POPULATION DYNAMICS OF THE JACKSON ELK HERD

BRUCE C. LUBOW,[1,2] Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA

BRUCE L. SMITH,[3,4] National Elk Refuge, P.O. Box 510, Jackson, WY 83001, USA

Abstract: We fit data on elk (*Cervus elaphus*) population size and composition, survival rates measured from their first week of life, reported harvest, and local weather to a series of alternative population models of the elk herd in Jackson, Wyoming, USA, for the period 1980–2002. Data were corrected for biases in aerial survey visibility, mis-classification of juveniles in ground surveys, and harvest reporting. The models included explanatory variables for sex, age, population size, weather, and autocorrelation of survival rates in different periods. Using information–theoretic model selection, we identified the most strongly supported models and effects. Model complexity ranged from 12 to 70 fitted parameters, and the best-supported model contained 25 parameters. We estimated annual natural survival (excluding harvest) of mature (≥1 yr) elk of 96.8% (SE = 1.5%) for males and 97.2% (SE = 2.2%) for females. Natality was 60.4 juveniles/100 mature females (SE = 3.9 juveniles/100 mature females). Sex ratio at birth strongly favored females (45.8% males, SE = 1.6%, Akaike weight = 99.9%). The dynamics of this population were well explained by annual variation in survival of neonates (birth to 31 Jul), juvenile survival during late winter (20 Feb–19 May), and harvest. Survival of neonates was correlated with several weather covariates that apparently affected nutritional status of their mothers. Survival of juveniles during late winter was related to weather conditions during the preceding summer and early winter. We found a compensatory effect of juvenile harvest on subsequent juvenile survival in late winter; 89% of increased juvenile harvest was offset by reduced natural mortality. We also found evidence for a decline in survival of neonates with increasing population size (density dependence). However, the density effect was weak at current population size and recent supplemental feeding rates. Thus, only continued or increased female harvest can maintain this population at current or lower levels if current feeding policies are continued—unless disease prevalence, predator impacts, or other factors substantially alter the historical dynamics. Simulations suggested that harvest rates of mature females must be increased to 15.1% from recent levels of 11.9% to reduce the current population of 15,680 elk (SE = 407) to the target population size of 11,029 set by the Wyoming Game and Fish Department (WGFD). Sensitivity of equilibrium population size at the WGFD target level to harvest rate was very high, requiring regular monitoring and adjustment of harvest to maintain a stable population.

Management of the Jackson elk herd (JEH) in northwestern Wyoming has been the subject of intense scrutiny since establishment of the National Elk Refuge (NER) in 1912 (Boyce 1989). Both federal and state governments have actively provided supplemental winter feed to this herd at several locations throughout this period. The population is a valuable resource producing both sustained harvests and abundant viewing opportunities in and near 2 national parks.

We constructed a population dynamics model of the JEH to characterize its recent history (1980–2002). In addition to annual monitoring data on population size, age and sex composi-tion, and harvest collected by the WGFD and Grand Teton National Park (GTNP), 2 3-year studies conducted in the 1990s provided data on survival of radiomarked juveniles beginning in their first week of life (Smith and Anderson 1996, 1998; Smith et al. in press).

Our primary objective was to model all available data to understand density-independent, density-dependent, and management influences on this population. Although model data were observational rather than experimental, we also expected the model to be useful in predicting future population responses to variable weather and alternative management policies.

FIELD METHODS

Study Area and Population

We conducted our study in the Jackson Hole and Gros Ventre valleys and foothills of northwest Wyoming, USA, lying between the Teton Mountains on the west, the Gros Ventre Mountains and

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[1] Present address: Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA.

[2] E-mail: Bruce@CNR.ColoState.edu

[3] Present address: 44 Duncan District Road, Sheridan, MT 59749, USA.

[4] E-mail: wapitimail@aol.com

Mount Leidy Highlands on the east, and the Pinyon Peak Highlands on the north (Boyce 1989). Elevations range from 1,950 to 2,450 m. Vegetation included sagebrush (*Artemesia* spp.) grasslands and aspen (*Populus tremuloides*) woodlands, interspersed with willow (*Salix* spp.) riparian zones and coniferous forests of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Douglasfir (*Pseudotsuga menziesii*), and Engelman spruce (*Picea engelmannii*). The climate was characterized by long, cold winters and short, warm summers.

Between 13,000 and 16,200 elk were counted by WGFD in the JEH during the 1990s. Prior population modeling indicated a herd size of 14,000–18,000 elk (Wyoming Game and Fish Department 2000). The WGFD's herd objective for the JEH is 11,029 elk. The elk occupy 4 relatively distinct geographical areas during summer: GTNP, southern Yellowstone National Park, the Teton Wilderness, and the Gros Ventre (Boyce 1989, Smith and Robbins 1994). About 60% of the elk herd winters on or adjacent to the NER. The remainder winter at 3 elk feedgrounds in the Gros Ventre operated by WGFD or on native winter ranges in the Gros Ventre, Spread Creek, or Buffalo Valley (Smith and Robbins 1994). Nearly 70% of the JEH and most GTNP elk are supplementally fed for 2–3 months each winter. Elk typically forage on new vegetative growth for several weeks following termination of winter feeding (about 1 Apr) before migrating to calving areas (Smith and Robbins 1994, Smith et al. 1997).

Harvest occurs in 10 harvest areas covering much of the JEH's distribution. The migratory nature of the herd and the influence of fall weather on the timing of migrations necessitate complex hunting seasons. Seasons are long, beginning as early as 10 September and extending into December in many harvest areas. Elk that summer in the Teton Wilderness and Gros Ventre occupy lands (primarily Bridger-Teton National Forest) that are open to big-game hunting during fall. Yellowstone National Park is closed to hunting, but elk that summer in the park are subject to harvest as they migrate south. Elk that summer in or migrate through portions of GTNP are harvested to assist with annual reductions in the size of the JEH. A limited elk hunt also is held on the northern half of the NER to control elk numbers.

Data Collection

Capture and Monitoring of Elk.—We captured elk during 2 periods: 1990–1992 and 1997–1999. Our experimental designs for capture and monitoring of elk during both periods were nearly identical and have been reported previously (Smith and Anderson 1996, Smith et al. in press). We monitored juvenile survival from birth through 31 August each year, but we report neonatal survival from birth through 31 July (neonate mortality was negligible after this date). We censored 19 of 164 juveniles and 1 of 154 adults during the early 1990s that cast their radiotransmitters. From 31 August to 1 December, we located radiomarked elk 3 times weekly from towers or weekly from aircraft. This same protocol applied during May–August 1993–1996 when we did not capture new neonates. Elk that wintered on the NER were located biweekly from the ground during 1 December–1 May. Those that wintered elsewhere were located from aircraft monthly. We investigated mortality signals of radiocollars, as described by Smith et al. (in press), to determine fate of animals.

Population Size and Recruitment.—Methods for collecting population data varied over the period analyzed and different geographic segments of the population. Observers determined elk population size and composition from censuses conducted from feed wagons at the NER and Gros Ventre elk feedgrounds each February (Wyoming Game and Fish Department 2000, Smith and McDonald 2002). Helicopters were used exclusively between 1989 and 2002 to conduct counts of elk that did not attend feedgrounds (Smith and Robbins 1994), while airplanes were used prior to 1987. Both airplanes and helicopters were used in 1987 and 1988 surveys

Harvest Data.—Harvest records were based on (1) annual mail survey of licensed hunters conducted by a contractor of the WGFD; (2) a permanent hunter check station east of the JEH unit along State Highway 26/287 at Dubois, Wyoming, operated during most elk hunting seasons; and (3) mandatory reporting of elk harvested by hunters who received permits to hunt in GTNP and the NER. Hunters in GTNP and the NER were either contacted by enforcement personnel in the field or required to return a portion of their permit with results of their hunt.

ANALYTICAL METHODS

Statistical and Modeling Approach

We constructed models to account for the major biological and methodological processes we expected to observe, and we fit these models to available data (White and Lubow 2002). This allowed us to fit models for the entire period of

interest despite missing observations. Our models were likelihood functions that compared field data to estimates. The likelihood functions contained submodels of biological or observational processes. Fitting consisted of finding parameter values (maximum-likelihood estimates) that maximized these likelihoods.

Clearly, multiple alternative hypotheses, or models, could explain the complexity inherent in this dataset. Therefore, we fit a series of alternative models of varying size. Models with fewer parameters assumed that some parameters in the general model were indistinguishable and could be set equal to each other or represented by a single default value to obtain more precise estimates of the remaining parameters. For example, in the most general model, we included individual juvenile survival rates during the neonatal period for each year, whereas in alternative models, we modeled these rates as functions of combinations of weather covariates, population size, time, or even a single constant. We applied information–theoretic methods using Akaike's Information Criterion, corrected for small sample bias (AIC$_c$; Burnham and Anderson 2002) to evaluate strength of evidence supporting each model.

Field Data Model

We were aware of—or anticipated—biases in the population and harvest data, incomplete records, and unavailability of measurement error (precision) estimates for some field data. We addressed these deficiencies in our analysis.

Population Count Biases.—Of the covariates known to affect sightability in aerial surveys (Samuel et al. 1987, Anderson et al. 1998, Lubow et al. 2002), only group-size data were available for the JEH. Therefore, we analyzed data from 2 studies of other elk populations (Lubow et al. 2002; F. Singer, U.S. Geological Survey, personal communication, unpublished data from Yellowstone National Park) to develop a sighting probability model based only on group size and applied this model to the JEH data. Field methodology and analysis for both studies was consistent with Lubow et al. (2002), which followed Steinhorst and Samuel (1989). We adjusted raw population counts using individual sighting probability estimates for each of 4 age–sex classes of elk, for 2 geographic areas (elk on and adjacent to the NER vs. all other areas) distinguished in aerial survey data, and for 4 years (1999–2002) for which group-size data were available. We applied the mean sighting probability over these 4 years, sep-arately for each age–sex– area combination, to all other years (1989–1999) when surveys used similar methodology (helicopters and complete geographic coverage). We assumed that sighting probability for airplane surveys was a constant proportion of mean helicopter survey sightability for each age and sex class; this proportion was a fitted model parameter. During 2 years of transition from helicopter to airplanes (1987–1988), we used linear interpolation to derive intermediate values of sighting probability.

