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DISEASE ECOLOGY

Supporting adaptive management with ecological forecasting: chronic wasting disease in the Jackson Elk Herd

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Abstract. Adaptive management has emerged as the prevailing approach for combining environmental research and management to advance science and policy. Adaptive management, as originally formulated by Carl Walters in 1986, depends on the use of Bayesian models to provide a framework to accumulate knowledge. The emergence of ecological forecasting using the Bayesian framework has provided robust tools and supports a new approach to informing adaptive management, which can be particularly useful in developing policy for managing infectious disease in wildlife. We used the potential infection of elk populations with chronic wasting disease in the Jackson Valley of Wyoming and the National Elk Refuge as a model system to show how Bayesian forecasting can support adaptive management in anticipation of management challenges. The core of our approach resembles the sex- and age-structured, discrete time models used to support management decisions on elk harvest throughout western North America. Our model differs by including stages for CWD-infected and unaffected animals. We used data on population counts, sex and age classification, and CWD testing, as well as results from prior research, in a Bayesian statistical framework to predict model parameters and the number of animals in each age, sex, and disease stage over time. Initial forecasts suggested CWD may reach a mean prevalence in the population of 12%, but uncertainty in this forecast is large and we cannot rule out a mean forecasted prevalence as high as 20%. Using recruitment rates observed during the last two decades, the model predicted that a CWD prevalence of 7% in females would cause the population growth rate (λ) to drop below 1, resulting in population declines even when female harvest was zero. The primary value of this ecological forecasting approach is to provide a framework to assimilate data with understanding of disease processes to enable continuous improvement in understanding the ecology of CWD and its management.

Key words: adaptive management; *Cervus canadensis;* chronic wasting disease; disease invasion; ecological forecasting; elk.

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INTRODUCTION

Adaptive management promotes a useful interplay among research, management, and policy at large scales (Walters 1986, Walters and Holling 1990). The approach has been applied to a wide range of problems in terrestrial, freshwater, and marine systems all over the world (reviewed by Westgate et al. 2013). Adaptive management as it was originally formulated in the seminal work of Walters (1986) depends on the use of models, specifically Bayesian models, to help inform alternatives for management action (e.g., Prato 2005, Nyberg et al. 2006, Nichols et al. 2007, Stauffer 2008).

The emergence of ecological forecasting using the Bayesian framework (Dietz 2017) has provided tools for adaptive management of wildlife (e.g., Hobbs et al. 2015, Raiho et al. 2015, Ketz et al. 2016, Andrén et al. 2020) that were computationally infeasible until relatively recently. We use the term forecast to mean predictions of the future accompanied by rigorous quantification of uncertainty. Model forecasting supports a new approach to informing management before anticipated challenges become realized.

It is often the case that problems in natural resource management can be anticipated before they occur. Particularly compelling, contemporary examples include biological invasions, disease outbreaks, and impacts due to climate change (e.g., Westgate et al. 2013). In these cases, the arrival of a pathogen or invasive species is expected to cause problems for management even though the agent has not yet arrived in the managed system. Model forecasts can be constructed to explore the behavior of a complex system before the problem occurs to clarify the potential need for management action and explore management options. The proper use of informed prior distributions within the Bayesian framework can allow reasonable forecasts on system behavior even when system-specific data are incomplete. Model forecasts also provide a framework for statistical inference as data on the emerging problem become available, and can be useful for designing monitoring programs.

Chronic wasting disease

Chronic wasting disease (CWD) is a fatal prion disease of the deer family (Cervidae) and is the only known prion disease to circulate in wild populations. It is primarily known to impact deer populations (Edmunds et al. 2016, DeVivo et al. 2017) but has also been shown to impact Rocky Mountain elk (*Cervus canadenis nelsoni*). CWD can meaningfully reduce growth rates of populations of elk by causing declines in individual survival (Sargeant et al. 2011, Monello et al. 2014). Prions may be spread directly or indirectly, mediated by strong environmental persistence (Georgsson et al. 2006), both of which may increase in high-density populations.

Chronic wasting disease was first reported in Colorado in 1967 but has since been identified in wild populations in 26 states and two Canadian provinces, as well as three Scandinavian countries (United State Geological Survey 2021). It has been described as a formidable threat to deer and elk populations in North America and continues to spread into new areas and achieve higher levels of prevalence in endemic areas. Managers are challenged to understand how they can respond to this emerging threat.

Chronic wasting disease was only recently detected in Rocky Mountain elk in northwestern Wyoming during the 2020 hunting season (Wyoming Game and Fish Department 2020*a*). Extensive surveillance recently detected the first positive elk case within the area near Jackson, WY, where infected mule deer have been observed for several years (Wyoming Game and Fish Department 2018). It appears to be a matter of time until the disease becomes more prevalent in the high-density elk population, which inhabits the National Elk Refuge and adjacent areas during winter, hereafter collectively referred to as the Jackson elk herd. Although this model was completed for managers in 2016 using data available at that time, the results remain valid and increasingly relevant in light of the recent detection of CWD.

We use the expected arrival of CWD on the National Elk Refuge as a model system to illustrate supporting adaptive management through model forecasting. We constructed a Bayesian state-space model of the elk population around Jackson, Wyoming. We use the model to forecast potential short-term effects of CWD on the population and to better understand the relationship between disease prevalence and elk population trajectory. We show how the model can inform alternatives for management and create a repository for data useful for monitoring the future effects of the disease.

