure 4). Adult male survival estimates were lower than adult female survival (Table 2) with state-wide estimates with a mean of 0.61 (SD = 0.02). State-wide recruitment was estimated to be 0.33 (SD =  $1.3 \times 10^{-3}$ ).

Geometric mean growth rates varied spatially, with some regions appearing to have grown over the 26 years, and others declined (Figure 5). Precision of annual growth rate estimates



was generally low ( $\text{mean}_{SD} = 0.016$ ,  $\text{range}_{SD} = 0.007\text{-}0.07$ ). Geometric means, as calculated from the best supported model, varied from a low of 0.91 ( $SD = 4 \times 10^{-3}$ ) to a high value of 1.07 ( $SD = 5 \times 10^{-3}$ ). The probability of the geometric mean being greater than one was above 0.5 in 22 of 51 GMU's (Figure 5, right panel). Thus, 43% of the GMUs were likely to have experienced growth between 1985 and 2011.

When considered in isolation, GMU 43 population size estimates were very similar as when this unit was considered in the most supported random effects model ( $\phi(G)\rho(\cdot)$ ). However, demographic parameter estimates were considerably less precise in the single unit analysis as illustrated by the increased dispersion of the posterior distributions (Figure 6). Consistent with the application of random effects we observed a small shift in estimates of demographic rates towards the global mean (i.e. shrinkage) in the random effect model (Figure 6).

## Discussion

This is the first time that many of the GMUs have estimates of demographic rates and growth rates. This has been previously impossible to do with incomplete data. With formal quantitative approaches to information sharing among GMUs combined with Integrated Population Model methodologies we can now allow for inference about poorly understood locations. Furthermore, the estimates of the well-studied places are likely even stronger than before because of the same information sharing. Given our model assumptions and model selection results, elk populations in Idaho respond most strongly to variation in adult survival, which experienced sufficient variability in the spatial dimension to render this model the most supported. Variation in adult survival likely stems from differences in harvest among years and/or units (Brodie *et al.* 2013). Recruitment data exhibited extreme variation in raw form, but recruitment parameters were routinely estimated as a consistent quantity in space and time (Table 2). Such information provides critical non-intuitive data-driven insights for the management of elk in Idaho.

Integrated population models accommodated the numerous disparities in our data while synthesizing multiple sources of information to provide precise estimates of population size and demographic rates. IPMs are the subject of active research to which we add the strength of hierarchical parameterization (Conn *et al.* 2008; Abadi *et al.* 2010b; a; Schaub & Abadi 2011). Our parameterization facilitates sharing of information from areas and times with abundant data to help make estimates in places and times of scarce data. We illustrated this point by showing the increased precision of demographic rate estimates in data poor GMU 43, though this sharing occurred everywhere, when using the random effect parameterization that leveraged data from the entire study area (Figure 6). In the context of population monitoring, a random effects parameterization facilitates estimation of low priority populations when monitoring or data collection is stratified by population. This is particularly relevant when one considers the potential for low priority populations to become high priority in the future and the subsequent need for modeling change under the future conditions.

In the single unit analysis of GMU 43, the relatively flat posterior distribution of the recruitment estimate signals little information contained in the weak dataset. One way to deal with this problem is by specifying an informative prior on the recruitment process (Lukacs *et al.* 2009). Under the assumption of exchangeability, random effect IPMs do not necessitate the use of informative priors for such situations because weakly identifiable parameters are subsumed by the hierarchical structure and thus are informed by data shared through random effects. In the biological sense, we defend the exchangeability assumption by noting that many biological drivers operate at scales larger than those at which populations are monitored, which suggests that each monitoring unit is in fact part of a single larger population. The random effects parameterization thus automatically handles “prior” construction by shrinking weakly informed unit specific estimates towards the global mean when insufficient data exists to override the global mean. In other words, this approach is conservative such that when a GMU has only a few data points that suggest catastrophic patterns (e.g., rapid declines or rapid increases that are different than elsewhere), the model addresses this by downplaying the weak data in favor of the state-

wide trend. In practice, confirming an apparent catastrophic pattern would require a focused data collection effort, something that the hierarchical model would also require.

The absence of continuous data collection limits our ability to accurately describe temporal variation. The data used for this study have very few observations in certain years, which forces estimation of temporal variability to rely on data from only a few populations. When study objectives emphasize temporal variability, a potential solution is to maintain a minimum sample size along the temporal axis. Despite information gains offered by IPMs, we imagine that detection of short-term changes in population dynamics will continue to prove difficult. If a desire exists to focus on short-term trend detection, extensive data will be required. However, given realized logistical and financial constraints of monitoring agencies, IPMs represent a significant gain in information obtained from existing data. Information gains come in the form of demographic rate estimates, annual population size estimates, derived parameters (such as probability that the GMU is growing) and quantification of uncertainty. The information gains touted here were once relegated to only the most technically well-informed practitioners, but readily available computing software has removed many of the obstacles that once separated decision maker from data and inference.

Incorporating harvest data would further our ability to accurately describe temporal variability in demographic rates and add realism. In our study, the influence of harvest was accounted for by the inclusion of telemetered animals that died from harvest. Unfortunately, elk are migratory in most of Idaho and harvest data does not align spatially with winter aerial surveys. Harvested populations are often monitored during the winter when visibility bias is minimized (Rabe, Rosenstock & deVos 2002). However, winter counts do not reflect the state of harvested populations if animals migrate among management units. IDFG designed the elk zone system, which clusters several GMUs, to combat this problem and to make population indices more meaningful to where harvesting occurs. Our models make it relatively simple to derive zone-wide estimates of population size. To calculate a zone-wide population estimate, one would simply need to sum the posterior distributions of each GMU that comprise the zone for each year monitored.

Alternatively, we can conceive of an open population model with seasonality that would overcome the migration problem and we suggest it as a next step for the management of migratory harvested wildlife populations that transcend administrative boundaries. Regardless of the approach pursued, the process of building an IPM provided critical insights into data structures and features of future monitoring protocols that will minimize alienation of existing data.

We assumed all populations were closed to immigration and emigration for the duration of the study. Given high levels of fidelity to winter range (i.e. where the animals are counted) observed in telemetry data (*unpublished data*) we suggest that the closure is an adequate approximation of reality. Regardless of fidelity to winter range, the model as presented could estimate a latent immigration term if telemetry data were sophisticated or complete enough as to permit incorporation of a multi-state survival likelihood that partitioned survival into spatial compartments (Abadi, Gimenez, Ullrich, et al. 2010, Schaub et al. 2010). A large portion of the telemetry data available for our study did not include location information, which precluded pursuing this model structure.

Populations of large ungulates respond most strongly to changes in adult female survival (Nelson & Peek 1982). However, a lack of variability in adult survival prompted investigation into the more variable recruitment process (Gaillard, Festa-Bianchet & Yoccoz 1998; Raithel, Kauffman & Pletscher 2007). Our results suggest that spatial variation in adult female survival has a meaningful effect on Idaho's elk populations. However, the main source of data available for this work consisted of aerial stage-structured counts with many missing values and a surrogate (calf:female ratio) for the recruitment process. The lack of data on the components of the recruitment process could have underrepresented variation and induced covariation between the recruitment parameter and adult survival (*sensu* (Morris & Doak 2004)). Such buffering would have the effect of smoothing the time-series and potentially downplaying the importance of recruitment. Our results are consistent with the work of (Brodie *et al.* 2013) who suggest that potentially dramatic spatial variation in adult female survival can be induced by harvest. (Johnson *et al.* 2010a) add further support with their work on endangered wild

sheep populations. The authors reported that for some populations variation in population growth was best explained by variation in adult female survival, while for other populations recruitment was the most informative vital rate.

Effective management of wildlife populations relies on detailed information describing demographic rates and population size. Regardless of data availability, our ability to learn from and defend management actions relies on a formalization of data and error structures. As noted by (Humbert *et al.* 2009), many simple approaches to population modeling rely on unrealistic assumptions, have trouble with missing data and we add cannot accommodate disparate sources of data. IPMs have enormous potential for synthesizing all available data for harvested, as well as endangered species. They do not however suggest continued collection of minimal disparate data, but rather by quantifying uncertainty they suggest the types of data that might be useful and provide incentive for improved species monitoring. The random effects parameterization explored here facilitates sharing of information, a key step towards modeling areas with severely limiting data. Quantifying key demographic rates and the state of the population is a meaningful first step towards continuous quantitative knowledge of biological systems.

Model	Deviance	pD	$\delta$ DIC
$\phi(G)\rho(.)$	20381.83	8416.44	0.00
$\phi(.)\rho(G)$	21047.93	9513.69	1763.35
$\phi(Y)\rho(Y)$	21023.18	9703.80	1928.71
$\phi(G)\rho(G)$	21009.75	10090.56	2302.05
$\phi(Y)\rho(.)$	21362.67	9903.93	2468.34
$\phi(.)\rho(Y)$	21886.32	10704.83	3792.87
$\phi(.)\rho(.)$	22244.15	11018.96	4464.84

Table 2-1 Model comparison results of integrated population models applied to elk populations in Idaho (1985-2011). Where G represents a spatial random effect delineated by game management unit and Y indicates a random effect of year on adult elk survival ( $\phi$ ) and recruitment of young ( $\rho$ ) respectively and a period indicates the parameter was held constant.

Model	Female Survival				Male Survival				Recruitment			
	Mean	SD	RE	RES D	Mean	SD	RE	RES D	Mean	SD	RE	RES D
$\phi(G)\rho(\cdot)$	0.85	0.0 0	0.2 1	0.02	0.61	0.0 2	0.36	0.0 4	0.33	0.0 0	--	--
$\phi(\cdot)\rho(G)$	0.86	0.0 0	--	--	0.61	0.0 0	--	--	0.32	0.0 3	0.32	0.0 3
$\phi(Y)\rho(Y)$	0.82	0.1 1	2.2 1	0.64	0.64	0.0 4	0.53	0.0 9	0.40	0.0 4	0.92	0.1 7
$\phi(G)\rho(G)$	0.89	0.0 3	1.5 9	0.27	0.61	0.0 3	0.58	0.1 0	0.36	0.1 1	0.62	0.1 2
$\phi(Y)\rho(\cdot)$	0.89	0.0 3	1.3 5	0.28	0.63	0.0 2	0.46	0.0 8	0.33	0.0 0	--	--
$\phi(\cdot)\rho(Y)$	0.85	0.0 0	--	--	0.60	0.0 0	--	--	0.32	0.0 1	0.30	0.0 5
$\phi(\cdot)\rho(\cdot)$	0.85	0.0 0	--	--	0.60	0.0 0	--	--	0.33	0.0 0	--	--

Table 2-2 Parameter estimates obtained from the seven fitted models for adult female survival ( $\phi^f$ ), adult male survival ( $\phi^m$ ), recruitment ( $\rho$ ) and random effects (RE). When parameters were assumed constant demographic rates represent the mean and standard deviation of the posterior distribution. When random effects were considered the estimate reflects the population level (i.e. global) mean and standard deviation of the posterior distribution. Columns with heading RE depict the standard deviation of the hierarchically centered random effect with the uncertainty about that estimate following in the RESD column. The -- denotes the exclusion of a parameter from a given model.