We hypothesized an additional bias in ground population classifications. On feedgrounds, observers classified elk as bulls (adult males), spikes (yearling males), cows (combined yearling and adult females, hereafter referred to as mature females), or calves (juveniles). Bias was suspected in misclassification of some female juveniles as mature females (Smith and McDonald 2002). To address this possible bias, we included a parameter in our models representing a constant proportion of total antlerless count consisting of juveniles mistakenly classified as adults.

Unclassified Elk.—During some surveys, not all elk could be classified. We allocated these to age and sex classes using 2 procedures. For surveys in which most elk were classified, we assumed that unclassified elk were a random subset and allocated them in the same proportions as classified elk. Prior to 1988, classification was not done outside of feedgrounds; therefore, we fit a regression line to ratios of elk in each count category to mature females for years when classification was done. We used the estimated ratio from this linear fit for the first year of available classification data (i.e., the intercept) to approximate the value in prior years.

Harvest Reports.—Trophy males hunted near the periphery of the JEH's range included substantial numbers that seasonally occupied the same range but did not winter with the JEH. Managers at WGFD also suspected over-reporting of adult male and under-reporting of mature female harvest. We used 2 parameters, defined as ratios of actual harvest to reported harvest, 1 for antlered elk and 1 for mature females, to estimate these potential biases. In addition, most harvest data did not distinguish yearling from adult females, or male from female juveniles. Therefore, we used records from harvest within GTNP that did provide this level of detail to apportion harvest for the entire population.

Measurement Errors.—We based standard errors for the aerial portion of population estimates on

the sightability model. In addition, we assumed error rates (CV) for our classification of unclassified elk of 10% for ground surveys and 30% for aerial surveys. We did not have precision estimates for feedground surveys because these were thought to be a perfect census. However, a recent evaluation (Smith and McDonald 2002)—where differences between pairs of observers making simultaneous counts were compared—cast doubt on this assumption. Although not a direct measure of count error rates, we used Smith and McDonald (2002) and personal experience to estimate error rates of 5% for classifications and 10% for total counts on feedgrounds.

General Population Dynamics Model

Model Structure.—We constructed a discrete-time, stage-structured population model and modeled each year as 5 discrete periods, beginning with the end of the mid-winter population survey. We defined seasons as late winter (20 Feb–19 May), neonatal (20 May–31 Jul), summer (1 Aug–9 Sep), harvest (10 Sep–31 Dec), and early winter (1 Jan–19 Feb). Elk age was modeled with 3 classes: juveniles (<1 yr), yearlings (≥1 and <2 yr), and adult (≥2 yr). Some quantities are computed for pooled yearlings and adults for comparison to field data, however, the model tracked yearlings and adults independently. We refer to the combined age classes as "mature." Ages were advanced between the end of late winter and the beginning of the neonatal period. Births of new juveniles occurred at the beginning of the neonatal period. We began modeling with the neonatal period in 1980 and ended with the population survey at the end of late winter 2002—a period of almost 22 years (excluding 1 late-winter period), or 109 seasonal periods. In all models, birth rates for yearling females were assumed to be 19.5% of the adult rate throughout the 22 years, based on Smith and Robbins (1994), because no additional data were available.

Alternative Model Complexity.—All models were part of a nested hierarchy derived from a single general model. The simplest model that we considered biologically plausible (designated M_0) contained 12 parameters: 1 birth rate parameter; 1 airplane sightability parameter; late-winter and neonatal juvenile and mature survival (4 parameters); summer and early-winter survival for all classes (2 parameters); and initial population size for adult males, yearling males, mature females, and juveniles (4 parameters). Initial estimates of the allocation between yearling and adult females

and between male and female juveniles were determined by applying the mean proportions of each class in harvest data from GTNP, in which these segments were identified and recorded.

Our largest model (M_H; 70 parameters, 58 for survival and 12 others) included parameters that we hypothesized might be necessary to explain the important biological and data collection processes inherent in the data. This model used birth rate and sex ratio (2 parameters), our adjustments to harvest and population data biases (4 parameters), and initial population estimates for each age and sex class (6 parameters). As many as 659 survival parameters were possible (6 age–sex classes in each of 5 seasons/year for 22 years except late winter of 2002). Clearly, estimation of this many parameters would be both impractical and unjustified by the size of the dataset. Therefore, we defined a reduced set of survival parameters by setting many survival rates equal. We assumed that harvest period mortality was solely determined by measured harvest, which could be removed directly, eliminating the need for estimating survival. Consequently, any unreported mortality during this period would be implicitly included with early-winter mortality in our models. We assumed that summer survival was high enough for adults that it could be fixed at 1.0, whereas we estimated separate constant values for each sex of juveniles (2 parameters). Early-winter survival was assumed to differ between juvenile and mature elk, but not by juvenile sex (2 parameters). Late-winter survival was modeled with a separate parameter for adult and yearling males and females (4 parameters) and annual survival rates for juveniles (22 parameters), plus an additive parameter for sex differences in juveniles (1 parameter). Neonatal survival was modeled similarly to late winter (27 parameters).

We fit 204 alternative models spanning a range of complexity. These models fell into 2 categories: historical and predictive. To be predictive, a model had to project future population dynamics based only on constant parameters and external covariates, such as weather. By contrast, an historical model could include estimates specific to each year, precluding forecasts because these specific rates must be observed rather than predicted. Thus, model M_0 was predictive, and the most complex model (M_H) was historical.

Most predictive models introduced several additional parameters as part of survival submodels. These submodels relate certain annual survival rates to covariates. For example, we mod-

eled late-winter juvenile survival as a logistic function with parameters for effects of sex, population size, weather, autocorrelation with harvest and neonatal period survival, and correlation with mature female harvest survival:

$$S(y) = \text{Logit}\left(\begin{array}{l} \beta_0 + \sum_{i=1}^{4}\beta_i W_i + \beta_5 I_S + \beta_6 S_N(y-1) + \beta_7 S_H(y-1) \\ + \beta_8 S_{H,AF}(y-1) + \beta_9 \dfrac{N_T(y)}{\bar{N}} \end{array}\right),$$

where the logistic function was given by

$$\text{Logit}(x) = \frac{1}{1 + e^{-x}} \quad,$$

and $S(y)$ was late-winter juvenile survival rate in (calendar) year y, W_i was the ith of 4 weather statistic, I_S was an indicator for sex (M = 1, F = 0), S_N was neonatal juvenile survival rate, S_H was juvenile harvest period survival rate, $S_{H,AF}$ was mature female harvest survival rate, N_T was total population size, and $\bar{N}$ was mean total population size over the course of the study (used here as a normalizing constant). The β_i were model parameters to be estimated. This formulation reduces the original 23 parameters for late-winter juvenile survival in M_H to a maximum of 10.

Neonatal juvenile survival was modeled in a similar fashion, including most of the effects considered for late-winter juvenile survival: sex, density, and weather. Unlike the late-winter juvenile survival model, we had no earlier survival periods to generate possible autocorrelations. The maximum number of parameters considered in this submodel was 10, including intercept and up to 7 weather covariates. With these 2 submodels replacing the 46 annual juvenile survival rates in M_H, we obtained the most complex predictive model (M_P) with 44 parameters.

Generation of Intermediate Complexity Models.—We sought more parsimonious models than M_H and M_P to improve parameter estimates. Considering all possible combinations of parameters would lead to $2^{(70-12)} \cong 2.9 \times 10^{17}$ models. Even if time permitted such an exhaustive search, Burnham and Anderson (2002) caution against this approach. Instead, we applied the following systematic process for testing the various parameters in models covering a range of complexity to identify those parameters best supported by the data and worthy of inclusion in more parsimonious models.

(1) Fitted a series of models, each identical to M_0 except for addition of 1 parameter.

(2) Fitted a series of models, each identical to M_H except for removal of 1 parameter.

(3) Identified those parameters that improved AIC_c when present in the models (as compared to the similar model without the parameter) in steps 1 or 2. We referred to these as helpful parameters.

(4) Constructed 2 new baseline models: (a) M_{H1} included all parameters from M_H except those that were found to be unhelpful in *either* test from step 1 or 2; and (b) M_1, based on M_0 plus every parameter found to be helpful in *both* steps 1 and 2.

(5) Repeated steps 1–4 using M_1 and M_{H1} in place of M_0 and M_H to construct M_2 and M_{H2}, and continued this iterative process until either M_{Hn} was identical to M_n, (n = iteration number) or no changes occurred during an iteration of this process.

(6) If M_{Hn} and M_n were not identical, we identified parameters shared by both models or present in only 1, then generated and fitted models with all shared parameters and all possible combinations of the unshared parameters.

We applied this same procedure to model M_P in place of M_H.

Weather Covariates.—We expected survival rates to fluctuate over time, especially those of juveniles during critical periods including their first months of life and first winter. We hypothesized that weather covariates would correlate with these fluctuations. Available weather data consisted of daily records of temperature (high, low, mean), precipitation, and snow depth for 3 stations (Moose, Moran, and Jackson, Wyoming) in the range of the JEH (National Oceanic and Atmospheric Administration 1992). Our first task was to identify combinations of these variables that best predicted survival during each period.