Study area

Although CWD has not reached epidemic levels in the Jackson elk herd, it has been detected in sympatric mule deer (*Odocoileus hemionus)* and in a single harvested elk in Grand

Teton National Park in 2020. Previous research suggests that the disease will continue to slowly spread in a fashion that has been described as an "epizootic with a protracted time-scale" (Miller et al. 2000). Observations from captive and free-ranging herds suggest CWD may have greater impacts on elk in relatively high-density settings (e.g., Peters et al. 2000, Williams and Miller 2002, Monello et al. 2014). Given the high winter density and the profound importance of the Jackson elk herd to ecosystem processes, human livelihoods, and recreational opportunities in this region, it is prudent to use existing data to help understand potential implications of CWD on this elk population and to plan for managing and monitoring its impacts.

Supplemental winter feeding of elk has occurred on the National Elk Refuge (hereafter the refuge) for over 100 yr. This practice typically results in a highly concentrated elk herd from January to April. The Bison and Elk Management Plan (2007) identified an overarching strategy of reducing reliance on supplemental feeding to achieve management goals and objectives. To date, reduction of elk population size and improvements to available natural standing forage have been unsuccessful in reducing elk density on the refuge winter range. This is due in part to a spatial redistribution of animals on to the refuge, which has maintained high winter densities and continues to pose a risk for disease transmission (see Cole et al. 2015 for more).

Models developed previously made long-term projections of the arrival and subsequent transmission of CWD in the Jackson Hole area that were highly uncertain, predicting an enormous range of outcomes (e.g., Osnas 2011). This uncertainty limits their value for guiding management and policy. Uncertainty about the effects of CWD on population dynamics of the Jackson Hole elk herd could be reduced by using extensive demographic data are available for elk in this region combined with data from studies of CWD in elk elsewhere in the Rocky Mountains. This approach is enabled by the use Bayesian state-space models of disease transmission (Hobbs et al. 2015) and recent CWD studies on free-ranging elk (Monello et al. 2013, 2014, and unpublished ongoing project data). The approach can inform managers about how differing levels of CWD will interact with elk recruitment and survival to determine the Jackson elk herd's population trajectory tempered by rigorous estimates of uncertainty.

We developed a Bayesian state-space model to achieve three goals:

1. Examine the potential impacts of CWD on dynamics of the Jackson elk herd.
2. Aid in designing future sampling for CWD in the population.
3. Provide a proactive framework for assimilating new data on herd health to guide adaptive management of the population (see Walters 1986).

METHODS

Modeling approach

Here, we provide a general overview of our inferential approach, leaving detailed, technical treatment of the mathematics and statistics to Appendix S1. Inference is based on a matrix population model that annually updates a state vector (Caswell 1988). The state vector consists of the number of individuals in four age and sex classes (juveniles, yearling and adult females, yearling males, and adult males) and two disease states (infected and not infected with CWD). The projection matrix is composed of parameters representing survival, recruitment, and disease transmission. The structure of our model closely resembles the matrix models used to inform decisions on harvest of ungulates throughout the Western United States (e.g., White and Lubow 2002) as well as models used to model other diseases of ungulates (Hobbs et al. 2015).

We fit the model using three sources of data on the Jackson population: annual counts, demographic classifications, and CWD test results (see Table 1 for details on data used). We use Markov chain Monte Carlo (MCMC) methods to approximate the marginal posterior distributions of all parameters and unobserved states conditional on the data. These distributions reveal uncertainty arising from the failure of the model to represent population and disease dynamics (process variance) and from sampling and calibration error in the data (observation variance). The process variance includes effects of alternative migratory segments of the population (Cole et al. 2015), which

Table 1. Data sets used for model fit. Note that no data were obtained after 2015 which results in years 2016 and following serving as model forecasts.

Data type	Amount available
Annual counts	18 yr (1998–2015)
Demographic classifications	18 yr (1998-2015)
CWD testing	3758 tests over 18 yr (1998–2015)
Harvest estimates	18 yr (1998–2015)

we did not incorporate explicitly into our disease-focused model.

Estimating process variance separately from observation variance enables forecasts of mean predictions of the future state of the population accompanied by rigorous, statistically defensible estimates of uncertainty conditioned on the model (Hobbs and Hooten 2015, Dietz 2017). These forecasts can be used to understand the short-term dynamics of the population infected with CWD before CWD actually arrives.

We make inference on the effect of CWD on population growth rate, the dominant eigenvalue of the linearized projection matrix, using the values of survival, recruitment, and probability of transmission of CWD at each MCMC iteration. We repeated this sampling for different levels of CWD prevalence in the population, allowing us to see how population growth rate would change with different levels of prevalence. We further examined the potential influence that CWD may have on population growth with and without harvest at past levels. When included, harvest was set equal to 2011–2015 hunting levels.

We used posterior predictive checks (Hobbs and Hooten 2015) to assure that the model is capable of giving rise to the data. Lack of fit was indicated if a discrepancy test statistic.

$$d = \sum_{t=1}^{T} \left(y_t - \hat{y}_t\right)^2 \tag{1}$$

calculated on data sets simulated at each MCMC iteration were consistently smaller or consistently larger than the same test statistics calculated from the observed data. We calculated the test statistic for all data sets used to fit the model.

We present some technical components of our model here, but leave much of the detail to Appendix S1. The overall structure resembles Hobbs et al. (2015); Ketz et al. (2016) and Raiho et al. (2015). The purpose of the model is to examine the potential disease impacts on the population's dynamics, to aid in designing future sampling for CWD in the population, and to provide a proactive framework for assimilating new data on herd health. This framework can be used to guide adaptive management of the population (Walters 1986).

