Greater Sage-Grouse Population Dynamics and Probability of Persistence

Final Report to Pew Charitable Trusts
18 March 2015

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Abstract. We updated our earlier comprehensive analysis of Greater Sage-Grouse (*Centrocercus urophasianus*) population dynamics and probability of persistence from 1965 to 2007 throughout the species range by accumulating and analyzing additional counts of males from 2008 to 2013. A total of 89,749 counts were conducted by biologists and volunteers at 10,060 leks from 1965 through 2013 in 11 states occupied by Greater Sage-Grouse. In spite of survey effort increasing substantially (12.6%) between 2007 and 2013, the reconstructed estimate for minimum number of breeding males in the population, using standard approximations for missing values from Colorado, fell by 56% from109,990 breeding males in 2007 to 48,641 breeding males in 2013. The best model of annual rates of change of populations estimated across the Sage-Grouse Management Zones was a stochastic density dependent Gompertz model with 1-year time lags and declining carrying capacities through time. Weighted mean estimates of carrying capacity for the minimum number of males counted at leks for the entire range-wide distribution, excepting Colorado, were 40,505 (SE 6,444) in 2013 declining to 19,517 (SE 3,269) in 30 years and 8,154 (SE 1,704) in 100 years. Starting with the estimated abundance of males counted at leks in 2007 a simple effort to evaluate the validity of future forecasts of abundance was conducted by forecasting abundance in 2013 from Gompertz density dependent models with 1-year time lag and declining carrying capacity models of 6 of the 7 management zone populations. Estimated mean abundance in 2013 predicted 97.8% of the variation in true abundance in management zones. Concerted efforts across both public and private land ownerships that are intended to benefit Greater Sage-Grouse show little current evidence of success but more will be required to stabilize these declining populations and ensure their continued persistence in the face of ongoing development and habitat modification in the broad sagebrush region of western North America.

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Introduction

The Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) is considered a "landscape species" with annual ranges that can encompass > 2,700 km^2 (Leonard et al. 2000, Holloran and Anderson 2005, Knick and Connelly 2011). Movements within breeding habitat can exceed 25 km, and seasonal ranges can be > 80 km apart (Connelly et al. 1988, Holloran and Anderson 2005). Populations throughout the species' range have been negatively affected by loss and fragmentation of habitat largely due to wildfire, invasive species and energy development (Doherty et al. 2008, Miller et al. 2011). Moreover, some populations have declined as a result of west Nile virus (Walker et al. 2004, 2007). Schroeder et al. (2004) estimated that sage-grouse have been extirpated from 44% of the species' likely historic range.

Despite substantial evidence indicating population declines and habitat loss (Braun 1998, Connelly et al. 2004, Schroeder et al. 2004), in 2005, the U.S. Fish and Wildlife Service (USFWS) determined that listing greater sage-grouse under the Endangered Species Act (ESA) was not warranted (Stiver 2011). However, a complaint filed in July 2006 by Western Watersheds alleged the 2005 finding was incorrect, arbitrary, and unwarranted (Ashe 2010). The U.S. District Court for Idaho subsequently ruled the USFWS determination was arbitrary and capricious and remanded the finding to the USFWS. In March 2010, the USFWS concluded that the sage-grouse was warranted for protection under ESA, but listing was precluded because of higher priorities (Ashe 2010); this agency agreed to issue a final determination by September 2015. The listing decision identified habitat loss/fragmentation, including habitat treatments, and lack of adequate regulatory mechanisms as the major factors contributing to declines in sage-grouse populations (Connelly 2014).

In addition to the work by Schroeder et al. (2004), other publications have assessed sage-grouse population change. Connelly and Braun (1997) concluded that by 1994 breeding populations had declined by 17-47% from long-term averages. Connelly et al. (2004) reported that sage-grouse populations declined at an overall rate 2.0% per year from 1965-2003. Similarly, an analysis by the Western Association of Fish and Wildlife Agencies (WAFWA 2008) indicated range wide declining trends for sage-grouse from 1965-2007. The most recent analysis (Garton et al. (2011) assessed long-term changes in sage-grouse populations by sage-grouse management zone (Stiver et al. 2006), reconstructed population abundance, and evaluated the likelihood of long-term persistence of populations. These authors' findings generally agreed with previous studies documenting declining populations of sage-grouse. Moreover, Garton et al. (2011) generated models that suggested at least 3 of 23 populations but no Sage-Grouse Management Zones (SMZs) may decline below effective population size of 50 within the next 30 years and at least 18 of 23 populations and 2 of 7 SMZs are likely to decline below effective population size of 500 within 100 years if current conditions and trends persist.

Recently, state and federal agencies have implemented a variety of conservation plans and programs to improve sage-grouse populations and habitats (NTT 2011, Baruch-Mordo et al. 2013, Copeland et al. 2013, Connelly 2014). Although federal conservation actions have been criticized (Connelly 2014) and some positive impacts of CRP on sage-grouse populations in Washington had been documented through 2010 (Schroeder and Vander Haegen 2011), no current evaluations of the status of sage-grouse at the population, SMZ, or range-wide scales exist that provide insight into current status of sage-grouse or that may allow an evaluation of effectiveness of conservation actions to date. If implementation of current conservation programs were effective and sufficient, we would expect that trends for many sage-grouse over the last 6 years would have begun to stabilize or in some cases may have begun to increase. With availability of 6 additional years of data since the Garton et al. (2011) publication, our objectives were to update the analyses of Garton et al. (2011) and evaluate our predictions. Thus, we 1) assess recent changes (2007-2013) in sage-grouse populations by SMZ; 2) reconstruct population abundance back to 1965 for each population, SMZ and range-wide; 3) evaluate the probability of persistence of sage-grouse populations; and 4) validate forecasts of future sage-grouse population abundance critical to estimating probability of persistence. We then examine these findings for evidence of stabilizing or increasing populations that could be attributed to recent conservation programs.

Methods

We obtained lek counts from 2007 to 2013 from each state fish and game agency except Colorado to reconstruct the sage-grouse populations for 6 additional years and use these estimates of the minimum number of males attending leks to model population changes and project probabilities of persistence for each population, SMZ population and the entire metapopulation using an analogous approach to that presented in Garton et al. (2011) and in a similar analysis for Lesser Prairie Chickens (Garton et al. in press). All states except Colorado contributed data on lek surveys that were combined with earlier data (Garton, et al. 2011:293) yielding a total of 89,749 surveys conducted from 1965 to 2013 at 10,060 individual leks. Detailed descriptions of each population and SMZ are provided in Garton et al. 2011.

Population Reconstruction

Leks surveyed in previous years (1965-2007) as well as leks added to the counts or discovered since 2007 were used to reconstruct an index of population abundance for each population (Fig. 1) and SMZ population ($N(t)$) based on the maximum count of males out of 3 or more surveys at each lek. The population index was estimated from the total number of males counted and the associated standard error from mean counts in 2007 to 2013, finite rates of change ($\lambda(t)$) and relative sizes of the previous years' populations ($\theta(t)$) in each pair of years using ratio estimators (Garton et al. 2011:301) to extend earlier estimates from 1965 to 2013. Only repeated counts of leks from consecutive years were included in the estimates to insure that they produce unbiased estimates of population size and rates of change. New leks added to the surveys or missed leks were included in estimation once they had been counted in successive years. New leks substantially increased the precision of the most recent estimates of minimum male abundance because of a 50% increase in the number of leks counted in most areas over the last 10 years of surveys. Confidence intervals for the reconstructed populations were calculated from the variance of mean lek counts in 2013 combined with the variances of successive ratios of previous year to current year abundance ($\theta(t)$) back to the year in question as in Garton et al. (2011:302). Thus we began at 2013 and reconstructed population sizes for each population and SMZ back to the earliest lek counts available to us, typically 1965. Finite rates of change ($\lambda(t)$) were transformed to instantaneous rates of change ($r(t)=\ln\lambda(t)$) to model population growth. These estimates provided an index of population abundance from 1965-2013 for modeling changes in population, population projections, and identifying the probability of the species persistence.

