

Wildlife mortality from infrastructure collisions: statistical modeling of count data from carcass surveys

BRYAN S. STEVENS¹ AND BRIAN DENNIS

Departments of Fish and Wildlife Science and Statistical Sciences, University of Idaho, Moscow, Idaho 83844 USA

Abstract. Anthropogenic infrastructure is a mortality source for many vertebrate species. Mortality is often measured using periodic counts of carcasses or remains at infrastructure segments, and bias from carcass removal is estimated via field experiments with wildlife carcasses. We describe a model for combining removal experiment and carcass count data to estimate underlying process parameters using joint likelihood. In the model, the instantaneous number of carcasses present is a stochastic birth–death process with Poisson arrivals (carcass addition) and proportional deaths (removal of carcasses). The approach accommodates modeling heterogeneity in the addition and removal processes using generalized regression. Results of fitting the model to a Greater Sage-Grouse (*Centrocercus urophasianus*) fence collision data set show that order of magnitude differences in expected carcass counts can be a function of spatial differences in removal and suggest caution for interpretation of many published studies. While the model assumption of negligible detection error may be tenable for some systems, the modeling framework provides a starting point for future state-space versions incorporating detection error.

Key words: carcass persistence; collision; fatality monitoring; fatality searches; fences; power lines; roadkills; road mortality; scavenger removal; vehicle collision; wind energy; wind turbines.

INTRODUCTION

Anthropogenic infrastructure causes substantial mortality for a variety of terrestrial vertebrate species (Forman and Alexander 1998). Ground level infrastructure such as roads and elevated structures such as wind turbines, power lines, fences, and communication towers kill ungulates (Groot Bruinderink and Hazebroek 1996), mesocarnivores (Grilo et al. 2009), amphibians (Langen et al. 2009), and birds and bats (Bevanger 1994, Kunz et al. 2007, Gehring et al. 2009). Forman and Alexander (1998) suggested automobiles alone may kill one million vertebrates per day on roads in the United States via automobile collision. Elevated infrastructure primarily kills flying vertebrates via mid-air collision (Bevanger 1994, Kunz et al. 2007, Kuvlesky et al. 2007). Localized effects of infrastructure mortality on wildlife demography can be severe, particularly for threatened and endangered species (Mumme et al. 2000, Haines et al. 2005). Moreover, the problem is exacerbated by the ubiquitous nature of existing infrastructure (e.g., roads and power lines; Bevanger 1994, Riitters and Wickham 2003) and the ongoing development of new structures (e.g., wind turbines; Kuvlesky et al. 2007).

Wildlife collision mortality is often measured using carcass surveys at infrastructure units, but carcass counts are biased low because of imperfect detection and removal of evidence prior to sampling (Smallwood 2007, Santos et al. 2011, Stevens et al. 2011). We define evidence removal bias as the removal of carcasses during the intervals between infrastructure collision surveys, and refer to the failure of field observers to locate carcasses conditional on their presence during sampling as detection error. Magnitude of errors caused by failed detection and removal of evidence are estimated via field experiments using randomly placed carcasses coupled with detection trials and persistence monitoring (Smallwood 2007, Santos et al. 2011, Stevens et al. 2011). Although field experimentation to estimate biases is common, the way this information is used to make inferences on collision risk varies (Arnett et al. 2008, Huso 2011). Much recent work has focused on the development of point estimation techniques for total fatality at a given site over time (Smallwood 2007, Huso 2011, Korner-Nievergelt et al. 2011). However, these estimators assume constant collision mortality across space and time and do not address methods to model heterogeneity in collision risk. Subsequently, many studies used uncorrected carcass counts to evaluate hypotheses regarding collision risk, assuming the raw counts adequately represent the collision mortality process (e.g., Gehring et al. 2009, Barrientos et al. 2011).

Determining what factors contribute to infrastructure mortality is a research and conservation need, and valid statistical methods are a prerequisite of this work (Kunz

Manuscript received 21 June 2012; revised 6 March 2013; accepted 12 March 2013. Corresponding Editor: K. B. Newman.

¹ Present address: Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources, East Lansing, Michigan 48824 USA.
E-mail: stev8930@vandals.uidaho.edu

et al. 2007, Kuvlesky et al. 2007). Thus, a framework to model infrastructure mortality and bias parameters directly as a function of covariates is warranted. Existing methods for combining removal experiment data with carcass counts from infrastructure surveys focus on estimating total fatality. Although some methods permit modeling heterogeneity in removal processes (e.g., Huso 2011), existing methods do not incorporate heterogeneity in carcass addition processes (i.e., collision mortality) adequately. Therefore, our objective was to develop a modeling framework to combine data from removal experiments with carcass counts that accommodates covariates on addition and removal rate parameters. We present likelihood-based models for the carcass count and removal experiment data sets and a joint-likelihood model to combine data sets and model heterogeneity in process parameters using generalized regression, under the assumption of perfect detection during sampling. The model under perfect detection, albeit unrealistic for many field studies, provides a theoretical process model and starting point for more complicated state-space models including detection error.

METHODS

Modeling count data and population change using a stochastic birth–death process

Let $X(t)$ denote the number of carcasses present and available for detection at time t . We treat $X(t)$ as a population of carcasses that changes in size according to a stochastic birth–death process. In this context, births and deaths are more appropriately thought of as additions and removals, where a mortality event for an individual animal represents a birth or addition to the population of carcasses. Similarly, removal of a carcass via scavenging or other factors represents a death or loss from the carcass population. Additions to the carcass population (i.e., births) are analogous to adding individuals to a population via immigration because they are independent of the current number of carcasses present (Huso 2011). Therefore, we modeled change in $X(t)$ as a stochastic linear immigration–death process (hereafter SLID), with rates for addition and removal of carcasses constituting the immigration and death rates (Bailey 1964, Matis and Kiffe 2000).

A deterministic version of the model is represented by the following differential equation:

$$\frac{dX}{dt} = \theta - \psi X \tag{1}$$

where θ is the addition rate, ψX is the state-dependent removal rate (proportional to the number of carcasses present), and ψ is the per carcass removal rate. Eq. 1 has the following solution:

$$X(t) = X_0 e^{-\psi t} + (1 - e^{-\psi t}) \frac{\theta}{\psi} \tag{2}$$

where X_0 is the initial number of carcasses present at time zero (i.e., $X(0) = X_0$). A deterministic differential

equation similar to Eq. 1 underlies the modified point estimator of total fatality evaluated by Huso (2011); however, the estimator is limited by the assumption of constant addition rate (θ).

