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Integrating population- and individual-level information in a movement model of Yellowstone bison

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Abstract. Throughout the world, fragmentation of landscapes by human activities has constrained the opportunity for large herbivores to migrate. Conflict between people and wildlife results when migrating animals transmit disease to livestock, damage property, and threaten human safety. Mitigating this conflict requires understanding the forces that shape migration patterns. Bison *Bos bison* migrating from Yellowstone National Park into the state of Montana during winter and spring concern ranchers on lands surrounding the park because bison can transmit brucellosis (*Brucella abortus*) to cattle. Migrations have been constrained, with bison being lethally removed or moved back into the park. We developed a state-space model to support decisions on bison management aimed at mitigating conflict with landowners outside the park. The model integrated recent GPS observations with 22 years (1990–2012) of aerial counts to forecast monthly distributions and identify factors driving migration. Wintering areas were located along decreasing elevation gradients, and bison accumulated in wintering areas prior to moving to areas progressively lower in elevation. Bison movements were affected by time since the onset of snowpack, snowpack magnitude, standing crop, and herd size. Migration pathways were increasingly used over time, suggesting that experience or learning influenced movements. To support adaptive management of Yellowstone bison, we forecast future movements to evaluate alternatives. Our approach of developing models capable of making explicit probabilistic forecasts of large herbivore movements and seasonal distributions is applicable to managing the migratory movements of large herbivores worldwide. These forecasts allow managers to develop and refine strategies in advance, and promote sound decision-making that reduces conflict as migratory animals come into contact with people.

Key words: adaptive management; Bayesian models; bison; culling; density; harvest; hierarchical Bayes; migration; movement model; snowpack; state-space model; Yellowstone National Park, USA.

INTRODUCTION

Large herbivore movements occur at multiple scales of time and space. Annual migration is the manifestation of choices made at the regional scale that allow animals to respond to changes in resources that cannot be exploited year round (Senft et al. 1987, Fryxell and Sinclair 1988). Migration is a regular, long-distance pattern of movement typically observed in systems with predictable, seasonal fluctuations in environmental conditions (Mueller and Fagan 2008). In montane environments, such movements along elevation gradients provide large herbivores access to newly emerging vegetation during the growing season, resulting in

increased long-term rates of energy gain (Albon and Langvatn 1992, Wilmshurst et al. 1995, Mysterud et al. 2001, Hebblewhite et al. 2008). Migratory movements may also diminish predation pressure as animals move beyond the boundaries of predator territories (Laundre et al. 2001, Fortin et al. 2004, Hebblewhite and Merrill 2007). Montane environments are characterized by a prolonged period when newly emerging vegetation is no longer available and decisions to move are often influenced by increased energy costs of locomotion and foraging with snowpack establishment (Parker et al. 1984, Larter and Gates 1991, Schaefer and Messier 1995, Fryxell et al. 2004, Doerr et al. 2005). Within-patch foraging movements are affected by localized heterogeneity, whereas migratory movements are typically driven by factors at the landscape scale (Ball et al. 2001, D'Eon and Serrouya 2005, Holdo et al. 2009, Zweifel-Schielly et al. 2009).

Human activities have fragmented landscapes throughout the world, severing historic pathways for

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migration of many species of large herbivores (Galvin et al. 2008, Hobbs et al. 2008). Rural landscapes supporting livestock production and agriculture often provide usable habitat for migrating large herbivores (Hansen and DeFries 2007). Road development (Nellemann et al. 2001, Ito et al. 2005, Fox et al. 2009, Holdo et al. 2011), fencing (Fox et al. 2009, Bartlam-Brooks et al. 2011, Li et al. 2012), natural resource extraction (Sawyer et al. 2009), and recreation-based development (Vistnes et al. 2004, Wittmer et al. 2007) now threaten many remaining long-distance migrations (Berger 2004). Furthermore, migratory wildlife may come into conflict with people beyond the boundaries of protected areas because wildlife transmit disease, damage property, or compete with livestock for forage. (Thouless 1995, Plumb et al. 2009, Metzger et al. 2010). Severing migrations has had adverse demographic effects on large herbivores and there is increasing support at regional and global levels to preserve these natural phenomena (Berger 2004). However, the interests of local economies often conflict with conservation goals. Maintaining migrations in the face of this conflict requires an understanding of the forces that shape migratory patterns.

Human hunting reduced plains bison (*Bos bison*) from an estimated 28 million animals to fewer than 100 by the end of the 19th century. Approximately 25 of these surviving bison occupied remote areas in Yellowstone National Park and the remainder were found in private preserves across the western United States. Beginning in 1902, a second herd was started in Yellowstone with 21 bison from two private reserves. Total bison abundance in Yellowstone has gradually increased through protection, husbandry, and relocation. Beginning in 1968, bison numbers were allowed to fluctuate in response to weather, predators, and resource limitations (Meagher 1973). Seasonal movements were reestablished as the population increased in size, and expansion of the winter range was detected by the 1980s (Meagher 1989). Yellowstone bison eventually began using lower-elevation winter ranges outside the park in Montana, where winter snowpack is less severe and it is easier to access forage. Range expansion much beyond the park boundary is now precluded by intense management intervention, due to concerns of brucellosis transmission to cattle (White et al. 2011).

Approximately 60% of the Yellowstone bison population has been exposed to brucellosis, a bacterial disease caused by *Brucella abortus* that may induce abortions or the birth of nonviable calves in livestock and wildlife (Rhyen et al. 2009). When livestock are infected, it also results in economic loss from slaughtering infected cattle, increased testing requirements, and possibly, reduced marketability of cattle. The U.S. government and the state of Montana agreed to an adaptive interagency bison management plan (USDI and USDA 2000a, b) for cooperatively managing the risk of brucellosis transmission from Yellowstone bison to cattle while conserving bison as a natural component of

the ecosystem and allowing some bison to migrate out of the park. Before cattle are stocked in the area during summer, bison that migrated into Montana during winter are hazed (i.e., moved) back into Yellowstone National Park, harvested by hunters, or captured and transported to slaughter (USDI and USDA 2000a, b).

Adaptive management is a structured decision-making approach for improving resource management by systematic learning from management actions and outcomes (Walters and Holling 1990). It involves the exploration of alternatives for meeting objectives; prediction of outcomes from alternatives using current understanding; implementation of at least one alternative; monitoring of outcomes; and using results to update our knowledge and adjust actions (Williams et al. 2007). Adaptive management provides a framework for decision-making in the face of uncertainty and a formal process for reducing uncertainty to improve management and outcomes over time.

White et al. (2011) provided an assessment of the Interagency Bison Management Plan indicating that migrations far exceeded expectations of initial models and that ~3200 bison were culled during 2001–2011. More than 20% of the population was removed during 2006 and 2008, contributing to a skewed sex ratio, gaps in the population age structure, and reduced productivity, which could threaten the integrity of the population if continued (White et al. 2011). These authors and stakeholders recommended reduced culling of animals at park boundaries and increased tolerance in adjacent areas in the state of Montana to support sport hunting. Managers agreed to reduce large-scale culls through gather-and-slaughter and requested a predictive model of trans-boundary movements to assess revised management alternatives.

Model development is a component of the structured decision-making process that brings together data and uncertainty through testable hypotheses representing our understanding of the system and effects of management alternatives. Uncertainty arises from our lack of understanding of the ecological process, measurement error, environmental variability, and our lack of complete control over management actions (Williams et al. 2007). Hierarchical models are particularly well suited for adaptive management because of the ability to appropriately incorporate data with different error structures and to identify both observation error and process variance. Bayesian techniques provide a particularly clear method for constructing these models.