*Notation.—*Matrices will be notated in uppercase bold font, vectors in lowercase bold, and scalars in plain font. Greek letters will be used to represent parameters. We will notate data using the convention $y^{\text{data type}}$. All other quantities are unobserved.

Deterministic model

*State vector.—*The state of the population at year t is represented in a seven-element vector $(\mathbf{n}_t)$ representing four sex and age classes and two disease states (Table 2).

Note that there are no infected juveniles, which represents the assumption that animals do not become infected with CWD before eight months of age. This assumption is consistent with studies of epidemiology of CWD in mule deer (Miller and Williams 2003, Miller and Conner 2005). We pool yearling and adult females into the same class because preliminary analyses revealed that the data do not allow us to separately identify these states. This results in two annual age classes for females; the first represents calves which are eight months old at census, and the second includes both yearlings (20 months old at census) and all older adults.

Table 2. Elements of column vector $(\mathbf{n}_t)$ representing the state at model census of the National Elk Refuge elk population.

State	Definition
$n_{1,t}$	Uninfected juveniles of both sexes aged six months
$n_{2,t}$	Uninfected yearling and adult females aged 18 months and older
$n_{3,t}$	Uninfected yearling males aged 18 months
$n_{4,t}$	Uninfected adult males aged 30 months and older
$n_{5,t}$	CWD-infected yearling and adult females aged 18 months and older
$n_{6,t}$	CWD-infected yearling males aged 18 months
$n_{7,t}$	CWD-infected adult males aged 30 months and older

Projection matrix.—The state of the population in the absence of harvest can be updated using the deterministic model.

$$\mathbf{n}_t = \mathbf{A}\mathbf{n}_{t-1} \tag{2}$$

where $\mathbf{A}$ is a seven × seven projection matrix (Table 3; Caswell 1988). If all harvest occurs immediately before census, then

$$\mathbf{n}_t = \mathbf{A}\mathbf{n}_{t-1} - \mathbf{g}_t, \tag{3}$$

where $\mathbf{g}_t$ is a seven-element column vector specifying the number of animals harvested from each state during $t-1$ to t. Note that we use the term census to refer to the modeled time point within the year, not a total count of all individuals.

The relatively brief interval between harvest (which occurs during November–December) and model census (which occurs in February) does not justify a more complex formulation for recruitment. Thus, we use Eq. 3 to represent effects of harvest on population dynamics. See Appendix S1: *Timing of harvest* for further discussion of this choice.

Stochastic model

Process model.—The deterministic model described here and more fully in Appendix S1 assumes that Eq. 3 is able to represent changes in the state of the population perfectly. This is to say that the model can account for all of the dynamics of the population based on annually varying harvest and time-invariant survival, recruitment, and CWD transmission. However, there are many influences on the population's dynamics that are indirectly incorporated through annual survey data, but not included explicitly in Eq. 3, notable among them predation, other diseases, weather, poaching, density dependence, and non-linearities of CWD transmission producing a time-varying transmission probability. The data necessary to fit a dynamic transmission model (e.g., density dependence) simply do not yet exist so we chose to avoid the numerous assumptions necessary to fit that model.

We represent all of these influences stochastically by including everything not represented in the deterministic model in a seven × seven variance–covariance matrix $\mathbf{\Sigma}_p$. This matrix contains four terms for process variance on the diagonal and zeros elsewhere. We estimate separate process variances for healthy juveniles, yearling and adult females, and yearling and adult males, as well as for infected adults. Process variances were combined for stages that should have similar responses to environmental variance (Gaillard et al. 1998, 2000). We assume that these process variances are uncorrelated which reduces the number of estimated parameters and allows for model convergence. Similarly, we did not include covariance terms to allow for convergence.

We can now represent the unobserved, true state of the population as a probability

Table 3. Non-zero elements of the projection matrix $\mathbf{A}$. See Table 5 for description of individual parameters.

Transition during $t-1$ to t	Element	Value
Offspring produced per uninfected yearling and adult female	$a_{1,2}$	$\phi_3^{\frac{1}{4}}\rho$
Offspring produced per CWD-infected yearling adult female	$a_{1,5}$	$\phi_4^{\frac{1}{4}}\rho$
Uninfected juveniles to uninfected yearling females	$a_{2,1}$	$(1-\alpha)\phi_1(1-\psi)$
Uninfected juveniles to uninfected yearling males	$a_{3,1}$	$\alpha\phi_1(1-\psi)$
Uninfected juveniles to CWD-infected yearling females	$a_{5,1}$	$(1-\alpha)\phi_1^{\frac{1}{2}}\psi\phi_2^{\frac{1}{2}}$
Uninfected juveniles to CWD-infected yearling males	$a_{6,1}$	$\alpha\phi_1^{\frac{1}{2}}\psi\phi_2^{\frac{1}{2}}$
Uninfected yearling and adult females to uninfected adult females	$a_{2,2}$	$\phi_3(1-\psi)$
Uninfected yearling and adult females to CWD-infected adult females	$a_{5,2}$	$\phi_3^{\frac{1}{2}}\psi\phi_4^{\frac{1}{2}}$
Uninfected yearling males to uninfected adult males	$a_{4,3}$	$\phi_5(1-\psi)$
Uninfected yearling males to CWD-infected adult males	$a_{7,3}$	$\phi_5^{\frac{1}{2}}\psi\phi_6^{\frac{1}{2}}$
Uninfected adult males to uninfected adult males	$a_{4,4}$	$\phi_5(1-\psi)$
Uninfected adult males to CWD-infected adult males	$a_{7,4}$	$\phi_5^{\frac{1}{2}}\psi\phi_6^{\frac{1}{2}}$
CWD-infected yearling and adult females to CWD-infected adult females	$a_{5,5}$	ϕ_4
CWD-infected yearling males to CWD-infected adult males	$a_{7,6}$	ϕ_6
CWD-infected adult males to CWD-infected adult males	$a_{7,7}$	ϕ_6

distribution reflecting the uncertainty that arises from influences on the true state that are not represented in the deterministic model using.