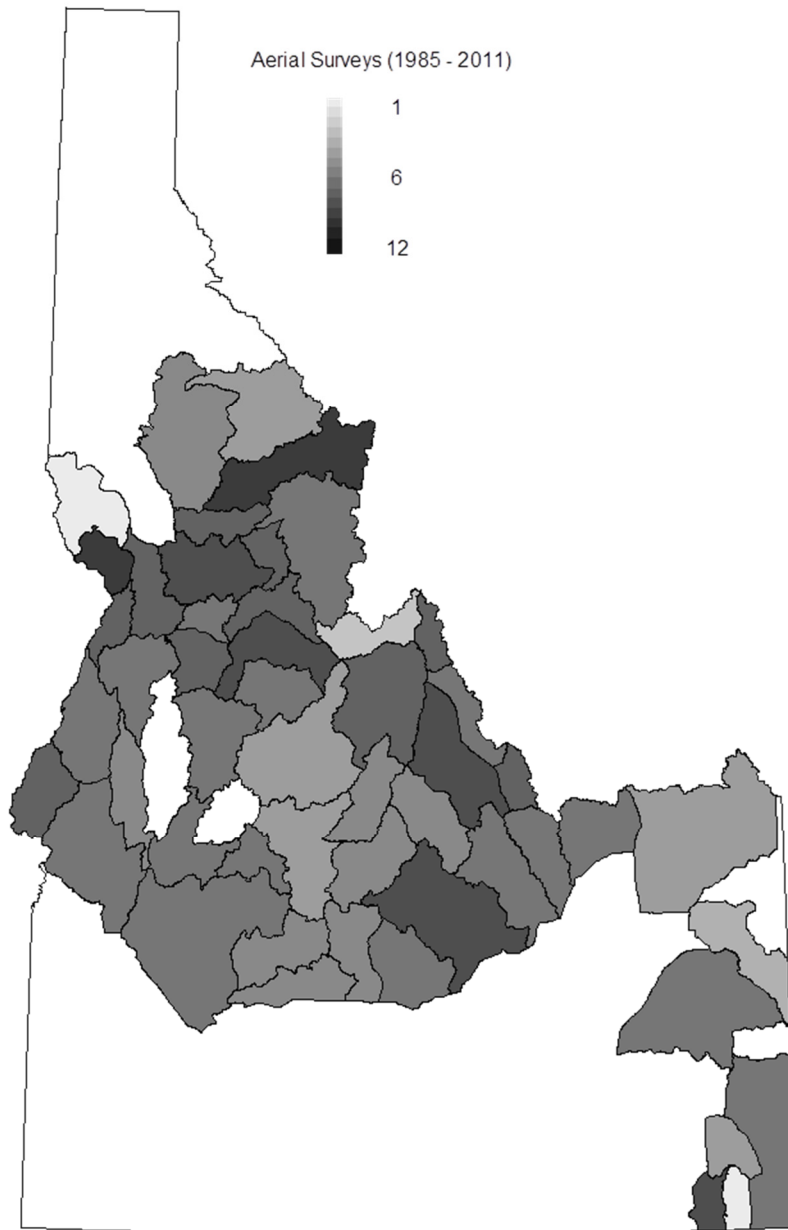


Figure 2-2 Spatial extent of the study area where shaded units indicate inclusion. Gray scale values also indicate the number of full aerial surveys conducted since 1985.

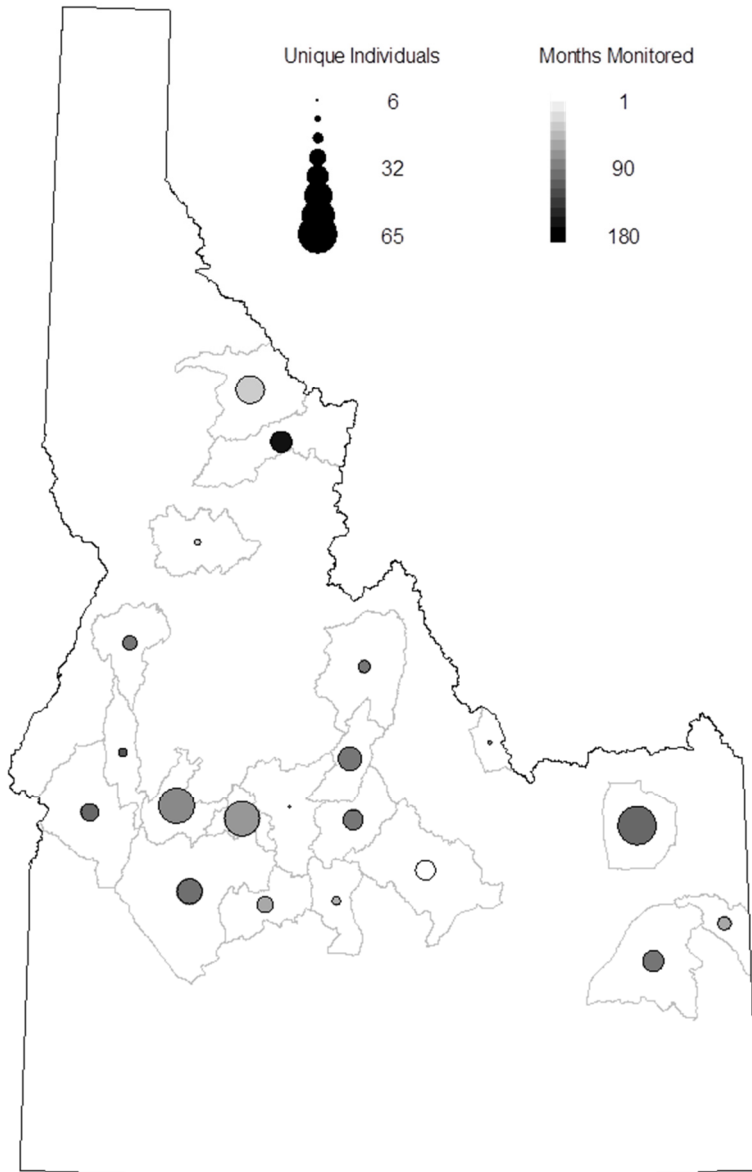


Figure 2-3 Telemetry data used in the study. The size of the dots represents the number of unique individuals monitored in the GMU while the grey scale of the dot is used to show the number of months the GMU had a sample size



Figure 2-4 Mean estimate of adult survival (Left: Female, Right: Male) by game management unit. Estimates taken from the most supported model. Darker colors correspond to lower survival, but note that while the scales are different the relative difference in survival is similar.

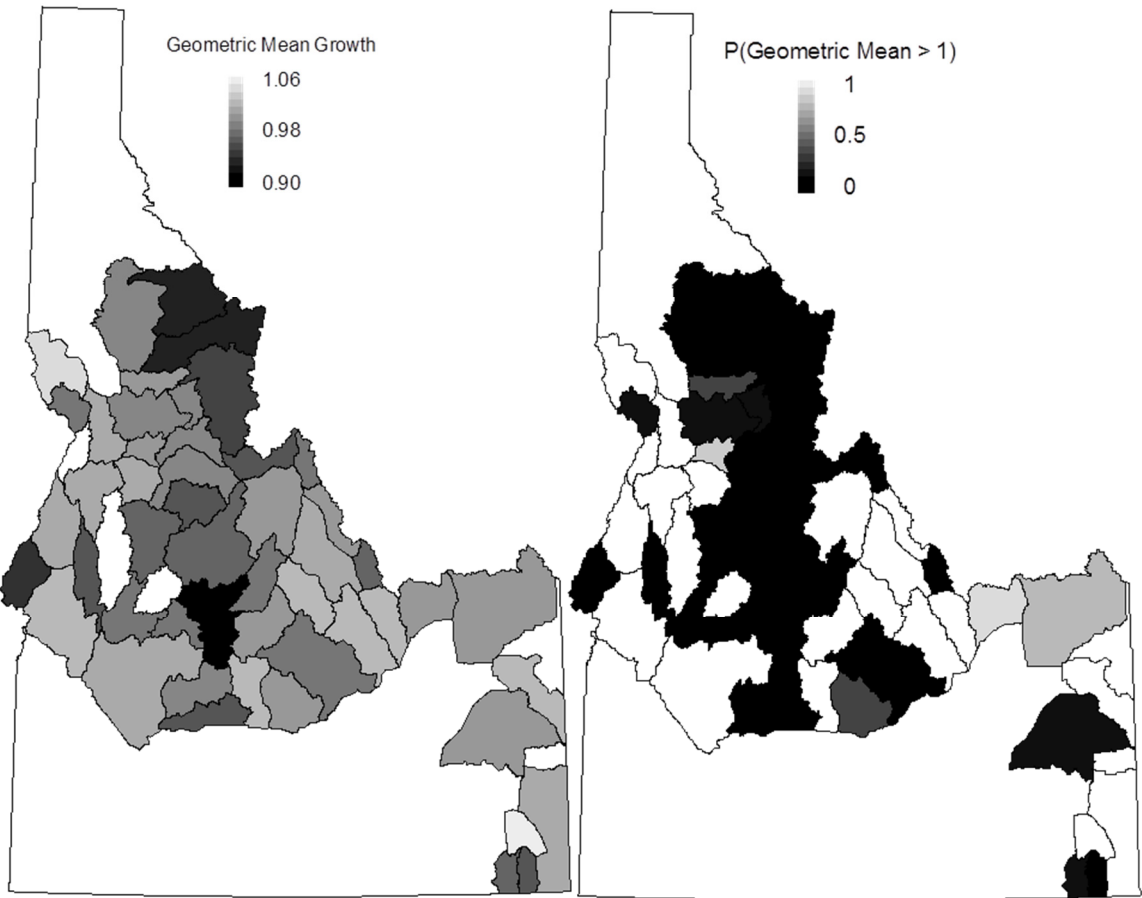


Figure 2-5 Geometric mean growth rate derived from annual population estimates from 1985-2011 presented on the left. The map on the right shows the probability that the value is > 1. Units in white were estimated to be growing with a probability of 1. Units in black represent those units with little to no chance of have experienced growth since 1985.