Here, we develop a hierarchical Bayesian model of regional-scale movements of Yellowstone bison. The structural connectivity of the bison range is identified by differentiating the landscape into wintering areas linked by migration paths. We used a state transition approach (Caswell 2001) in discrete time to estimate monthly distributions during 1990–2012 and to relate transition probabilities to environmental covariates. Future migrations are forecasted under different scenarios of

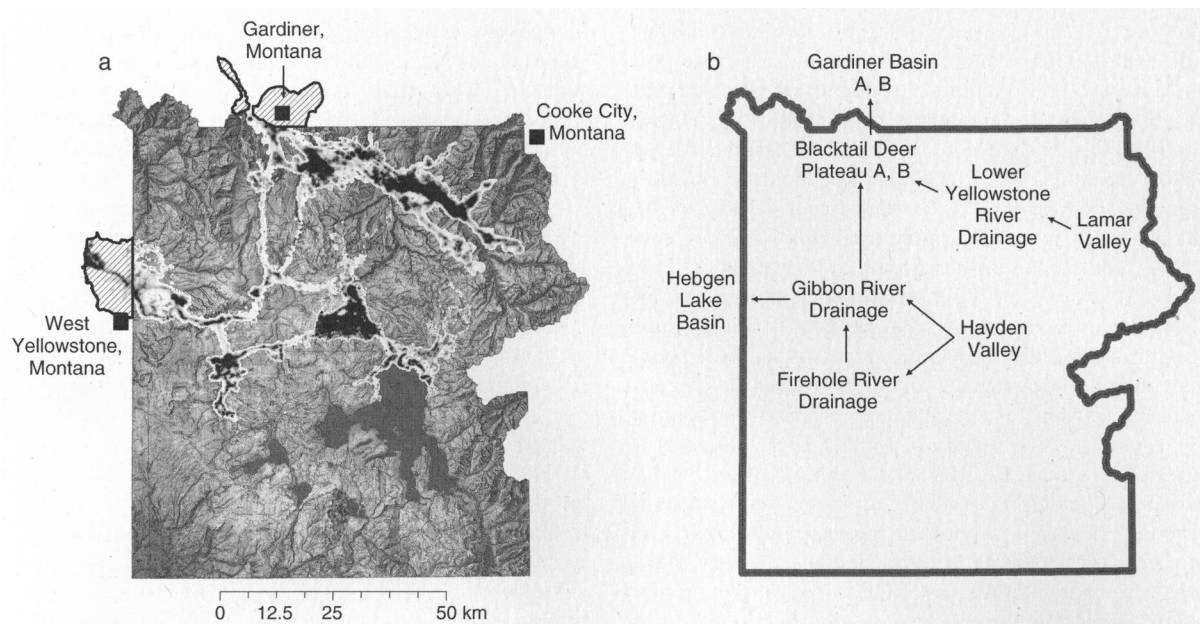


FIG. 1. (a) Cumulative utilization distribution of bison use (darker colors represent increased use) in and surrounding Yellowstone National Park during 2004–2012. Hashed areas are out-of-park bison management areas where animals are harvested, gathered into livestock-like handling facilities, and can come into contact with cattle. (b) Graph of wintering areas and migration paths (arrows) created from the cumulative utilization distribution. The uppercase letters A and B indicate separate wintering areas for central and northern herd animals occupying the same geographic area. These wintering areas and migration paths served as a basis for modeling movements.

environmental conditions and herd sizes to identify the timing and magnitude of movements, and to assess the appropriateness of alternative management interventions. This approach of using Bayesian inference in support of adaptive management is applicable to addressing trans-boundary movements of wildlife worldwide.

STUDY AREA

Yellowstone bison live in a single population of ~2500–5000 bison in at least two breeding herds (central and northern). The central herd occupies the central plateau of Yellowstone National Park, extending from the Hayden Valley and nearby grasslands in the east to the lower-elevation and thermally influenced Gibbon (also referred to as Madison) River drainage and Hebgen Lake basin in the west (Fig. 1). The central plateau is characterized by several large meadow complexes located along an east–west gradient of decreasing elevation linked by narrow travel corridors that coincide with rivers. At the highest end, the Hayden Valley is characterized by highly productive upland grass communities, with the majority of habitat classified as big sagebrush (*Artemisia tridentata*)/Idaho fescue (*Festuca idahoensis*) or silver sagebrush (*A. cana*)/Idaho fescue. Elevations exceed 2450 m and snow water equivalents are more severe than alternative areas used by bison, with refuge areas provided by windswept hills and geothermal-influenced areas during winter. The

mid-elevation Firehole River drainage (2225 m) encompasses several interconnected, thermally influenced geyser basins, with ground cover dominated by sedges at the base of the basins and cool season grasses on the slopes. The Gibbon Valley and Hebgen Lake basin are a series of small and disjoint meadows spanning a decreasing gradient from 2200 m in the east to 2050 m at the western boundary of the park north of West Yellowstone, Montana.

The northern herd congregates in the Lamar Valley and on adjacent plateaus in northern Yellowstone during the breeding season (15 July–15 August; Fig. 1). During the remainder of the year, these bison use habitats in the Yellowstone River drainage, which extends 100 km between Cooke City and the Paradise Valley north of Gardiner, Montana. This area is characterized by a large expanse of upland grassland meadows occurring along a decreasing elevation gradient from east (2200 m) to west (1650 m). This area has drier and warmer summers and less severe winters than the central interior of the park. There is limited geothermal influence and the majority of the habitat is characterized as big sagebrush/Idaho fescue. The western extent of these northern grasslands occurs near Gardiner, Montana. Although it is the least productive wintering range, it generally contains snow-free areas during most winters, so forage availability can be high even though production is low.

METHODS

Movement data

Sixty-six bison >1 year of age were captured in autumn during the years 2004–2012 by immobilization with carfentanil and xylazine (Rhyan et al. 2009), or at handling facilities near the boundary of the park (USDI and USDA 2000a, b). Individuals were fit with a store-on-board GPS collar (Telonics, Mesa, Arizona, USA) that collected between two months and five years of information. Bison were captured from the central herd during 2004–2012 and from the northern herd during 2006–2012. GPS devices were programmed to collect one location every 48 min during 2004–2005 and one location every 2 h during 2005–2012. In total, 512 621 locations were collected.

Migration paths used by bison in the central portions of Yellowstone generally passed through constricted regions at some point, and remotely triggered camera stations (PM-175, Silent Image, Reconyx, Holmen, Wisconsin, USA) were installed in these areas during the months of November–April in 2010–2012 to record total numbers of bison and their direction of travel. Cameras were visited biweekly to download images and replace batteries. Pictures were viewed using Mapview (Reconyx).

Aerial counts

During 1990–2012, 136 aerial counts were completed to estimate population size, whereby observers recorded the location and size of encountered bison groups during systematic surveying of wintering areas (Hess 2002). Counts occurred monthly from 1990 to 1997, approximately quarterly from 1998 to 2006, and again monthly from 2007 to 2012.

Model covariates

Three movement covariates were observed throughout the duration of this research: herd size, snowpack, and standing crop. (1) Between two and three annual aerial counts of bison on breeding areas were completed to estimate herd sizes. (2) Daily snow estimates were generated using a simulation model that predicted 28-m² resolution surfaces of snow water equivalents (Watson et al. 2006, Geremia et al. 2009). Daily snow surfaces of the bison utilization distribution area across the central and northern portions of the park were averaged to single north and central values for each day of the year. We added these averaged, daily values across the year to create single, annual snowpack values for the northern and central regions. (3) Standing crop estimates at the conclusion of the growing season were generated using a simulation model that predicted 30-m² resolution surfaces of modeled monthly net primary productivity from NASA's Carnegie-Ames-Stanford-Approach (Potter et al. 2007, Geremia et al. 2011). CASA, a biophysical ecosystem model, incorporates temperature, precipitation, solar radiation, vegetation cover, and the

normalized differentiation vegetation index from Landsat satellite data as inputs during April through October (Potter and Klooster 1999, Crabtree et al. 2009, Huang et al. 2010). Values were averaged across central and northern grassland regions of the bison utilization distribution for each year.

Bison utilization distribution

Brownian bridge movement models were used to approximate the continuous movement path of individual adult female bison between successive locations recorded by store-on-board global positioning system (GPS) devices (Horne et al. 2007). For each individual, we created utilization distributions that were two-dimensional gridded surfaces representing relative use according to frequency of visits to, and movement rate through, areas. A single cumulative utilization distribution for the entire population was created by summing across each individual utilization distribution (Sawyer et al. 2009; Fig. 1).

Structural connectivity

We used a graph theoretic approach to define the structural connectivity of Yellowstone bison (Urban and Keitt 2001). We differentiated the landscape into a set of nodes that were wintering areas connected by edges that were migration paths. Wintering areas and migration paths were determined by looking at the cumulative utilization distribution and identifying the two types of areas. GPS histories of individually marked animals were then examined to confirm our classification. Our graph included 10 wintering areas connected by eight migration paths (Fig. 1).

Statistical approach

State-space models can be used to join stochastic models of observations with a stochastic model portraying the underlying mechanisms of movement (Patterson et al. 2008, Schick et al. 2008). In the state-space approach, we assume that there is a time series of unobserved, true states such that the current state directly influences the state at the next time. A second time series, running in parallel, includes the observations of the true states. We assume that the observations fail to represent the true state perfectly because they are made with error. Hierarchical Bayesian methods provide a framework for factoring highly dimensional problems into lower-dimensional ones (Berliner 1996). These techniques decompose a problem into data, the underlying process, and parameters, and identify uncertainty associated with each component. The following sections describe the decomposition of the problem into process, data, and parameter models.

Process model

The true numbers of bison in wintering areas and movement probabilities between areas were estimated using a state-transition model (see also Harrison et al.