$$\log(\mathbf{n}_t) \sim \text{multivariate normal} \left(\log\left(\mathbf{A}\mathbf{n}_{t-1} - \mathbf{g}_t\right),\ \boldsymbol{\Sigma}_p\right). \qquad (4)$$

Eq. 4 represents the true state of the population at time t as a seven-element vector of continuous and non-negative, log-normally distributed random variables with medians $\mathbf{A}\mathbf{n}_{t-1} - \mathbf{g}_t$ and variances $\boldsymbol{\sigma}_p^2 = \left(\sigma^2_{p.\text{juvenile}},\ \sigma^2_{p.\text{female}},\ \sigma^2_{p.\text{male}},\ \sigma^2_{p.\text{CWD}}\right)$.

See Appendix S1 for further technical model details.

RESULTS

The diagnostics of Brooks and Gelman (1998) and Heidelberger and Welch (1983) indicated that all MCMC output retained for inference had converged on marginal posterior distributions of parameters and other unobserved quantities. We observed no evidence of lack of fit (Table 4).

The posterior distributions for demographic parameters diverged from the priors, indicating that the demographic data resulted in parameters more specific to the Jackson elk herd for uninfected juvenile survival, uninfected yearling and adult male survival, proportion of juveniles surviving to the yearling stage that are male, recruitment, and probability of transmission. Specificity of parameters is evidenced by the modified posterior distributions of parameters relative to priors (Fig. 1, Table 5 and Appendix S1: Table S2). The estimated parameter for disease transmission risk also shifted toward zero because of extensive testing data showing no positive cases in the Jackson elk herd. This resulted in the posterior distribution of probability of transmission shifting away from the prior distribution and toward zero. Data caused small shrinkage around the means of yearling and adult female survival, confirming prior knowledge.

Table 4. Posterior predictive checks using the discrepancy statistic (Eq. 1). Lack of fit is indicated by Bayesian P values close to 0 or 1.

Observation	Bayesian P value
Total counts	0.22
Proportion juveniles	0.45
Proportion yearling and adult females	0.52
Proportion yearling males	0.49
Proportion adult males	0.45

The population was fairly stable from 1998 to 2005 and then showed a weak downward trend until 2015 (Fig. 2; note that 2016 was treated as a forecast due to pending CWD test results at the time of the original report). Model predictions were strongly influenced by sex and age classification data (Fig. 3).

Eigen analysis revealed that infection of the population with CWD is likely to drive the population growth rate (λ) below one (Fig. 4), indicating a decline in elk numbers over time. A declining population becomes more probable with increasing disease prevalence. We also examined the relationship between CWD prevalence and growth rate with and without past levels of hunting. The most probable threshold between an increasing and a declining population ($\lambda = 1$) occurred when prevalence of CWD in yearling and adult females reached 7%. However, we cannot rule out a threshold as high as 23% prevalence before λ falls below one. The probability that the current population growth rate, in the absence of both hunting and CWD, is less than one is 0.055. Recent (2011–2015) levels of hunting reduced the population growth rate significantly, but this is by design, as the state and federal agencies were seeking to reduce abundance of the Jackson elk herd. The addition of CWD into the model leaves little possibility that the population will grow (Fig. 4).

Model forecasts showed the potential for CWD to reduce the abundance of the Jackson elk herd (Fig. 5) if transmission is similar to the level (0.08; BCI = 0.05, 0.12) observed by Monello et al. (2014). This decrease corresponded to a population growth rate less than one at the predicted asymptotic prevalence of ~12% (see predicted prevalence in Fig. 5 and its relationship to population growth rate in Fig. 4). Although there is significant overlap in the forecasts for an infected and uninfected population, it is clear that CWD has the potential to decrease the population size.

DISCUSSION

Forecasts for the Jackson elk herd suggest that the effects of CWD on population abundance are