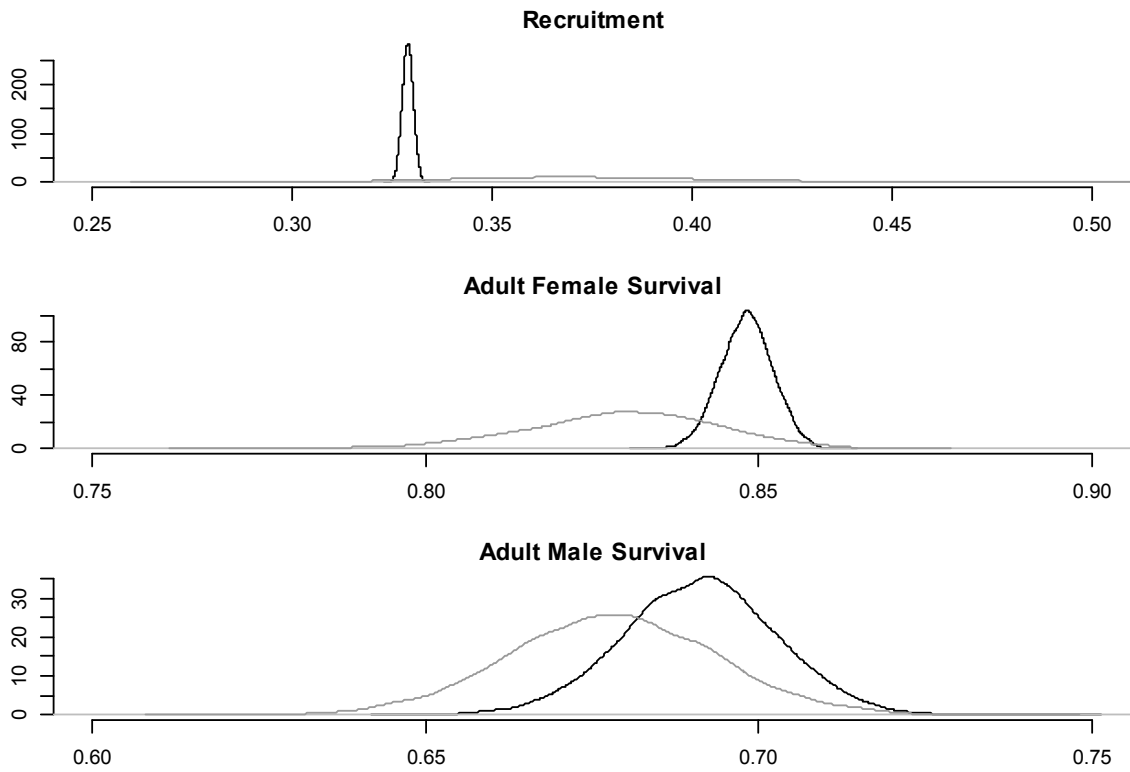


Figure 2-6 Comparison of demographic rate estimates from GMU 43 as suggested by the most supported model ( $\phi(G)\rho(\cdot)$ ) and a model considering GMU 43 in isolation with constant demographic rates. Black lines show posterior densities estimated by the random effects model while the gray lines depict the single unit analysis. This analysis is included to illustrate the data sharing qualities of a random effects parameterization.



# Chapter 3. Relating Habitat Selection and Use to Fitness

## Résumé

Puisque les résultats des études de sélection d'habitats sont appliqués de manière normative et ne donnent pas nécessairement des informations sur la qualité de l'habitat ou la performance individuelle, il est important de tester ces hypothèses. L'assomption que les résultats de la sélection de l'habitat maximisent la valeur adaptative est supportée empiriquement en écologie. Toutefois, en écologie la théorie suggère également l'existence d'une sélection non idéale des ressources. Afin d'améliorer la gestion du Wapiti, nous avons testé le lien entre la sélection des ressources au niveau de l'individu et au niveau de la population à la survie. Au niveau de la population, nous nous sommes appuyés sur la variation dans les coefficients de sélection au travers du temps pour expliquer la variation dans la survie. Nous avons par la suite créé des mesures d'habitat rencontrées puisque les bénéfices conférés aux individus dépendent probablement de la durée et de la fréquence d'utilisation de la ressource. Les mesures d'habitats rencontrés ont fourni une hypothèse alternative à l'échelle de l'individu et de la population. Nous avons trouvé que notre caractérisation de la sélection des ressources n'était pas corrélée avec la survie, tant au niveau individuel qu'au niveau de la population. Toutefois, les mesures d'habitat rencontré ont été soutenues par des procédures de sélection de variables. Au niveau individuel, la sélection des variables a appuyé les modèles contenant des variables auxiliaires pour la présence du loup et de la verdure végétative. Au niveau des populations, la sélection des variables a soutenu un modèle incluant les effets du loup et des zones récemment brûlées. Nos résultats indiquent que l'endroit où se trouve un animal est mieux expliqué par sa performance individuelle que là où il veut être. Nos résultats devraient encourager les gestionnaires des ressources à valider les résultats d'analyses de sélection d'habitats avant d'appliquer de manière normative les résultats des études.

## **Abstract**

Because the results of habitat selection studies are applied prescriptively and do not necessarily convey information about habitat quality or individual performance we require tests of these assumptions. The assumption that habitat selection results in maximized fitness is well founded in ecological theory. However, ecological theory also suggests the existence of non-ideal resource selection. To inform elk habitat management we related resource selection at the individual and population level to survival. At the individual level, we related differences between each individual and population level resource selection coefficients to survival. Considering the population level, we leveraged variation in selection coefficients through time to explain variation in survival. We then created metrics of habitat encountered because benefits conferred to individuals by resources likely relate to the duration and frequency of resource use. Metrics of habitat encountered provided an alternative hypothesis at both the individual and population levels. We found that our characterization of resource selection did not correlate with survival at the individual or population level. Meanwhile, metrics of habitat encountered found support from variable selection procedures. Variable selection supported retention of surrogates for wolves and vegetative greenness at the individual level. Population level variable selection supported a model including the effects of wolves and recently burned areas. Information criterion showed the most support for the individual level model incorporating each individual's propensity to encounter wolves and green open areas. Our results indicate where an animal is (habitat use) better explains individual performance than where it wants to be (habitat selection). The results also encourage resource managers to validate the habitat performance relationship before prescriptively applying the results of habitat selection studies.



## Introduction

Animals must consume resources and mitigate risk to sustain life. Movement is the mechanism by which animals adjust their spatial location and in heterogeneous environments alter exposure to resources and risks (Hooten *et al.* 2010). Spatial patterns arising from movements are typically assumed indicative of an animal's desire to meet life history goals (Manly, McDonald & Thomas 1993). To examine these patterns researchers often couple habitat use with a measure of habitat availability, which results in a resource selection function (RSF). A RSF quantifies habitat selection from disproportionate use of habitat relative to availability (Manly, McDonald & Thomas 1993). Estimates of selection are then taken to be the outcome of a series of behavioral processes by which animals seek to maximize fitness. However, it is habitat use, not selection, that ultimately determines the benefits conferred to the individual by habitat because energetic gains and costs afforded by habitats vary with the frequency and duration of habitat use (Gaillard *et al.* 2010). The ability of habitat selection to predict individual performance is consequently dependent upon the level of agreement between selection and use (Keim, DeWitt & Lele 2010). Thus, an implicit relationship between habitat use, selection and individual performance is a common and typically untested feature of habitat selection studies (Arlt & Pärt 2007; McLoughlin *et al.* 2010; Gaillard *et al.* 2010; Keim, DeWitt & Lele 2010; DeCesare *et al.* 2013). Because the results of habitat selection studies are applied prescriptively and do not necessarily convey information about habitat quality or individual performance we require tests of these assumptions.

The assumption that habitat selection results in maximized fitness is well founded in ecological theory. Over evolutionary time habitat selection is suggested to maximize fitness if animals follow the Ideal Free Distribution (IFD) (Fretwell & Jr 1969; Morris 2003). Such exact habitat selection would ensure relatively uniform and maximized fitness. Consequently, one would not expect variations in space use to be predictive of individual performance. When animals are distributed in accordance with the IFD density should reliably indicate habitat quality (Horne 1983). On time scales relevant to species

management, fluctuations in the abundance of animals seem likely given the dynamic nature of the landscapes upon which they rely. As such, failure to corroborate habitat selection with other measures of individual performance limits inference and questions prescriptive application in matters of species conservation (Keim, DeWitt & Lele 2010).

Recent evidence suggests that despite a desire to fulfill life history goals, animals may not employ the “best” strategy that results in maximized fitness (Arlt & Pärt 2007; DeCesare *et al.* 2013). Here we define the term non-ideal habitat selection to describe a lack of 1:1 correspondence between habitat selection and fitness. One hypothesized pathway to non-ideal habitat selection involves intentional and inadvertent social cues from successful conspecifics. In practice, such “public information” can lead to aggregation above that expected by the IFD and has subsequently gained popularity as a remedial hypothesis bridging the gap between IFD and field observations (Boulinier & Danchin 1997; Danchin, Boulinier & Massot 1998; Frederiksen & Bregnballe 2001; Doligez, Danchin & Clobert 2002). Acting on public information could be a selfish endeavor if certain individuals benefit while population fitness (i.e. growth) declines. For example, one can imagine individuals utilizing grouping as an anti-predatory strategy which dilutes individual risk while simultaneously increasing conspicuousness of the group, which results in increased per capita kill rates and reduces efficacy of positive density dependent effects (Allee 1931; Holling 1959). Finally, we note that habitat selection strategies, and space use in particular, resulting from public information are likely to persist in the short-term if habitat selection is a learned behavior (Nielsen *et al.* 2013). Through learning a non-ideal selection strategy could persist until no individual exists to “teach” the strategy. Such may be the case for many imperiled species that temporarily occupy habitat no longer capable of supporting the species.