Modeling Population Growth

We fit the same suite of 26 stochastic population growth models as described by Garton et al. (2011:302) to the time series of reconstructed minimum male population indices for each SMZ and population. The first 2 models are a more efficient and realistic version of the classic trend models (WAFWA 2008) assuming no density dependence in the rates of population change but either a single trend through time portraying exponential growth with process error (EGPE; Dennis et al. 1991) or exponential growth with differing mean rates of change between two time periods (period 1 = 1967–1987, period 0 = 1987–2013). We also fit density-dependent models of annual rates of change based on either Ricker-type density dependence in population growth (Dennis and Taper 1994) in which rates of change decline in proportion to abundance, or Gompertz-type density dependence in population growth (Dennis et al. 2006) in which rates of change decline logarithmically in proportion to abundance. Because of the apparent cyclic pattern of population growth observed in come populations and management zones (Rich 1985, Garton et al. 2011) we incorporated either 0,1 or 2 year time lags (Δ)into the density dependent Ricker and Gompertz models. To portray the apparent difference in growth patterns through time as either a difference between the 2 time periods identified above or as a continuously changing carrying capacity, each density dependent model was combined with a period effect (period, as described above), and a time trend in population carrying capacity (year) or both (Garton et al. 2011:302). Letting $N(t)$ be the observed population index at time t ,$Y(t)$ = log[$N(t)$], and the annual growth rate $r(t) = Y(t+1) - Y(t)$. The global stochastic model incorporating Ricker-type density dependence was

$$r(t) = a + b \times N(t-\Delta) + c \times Year + d \times Period + E(t), \qquad (1)$$

and the analogous model for Gompertz-type density dependence was

$$r(t) = a + b \times \ln\left(N(t-\Delta)\right) + c \times Year + d \times Period + E(t) \qquad (2)$$

where $Y(t) = \log[N(t)]$, the annual growth rate $r(t) = Y(t+1) - Y(t)$.

The global statistical model incorporated a difference in time periods by setting Period = 1 if Year = 1965 – 1996 and Period = 0 if Year = 1997 – 2013. *E*(t) represented environmental (i.e., process) variation in realized growth rates and was a normally distributed random deviate with mean = 0 and variance = σ^2. These models yielded five parameters (i.e., *a, b, c, d,* and σ^2) that were estimated via maximum likelihood using the indices to past abundance data estimated from the population reconstruction.

The only difference between the Ricker and Gompertz models is that the Ricker assumes growth rates are a linear function of population size and the Gompertz assumes growth rates are a linear function of the natural log of population size. Density dependent models such as Gompertz and Ricker provide an objective approach to estimate a carrying capacity or quasi-equilibrium (hereafter carrying capacity), which is defined as the population size at which the growth rate is 0. This carrying capacity represents a turning point in abundance below which population size tends to increase and above which population size tends to decrease. Adding period or year effects to these density dependent models evaluate the possibility that carrying capacity varied between the early time period and more recently or that it has changed through the years or both. This set of 24 density dependent models produce an efficient approach to evaluate and estimate 2 types of density dependence (arithmetic vs logarithmic for Ricker vs Gompertz) with 3 lags (0, 1 or 2 years) with potential differences in periods of time (2 periods) with constant or continuously changing carrying capacities (changing or constant, i.e. year or no year effect) yielding 2 by 3 by 2 by 2 combinations or 24 total density dependent models that we would hypothesize might best describe the observed reconstructed population abundance indices through time. Note that the 2 density independent models appear superficially similar to classic trend models obtained by simply converting reconstructed annual abundance indices to logarithms and regressing log abundance on year to “fit a trend line” through the data or as done by WAFWA (2008) fitting separate trend lines to the 2 time periods but at the conceptual level they differ fundamentally. Fitting a single or 2 trend lines is far less efficient (Humbert et al. 2009) and falsely treats error around the regression line as errors in observation, while our approach to estimating trend estimates logarithmic rates of change *r(t)* in each year and then estimates the average or an average for each time period as an efficient estimator of trend, treating errors in the estimates as estimates of process error rather than observation error. Estimating process error in this way provides a straight-forward approach to forecast future abundance incorporating process error (see below) whereas observation error estimated by regression is not useful for forecasting future patterns of abundance.

Parameter Estimation

To each set of observed abundance data, we fit these 26 models using general linear mixed models in the statistical computing program R (R Development Core Team 2014) and mixed procedure of Program SAS (SAS Institute 2003) in the same manner as applied earlier to sage-grouse (Garton et al. 2011:303 eq. 15.10) and applied to Lesser Prairie Chicken (*Tympanuchus pallidicinctus*, Garton et al. in press). These stochastic growth models treat annual rates of change (r_t) as mixed effects of fixed effects (year and period) and random effects (reconstructed population index with or without log transformation and time lags). Residual annual rates of change (r_t) were consistently described well by a normal distribution. We used Akaike's Information Criteria corrected for small sample size (AICc) to rank the relative performance (i.e., predictive ability) of each model (Burnham and Anderson 2002). Likewise, we followed Akaike (1973,), Buckland et al. (1997) and Burnham and Anderson (2002:75) in calculating AICc weights (w_i), which we treated as relative likelihoods for a model given the data

$$w_i = \frac{\exp(-0.5 \times \Delta_i)}{\sum_{i=1}^{R} \exp(-0.5 \times \Delta_i)} \tag{3}$$

where Δi was the difference between the AICc for model i and the lowest AICc of all R models. For a given analysis unit, we report a 95% confidence set of models based on the best model using the sum of model weights ≥0.95 (Burnham and Anderson 2002). This approach reduced the number of models reported for all analysis units to those models with some potential of explaining the data but did not necessarily drop all models with ΔAICc less than 2 or 3. All models and resulting parameter estimates are reported in Appendices 1 and 2.

We used this same approach based on maximum likelihood estimation of general linear mixed models to estimate a weighted mean carrying capacity for each population where weights were based on Akaike weights defined above. We combined SMZ population estimates into a range-wide estimate by treating SMZ populations as strata within a stratified random population estimate of range-wide abundance and carrying capacity. From these base models, several plausible scenarios for population growth can be realized. Models involving time trends (+ Year) and period differences (+ period) can be interpreted as inferring that the carrying capacity is changing through time (i.e., negative slopes imply declines through time) or differs between time periods. For example, the parameter estimates from the Ricker model with a time trend (Year) and period effect (Period) can be used to estimate a carrying capacity as follows:

$$\hat{K} = -\hat{b}^{-1}(\hat{a} + \hat{c}Year + \hat{d}Period) \tag{4}$$

The hat (^) notation over a parameter indicates this value was the maximum likelihood estimate for that parameter when fit to past abundance data. When parameters *b* and *c* are set to 0, these models reduce to the EGPE model (Dennis et al. 1991) and including Period simply allows for differing carrying capacities between the two time periods. All forecasts assume that period effects estimated for the final time period and future year effects continue into the future at constant annual rates of change.