Addition and removal of carcasses to the population are stochastic processes that depend on a number of factors (e.g., target species and scavenger movement patterns, local weather). Therefore, we modeled carcass population size using a stochastic version of Eq. 1, with the assumption that only process error is present. The SLID model assumes population size $X(t)$ is a continuous-time, homogenous Markov process, with birth rate θ and state-dependent death rate ψx , where x is any given nonnegative integer state of $X(t)$. Thus, the length of time until the next addition or removal, given $X(t) = x$, has an exponential distribution with a mean of $1/(\theta + \psi x)$ (for instance, Allen 2003). The model assumes adding carcasses to the population is a Poisson process, whereas lifetimes of individual carcasses in the population have an exponential distribution (i.e., constant hazard rate). Under the Markov property, the probability distribution of future carcass population size depends only on the current number of carcasses and model parameters θ and ψ (Matis and Kiffe 2000). Let $p(x, t | X_0)$ be the so-called transition probability density function for $X(t)$; that is, the probability x carcasses are present after time t given the initial population size of X_0 . Fitting the model to data requires stochasticity to describe departure of data from the model, and the transition probability density function is the key to connecting the model with data to estimate process parameters.

To develop likelihoods for this model we assumed that carcass count surveys occur at J infrastructure units on K occasions over a relevant time period, and all remains (e.g., carcasses, feathers) are removed at each occasion by investigators. Perfect detection and removal of remains implies the population of carcasses grows from zero after each sampling occasion. For the SLID model where $X_0 = 0$, $X(t)$ has a Poisson distribution with time-dependent mean function $\lambda(t)$ (written $X(t) \sim \text{Poisson}(\lambda(t))$; Cox and Miller 1965, Matis and Kiffe 2000), with

$$\lambda(t) = (1 - e^{-\psi t}) \frac{\theta}{\psi} \tag{3}$$

Thus, each sampling-interval time provides a unique Poisson distribution for the observed number of carcasses. Because carcasses are removed, the transition probability for future population size becomes conditional on the population size of zero instead of the population size observed on the current sampling occasion (i.e., after $X(t)$ is set to 0), and the conditional probabilities for $X(t+s)$ equal the marginal probabilities associated with a starting population size of zero (i.e., $p(x, t+s | X(t) = 0) = p(x, s | X_0 = 0)$). This effectively changes the time series of carcass count observations at each sample unit from a Markov chain to a series of

independent counts. If carcass counts for sample unit j are denoted x_1, x_2, \dots, x_K , the likelihood for this data is a product of Poisson transition density functions

$$L(x_1, \dots, x_K | \alpha_1, \dots, \alpha_K, \theta) = \prod_{k=1}^K \frac{(\theta \alpha_k)^{x_k} e^{-\theta \alpha_k}}{x_k!} \quad (4)$$

where $\alpha_k = (1/\psi)(1 - e^{-\psi t_k})$ and t_1, t_2, \dots, t_K are the lengths of time since the previous sampling event (i.e., the length of time of carcass accumulation). Carcass population size $X(t)$ has a unique stationary distribution as $t \rightarrow \infty$ that assumes $X(t)$ has reached stochastic equilibrium (hereafter stationarity). Equilibrium population size (X^*) has a unique stationary Poisson distribution

$$X^* \sim \text{Poisson}\left(\frac{\theta}{\psi}\right). \quad (5)$$

The stationary distribution of X^* is independent of the initial population size (X_0) and the length of time carcasses have been accumulating (t), and the length of time required to reach stationarity for this model depends on the ratio θ/ψ (Fig. 1; Bailey 1964, Matis and Kiffe 2000). Therefore, if time intervals between count observations at a given sample unit are long enough for the SLID process to approach equilibrium, Eq. 5 could be a useful model for all count observations.

A challenging reality exists with real carcass count data where the length of time for carcass accumulation is unknown at the first sampling event (i.e., t_1 is unknown). This difficulty results in many studies discarding data from the first sampling occasion (i.e., clean-out searches; Korner-Nievergelt et al. 2011), and precludes the use of Eq. 4 as the likelihood for data from the first sampling occasion. However, data are expensive and time consuming to collect, and our modeling framework can accommodate observations from $k = 1$ if we assume they follow the stationary distribution (Eq. 5), which is time independent. Thus, the likelihood for all observations at sample unit j becomes the product of density functions for $k = 1$ and $k > 1$ as follows:

$$L(x_1, \dots, x_K | \alpha_2, \dots, \alpha_K, \theta) = \frac{\left(\frac{\theta}{\psi}\right)^{x_1} e^{-\frac{\theta}{\psi}}}{x_1!} \prod_{k=2}^K \frac{(\theta \alpha_k)^{x_k} e^{-\theta \alpha_k}}{x_k!}. \quad (6)$$

Similarly, the likelihood for all collision count observations is the product of likelihoods for each of the J sample units

$$L(x_{11}, \dots, x_{JK} | \alpha_{12}, \dots, \alpha_{JK}, \theta) = \prod_{j=1}^J \left[\frac{\left(\frac{\theta}{\psi}\right)^{x_{j1}} e^{-\frac{\theta}{\psi}}}{x_{j1}!} \prod_{k=2}^K \frac{(\theta \alpha_{jk})^{x_{jk}} e^{-\theta \alpha_{jk}}}{x_{jk}!} \right]. \quad (7)$$

If intervals between subsequent observations at a given sample unit are long enough for $X(t)$ to approach