Other hypothesized pathways to non-ideal habitat selection focus on a lack of information, ecological traps and metapopulation dynamics. A lack of information regarding the larger landscape could preclude individuals from seeking the best habitats (Lima & Zollner 1996). In their seminal work, Lima and Zollner (1996) point out that where an animal is and where it wants to be are not necessarily equivalent and the difference holds very real

consequences for the ignorant individual. Decoupling of habitat selection from individual performance is also illustrated by ecological traps (Schlaepfer, Runge & Sherman 2002; Battin 2004). Several examples exist in the literature concerning the order Odonata. Odonates use visual cues to select habitat for oviposition (Wildermuth 1998). Dishonest visual cues have led researchers to find Odonates depositing eggs on oil lakes (Horváth & Zeil 1996; Horváth, Bernhardt & Molnár 1998), glass buildings (Kriska *et al.* 2008), certain colors of gravestones (Horváth *et al.* 2007) and cars (Wildermuth & Horváth 2005). A recent study by Raebel *et al.* (2010) described Odonates depositing eggs in farm ponds irrespective of quality. In each of the Odonate examples the behavioral mechanism that led to habitat use was not indicative of individual performance. The same pattern can be observed within the context of a metapopulation where the presence of a sink or so-called attractive sink confuses the habitat-performance relationship by directing animals towards habitats that are detrimental to individual fitness (Pulliam & Danielson 1991; Delibes, Gaona & Ferreras 2001).

Habitat selection inquiries often employ a resource selection probability function (RSPF) or a resource selection function (Johnson 1980; Manly, McDonald & Thomas 1993), but other techniques could also be utilized (Johnson *et al.* 2008; Elith & Leathwick 2009; Johnson, Hooten & Kuhn 2013). The RSPF quantifies habitat selection; the probability that a resource unit of a given type is selected when encountered (Lele *et al.* 2013). The RSPF is not a process based model (Austin 2002). A process based model of habitat selection would better align with definitions of resource selection that consider selection the outcome of a behavioral process. Nevertheless, under the RSPF framework estimates of selection arise from measures of available and used habitat units. The concept of a selection ratio,  $w(\underline{x}) = \frac{f^U(\underline{x})}{f^A(\underline{x})}$  illustrates this point and is equivalent to a RSF. The numerator of the selection ratio ( $f^U(\underline{x})$ ) is the distribution of habitat use. Habitat use can be defined as the collection of resources encountered and selected during the course of study (Lele *et al.* 2013). Here we use the preceding definition within the context of resource selection, but otherwise consider habitat use as representative of resources. The denominator of the selection ratio  $f^A(\underline{x})$  represents the distribution of available resources or those units that

could be encountered by the animal (Lele *et al.* 2013). Researchers must determine available resource units, which has nontrivial effects on estimates of selection (Beyer *et al.* 2010; Lele *et al.* 2013). Considering habitat selection a hierarchical process has led many researchers to evaluate the RSF at multiple spatial scales. Such analyses quantify how selection changes as a function of availability, but the biological interpretation is unclear if the observed change is a statistical consequence of altered availability (Beyer *et al.* 2010).

Here, we quantify 2<sup>nd</sup> order habitat selection, which defines the home range of an individual within a landscape (Johnson 1980) and habitat encountered by elk (*Cervus elaphus*) and then apply these metrics of resource acquisition and risk avoidance to model survival (a surrogate for fitness). Here we define habitat encountered as those resource units in which an individual was observed. The first question we address is whether habitat selection, as characterized by the RSF posed here, correlates positively with survival. We would characterize selection as non-ideal if a resource selection coefficient had a negative effect on survival. The analysis first takes place at the population level allowing selection coefficients to vary through time, but no variation among individuals. We then repeat the analysis at the individual level to examine if individual variation is a better predictor of survival. According to the IFD variation among individuals should have no profound effect on fitness.

The second question concerns whether habitat selection or habitat encountered better explains variation in survival. To answer this question we compare the most supported habitat selection model to simple metrics of habitat encountered when modeling survival. Habitat encountered provides a robust alternative model to habitat selection. In each of the above mentioned examples of non-ideal habitat selection, selection was not a reliable indicator of individual performance, but habitat encountered remained predictive of fitness. Thus, one might expect metrics of habitat encountered to better align with what individual animals experience in their daily activities. Coefficient estimates from this model provide a metric of habitat quality, which we predict will be highest in areas with low probability of encountering a wolf and high levels of green vegetation. Other environmental variables considered likely help to predict space use, but have little to no direct impact on individual

fitness. The importance of this work rests in enhancing understanding of habitat studies for prescriptive application because long-term management plans are typified by habitat centric approaches. If habitat studies are to suggest a course of action to conserve species then results of these studies should relate to individual performance.

## Methods

To evaluate the relative abilities of our habitat selection model and metrics of habitats encountered to explain variation in survival we first compiled environmental data of interest, then combined that data with telemetry data from elk and finally fit a series of RSF models. The estimated coefficients of the RSF models and summaries of habitat encountered were then used as data to model survival. Model selection and averaging were relied upon to choose the most supported description of habitat selection. At the survival modeling stage model selection arbitrated among competing models.

### Study Area

The study area was west central Idaho, an area of almost entirely public land with a vast array of users and activities. Elevations range from 792 to 2987 meters. Annual precipitation averages 65.64 cm. Conifer forests cover much of the study area. Tree species include ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*), subalpine fir (*Abies lasiocarpa*), western larch (*Larix occidentalis*) and whitebark pine (*Pinus albicaulis*). Shrubs and grasses grow in the non-forested areas.

Elk in the study area exhibited migratory behavior transiting between high elevation subalpine/alpine environments during summer and lower elevation ponderosa pine and douglas fir dominated forests during winter. Local anecdotes suggest that elk migrated much further distances than current patterns of migration suggest. Supplemental feeding in the last 40 years encouraged elk to stop short of traditional winter range. As is true of

much of Western North America, the distribution of elk is most likely the result of human activity patterns as opposed to a naturally evolved distribution (Toweill, Thomas & Metz 2002).

## Environmental Data

A desire to make our results applicable to elk across Idaho compelled us to focus on continuous variables for which we could compile freely available data that covered the entire state. Habitat variables were selected according to their availability, spatial coverage and past use in studies of elk habitat selection. We considered five variables.

The first variable of interest was road density. We intended to include this variable as a measure of anthropogenic risk experienced through hunting and more generally year round disturbance (Edge, Marcum & Olson-Edge 1987; Cole, Pope & Anthony 1997; Hayes, Leptich & Zager 2002). Interest in roads also exists because managing agencies can manipulate the number of roads. Roads may also influence predation risk given previous work describing preferential use of linear features by wolves (Latham *et al.* 2011; McKenzie *et al.* 2012). Because the relationship between road density and humans is not unique, we chose to interpret road density as another surrogate for risk whereby we do not attempt to disentangle anthropogenic and natural predator risk within the variable. We quantified road density by counting the number of roads in each 250m by 250m cell of a grid covering the state. Road data was created by merging road data from the Boise National Forest and the road transportation of Idaho data published by the Idaho Geospatial Office (<http://inside.uidaho.edu/>). We consider this metric a conservative approach to the influence of roads.

The second variable represented forage resources on the landscape. For this variable, we chose the enhanced vegetative index (EVI) as measured by the Terra Satellite carrying the moderate-resolution imaging spectroradiometer payload (MODIS, <http://modis.gsfc.nasa.gov/>). Data collection occurred at near daily intervals with 16-day mosaics routinely published for end users. From the EVI mosaics we created a grid for

each month from January 2008 through December 2011. All mosaics falling within each month were combined by calculating the mean of each grid cell. Because treed areas we hypothesized that treed areas provided less forage than open meadows we weighted EVI grids by multiplying by the inverse of canopy cover. The grids assumed the finest possible grain of 250m by 250m. We note that other remotely sensed options had clear advantages, but large amounts of missing data due to faulty hardware precluded their use while MODIS facilitated analysis while restricting our inquiry of habitat selection to coarser scales.

Fire was the third variable we considered. With this variable we aimed to capture the influence of historic fires on elk space use. Controlled burns and their postulated benefits remain a popular means of habitat manipulation in the American West. We gathered recent fire data from the United State Forest Service Region 1 GIS clearing house ([www.fs.usda.gov](http://www.fs.usda.gov)), which provided coverage from 1985 to 2012. We merged these data with historic data from the same clearinghouse that dates back to 1889. The data were then gridded in a manner that aligned them with other variables. In some areas, multiple fires occurred within a single grid cell, when this was the case we assigned the grid cell the most recent value. We report the calculation of years since fire later under the *Elk Telemetry* data heading.

Our fourth variable aspect, was meant to represent the thermal and vegetative differences that occur on North versus South facing slopes in mountainous terrain. Unlike some of the other variables aspect did not change through time and so represented a static measure of selection and use. The data came from the LANDFIRE project's digital elevation model (<http://www.landfire.gov/>). In raw form, the data represent azimuth of sloped surfaces, but because our intent was to represent north and south facing slopes we applied a cosine transformation to the data. This simple transformation resulted in values for north being close to 1 and more south facing slopes assuming values near -1. Finally, the aspect grid was resampled to achieve the same grain as other variables.

The fifth and final variable in our model was an index of wolf space use. Concurrent with data collection on elk, Idaho Department of Fish and Game (IDFG) closely monitored wolf packs in the area. IDFG had a proposed goal of maintaining at least 1 GPS/ARGOS collar in each wolf pack for the duration of the study. This goal was largely met with most packs retaining at least 1 collar for the period considered here. We sought to characterize wolf space use, our surrogate for predation risk, with utilization distributions (UD(Winkle 1975; Worton 1989). Despite IDFG's monitoring success, data were not abundant enough to calculate unique monthly UD's for the entire period. To solve this problem we elected to calculate monthly UD's with data aggregated over years. For example, a January wolf UD was calculated using data from all 4 Januarys in the study. Calculations were performed using the R package *adehabitatHR* (R Development Core Team 2013). Given that we binned data into months, but not years, we chose to fit standardized UD's at the individual level, which had the advantage of alleviating concerns over wrongly assigning individuals to packs. To estimate the UD we implemented the Epanechnikov kernel using a fixed bandwidth of 3 km following (Fortin *et al.* 2005). Each individual UD was standardized such that the area under the curve summed to 1, which helped account for sample size differences among individuals. To combine individual UD's into a population level measure we created monthly grids such that a given cell took the maximum value observed in that cell and month. It is worth noting that the UD's were fit using a grid that matched the extent of the study area and grain of other environmental variables.