We used the series of annual survival estimates from the historical model with the lowest AIC_c and computed correlation coefficients between these and a series of summary weather statistics. We computed the mean of daily weather statistics for periods of 3–40 weeks ending on each day of the year, from the last day of the survival period to 2 years prior to that day for all combinations of weather statistic and station. This resulted in 2 years × 365 days/year × 38 weeks × 5 variables × 3 stations = 438,000 sets of annual weather statistics. We computed correlation coefficients between each of these summary statistics and each juvenile survival rate (neonatal or late winter). Plotting these correlations as a function of end date and period duration provided a topography of correlations. From these plots, we inspected regions of day–duration space with strong correlations and identified points

of (local) maximum positive or negative correlation. We screened these candidates further to consider only 1 of several statistics when several local peaks were associated with the same general period. This produced 4 statistics for late-winter juvenile survival and 7 candidates for neonatal juvenile survival. We then used the weather summary statistics associated with these high correlations as potential covariates in our predictive population models.

Model Fitting and Selection

Likelihood Model.—Following White and Lubow (2002), we constructed a likelihood model of the observed data. Errors in estimates of population segments were assumed to be normally distributed producing the first component of the likelihood (L_1):

$$\ln(L_1) = -\frac{n}{2}\ln\left(\frac{\sum_j \sum_y \frac{\left(\tilde{N}_{jy} - \hat{N}_{jy}\right)^2}{\widetilde{SE}(\tilde{N}_{jy})}}{n}\right),$$

where the $\tilde{N}_{jy}$ were field-based estimates of elk in age–sex class j in year y, $SE(\tilde{N}_{jy})$ were corresponding standard errors, $\hat{N}_{jy}$ were corresponding model estimates of these quantities, and n was the total number of such observations in the data set and summations were over all j and y for which data were available. We combined model estimates of adult and yearling females for comparison to field estimates of females, and we pooled juveniles over sex for comparison to field data. This formula differs from White and Lubow (2002) because we did not assume that error variance was known and equal to 1.0.

We assumed errors in survival rate estimates were binomially distributed, leading to the second component of the likelihood (L_2):

$$\ln(L_2) = \sum_j \sum_{y.s}\left[\begin{matrix} x_{j,y.s}\ln(\hat{S}_{j,y.s}) \\ + (X_{j,y.s} - x_{j,y.s})\ln(1 - \hat{S}_{j,y.s}) \end{matrix}\right],$$

where summation was over all age–sex classes j in year and season $y.s$ for which data existed, $\hat{S}_{j,y.s}$ were model-based estimates of survival rate, $X_{j,y.s}$ were the number of radiomarked elk available for the survival study, and $x_{j,y.s}$ were numbers of those that survived the period $y.s$. Combining these independent likelihoods provided total likelihood to be maximized, $\ln(L) = \ln(L_1) + \ln(L_2)$.

Parameter Estimation by Model Fitting and Selection.—The models were implemented in an Excel® spreadsheet (Microsoft 1999). Each was fit by maximizing the likelihood function using Premium Solver® (Frontline Systems 2000), an upgraded version of the numerical optimizing tool in the Excel®. We compared alternative models using AIC_c to examine relative support in the data for different ecological parameters involved in elk population dynamics. We also computed final parameter estimates as AIC_c model-weighted averages over all models (Burnham and Anderson 2002).

We computed estimates of precision for each model by inverting the information matrix (second partial derivatives of the log-likelihood function with respect to each parameter) to obtain the variance–covariance matrix. Precision of derived parameters (i.e., those not part of the fitted model but computed from them, such as equilibrium population size) were computed using the Delta Method (Cox 1998), which requires first partial derivatives of derived parameter with respect to all model parameters in addition to the variance–covariance matrix. All derivatives and matrix computations were computed numerically in Excel® (Microsoft 2002) with Visual Basic® (Microsoft 1999) using numerical methods described by Abromowitz and Stegun (1970) and Press et al. (1992). We computed unconditional precision of model-weighted parameter estimates as described by Burnham and Anderson (2002:162).

Projections and Simulation.—We used the best model selected by AIC_c to project consequences of a range of harvest management alternatives. In these projections, we extended the timeframe of the model by 250 years. Weather for future years was selected randomly from weather observed in 1 of the 22 years of our dataset with all weather statistics from each past year applied to a future year, thereby maintaining any covariances among weather variables. We varied harvest of mature females according to the scenario under evaluation, held adult and yearling male harvest rates (as a proportion of each age–sex class' size) at the 5-year mean for 1997–2001, and fixed ratios of yearling female and juvenile harvest to mature female harvest at the mean for the same period. We estimated temporal variation as the variance over 1,000 simulations and total uncertainty as the combined parameter uncertainty and temporal variation, computed by summing respective variances.

RESULTS

Data Biases and Extrapolations

By applying sightability corrections, allocating unclassified elk, and adjusting for misclassified

juveniles, we obtained corrected estimates of observed population size by class (Fig. 1). Logistic regression of sighting probability as a function of elk group size based on 175 test groups in Yellowstone National Park and Rocky Mountain National Park produced the model

$$p = \frac{1}{1 + e^{-0.3388 + 0.336G}} \ ,$$

where p was sighting probability for an elk group of size G. The group-size effect was strongly supported by comparison to a model with an intercept only (ratio of AIC_c weights = 345,089). Differences between the 2 locations were only weakly supported (ratio of AIC_c weights = 0.14). Group-size data were recorded for the JEH during aerial surveys in 1999–2002 and ranged from 1 to 343 elk. Applying the above model to correct for sightability during these years resulted in estimates of sightability ranging from 50.3% (adult males near NER in 2001, SE = 26.3%) to 74.5% (yearling males near the NER in 2001, SE = 13.1%). Combining years, overall sightability esti-

mates were 67.3% (SE = 14.0%) near the NER and 66.3% (SE = 11.3%) on other native winter range areas. Sightability was highest for mature females (69.7, SE = 15.4% on NER; 68.3, SE = 12.0% elsewhere) and lowest for adult males (61.1, SE = 19.9% on NER; 53.8, SE = 22.5% elsewhere). Sightability of elk during airplane aerial surveys was estimated to be 41.8% (SE = 4.7%) for adult males, which was 68.1% of mean sighting rate estimated for helicopter surveys near the NER. Variance of sightability estimates was attributed to the binomial sighting process (39.2% of variance) and to estimation of sighting probability (60.8%). Overdispersion was mild ($\hat{c} = 1.20$), so we made no adjustment to variance estimates. All standard errors incorporated both mean annual measurement error and between-year temporal variation.

Evidence of bias in antlered elk harvest reports was strong (AIC_c weight ≈ 100.0%) and was estimated to be 25.9% = (1 − 0.794)/0.794 higher than the actual harvest (Table 1). Support for bias in mature female harvest was minimal (AIC_c weight =
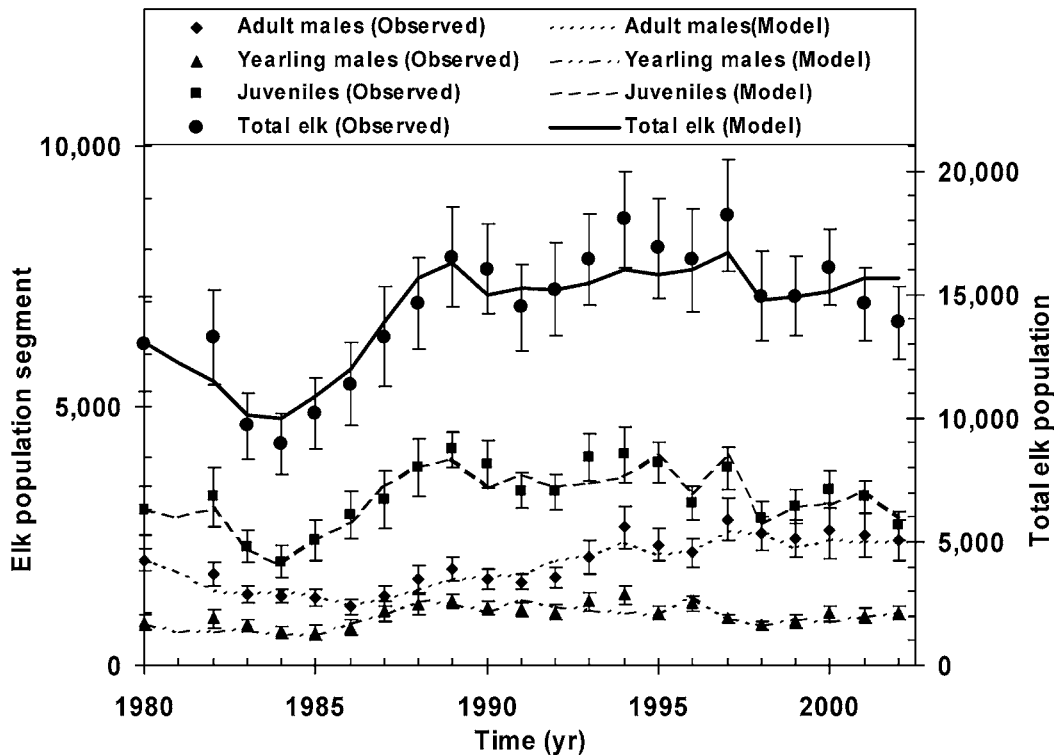

Fig. 1. Total population size (right axis) of the Jackson elk herd (Jackson Hole, Wyoming, USA) and its composition (left axis) of adult males, yearling males, and juveniles (male and female) for 1980–2002. Lines are estimates from the best population dynamics model based on Akaike's Information Criterion and points are annual field observations based on combined data from ground and aerial surveys adjusted for sightability bias and misclassification of juveniles as mature females as estimated in fitting the population model. Error bars represent 95% confidence intervals for the field data.