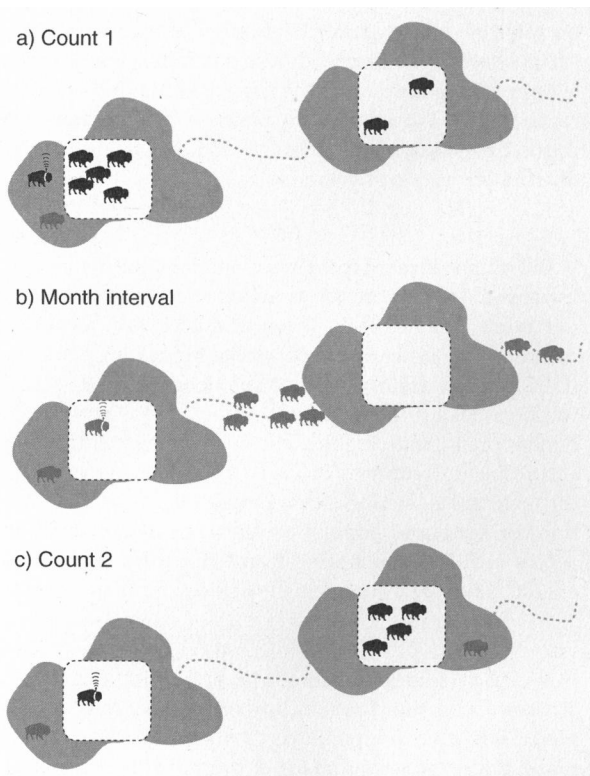


FIG. 2. We present a conceptual diagram of our model. Aerial count units (dashed-line boxes) did not completely overlap wintering areas (gray-shaded region). (a) At count 1, bison were observed in aerial count units or in wintering areas based on GPS devices fit to animals. Uncollared bison outside of count areas were not observed, which we represent using the transparent (gray) icon. (b) Movements between wintering areas during the ensuing month were not observed (gray icons). (c) One month later at count 2, bison were again observed in aerial count units or in wintering areas based on GPS devices fit to animals. Unobserved quantities including the true number of bison in wintering areas at the time of counting and movements between counts were estimated. These unobserved quantities (e.g., movements) were related to covariates mainly reflecting food availability.

2006, Morrison and Bolger 2012) in discrete time (Fig. 2). The model updated on a monthly time step. The initial spatial distribution of bison for each year was estimated during July, when bison were congregated on breeding areas for the rut. Model updates were generated each subsequent month through peak migration, which occurred when the highest numbers of bison were located on alternative wintering areas. The column vector $\mathbf{z}_{t,j}$ represents the true number of bison in each wintering area during month t and year j . The matrix \mathbf{A} represents transitions of bison between wintering areas (e.g., survival and movement along migration paths) during Δt (Appendix). We assume that $\mathbf{z}_{t,j}$ follows a gamma distribution with rate β and shape $\mathbf{A}_i \mathbf{z}_{t-1,j} \beta$, where \mathbf{A}_i is the i th row vector of \mathbf{A} , and $\mathbf{z}_{t-1,j}$ is a column vector. The parameters of the gamma distribution are the rate and shape, which correspond to the mean $\mathbf{A}_i \mathbf{z}_{t-1,j}$

and process variance $(1/\beta)(\mathbf{A}_i \mathbf{z}_{t-1,j})$ using moment matching (Appendix).

Survival and movement determined the number of bison remaining in each wintering area at the next time step. The monthly probability of survival is ϕ and the monthly movement probability along the i th migration path is γ_i . Each movement probability is related to covariates using the logistic model, which reflects increased energy costs of locomotion and foraging during winter (Appendix). These covariates include days since the onset of snow cover, annual snowpack magnitude, herd size, standing crop at the conclusion of the growing season, and year of study. Days since the onset of snow cover is represented using a quadratic term. This allows movement probabilities to reach minima corresponding to optimal times of the year for wintering area use. Year was included as a covariate to allow annual movement probabilities to steadily increase or decrease throughout the duration of our research.

Initial conditions

The number of bison in each wintering area at the current time $\mathbf{z}_{t,j}$ was conditioned on the number of bison at all previous times, but could be expressed by conditioning only on the most recent time. Then, the joint distribution of the movement process could be factored as $[\mathbf{z}_{1:t,j}] = [\mathbf{z}_{t,j} | \mathbf{A} \mathbf{z}_{t-1,j}] [\mathbf{z}_{t-1,j} | \mathbf{A} \mathbf{z}_{t-2,j}] [\mathbf{z}_{t-2,j} | \mathbf{A} \mathbf{z}_{t-3,j}] \dots [\mathbf{z}_{1,j}]$. We needed to specify prior distributions on the initial numbers of bison in each wintering area $\mathbf{z}_{1,j}$ during each year. We chose informative priors that were based on the numbers of bison observed during initial counts, where $\log(\mathbf{z}_{1,j}) \sim N(\log(\mathbf{y}_{1,j}), 0.5)$ (see Appendix).

Data models

Aerial counts did not occur exactly one month apart, and we adjusted our process model to have a variable time step. Model updates occurred on the day of counting or on the 15th day of the month when counts did not occur. To align the intervals in the process model with the intervals in observed counts, transition probabilities were scaled by the fraction of elapsed time to the monthly time step. We defined $\Delta t_{t,j}$ as this proportion and scaled survival using $\phi^{\Delta t_{t,j}}$ and movement using $1 - \gamma_i^{\Delta t_{t,j}}$. For example, if counting occurred 45 days (e.g., 1.5 months) after the previous model update, then survival during that interval was estimated as $\phi^{1.5}$ and movement as $1 - \gamma_i^{1.5}$.

Counts of wintering areas were assumed to follow a Poisson–gamma mixture distribution. Count areas overlapped wintering areas and the relation matrix \mathbf{B} was created to align counting and wintering areas (Appendix). The vector $\lambda_{t,j}$ was the true average number of bison in count areas during month t and year j ; $\mathbf{y}_{1:t,j}$, a column vector, was the observed aerial count. We assumed that $\lambda_{t,j}$ follows a gamma distribution with rate α and shape $\mathbf{B}_k \mathbf{z}_{t,j} \alpha$, where \mathbf{B}_k is the k th row of \mathbf{B} . Then, each element of $\mathbf{y}_{1:t,j}$ follows a Poisson distribution with intensity $\lambda_{t,j}$ (Appendix). The shape parameters of the

gamma distribution correspond to the mean ($\mathbf{Bz}_{t,j}$) and observation variance ($(1/\alpha)(\mathbf{Bz}_{t,j})$) using moment matching. Our specification assumed that observers had perfect detection during counting which was based on >0.97 sightability reported by Hess (2002). Discrepancies between process model predictions and counts were attributed to sampling error, such as bison moving outside of count unit boundaries or incomplete surveying of units due to inclement weather.

Monthly locations of all bison fit with GPS devices were assumed to follow a multinomial distribution, with the column vector $\mathbf{y}_{2t,j}$ as the number of individually marked bison located by GPS in each wintering area during month t and year j . Multinomial probabilities were the proportion of bison in each wintering area predicted by the process model where the probability for the i th wintering area was $z_{t,j,i}/\sum_i z_{t,j,i}$ (Appendix). This approach integrated observations from a small subset of individual animals over a comparatively short time period with 22 years of park-wide counts in the likelihood of process model predictions.

Covariates were treated as being measured with error. We assumed that observations (x) of annual snowpack magnitude, standing crop at the conclusion of the growing season, and herd size followed normal distributions. The vector $\boldsymbol{\mu}_x$ represented latent snow, herd, and standing crop conditions during year j (Appendix). The vector of standard deviations of observed covariate conditions, $\boldsymbol{\sigma}_x$, had one element for each latent covariate type (Appendix). Informative prior distributions were chosen for standard deviations of snowpack magnitude and standing crop conditions (see *Parameter models*). Up to three replicate observations of herd sizes were recorded annually and diffuse prior distributions were specified for standard deviations of herd sizes (see *Parameter models*). Covariates were standardized to improve model convergence, reduce auto correlation, and facilitate comparison of covariate effects. Because covariates were treated as latent quantities, standardization occurred during each MCMC update. The difference of each current covariate value and mean of all current covariate values were divided by the standard deviation of all current covariate values.

Parameter models

We assumed that monthly survival followed a Beta(97,0.98) distribution, based on previous research identifying survival in Yellowstone bison using mark-recapture techniques (Geremia et al. 2009). Note that the posterior distribution of the survival parameter was identical to the prior distribution and, as a result, we do not discuss this result further. Model-generated metrics for snow were produced for sites corresponding with four SNOTEL stations located within and surrounding Yellowstone. Predictions were compared to reported values to create informative $N(1.60,0.10)$ prior distributions for log-transformed standard deviations of snow conditions. Standing crop measures were collected at the

conclusion of the growing season from across Yellowstone and were compared to forage model predictions to create informative $N(1,0.10)$ prior distributions for log-transformed standard deviations of standing crop conditions. Otherwise, the diffuse prior distribution $N(0,1000)$ was assumed for all model parameters including: the logistic model coefficients relating covariates to movement probabilities; the log-transformed parameters of gamma distributions for the true (β) and observed (α) numbers of bison occupying wintering areas; the log means ($\boldsymbol{\mu}_x$) of annual herd size, snow, and standing crop conditions; and the log-transformed standard deviations of herd size conditions ($\boldsymbol{\sigma}_x$; Appendix).