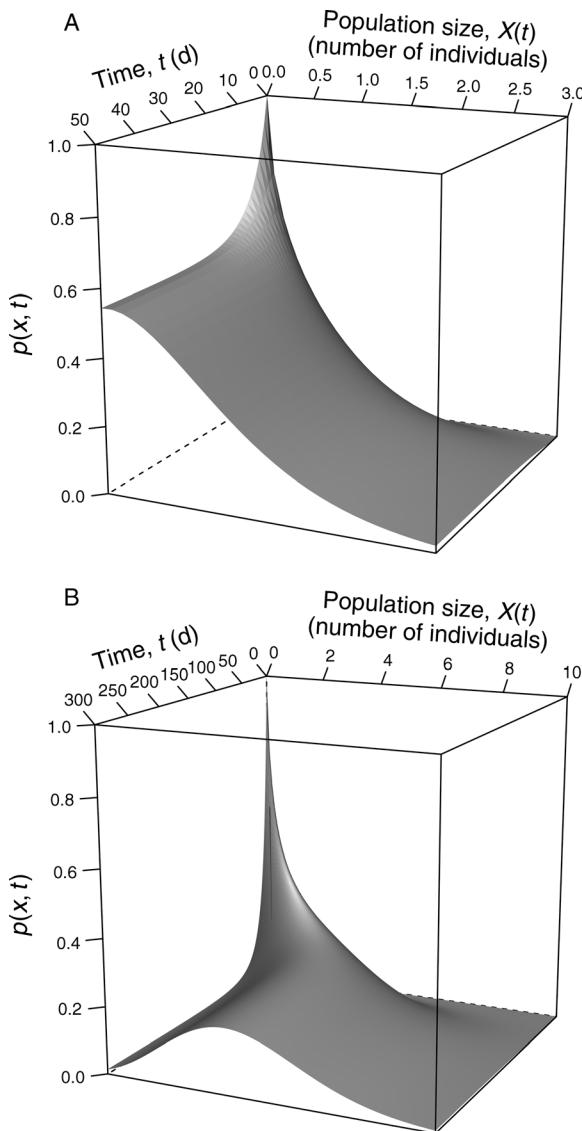


FIG. 1. Plots of the transition probability density function [$p(x, t) | X_0 = 0$] of population size at time t , $x(t)$, approaching its stationary distribution over time (measured in days) from the stochastic linear immigration–death (SLID) model. $X(t) \sim \text{Poisson}[\lambda(t)]$, where $\lambda(t) = \theta/\psi \times (1 - e^{-\psi t})$ for the SLID model when the population starts growing from size zero. These plots show the distribution of $X(t)$ for $\theta = 0.09$ and (A) $\psi = 0.148$ or (B) $\psi = 0.021$, and they illustrate the role of θ/ψ in determining the speed that stationarity is reached. Values of θ and ψ used to generate plots come from example model fitting, and plots are smoothed versions of discrete distributions. See the *Methods: Modeling count data and population change using a stochastic birth-death process* for further clarification of variables.

stationarity, a simplified version of the count-data likelihood is

$$L(x_{11}, \dots, x_{JK} | \theta, \psi) = \prod_{j=1}^J \prod_{k=1}^K \frac{\left(\frac{\theta}{\psi}\right)^{x_{jk}} e^{-\frac{\theta}{\psi}}}{x_{jk}!}. \quad (8)$$

Under this model, the length of time between observa-

tions required to achieve independent carcass counts depends on the average per carcass survival time ($\sim 1/\psi$; Cox and Miller 1965).

Combining carcass counts with auxiliary data from removal experiments

In practice, a carcass count data set alone may or may not be able to estimate θ or ψ uniquely, and researchers collect auxiliary information about ψ using carcass removal experiments. Commonly used point estimators of fatality estimate removal using field experiment data, and often propagate the effects of removal uncertainty on fatality estimates using bootstrapping (Huso 2011). We developed a model and likelihood for this auxiliary data set and combined the carcass count and removal experiment data sets using joint-likelihood techniques. If carcasses are placed randomly on study areas and monitored over time (not necessarily at regular intervals or daily), the removal experiment observations are analogous to observing the size of a population that is changing through time via a stochastic death process. Bailey (1964) showed that lifetimes of individuals with a constant hazard rate (i.e., constant removal probability through time) follow an exponential distribution. Using this model for the carcass removal experiment assumes removal probability for individual carcasses is independent of carcass age. Under these assumptions, the number of carcasses in the population remaining after time t follows a binomial distribution (Bailey 1964). If c carcasses are deposited and evidence from r carcasses remains after time t , then

$$p(r | c, t, \psi) = \binom{c}{r} e^{-r\psi t} (1 - e^{-\psi t})^{c-r} \tag{9}$$

where per carcass survival probability for t units of time equals $e^{-\psi t}$. Removal experiments typically monitor for more than one occasion (e.g., Smallwood 2007, Stevens et al. 2011). Therefore, the likelihood for the entire removal experiment is a product binomial, where carcasses are monitored for M occasions after initial placement as follows:

$$L(r_1, \dots, r_M | t_1, \dots, t_M, c_1, \psi) = \prod_{m=1}^M \binom{c_m}{r_m} e^{-r_m \psi t_m} (1 - e^{-\psi t_m})^{c_m - r_m} \tag{10}$$

where c_m is the number of carcasses remaining at the start of each interval, r_m is the number of those carcasses remaining after time t_m , and $c_m = r_{m-1}$ for $m > 1$. This model again assumes population size is a first-order Markov process, and observations of this process through time represent a Markov chain resulting in the likelihood of Eq. 10 (i.e., $P(r_1 | t_1, c_1, \psi)P(r_2 | r_1, t_2, \psi) \dots P(r_M | r_{M-1}, t_M, \psi) = L(r_1, \dots, r_M | t_1, \dots, t_M, c_1, \psi)$). Careful attention is needed for proper use of Eq. 10 when carcasses are not placed and monitored at the same time (e.g., staggered entries). In this case, the product binomial is

still a valid likelihood under the assumption of independence between different sets of monitored carcasses. Thus, each set of carcasses would result in a separate product-binomial likelihood, and the likelihood for all carcass removals would be the product of the individual likelihoods of the form of Eq. 10. In this case monitoring the interval lengths for each group of carcasses separately is necessary, and M for the full likelihood becomes the total number of monitoring events for all sets of carcasses.