6.3%). We also found strong evidence (AIC$_c$ weight ≈ 100.0%) of a bias in classification counts of juveniles on feedgrounds with an estimated 5.0% (SE = 1.1%) of antlerless elk consisting of juveniles misclassified as mature females.

Linear regression produced estimates of classification ratios for the earliest year (1989) of classification data on and adjacent to the NER of 32.2 adult males/100 mature females, 32.9 yearling males/100 mature females, and 70.4 juveniles/100 mature females. On other natural winter range areas, we estimated 11.6 adult males/100 mature females, 14.8 yearling males/100 mature females, and 41.7 juveniles/100 mature females for 1988 (the year classifications began).

Historical Models and Survival Correlations with Weather

We fit 102 historical models (those containing annual estimates of survival for neonatal and late-winter juvenile survival). The best historical model used 58 parameters, 44 for annual estimates of neonatal and late-winter juvenile survival. This model was a substantial improvement over the full historical model with 70 parameters

(ratio of AIC$_c$ weights > 1.2 × 10^6). These models fit observed data very well with a variance inflation factor ($\hat{c}$ = 1.15) only slightly exceeding the nominal value of 1.0. Consequently, we did not adjust for overdispersion in other models. Using the 2 time series of juvenile survival rates from the best historical model, we computed correlations with corresponding annual weather data. This produced a list of candidate covariates for further testing in predictive models (Table 2).

Predictive Models

The full predictive model had 44 parameters but was strongly disfavored relative to more parsimonious predictive models. The best predictive model contained only 25 parameters and received 3.0 × 10^6 times the support of the full predictive model and 4.2 × 10^4 times the support of the best historical model. Thus, the best models overall were predictive models. The best predictive model fit nearly as well as the full historical model ($\hat{c}$ = 1.23) as can be seen in comparisons of the model to observations (Figs. 1, 2). No extreme outliers were evident in residuals of the fitted model, the largest being the yearling male

Table 1. Maximum-likelihood estimates (MLE) of model parameters for the full predictive model, best model (based on Akaike's Information Criteria adjusted for sample size [AIC$_c$]), and the model-weighted average estimates of all parameters for alternative population dynamics models of the Jackson, Wyoming, USA, elk herd for 1980–2002.

Model parameter	Weight of evidence[a] (%)	Full predictive model, M$_P$ MLE	SE	CV (%)	Best model[b] MLE	SE	CV (%)	Unconditional[c] Est.	SE	CV (%)
Survival, early winter										
Adults	*	0.993	0.0037	0	0.993	0.003	0	0.993	0.0031	0
Juveniles	3.3	0.995	0.0051	1				0.993	0.0051	1
Survival, late winter, nonjuveniles										
Adult males	*	0.986	0.016	1.7	0.990	0.005	0.5	0.980	0.014	1.5
Mature females	71.9	0.996	0.005	0.5				0.994	0.008	0.8
Yearling males	1.1	0.981	0.022	2.3				0.980	0.026	2.6
Yearling females	71.9	0.983	0.019	2.0				0.994	0.008	0.8
Survival, late winter, juveniles[d]										
Male intercept	*	5.96	4.02	67	9.46	2.41	25	8.93	2.73	31
Female intercept	3.9	5.99	4.01	67				8.94	4.23	47
Density slope	0.6	0.00	0.10	–3,069	–	–	–	0.00	0.11	3,144
$S_N(t-1)$[e] slope	11.1	–0.36	1.82	–504	–	–	–	–0.23	1.91	845
$S_H(t-1)$[e] slope	99.6	–4.74	4.91	–104	–8.89	2.54	–29	–8.40	2.80	33
$S_{H,F}(t-1)$[e] slope	3.8	0.13	3.31	2,625	–	–	–	0.12	3.36	2,825
W_1 slope	100.0	–10.38	2.29	–22	–8.86	1.48	–17	–8.83	1.52	17
W_2 slope	3.0	0.00	0.00	–1412	–	–	–	0.00	0.00	1,490
W_3 slope	8.4	0.01	0.07	1,092	–	–	–	0.01	0.07	1,232
W_4 slope	100.0	30.26	12.0	40	33.49	7.85	23	33.03	8.23	25
Survival, neonatal period, mature										
Adult males	*	1.000	0.044	4	0.987	0.004	0	0.988	0.005	1
Yearling males	11.0	0.986	0.006	1				0.987	0.006	1
Adult females	10.3	0.963	0.021	2				0.985	0.021	2
Yearling females	14.2	1.000	0.288	29				0.988	0.0288	29

Table 1. (continued)

Model parameter	Weight of evidence[a] (%)	Full predictive model, M_P			Best model[b]			Unconditional[c]		
		MLE	SE	CV (%)	MLE	SE	CV (%)	Est.	SE	CV (%)
Survival, neonatal, juvenile[e]										
Male intercept	*	12.05	2.65	22	11.90	2.82	24	11.93	3.00	25
Female intercept	96.3	12.40	2.62	21	12.31	2.80	23	12.31	2.99	24
Density slope	67.4	−1.00	0.98	−97	−1.27	0.68	−54	−0.82	0.88	108
W_1 slope	2.8	0.00	0.00	−2073	–	–	–	0.00	0.00	2,123
W_2 slope	100.0	−0.20	0.04	−21	−0.20	0.04	−22	−0.20	0.05	22
W_3 slope	97.0	0.04	0.03	60	0.05	0.02	44	0.05	0.02	51
W_4 slope	99.5	8.16	3.67	45	10.56	3.03	29	9.56	3.27	34
W_5 slope	96.0	9.33	6.84	73	8.62	4.13	48	7.77	4.46	57
W_6 slope	99.9	−6.41	1.91	−30	−5.40	1.63	−30	−6.01	1.78	30
W_7 slope	3.0	−0.07	2.31	−3487	–	–	–	−0.07	2.34	3,589
Survival, summer, juvenile										
Male	*	0.991	0.009	1	0.996	0.004	0	0.995	0.004	0
Female	7.8	1.000	0.000	0				0.996	0.000	0
Reproduction										
Birth rate	*	0.578	0.070	12	0.624	0.038	6	0.604	0.039	6
Birth sex ratio	99.9	0.457	0.032	7	0.454	0.015	3	0.458	0.016	3
Harvest rate, actual vs. reported										
Yearling males and adult males	100.0	0.794	0.113	14	0.768	0.026	3	0.737	0.032	4
Mature females [f]	6.2	0.993	0.134	13	–	–	–	0.996	0.0135	14
Initial population										
Adult males	*	2,001	135	7	2,048	108	5	2,029	109	5
Adult females	*	6,385	1,056	17	6,481	309	5	6,606	351	5
Yearling males	*	811	103	13	829	91	11	818	91	11
Yearling females[g]	2.9	1,127	1,195	106	688	–	–	713	1,197	168
Juvenile males	*	1,258	276	22	1,340	124	9	1,314	125	10
Juvenile females[h]	2.7	1,601	505	32	1,660	–	–	1,628	505	31
Observation biases										
Misclassification (yearlings as mature females)	100.0	0.042	0.034	80	0.056	0.011	19	0.050	0.011	22
Sightability		0.396	0.049	12	0.416	0.046	11	0.418	0.047	11

[a] Sum of AIC_c model weights for models containing a given parameter. Sum indicates the strength of support for the parameter; 1 minus weight indicates support for excluding parameter. An asterisk indicates support for excluding parameter. An asterisk indicates parameters considered essential, a priori, and not tested by removal from any model; thus these 12 parameters were the only parameters included in the simplest model, M_0.

[b] Parameters not included in the best model were indicated by a dash. A vertical line connecting a group of parameters indicates that they were set equal to each other. Parameters not included in a particular model and not set equal to others were set to default value (zero in most cases).

[c] Parameter estimates averaged over all 102 predictive models considered and weighted by AIC_c model weights.

[d] These were parameters of a logistic survival submodel, not survival rates.

[e] Coefficients for autocorrelations or correlations with indicated survival rates.

[f] Default value for model with parameter excluded was 1.0.

[g] Default value for models where parameter was excluded was a fixed proportion of mature females based on the mean ratios of yearling to mature females and male and female juveniles harvested in harvest data from Grand Teton National Park.

[h] Default value for models where parameter was excluded was a fixed ratio of male to female juveniles harvested in harvest data from Grand Teton National Park.

estimate in 1994, which differed from observed by 3.6 SE. Furthermore, we found no visually obvious temporal patterns in residual errors and linear regression of residuals versus time had negligible support ($R^2 < 2\%$).

In contrast, model M_0 fit the data poorly ($\hat{c} = 1.8$) and was disfavored relative to the best model by a strength of evidence ratio of $>3.3 \times 10^{35}$. Addition of 5 parameters to M_0 (sex ratio at birth, sex differences in neonatal and late-winter sur-

vival, antlered harvest reporting bias, and juvenile misclassification bias) improved fit ($\hat{c} = 1.5$) and was supported by a factor of 2.3×10^{16} over M_0, but was still inferior to the best model by a ratio of 1.4×10^{19}. The difference between this slightly more complex (17 parameter) model and the best (25 parameter) model was addition of 9 parameters for submodels that described annual variation in juvenile survival and removal of 1 parameter for adult survival difference by sex.

Table 2. Candidate summary weather statistics strongly correlated with annual late-winter or neonatal juvenile survival for the elk herd in Jackson Hole, Wyoming, USA, 1980–1992.

