Melding wildlife surveys to improve conservation inference

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Abstract
Integrated models are a popular tool for analyzing species of conservation concern. Species of conservation concern are often monitored by multiple entities that generate several datasets. Individually, these datasets may be insufficient for guiding management due to low spatio-temporal resolution, biased sampling, or large observational uncertainty. Integrated models provide an approach for assimilating multiple datasets in a coherent framework that can compensate for these deficiencies. While conventional integrated models have been used to assimilate count data with surveys of survival, fecundity, and harvest, they can also assimilate ecological surveys that have differing spatio-temporal regions and observational uncertainties. Motivated by independent aerial and ground surveys of lesser prairie-chicken, we developed an integrated modeling approach that assimilates density estimates derived from surveys with distinct sources of observational error into a joint framework that provides shared inference on spatio-temporal trends. We model these data using a Bayesian Markov melding approach and apply several data augmentation strategies for efficient sampling. In a simulation study, we show that our integrated model improved predictive performance relative to models for analyzing the surveys independently. We use the integrated model to facilitate prediction of lesser prairie-chicken density at unsampled regions and perform a sensitivity analysis to quantify the inferential cost associated with reduced survey effort.

KEYWORDS
conservation biology, data augmentation, integrated modeling, lesser prairie-chicken, Markov melding

1 | INTRODUCTION

Integrated models that allow for the unified analysis of multiple datasets have been described as integrated analysis (Maunder & Punt, 2013), integrated distribution models (Isaac et al., 2020), shared parameter models (Rizopoulos et al., 2008), joint models (Wulfsöhn & Tsiatis, 1997), Markov combination (Dawid & Lauritzen, 1993), Bayesian melding (Fuentes & Raftery, 2005), data assimilation (Ghil & Malanotte-Rizzoli, 1991), data reconciliation (Hanks et al., 2011), and data fusion (Kedem et al., 2017) and have applications in econometrics, biostatistics,
conservation biology, atmospheric sciences, and oceanography. The joint likelihood of integrated models conditions multiple datasets on link parameters in a way that can often improve predictive performance and parameter precision (Schaub & Abadi, 2011).

Markov combination (Dawid & Lauritzen, 1993) facilitates joint inference on a link parameter expressed in several submodels but is not applicable when the prior marginal distributions of the link parameter differ across submodels. Goudie et al. (2019) introduced Markov melding for combining related submodels that have differing marginal distributions for the link parameter. In this setting, the joint model is constructed through marginal replacement, where the prior marginal distributions for the link parameter across submodels are replaced with a common pooled prior marginal distribution. Markov melding facilitates joint inference on a link parameter in one submodel that can be expressed as non-invertible functions of other submodel parameters. For example, suppose we have submodels for learning about adult and juvenile survival, but we are interested in learning about aggregate survival, which is a weighted average of the two. Markov melding uses marginal replacement to form a melded posterior distribution for the link parameter that accounts for its implied prior and likelihood in each submodel. Recently, Manderson and Goudie (2022a) proposed chained Markov melding, an extension that facilitates joint inference for a sequence of submodels connected by multiple link parameters.

The earliest applications of integrated modeling frameworks in the context of wildlife management arose in fisheries science (Fournier & Archibald, 1982), but wide adoption of the framework in the broader fields of conservation biology and ecology began in the early 2000s (Maunder & Punt, 2013; Zipkin & Saunders, 2018). In particular, integrated population models (IPMs), which are an application of integrated models, have been used to understand population dynamics for species of conservation concern (Schaub & Abadi, 2011; Zipkin & Saunders, 2018). In an IPM, population counts are analyzed in conjunction with surveys of survival, fecundity, and harvest by conditioning all datasets on a shared latent process that describes population dynamics (Schaub & Abadi, 2011; Schaub & Kery, 2021; Zipkin & Saunders, 2018). For example, Broms et al. (2010) specified an IPM for greater sage-grouse (Centrocercus urophasianus) that leveraged count, telemetry, and harvest data to understand drivers of abundance. By accounting for uncertainty in multiple datasets, IPMs can provide novel insights into population dynamics that help inform conservation (Schaub & Kery, 2021).

Despite the success of IPMs, few other integrated modeling approaches have been proposed in conservation biology. One persistent challenge is the lack of spatial and temporal conformity across datasets. Additional methodological challenges include differences in the quantity or observational uncertainty of the data sources, and sampling bias in one or more datasets (Isaac et al., 2020; Simmonds et al., 2020; Zipkin et al., 2021). Such challenges are encountered when developing integrated models for SCC because of their elusiveness, restricted range, or small population size (Lomba et al., 2010).