Stochastic population projections

For each population, we used parametric bootstraps in SAS and R by projecting 4,000 replicate abundance trajectories for 30 and 100 years post 2013 using

$$N(t+1) = N(t) + e^{\hat{r}(t)} \tag{5}$$

where $\hat{r}(t)$ was the stochastic growth rate calculated using maximum likelihood parameter estimates for the given model. For example, to project based on the Ricker model with no time lag, a time trend in carrying capacity and a difference between periods, we used

$$N(t+1) = N(t) \times e^{\hat{a} + \hat{b}N(t) + \hat{c}Year + \hat{d}Period + E(t)} \tag{6}$$

where $N(0)$, the initial abundance for the projections, was the final observed population size index (i.e., male sage-grouse counted in 2013), Period = 0 indicating that future change (growth or decline) would be analogous to what occurred from 1987 to 2013 and $E(t)$ was a random deviate drawn from a normal distribution with mean 0 and standard deviation equal to $\hat{\sigma}$ (square root of maximum likelihood estimate of mean squared error remaining from mixed model). These parametric bootstraps (replicate stochastic time series) were then used to calculate the probability that the population would decline below a quasi-extinction threshold corresponding to minimum counts of 20 and 200 males for comparison to earlier estimates (Garton et al. 2011) or 77 and 767 males at leks (effective population sizes of 50 and 500 of Franklin (1980) and Soule (1980); see next paragraph for details). Probability of quasi-extinction was the proportion of replications in which population abundance fell below the quasi-extinction threshold at some point during the time horizon (30 or 100 years).

We calculated thresholds for estimation of probability of persistence in two different manners for this analysis. First, for comparison to earlier bootstraps of probability of persistence we used the same thresholds of quasi-extinction of 20 and 200 males representing breeding lek attendance of 50 and 500 sage-grouse (Garton et al. 2011:304). Secondly, we estimated persistence defined as probability of falling below effective population size (N_e) of 50 and 500 as proposed by Franklin (1980) and Soule (1980), respectively. We used the average of three independent approaches to estimating breeding sex ratio applied to Sewall Wright's (1938) estimator of effective population size:

$$N_e = \frac{1}{\frac{1}{N_m} + \frac{1}{N_f}} \tag{7}$$

where N_m = number of males successfully breeding and N_f = female breeders. Patterson's (1952) historic work in Wyoming suggested that sex ratio at leks is 2.5 adult plus yearling females per male producing an estimate of 70 males counted at leks corresponding to an effective population size of 50 or 699 males for N_e of 500. Aldridge (2001) estimated N_e of 88 for sage-grouse in Alberta based on estimates of breeding success applied to his counts of 140 males and 280 females attending 8 leks. This suggests a count of 79 males required for an effective population size of 50 and 795 for N_e of 500. Schroeder et al. (1999) reviewed banding data on 3671 females and 5468 males banded in Colorado, Idaho and Wyoming indicating average annual survival rates of yearlings and adults combined of 61.7% for females and 49.2% for males. Applying these average rates in a simple lifetable for yearlings and adults yields an estimate of 1.64 females per male in the populations of breeding age sage-grouse. Using Wright's formula, this sex ratio implies 80 males are required at leks for an effective population size of 50 and 804 males for an effective population size of 500. Averaging these 3 independent estimates of effective population size yields thresholds of counts of 77 males at leks required for an effective population size of 50 and 767 for N_e of 500.

Based on our comparison of AICc values, most populations had >1 model that could be considered a competing best model by scoring within the 95% set; this generally meant ΔAICc < 3. Therefore, to incorporate model selection uncertainty into forecasts of population viability, we projected future population abundances using each of the 26 models and used model averaging (Burnham and Anderson 2002:159) to generate an overall (i.e., based on all fitted models) estimate of the probability of quasi-extinction. Generally, a “model averaged” prediction can be obtained by calculating the predicted value of a parameter of interest (e.g., probability of quasi-extinction) for each model and taking a weighted average of the predictions where the weights are the relative likelihoods of each model,

$$\hat{\Pr}(Extinction) = \sum_{i=1}^{R} \left\langle \hat{\Pr}(Extinction \middle| Model_i \right\rangle \times w_i) \tag{8}$$

Probability of extinction under a particular model is conditional on that model and its maximum likelihood parameter estimates. To assess the precision of model averaged probabilities of quasi-extinction, we calculated a weighted variance for these probabilities of extinction (Krebs 1999:276) similar to the variance of a mean for grouped data (Remington and Schork 1970:46)

$$V\hat{a}r\left[\hat{\Pr}(Extinction)\right] = \sum_{i=1}^{R} w_i^2 \times [\hat{\Pr}(Extinction) - \hat{\Pr}(Extinction \mid Model_i)]^2 \tag{9}$$

Metapopulation Analyses

We analyzed viability of the metapopulation of sage-grouse across all 6 management zones similarly to the analysis for individual SMZs with three exceptions. First, instead of basing population projections on all 26 models, we used only the highest ranked AICc model across all 6 SMZ populations, Gompertz density dependent models with one year time lag and declining trend in carrying capacity through time. Second, the metapopulation model required estimated dispersal rates among SMZs. Movements were modeled using the same approach developed in earlier work (Garton et al. 2011:367) with the modification that Colorado Parks and Wildlife’s failure to participate required dropping those potential movements and connections. Lastly, correlated dynamics among SMZs were modeled by including a covariance in the random deviates used to portray environmental stochasticity.

Specifically, the metapopulation was projected through time using

$$N_{Meta}(t+1) = \sum_{j=1}^{7} N_j(t+1) \tag{10}$$

where *Nj* is the abundance of SMZj. Abundance of each SMZ was projected using

$$N_j(t+1) = N_j(t) \times e^{r_j(t)} + \sum_{i=1 \neq j}^{7} N_i(t) \times D_{ij} - \sum_{i=1 \neq j}^{7} N_j(t) \times D_{ji} \tag{11}$$

where *Dij* is the dispersal rate between SMZ i and j. We followed the approach developed by Knick and Hanser (2011) to estimate dispersal rates between populations within SMZs. The probability of connectivity between every pair of leks was estimated using graph theory, based on distance between known leks, the difference in size between adjacent leks, and the product of all probable steps (dispersal limited to 27 km) between the pair of leks (Knick and Hanser 2011). We expressed the estimated number of probable connective links between leks in adjacent SMZs, based on graph theory, as a proportion of all the links shown between any pair of SMZs

(N = 112). These proportions were standardized to an estimated maximum dispersal rate at a distance of 27 km of 0.05 (Knick and Hanser, 2011). The random deviate, *Ej(t)*, for the growth rate of the jth SMZ, $r_j(t)$, was drawn from a multivariate normal distribution with mean = 0 and the six by six variance/covariance matrix estimated from past abundance trajectories. We obtained estimates of covariance by correlating the residuals of the information-theoretic best model for each management zone pair. We used a program similar to the SAS and R routines performing parametric bootstraps in SAS for metapopulation projections.

Data Considerations and Limitations

A key issue in analyzing lek data concerns the magnitude of sampling error in sage-grouse lek counts as sampling error could inflate estimates of process error leading to stochastic forecasts of future population viability that are excessively conservative. We evaluated this question by analyzing each reconstructed population time series using an approach that simultaneously estimates observation and process error (Dennis et al. 2006) and found that the population reconstruction time series provide unbiased estimates of process error just as they did for sage-grouse and for Lesser Prairie Chicken in earlier analyses (Garton et al. 2011, Garton et al. in press) with sampling error from combining counts at tens to hundreds of leks approaching 0. Only 3 small populations with limited numbers of leks indicated a non-zero value for observation error and those were exceedingly small (σ^2<0.002). Thus, we were able to take the same approach applied successfully to sage-grouse earlier (Garton et al. 2011) of estimating parameters and likelihoods for models including observation error within a single error term combining both process (stochastic environmental and demographic) error and sampling error. Consequently, forecasts from these models of probability of persistence will be slightly conservative, implying that probability of persistence is at least as large as our estimates or slightly larger.