We use joint-likelihood techniques to combine data from carcass counts and removal experiments to estimate process parameters of the SLID model. Information about ψ is provided from both the carcass counts and removal experiment, and the joint-likelihood model is

$$L(x_{11}, \dots, x_{JK}, r_1, \dots, r_M | \alpha_{12}, \dots, \alpha_{JK}, t_1, \dots, t_M, c_1, \theta, \psi) = \prod_{j=1}^J \left[\frac{\left(\frac{\theta}{\psi}\right)^{x_{j1}} e^{-\frac{\theta}{\psi}}}{x_{j1}!} \prod_{k=2}^K \frac{(\theta \alpha_{jk})^{x_{jk}} e^{-\theta \alpha_{jk}}}{x_{jk}!} \right] \times \prod_{m=1}^M \binom{c_m}{r_m} e^{-r_m \psi t_m} (1 - e^{-\psi t_m})^{c_m - r_m}. \tag{11}$$

If we assume all counts come from the stationary Poisson distribution, the joint likelihood reduces to

$$L(x_{11}, \dots, x_{JK}, r_1, \dots, r_M | t_1, \dots, t_M, c_1, \theta, \psi) = \prod_{j=1}^J \prod_{k=1}^K \frac{\left(\frac{\theta}{\psi}\right)^{x_{jk}} e^{-\frac{\theta}{\psi}}}{x_{jk}!} \prod_{m=1}^M \binom{c_m}{r_m} e^{-r_m \psi t_m} (1 - e^{-\psi t_m})^{c_m - r_m}. \tag{12}$$

Maximum-likelihood estimators for θ and ψ in Eqs. 11 and 12 must be optimized numerically. Moreover, models fit using the transient and stationary carcass count likelihoods can be compared with the data using goodness-of-fit measures or model selection criteria.

Modeling heterogeneity in process parameters and evaluating model fit

A primary advantage of a likelihood-based model is the ability to include covariates on addition and removal parameters using the techniques of generalized regression. Under the model the addition rate (θ) is assumed a positively valued Poisson process parameter. Thus, it is natural to model θ as a function of covariates in a Poisson regression using the log link function:

$$\log(\theta) = \beta_0 + \beta_1 Y_1 + \dots + \beta_q Y_q$$

where β_i are coefficients for the intercept and q hypothesized covariates. The removal rate (ψ) is defined as the rate parameter for the exponential model of individual lifetimes, and is similarly bound to be positively valued. Thus, we also modeled ψ as a function

of covariates using the log link function. In practice, researchers are often interested in the number of additions to the system over a time period. After fitting models of interest, maximum-likelihood estimates of the number of additions over a relevant time period (e.g., total mortality per season) can be derived as a function of the regression covariates by multiplying $\hat{\theta}$ by the period length. For example, if θ is reduced by a mitigation method (e.g., fence or power line marking), one could evaluate hypotheses regarding mitigation treatment effects and obtain maximum-likelihood estimates of total mortality over a relevant season for infrastructure with and without mitigation efforts.

Residual analyses can also be used to evaluate the Poisson model assumption of the carcass count data. Standard residual analyses can be performed using the Freeman-Tukey (FT) residual for Poisson models given by

$$\sqrt{x_i} + \sqrt{x_i + 1} - \sqrt{4\hat{\lambda}_i + 1}$$

where x_i are observed carcass counts and $\hat{\lambda}_i$ are model-fitted values (Bishop et al. 1975). The FT residual is approximately normally distributed with constant variance if the data come from a Poisson model (Bishop et al. 1975). Thus, FT residuals can be used to evaluate model assumptions using quantile comparison and residual-by-fitted-value plots (Fox 2008).

Goodness-of-fit tests for the SLID model can be constructed using the model deviance statistic. McCullagh and Nelder (1989) showed the generic deviance expression for a Poisson model reduces to

$$2 \sum_{i=1}^n \left\{ [x_i \ln(x_i/\hat{\lambda}_i)] - (x_i - \hat{\lambda}_i) \right\} \quad (13)$$

for n counts, whereas deviance for the binomial model reduces to

$$2 \sum_{m=1}^M \left\{ [r_m \ln(r_m/\hat{\delta}_m)] + (c_m - r_m) \ln[(c_m - r_m)/(c_m - \hat{\delta}_m)] \right\} \quad (14)$$

where $\hat{\delta}_m$ are model fitted values (i.e., $\hat{\delta}_m = c_m e^{-\psi^m}$), and M is the number of binomial trials, each with r_m successes and c_m trials. Thus, deviance for our joint-likelihood model is twice the sum of deviance for collision counts and the carcass removal experiment

$$D = 2 \left[\sum_{i=1}^n \left\{ \left[x_i \ln \left(\frac{x_i}{\hat{\lambda}_i} \right) \right] - (x_i - \hat{\lambda}_i) \right\} + \sum_{m=1}^M \left\{ [r_m \ln(r_m/\hat{\delta}_m)] + (c_m - r_m) \ln \left[(c_m - r_m) / (c_m - \hat{\delta}_m) \right] \right\} \right]. \quad (15)$$

For the null hypothesis that the model fits the data, D

has an asymptotic χ^2 distribution, and the saturated model has $n + M$ parameters (Wilks 1938).

EXAMPLE USING GREATER SAGE-GROUSE FENCE COLLISION DATA

Data and model descriptions

We fit the SLID model to a Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter sage-grouse) fence collision data set from southern Idaho, USA. Stevens et al. (2011) showed detection bias during sage-grouse fence collision surveys can be large; however, the data set is useful for the purpose of illustrative model fitting. Stevens et al. (2012) described a field experiment where the effectiveness of reflective markers at reducing sage-grouse fence collision was tested, and our example used this data set. In this study, the fate of all collision victims was not ascertained (some collisions recorded were just feathers and tissue on the fences), thus, θ is interpreted as a collision rate, not a true mortality rate (Stevens et al. 2012). The field experiment consisted of 48 500-m fence segments spread across breeding areas of southern Idaho, where 24 fence segments were randomly marked and 24 were unmarked controls (Stevens et al. 2012). Study locations for fence marking were selected using pilot surveys of fences across southern Idaho (Stevens et al. 2012). Specifically, areas were included in this study where >2 collisions/km of fence were recorded during pilot surveys. Thus, study fence segments were selected independent of site-specific sage-grouse space-use data. The fence-marking treatment consisted of reflective vinyl markers attached to the top fence strand at 1-m intervals, whereas unmarked controls were simply unmodified barbed-wire fence segments (Stevens et al. 2012). Each 500-m segment was sampled on five occasions during the 2010 breeding season at approximate two-week intervals (range = 11–16 days), resulting in 240 collision count observations. Sage-grouse exhibit a lek mating strategy, where traditional display leks are often used for many years (Dalke et al. 1963). Although study fences were selected independent of lek location and local abundance data, we hypothesized a priori these factors would contribute to sage-grouse collision risk. Thus, covariates used to model θ included fence-marking treatment (binary indicator variable), distance from the midpoint of each 500-m segment to the nearest sage-grouse lek (range = 104–4650 m), and number of sage-grouse displaying at the nearest lek (range = 1–127 birds; Stevens et al. 2012). Moreover, we did not hypothesize additional regional effects on sage-grouse fence collision risk, and assumed spatial variation in collision rate would be described by lek location and local abundance covariates.