We developed an integrated model that facilitates joint inference of aerial and ground surveys of lesser prairie-chicken (Tympanuchus pallidicinctus; hereafter LEPC), an SCC that has experienced range and population declines since the 1980s (Hagen et al., 2004, 2017; U.S. Fish and Wildlife Service, 2021). Joint modeling of these data is challenging because LEPC are simultaneously monitored by several entities who operate independently in different regions. As a result, the surveys vary in their spatial and temporal resolution, sample size, and observational uncertainty. Additionally for some surveys, LEPC were preferentially sampled in regions presumed to have high abundances which may bias inference (Diggle et al., 2010).

We facilitated shared inference of multiple LEPC surveys by chained Markov melding (Manderson & Goudie, 2022a) density estimates derived from submodels describing the observation processes of the aerial and ground surveys into a joint response model. Melding refines the submodel density estimates to those that agree with the spatio-temporal patterns observed in both surveys. By joining the submodels through derived quantities, we addressed the differences in the spatial and temporal scales of the surveys. Accommodating these differences in scales with a traditional integrated model is difficult because density is a non-invertible function of submodel parameters. Our modeling approach attenuated the impacts of potential sampling biases and accounted for the distinct sources of observational error, so that all data sources can be assimilated to improve predictive performance. Lastly, the Markov melding approach improved computation by enabling submodel specific data augmentation techniques and avoiding high-dimensional parameter updates by fitting the integrated model in stages.

The paper is organized as follows. In Section 2, we provide a brief history of LEPC conservation and discuss current needs for informing management. Section 3 details the sampling protocols of the aerial (3.1) and ground (3.2) surveys. Section 4 describes submodels accounting for the observation process of each survey and a joint response model for linking inference across surveys. In Section 5,
we describe the Markov melding techniques used to facilitate posterior inference for our integrated model. Section 6 includes the results our simulation study and LEPC abundance analysis. Section 7 concludes with a discussion of our findings.

2 | LESSER PRAIRIE-CHICKEN CONSERVATION

The LEPC is a member of the family Phasianidae and is indigenous to the southern Great Plains of the United States. Like other species in its family, the LEPC has experienced range and population declines since the 1980s primarily due to habitat loss, degradation, and fragmentation (Hagen et al., 2004, 2017; U.S. Fish and Wildlife Service, 2021), but curtailment of natural fires, overgrazing, and climate change have also contributed (Haukos & Boal, 2016).

We studied spatio-temporal patterns in LEPC abundance across the state of Kansas because an estimated 70% of the total LEPC population resides in the state (Van Pelt et al., 2013). Our modeling approach, however, can accommodate data sources from the other states in the LEPC range. In Kansas, LEPC inhabit Sand Sagebrush Prairie (SSPR), Mixed-Grass Prairie Ecoregion (MGPR), Short-Grass Prairie/Conservation Reserve Program Mosaic Ecoregion (SGPR) ecoregions, which cover the southwest, southeast, and northern regions of western Kansas, respectively.

Recently, the United States Fish and Wildlife Service listed the LEPC for federal protections under the Endangered Species Act (U.S. Fish and Wildlife Service, 2023). The Northern Distinct Population Segment, which encompasses the SSPR, MGPR, and SGPR ecoregions, is categorized as threatened. Improved estimation of spatio-temporal population change, especially range-wide, would help inform conservation practices for the species (Van Pelt et al., 2013).

Population monitoring of LEPC relies on spring counts of individuals on leks (McDonald et al., 2014). A lek is an aggregation of males defending a small territory and communally calling and performing displays to attract and mate with females (Haukos & Boal, 2016). Leks are generally located in sparse vegetation on hilltops and ridgelines and commonly include more than 10 individuals which makes detection by audio and visual cues of the otherwise cryptic individuals easier (Haukos & Boal, 2016).

Historically, LEPC populations have been monitored using counts of individuals at leks from ground surveys conducted by state wildlife agencies. Lack of spatial randomness in the ground surveys, however, makes inferring species–habitat associations difficult and density estimates imprecise and potentially biased (Diggle et al., 2010). Since 2012, several entities have collectively supported annual range-wide aerial surveys of LEPCs. The aerial surveys follow a spatially random sampling design and have thereby improved range-wide density estimates (McDonald et al., 2014; Nasman et al., 2021). Two drawbacks of the aerial surveys are that they encounter fewer individuals per unit of area searched and have higher operating costs. These limitations have led managers to consider integrated models that could leverage ground survey data and reduce reliance on aerial surveys.

Over the last two decades, there have been numerous studies related to LEPC conservation but few have assimilated multiple data sources due to the methodological challenges described by Zipkin et al. (2021). Ross et al. (2018) developed an IPM for assimilating count, survival, and fecundity data that suggested observed declines in LEPC abundance following droughts (Ross et al., 2016) were driven by higher juvenile and chick mortality. The findings of Ross et al. (2018) prompted managers to consider habitat improvements that focus on increasing and maintaining grasslands that can buffer the population against the harmful effects of severe drought. By melding available data sources, we improve spatio-temporal density estimates and facilitate prediction at unsampled regions to identify vulnerable populations and prioritize landscapes for conservation action. Our approach can also quantify the inferential cost and reduced predictive performance associated with less frequent aerial surveys. In what follows, we describe the aerial and ground survey protocols.