All US states supporting populations of sage-grouse (Fig. 1) provided results of lek surveys they conducted except Colorado. Colorado Parks and Wildlife denied requests for results of lek counts (email from Jeffrey M. Ver Steeg, Assistant Director Research, Policy and Planning, Colorado Parks and Wildlife, dated 19 January 2015) making it necessary to substitute the best reasonable estimate of current numbers of breeding males counted at leks in 2013 in Colorado for the observed counts. We used a standard approach for missing values by replacing them with the best available estimate closest in time to the missing value. For 307 leks in Colorado included in the Wyoming Basin population and Wyoming Basin SMZ, we used the last available abundance of sage-grouse counted at these 307 leks: 4103 males were counted in Colorado at 213 of the leks in 2007 (Garton et al. 2011:35). The final estimate for abundance of males in this region in 2013 was then corrected to include both the total number of males observed in surveys in Wyoming and Utah in 2013 plus this estimated number of males present on the Colorado leks not reported, 4103 in 2007. This corrected estimate of male attendance at surveyed leks in 2013 was used as the base survey for population reconstruction back to 2007 and beyond to the earliest surveys in 1965 for Wyoming Basins population and SMZ II. For the Colorado Plateau (SMZ VII) we noticed that the earlier analysis of lek data (Garton et al. 2011:363) identified 2 best models of stochastic growth with no time trend, i.e., stochastic density dependent Ricker and

Gompertz models. Therefore we used an average of the predicted stochastic carrying capacity from each of these models and the last population estimate in 2007 at 73 leks as a best estimate of the missing abundance for this SMZ in 2013.

Results

Great Plains Management Zone

Dakotas Population

Sampling effort for leks in this population occupying western portions of North and South Dakota and small parts of southeastern Montana and northeastern Wyoming increased 16.5%. The average number of leks counted per year from 2008-2013 was 83 leks, up from 56 leks counted per year on average from 2000-2007. The estimated minimum population size was 311 males (SE = 55) which represented a 72% decline from the reconstructed estimate of 1,112 males (SE = 307) based on counts at 85 leks in 2007. The last 6 years showed a continuous (Fig. 2a) decline to reach abundances lower than ever observed before and approximately 16% of average values of about 1,917 males counted in the 1970s and 1980s (Fig. 2a). The best model characterizing the dynamics of this population was a Gompertz model ($r_t = 35.8948 - 0.3942 \ln(N_t) - 0.017$ year, $r^2 = 0.189$) with a declining year trend of 1.7% per year which successfully portrayed 19% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 32%. Quasi-equilibriums were estimated at 280 males (SE 79.2) in 2013, 97 males (SE 30.6) in 30 years and 45 males (SE 17.7) in 2113. Parametric bootstraps imply that the minimum count of males has a 21.5% (SE 7.7%) chance of declining below 20 males in 30 years, lower than estimated with data through 2007 (29%) but not significantly lower. Model weighted probabilities of declining below effective population sizes of 50 (35.4%, SE 7.4%) in 30 and 100 years (72.5%, SE 8.5%) were higher.

Northern Montana Population

Sampling effort for leks in this population occupying parts of north-central Montana, southeast Alberta, and southwest Saskatchewan declined 11.4 %. This is partially due to Canadian counts included in the 2007 data and analysis but excluded from our current data set. If Canadian counts are removed, sampling effort increased by 6.2%. The average number of leks counted per year from 2008-2013 was 138 leks per year, down from 162 leks counted per year on average from 2000-2007. The estimated minimum population size was 1,667 males (SE = 165) which represented a 54% decline from the reconstructed estimate of 3,615 males (SE = 573) based on counts at 175 leks in 2007. The last 6 years showed a continuous (Fig. 2b) decline to reach abundances as low as those in the 1970s and early 1980s of approximately 1,600 males. Current estimates are about 40% lower than the average counts shown from 1984-2007, which showed a slight increase in abundance males over the preceding 10 years (Fig. 2b). The best model for the dynamics of this population was a Gompertz model with a one year time-lag and a period effect ($r_t = 2.8591 - 0.3347 \ln(N_{t-1}) - 0.3066$ period, $r^2 = 0.352$) and showed a probability of being the correct model of 36%. Quasi-equilibrium estimated at 4353 (SE 1,394) in 2013, 3,714 (SE 1,122) in 30 years and 3,380 (SE 992) in 2113. Parametric bootstraps imply that the minimum count of males has a 2.7% (SE 2.1%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (5.6%, SE 4.4%) in 30 and 100 years (7.2%, SE 5.1%) are all quite low.

Powder River Basin Population

Sampling effort for leks in this population, occupying parts of southeastern Montana and northeastern Wyoming, remained fairly steady between 2007 and 2013, with only a 2.1% increase in the number of leks counted. The average number of leks counted per year, however, from 2008-2013 was 395 leks per year, up from 239 leks counted per year on average from 2000-2007, a 65% increase between the 2 periods. The estimated minimum population size was 1651 males (SE = 155) which represented a 76% decline from the reconstructed estimate of 6804 males (SE = 919) based on counts at 384 leks in 2007. The last 6 years showed a continuous (Fig. 2c) decline to reach abundances lower than ever observed before and approximately 4% of average values close to 38,500 males counted in the 70s and 80s. The best model for the dynamics of this population was a Gompertz model with a one-year time lag and an effect of year ($r_t = 67.1015 - 0.396 \ln(N_{t-1}) - 0.0318$ year, $r^2 = 0.317$) with a declining year trend of 0.3% per year which successfully portrayed 32% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 63%. Quasi-equilibriums were estimated about 2,273 (SE 618) in 2013, 240 (SE 78) in 30 years and 36 (SE 24) in 2113. Parametric bootstraps imply that the minimum count of males has a 2.9% (SE 2.3%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (98.7%, SE 2.2%) in 30 and 100 years (98.8%, SE 2.1%) suggest that is fairly certain to happen.

Yellowstone Watershed Population

Sampling effort for leks in this population occupying southeastern Montana and northeastern Wyoming increased 83% from 327 leks in 2007 to 625 leks counted in 2013. The estimated minimum population size was 3045 males (SE = 106) which represented a 29% decline from the reconstructed estimate of 8747 males (SE = 949) based on counts at 327 leks in 2007. The last 6 years showed a continuous (Fig. 2d) decline to reach abundances lower than ever observed before and approximately one quarter of average values close to 12,000 males estimated in the 70s and 80s. The best model for the dynamics of this population was a Ricker model ($r_t = 32.4125 - 0.00006027 N_t - 0.016$ year, $r^2 = 0.364$) with a declining year trend of 1.6% per year as in earlier analyses (Garton et al. 2011:313) which successfully portrayed 36% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 68%. An estimate of carrying capacity for the population in 2013 is 3,087 (SE =788) but the estimate for 2043 indicates a decline to 241 (SE =172) and to 136 (SE =97) in 2113. Compared to results in 2007 when there was negligible chance of the population count falling below 20 males at leks in the short term (30 years, Garton et al. 2011:313) declines during the last 6 years have increased the probability to 15.6% (SE = 2.1%) with the probability of declining below effective population size of 50 now above half (54.5 % with SE = 7.2%). Long term probabilities (in 100 years) of declining below counts of either 20 or 200 males attending leks or effective population sizes of 50 or 500 all exceed 89% (Table 6).