## Elk Telemetry Data

In the winter of 2008 IDFG began collaring elk with intent of maintaining a sample of 50 cow elk, 50 bull elk and 50 calf (~ 6 months old at time of capture) elk. The majority of capture was accomplished by means of helicopter darting, but corral traps were used to supplement samples when needed. Collar manufacturer varied, but those present included Lotek (Newmarket, Ontario, CA), Telemetry Solutions (Concord, California, USA), Telonics (Mesa, Arizona, USA) and Vectronic Aerospace (Berlin, Germany). All telemetry collars were equipped with GPS tracking units, VHF beacons and mortality switches. Collar deployment length varied as a function of GPS fix interval. Lotek and Telonics



collars took fixes every 4 hours with an anticipated deployment of two years. Vectronic collars allowed more flexible programming due to two-way communication via satellite modem. Because of this feature, Vectronic collars took fixes at irregular intervals ranging from every 30 minutes to one fix per day with fixes staggered such that battery life enabled a one-year deployment. Programming of Telemetry Solutions collars initially took a different approach where fix intervals were sampled from a negative binomial distribution with the intent of achieving more random sampling through time. The initial 11 collars all failed and so no data from these collars was incorporated in this study. A second set of 11 collars from telemetry solutions collars was deployed programmed to attempt regular fix intervals of 3 hours or a more randomized schedule that altered between fine (30 minute) and coarse (5 hours) fix intervals.

IDFG personnel monitored collars by fixed wing aircraft every other week and upon hearing a VHF beacon noted the state (i.e. alive or dead) of the mortality switch. Upon detecting a mortality signal, aircraft crew established the animal's location. Whenever possible, ground crews would investigate mortalities within 48 hours to determine cause of death. Monitoring flight data was subsequently combined with recovered GPS collars to build encounter histories for each animal at monthly intervals. Encounter histories represent the state of the animal at each time step where a 1 denotes the animal as alive and a 0 dead, application of these data is described under the heading *Survival Models*.

Our sampling scheme produced an initial collection of 442,196 GPS points from 133 individual elk. The number of successful fixes suggested an estimated fix rate of approximately 93%, which is less than a 10% data loss and the point at which coefficients are likely biased by data loss (Frair *et al.* 2004). However, we further filtered fixes by eliminating all fixes with a dilution of precision  $> 5$ , which removed 81,878 fixes (Lewis *et al.* 2007).

Finally, we related GPS fixes to environmental variables by sampling grids at the time and location of the fix using packages raster, rgdal and sp in program R. For static variables

like roads and aspect, time was not a consideration and the value of the grid cell within which the point fell was related to the fix. For temporally varying variables the month within which a fix was taken was related to the state of environmental variable in the same month. Years since fire was calculated by subtracting the year of the fire from the year of the GPS fix. Time varying environmental variables included EVI, fire and wolves, while aspect and roads remained constant in time.

## Resource Selection Models

We chose to estimate resource selection functions using the classic exponential link (McDonald 2013). It is this form of resource selection that appears to receive the most use in the literature and because of its simplicity and ease of implementation we assume it most likely to be used for conservation. We fit all RSF models using the readily available R package lme4 (R Development Core Team 2013).

Resource selection functions require a set of available points. Given availability of habitat data and a desire to examine the consequences of differential space use, our chosen scale of inference was equivalent to Johnson's 2<sup>nd</sup> order (Johnson 1980). We randomly selected points from the landscape to achieve a ratio of 4 random points for every used point in each period. The landscape, or study area, was defined by first calculating a 100% minimum convex polygon (MCP) using all elk points and then extracting the smallest square that the MCP fit inside. The last step was to buffer the MCP bounding box by 2 times the 99th quantile of the distance moved by elk in 4 hours. This arbitrary definition of the landscape accomplished two things 1) it expanded the area of consideration to encompass unused areas and 2) the reliance on the MCP made the procedure repeatable. We prevented random points from falling within bodies of water. Random points were assigned the time of the associated used point so that the same landscape, in time, would be sampled. Assigning a time to each available point was important because measures of the landscape changed through time. Environmental variable sampling followed the same procedure as that described under the *Elk Telemetry Data*

Model building began by fitting a univariate RSF for each month of the study and each of the five environmental variables with a random slope indexed by individual. Estimates of random slopes were then averaged over each individual to obtain the individual's propensity for selecting an environmental variable more or less than the population. After fitting univariate models, we proceeded to fit a suite of monthly multivariate models with random intercepts for each individual. However, prior to fitting multivariate models, we calculated Pearson's product-moment correlation coefficient to screen for multicollinearity and standardized covariate data. Standardization followed the recommendation of Gelman and Hill (2006) whereby we subtracted the mean value and divided by 2 times the standard deviation of covariate data. We fit the multivariate models and employed model averaging by AIC weight to obtain population level time varying monthly selection coefficients for each environmental variable. Model averaging ensured consistent model dimensions through time. The ability of model averaged estimates to predict space use was evaluated using K-fold cross validation with 5 folds (Boyce *et al.* 2002). Spearman rank correlations were calculated within each month and through time.

We used a random effects parameterization of the resource selection function. In our study random effects had several advantages including accounting for discrepancies in sample size among individuals, repeated measures within individuals, differences in individual selection patterns and autocorrelation among GPS fixes (Gillies *et al.* 2006). Furthermore, population level estimates allowed exploration of the temporal changes at large scales of organization. Inference from multivariate models concentrated on the temporal change in population selection because a separate RSF was fit for each month of the study. Whereas the random individual-specific slopes estimated in the univariate models provided a measure of individual variation from the population mean. Thus, we evaluated the relationship between resource selection and survival at the population level using variation in time and at the individual level using each individual's deviation from the population mean estimate.

## Habitat Encountered

To compare habitat selection to habitat encountered we needed to summarize the attributes of the resource units in which each animal was sampled by the GPS collar. This calculation followed the foci of the RSF analyses. To prepare the data we first calculated the mean value of habitat encountered by each individual in each period, which resulted in a monthly rate of acquisition for each individual. We then summarized these values at the population scale by taking the time indexed mean of habitat encountered across individuals. We captured individual differences by computing a unique mean for each individual. The data mirrored the RSF analyses in that we had a time-varying population level metric of habitat encountered and an individual level propensity to encounter a particular environmental variable.

## Survival Modeling

Survival was modeled by borrowing from Mark Recapture protocols (Lebreton *et al.* 1992) and assumed all fates known. It was necessary to assume known fate because the data available for this study consisted of collar deployment summaries. Nevertheless, we described survival as a binary random variable influenced by covariates that entered the model through a linear predictor with an inverse logit link to bound predictions between 0 and 1. Survival was further assumed to follow a Markovian structure whereby

$$\text{logit}(\mu_{i,t}) = B_{0,age} + B_{i,j}X_j + \gamma_i$$

$$y_{i,t} \sim \text{Bern}(\mu_{i,t} * y_{i,t-1}).$$

Thus, the state of animal  $i$  at time  $t$  ( $y_{i,t}$ ) is conditional on its state at  $t-1$  and a function of the current value of the linear predictor ( $\mu_{i,t}$ ). As shown above, the linear predictor was comprised of an age specific intercept ( $B_{0,age}$ ), coefficients ( $B_{i,j}$ ) and an individual specific random effect ( $\gamma_i$ ). This formulation of the model allowed us to accommodate animals

entering the study at different times and leaving the study before death. Further, all models incorporated separate intercepts for 5 age-at-capture categories and an indicator variable for animal sex. The 5 age-at-capture categories represented animals approximately 6 months of age, 18 months of age, 2-9 years of age, 10-14 years of age and a last category for animals greater than 15 years of age. All ages reference age-at-capture.

We used a Bayesian framework to fit survival models. Adopting a Bayesian perspective eased incorporation of uncertainty in population level RSF coefficient estimates and implementation of individual random effects. Because some of the covariate data were actually RSF model estimates, we included an observation model to admit uncertainty by assuming estimates normally distributed with a mean equal to the mean of the estimate and variance equal to the variance of the coefficient estimate. The value of the covariate was then drawn from this distribution at each iteration of the MCMC simulation to approximate the uncertainty of the RSF coefficient. Covariate data were centered and scaled using the same procedure as RSF modeling (Gelman & Hill 2006). Before fitting models, we examined covariate data for multicollinearity by calculating Pearson's product-moment correlation coefficient for all combinations of data. For comparison, we also fit the models without incorporating covariate error.

Bayesian survival models required prior distributions. We chose distributions with compact support,  $Unif(-10, 10)$ , for the effect of covariates ( $B_{i,j}$ ) and a  $Unif(0, 1)$  prior for the intercept of the linear predictor ( $B_{0,age}$ ), which was back transformed using  $\log(x/(1 - x))$ . Individual random effects were hierarchically centered and drawn from a normal distribution with standard deviation  $\sigma$ , which had a prior specification of  $Unif(0, 50)$ .

$$\gamma_i \sim Norm(0, \sigma)$$

Where  $\gamma_i$  is the deviation of individual  $i$  from the population mean.

### *Survival Model Variable Selection*

We used a Bayesian variable selection procedure following the framework of (Kuo & Mallick 1998). For each variable in the linear predictor we introduced an indicator variable  $w$  having a  $Bern(0.5)$  prior distribution and multiplied each variable by  $w$  such that the usual linear predictor

$$\text{logit}(\mu_{i,t}) = B_0 + B_j * x_{i,t},$$

became,

$$\text{logit}(\mu_{i,t}) = B_0 + w_j * B_j * x_{i,t}.$$

Using an indicator variable allowed us to calculate a posterior probability of inclusion for each environmental variable. The probabilities were computed by dividing the number of times the variable appeared in the model by the number of iterations in the MCMC simulation. Following the same procedure, it was also possible to calculate posterior model probabilities for a collection of variables. We used the variable selection procedure to determine the model with the highest posterior probability.

### *Survival Model Selection*

Following variable selection we fit the most supported habitat use and habitat selection models and compared them using deviance information criterion (DIC, (Spiegelhalter *et al.* 2002)). DIC is a Bayesian analog of the more familiar Akaike Information Criterion. The criterion attempts to balance model complexity with model fit by combining a measure of model complexity  $pD$  with model fit described by the deviance ( $D(\bar{\theta})$ ). The equation for DIC used was

$$DIC = D(\bar{\theta}) + 2pD$$

where

$$pD = \frac{1}{2} \text{var}(D(\bar{\theta})).$$

## *MCMC*

Bayesian survival models were updated for 130,000 iterations with the first 30,000 discarded. Three chains were thinned such that every fifth iteration was retained resulting in 20,000 samples of the posterior distribution. MCMC sampling was accomplished by calling JAGS from R through the package R2jags (Plummer 2003).