3 | SURVEY PROTOCOLS

3.1 | Aerial

The Kansas estimated occupied range (EOR) for LEPC was partitioned into $n^A = 299$, $15 \times 15 = 225$ km$^2$, survey blocks (McDonald et al., 2014). A spatially random subset of blocks were selected for sampling, and the subset selected differed by year (Figure 1). No blocks were surveyed in 2019.

Two north–south oriented, 15-km transects were surveyed by helicopter in blocks selected for sampling. Selected transects were surveyed once during the LEPC breeding season (March 15–May 15) and within 0.5 h prior to and 2 h after sunrise to maximize detection of individuals present at leks. The helicopter was operated by one pilot and three observers. As the pilot flew at a speed of 60 km/h and altitude of 25 m above ground, observers attempted to visually locate prairie-chicken. When one or more prairie-chicken were located, the pilot navigated to the location.
and recorded the geographic coordinate and number of individuals observed. For an in-depth description of the aerial survey protocol and design, see Nasman et al. (2021) and Van Pelt et al. (2013).

3.2 | Ground

Kansas Department of Wildlife and Parks (KDWP) preferentially located 21 ground survey routes for monitoring LEPC in representative, high-quality LEPC habitat across Kansas EOR. Each route was approximately 16 km long and the ground survey attempted to census all leks within 1.6 km of the road for a region of approximately 51.2 km². Routes were surveyed (March 20–April 20) and within 0.5 h prior to and 1.5 h after sunrise.

All routes were surveyed at least twice per year in two parts. First, the listening portion of the route was conducted; leks were audibly detected and their locations approximated, but not confirmed. On the same morning, the surveyor navigated to each lek detected, prompted the individuals to take flight (flushed), and recorded the count of individuals and location. Surveyors also revisited sites at which leks were previously recorded because LEPC are known to return to historical lek sites (Haukos & Boal, 2016). The ground survey is a census of the leks in the survey area, but it is not a census of the population because some individuals may not be present at their lek at the time it was flushed.

4 | METHODS

In northwestern Kansas, the LEPC EOR overlaps with the range of its sister species the greater prairie-chicken (Tympanuchus cupido; hereafter GEPC). Species verification was sometimes infeasible for the aerial and ground surveys and observations of GEPC are included in both datasets. We proposed distance sampling (Section 4.1) and N-mixture (Section 4.2) submodels that analyzed counts of prairie-chicken (LEPC and GEPC). We then derived the block-level densities of LEPC in northwestern Kansas by multiplying the combined LEPC and GEPC density estimates by known LEPC proportions (Section 4.3). The spatio-temporal submodel assimilates the LEPC density estimates derived from the other two submodels.
in a joint response that induced the integrated model. The integrated model accounted for the uncertainty in both datasets, the underlying ecological processes, and the parameters.

4.1 Aerial distance sampling submodel

We developed a distance sampling model to describe the observational uncertainty associated with aerial surveys of prairie-chickens. We let $v_{ilt}$ represent the number of observers who detected group $l = 1, \ldots, L^A$ in the sampling region $i = 1, \ldots, n^A$ during year $t = 1, \ldots, T^A$. Assuming all observers had equal skill in detecting prairie-chicken groups and observers detected the groups independently, a model for $v_{ilt}$ is

$$v_{ilt} \sim \text{Binomial}(B_{ilt}, \rho_{ilt}),$$

where $B_{ilt}$ is the total number of observers for which group $l$ was visible and $\rho_{ilt}$ is the observer detection probability for group $l$, assumed to be identical for all observers. The visibility of group $l$ to each observer depended on their distance from the transect, $d_{ilt}$, and side of the transect, $e_{ilt}$ ($e_{ilt} = 1$ indicates group on left side). Groups more than 7 m left of the transect were visible to both the front and rear left-hand side observers; groups within 7 m of the transect were only visible to the front left-hand side observer; and groups more than 7 m right of the transects were only visible to the right-hand observer. Hence, $B_{ilt} = 2$ for $e_{ilt} = 1$ and $d_{ilt} > 7$, but $B_{ilt} = 1$ otherwise. Detected prairie-chicken groups were announced only after they were out of view for all observers to ensure independent detections.