Great Plains Management Zone Comprehensive Analysis

Biologists dramatically increased their efforts (33% increase) to count sage-grouse leks from 2007 (957 leks) to 2013 (1,271 leks) producing a reconstructed population estimate of the minimum number of male sage-grouse of 20,016 (SE = 1462) in 2007 which was almost 50% larger than the estimate obtained from counting fewer leks earlier (Garton et al. 2011:314). In spite of this dramatic increase in effort, the estimated minimum male numbers attending leks fell by two-thirds to 6,674 (SE = 312) in the 6-year interval to 2013. This population is continuing its downward trajectory (Figure 2e) with an irregular pattern of peaks separated by periods varying in length from 3 to 16 years. As before (Garton et al. 2011:315) the 4 best models all include Gompertz and Ricker models with declining time trends with and without 1-year time lags that are not significantly better than each other by likelihood ratio tests (Appendix 1). The very top model by information criteria was a Ricker with decreasing time trend ((r_t = 30.2053 – 0.0.00001673 N_t – 0.015 year, $\sigma = 0.148$, $r^2 = 0.239$) implying a 1.5% decrease in carrying capacity each year. Across the best models carrying capacity was estimated as a minimum count of males of 3798 (SE 1378) currently, declining to 1,444 (SE 546) in 2043 and further to 481 (SE 193) in 100 years. With 6 additional years of declining counts at leks the estimates of carrying capacity for this management zone have decreased by half. Forecasts of probability of persistence suggest likelihood of falling below counts of 20 or 200 males have risen to almost 50% (Table 6) while long term probability of falling below effective population sizes of 50 or 500 are now in the range 55% (SE 9.8%) to 93% (SE 5.1%).

Wyoming Basin Management Zone

Wyoming Basin Population

Sampling effort to count leks in this population occupying much of Wyoming, part of southern Montana, northeast Utah and northern Colorado increased by 5% excluding Colorado data. The estimated population size was 15,767 males (SE = 644) in 2013 based on counts at 1158 leks which represented a 63% decline from the reconstructed estimate of 43,040 males (SE = 2727) based on counts at 1,106 leks in 2007, again excluding Colorado. The last 6 years showed a continuous (Fig. 3c) decline to reach abundances lower than ever observed before and approximately 25% of average values approximating 63,000 males counted in the 70s and 80s. The best model for the dynamics of this population was a Gompertz model with a one year time lag and a year effect (r_t = 23.619 – 0.2946 ln(N_{t-1})– 0.0103 year, $r^2 = 0.246$) indicating a declining trend of 1.0% per year which successfully portrayed 25% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 36%. Quasi-equilibriums were estimated about 16,078 (SE 4,982) in 2013, 6,158 (SE 2,020) in 30 years and 2,209 (SE 913) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.1% (SE 0.06%) chance of declining below 20 males in 30 years but model weighted probabilities of declining below effective population sizes of 50 (4.7%, SE 1.9%) in 30 and 100 years (21.0%, SE 8.1%) are somewhat higher though still well below 50%.

Wyoming Basin Management Zone Comprehensive Analysis

This enormous population constituting a minimum of 54,282 (SE 2636) males in 2007 has dropped precipitously (63% decline) through 2013 to a minimum of 20,006 males (SE 646) counted at 1258 leks if we replace the missing surveys of Colorado leks with the last count available to us in 2007 of 4103 males counted at 213 leks. Alternately, simply ignoring the missing lek surveys from Colorado produces an estimate for this SMZ of 43,149 males declining 63% to 15,903 males in 2013. Sampling effort appeared to decrease by 5.2% between 2007 and 2013 due to failure to report by Colorado, but excluding the 213 Colorado leks counted in 2007 reveals effort in the other states actually increased by 13%. The average number of leks counted from 2007-2013 was 1,161 leks per year a decrease from 1,321 from 2000-2007, again due to failure to report by Colorado. Excluding the 307 total Colorado leks suggests increased effort of 14% in average number of leks surveyed in the recent time interval. The last 6 years showed a continuous (Fig. 3d) decline to reach abundances lower than ever observed before and approximately 33% of average values close to 62,368 males counted in the 70s and 80s. From a reconstructed minimum male population estimate approaching 175,000 birds in the late 1960s the last minimum male population estimate has fallen by an order of magnitude (Fig. 3d). The 10-year interval between peaks in this population appears to have shortened to an 8 or 9 year interval and the low estimate in 2013 is approximately 2000 males below the previous low in the cycle in 1996 though this difference is not statistically significant because of the large SE (4,798) of that earlier low estimate in the cycle.

The best stochastic growth model for this management zone population is a Gompertz model with one year time lag and a carrying capacity declining at approximately 1% per year (r_t = 23.58 – 0.298 ln(N_{t-1}) – 0.0102 year, σ = 0.148, r^2 = 0.247). This model has a relative likelihood of 37% followed closely by the comparable Ricker model with declining year trend in carrying capacity. The best stochastic growth models imply that the population of sage-grouse will fluctuate around the current carrying capacity of 18,899 (SE 5518) which will decline to 8,285 (SE 2,619) in 2043 and 2,798 (SE 1,147) in 2113 if this yearly rate of decline persists. Parametric bootstraps forecasting the likelihood of this management zone population falling below 20 or 200 males attending leks are less than 25% (Table 7) but chances for declines below effective population sizes of 50 and 500 in 100 years have grown to 22.1% (SE 8.2%) and 65.3% (SE 7.6%) respectively. These probabilities of extinction are two to three times as large as they were at the end of 2007.

Southern Great Basin Management Zone

Mono Lake, California-Nevada, Population

Sampling effort for leks in this small population straddling the California-Nevada border increased by 138% to 50 leks in 2013. The average number of leks counted increased to 46 leks per year, up from 24 leks per year from 2000-2007. The estimated minimum population size was 543 males (SE = 157) which represented a 25% increase from the reconstructed estimate of 435 males (SE = 266) based on counts at 21 leks in 2007. The last 6 years showed an increase until 2013 (Fig. 4a) to reach abundances approximately 83% larger than average values close to 300 males counted in the 1970s and 1980s. The best model for the dynamics of this population was the Gompertz model (r_t = 3.1176 – 0.5521 ln(N_t), r^2 = 0.267) and showed a probability of being the correct model of 37%. Quasi-equilibriums reached about 330 (SE 120) in 2013, 576 (SE 216) in 30 years and 4,059(SE 1,678) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.09% (SE 0.25%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (7.7%, SE 1.6%) in 30 and 100 years (21.5%, SE 4.3%) are low.

South Mono Lake, California, Population

Sampling effort for leks in this small population in eastern California increased 16.7% from 12 leks in 2007 to 14 leks in 2013. The estimated minimum population size was 264 males (SE = 102) which represented a 6% decline from the reconstructed estimate of 282 males (SE = 161) based on counts at 12 leks in 2007. The last 6 years showed slight overall (Fig. 4b) decline to reach abundances approximately equal with average values close to 270 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model ($r_t = 2.491 – 0.4528 \ln(N_t)$, $r^2 = 0.228$) and garnered a 38% probability of being the correct model. Quasi-equilibriums reached about 258 (SE 84.5) in 2013, 275 (SE 91.7) in 30 years and 336 (SE 118.3) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.26% (SE 0.42%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (7.9%, SE 2.1%) in 30 and 100 years (21.3%, SE 3.9%) are fairly low.

Northeast Interior Utah Population

Sampling effort for leks in this population decreased 18% from 32 leks in 2007 to 26 leks in 2013. The average number of leks counted from 2007-2013 was 27 leks per year an increase from 25 from 2000-2007. The estimated minimum population size was 241 males (SE = 71) which represented a 42% decline from the reconstructed estimate of 412 males (SE = 192) based on counts at 32 leks in 2007. The last 6 years showed a continuous (Fig. 4c) decline to reach abundances 50% of average values close to 486 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Ricker model with period effect ($r_t = 0.2812 – 0.0012(N_t) + 0.3498$ period, $r^2 = 0.222$) and showed a probability of being the correct model of 19%. Quasi-equilibriums reached about 241 (SE 67) in 2013, 304 (SE 85) in 30 years and 705 (SE 204) in 2113. Parametric bootstraps imply that the minimum count of males has a 1.4% (SE 1.0%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (13.9%, SE 4.5%) in 30 and 100 years (27.5%, SE 6.7%) are fairly low.