Stevens et al. (2011) conducted a carcass removal experiment to estimate removal bias in sagebrush-steppe habitats. This study placed 100 pen-raised hen Ring-necked Pheasant (*Phasianus colchicus*) carcasses (surrogates for sage-grouse) randomly along fences and monitored their persistence every 1–3 d for a maximum

TABLE 1. Model rankings for stochastic linear immigration–death (SLID) model fit to the Greater Sage-Grouse (*Centrocercus urophasianus*) fence collision data set from southern Idaho, USA.

Model†	Likelihood‡	K§	ΔAIC	AIC
$\theta(\text{trt} + \text{lsize} + \text{distance}), \psi(\text{region})$	SD	6	0	356.534
$\theta(\text{trt} + \text{lsize} + \text{distance}), \psi(\text{region})$	TD	6	9.844	366.378
$\theta(\text{trt} + \text{lsize} + \text{distance}), \psi(\cdot)$	TD	5	84.291	440.825
$\theta(\text{trt} + \text{lsize} + \text{distance}), \psi(\cdot)$	SD	5	86.557	443.091
$\theta(\cdot), \psi(\cdot)$	TD	2	168.176	524.710
$\theta(\cdot), \psi(\cdot)$	SD	2	170.168	526.702

Note: Covariates were fence-marking treatment (trt), size of nearest lek (lsize), distance to nearest lek (distance), and intercept only (·).

† The model form is $\log(\theta) = \beta_0 + \beta_1 Y_1 + \dots + \beta_k Y_k$ and $\log(\psi) = \gamma_0 + \gamma_1 Y_1 + \dots + \gamma_k Y_k$, where θ is the daily collision rate and ψ is the per carcass daily removal rate.

‡ SD is the joint likelihood assuming all collision counts are from stationary Poisson distribution (Eq. 12). TD is the joint likelihood using the transition probability distribution for collision counts for observations after the first sampling occasion (Eq. 11).

§ Number of model parameters.

of 31 days (Stevens et al. 2011). Survival of collision remains was defined as presence of carcasses, scavenged remains, or ≥ 5 feathers at the location of carcass placement. Sage-grouse are a species of conservation concern across Idaho and many parts of the Intermountain West; thus, it was not feasible to obtain sage-grouse carcasses for removal experiments. Hen pheasants used in this study were the most similar available in size and cryptic plumage to sage-grouse, which should have minimized error caused by using a nontarget species to estimate carcass removal (Osborn et al. 2000, Smallwood 2007). Moreover, carcasses were placed along >54 km of discontinuous fence spread over $>15\,000$ ha of sagebrush steppe across two study regions (Stevens et al. 2011). Thus, predator swamping effects of carcass placement should be minimal. Stevens et al. (2011) provided evidence for regional variation of removal; thus, we modeled ψ as a function of a binary variable indicating region (1 = southeast Idaho, 0 = Magic Valley region), and combined removal and collision count data sets to estimate SLID model parameters. For the purposes of region-specific removal rates, fences west of Craters of the Moon National Monument were considered in the Magic Valley region, whereas fences east of this location were located in southeast Idaho. This resulted in 12 500-m segments in the Magic Valley (six marked and six unmarked) and 36 500-m segments in southeast Idaho (18 marked and 18 unmarked).

We fit six models to the sage-grouse data sets and compared them using Akaike’s Information Criterion (hereafter AIC; Akaike 1973). We fit models with three different covariate combinations: (1) constant θ and ψ , (2) covariates on θ but constant ψ , and (3) covariates on θ and ψ . We fit each of these models using the transition (Eq. 11) and stationary (Eq. 12) distribution joint likelihoods. For models with constant θ and ψ , we used analytical maximum-likelihood estimators (Appendix A) as starting θ values for numerical optimization. Starting ψ values were generated by fitting the carcass removal likelihood (Eq. 10) to the carcass experiment

data. We generated starting θ values with Poisson regression for all models with covariates. Initial model fitting and evaluation suggested multimodal likelihood surfaces for models with covariates, thus, all optimizations were conducted using a two-stage process in attempt to locate global optima. First, we fit models using 100 000 (covariates on θ) or 250 000 (covariates on θ and ψ) iterations of a simulated annealing stochastic search algorithm (Belisle 1992). Next, we used parameter estimates from simulated annealing as starting values for optimization using the Nelder-Mead simplex method (Nelder and Mead 1965). We generated profile likelihood confidence intervals for model parameters and conducted goodness-of-fit testing for the most supported model. We used R version 2.15.1 for all model fitting (i.e., numerical likelihood maximization) and analyses (R Core Development Team 2012), and code is provided (Supplements 1 and 2).