Model implementation

Marginal posterior distributions of latent states and parameters were estimated using Markov chain Monte Carlo (MCMC) methods. Samples were drawn from the posterior distribution of each parameter and latent state using a hybrid Gibbs sampler with Metropolis-Hastings steps. All analyses were completed using program R (R Core Development Team 2013); we have included code to simulate data and implement our model in the Supplement.

Each of three MCMC chains was run for 500 000 iterations; the first 250 000 iterations were discarded to allow for burn-in. We confirmed convergence, using the Gelman and Rubin test statistic, by assuring that the potential scale reduction factor was <1.02 for each variable (Gelman and Rubin 1992). Trace plots of marginal posterior distributions were inspected to ensure reasonable exploration of the parameter space. Metropolis-Hastings acceptance rates were tracked to assure values near 0.40.

Posterior predictive checks help to assess whether observed data are consistent with the model (Gelman et al. 1996, Gelman and Hill 2007). Posterior predictive realizations of count observations were obtained during each MCMC update after the burn-in period. These realizations can be conceptualized as replicated data produced by the model. We assessed how replicated data resembled the distribution of the real data by defining test statistics and calculating Bayesian P values as the proportion of MCMC iterations for which the test statistic of the replicated data was more extreme than the observed data. One test statistic was created as the proportion of bison in each count area to indicate discrepancies in central tendency. Mean squared error was defined as an additional test statistic to indicate discrepancies in dispersion.

Posterior predictive realizations of counts should exhibit a strong linear relationship to observed counts. We estimated the posterior predictive distribution of r between the observed and replicated data during each MCMC iteration after the burn-in period. Out-of-sample prediction was also used to assess model performance by comparing predicted numbers of bison

moving along migration paths to numbers of bison recorded using remote camera stations.

Predictions for adaptive management

Bayesian inference provides a framework for prediction that estimates the uncertainty in the model parameters, process error, and observation error (Clark 2007). The same model that is used for estimating the parameters is used to make predictions. This is done by conditioning the predictive distribution of future numbers of bison in wintering areas on the parameters, process error, and future covariate variables. Because these covariate variables are not known in advance, an additional source of uncertainty enters, which we refer to as scenario uncertainty (Clark 2007). Future snow and standing crop conditions can be conditioned on what has been observed. For example, \tilde{x} is a predicted covariate and we assume that \tilde{x} follows a normal distribution with the mean and standard deviation of previously observed snow or standing crop conditions. It is more challenging to estimate future herd sizes, which depend on herd size during the previous year, \tilde{x}_{j-1} ; population growth, $\tilde{\lambda}$; and removals, \tilde{r}_j such that $\tilde{x}_j = \tilde{\lambda}(\tilde{x}_{j-1} - \tilde{r}_j)$. Population growth can be estimated as a derived quantity in our model by calculating this quantity for each year since 1990. Then, predictions of $\tilde{\lambda}$ follow a normal distribution with the mean and standard deviation of these derived quantities. Management reductions occur through hunting or gather-and-consignment, in which bison are moved into livestock facilities and shipped to slaughter, terminal pastures, or research or quarantine facilities. Managers have complete control over gather-and-consignment, because riders on horseback are used to haze targeted animals into processing facilities. Therefore, we do not need to incorporate uncertainty in \tilde{r} for predicting removals occurring through gather-and-consignment. However, there is uncertainty in predicted hunter success because not all bison occupying hunting districts are harvested by hunters. Observations during 2005–2012 indicated that it is reasonable to assume that the probability of harvest of bison occupying hunt areas follows a Beta(1,5) distribution. Using these steps, we were able to incorporate all reasonable sources of scenario uncertainty in forecasting future movements.

Bison distributions were forecasted for the 15th day of each month during August–March on the northern portions and during August–May on the central portions of Yellowstone in 2013–2017. Starting bison population size during August 2012 was assumed as 4170–4230 (~1600 central and ~2600 northern) based on aerial counting.

Five management alternatives were compared, as follows:

- 1) *Low hunting* supported recent levels of public and treaty hunting that included 50 total permits issued

during early (November–January) and late (February–March) seasons.

- 2) *Moderate hunting* included 50 permits issued for the western management area and 300 permits for the northern management area during early and late seasons.
- 3) *Moderate consignment* consisted of gather-and-consignment of up to 350 bison near the northern park boundary during early March.
- 4) *Aggressive consignment* consisted of gather-and-consignment of up to 1000 bison near the northern park boundary during early March.
- 5) *Moderate hunting-supplemental consignment* had hunting as described in alternative 2, with supplemental gather-and-consignment during early March such that total removals did not exceed 350 bison.

Plumb et al. (2009) recommended maintaining the bison population between 2500 and 4500 individuals to satisfy collective interests concerning the park's forage base, bison movement ecology, retention of genetic diversity, brucellosis risk management, and prevailing social conditions. Furthermore, White et al. (2011) found that increased conflict with humans occurred in Montana when more than 500 bison exit either park boundary. We established three constraints on model output; that total population size was kept between 2500 and 4500, that individual herd size was 1250–1750 animals, and that the number of migrants (excluding harvests and culls) was below 500.

RESULTS

Assessment of model performance

We begin by assessing model performance to confirm that our model appropriately portrayed bison movements. Comparison of posterior predicted realizations of counts to 819 real count observations indicated an r value of 0.82 (0.79–0.85, 95% credible interval). The Bayesian P value of the proportion of bison in any single count area assessed across all count observations was 0.30, but the Bayesian P value based on mean squared error was <0.01 . These test statistics show that our model was able to generate replicated data with average numbers of bison in wintering areas similar to the observed data. However, mean squared error between replicated data and true numbers of bison in each wintering area were greater than mean squared error between the observed data and true numbers of bison. Replicated MSE values were probably larger because errors propagate across levels of the modeling hierarchy. Overestimating uncertainty at the parameter level produces over-dispersed estimates of latent states, and subsequent replicated data would be over-dispersed compared to the observed data. This finding was not unexpected, given the large numbers of parameters and latent states that were estimated.

Derived quantities of numbers of bison moving along migration paths were compared to observations record-

ed by remotely triggered camera stations. Our process model only allowed for one-directional moves along edges that linked nodes representing wintering areas. Camera observations verified that back-and-forth movements occurred. However, net movements were in the direction of the process model in 94% (51/55) of monthly observations and generally within 95% credible intervals of derived quantities (Fig. 3). Thus, our model was capable of predicting movements similar to those recorded by an independent data set.

Process variance was estimated as $(1/\beta)(A_i z_{i-1,j})$ and aerial counting error was estimated as $(1/\alpha)(z_{i,j,k})$ using moment matching. Each of these quantities depended on numbers of bison in wintering areas (Table 3). To provide an illustration of the relative contribution of each of these sources of uncertainty, a process model prediction mean of 500 animals in a wintering area corresponded to a 95% credible interval of 230–861 animals truly present. The corresponding average count would be 490 with a standard deviation of 251 (Figs. 4 and 5).

Individual animal movements

Individual animal movement histories were used to develop a graph of wintering areas and migration paths from the cumulative distribution of bison use. Alternative graphs of wintering areas and migration paths were compared against GPS histories of adult female bison. We identified a graph (Fig. 1) that matched >90% of monthly locations of individual animals, which served as our state-transition matrix for predicting monthly distributions and movements. This graph was appropriate for the entire study period because migration routes were reestablished by 1990 after nearly a century of recovery and population increase (Meagher 1989, 1998). Also, telemetry locations of adult female bison recorded since 1995 (Fuller et al. 2007, Olexa and Gogan 2007, Geremia et al. 2009) indicated that identified migration paths were present and used extensively during our study.