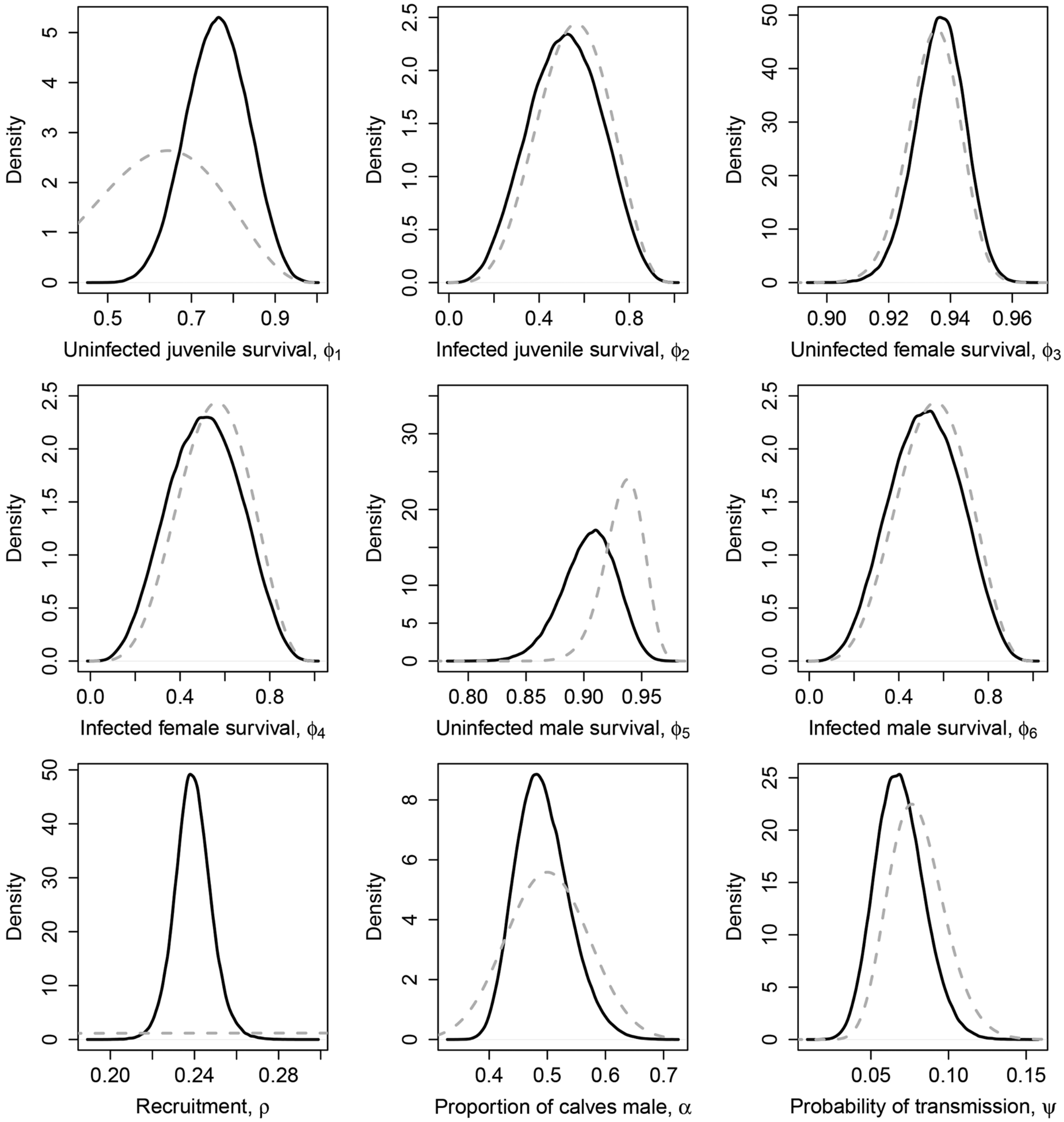

Fig. 1. Marginal posterior distributions (solid lines) and prior distributions (dashed lines), of model parameters. Note that female and male refer to yearlings and adults and exclude calves.

likely to be slow to develop and difficult to detect; there is strong overlap between predictive process distributions for populations with and without CWD (Fig. 5). The assumption of a constant transmission probability over time drives the observed forecasts. Time-invariant transmission is almost certainly not the case but represents a starting point for transmission modeling until parameters in a dynamic model can be estimated from data specific to the Jackson elk herd following infection. The refuge may offer an unusual opportunity to obtain those data given a long history of monitoring for CWD, with the arrival of CWD presenting a unique opportunity

Table 5. Marginal posterior distributions of model parameters are summarized with means, standard deviations (SD), and lower (2.5%) and upper (97.5%) highest posterior density intervals.

Model parameter	Mean	SD	2.5%	97.5%
Recruitment α	0.49	0.046	0.41	0.58
Uninfected juvenile survival ϕ_1	0.76	0.072	0.62	0.9
Infected juvenile survival ϕ_2	0.51	0.16	0.21	0.81
Uninfected yearling and adult female survival ϕ_3	0.94	0.008	0.92	0.95
Infected yearling and adult female survival ϕ_4	0.51	0.16	0.21	0.81
Uninfected yearling and adult male survival ϕ_5	0.91	0.023	0.86	0.95
Infected yearling and adult male survival ϕ_6	0.52	0.16	0.22	0.82
Probability of transmission ψ	0.067	0.015	0.038	0.098
Recruitment ρ	0.24	0.009	0.22	0.26
Process standard deviation for yearling and adult females σ_{pf}	0.11	0.03	0.055	0.17
Process standard deviation for juveniles σ_{pj}	0.093	0.05	0	0.17
Process standard deviation for yearling and adult males σ_{pm}	0.21	0.035	0.14	0.28