## **Results**

### Resource Selection Models

We fit multivariate and univariate RSF's for each month of the study period. More than 20 collared animals contributed data in the average month, but sample sizes diminished rapidly in the final few months of the study (Fig. 1). The age distribution of collared animals fluctuated throughout the study with animals 10-14 years of age comprising a majority of the sample initially and animals > 15 years of age dominating the sample in the last year (Fig. 1).

Model averaged results suggest that at large scales elk in our study area select most strongly for areas of high wolf concentrations in the winter months, December through April (Fig. 2). The magnitude of selection estimates for our wolf index suggested that other variables had less influence during these months. During the remaining months of the year, a more equitable influence of multiple environmental variables determined elk habitat selection, as evidenced by reduced variation in the magnitude of effect sizes (Fig. 2).

Direct comparison of the magnitude of effect among variables is possible because we standardized data prior to fitting models.

Temporal variation in habitat selection followed regular, if not cyclical, patterns through time (Fig. 2). Elk selection for EVI, fire and wolves remained largely positive in all months of the year, while selection for aspect and roads vacillated between positive and negative correlations (Fig. 2). Elk selection for EVI peaked in April each year of the study. Coefficient estimates for the effect of aspect suggested selection for southern aspects during cool winter months, but relatively equal use of north and south aspects during the warm summer months.

Cross-validation of the multivariate model exhibited high predictive power across months (Spearman rank = 1.0). Within any given month correlations proved highly variable (range = 0.4-1.0) and correctly ranked fixes moderately well with approximately 64% of models achieving a correlation of 0.8 or greater.

## Survival Models

Survival models converged within 10,000 iterations, exhibited adequate chain mixing and smooth unimodal posteriors. Convergence diagnostics obtained values below 1.1 for all parameters. Common to all survival models were strong effects of animal sex and age (Appendix 3-2). Estimates of the effect of sex were large and consistently positive, meaning that female elk survive at higher rates than males (Appendix 3-2). Age effects also followed very regular patterns. The youngest age class consistently exhibited the lowest survival (Appendix 3-2). Moving up the age classes survival increased from the first to the third age class before beginning a monotonic decline from the third to the fifth (Appendix 3-2).



### *Habitat Selection – Survival Model*

When considered with and without estimation uncertainty, habitat selection coefficients proved insignificant in describing variation in survival. Support for this conclusion comes from the posterior model probabilities displayed in Table 1. Neither the population level time varying nor the individual propensity selection coefficients warranted inclusion in any of the models. Relative to the amount of variation described by sex and age-at-capture RSF coefficients were an unsupported complication. Analyses stopped at the variable selection stage because of a lack of support for selection coefficients.

### *Habitat Encountered – Survival Model*

At the individual level, the model selection technique employed showed support for a model describing increased survival as a function of an individual's propensity to overlap spatially with wolves ( $\mu = -2.75$ ,  $SE = 0.37$ ) and high values of EVI ( $\mu = 0.95$ ,  $SE = 0.38$ ). Although, a second model that only included wolf avoidance received relatively similar support (Table 1).

At the population level, the most supported model again included wolf avoidance ( $\mu = -2.30$ ,  $SE = 0.63$ ), but at this level of organization using recently burned areas ( $\mu = 2.02$ ,  $SE = 0.61$ ) was more influential than EVI. Relative to the individual propensity model (DIC = 536.8, pD = 53.7), the time varying population level survival model had a much higher DIC value (DIC = 639.0, pD = 163.5,  $\Delta DIC = 102.2$ ).

## **Discussion**

We quantified resource selection and found a lack of relationship between resource selection coefficients and survival. The result held at both the population level and when allowing for individual variation. We also considered an alternative model that related survival to habitat encountered. The habitat encountered model proved useful in describing

the effects of wolves, EVI and fire year on elk survival. While the RSF models quantify relative probability of use, the habitat encountered model attempted to quantify the frequency and duration of habitat use. The two approaches quantify habitat in fundamentally different ways.

At the individual level, those animals showing high spatial overlap with wolves experienced lowered survival, but the negative effect of wolves was balanced in part by heightened survival with exposure to high values of EVI. Considering the population level, we found a similar negative effect of wolves and a contrasting positive effect of recently burned areas. In this way both the individual and population levels models point to a trade-off between areas of high predation risk and those areas with high potential for forage production, which may be the same spatial location. However, the magnitude of the estimates indicates that predation risk is a more influential factor than forage production.

We used DIC to compare individual and population models. We found the most support for models including individual level variation. Time-varying population level models lagged in their ability to explain variation in survival as a function of habitat encountered. As noted at the outset, individual's occupying heterogeneous landscapes have the opportunity to adjust their exposure to resources and risk by moving (Hooten *et al.* 2010). Inclusion of the wolf and EVI covariates in the most supported model suggests that how an individual chooses to adjust this exposure holds consequences for fitness (DeCesare *et al.* 2013). In addition, the overwhelming support for an individual based model implies that an animal's utilization of certain habitats is more predictive of survival than temporal fluctuations in resource availability or predation risk. Simply put, some habitats are consistently of higher quality than others and regardless of temporal fluctuations those individuals occupying high quality habitat will realize higher survival rates. This point reiterates the sentiment of Gaillard *et al.* (2010) who suggested that fitness derives from frequency and duration of resource use. Our results suggest that where an animal is on the landscape is likely more influential in determining its fitness than where it wants to be.

Several authors have identified pathways to non-ideal habitat selection and decoupling of habitat preference from realized fitness. Briefly, selection may decouple from fitness because of public information or social cues (Boulinier & Danchin 1997), a lack of information of the greater landscape (Lima & Zollner 1996), ecological traps (Schlaepfer, Runge & Sherman 2002) and attractive sink habitats (Pulliam & Danielson 1991). Elk are a social species that are likely subject to the effects of social cues, which may also foster a general lack of information of the larger landscape. We would also expect elk to be relatively ignorant of the larger landscape if sociality reduces exploration of the landscape by individuals. This behavior may also be similar in function to what (Nielsen *et al.* 2013) described as learning. At this time at least two other studies show a similar lack of correspondance between resource selection and fitness (Arlt & Pärt 2007; DeCesare *et al.* 2013), but (McLoughlin *et al.* 2006) found a positive relationship. Certainly more tests of the assumption that habitat selection is indicative of fitness seeking behavior are needed.

One reason to include a sample of available habitats in an analysis of habitat selection is to obtain a measure of the species' or individual's preference for a given habitat (Johnson 1980). The problem with including a measure of availability is the definition of this term because analysis results can be sensitive to the choice of available habitat (Johnson *et al.* 2008; Beyer *et al.* 2010). On the other hand, simple measures of use do not allow researchers to determine preference and as such represent a loss of information, but they also relieve investigators from the arbitrary assignment of availability. When preference is the desired outcome of investigation a used-available design is preferred. However, when the response of interest is fitness, or some surrogate of, there is no obvious choice of study design.

Results of the RSF analysis suggest that elk use areas of high wolf occurrence disproportionate to their availability. This result is perhaps surprising, but an alternative explanation is that the RSF is unable to tease apart the wolf following the elk from the elk following the wolf. In light of this idea, perhaps our results suggest that at large scales wolves do a better job of following elk than elk do of avoiding wolves. As mentioned in the introduction, Austin (2002) called the RSF a pattern based model. This statement

highlights that our result, that elk select for wolves, is free from perspective and process. The results of the RSF models simply relate the locations of elk to wolves in a phenomenological manner. As we highlighted with the odonate examples (Horváth & Zeil 1996; Wildermuth & Horv  th 2005; Kriska *et al.* 2008), a key advantage of the habitat encountered model is fidelity to fitness. The RSF suggests that elk encounter and select for areas with high concentrations of wolves while the habitat encountered model suggests that where the two species overlap elk accrue risk more rapidly. We say accrue risk because the mean, as calculated here, of habitat encountered by an individual is equivalent to a rate of acquisition and the metric proved useful in predicting decreased survival.

The approach used here to relate habitat selection and use to a fitness component differs from that of previous work. The work of (McLoughlin *et al.* 2006) quantified resource selection in a univariate fashion using selection ratios and lifetime reproductive success. Later, DeCesare *et al.* (2013) developed a multivariate approach that used a predictive map generated by a hierarchical RSF to quantify the instantaneous and cumulative acquisition of RSF values by individuals. The latter approach incorporated uncertainty by considering the mean and boundaries of coefficient confidence intervals. Key features of our approach include the ability to incorporate uncertainty in selection coefficient estimates and a model selection technique that allows the independent evaluation of each covariate and the model as a whole without the need to separately consider each possible combination of covariates. Further, we incorporated individual variation by using the residuals of marginal random effect estimates, but inclusion of error from these estimates remains a topic for future research.

We chose to evaluate habitat at a single scale. Relating habitat selection to survival involves quantifying differences among individuals. We chose a large scale of availability to quantify the differences in monthly space use because it allowed us to hold availability constant among individuals while use changed on an individual basis. Taking this approach ignores issues of accessibility, but has the advantage of simplifying the RSF (Beyer *et al.* 2010). The interpretation of habitat selection coefficients collected at this scale relates an individual's home range to resources available on the landscape.

Consequently, we interpret the coefficients of the survival modeling exercise to be related to the differences in quality among individual home ranges. Future efforts might standardize differences in availability at finer scales by leveraging the concept of functional resource selection (Myserud & Ims 1998).

Prescriptive application of habitat studies to matters of conservation requires validation of key model assumptions and ideally an understanding of how they relate to population dynamics. A desire to formulate long-term management plans challenges researchers to solidify these connections and facilitate meaningful and efficient preemptive action. The methods presented here represent another effort to make this connection between habitat and populations.