Results

Modeling identified fence marking, lek size, and distance to lek effects on collision rates, and regional differences in removal of collision evidence ($\Delta\text{AIC} = 0$; Table 1). The stationary process model was most supported by the data, whereas the transient version of the top model received weaker support ($\Delta\text{AIC} = 9.844$), as did all models without covariates on ψ or assuming constant θ and ψ ($\Delta\text{AIC} > 84$). Confidence interval coverage was similar for Wald and profile-likelihood intervals (Appendix B), and all covariates in the top model were significant at the $\alpha = 0.05$ level (i.e., no 95% confidence intervals overlapped zero). Expected numbers of collisions evidenced per 500 m at equilibrium (θ/ψ) from the top model were >1 order of magnitude higher in southeast Idaho because of reduced removal rates (for Magic Valley, $\psi = 0.145$; for southeast Idaho, $\psi = 0.014$). Expected numbers of carcasses at equilibrium (θ/ψ) were 0.004 (marked fences) and 0.021 (unmarked fences) in the Magic Valley and 0.037 (marked fences) and 0.216 (unmarked fences) in southeast Idaho, holding lek size and distance to lek at

their mean values (for lek size, $\bar{x} = 47.1$ birds; for distance, $\bar{x} = 1364.4$ m). Estimated number of collisions per km of fence over the 78-day lekking season increased with lek size and decreased with increasing distance from lek (Appendix B). Goodness-of-fit testing failed to reject the hypothesis that the top model fit the data ($P = 0.92$, $D_{264} = 232.52$); however, analysis of FT residuals provided some evidence for non-normality, likely caused by the large number of zero observations ($n = 207$; Appendix C). The second best model predicted equilibrium number of collisions was reached after approximately three weeks in the Magic Valley ($\psi = 0.148$), whereas equilibrium was not reached in southeast Idaho until ~ 150 days because of reduced removal rates ($\psi = 0.021$; Appendix B).

DISCUSSION

We developed a likelihood-based approach for modeling heterogeneity in count data from wildlife–infrastructure collision mortality surveys. The method combines data from removal experiments with carcass counts using joint likelihood, and facilitates modeling heterogeneity in process parameters by allowing both categorical and continuous covariates. This approach shifts the emphasis from point estimation of fatality to understanding heterogeneity in the underlying data-generating processes, and provides a framework for evaluating hypotheses regarding wildlife–infrastructure collision risk. Our example using sage-grouse collision data found evidence for heterogeneity in both collision and removal processes, and suggested the top model fit the data adequately despite known detection error (Stevens et al. 2011).

Previous authors have discussed similarities of estimating total mortality from carcass surveys with estimating the size of an animal population (Hels and Buchwald 2001, Huso 2011). However, modeling carcass counts is complicated by the temporally changing number of carcasses, violating closure assumptions of many estimation techniques. Our approach is based on observations of the state process through time and is not limited by a closure assumption. Huso (2011) suggested that the addition of carcasses to the system may be analogous to stochastic immigration, but that investigators are interested in the total number of additions over a time interval, not the instantaneous population sizes. We provide a model whereby instantaneous population sizes provide information for maximum-likelihood estimation of addition and removal rate parameters. Moreover, this approach facilitates maximum-likelihood estimation of total additions to the population over time at desired values of hypothesized covariates.

Several fatality estimation procedures are commonly used to estimate wildlife mortality from carcass survey data (e.g., Flint et al. 1999, Ford 2006, Huso 2011, Korner-Nievergelt et al. 2011). These estimators operate under various assumptions concerning search intervals

(e.g., regular intervals), carcass removal distributions (e.g., exponential lifetimes), and collision mortality rate. However, variable assumption violation through space and time makes comparability of results across studies difficult (Huso 2011). Simulation studies suggested precision and bias of commonly used fatality estimators can vary with sampling strategies, form of carcass removal distributions, and number of zero count observations, and that an estimator optimal under all sampling scenarios may not exist (Huso 2011, Korner-Nievergelt et al. 2011). These metrics all estimate total fatality as an algebraic function of the number of observed carcasses, the estimated removal and detection probabilities, and an underlying mortality rate that is assumed constant (Flint et al. 1999, Ford 2006, Huso 2011, Korner-Nievergelt et al. 2011). In essence, these estimators are attempting to census all of the additions to the carcass population through time at each sample unit as a function of the number observed carcasses and their assumptions.

Our model-based approach uses observed count data and specific assumptions regarding addition and removal processes, but the framework is fundamentally different than common point estimation procedures. We shift the objective from point estimation of fatality to estimating parameters of a theoretical parametric model of the biological and data generating processes. This model was derived from the theory of stochastic population models and stochastic processes, and shifts the focus to understanding process heterogeneity instead of estimating the outcome. In reality, carcass counts are indices to the number of carcasses added to the population; relationships to the true number of additions likely vary with a number of factors (e.g., relative rates of carcass removal and addition). The number of carcasses present at any point in time is a random variable that depends on stochastic addition and removal processes, not the result of a deterministic population process. Our models treat it as such, and do not attempt to census carcass additions over time at each sample unit. Rather, counts are observations of the stochastic process and are used to estimate the underlying parameters of the model. We did not simulate data to evaluate bias of model parameter estimates; however, previous studies have suggested that estimates may be influenced by the combination of sampling strategy and relative rates of carcass addition and removal through the number of zero count observations (Korner-Nievergelt et al. 2011). Regardless, treating counts as observations from a stochastic model provides a natural likelihood-based framework for modeling heterogeneity in both addition and removal processes using tools from generalized regression.

Many previous studies have used uncorrected carcass count data for hypothesis testing, regression modeling, or spatial analyses. Use of uncorrected carcass count data to evaluate hypotheses regarding aggregated-

infrastructure mortality (e.g., Grilo et al. 2009, Langen et al. 2009) or mitigation effectiveness (e.g., Gehring et al. 2009, Barrientos et al. 2011) is ubiquitous in the applied-ecology literature. However, spatiotemporal variation in removal obfuscates interpretation and could lead to misleading results (Huso 2011, Santos et al. 2011). We found differences greater than one order of magnitude for expected sage-grouse collision counts that were based on removal variation between regions. Thus, models constructed with uncorrected data from different regions or time frames lack comparability and are difficult to interpret at best, and could result in erroneous inferences and conservation decisions (Huso 2011, Korner-Nievergelt et al. 2011).