Affected juvenile survival rate	Description[a]	Weather station[b]	Statistic[c]	Lag[d]	End date[e]	Duration[e] (no. of weeks)	Correlation of survival with weather	Included in best AIC$_c$ model
Late-winter								
W_1	Dry winter	Moran	P	0	12 Feb	8	−67.0%	Y
W_2	Cold summer, fall, and winter	Jackson	T_{Max}	0	1 Jan	34	−52.8%	N
W_3	Warm spring green-up period	Moose	T_{Max}	0	25 Mar	7	57.8%	N
W_4	Wet previous summer and fall	Moran	P	−1	27 Oct	16	74.3%	Y
Neonatal								
W_1	Cool summer	Jackson	T_{Min}	0	13 Aug	6	−58.6%	N
W_2	Cool previous summer	Jackson	T_{Mean}	−1	31 Aug	6	−55.8%	Y
W_3	Warm spring green-up period	Jackson	T_{Max}	0	17 Apr	10	50.8%	Y
W_4	Wet spring green-up period	Jackson	P	0	22 May	6	58.5%	Y
W_5	Wet previous spring green-up period	Jackson	P	−1	26 May	7	63.7%	Y
W_6	Light January snowfall	Jackson	P	0	17 Jan	5	−55.0%	Y
W_7	Light early-winter snowfall in prior year	Jackson	P	−1	26 Feb	14	−68.2%	N

[a] Conditions stated were those favorable to survival.
[b] Data taken from 3 National Oceanic and Atmospheric Administration weather stations near wintering areas in the Jackson Hole and Gros Ventre valleys, Wyoming (National Oceanic and Atmospheric Administration 1992).
[c] Raw statistics are daily values of Precipitation (P) and minimum (T_{Max}), maximum(T_{Min}), and mean (T_{Mean}) temperature.
[d] Lag 0 indicates that start date of weather included in mean was in the same calendar year as the juvenile survival period; −1 indicates prior year.
[e] Weather covariates used were annual statistics computed as the mean of daily values over the period defined by the end date and duration given in the table.

Many of the 102 alternative predictive models tested with complexity similar to the best predictive model (23–27 parameters) had support approaching that of the best model. Consequently, a weighted average of parameter estimates provided the most reliable final estimates, unconditional on the specific model (Table 1). Total weights for models containing each parameter indicated minimal support (3.3%) for a difference between adult and juvenile survival rates during the early-winter period and the best model estimated these as a single parameter (Table 1). Similarly, differences in late-winter survival between yearlings and adults were not well supported (1.1%); however, sex differences were moderately supported (71.9%) but were not included in the best model. We found weak support (<14.2%) for age and sex differences in adult survival during the neonatal period and for sex differences in juvenile survival during summer (7.8%).

Annual natural survival rates of adult elk were very high. Combining estimates for the 4 periods, excluding harvest, we obtained estimates of 96.8% (SE = 1.5%) for adult males and 97.2% (SE = 2.2%) for mature females. Reproductive rate, based on juveniles alive when survival monitoring began, was estimated as 60.4 juveniles/100 mature females (SE = 3.9 juveniles/100 mature

females). This rate of reproduction was after prenatal and perinatal mortality occurring in the few days before captures. Sex ratio at birth strongly favored females (45.8% males, SE = 1.6%, AIC$_c$ weight = 99.9%). Evidence for initial (1980) yearling:adult female and male:female juvenile ratios differing from the long term mean was weak (<2.9%) and not included in the best model.

A final estimate of total population size in 2002, based on the cumulative evidence provided by a 22-year history and multiple sources of data, was 15,680 elk (SE = 407). This differed significantly from the single-year estimate (Fig. 1) of 13,868 (SE = 751), which was the most deviant annual estimate of population size in the time series.

Juvenile Survival Submodels

Submodels of juvenile survival during late winter and neonatal periods supported several explanatory covariates. Difference between sexes was strongly supported (96.3%) for neonatal juvenile survival but poorly supported (3.9%) for late-winter juvenile survival. Density dependence was moderately supported (67.4%) for neonatal juvenile survival (Fig. 3) but not for late-winter juvenile survival (0.6%). We found strong support for a negative autocorrelation between survival of juveniles in late winter and their prior survival
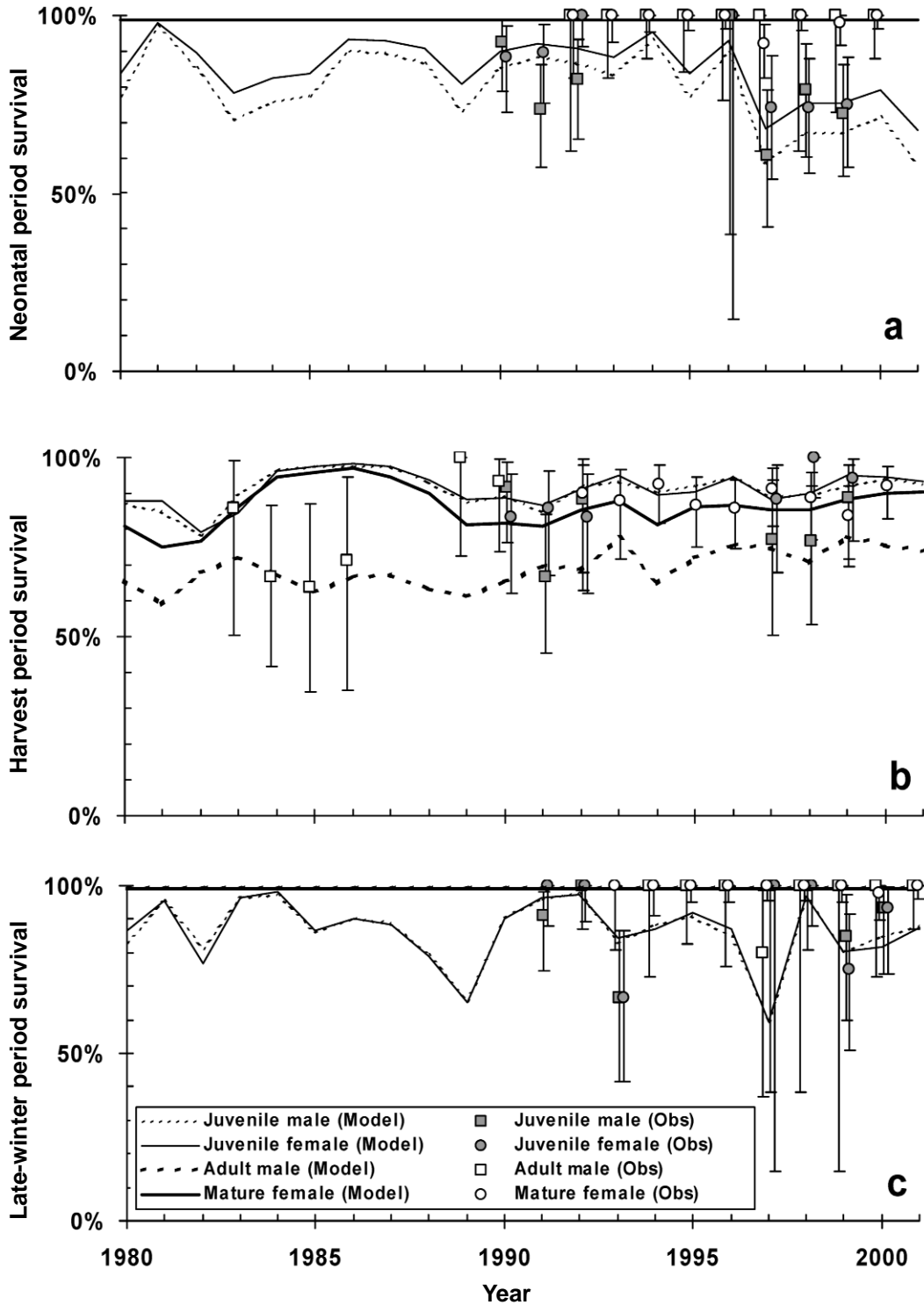
Fig. 2. Elk survival rates during: (a) neonatal (20 May–31 Jul), (b) harvest (10 Sep–31 Dec), and (c) late-winter (20 Feb–19 May) periods based on the best model selected by Akaike's Information Criterion (lines) and directly observed in radiomarked elk (points) from Jackson Hole, Wyoming, USA, including 95% confidence intervals for observed points.
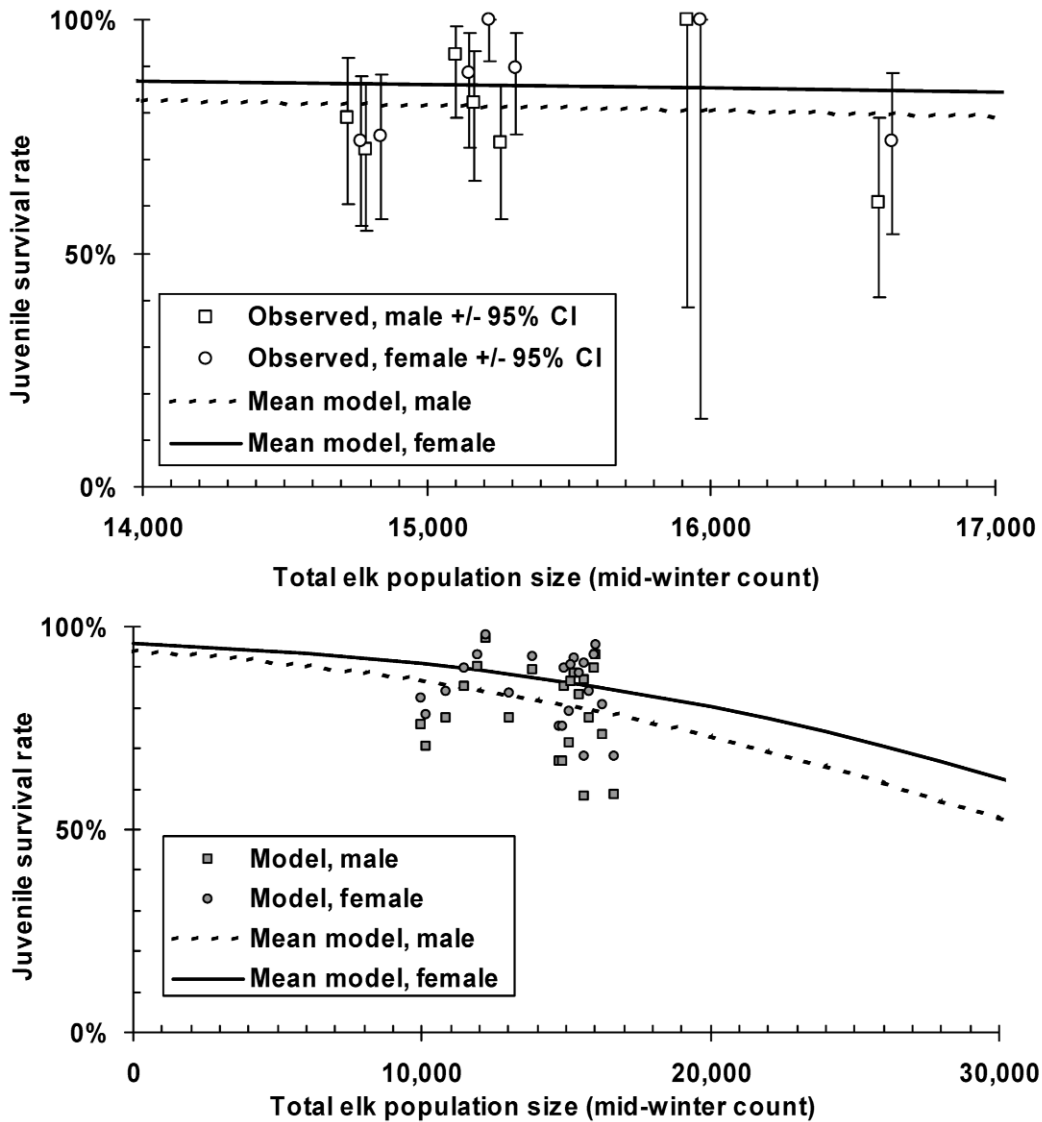
Fig. 3. Late-winter elk juvenile survival rate shown as a function of population size directly observed in radiomarked elk (open symbols) from Jackson Hole, Wyoming, USA, including 95% confidence intervals, compared to model predictions (filled symbols) using the best model selected by Akaike's Information Criterion. Model predictions based on average values for all covariates except density are also shown for comparison (lines). Upper graph is an enlargement of the x-axis to emphasize the observed field data.