Radio-collared adult female bison from the central herd congregated in non-forested areas of the Hayden Valley for the breeding season, after which most animals began to travel regularly between the Hayden Valley and alternative areas along the north shore of Yellowstone Lake and within the Pelican Valley. During most years, all animals exited these higher-elevation areas directly to the Firehole River drainage by the conclusion of winter. Some brief return movements to the Hayden Valley occurred, and a few bison directly accessed the Gibbon River drainage from the Hayden Valley. From the Firehole River drainage, bison accessed several disjoint meadows along the Gibbon and Madison rivers. Movements were fluid between these areas, resulting in low residence time in any single meadow. Bison next moved toward the western park boundary (23 of 46 bison fit with GPS devices) or accessed the western portion of the grasslands in northern Yellowstone by

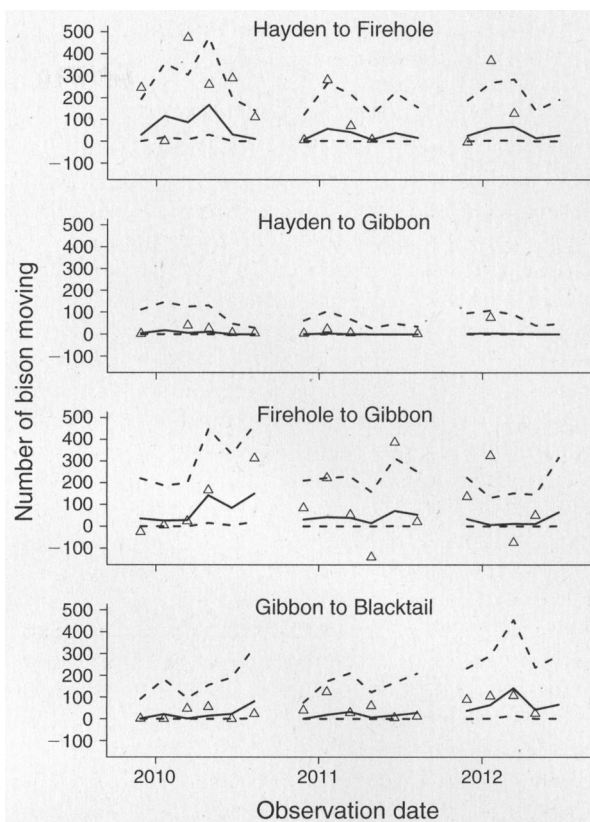


FIG. 3. Estimated numbers of bison moving along migration paths were generated as derived quantities and compared to net observed movements recorded by remote camera stations (open triangles) during the period November 2009–March 2012. Solid and dashed lines represent medians and 95% credible intervals of model predictions.

moving north along the road connecting Mammoth Hot Springs and the interior of the park (23/46 bison). Most (40/46) females from the central herd exhibited strong fidelity to breeding sites and wintering areas. However, six individuals that migrated to the northern portions of Yellowstone moved to the Lamar Valley during the following summer, interbreeding with the northern herd.

Use of northern Yellowstone by adult female bison fit with telemetry devices showed that animals fluidly moved across an approximately 40-km region along the Lamar River, from Cache Creek in the east to west of the confluence of the Yellowstone River in the west. Use was concentrated in the eastern portions of this area and adjacent higher-elevation slopes during the breeding season and early autumn, and was concentrated in the western portions during winter. During some years, most, if not all individuals, moved northwest to the Blacktail Deer Plateau. Several movement corridors connected these areas. Bison also moved farther north to the lower-elevation Gardiner basin during many of these years. These movements were made along several pathways that followed the Yellowstone and Gardner rivers. Females from the northern herd exhibited strong

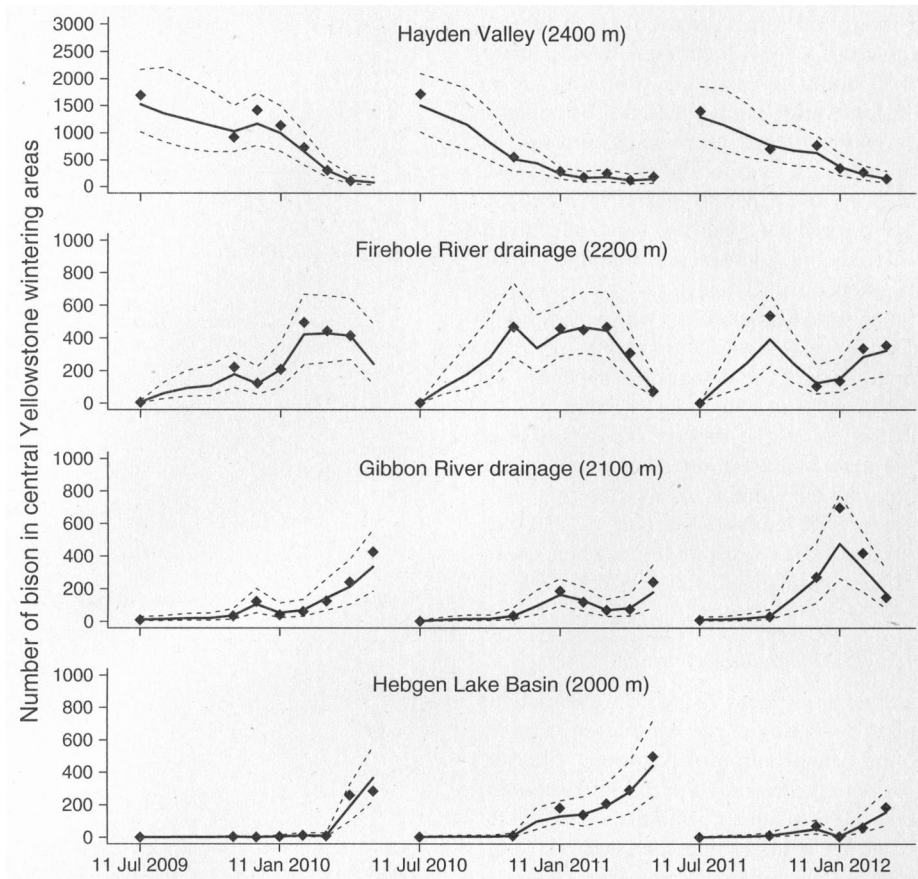


FIG. 4. Counts (solid diamonds) and means (solid lines) with 95% credible intervals (dashed lines) of marginal posterior distributions of numbers of bison occupying wintering areas in central Yellowstone during the period July 2009–May 2012. Return migrations began earlier during 2012. Breaks in lines represent times when bison were returning to breeding areas for the rut. Panels are aligned from top to bottom to show wintering areas that are progressively lower in elevation.

fidelity to breeding sites (19/20 individuals), but within-year variation in use of wintering areas. Only a single individual from the northern herd was observed using the central interior of the park.

Estimation of population-level parameters

Monthly estimated abundance of bison on wintering areas suggested that migrations followed a movement cascade, with animals moving progressively from higher- to lower-elevation areas. Abundance on breeding areas that corresponded to the highest-elevation wintering areas steadily decreased after the conclusion of the rut in September. Abundance on mid-elevation wintering areas peaked during migration periods, suggesting that these areas were used much like stopover sites. Abundance on wintering areas at the termination of migration paths peaked during May and June in the Hebgen Lake basin and during February–April in the Gardiner basin. Similar numbers of bison tended to remain on higher-elevation wintering areas at the conclusion of migration periods along central migration paths (Fig. 4). The timing, magnitude, and extent of movements along northern migration paths was more variable between years. Most, if not all, bison remained

on middle-elevation wintering areas during some years, with nearly all animals exiting to the lower-elevation areas during other years (Fig. 5).

We found strong seasonality of monthly movement probabilities along central migration paths, based on days since the onset of snow cover (Table 1). Movement probabilities reached minima during the migration period, supporting that early migrants exhibited higher probabilities of movement to subsequent wintering areas. Minima corresponded to optimal times of use of wintering areas, which occurred at a similar time after snow onset each year. Thereafter, movement probabilities rapidly increased. Seasonality of movement probabilities along northern migration paths was less apparent (Table 2), with increased interannual variation related to herd size, snowpack magnitude, and standing crop (Figs. 6 and 7).

The size of the northern herd was related to increases in monthly movement probabilities. There was a 0.85 probability that the northern herd covariate coefficient was greater than zero for movements between the Lamar Valley and the lower Yellowstone River drainage, and a 0.87 probability for movements between the Lower Yellowstone River drainage and Blacktail Deer Plateau.