Inferences from carcass count surveys can also be affected by length of time intervals between samples (Kuvlesky et al. 2007, Santos et al. 2011). Appropriate search intervals likely depend on the target species, and total-fatality estimators can be less susceptible to removal induced bias when sampling intervals are short (Huso 2011, Korner-Nievergelt et al. 2011). Removal can be so great that some have suggested daily carcass searches are necessary, particularly for small species (Santos et al. 2011). However, the underlying assumption of this recommendation is that a complete census of victims is necessary to understand the addition process or estimate total mortality through time. While our model does not attempt to census collision events through time, the longer sampling intervals used in our carcass surveys (range 11–16 days) likely increased reliance on distributional assumptions of the model, particularly with respect to the carcass removal rate. Yet, the auxiliary removal experiment data with short observation periods (1–3 days) allowed precise estimation and separability of model parameters. A critical assumption with all removal studies is that the removal experiments accurately capture true removal of wildlife carcasses. Careful consideration of removal experiment design is warranted to guard against bias when carcass count sampling intervals are long and removal experiments are relied on heavily for estimating model parameters. However, when the field experiment accurately captures the removal process long sampling intervals should not be problematic for estimating parameters of the SLID model. In fact, allowing more time between searches allows the carcass population to approach equilibrium and simplifies the likelihood. This of course assumes the underlying process model itself is correctly specified, and thus, a unique stationary distribution exists. If the process model is mis-specified stationarity may not exist, and biased parameter estimates could result from empirical model fitting under the assumed model (Light 2010). However, the stationary version of our model was more supported by the data than the model using the transient Poisson distribution for collision counts, likely due to our long sampling intervals relative to θ/ψ . Daily carcass surveys are unrealistic under common logistical and financial

constraints, and previously collected field or pilot data could be used to determine approximate sampling interval lengths necessary for the carcass population to reach equilibrium. Moreover, there is a trade-off between temporal frequency and spatial extent of sampling (Ford 2006). It remains unclear if a greater sampling frequency is worth its cost in spatial replication, or vice versa, and more research is necessary to evaluate these trade-offs.

The stochastic population model used to model carcass population change is a time-homogenous Markov process, which may be unrealistic for many applications. Time homogeneity implies constant θ and ψ throughout the study, an assumption that could be violated frequently with real collision data. For example, the true collision rate may vary as a linear or quadratic function across a breeding or migration period due to the behavior or movement patterns of target species. Field studies sampling infrastructure over multiple seasons or field experiments testing mitigation methods using a before–after/control–impact design may wish to test the hypothesis that collision varies categorically through time. Similarly, assuming constant removal rate and exponentially distributed lifetimes for individual carcasses may not always represent the true removal processes (Bispo et al. 2012), and removal could vary with carcass age (e.g., stale carcasses with reduced removal probability). Bispo et al. (2012) suggested the Weibull distribution (decreasing risk with age), as well as the log-normal and log-logistic distributions (initial increase followed by decreasing risk with age) as alternative survival models for carcass lifetimes. Unfortunately, generalizing our stochastic birth–death process to accommodate other survival distributions would likely result in un-tractable likelihood functions. However, one solution for evaluating models with temporally changing θ and ψ comes through use of time-varying covariates in the regression functions. For example, a continuous covariate representing time since the beginning of the study or a season of interest could be included to model either linear or quadratic time trends in θ and ψ . Moreover, categorical indicator covariates representing different seasons or before–after treatments could be used to model categorical changes in θ . Although less desirable than explicit likelihoods for models with time-varying θ and ψ , this approach is commonly used to model time trends in applied mark–recapture and survival analyses (e.g., Dinsmore et al. 2002).

Assuming perfect detection during infrastructure surveys is an unrealistic limitation of the model under many sampling conditions. Detection error during carcass surveys can be large, and likely varies with the local vegetation conditions and size of target species (Smallwood 2007, Stevens et al. 2011). This model is directly applicable where detection bias is not a strong component of sampling (e.g., large animals, sparse vegetation), and our example using sage-grouse fence

collisions showed a reasonable model fit despite known detection error. Despite the reasonable model fit, our parameter estimates could be biased by ignoring the realities of imperfect detection. However, we provide a starting point for further development incorporating detection error. Hierarchical statistical models provide a framework for explicitly modeling ecological and observation processes (Royle and Dorazio 2008), and hierarchical SLID models treating $X(t)$ as a partially observed state process should be a research objective to increase the realism of wildlife–infrastructure collision modeling.

Conclusions

Infrastructure surveys to count wildlife remains are used for purposes ranging from basic research to environmental impact and mitigation assessment. A large degree of uncertainty remains concerning quantitative estimates of mortality and interpretation of modeling results because of variable methods for correcting biases and analyzing data (Kunz et al. 2007, Kuvlesky et al. 2007, Smallwood 2007, Arnett et al. 2008, Huso 2011). A number of hypotheses exist regarding factors related to infrastructure mortality (e.g., Bevanger 1994, Cryan and Barclay 2009), and statistically rigorous methods are necessary to confront these hypotheses with data (Kuvlesky et al. 2007, Arnett et al. 2008). Our stochastic process model formally combines carcass counts with removal experiment data, accommodates covariates on addition and removal parameters, and provides a likelihood-based framework for evaluating collision risk hypotheses using carcass counts from infrastructure surveys.

ACKNOWLEDGMENTS

This work was supported by a grant from the United States Department of Agriculture Natural Resources Conservation Service Sage-Grouse Initiative (SGI). We thank D. Naugle and T. Griffiths for aide in securing funds for this work; J. Connelly and D. Musil for support during the original project generating the Sage-Grouse data; and C. Williams, K. Reese, and two anonymous reviewers for comments that improved the manuscript substantially. Data sets used for our example model fitting were contributions from Idaho Federal Aid in Wildlife Restoration Project W-160-R.