during harvest (Fig. 4a)—an apparent compensatory response to harvest. The magnitude of this effect was 89.3%, meaning that additional harvest of 100 juveniles would result in reduced winter mortality of 89 juveniles, a net loss of only 11 juveniles/100 harvested. Autocorrelation with prior neonatal survival was poorly supported (11.1%). Correlation of juvenile survival with harvest survival of their mothers was not supported (3.8%).

Of the 4 weather covariates considered for late-winter survival (Table 2), 2 were strongly supported (approx 100%) and 2 poorly supported (<8.4%). We found support (Table 1) for increased survival in dry winters (Fig. 4b) and wet weather during the prior summer and fall (Fig. 4c). Of the 7 candidate weather covariates for neonatal survival (Table 2), 5 were included in the best model (Table 1) and received strong
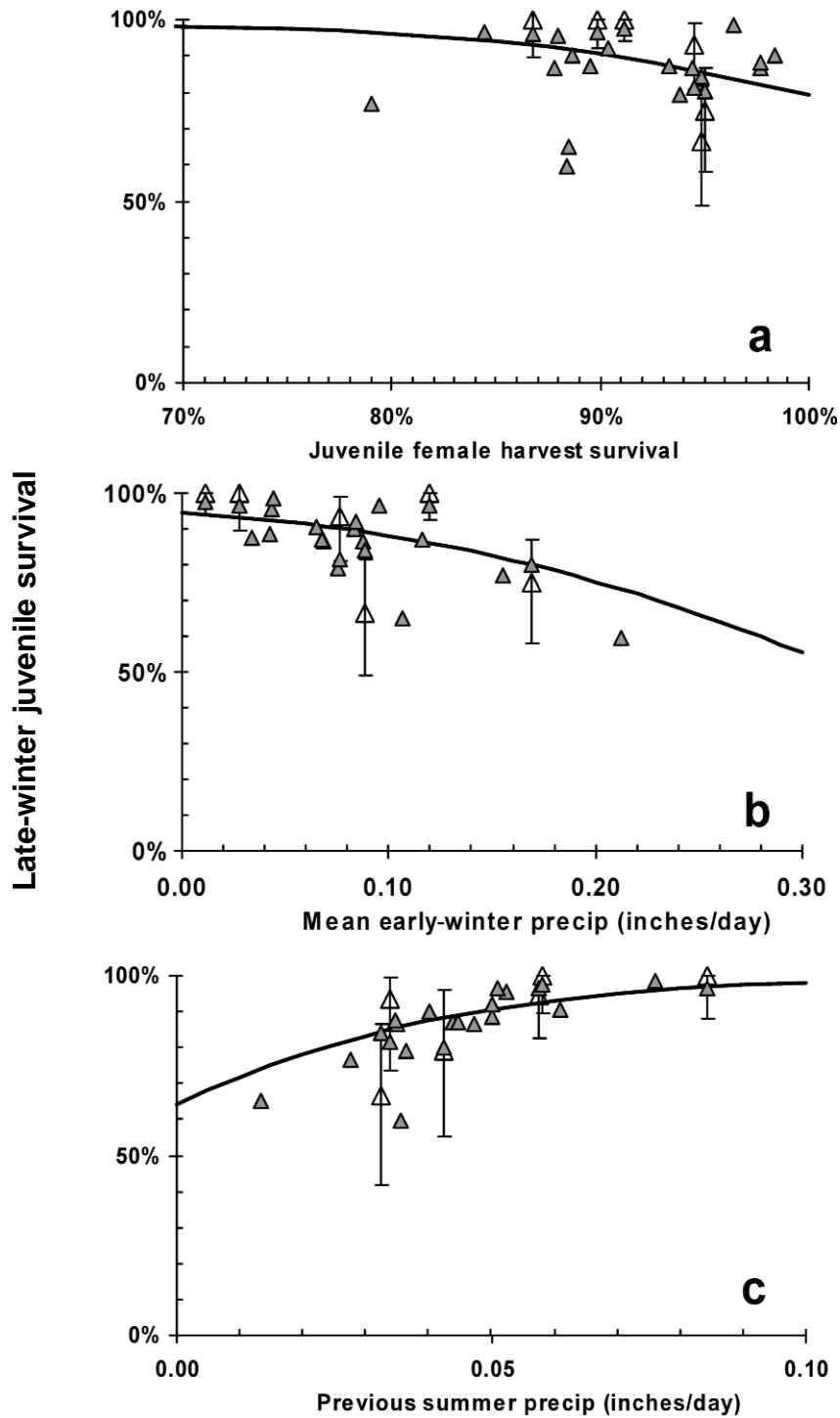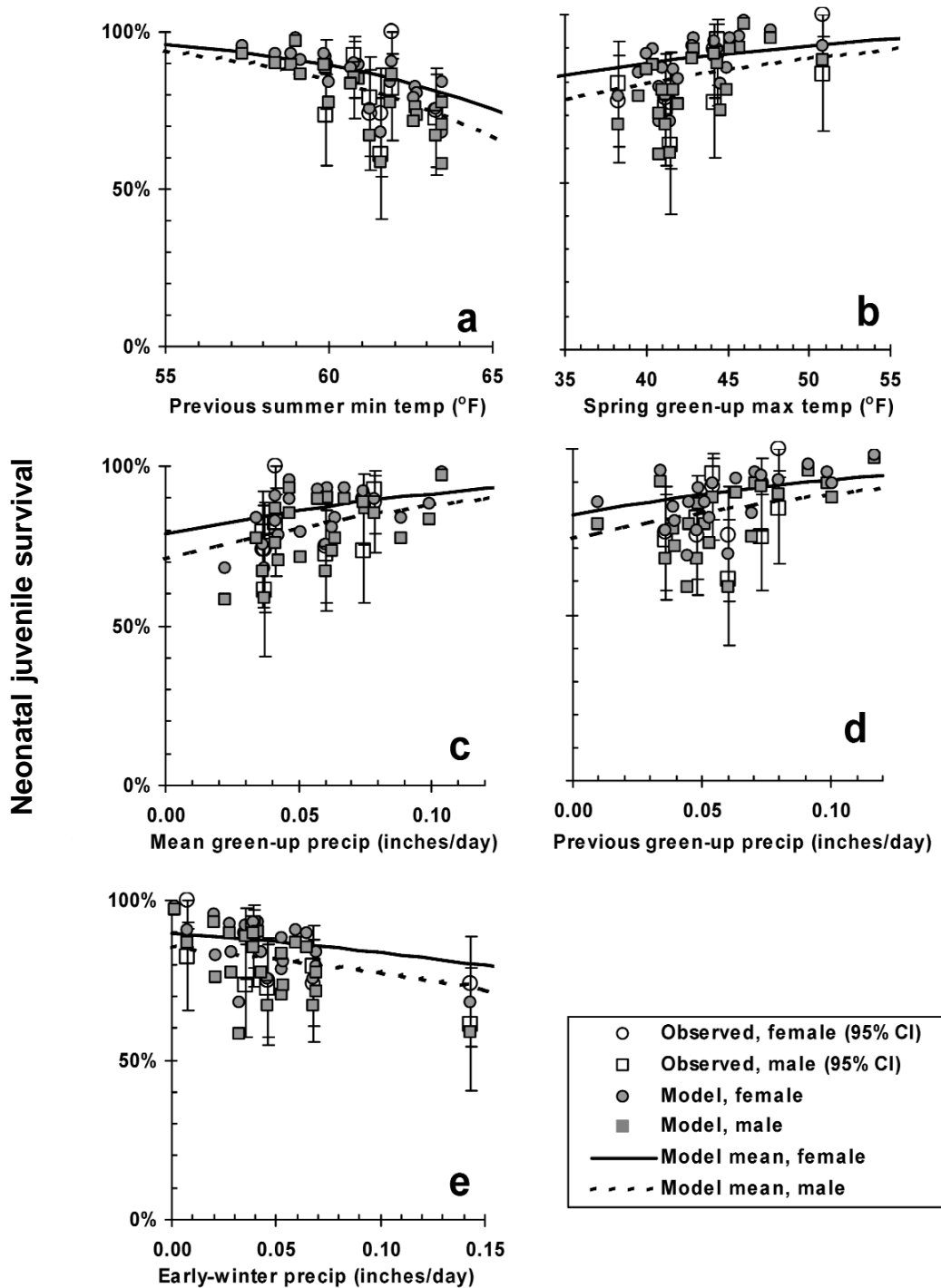
Fig. 4. Late-winter elk juvenile survival as a function of 3 covariates included in the best model (based on Akaike's Information Criterion): (a) female juvenile harvest period survival, (b) mean early-winter precipitation, and (c) previous summer precipitation. Directly observed values (open symbols) based on radiomarked elk from Jackson Hole, Wyoming, USA, including 95% confidence intervals are compared to model predictions (filled symbols) using the best model and model predictions based on average values for all covariates except the weather covariate depicted in each graph (lines).
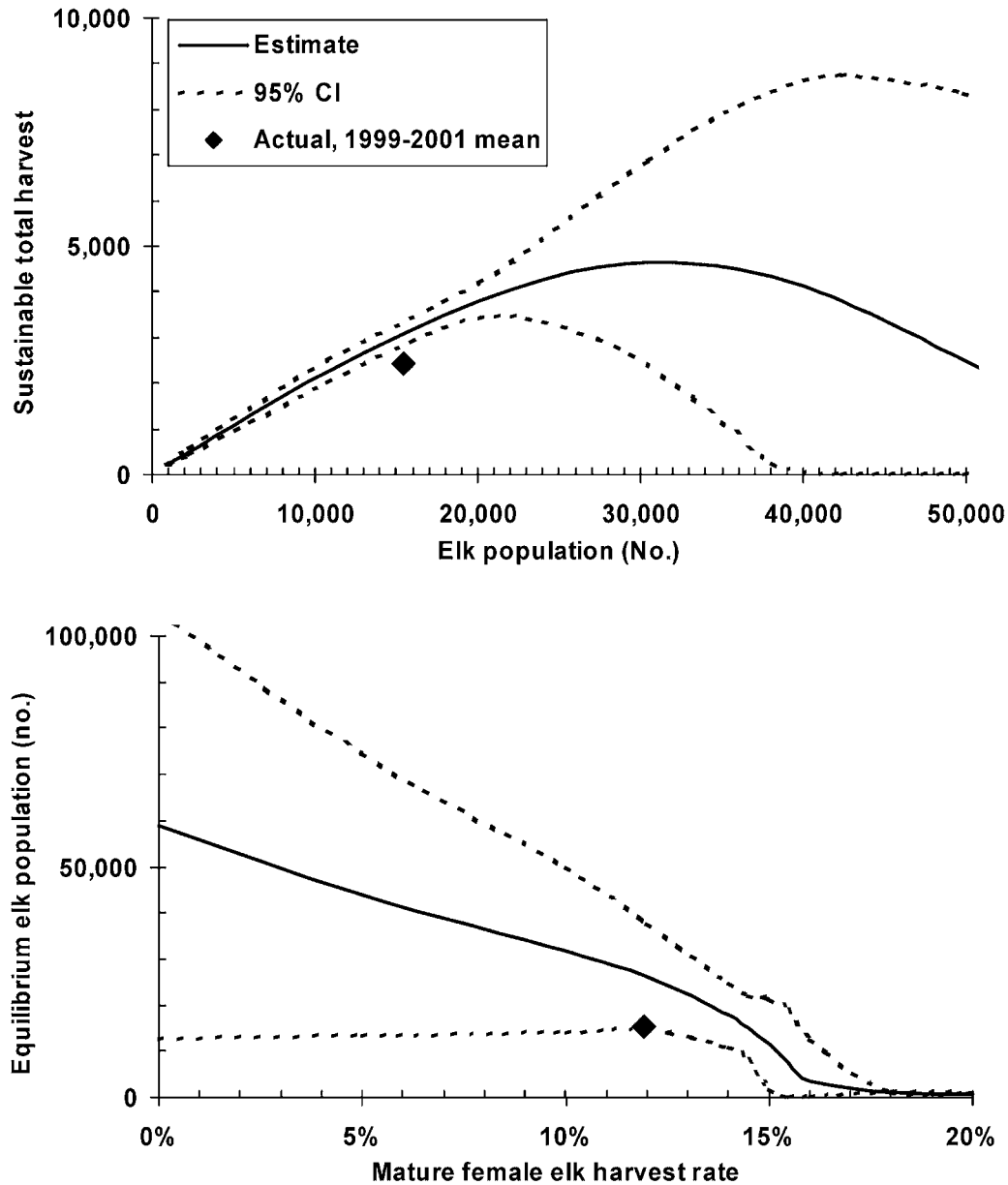
Fig. 5. Neonatal elk juvenile survival as a function of 5 weather covariates included in the best model (based on Akaike's Information Criterion): (a) previous summer minimum temperatures (min temp), (b) spring green-up maximum temperatures (max temp), (c) green-up precipitation (precip), (d) prior year green-up precipitation, and (e) early-winter precipitation. Directly observed values based on radiomarked elk (open symbols) from Jackson Hole, Wyoming, USA, including 95% confidence intervals, are compared to model predictions (filled symbols) using the best model and model predictions based on average values for all covariates except the weather covariate depicted in each graph (lines).