Sanpete-Emery Counties, Utah, Population

From 2007 to 2013, only 2 to 3 leks were counted, consistent with counts since approximately 1987. The estimated minimum population size was 48 males (SE = 19) which represented a 100% increase from the reconstructed estimate of 24 males (SE = 26) based on counts at 2 leks in 2007. The last 6 years showed a slight increase (Fig. 4d) for this small, isolated population.

South-Central Utah Population

Sampling effort for leks in this population decreased 18% from 51 leks in 2007 to 42 leks in 2013. The average number of leks counted from 2007-2013 was 51 leks per year, an increase from 38 from 2000-2007. The estimated minimum population size in 2013 was 737 males (SE = 208) which represented a 51% decline from the reconstructed estimate of 1501 males (SE = 570) based on counts at 51 leks in 2007. The last 6 years showed an overall (Fig. 4e) decline to reach abundances approximately 53% of average values close to 1382 males counted in the 1970s and 1980s. The best model characterizing the dynamics of this population was a Gompertz model ($r_t = 2.2129 - 0.3196 \ln(N_t)$, $r^2 = 0.186$) and garnered a probability of being the correct model of 19%. Quasi-equilibriums reached about 944 (SE 248.1) in 2013, 802 (SE 209.4) in 30 years and 680 (SE 177.2) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.11% (SE 0.16%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (0.9%, SE 0.7%) in 30 and 100 years (18.7%, SE 7.6%) are low.

Summit-Morgan Counties, Utah, Population

Sampling effort for leks in this population decreased 14% from 7 leks in 2007 to 6 leks in 2013. The average number of leks counted from 2007-2013 was 8 leks per year, a decrease from 9 from 2000-2007. The estimated minimum population size was 65 males (SE = 19) which represented a 25% decline from the reconstructed estimate of 87 males (SE = 67) based on counts at 7 leks in 2007. The last 6 years showed a decline (Fig. 4f) to reach abundances approximately 85% of average values close to 77 males counted in the 1970s and 1980s.

Toole-Juab Counties, Utah, Population

Sampling effort for leks in this population increased 29% from 7 leks in 2007 to 9 leks in 2013. The average number of leks counted from 2007-2013 was 9 leks per year an increase from 6 from 2000-2007. The estimated minimum population size was 57 males (SE = 18) which represented a 78% decline from the reconstructed estimate of 257 males (SE = 237) based on counts at 7 leks in 2007. The last 6 years showed a decline (Fig. 4g) to reach abundances approximately 23% of average values close to 244 males estimated in the 2000.

Southern Great Basin Population

Sampling effort for leks in this population decreased in 2013 by 12.1% to 269 leks, down from 306 in 2007. Since 2007 however, the average number of leks counted per year increased from 233 leks per year from 2000-2007 to 281 leks per year from 2008-2013 and overall showed a greater sampling effort. The estimated minimum population size was 3,388 males (SE = 259) which represented a 33% decline from the reconstructed estimate of 5,084 males (SE = 691) based on counts at 306 leks in 2007. The last 6 years showed an overall (Fig. 4h) decline to reach abundances approximately 43% of average values close to 7,855 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model with a 2-year time lag and a year effect ($r_t = 28.088 - 0.4317\ln(N_{t-2}) - 0.0123$ year, $r^2 = 0.357$) with a declining year trend of 1.2% per year which successfully portrayed 36% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 50%. Quasi-equilibriums reached about 2,702 (SE 961) in 2013, 1,417 (SE 551) in 30 years and 543

(SE 267) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.14% (SE 0.16%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 are 1.3% (SE =1.5%) and 10.4% (SE =3.5%) in 30 and 100 years.

Southern Great Basin Management Zone Comprehensive Analysis

The population estimate for the entire Southern Great Basin Management Zone declined from a peak in the 6-9 year cycle exceeding 15,000 males in 1970 to a low point of less than 4,000 males in mid-1990s. The 33% decline from an estimated minimum number of males of 8202 (SE 971) in 2007 to 5485 males (SE 382) in 2013 exemplifies the observed declines over the last 2 decades (Fig. 4i). Sampling effort fell 4.0% in that same period. The best stochastic growth model of dynamics of this management zone population was a Gompertz model of density dependence with a 1-year time lag and declining carrying capacity through time ($r_t = 15.2114 - 0.3777 \ln(N_{t-1}) - 0.006$ year, $\sigma = 0.13$, $r^2 = 0.34$). This best model implies that the carrying capacity for sage-grouse in the Southern Great Basin Management Zone is declining very slowly at 0.6% per year. Weighted mean estimates of carrying capacity for the management zone across all 24 density dependent models is 4862 (SE 1514) for 2013, 3722 (1175) for 2043 and 2649 (SE 875) for 2113. Parametric bootstraps of probability of declining below counts of 20 and 200 males in 30 years are nil (0%) but grow somewhat for declining below effective population sizes of 50 and 500 in100 years (10.0% with SE 6.0% and 25.3% with SE 6.3%).

Snake River Plain Management Zone

Baker, Oregon, Population

Sampling effort for leks in this small population in eastern Oregon increased by 6.3% to 49 leks in 2013. The average number of leks counted per year increased to 21 leks per year from 2008-2013 up from 15 leks per year from 2000-2007. The estimated minimum population size was 49 males (SE = 18) which represented a 64% decline from the reconstructed estimate of 137 males (SE = 92) based on counts at 16 leks in 2007. The last 6 years showed a continuous (Fig. 5a) decline to reach abundances lower than ever observed before and approximately 25% of average values close to 200 males counted from 1993-2007.

Bannack, Montana, Population

The small population in Bannack, Montana, estimated at a minimum of 219 (SE 81) males in 2007 declined 19% to a minimum of 177 (SE 35) males observed at 15 leks in 2013, a 37.5% decline in leks counted since 2007 (Fig. 5b). The best models of the dynamics of this small population were Gompertz models with a combination of Period and Year effects ($r_t = 16.2963 - 0.4031 \ln(N_t) - 0.0071$ year$- 0.1995$ period, $r^2 = 0.212$) indicating a very slow decline at approximately 0.7% per year to a quasi-equilibrium about 146 (SE 40.1) in 2013, 109 (SE 30.2) in 30 years and 86 (SE 24.6) in 2113. Parametric bootstraps imply that the minimum count of males has a 6.6% (SE 4.2%) chance of declining below 20 males in 30 years but is already below 200. Model weighted probabilities of declining below effective population sizes of 50 (37.3%, SE 8.3%) in 30 and 100 years (48%, SE 9.0%) are uncomfortably large while long-term persistence based on probability of declining below an effective population size of 500 is nil.

Red Rocks Lake, Montana, Population

Sampling effort for leks in this small population occupying southwestern Montana just north of the Idaho border decreased by 30% from 30 leks counted in 2007 to 21 leks counted in 2013. The average number of leks counted per year from 2008-2013 was 18 leks per year, down slightly from 20 leks counted per year on average from 2000-2007. The estimated minimum population size was 357 males (SE = 113) which represented a 37% increase from the reconstructed estimate of 260 males (SE = 202) based on counts at 30 leks in 2007 (Fig. 5c). The last 6 years showed an increase (Fig. 5c) to reach abundances approximately 35% larger than average values of 265 males counted in the 1970s and 1980s.

Snake-Salmon-Beaverhead, Idaho, Population

Sampling effort for leks in this population increased by 67.1% to 620 leks up from 321 leks in 2007. The average number of leks counted per year from 2008-2013 was 505 leks, up from 323 leks counted per year on average from 2000-2007. The estimated minimum population size was 6,126 males (SE = 229) which represented a 30% decline from the reconstructed estimate of 8,734 males (SE = 1157) based on counts at 371 leks in 2007 (Fig. 5e). The last 6 years showed a decline (Fig. 5e) to reach abundances approximately 39% of average values of approximately 16,000 males counted in the 70s and 80s. The best model characterizing the dynamics of this population was a Gompertz model with a one-year time lag and a period effect ($r_t = 3.0269 - 0.3423 \ln(N_{t-1}) + 0.2949$ period, $r^2 = 0.371$) and showed a probability of being the correct model of 36%. Estimated quasi-equilibriums reached about 5,727 (SE 1,823) in 2013, 5,074 (SE 1,538) in 30 years and 4,719 (SE 1394) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.36% (SE 0.3%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (3.3%, SE 2.7%) in 30 and 100 years (16.5%, SE 7.4%) are low.