We modeled the detection probability of group $l$, $\rho_{ilt}$, as a function of the group’s distance from the transect at detection, $d_{ilt}$, count of individuals at detection, $N_{ilt}$, and ecoregion, such that $\text{logit}(\rho) = (X_\rho, N^A, d) \beta_\rho$, where $X_\rho$ is a binary matrix with unique intercepts for each ecoregion, and $(\cdot)$ denotes a column-wise bind of the listed matrices. The regression model provides additional flexibility for estimating the detectability of prairie-chicken groups, and the entries of $\beta_\rho$ are identifiable under the double observer design (Borchers et al., 2006). We treat detections of the two left-hand observers as fully independent but alternative approaches that allow for dependence in detectability as a result of unmeasured covariates and animal movement have been proposed (Buckland et al., 2010; Borchers et al., 2022). Under our modeling framework, we assume that heterogeneity in the prairie-chicken group detectability is well characterized by distance from the transect and size of the group. We also assumed that groups are stationary, but note that there were a small number of transiting individuals.

Some groups for which $v_{ilt} = 0$ were not in the dataset because they went undetected. To account for these missed individuals, we employed a parameter expanded data augmentation (PX-DA) approach (Royle et al., 2009). Specifically, we augmented the dataset with many undetected groups and let $z_{ilt} \in \{0, 1\}$ indicate whether group $l$ belonged to the sample population of groups in region $i$. If a group was detected (i.e., $v_{ilt} > 0$), then it must be part of the sample population in region $i$ (i.e., $z_{ilt} = 1$).

For undetected groups, $z_{ilt}, N_{ilt}^A, d_{ilt}$, and $e_{ilt}$ were all unknown and hence estimated. To denote the observed and unobserved components of partially latent parameters, we use the superscripts $o$ and $u$, respectively. Heuristically, we conceptualize the model as proposing groups of prairie-chicken that the aerial survey may have missed: we proposed a group of prairie-chicken with count $N_{ilt}^A$, distance from the transect $d_{ilt}$, and on side $e_{ilt}$ of the transect, and then used the observations from our detected groups (i.e., $N_{ilt}^A, d^o, e^o$) to determine if group $l$ could have been part of our sample population (i.e., $z_{ilt} = 1$) but went undetected (i.e., $v_{ilt} = 0$). We chose the prior distributions for $d_{ilt}$ and $e_{ilt}$ to induce a uniform distribution of groups within the survey region. See Web Appendix A for a full description of prior distributions. Royle et al. (2009) referred to the total number of both observed and unobserved groups as the super-population, and the size of the super-population, $M$, must be specified a priori. Web Appendix B discusses recommendations for choosing $M$. We calculate the total number of groups in the sample population of region $i$ during year $t$ as the derived quantity $L^A_{ilt} = \sum_{l=1}^M z_{ilt}$. Note that in this data augmentation framework $L^A_{ilt}$ includes the detected groups as well as groups that may have existed in the survey region but went undetected.

The aerial survey was conducted during the breeding season to maximize detection of leks, but smaller, non-lekking groups as well as individual prairie-chicken were also detected. We accounted for the occurrence of lek and non-lek observations in the observed prairie-chicken counts using a zero-truncated Poisson (ZTP) mixture model

$$N_{ilt}^A \sim \begin{cases} \text{ZTP}(\lambda_{ilt}), & \text{for } \omega_{ilt} = 1 \\ \text{ZTP}(\lambda_0), & \text{for } \omega_{ilt} = 0 \end{cases},$$

$$\omega_{ilt} \sim \text{Bernoulli}(p_\omega),$$

where $\omega_{ilt}$ is the indicator of whether group $l$ is a lek, $\lambda_{ilt}$ is the mean number of individuals per lek in region $i$ during year $t$, and $\lambda_0$ is the homogeneous mean number of individuals for non-lek observations. Both distributions in the Poisson mixture, equations (2) and (3), are zero-truncated because if a group exists, it must have $\geq 1$ individuals.
We treated $\omega_{it}$ as a latent variable because it was often infeasible to determine the lek status of a prairie-chicken group from the air. For monitoring purposes, KDWP defines a lek as 3 or more individuals on a display site (Jennison et al., 2011). In our case, the latent lek indicators $\omega_{it}$ accommodated the bimodality of the count data and carried fewer assumptions regarding the composition of a lek.

Mean lek size varies temporally and with environmental factors (Hagen et al., 2009, 2017). We specified a heterogeneous mean lek size across sites $i$ and years $t$, $\lambda_{it}$, which we modeled with covariates (i.e., $\log(\lambda) = X_{it}\beta_{\lambda}$). The design matrix $X_{it}$ includes unique intercepts for each ecoregion and additional continuous covariates. The covariates capture heterogeneity in mean lek size related to landcover, habitat patch size, anthropogenic disturbance, and climatic stochasticity. See Web Appendix C for a description of all covariates, and how they were collected.

We specified a binomial model to account for variability in the number of prairie-chicken groups such that

$$L_{it}^A \sim \text{Binomial}(M, \psi_{it}),$$

where $\psi_{it}$ is the probability that a group belonged to the sample population of region $i$ during year $t$. The parameter $\psi_{it}$ controls the number of prairie-chicken groups within a region, with greater $\psi_{it}$ implying more groups. Heterogeneity in prairie-chicken use of habitat within the EOR has also been documented (Hagen et al., 2016), motivating the logit model, $\logit(\psi) = X_{it}\beta_{\psi}$. We chose the same suite of covariates for explaining heterogeneity in the number of groups as those used for explaining lek size (i.e., $X_{it} = X_{\lambda}$).