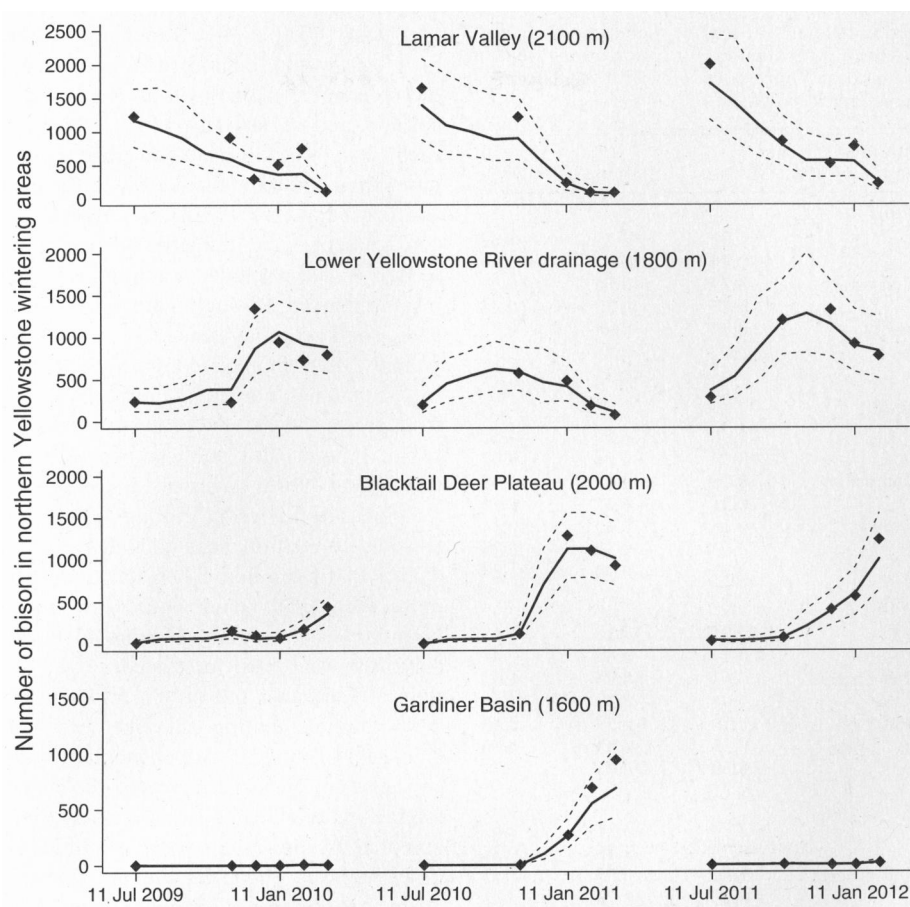


FIG. 5. Counts (solid diamonds) and means (solid lines) with 95% credible intervals (dashed lines) of marginal posterior distributions of numbers of bison occupying wintering areas in northern Yellowstone during the period July 2009–March 2012. Return migrations began earlier in northern compared to central Yellowstone. Breaks in lines represent times when bison were returning to breeding areas for the rut. Panels are aligned from top to bottom to show wintering areas that are progressively lower in elevation.

The effect of central herd size was less clear. Movement probabilities from the breeding area for the central herd decreased with herd size, suggesting that larger herd sizes prolonged congregation on the breeding area. Perhaps bison cooperatively displace snow, thereby facilitating foraging and locomotion early in winter. Central herd animals moved to the northern or western park boundaries from the Gibbon River drainage. Movements toward the northern park boundary were believed to be infrequent prior to the central herd increasing in size after large-scale reductions during 1996–1997 (Gates et al. 2005). We found a 0.90 probability that the central herd covariate coefficient was greater than zero for movements to the north, and a 0.89 probability that the central herd covariate was less than zero for movements to the west. Thus, as the central herd increased in size, use of the northern migration pathway increased (Table 1).

Snowpack magnitude was related to increased monthly movement probabilities along northern migration paths, with a 0.94 probability that the northern snowpack covariate coefficient was greater than zero

for movements between the Lower Yellowstone River drainage and Blacktail Deer Plateau and a 0.86 probability for movements between the Blacktail Deer Plateau and Gardiner basin (Table 2). Snowpack magnitude effects were in opposition across central migration paths. Snow was related to increased movements from the Hayden Valley to the Firehole River drainage (0.89 probability) and the Gibbon River drainage to the Hebgen Lake basin (0.81 probability), but decreased movements from the Firehole to Gibbon River drainages (1.00 probability; Table 1). The Firehole River drainage is characterized by thermally influenced areas that probably offset the negative effects of snow on accessing food.

The effects of standing crop at the conclusion of the growing season were ambiguous. Although nearly all coefficients were in the expected direction, with increases in standing crop related to decreased per capita movements, all credible intervals broadly spanned zero (Tables 1, 2, and 3). Monthly movement probabilities along most central migration paths increased through the duration of our research, but probabilities from the

TABLE 1. Posterior estimates of logistic model coefficients of monthly movement probabilities for bison along central Yellowstone migration paths; covariates with >0.85 probability of an effect are in boldface.

Migration path and parameter	Median	0.025%	0.975%
Hayden to Firehole			
Intercept	-1.91	-2.24	-1.62
Snow onset	0.74	0.48	0.99
Snow onset (2nd order)	-0.27	-0.56	-0.01
Herd size	-0.17	-0.38	0.03
Snowpack severity	0.13	-0.08	0.33
Standing crop	-0.02	-0.25	0.19
Year of study	0.03	-0.21	0.27
Gibbon to Blacktail			
Intercept	-2.55	-1.99	-1.50
Snow onset	-0.14	-0.66	0.32
Snow onset (2nd order)	0.78	0.07	1.48
Herd size	0.21	-0.17	0.60
Snowpack severity	-0.16	-0.49	0.14
Standing crop	-0.02	-0.39	0.34
Year of study	0.77	0.30	1.24
Firehole to Gibbon			
Intercept	-2.21	-3.11	-1.61
Snow onset	-0.25	-0.80	0.41
Snow onset (2nd order)	0.62	0.25	1.03
Herd size	0.06	-0.38	0.50
Snowpack severity	-0.19	-0.59	0.18
Standing crop	-0.35	-0.84	0.05
Year of study	0.30	-0.09	0.78
Gibbon to Hebgen			
Intercept	-2.24	-3.11	-1.61
Snow onset	-0.78	-1.45	-0.22
Snow onset (2nd order)	1.06	0.55	1.72
Herd size	-0.27	-0.78	0.21
Snowpack severity	0.18	-0.23	0.61
Standing crop	0.01	-0.53	0.48
Year of study	0.44	-0.11	1.08

Note: For snow onset, "2nd order" indicates a second-order polynomial term.

Blacktail Deer Plateau to the Gardiner basin decreased (Tables 1 and 2)

Adaptive management

Continued large-scale gather-and-consignment (alternative 4), as has occurred sporadically since the inception of the Interagency Bison Management Plan, exhibited the highest probability of reducing herd sizes below targeted levels (Table 4). Alternatives that relied exclusively on hunting were the least likely to meet decision criteria (alternatives 1 and 2). Under low levels of hunting (alternative 1), herd sizes increased and there was a high probability of more than 1500 migrants moving beyond park boundaries. Issuing more annual hunting permits (alternative 2) increased the probability of meeting decision criteria. However, there was large variation in forecasted herd sizes due to broad uncertainty in hunter success rate.

Supplementing increased numbers of state and tribal hunting permits with moderated late-winter gather-and-consignment (alternative 5) provided the highest certainty of meeting key management criteria over the next

five years (Table 4). Under this alternative, tribal members would be afforded greater opportunity for the consumption of bison as food, and the associated cultural and spiritual benefits. By issuing 350 permits each year, we forecasted average hunter harvests of more than 100 animals in each of the next five winters. In turn, numbers of bison removed by gather-and-consignment were reduced by one-half compared to scenarios that excluded hunting. Reduced numbers of bison removed through gather-and-consignment mitigates social conflicts that arise from slaughtering wild animals. Also, managers are provided increased flexibility for pursuing nonlethal alternatives, such as transport to quarantine facilities for eventual supplementation of tribal, private, and publicly owned bison populations throughout North America.

Under alternative 5 (hunting and consignment) and a starting population near 4200 bison, we found a 29% chance that more than 500 bison, and a 10% chance that more than 1000 bison would exit the northern park boundary (in addition to removals) within one year. After five years, we forecasted a 18% chance of more than 500 animals and only a 5% chance of more than 1000 animals exiting the northern park boundary. Consistent hunting, supplemented with gather-and-consignment of bison, increased the chances that future migrations would not surpass levels that are generally accepted by prevailing social conditions. At the same time, harvests and culls did not remove all migrants during most years. Consequently, managers would be

TABLE 2. Posterior estimates of logistic model coefficients of monthly movement probabilities for bison along northern Yellowstone migration paths; covariates with >0.85 probability of an effect are in boldface.

Migration path and parameter	Median	0.025%	0.975%
Lamar to Lower Yellowstone			
Intercept	-1.20	-1.88	-0.66
Snow onset	0.36	-0.74	1.02
Snow onset (2nd order)	-0.87	-2.16	0.17
Herd size	0.29	-0.25	0.84
Snowpack severity	-0.05	-0.26	0.15
Standing crop	-0.16	-0.47	0.16
Year of study	-0.10	-0.71	0.51
Lower Yellowstone to Blacktail			
Intercept	-2.20	-2.74	-1.73
Snow onset	-0.17	-0.67	0.31
Snow onset (2nd order)	-0.84	-0.20	0.39
Herd size	0.36	-0.28	1.04
Snowpack severity	0.19	-0.05	0.44
Standing crop	0.14	-0.24	0.52
Year of study	-0.14	-0.87	0.54
Blacktail to Gardiner			
Intercept	-0.47	-1.06	0.14
Snow onset	-0.26	-0.69	0.14
Snow onset (2nd order)	0.39	-0.29	1.07
Herd size	-0.11	-0.54	0.28
Snowpack severity	0.13	-0.12	0.39
Standing crop	0.03	-0.38	0.48
Year of study	-0.68	-1.05	-0.35