LITERATURE CITED

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Czaki, editors. Second International Symposium on information theory. Akademiai Kiado, Budapest, Hungary.
- Allen, L. J. S. 2003. An introduction to stochastic processes with applications to biology. Pearson Education, Upper Saddle River, New Jersey, USA.
- Arnett, E. B., et al. 2008. Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management* 72:61–78.
- Bailey, N. T. J. 1964. The elements of stochastic processes. Wiley Publications in Statistics, John Wiley and Sons, New York, New York, USA.
- Barrientos, R., J. C. Alonso, C. Ponce, and C. Palacin. 2011. Meta-analysis of the effectiveness of marked wire in reducing avian collisions with power lines. *Conservation Biology* 25: 893–903.
- Belisle, C. J. P. 1992. Convergence theorems for a class of simulated annealing algorithms on R^d . *Journal of Applied Probability* 29:885–895.
- Bevanger, K. 1994. Bird interactions with utility structures: collision and electrocution, causes and mitigating measures. *Ibis* 136:412–425.
- Bishop, Y. M. M., S. E. Fienberg, and P. W. Holland. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, Massachusetts, USA.
- Bispo, R., J. Bernardino, T. A. Marques, and D. Pestana. 2012. Modeling carcass removal for avian mortality assessment in wind farms using survival analysis. *Environmental and Ecological Statistics* 20:147–165.
- Cox, D. R., and H. D. Miller. 1965. The theory of stochastic processes. Wiley Publications in Statistics, John Wiley and Sons, New York, New York, USA.
- Cryan, P. M., and R. M. R. Barclay. 2009. Causes of bat fatalities at wind turbines: hypotheses and predictions. *Journal of Mammalogy* 90:1330–1340.
- Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* 27:811–841.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.
- Flint, P. L., A. C. Fowler, and R. F. Rockwell. 1999. Modeling bird mortality associated with the M/V Citrus oil spill off St. Paul Island, Alaska. *Ecological Modelling* 117:261–267.
- Ford, R. G. 2006. Using beached bird monitoring data for seabird damage assessment: the importance of search interval. *Marine Ornithology* 34:91–98.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207–231.
- Fox, J. 2008. Applied regression analysis and generalized linear models. Second edition. Sage Publications, Thousand Oaks, California, USA.
- Gehring, J., P. Kerlinger, and A. M. Manville II. 2009. Communication towers, lights, and birds: successful methods of reducing the frequency of avian collisions. *Ecological Applications* 19:505–514.
- Grilo, C., J. A. Bissonette, and M. Santos-Reis. 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. *Biological Conservation* 142:301–313.
- Groot Bruinderink, G. W. T. A., and E. Hazebroek. 1996. Ungulate traffic collisions in Europe. *Conservation Biology* 10:1059–1067.
- Haines, A. M., M. E. Tewes, and L. L. Laack. 2005. Survival and sources of mortality in ocelots. *Journal of Wildlife Management* 69:255–263.
- Hels, T., and E. Buchwald. 2001. The effect of road kills on amphibian populations. *Biological Conservation* 99:331–340.
- Huso, M. M. 2011. An estimator of wildlife fatality from observed carcasses. *Environmetrics* 22:318–329.
- Korner-Nievergelt, F., P. Korner-Nievergelt, O. Behr, I. Niermann, R. Brinkmann, and B. Hellgriegl. 2011. A new method to determine bird and bat fatality at wind energy turbines from carcass searches. *Wildlife Biology* 17:350–363.
- Kunz, T. H., E. B. Arnett, W. P. Erickson, A. R. Hoar, G. D. Johnson, R. P. Larkin, M. D. Strickland, R. W. Thresher, and M. D. Tuttle. 2007. Ecological impacts of energy development on bats: questions, research needs, and hypotheses. *Frontiers in Ecology and the Environment* 5:315–324.
- Kuvlesky, W. P., Jr., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, and F. C. Bryant. 2007. Wind energy development and wildlife conservation: challenges and

- opportunities. *Journal of Wildlife Management* 71:2487–2498.
- Langen, T. A., K. M. Ogden, and L. L. Schwarting. 2009. Predicting hot spots of herpetofauna road mortality along highway networks. *Journal of Wildlife Management* 73:104–114.
- Light, G. L. 2010. Regression, model misspecification and causation, with pedagogical demonstration. *Applied Mathematical Sciences* 4:225–236.
- Matis, J. H., and T. R. Kiffe. 2000. Stochastic population models: a compartmental perspective. Springer Lecture Notes in Statistics, Springer-Verlag, New York, New York, USA.
- McCullagh, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall, New York, New York, USA.
- Mumme, R. L., S. J. Schoech, G. E. Woolfenden, and J. W. Fitzpatrick. 2000. Life and death in the fast lane: demographic consequences of road mortality in the Florida scrub-jay. *Conservation Biology* 14:501–512.
- Nelder, J. A., and R. Mead. 1965. A simplex algorithm for function minimization. *Computer Journal* 7:308–313.
- Osborn, R. G., K. F. Higgins, R. E. Usgaard, C. D. Dieter, and R. D. Neiger. 2000. Bird mortality associated with wind turbines at the Buffalo Ridge Wind Resource Area, Minnesota. *American Midland Naturalist* 143:41–52.
- R Core Development Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Riitters, K. H., and J. D. Wickham. 2003. How far to the nearest road? *Frontiers in Ecology and the Environment* 1: 125–129.
- Royle, J. A., and R. M. Dorazio. 2008. Hierarchical modeling and inference in ecology: analysis of data from populations, metapopulations and communities. Academic Press, London, UK.
- Santos, S. M., F. Carvalho, and A. Mira. 2011. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE* 6:e25383.
- Smallwood, K. S. 2007. Estimating wind turbine-caused bird mortality. *Journal of Wildlife Management* 71:2781–2791.
- Stevens, B. S., K. P. Reese, and J. W. Connelly. 2011. Survival and detectability bias of avian fence collision surveys in sagebrush steppe. *Journal of Wildlife Management* 75:437–449.
- Stevens, B. S., K. P. Reese, and J. W. Connelly. 2012. Greater Sage-Grouse and fences: does marking reduce collisions? *Wildlife Society Bulletin* 36:297–303.
- Wilks, S. S. 1938. The large-sample distribution of the likelihood ratio for testing composite hypotheses. *Annals of Mathematical Statistics* 9:60–62.

SUPPLEMENTAL MATERIAL

Appendix A

Analytical maximum-likelihood estimators of θ from Eqs. 7 and 8 ([Ecological Archives E094-190-A1](#)).

Appendix B

Parameter estimates, confidence intervals, and figure results from fitting the stochastic linear immigration–death model to example sage-grouse fence collision data set ([Ecological Archives E094-190-A2](#)).

Appendix C

Profile-likelihood plots for regression coefficients and model-evaluation plots for the top stochastic linear immigration–death model fit to example sage-grouse fence collision data set ([Ecological Archives E094-190-A3](#)).

Supplement 1

R code for fitting the stochastic linear immigration–death model to example sage-grouse fence collision data ([Ecological Archives E094-190-S1](#)).

Supplement 2

R code for constructing profile likelihood confidence intervals and evaluating fit of the stochastic linear immigration–death model fit to example sage-grouse fence collision data ([Ecological Archives E094-190-S2](#)).