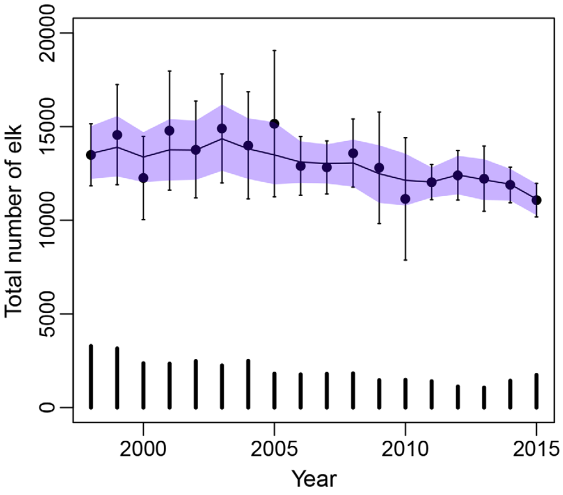

Fig. 2. Number of elk in the Jackson Elk Herd during 1998 to 2015. The population showed a weak downward trend during this time, coinciding with management efforts to reduce abundance. Filled circles are mean counts, and vertical bars are ± 2 standard deviations. Solid line is the median estimate of the true, unobserved population size, and shaded areas give 95% equal-tailed credible intervals. Vertical bars show total harvest preceding census.

to understand the epidemic behavior of the disease over time. The Bayesian model reported here would facilitate the development of the understanding of dynamic transmission probability after disease invasion by providing a way to assimilate data from multiple sources, including annual count data and data from prior studies in other locations. It enables the comparisons of multiple theoretical models of dynamic disease transmission with minor modification to the transmission function (See Miller et al. 2006, Hobbs et al. 2015). It can also be used annually to update the role of harvest and disease and provide managers with the probability of attaining population goals in the ensuing 1–3 yr (Ketz et al. 2016, Andrén et al. 2020). Regardless, the model reveals that hunting and disease mortality will likely act additively resulting in higher mortality than would be present in the absence of one or the other if CWD becomes established and increases. Establishment and increases in CWD prevalence are almost certainly more likely in areas of high population density.

It is impossible to predict when or if CWD will reach endemic levels in the Jackson elk herd. However, there is no evidence to suggest the performance of this herd will not be affected by the disease in a way that resembles other elk populations (Sargeant et al. 2011, Monello et al. 2014). In particular, we expect reduced adult survival and population growth rate with increasing disease prevalence. There is evidence that these effects might be even greater for high-density populations, like those using the refuge within the Jackson valley.

Model forecasts showed disease prevalence increasing to an asymptote, but this result depends on the assumed constant transmission probability. It is reasonable to expect the modeled transmission probability is excessively high

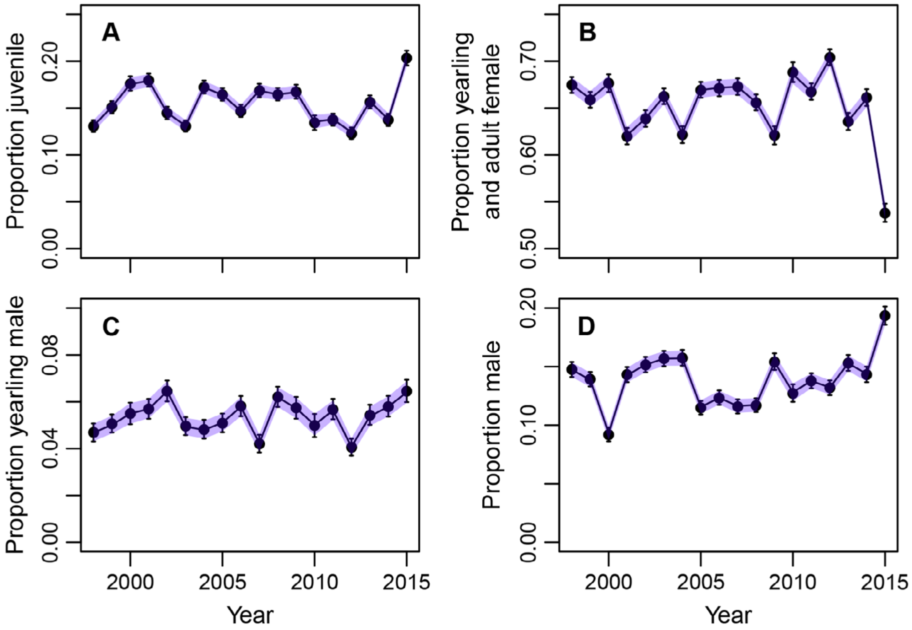

Fig. 3. Model fit to data on population composition: (A) juveniles, (B) yearling and adult females, (C) yearling males, and (D) adult males. Filled circles are the proportion observed in annual classification counts, and vertical bars are ± two standard deviations of the proportion. Solid line is the median of the unobserved, true population composition. The shaded area gives 95% highest posterior density interval of the true proportion. High precision results from the large amount of demographic data used, shown in Table 1.