Fig. 6. Upper graph shows projected equilibrium population size for the Jackson elk herd, Wyoming, USA, for various rates of adult elk female harvest. Lower graph depicts estimated sustainable total (all age and sex classes) harvest for various population sizes. Projected harvests and population sizes are based on the best model selected by Akaike's Information Criterion. Confidence intervals account for both parameter uncertainty and stochastic variation due to weather. Mean harvest and population size from 1999 to 2002 are shown for comparison.

overall support (>96.5%), and the remaining 2 received little support (<3.0%). Supported weather effects enhancing neonatal juvenile survival all occurred prior to calving. These effects were cool previous summers (prior to the pregnancy resulting in the current juveniles; Fig. 5a), warm (Fig.

5b) and wet (Fig. 5c) current spring green-up periods (just prior to juvenile births), wet previous spring green-up (Fig. 5d), and light snowfall in the January prior to birth (Fig. 5e).

Estimated neonatal density dependence provided a basis for projecting equilibrium popula-

tion (carrying capacity), assuming that no other density-dependent factors emerge at large population sizes. On this basis, we estimated an equilibrium population size of 59,000 elk (SE = 23,000 elk). Projections of sustainable harvest based on this same density relationship suggested a maximum sustainable yield of 4,600 elk (SE = 1,500 elk) at a population size of 33,000 elk (Fig. 6). Harvest rate of mature females required to achieve maximum sustainable yield was 9.5%, and harvest rate required to maintain the population at the target level of 11,029 elk was 15.1%, which would produce an estimated total elk harvest of 3,900 elk/year (SE = 300). Thus, the actual mean harvest rate in 1999–2002 of 11.9% of mature females fell approximately midway between these 2 goals.

Projection of equilibrium population size was extremely sensitive to adult female harvest rate for population sizes near the WGFD target: estimates ranged from 3,600 to 18,000 elk for harvest rates of 14–16% of mature females. Near the target population size, each additional adult female elk harvested annually would reduce equilibrium population by 13 elk. Continuation of the recent harvest rate of 11.9% would yield a harvest of 1,619 antlerless elk (all females plus male juveniles) in 2003, but would climb to 2,627 elk/year at an equilibrium population of 26,395 elk. Increasing harvest rate to 15.1% would lead to harvesting 1,985 antlerless elk in 2003, but this would decline to 1,344 antlerless elk/year as the population approached the target of 11,029 elk.

DISCUSSION

The good fit of the models suggests that the important dynamics occurring in this population during the past 22 years have been effectively captured by the relationships modeled. This does not preclude additional smaller effects, nor does it preclude the possibility that some covariates do not represent true causal effects but rather are indirect indicators of an underlying phenomenon or simply spurious correlations. We also caution that the specific periods of weather identified as most strongly correlated with survival resulted from an exploratory analysis and should be confirmed by additional data on these relationships. However, predictive covariates found to be important in the model represent plausible causal effects. Nevertheless, uncertainty about cause and effect will always exist in the absence of manipulative studies. Although not possible for weather effects, management-scale manipulations are conceivable for predation and density effects.