	Individual Propensity						Population Time Varying					
	Aspect	EVI	Fire Year	Road Density	Wolf	Posterior Model Probability	Aspect	EVI	Fire Year	Road Density	Wolf	Posterior Model Probability
RSF	0	0	0	0	0	0.60	0	0	0	0	0	0.58
	0	0	0	1	0	0.18	0	0	0	1	0	0.20
	0	0	0	0	1	0.04	0	1	0	0	0	0.04
	0	1	0	0	0	0.04	0	0	0	0	1	0.04
	1	0	0	0	0	0.04	0	0	1	0	0	0.03
Use	0	1	0	0	1	0.42	0	0	1	0	1	0.53
	0	0	0	0	1	0.37	0	0	0	0	0	0.15
	1	1	0	0	1	0.05	1	0	1	0	1	0.05
	0	1	0	1	1	0.04	0	1	1	0	1	0.05
	0	0	0	1	1	0.03	0	1	0	0	0	0.04

Table 3-1 Top five elk survival models for each combination of data considered. The top sets of five models related resource selection coefficients to survival while the bottom sets of five considered habitat encountered. Similarly, the left side of the table represents models focusing on individual variation and the right side considers time varying population level effects. Each row of the table depicts a unique model. Models are defined by 1/0 indicating the presence/absence of a variable. For example, a model coded as 00110 would include the effects of fire year and road density. The furthest right column contains posterior model probabilities. Note that the intercept always considered 5 age classes and animal sex was always included as an indicator variable.

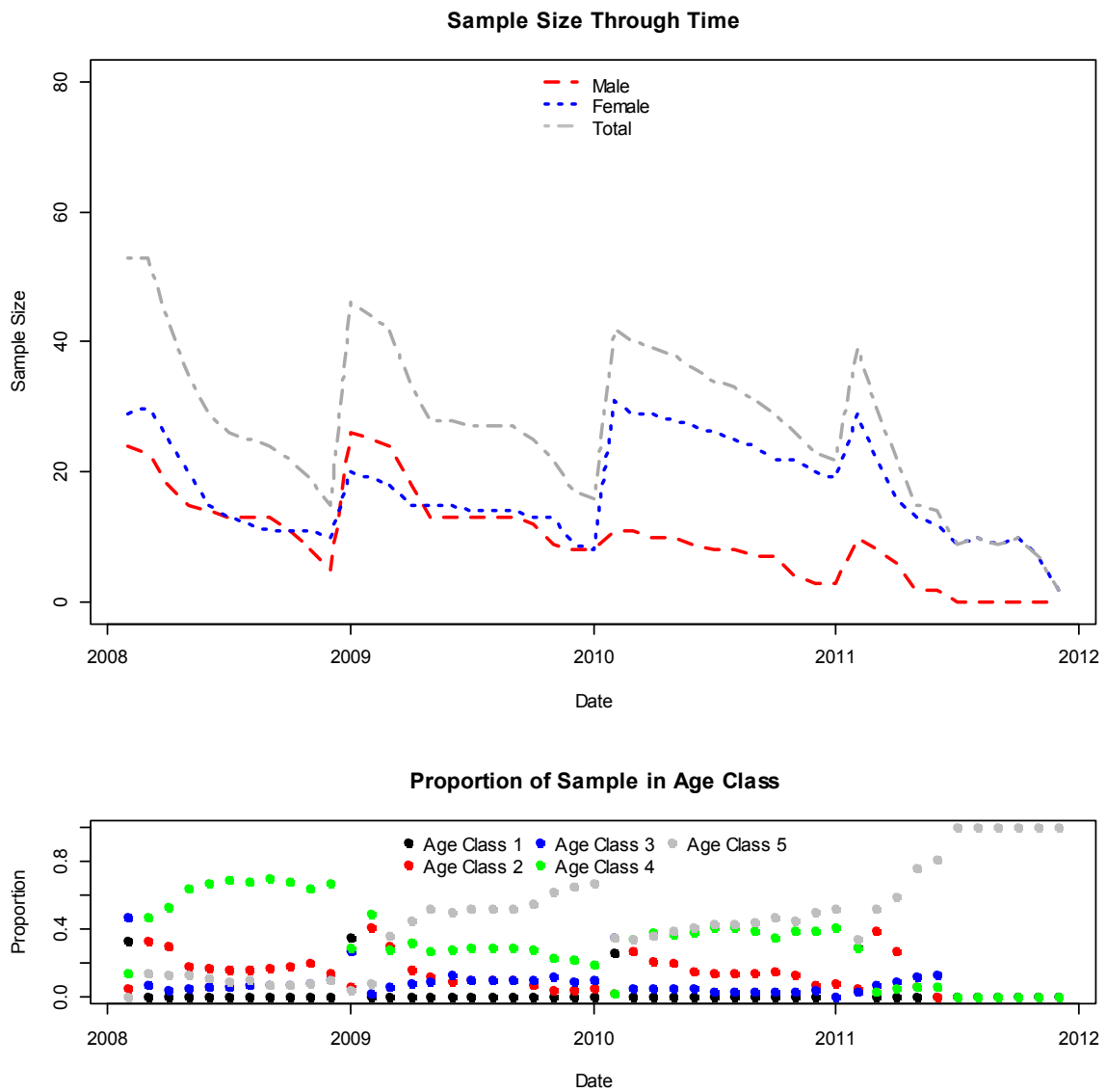


Figure 3-1 A plot of the changing sample size through time and the proportion of the sample comprised of 5 age classes used to model survival. The top panel displays the number of collared male elk with a dashed red line, while the number of collared female elk is represented with a dotted blue line. Atop both of these lines is the total sample size or the total number of collared elk in each month. Resource selection models were fit with data from both sexes (dashed and dotted gray line). The bottom panel shows which age classes comprise the sample. The five age classes were delineated such that animals  $\leq 1$  year of age were placed in age class 1, animals  $> 1$  and  $\leq 2$  years of age in age class 2 and so on until age class five, which represents animals older than 4 years of age. To create the plot we started the animal at the estimated age at capture and subsequently aged the animal each year.

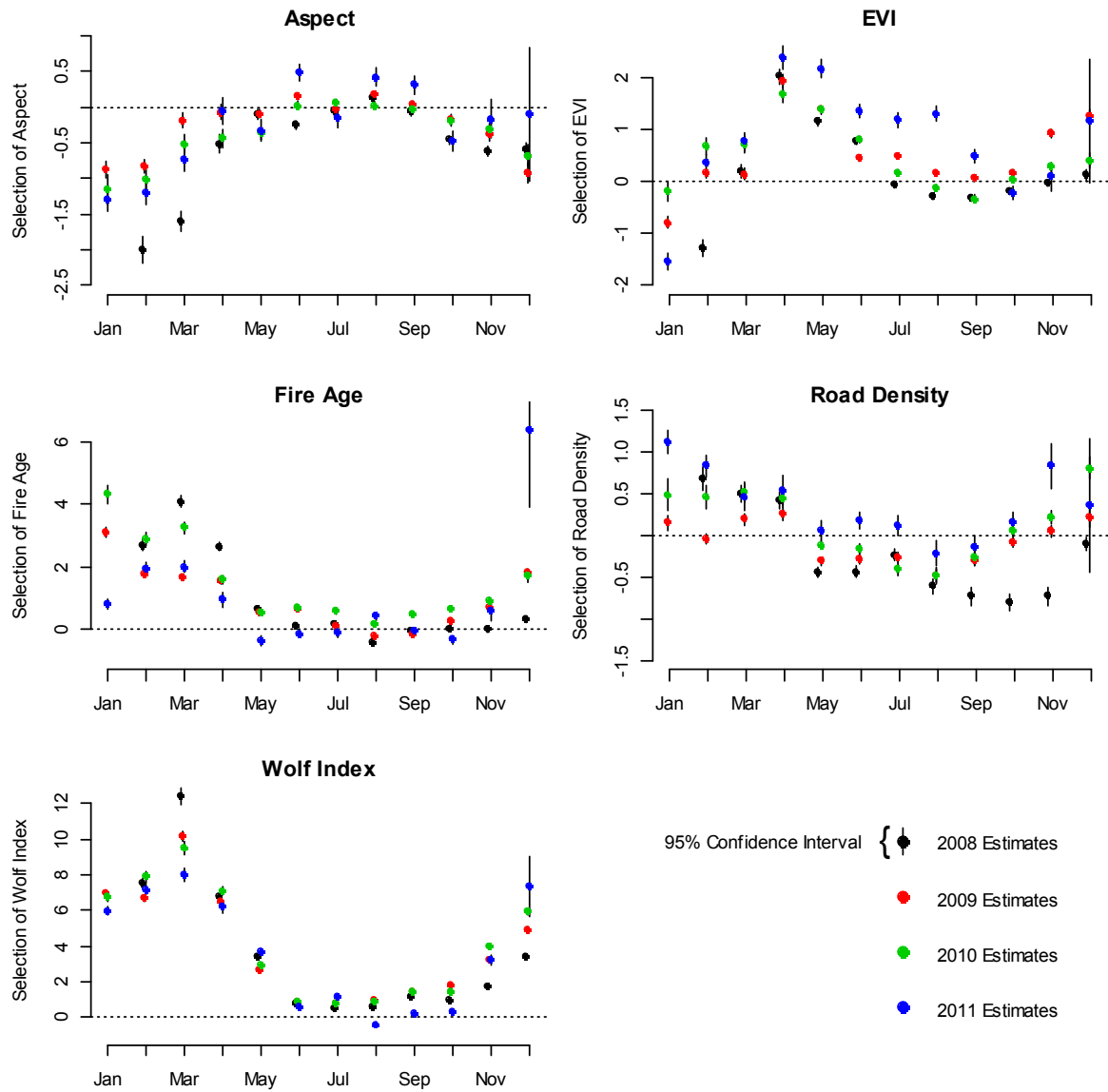
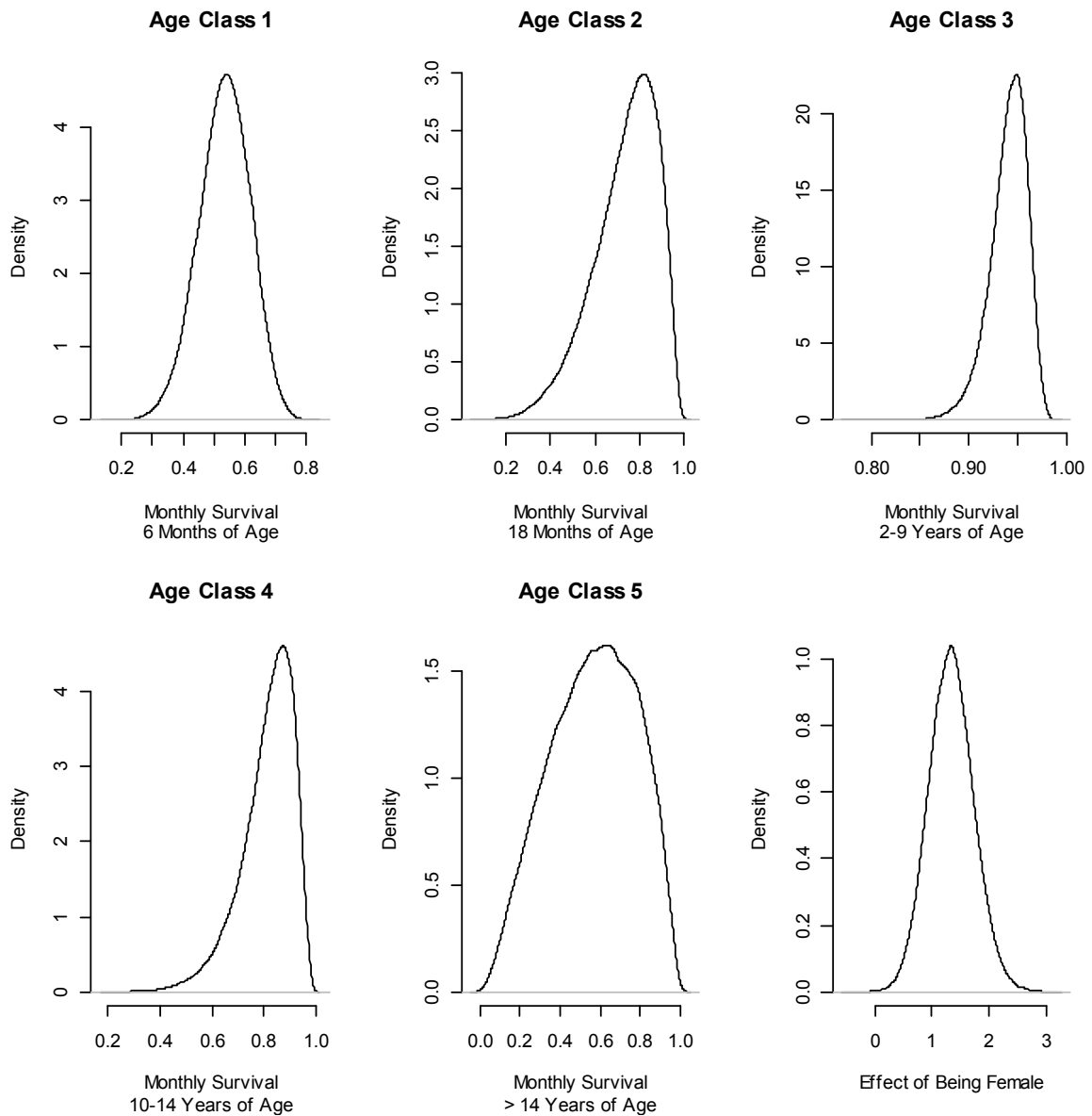