We specified diffuse exchangeable Gaussian priors for the regression coefficients $\beta_{\psi}$, $\beta_{\lambda}$, and $\beta_{\psi}$. We used a vague Uniform(0,1) prior for the proportion of prairie-chicken groups that are leks, $p_{\psi}$, and an informative Gamma(1.78, 0.675) prior for the mean number of individuals for non-lek observations $\lambda_0$. A full description of the priors is in Web Appendix A.

### 4.2 N-mixture submodel

We developed a submodel for describing observational uncertainty in KDWP prairie-chicken ground surveys. We let $F_{itlj}$ denote the ground count of male prairie-chicken on occasion $j$ at lek site $l$ in sampling region $i$ during year $t$. To account for variability in the counts induced by imperfect male lek attendance, we adopted an N-mixture model (Royle, 2004),

$$F_{itlj} \sim \text{Binomial}(N_{itlj}^G, p) \text{ for } j = 1, \ldots, J_{it},$$

where $p$ represents the homogeneous probability that a male belonging to lek site $l$ was present at the lek when it is surveyed. We assumed a Poisson model for the latent lek abundances, $N_{itlj}^G \sim \text{Poisson}(\exp(\mathbf{w}_{it}^G, \eta))$, where $\mathbf{w}_{it}$ is the same set of covariates used in the aerial model but with unique measurements because the aerial and ground sample regions differed. Note that zero abundances, $N_{itlj}^G = 0$, were possible because surveyors revisited historical lek sites that may not have been visited by any individuals in year $t$. It follows that $\exp(\mathbf{w}_{it}^G, \eta)$ is the expected number of individuals per lek site rather than the expected number of individuals per active lek, and the regression coefficient $\eta$ dictates the relationship between the expected number of individuals at a lek site and the covariates associated with that lek site. We specified a diffuse exchangeable Gaussian prior for $\eta$ and a vague Uniform(0,1) prior for the male lek attendance probability $p$ (see Web Appendix A for more details of the prior specification).

### 4.3 Integrated model

We induced an integrated model for the aerial and ground surveys by specifying a spatio-temporal submodel that couples the survey specific density estimates in a joint response. While density is not a parameter in either the aerial distance sampling model (ADSM) or N-mixture submodel, each submodel includes density as a derived quantity. For the ADSM, samples of block-level LEPC density in the aerial lattice are obtained by

$$y_{it}^A = f(N_{it}^{A,o}, z_{it}^o, N_{it}^{A,u}, z_{it}^u) = \sum_{i=1}^{M} N_{it}^{A}x_{it}k_{\lambda}/S^{A},$$

where $S^{A}$ is the prespecified area of the sampling region (Web Appendix B) and $k_{\lambda}$ is the proportion of LEPC in sampling region $i$ (Nasman et al., 2022). Proportions vary from 0.001–1 for blocks in the SGPR but equal 1 for all blocks in the MGPR and SSPR. Likewise, for the N-mixture submodel,

$$y_{it}^G = g(N_{it}^G) = \sum_{i=1}^{L_{it}} 2N_{it}^{G}x_{it}/S_{i},$$

where $S_{i}$ is a survey route $i$, $L_{it}^G$ is the number of lek sites at site $i$ in year $t$, and the 2 assumes equal sex ratios in the LEPC population (Campbell, 1972). Equation (7) also assumes that no females were present at the time the lek site was flushed which is a common assumption but could lead to inflated estimates of $y_{it}^G$. Both $y_{it}^A$ and $y_{it}^G$ are unobserved because they are functions of, at least partially, unobserved submodel parameters.
Given the annual density estimates for the $n^A = 299$ aerial blocks arranged in a lattice as well as the $n^G = 21$ ground survey routes (Figure 1), we proposed a joint response model for annual density at the $n^A + n^G = 320$ sampling regions. Omitting the superscripts $A$ and $G$, we let $y_{it}$ represent the density of LEPC in sampling region $i$ during year $t$. Because some sampling regions can have an LEPC density of exactly zero, we considered the following tobit model (Amemiya, 1984):

$$y_{it} = \begin{cases} 
\xi_{it}, & \text{for } \xi_{it} > 0 \\
0, & \text{for } \xi_{it} \leq 0
\end{cases}$$

(8)

$$\xi_{it} \sim \mathcal{N}(\xi_{it}, \sigma_d^2 R_d(\phi)).$$

(9)

Tobit models are often used in the context of censoring where the true state of interest, $\xi_{it}$, is only observable in a certain range. Our density data were not censored explicitly, but the tobit model accounted for the mixture of discrete and continuous components in the response and promoted conjugacy of the latent states $\xi_{it}$ and $\xi_{it}$. Both $\xi_{it}$ and $\xi_{it}$ may be viewed as the latent density of LEPC in a region with negative values indicating the relative probability that the density is zero. To account for the spatial structure, we assumed an exponentially decaying correlation matrix $R_d(\phi)$, where the entry in the $i$th row and $j$th column is defined as $r_d(i, j, \phi) = \exp(-d_{ij}/\phi)$, $d_{ij}$ is the Euclidean distance between sampling regions $i$ and $j$ in meters, and $\phi$ is the spatial range parameter.