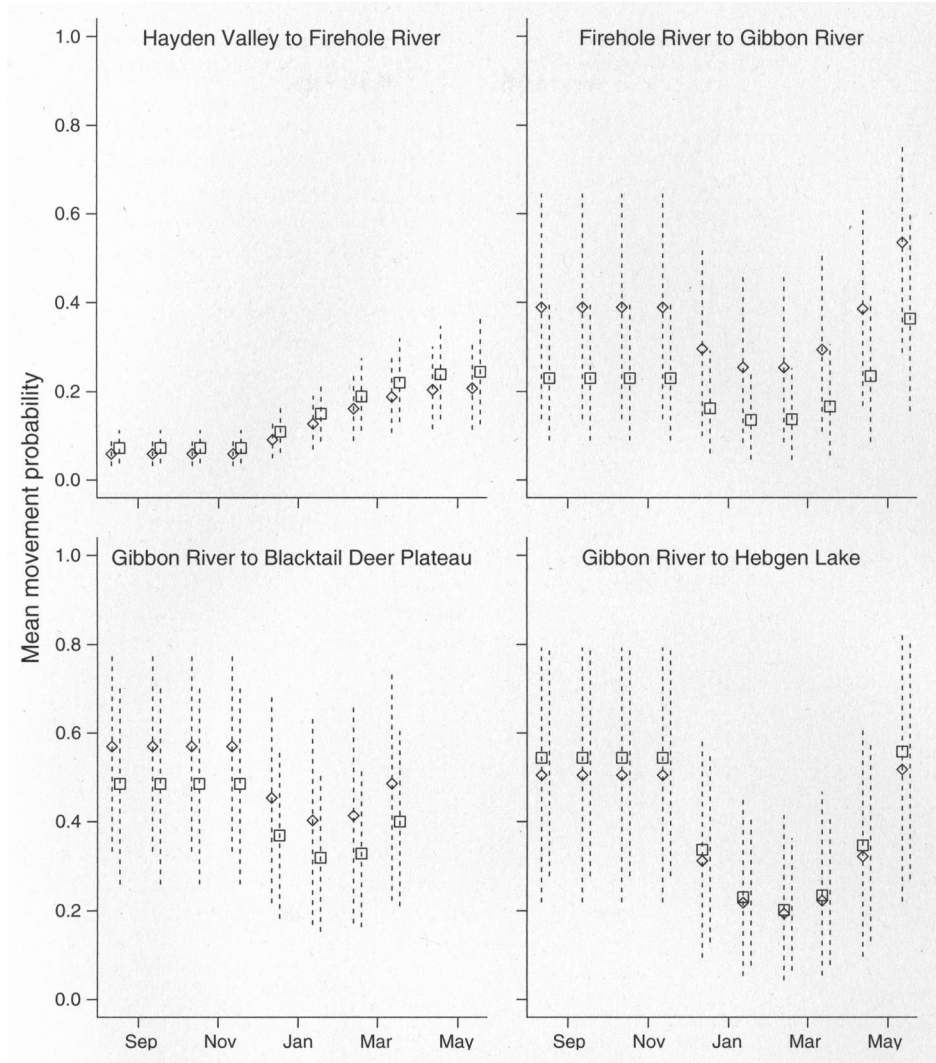


FIG. 6. Mean posterior predicted monthly movement probabilities along migration paths in central Yellowstone, assuming below-average (open diamonds) and above-average (open squares) covariates reflecting food availability. Dashed lines represent 85% quantiles (see Table 1).

afforded the opportunity to selectively remove animals through gather-and-consignment. Culls could be targeted at desired age and sex classes to offset potential adverse effects of selective hunting (e.g., by sex or herd) or to reduce brucellosis infection through removing individuals capable of transmitting infection to livestock or other wildlife (Treanor et al. 2011, White et al. 2011).

In contrast to the northern park boundary, management alternatives that reduced herd sizes to the targeted range of 1250–1750 animals did little to moderate numbers of bison migrating to the western park boundary. Further, these movements coincided with the calving period, when bison are most likely to transmit brucellosis by shedding infectious material onto the landscape through parturition. Therefore, successful trans-boundary management must focus on spatiotemporal separation of livestock and bison, rather than on removing migrants through harvest or gather-

and-slaughter. Fencing or hazing bison away from areas soon to be occupied by cattle, and targeted gather-and-haze of bison from these potential conflict areas, should create this separation. Also, current management policies attempt to gather-and-haze all bison back into the park by 15 May. However, movement probabilities out of the park peak at this time, thereby complicating management efforts. Fostering increased tolerance in regions where bison cannot come into contact with cattle until bison naturally return to breeding areas may be a sensible alternative.

DISCUSSION

We provide a first assessment identifying regional-scale movements of bison throughout Yellowstone and nearby areas of Montana. This research extends existing work that determined relationships between numbers of bison exiting the park, herd sizes, snowpack severity,

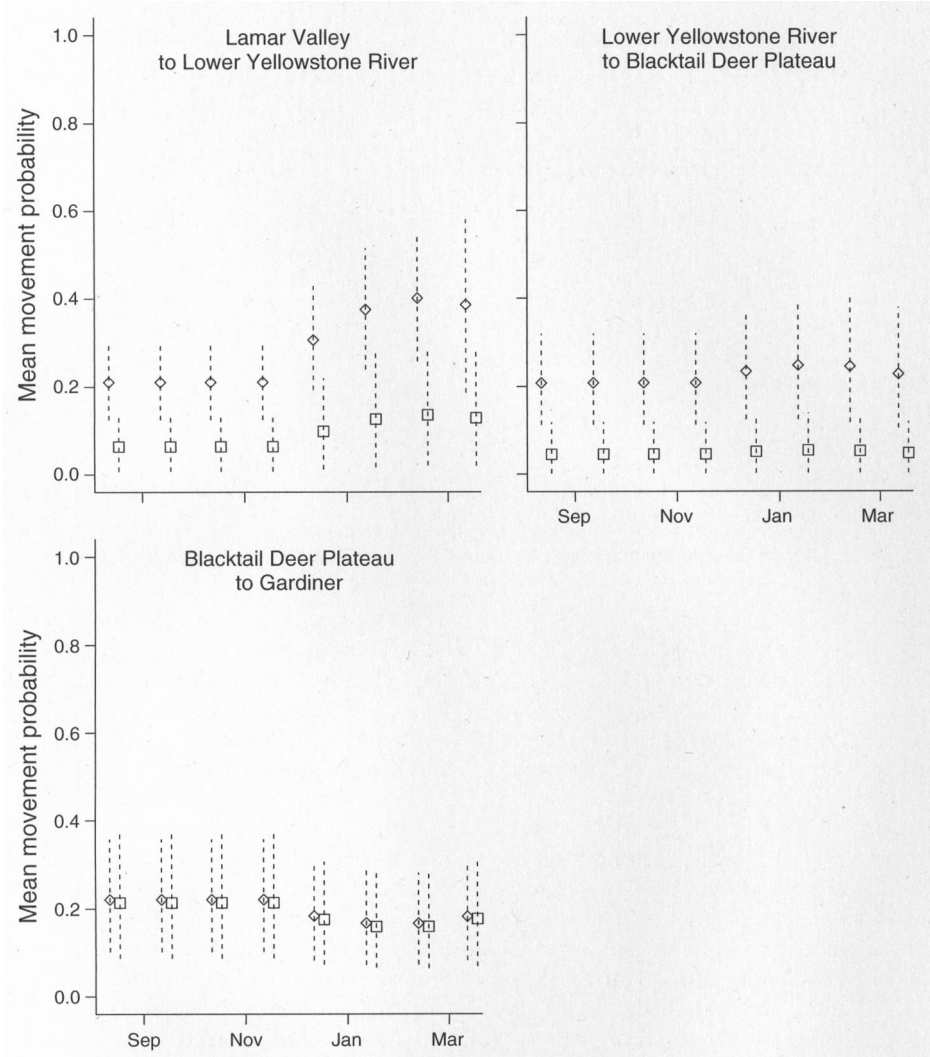


FIG. 7. Mean posterior predicted monthly movement probabilities along migration paths in northern Yellowstone, assuming below-average (open diamonds) and above-average (open squares) covariates reflecting food availability. Dashed lines represent 85% quantiles (Table 1).

TABLE 3. Posterior estimates of model parameters representing process uncertainty and observation error for bison.

Parameter	Definition	Median	0.025%	0.975%
β	process uncertainty, $(1/\beta)(\mathbf{A}_i\mathbf{z}_{t-1,j})$	0.018	0.016	0.021
α	counting error, $(1/\alpha)(\mathbf{z}_{t,j,k})$	0.012	0.011	0.013
σ_x (central)	herd abundance	141.97	114.61	181.37
	snowpack magnitude	5.16	4.20	6.38
	standing crop	2.20	1.81	2.68
σ_x (northern)	herd abundance	165.60	132.67	216.72
	snowpack magnitude	7.28	5.85	8.74
	standing crop	2.20	1.81	2.68

Notes: Process uncertainty and counting error are functions of estimated parameters where \mathbf{A} is a transition matrix of movement and survival probabilities, $\mathbf{z}_{t,j}$ is a column vector of true numbers of bison in each wintering area during month t and year j , and k are count areas. Here, σ_x is a vector of the standard deviations of observed covariate conditions, with an element for each of six covariate types, including central snow, northern snow, central standing crop, northern standing crop, central herd size, and northern herd size.