Northern Great Basin Population

Sampling effort for leks in this population occupying portions of Nevada, southeastern Oregon, southwestern Idaho, and Northwestern Utah declined by 9.4% to 951 leks down from 1,008 in 2007. The average number of leks counted per year from 2008-2013 was 951 leks per year, up from 595 leks counted per year on average from 2000-2007. The estimated minimum population size was 6,580 males (SE = 376) which represented a 34% decline from the reconstructed estimate of 9,927 males (SE = 1,144) based on counts at 1,008 leks in 2007. The last 6 years showed a decline (Fig. 5f) to reach abundances lower than ever observed before and approximately 23% of average values close to 28,618 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model with a one-year time lag and a year effect ($r_t = 49.056 - 0.5015 \ln(N_{t-1}) - 0.0222$ year, $r^2 = 0.514$) with a declining year trend of 0.2% per year which successfully portrayed 51% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 77%. Quasi-equilibriums reached about 6,214 (SE 1,565) in 2013, 1,664 (SE 424) in 30 years and 77 (SE 20.3) in 2113. Parametric bootstraps imply that the minimum count of males has a 0.05% (SE 0.4%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (0.06%, SE 0.5%) in 30 and 100 years (83.6%, SE 2.8%) differ dramatically.

Snake River Plain Management Zone Comprehensive Analysis

The estimated minimum number of males attending leks in the Snake River Plain Management Zone declined 31% from 2007 (19,510 SE 1404) to an estimated 13,371 (SE 550) in 2013 (Figure 5h). Sampling effort in this interval increased 9.9% from counting 1480 leks in 2007 to 1,627 leks in 2013 and this increased effort substantially increased the estimated minimum number of males attending leks from the population reconstruction by almost 4,000 males compared to the earlier population estimate (Garton et al. 2011:351). The best stochastic growth model for the reconstructed population was a Gompertz with 1-year time lag and both year and period effects on carrying capacity ($r_t = 25.4738 - 0.4124 \ln(N_{t-1}) - 0.0107\ year + 0.1566\ period$, $\sigma = 0.1319$, $r^2 = 0.448$) which estimated carrying capacities for the management zone declining at 1.07% per year from 13,275 (SE 4,008) in 2013, to 6,420 (SE 2,083) in 2043 and further to 2,330 (SE 1,111) in 100 years.

Northern Great Basin Management Zone

Central Oregon Population

The Central Oregon population of sage-grouse has declined 33% since 2007 to a minimum estimated number of males attending leks of 559 (SE 95) along with a 17% decrease in number of leks counted to 80 down from 97 in 2007. The average number of leks counted per year from 2008-2013 was 86.8 leks per year, down from 96 leks counted per year on average between 2000 and 2007. The last 6 years showed a decline to reach abundances lower than ever observed before and approximately 23% of average values close to 2,424 males counted in the 1970s and 1980s (Fig 6a). This final survey is less than one tenth of the peak estimates for the late 1960s which reflects fairly continuous declines through time. The best models characterizing dynamics of this population were Gompertz density-dependent models with either period or year or both parameters indicating a 1.1% decline per year but the best of these models only described slightly more than 20% of the variation in annual estimates of abundance and suggested a carry-capacity currently less than half of current numbers (146, SE 40). Consequently parametric bootstraps imply a 6.6% (SE 4.2%) probability of falling below male counts of 20 and 100% probability below 200 in the short term. Probabilities of declining below effective population sizes of 50 in the long term climb to 48% (SE 9%) while long-term persistence is unlikely if the population continues this pattern of decline.

Northwest-Interior Nevada Population

Sampling effort for leks in this small, scattered population, occurring in north-central Nevada decreased by 23.1% to 50 leks down from 65 leks counted in 2007. The average number of leks counted per year from 2008-2013 was 30.2 leks per year, down from 40 leks counted per year on average from 2000-2007. The estimated minimum population size was 79 males (SE = 29) which represented a 32% decline from the reconstructed estimate of 117 males (SE = 102) based on counts at 65 leks in 2007. The last 6 years showed a decline (Fig. 6b) to reach abundances lower than ever observed before and approximately 52% of average values close to 153 males counted from 1999-2007 (Fig. 6d). The best model for the dynamics of this population was a Gompertz model (r_t = 4.9614 – 1.0683 ln(N_t), r^2 = 0.70) and showed a probability of being the correct model of 69%. . Parametric bootstraps imply that the minimum count of males has a 100% (SE 0%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (100%, SE 0%) in 30 and 100 years (100%, SE 0%) imply that is certain.

Western Great Basin Population

Sampling effort for leks in this population decreased by 1.7% to 396 leks in 2013 down from 403 leks in 2007. The average number of leks counted per year from 2008-2013 was 330 leks per year, up from 285 leks counted per year on average from 2000-2007. The estimated minimum population size was 1,934 males (SE = 212) which represented a 69% decline from the reconstructed estimate of 6,327 males (SE = 1,345) based on counts at 403 leks in 2007 (Fig. 6d). The last 6 years showed a decline (Fig. 6c) to reach abundances lower than ever observed before and approximately 16% of average values close to 11,765 males counted in the 1970s and 1980s. The best model characterizing the dynamics of this population was a Gompertz model with a one-year time lag and period effect (r_t = 2.5868 – 0.3036 ln(N_{t-1})+ 0.2514 period, r^2 = 0.241) and showed a probability of being the correct model of 44%. Quasi-equilibriums reached about 2,548 (SE 812) in 2013, 701 (SE 228) in 30 years and 40 (SE 14.8) in 2113. Parametric bootstraps imply that the minimum count of males has a 13.1% (SE 6.7%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (13.1%, SE 6.75%) in 30 and 100 years (96.2%, SE 1.1%) are polar opposites.

Northern Great Basin Management Zone Comprehensive Analysis

From an abundance of an estimated 40,000 males attending leks in 1965 this management zone population has shown a continuing decline overlaid on 10-year or longer cycles which extended dramatically in length in the most recent period (Figure 6d). The estimated minimum abundance in 2007 of 7,429 (SE 1,312) males, declined 65% by 2013 to 2,573 (SE 468) males even though sampling effort was close to 500 leks counted in both of those years. The best stochastic growth model for the Great Basin management zone population is again a Gompertz model with 1-year lag and a decreasing trend through time (r_t = 27.4378 – 0.33 ln(N_{t-1}) – 0.0123 year, σ = 0.1947, r^2 = 0.221). Weighted mean estimates of carrying capacity for this management zone suggest that the abundance will fluctuate around 2,796 (SE 835) males in 2013, 1,027 (SE 330) males in 2043 and 382 (SE 152) males in 2113. Parametric bootstraps forecast that chances of declining below male attendance at leks of 20 and 200 in the short term (30 years) are only 9.9% (SE 5.3%) and 13.6% (SE 6.7%) but long term extinction defined as falling below effective population sizes of 50 and 500 are very likely at 72.2% (SE 6.2%) and 92.3% (SE 4.9%).