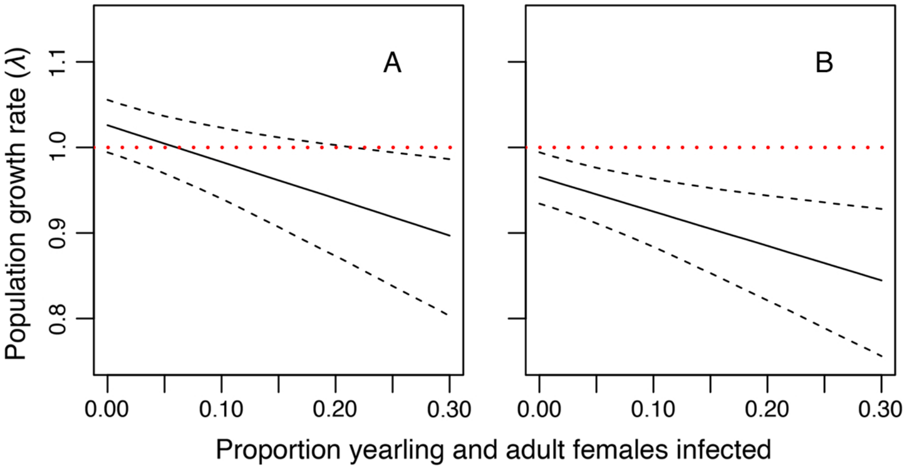

Fig. 4. Estimated potential effects of chronic wasting disease on the growth rate of the Jackson elk herd population differ with assumptions about hunting. Solid lines are the median of the marginal posterior distribution of the discrete time population growth rate λ. Dashed lines give 95% equal-tailed credible intervals. The horizontal dotted line is the threshold between population increase and decline. (A) Population growth rate assuming no hunting and using recruitment estimated in this study. (B) Population growth rate with hunting and recruitment estimated in this study. Hunting is estimated as a random variable from hunting removals observed during 2011–2015 and is included in survival of healthy and infected animals.

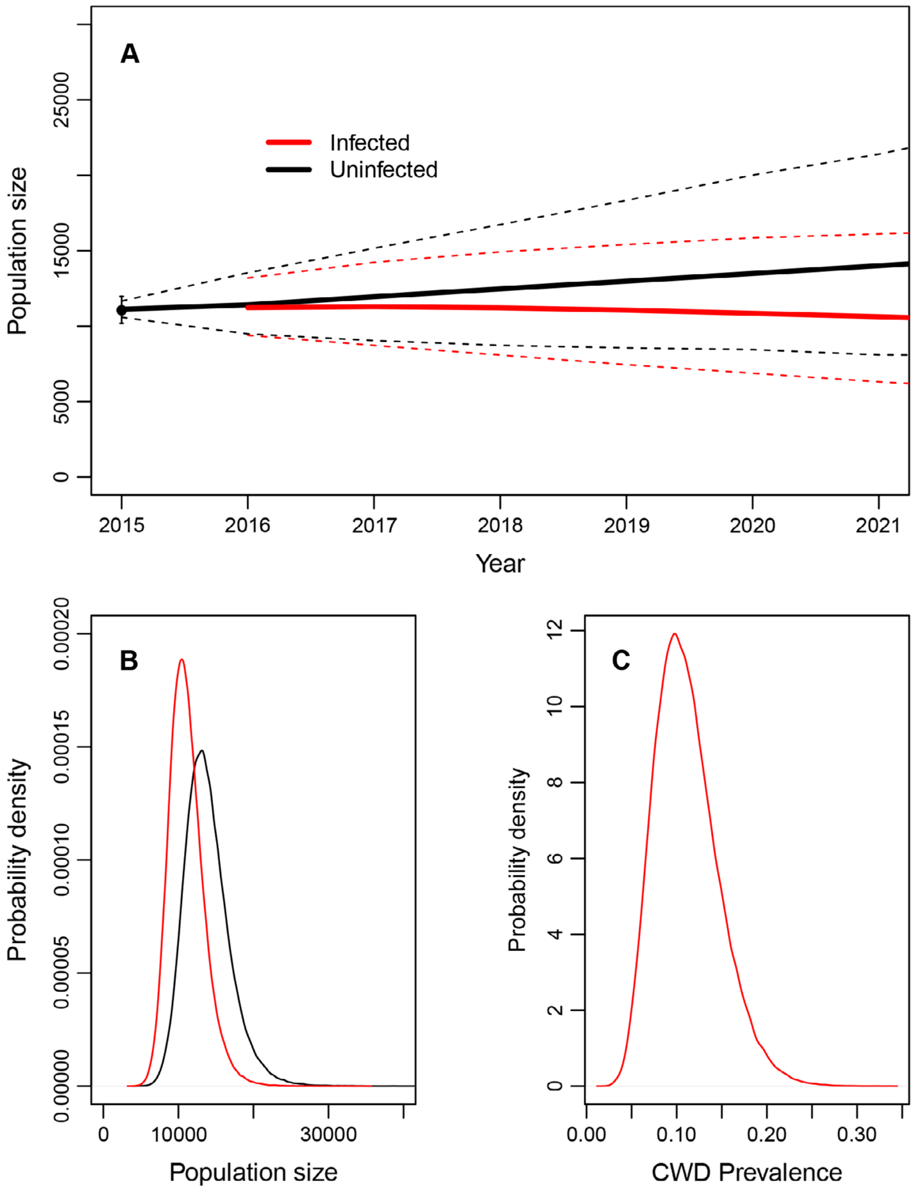

Fig. 5. Forecast of the population size of the Jackson elk herd during 2016–2021 with and without CWD infection (upper panel) assuming CWD invades in 2016 with time-invariant disease transmission similar to that observed in Rocky Mountain National Park (Monello et al. 2014). (A) Predictive process distributions of population size with and without CWD present. Years 2016 and after reflect model forecasts, as 2015 was the last year new data were obtained. Solid lines are the median of the predictive process distribution. Dashed lines are 95% equal-tailed credible intervals. (B) Predictive process distributions of numbers of individuals in healthy and infected populations in 2021. (C) Predictive process distributions of CWD prevalence in the infected population in 2021.

in the years immediately after the arrival of CWD, if environmental contamination becomes the dominant mode of transmission, and excessively low in later years. Data used from Rocky Mountain National Park to estimate transmission probability were collected well after the initial CWD outbreak, giving time for disease establishment. However, the density of elk in Rocky Mountain National Park in winter is likely substantially lower than that on the refuge and on feed grounds specifically. We hypothesize that this higher density would lead to elevated rates of disease transmission on the refuge, increasing impacts on abundance.