We accounted for temporal dependence by specifying autoregressive random effects in Equation (9)

$$\xi_{it} \sim \mathcal{N}(\xi_{i,t-1}, W_{t-1} \alpha, \Sigma)$$

(10)

where $W_{t-1}$ is a matrix of covariates measured across all sampling regions in year $t-1$, and we modeled the initial state as $\xi_0 = X_0 \gamma$. Many environmental factors known to be associated with LEPC density were constant over the $T = 17$ years considered in our analysis, and so the set of covariates used in $W_t$ is reduced from those in $X_0$ (see Web Appendix C). In addition to the landcover and climatic covariates used in the ADSM and N-mixture submodel, we also included a binary covariate that indicated whether a survey block or ground site was north of Interstate 70. LEPC to GEPC ratios decrease sharply north of Interstate 70 (Nasman et al., 2022), and the binary covariate was helpful for explaining spatial heterogeneity in LEPC density that was difficult to characterize with the other covariates. We considered a block diagonal structure for $\Sigma_t$ with distinct covariance matrices $\sigma_t^{2A} R_t^A$ and $\sigma_t^{2G} R_t^G$ for the aerial and ground survey regions, respectively. We let $R_t^A = \text{diag}(A^t) - \rho(A)^{-1}$, where $A$ is the adjacency matrix from the aerial survey lattice, which has entries $a(i, j) = 1$ if blocks $i$ and $j$ are neighboring and $a(i, j) = 0$ otherwise, and $\text{diag}(A)$ denotes the diagonal matrix of the row sums of $A$. We specified $\rho \rightarrow 1$ to induce an intrinsic conditional autoregressive covariance matrix that allows for dependence among regions organized in a lattice (Ver Hoef et al., 2018). For the ground sites, we designated a simple diagonal structure $R_t^G = I$. We used diffuse exchangeable Gaussian priors for the regression coefficients $\gamma$ and $\alpha$, a discrete uniform prior for $\phi$, and vague inverse-gamma priors for the variance parameters $\sigma_d^2, \sigma_t^{2A}, \sigma_t^{2G}$.

The joint posterior distribution associated with our full integrated model is

$$\begin{align*}
\alpha \propto & \prod_{i=1}^{T^G} \prod_{l=1}^{n^G} \prod_{l=1}^{L^G} \left( \prod_{j=1}^{J^G} \left( \prod_{i=1}^{P} \left( N_{i|l|} | \sigma^{2A}, \sigma^{2G}, \phi \right) \right) \right) \left( N_{i|l|} | \eta \right) \left[ \eta \right] \left[ p \right] \\
\times & \prod_{i=1}^{T^G} \prod_{i=1}^{T^G} \prod_{l=1}^{n^A} \prod_{l=1}^{L^A} \left( \prod_{j=1}^{J^A} \left( \prod_{i=1}^{P} \left( N_{i|l|} | \sigma^{2A}, \sigma^{2G}, \phi \right) \right) \right) \left( N_{i|l|} | \eta \right) \left[ \eta \right] \left[ p \right] \\
\times & \prod_{i=1}^{T^G} \prod_{i=1}^{T^G} \prod_{l=1}^{n^A} \prod_{l=1}^{L^A} \left( \prod_{j=1}^{J^A} \left( \prod_{i=1}^{P} \left( N_{i|l|} | \sigma^{2A}, \sigma^{2G}, \phi \right) \right) \right) \left( N_{i|l|} | \eta \right) \left[ \eta \right] \left[ p \right]
\end{align*}$$

(11)

where we use the bracket notation to denote probability distributions (Gelfand & Smith, 1990). The joint distributions of the ADSM, N-mixture submodel, and spatio-temporal tobit submodel (STTM) are given by Equations (12)–(14), respectively. The three submodels induced the integrated model through the link parameters $y_{it}^A = f(N_{i|l}^{A,G}, z_{i|l}, N_{i|l}^{A,A}, z_{i|l}^G)$ and $y_{it}^G = g(N_{i|l}^G)$. A directed acyclic graph of our integrated model is shown in Figure 2, and a full model statement with priors is provided in Web Appendix A.