Figure 3-2 Plots of monthly habitat selection by elk in Idaho, USA. Colored dots show mean estimates while vertical bars depict 95% confidence intervals. Dots are coded such that the color signifies the year of the estimate where black, red, green and blue represent 2008, 2009, 2010 and 2011 respectively. A dashed line is included in each plot to mark 0, the point at which environmental variables are used equal to their availability.



## Appendix 3-1



Appendix 3-1 Age and sex specific elk survival estimates. Ages reference age-at-capture. An indicator variable represented whether an animal was a female or not. Models used a means parameterization for age and an effects parameterization for the effect of sex. Models that produced the estimates shown here did not include any habitat covariates.



## **GENERAL CONCLUSION**

Aldo Leopold (1933) defined wildlife management as “...the art of making land produce sustained annual crops of wild game for recreational use.” The contemporary wildlife manager works to provide sustainable yields of game in an increasingly litigious society. Further, they must defend their decisions to a well-informed public with strong opinions. The chapters detailed herein arm managers with tools that promise more and higher quality information than is available from summaries of raw data. They also bring methodological rigor to the decision making process. In sum, better information and employment of rigorous methodology suggest not only defensible decisions, but also a more informed and potentially effective decision-making process. These applied niceties come while explicitly accounting for species life history. Such overt accounting of the biology underlying population growth promises to lead to a deeper understanding of system dynamics and more accurate predictions. Diminishing knowledge gaps signal progress in achieving comprehensive system knowledge. Meanwhile the ability to address both short- and long-term strategies takes us one-step closer to proactive management.

### **Perceptions of Too Little Data**

Chapter 1 used simulation to quantify the effects of missing data and model misspecification when fitting population models. The primary conclusion of this chapter was that under typical circumstances wildlife managers could faithfully employ integrated population models (IPM) and inverse methods of model fitting. This conclusion should encourage managers to adopt similarly consistent and rigorous methods for estimating population parameters. Perceptions of insufficient data likely stifle the application of IPMs. However, our simulations clearly delivered the optimistic message that missing data and model misspecification carry minimal consequences (over the range of values considered). The methods also bring the benefit of a consistent model framework that, in this case, can be applied to the entire state. A consistent modeling framework is important for comparative studies and standardization of formal decision making protocols.

In this chapter, we promoted a model fitting approach. A primary advantage of model fitting is the ability to isolate observation error from process error. Error parsing facilitates predictions that do not include observation error while retaining process error (Calder *et al.* 2003; Clark & Bjørnstad 2004). Then too, model fitting avoids the pitfalls and advocacy associated with trial and error parameter optimization (White & Lubow 2002). IPMs and inverse methods also provide a non-invasive means of estimating demographic rates for long-lived species with slow to moderate reproductive rates. These ideas were put to work when fitting models to 51 elk management units in Idaho, USA. The estimates were the first of their kind for a majority of the units. In addition to being novel, the estimates also increased the quantity of information available in each unit.

Where model misspecification is likely large, fidelity of geometric mean growth rate suggested that at a minimum the method could be used to identify areas or species of concern. A mean growth rate contains similar information as trend estimation. Trend monitoring relegates management to a reactionary posture. Therefore, this result demonstrates need for methods that incorporate prior information or that share information in time and space.

## **Sharing Information**

The second chapter demonstrated the power of placing random effects on demographic parameters, which served as a means of sharing information in time and space. We also compared a suite of models that allowed recruitment and adult survival to vary in time or space. Deviance information criterion (DIC) arbitrated among models. The most supported model of elk population dynamics was a model that held recruitment constant and let adult survival vary in space. We also demonstrated increased precision with an IPM approach by comparing inverse methods of model fitting within a single data deficient unit.

The novelty of the random effects parameterization lies in the reliance on shrinkage to inform weakly identifiable parameters. Elk monitoring data available for this study

consisted of aerial surveys collected at low temporal frequency. Furthermore, supplementary data existed for only a small subset of management units. The random effects parameterization provided a means of sharing supplementary data through a hyperparameter characterizing the population's mean level of each demographic rate.

The model also estimated demographic rates within individual units, which is the level of organization of interest for management purposes. However, a recent shift in focus has managers considering aggregations of management units. This shift in focus poses no additional difficulties for the models presented here. Calculation of derived parameters will allow managers to scale parameter estimates and consider aggregations of units with associated uncertainty. A related issue is the potential for currently low priority units to become high priority in the future. The random effects IPM considered here retains the ability to switch emphasis without sacrificing the ability to estimate parameters.

## **Integrated Population Models – Future Directions**

Several unresolved issues remain for IPMs. First, the performance of model selection techniques remains unevaluated. The primary issues that suggest evaluation include missing data and the combination of several likelihoods. Future efforts using an iterative weighting process may prove more useful than model selection given that the application of IPMs typically focuses on prediction. Second, we did not consider density dependence or the incorporation of covariates to explain spatial or temporal variation in demographic rates. Third, we made the assumption of population closure. Open population variants of the models presented here exist, but they typically require special data that would be logistically onerous to collect. To this end, it would be simpler and cheaper to evaluate the scale at which biological processes occur. Again, the quantification of covariation in demographic rates seems a fruitful approach. Fourth, implementation of IPMs requires technical expertise. Biologist lacking the skills to implement such models could still benefit from their existence. Development of a simple user interface would increase accessibility of the models and promote their adoption by agency personnel. Fifth, the

incorporation of harvest data presents something of a crossroads. Evaluations of the additivity of harvest mortality typically focus on mortality or its complement survival. However, in the context of population modeling it would seem more useful to characterize mortality as additive on abundance. When harvest mortality is additive on abundance, say by subtracting number harvested from abundance, survival need not change rendering it compensatory. Unfortunately, ecological theory has little to offer this quandary.

## **Linking Habitat to Population Growth**

The third chapter focused on relating habitat selection and habitat encountered to survival (a surrogate of fitness). Habitat selection was quantified at the population and individual levels. We found no correlation between habitat selection coefficients and elk survival. A competing hypothesis suggested that the frequency and duration of habitat encountered better relates to the benefits conferred to individuals. This competing hypothesis was evaluated at the population and individual scales. Metrics of habitat encountered proved useful in describing variations in survival. Specifically, a model considering an individual's propensity to encounter wolves and green vegetation in open areas received the most support. These results suggest that where an animal wants to be is less predictive of individual performance than where it has been.

The prescriptive application of habitat studies is a long-term management tool that has the potential to increase recruitment rates and survival of all demographics. However, the assumption that habitat selection relates to fitness is rarely tested. We tested this assumption and found no evidence that habitat selection (as characterized here by resource selection functions) related to fitness. The Ideal Free Distribution suggests that density dependence will create relatively equal fitness across a landscape. Our results suggest the opposite is true. We found the most support for a model that described survival as a function of individual variation.

Quantifying the relationship among habitat and fitness components remains an open field. Few studies have pursued this course of inquiry in the field. Because of this many questions remain. For example, the work of (DeCesare *et al.* 2013) used the outcome of the selection process to quantify an individual's selection. Here, we used individual selection coefficients because we did not assume that all coefficients influenced survival. The difference is subtle, but likely important to overall model performance. Simplifying the models and providing useful guidance for validation of habitat studies should remain a priority.

## **Put It All Together**

Estimating population parameters from limited noisy data is a challenge. Here we have described a validation of methods and application of a novel model. Then we related habitat to fitness. Together these components suggest the application of IPMs as a consistent framework for management at large and small spatial scales. The models allow managers to make predictions, test hypotheses, and iteratively manage populations. Further, the application of a single scalable modeling framework provides consistency. In short, the models efficiently extract maximum information from limited data and make possible data informed decision-making.





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