TABLE 4. Forecasted conditions during the next five years (Yr 1 and Yr 5), assuming a starting population size of 4200 bison and five different annual management alternatives (Altern.).

Key criteria	Altern. 1		Altern. 2		Altern. 3		Altern. 4		Altern. 5	
	Yr 1	Yr 5	Yr 1	Yr 5	Yr 1	Yr 5	Yr 1	Yr 5	Yr 1	Yr 5
Probabilities of numbers of bison in conflict areas (excluding removals)										
>500 Gardiner basin	0.52	0.72	0.45	0.56	0.30	0.19	0.11	0.02	0.29	0.19
>500 Hebgen Lake basin	0.31	0.35	0.31	0.34	0.34	0.39	0.34	0.36	0.31	0.33
>1000 Gardiner basin	0.20	0.44	0.15	0.26	0.10	0.05	0.02	<0.01	0.10	0.05
Probabilities of end-of-winter abundance										
1250–1750 northern	0.17	0.11	0.18	0.14	0.19	0.20	0.21	0.20	0.20	0.20
1250–1750 central	0.21	0.21	0.21	0.20	0.21	0.20	0.21	0.20	0.21	0.20
2500–3500 park-wide	0.51	0.38	0.51	0.43	0.52	0.49	0.53	0.48	0.52	0.50
Average annual harvest (no. bison)										
Gardiner basin			114	130	0	0	0	0	119	98
Hebgen Lake basin, mean			31	32	0	0	0	0	31	32
Average annual gather-and-consignments (no. bison)										
Gardiner basin	0	0	0	0	268	241	449	265	153	145

Note: The alternatives are: 1, issuing 50 hunting permits; 2, issuing 350 hunting permits; 3, gather-and-consignment of up to 350 bison; 4, gather-and-consignment of up to 1000 bison; and 5, using harvests and gather-and-consignment to remove up to 350 bison.

and forage production (Gates et al. 2005, Bruggeman et al. 2009, Kilpatrick et al. 2009, Geremia et al. 2011). We used a hierarchical approach, which allowed us to bring together detailed movement history data collected on individual animals over relatively brief periods of time with long-term monitoring data of seasonal distributions, and to account for uncertainty resulting from each component. By treating this as a hierarchical problem, we were able to estimate monthly distributions during more than two decades in the face of incomplete data, and to identify changes in monthly movement probabilities between bison wintering areas. Our approach allowed a clearer understanding of the forces that shape migratory patterns, which is necessary for managing trans-boundary movements of wildlife where there are disease, property, or safety concerns.

Bison select habitats that facilitate group formation to reduce predation risk and support cooperative displacement of snow (Fortin et al. 2009). Meagher (1998) referred to this phenomenon as a desire for bison to maintain their social bonds. We found that bison were congregated on high-elevation breeding areas at the conclusion of the rut. Foraging efficiency in these areas probably declined as food was consumed and snow accumulated, and bison made coordinated movements to lower-elevation areas, which provided improved access to food. Animals rapidly accumulated in lower-elevation areas. As food accessibility declined in these areas due to consumption and snow accumulation, animals moved to areas progressively lower in elevation.

The net effect of snow and herd size conditions on northern migration pathways resulted in dramatic year-to-year differences in numbers of bison moving to the Gardiner basin wintering area. This finding is corroborated by previous research that indicated snow, standing crop, and herd size as significant predictors of

the numbers of bison exiting Yellowstone (Gates et al. 2005, Kilpatrick et al. 2009, Geremia et al. 2011). We found little net effect of snow and herd size conditions on monthly movement probabilities along central migration pathways. Central herd animals moved to wintering areas that span park boundaries across all observed central herd sizes. More animals moved sooner with larger herd sizes, which corroborates earlier work by Bruggeman et al. (2009), and increases were proportional to changes in herd size.

Our findings could be interpreted as showing that snow acts as a stronger control on movements in northern Yellowstone. However, snow conditions clearly are more severe in central Yellowstone, with earlier and deeper snowpack establishment (Meagher 1973, Gates et al. 2005, Watson et al. 2006, Geremia et al. 2009). Our northern snow covariate levels averaged 32% lower than central snow conditions. Covariate levels were standardized, such that we compared the effect of a condition relative to the average. We believe snow conditions in central Yellowstone reached levels that affected movements each year. Therefore, year-to-year variations had little additional effect.

Emergent seasonal distributions during years characterized by above- or below-average snow conditions were similar in central Yellowstone and variable in northern Yellowstone. Fidelity to summering and wintering locations declines as conditions affecting foraging become less predictable (Mueller and Fagan 2008). Wildebeest (*Connochaetes taurinus*) in the Serengeti provide an excellent example; animals make nomadic movements during the wet season, tracking highly unpredictable vegetation dynamics in response to rainfall (Holdo et al. 2009). When conditions affecting foraging are highly predictable from year to year, experience and learning play an increasingly important

role in movement decision-making (Bailey et al. 1996, Mueller and Fagan 2008). Such behavior has been observed in large herbivores in snow-limited environments, including elk (*Cervus elaphus*; Morgantini and Hudson 1988, Hebblewhite et al. 2008), mule deer (*Odocoileus hemionus*; Nicholson et al. 1997), white-tailed deer (*Odocoileus virginianus*; Nelson and Mech 1991), pronghorn (*Antilocapra americana*; White et al. 2007), and caribou (*Rangifer tarandus*; Mueller et al. 2011).

It is difficult to determine if moving herbivores are responding to food or basing their decisions on experience. We did not directly test whether experience affected movements in our model. GPS histories of central-herd adult female bison indicated that animals increased fidelity to movement patterns with age, which is suggestive of learning. We also found strong year effects on most central Yellowstone migration paths, suggesting that routes became increasingly entrenched over time. The central herd reached record abundance in 2005, which coincided with a winter characterized by above-average snowpack. Concurrently, changes in management policy allowed increased use of the Hebgen Lake basin wintering area, which afforded bison access to newly emerging vegetation while high-elevation areas remained snow covered. Range expansion as the result of food limitation caused by the record population abundance and above-average snowpack is probably what facilitated bison in pioneering new areas. Movements out of the central interior to northern portions of the park and expanded use of areas adjacent to the western park boundary became established and likely persisted due to experience and learning.

Posterior predictive checks indicated that our model accurately estimates the mean. Unsurprisingly, the variance estimates are slightly too large. Snowpack estimates were averaged over the entire year across large areas. Snow is a highly local variable, and consideration of snow in each wintering area per month may provide better spatiotemporal resolution of the covariate. Additional covariates could be developed as we continue this research. For example, wolves (*Canis lupus*) were reintroduced to Yellowstone during 1995–1997. Wintering areas with increased wolf occurrence during times of increased snow may affect bison movements. Elk numbers have also declined substantially since the return of the wolf, which may provide increased foraging opportunities for bison. It would also be interesting to develop a metric for management pressure to test if bison are learning and possibly avoiding certain types of interventions. However, additional data are needed before these covariates based on recent changes in the system can be adequately addressed.

Our research suggests that population size and out-of-park abundance objectives can be met using hunting and gather-and-consignment, with removal actions limited to bison that exit the northern boundary. Spatial and temporal separation of livestock and bison that exit the

western boundary has effectively prevented disease spillover. Beyond Yellowstone, our research provides some general insight of managing migratory wildlife populations in fragmented landscapes. Managers should acknowledge that they have limited control, because movements are themselves affected by unpredictable variation (e.g., weather). As a result, a clear, single best management strategy does not exist, or is not identifiable. Instead, it is essential to work over short time frames with continual reassessment of management guidelines and outcomes. Management is further complicated when animals seasonally occupy protected areas such as national parks. These areas serve many purposes, one of which is providing visitors with an opportunity to view wildlife in a natural setting. Management interventions (e.g., culls, harvests, sterilization, contraception) are often limited within these areas, with the unintended consequence of population growth, which increases movements and the chances of episodic reductions outside these protected areas. Learning and experience may affect movements by allowing a behavior such as the use of a migration path or wintering area to become increasingly entrenched. If a particular learned behavior increases conflict, it may be reasonable to target animals that exhibit the behavior for removal. We developed a tool to make probabilistic forecasts of migratory ungulate distributions. These forecasts promote sound decision-making by allowing managers to develop and refine strategies in advance. Models are unique to each situation, but the framework that we used is applicable to the global concern of managing wildlife in fragmented habitats.

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SUPPLEMENTAL MATERIAL

Appendix

Model specification and Markov chain Monte Carlo algorithm (*Ecological Archives* A024-020-A1).

Supplement

Program R code to fit a movement model to simulated data (*Ecological Archives* A024-020-S1).