5 | POSTERIOR INFERENCE

The crux of fitting our integrated model was that the link parameters $y_i^A$ and $y_i^G$ are non-invertible functions of the submodel parameters $z$, $N^A$, and $N^G$. We adopted a chained Markov melding approach (Manderson & Goudie, 2022a) that facilitated joint inference for $y^A$ and $y^G$ accounting for the data, prior information, and assumptions in all three submodels. We derive the joint melded
distribution for $y = (y^A', y^G')'$ as follows (Manderson & Goudie, 2022a):

$$[y, .]_{meld} = [y]_{pool} \cdot [y]_{ADSM} \cdot [y]_{STTM} \cdot [y]_{N-mix}, \quad (15)$$

where “.” is a placeholder for all parameters other than $y$ in the joint and conditional distributions, $[y]_{pool}$ is the pooled prior marginal distribution, and $[y]_{M}$ and $[y]_{M'}$ denote the joint and prior marginal distribution of $y$ in submodel $M$, respectively. In the first equality, equation (15), we perform marginal replacement to establish a common prior marginal distribution for $y$ across all submodels (Goudie et al., 2019). Goudie et al. (2019) proved that marginal replacement minimizes the Kullback–Leibler divergence between the melded distribution and original joint distribution under the constraint that the updated joint distribution admits $[y]_{pool}$ as a marginal therefore we can view equation (15) as the minimally modified joint distribution with marginal $[y]_{pool}$. Note that neither of the conditional distributions $[y]_{ADSM}$ or $[y]_{N-mix}$ in equation (15) have an analytical closed form because both $f$ and $g$ are non-invertible equations (6) and (7). We therefore rewrite the joint melded distribution as a product of the submodel joint distributions over the prior marginals for posterior inference, equation (16).

Another difficulty in posterior inference is that all three submodel marginals in equation (16) are analytically intractable. Goudie et al. (2019) recommended approximating the submodel marginals with kernel density estimators, but this approach can lead to numerical instabilities in implementation (Manderson & Goudie, 2022b). We obviated approximating the submodel marginal distributions by constructing $[y]_{pool}$ using chained product of experts (PoE) pooling (Manderson & Goudie, 2022a),

$$[y]_{pool} = \frac{1}{K}[y^A]_{ADSM}[y]_{STTM}[y^G]_{N-mix}, \quad \text{for } K$$

where $K$ is the number of submodels. Under PoE pooling, the melded posterior for $y$ is proportional to a product of the submodel joint distributions, which simplifies implementation. One caution regarding PoE is that the pooled prior is often unintuitive and may not be a good summary of the submodel marginals (Goudie et al., 2019). We simulated draws from $[y^A]_{ADSM}, [y]_{STTM}$, and $[y^G]_{N-mix}$ using standard (forward) Monte Carlo methods and found that the implied prior marginals were vague because the specified priors for submodel parameters $\beta_i, \alpha, \eta$, etc., were also vague. Because of the limited impact of prior information and pooling function on posterior inference for $y$, we used PoE pooling for computational convenience, but see Goudie et al. (2019) for a suite of other pooling options.

Targeting $[y, .]_{meld}$ with a standard Markov chain Monte Carlo (MCMC) algorithm would involve computationally infeasible block updates for $N^A, N^G$, and $z$ because $y^A = f(N^A, z)$ and $y^G = g(N^G)$. We avoided high-dimensional parameter updates by targeting the melded posterior with a multistage MCMC algorithm. We sampled from $[y^A, .]_{ADSM}$ and $[y^G, .]_{N-mix}$...
using two independent Metropolis–Hastings-within-Gibbs algorithms. We promoted conjugacy of the linear predictor, $\beta_y$, using Pólya–Gamma data augmentation (Polson et al., 2013), which can improve sampling efficiency in ecological binary regression models (Clark & Altewegg, 2019). Web Appendix B includes additional implementation details for the first-stage sampler.

In the second-stage, density samples from the first-stage were used as the proposals in the STTM, equation (14). For MCMC iteration $k$ in the second-stage, we drew a subsample denoted by $y^{X,(k)}$, $X \in \{A, G\}$ from the first-stage samples of submodel $M$, $M \in \{ADSM, N$-mix$\}$, randomly with replacement, and the Metropolis–Hastings ratio was

$$\frac{[y^{X,(k)}]}{[y^{X,(k-1)}]} = \frac{[y^{X,(k)}]}{[y^{X,(k-1)}]}$$

where $y^{X,(k-1)}$ is the current value of $y^{X}$ in the chain. The refined samples from the second-stage constitute draws from $[y^{X}, \cdot]_{\text{merge}}$. A heuristic for the multistage MCMC algorithm is that it further refines $[y^{X}, \cdot]_{\text{merge}}$ by selecting samples that conform with the spatio-temporal trends observed in both datasets. To improve mixing, we updated the elements of $y^{X}$ one at a time. See Web Appendix B for a complete description of the second-stage sampler and implementation details.