Selection for genotypes with a longer incubation period for CWD that allows infected elk to persist longer and continue reproducing has been suggested to be able to decrease the disease impact over a long timescale of more than 50 yr (Williams et al. 2014). The potential for selection of genotypes with a longer CWD incubation time was not incorporated into our model. However, we used survival and infection data from infected cow elk that lived in a relatively high-density population that has been exposed to CWD for 30–50 yr (Monello et al. 2014) and the effects of such selection would be incorporated in survival outcomes. This means that the modeling results in this paper are unlikely to be largely influenced by prion genotype selection in the next several decades, suggesting CWD-related declines in population growth rate may at a minimum be prolonged over that time frame. This is consistent with work to date that suggested the effects of selection on prion genotypes will only take root after 75–100 yr based on a scenario that used “worst-case” transmission rates from a captive population that was confined to contaminated pens and “best-case” genetic resistance with no trade-off or interaction with disease dynamics or prion strains (Williams et al. 2014).

The model also does not currently consider the potential decreases in recruitment by CWD-infected females. This effect would further exacerbate the decline in growth rate with increasing prevalence (see Dulberger et al. 2010), that would in turn increase disease impacts on abundance. This is one area where observation after CWD invasion would provide valuable insight to clarify the disease impact. Continued use of this model along with annual counts and disease data will provide valuable information on the potential impacts of both selection and recruitment.

The potential outcomes of CWD invasion into the Jackson elk herd are complicated by the different migratory segments of the population and their differential recruitment (Cole et al. 2015). Disease processes may differ in these groups, with the long-distance migrants perhaps having a slight advantage by spending more time over a larger area and at lower densities, thereby decreasing prion exposure. However, both population segments intermix at high densities on the winter grounds which may negate such benefits. Alternatively, improved body condition on feed grounds may modify the disease process, or interact with it in unexpected ways. For example, higher body condition may keep infected animals alive longer leading to increased prion shedding or allowing for further reproduction before death. There also exists the possibility that the higher observed recruitment for short-distance migrants (Cole et al. 2015) may mitigate the disease impacts on population growth rate as long-distance migrants are lost. There are foreseen drawbacks to an increase in short-distance migrants in the population, however, including more vehicle collisions, more commingling with livestock and property damage, and decreased hunting opportunity.

We expect that the effects of CWD on other elk populations in northwest Wyoming will be similar to those described here. This model could be fit to demographic data from other herds to examine those differences but until we have a better understanding of the dynamic relationship between density and disease transmission the likely important differences in disease risk for fed and unfed populations could not be included without strong assumptions.

The model framework presented here is a first step toward informing managers of the Jackson elk herd of the possible population-level effects of CWD. Given that the CWD effects in the model were based on Rocky Mountain National Park in a lower density elk population, it would seem advisable to reduce the areas of higher concentration on the refuge before CWD reaches endemic levels, which may prove to have a much larger impact than that estimated here on crowded herds typical of feed ground populations. Lower population densities may also have the added benefit of increasing recruitment rates (Proffitt et al. 2014), which are relatively low in this population, and allow the population to both handle a higher prevalence of CWD before λ is reduced below 1 and allow for a greater proportion of elk to be sustainably harvested on an annual basis. As disease impacts become more clear and if recruitment changes, newly available data can be incorporated into the existing model framework on an annual basis, which will enable adaptive management as it was originally conceived by Walters (1986).

This model could support decision-making regarding adaptive management as described in the current approved management plans of the Wyoming Game and Fish Department (Wyoming Game and Fish Department 2020*b*) and the National Elk Refuge (United States Fish and Wildlife Service 2007). Specifically, the model may be useful as the agencies evaluate experimental management actions to slow the spread and/or reduce prevalence of CWD. A plausible adaptive management cycle may look like this: Model predictions motivate a management action (e.g., reduce density), the population is monitored, monitoring data are used to improve the model (e.g., the transmission function) which is then updated for new predictions.

As future hunting season proposals are developed, managers could evaluate harvest rates on various herd segments of the population relative to estimated annual CWD prevalence. A key question of interest would be, what levels of cow harvest would be most likely to maintain the population at objective levels or a growth rate of interest given the current disease prevalence?

If managers wish to implement and evaluate management actions to slow the spread and/or reduce/limit prevalence of the disease, this model could help them track disease progression over time and disentangle the effects of management actions. Those actions could potentially include any of those discussed here, as well as others, but would need to undergo the full process in place by those managers, including public comment and approval from decision makers.

Ecological forecasting fills an important functional role in the implementation of adaptive management. Forecasting incorporates a quantification of uncertainty given assumptions about system behavior, and can inform managers about potential outcomes for unobserved future states. The many advances in the field of Bayesian hierarchical modeling offer one tool for managers hoping to implement adaptive management. The progress of work in this field, when combined with modern computational power, allows managers to explore the potential relationships in unobserved systems by combining data from multiple sources. This can prove useful to managers in many scenarios, including biological invasions, previously unexplored management actions, and as our example illustrates, disease invasions.

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DATA AVAILABILITY

Data are available from Mountain Scholar: http://dx.doi.org/10.25675/10217/233650

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3776/full