Only models including annual variation in winter juvenile survival received support from the data. Winter juvenile survival should be improved by both access to winter forage and improved nutritional status at the start of winter (Hobbs 1989). Weather covariates identified in our analysis directly relate to these 2 factors. Low precipitation in early winter leads to shallow snowpack, facilitating access to native forage and reduced catabolism of energy reserves. High precipitation during the previous growing season favors increased forage quality and quantity, enhancing elk juvenile growth and nutritional status prior to winter. We also observed a compensatory response to juvenile harvest, unrelated to population density: increased harvest led to increased winter survival. This suggests that either (1) some set of traits predisposed certain individuals to mortality—those most likely to be harvested were also most likely to die of natural factors in late winter; or (2) removal of some juveniles reduced competition among remaining juveniles, thereby increasing their chance of survival.

Neonatal juvenile survival was predicted well by weather factors affecting nutrition of mothers. New vegetative growth generally first appears in Jackson Hole in April and was significantly more nutritious and digestible than rations of alfalfa elk received on the NER (Smith et al. 1997). Warm, wet conditions during spring green-up lead to earlier plant growth during gestation and prior to lactation. Light snow in January could improve access to forage during winter and delay reliance on energy reserves. Cool conditions during the prior summer and wet conditions in the prior spring green-up could lead to improved nutrition for mature females entering pregnancy, leaving them less vulnerable to nutritional deprivation during winter. These results are consistent with studies of red deer (*Cervus elaphus*; Albon et al. 1987), which found that April temperatures positively affected neonatal survival. In an earlier study using some of the same data used in our analysis, Smith et al. (1997) found a positive effect of April temperatures on cohort birth weights and inferred that better nourished neonates experienced higher survival.

The combination of weather and density explains observed patterns in survival well. For example, neonatal survival was lower during the later survival study (1997–1999) than the earlier

study (1990–1992). However, the later period also exhibited less favorable weather. In particular, 1997 and 1999 had much higher than normal January precipitation, and 1996 and 1998 also were above average, producing a 4-year string of relatively severe winters. Cooler green-up periods and warmer summers occurred as the 1990s progressed. These patterns correlate well with observed changes in juvenile survival and have plausible mechanistic links to survival.

However, alternative hypotheses explaining observed patterns cannot be conclusively ruled out. An alternative hypothesis, suspected by Smith et al. (in press), was that predation was higher and contributed to lower survival in the second period. Gray wolves (*Canis lupus*), introduced to Yellowstone National Park in 1995 and 1996, began colonizing summer ranges used by the JEH in late 1998, and 2 packs established territories in 1999. Due to the small number of wolves (<25) relative to the tremendous ungulate prey base in Jackson Hole, wolves exerted little influence on elk population during our study. Higher predation mortality of neonates during the late 1990s was likely compensatory and consequent to poorer growth rates of neonates (Smith et al. in press). The fact that juvenile harvest was clearly compensatory in the models also supports this hypothesis relative to predation. Therefore, we conclude that if predation played any role in the decline, it was a more speculative hypothesis that was confounded with weather patterns. If wolf populations increase over time, they may dampen population growth of the JEH to some unknown degree.

Evidence for density dependence in this study was weak, both statistically and biologically. This was not surprising for 4 reasons:

(1) Winter food supplementation of much of the JEH likely reduced effects of density.

(2) The range of population size observed during this study covered only a small fraction of the range between zero and the projected equilibrium (Fig. 6), making the response of survival rates to density difficult to detect.

(3) Based on our estimated equilibrium population, the JEH has been maintained at a level <30% of equilibrium where density effects were unlikely to be important. Detection may require that populations approach or exceed carrying capacity due to the nonlinearity of density dependence (Caughley 1977, Fowler 1987). Density response could also occur in other survival rates, such as late-winter juvenile survival, at higher densities than have

been observed in the JEH, as reported by Singer et al. (1997) and Taper and Gogan (2002) for Yellowstone National Park and by Lubow et al. (2002) for elk in Rocky Mountain National Park.

(4) As Sæther (1997) noted, density dependence is particularly difficult to detect in ungulates that are long-lived and show a high degree of age dependence in fecundity and mortality. These age-specific effects may generate time lags in density-dependent responses of 3–10 years and increase the length of study required to detect them.

Sauer and Boyce (1983) and Boyce (1989) concluded that density dependence was operating in this same population at an earlier time. Coughenour and Singer (1996), Houston (1982), and Singer et al. (1997) found that both climate and population density influenced neonatal survival of Yellowstone elk. Clutton-Brock and Albon (1989), Clutton-Brock et al. (1982), and Sæther (1997) concluded that density had a more significant influence on winter survival than on neonatal survival. Lubow et al. (2002) also found that a combination of density together with winter and summer weather—presumed to be related to plant growth and elk nutrition—influenced survival of elk during their first year. Our results also corroborate findings of Singer et al. (1997) and Lubow et al. (2002) that density affects neonatal juvenile survival more strongly and at lower densities than does late-winter survival.

Our estimate of natality (60.4 juveniles/100 mature females, SE = 3.9%) was lower than the 67.8% estimated by Smith and Robbins (1994). However, Smith and Robbins' (1994) estimate was based on pregnancy rates of mature females captured during March and early April. Differences might be due to actual biological changes between the earlier study (1978–1982) and ours. However, more likely is that differences in natality were due to unmeasured losses from Brucellosis-caused abortions or perinatal mortality preceding capture of juveniles. Smith and Robbins (1994) suggested that abortion due to Brucellosis infection could terminate 7% of pregnancies and revised their natality estimate to 63 juveniles/100 mature females, thus placing their estimate well within the 95% confidence interval of our estimate.

MANAGEMENT IMPLICATIONS

The wide confidence interval on the projected equilibrium population (59,000, SE = 23,000 elk) from our model reflects relatively poor information available in this dataset regarding true effects

of large population size on survival. We do not preclude the possibility that additional or stronger (nonlinear) responses to larger populations than those observed to date would limit equilibrium population size at a level substantially below our projection. Consequently, we strongly discourage use of our projection for management purposes without adequate monitoring to provide additional information to improve this prediction. Nevertheless, we can say with confidence that no density response observed to date is sufficient to prevent growth of the JEH, given continuation of supplemental feeding. Only female harvest can maintain this population at current or lower levels given current feeding policies.

The difference between the recent harvest rate and the rate required to achieve the WGFD target population of 11,029 elk amounts to harvesting only 366 additional antlerless elk in 2003. Furthermore, required antlerless harvest would decline over time as the population declined toward the WGFD target, ultimately becoming approximately half the current level. The extreme sensitivity of equilibrium population to female harvest indicates the importance of continued monitoring and adjusting harvest regulations to observed fluctuations. A single harvest rate cannot maintain a relatively constant population, given the combination of natural stochasticity due to weather and estimated sensitivity to harvest rate. Thus, we recommend a process of adaptive management that uses annual feedback of observed population size to further improve our model and recommended harvest rate. However, the need for a higher harvest rate to achieve the target population size was supported by the observation that the JEH has not been at or below this level since 1985. Risk of overharvest should not be an impediment to testing higher harvest rates because rapid population recovery is possible in this population at its current size— 14% growth in 1 year if antlerless harvest were temporarily halted.

Population estimates for the JEH are the cause of some controversy. The WGFD issues annual estimates of this population based on much of the same data analyzed in this study. Field biologists, assisted by models developed in POPII (Fossil Creek Software, Fort Collins, Colorado, USA [http://weba.viawest.net/~fcs/p2]), generate these estimates. In 2002, WGFD estimated 13,318 elk, compared to our model-based estimate of 15,680 elk (SE = 407). However, our bias-corrected field estimate of 13,868 (SE = 751) does not differ significantly from the WGFD estimate. In other words, the isolated field population estimate for 2002 was not consistent with maximum-likelihood estimates based on the totality of evidence from the entire time series of survival, composition, harvest, and weather data. We are confident that our model-based estimates are the best available, given limitations of the data. Thus, the discrepancy between our isolated population estimate for 2002 and our model-based estimate indicates that 2002 was an anomaly. In fact, the 2002 population estimate was the only 1 of the 22 estimates in this time series with 95% confidence intervals that do not encompass the model-based estimate (Fig. 1). This suggests that sighting conditions were abnormally low in 2002. Our sightability corrections were based on group size only because additional covariates found to be important predictors of sighting probability have not been collected in aerial surveys of the JEH. However, we cannot exclude a recent qualitative change in vital rates caused by previously unimportant factors, such as epizootic disease. We believe that the only reliable way to resolve this discrepancy is to adopt statistically valid survey methods.

Several deficiencies in the data available on the JEH limit the value of our study and the ability of managers to make informed decisions. We found important biases in aerial and ground population counts and reported harvest data. Although we adjusted for these using evidence provided by the data, some uncertainty remains about the validity of these adjustments and the possibility of alternative explanations. The sightability corrections we used were based on studies of other populations under potentially different sighting conditions. Previous studies have found covariates, such as snow cover and elk activity (Lubow et al. 2002) and vegetation cover (Samuel et al. 1987), in addition to group size, to be important predictors of elk sightability. The unavailability of these covariates and lack of replication in current survey methods resulted in inadequate information for computing precision of estimates. Although ground counts were intended to be a complete census, some error has been documented (Smith and McDonald 2002). These data also are not currently collected in a manner that provides a basis for estimating precision. Age distributions of female elk harvested in GTNP were assumed to represent the entire population; this assumption should be verified through a population-wide, random sample of harvested females. Finally, we

note that birth rates, by sex, remains the 1 important set of vital rates that has not been directly estimated in this population.

Unless new and important qualitative changes arise that alter the fundamental dynamics of this population (e.g., epizootic disease, major natural or artificial landscape or climate changes, or biologically important shift in predator community), our model should reliably project future, short-term, population changes and responses to management. We recommend that our model, or a similar model fitted to all available data in a statistically rigorous manner, be used for evaluating future management decisions regarding the JEH. Such models can provide defensible predictions of management alternatives, ecological changes such as increase of predators, or potential climate changes.

ACKNOWLEDGMENTS

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