6 | RESULTS

6.1 | Simulation study

We performed a simulation study to access the predictive performance of our integrated model for site level density estimates. The integrated model maintained the same empirical coverage rate of the ADSM and $N$-mixture submodel and reduced uncertainty and bias. We also assessed the impact of reduced aerial survey effort on predictive performance. Overall, site level density estimates were more sensitive to reduced survey effort than range-wide estimates. Both site level and range-wide predictions were occasionally poor for years during which no aerial surveys were conducted. A full description of the simulation study and its results is available in Web Appendix D.

6.2 | Case study

The melded density estimates for the Kansas EOR from the integrated model are similar to the density estimates of the ADSM but have reduced uncertainty and are shifted slightly for some years (Figure 3). Shifts in the melded posterior tend to mirror trends estimated from the ground surveys. For example, from 2015–2016 there was an estimated decline in LEPC densities according to the aerial survey data, but densities increased across the ground sites. The melded posterior for 2016 incorporates trends from the ground survey and shifts the posterior right. The largest fluctuation in LEPC density was in 2013 following the extreme drought conditions of 2011 and 2012 (Hagen et al., 2017). Both the raw aerial and melded density estimates show a decline, but the fluctuation in the melded estimates is more nuanced. In general, the melded densities estimate have a smoother temporal trajectory compared to the raw aerial estimates. We also compared the estimates of our ADSM with those of Nasman et al. (2021) in Web Appendix E. See Web Appendix F for posterior inference for covariate associations in the STTM.

The integrated model facilitates inference for LEPC density at unsampled regions via the joint melded distribution so that annual density estimates across Kansas EOR during years which no aerial survey was conducted (2005–2011 and 2019) can still be inferred. The Kansas EOR density estimates from 2005–2011 exhibit greater uncertainty but have long right tails to reflect higher densities observed at the ground survey regions. A map of estimated LEPC across Kansas EOR is given in Figure 4. The southwest region of the SGPR consistently boasted the highest densities followed by the western portion of the MGPR. The SSPR had the lowest densities and show a decreasing pattern over time. Mean estimates were higher in the northern region of the SGPR from 2005–2011 but have large uncertainty because of no aerial or ground surveys during that period (Figure 1).
joint inference on quantities that are multivariate non-invertible functions of submodel parameters. This quality is especially appealing in ecology where many popular models provide inference on the parameter of interest through derived quantities. Markov melding may also reduce computation time when submodels handling the observational uncertainty of each dataset are fit in parallel.

The integrated model allowed us to reduce uncertainty in annual density estimates by refining the initial density posterior distributions from the submodels to concur with spatio-temporal trends observed across both datasets. Through the melded joint distribution, the integrated model also provided inference for density at unsampled regions that account for the contributions of both datasets. Inferring annual density estimates from the ground sites alone would be inaccurate because of preferential sampling (Diggle et al., 2010). The historical density estimates of the integrated model, however, accounted for the uncertainty in both datasets and leveraged trends in temporal dependence and covariate associations learned from the aerial survey data. The historical density estimates, which provide insights about longer scale trends in LEPC density, are important for assessing recovery of the species (Van Pelt et al., 2013).

We developed a modeling approach for integrating inference from aerial and ground surveys of LEPC in Kansas, but our approach can be generalized to accommodate other surveys. Most immediately, our approach can accommodate the ground surveys from the other states in the LEPC range. Ground surveys are distinct by state, but each survey produces estimates of density in a particular region and our approach can accommodate differences in observational error. Furthermore, we could extend our current model to account for population dynamics by including an additional submodel that characterizes changes in site-level counts due to annual variability in survival, fecundity, and immigration. The extended IPM could produce spatio-temporal predictions that explicitly account for the contributions of recruitment and survival which could help understand the driver of population change and inform conservation practices for the species (Van Pelt et al., 2013).

Accounting for observational error is often a necessity when developing models for SCC (Fernandes et al., 2019). By taking a Markov melding approach, we showed how surveys with unique observational uncertainties and scales can be incorporated into a joint response. Furthermore, we facilitated computation by fitting the model in stages.
which obviated high-dimensional parameter updates and induced conjugacy for several parameters in the submodels. Another computational advantage of Markov melding is that it enabled model specific data augmentation strategies such as PX-DA in the ADSM and tobit regression in the STTM. Our scalable approach for joint Bayesian inference serves as a foundation for developing future integrated models for mixed surveys of wildlife abundance in other studies.

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DATA AVAILABILITY STATEMENT
The data that support the findings in this paper can be requested from Kansas Department of Wildlife and Parks (KDWP) at kdwpt.openrecords@ks.gov.

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**SUPPORTING INFORMATION**

Web Appendices referenced in Sections 4–6 and code for fitting the melded model to the lesser prairie-chicken data and conducting the simulation study and sensitivity analysis are available with this paper at the Biometrics website on Wiley Online Library.

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