Columbia Basin Management Zone

Moses Coulee, Washington, Population

Sampling effort for leks in this small population decreased by 46.9% to 17 leks in 2013, down from 32 leks in 2007. The average number of leks counted per year from 2008-2013 was 20.2 leks per year, down from 33 leks counted on average from 2000-2007. The estimated minimum population size was 202 males (SE = 39) which represented a 12% decline from the reconstructed estimate of 230 males (SE = 84) based on counts at 32 leks in 2007. The last 6 years showed a decline (Fig. 7a) to reach abundances approximately 33% of average values of approximately 609 males counted in the 1970s and 1980s. The best model for the dynamics of this population was a Gompertz model with a one-year time lag and a year effect ($r_t = 27.7956 - 0.3647 \ln(N_{t-1}) - 0.0129$ year, $r^2 = 0.199$) with a declining year trend of 1.2% per year which successfully portrayed 20% of the variation in the data from 1965 to 2013 and garnered a probability of being the correct model of 31%. Quasi-equilibriums were about 172 (SE 49.9) in 2013, declining to107 (SE 34.6) in 2043 years and 77 (SE 27.7) in 2113. Parametric bootstraps imply that the minimum count of males has a 7.4% (SE 3.6%) chance of declining below 20 males in 30 years. Model weighted probabilities of declining below effective population sizes of 50 (71.6%, SE 7.8%) in 30 and 100 years (81.0%, SE 6.2%) are both greater than 50%.

Yakima, Washington, Population

Sampling effort for leks in this small population increased by 55% to 17 leks in 2013, up from 11 leks in 2007. The average number of leks counted per year from 2008-2013 was 13 leks per year, up from 10 leks counted per year on average from 2000-2007. The estimated minimum population size was 89 males (SE = 36) in 2013 which represented an 11.7% increase from the reconstructed estimate of 80 males (SE = 50) based on counts at 10 leks in 2007. The last 6 years showed small fluctuations (Fig. 7b) but typical numbers of males attending leks reached abundances lower than ever observed before and approximately 24% of average values close to 350 males counted in the 1970s and 1980s.

Columbia Basin Management Zone Comprehensive Analysis

Estimated numbers of males attending leks in the Columbia Basin management zone were close to 2,000 in 1965 but showed an approximately 10-year cyclic pattern imposed over a continuous decline to the present. From a 2007 reconstructed, male population estimate of 310 (SE 98) the population declined approximately 6% to an estimated 291 (SE 56) males in 2013 (Fig. 7c). Surveying effort fell to 34 leks counted in 2013 compared to 43 counted in 2007. The best stochastic growth model for the Columbia Basin management zone population is again a Gompertz model with 1-year time lag and declining year trend in carrying capacity ($r_t = 27.8921 - 0.3956 \ln(N_{t-1}) - 0.0128$ year, $\sigma = 0.209$, $r^2 = 0.208$). Weighted mean estimates of carrying capacity for this management zone suggest that the abundance will fluctuate around 233 (SE 69.7) males in 2013, 12 (SE 38.9) males in 2043 and 64 (SE 24.2) males in 2113. Parametric bootstraps forecast that chances of declining below male attendance at leks of 20 and 200 in the short term (30 years) are only 11.8% (SE 6.1%) and 85.2% (SE 6.0%) but long term extinction, defined as falling below effective population sizes of 50 and 500 in 100 years are almost certain at 80.2% (SE 7.5%) and 100% (SE 0%).

Colorado Plateau Management Zone

Colorado Plateau Management Zone Comprehensive Analysis

Colorado Parks and Wildlife denied our requests for results of lek counts on 4 separate occasion because of a decision of the leadership team (3 emails and 1 conversation with Kathy Griffin on 1/6/15) making it necessary to substitute the best reasonable estimate of current numbers of breeding males counted at leks in 2013: 244 calculated as average of last count (241 in 2007), estimated carrying capacity from best model (248 from Ricker model, Garton et al. 2011:381) and second best model (241 from Gompertz model, Garton et al. 2011:381) based on earlier studies (Garton et al. 2011:363). This lack of cooperation makes it impossible to provide any improved estimates or discussion of changes from 2007 to 2013.

Range-wide Summary Including All Sage-Grouse Management Zones

Comparing the estimated minimum male population size between 2007 and 2013 from population reconstructions of all evaluated populations showed declines in population size from 6% to 100% except for 4 small populations of less than 500 males which exhibited increases of 2% to 100% (Table 1). The total numbers estimated by summing across all 27 populations with sufficient data to analyze but excluding Colorado leks, suggest a minimum total of 98,740 males breeding in 2007 declined 55% to a total of 44,209 males breeding in 2013 (Table 1) whereas corrected total estimates including Colorado suggest a 56% decline from 109,990 in 2007 to 48,641 in 2013 (Figure 8). Placing the declines during these last 6 years in proper perspective requires looking more broadly at range-wide population changes over the last 5 decades (Fig. 9) which strongly suggests that this last 6-7 years represent the latest downward swing in the cycles of approximately 10-11 year intervals (statistically significant lows in 1965, 1975, 1985, 1996, 2002 and 2013) with the periodic low in 2002 coming 4 years early. The last 3 decades period appear to represent a multi-decadal periodic pattern where relative magnitude of change between highs and lows has decreased during an overall decline until 2013 where lek counts reached their lowest magnitude (48,641 males counted) in 50 years of records. Examination of SMZ population reconstructions reveal fairly, but not perfectly, simultaneous peaks and lows at 9-11 year intervals excepting the missing peak around 2000.

Estimated minimum male sage-grouse attending leks in various SMZs declined from 6% to 67% between 2007 and 2013 with largest declines occurring in the more northern regions excepting the Columbia Basin where numbers were already quite low in 2007(Table 2). Combining estimates across all the regions except Colorado Plateau the range-wide population declined 55% from an estimated 98,603 (SE 3,736) males in 2007 to 44,252 (SE 1,019) males in 2013.

The best stochastic growth model to describe annual changes in sage-grouse populations (Appendix 1) and SMZ populations (Appendix 2) was a stochastic density dependent Gompertz model with 1-year time lag and declining yearly trend in most cases (36% of populations and 66% of SMZ populations). Combining information theoretic measures across SMZs for all 26 models (Table 3) identified this model as significantly better than any of the alternative models (AICc difference > 2.0 indicates significant difference by likelihood ratio test at $\alpha=0.05$, Burnham and Anderson 2002). When these best models are used to forecast present and future carrying capacity of each population (Table 4) and SMZ (Table 5) they estimate that current populations of SMZs exceed carrying capacity by 3,800 males and that future SMZ carrying capacities will decline from approximately 40,000 males to 20,000 in 30 years and 8,000 males in 100 years if current trends portrayed by stochastic growth models hold that far into the future (Table 5).

Validation

Results of a validation test comparing predicted abundances in 2013 (Z_{2013}) to observed abundances (N_{2013})based on forecasts from Gompertz models with one-year lag and long-term annual trend in carrying capacities (Gompertz t-1 with year models) for each SMZ starting with abundances in 2007 (Fig. 8) indicated that the models ($Z_{2013}=256 + 0.9585\, N_{2013}$, $r^2=0.978$) predicted 97.8% of the variation in 2013 SMZ population abundances.

Parametric bootstraps forecasting future abundance of each population (Table 6) and SMZ population (Table 7) yielded higher probabilities of the minimum count of males attending leks falling below 20 or 200 compared to earlier projections based on models and parameters estimated in a previous analysis for lek surveys through 2007 (Garton et al. 2011:293 ff.). Only the Great Plains and Columbia Basin SMZs showed high probability of declining below these levels of abundance but the likelihoods increase for effective population sizes of 50 and 500 for both of these SMZs. Long-term (100 year) probability of abundance less than these levels are higher than 50% for the Wyoming Basin and Northern Great Basin as well as for the Great Plains and Columbia Basin management zones.

Metapopulation Persistence

Metapopulation projections of the probability of persistence depended on the level of independence in demographic rates amongst SMZ populations (Table 8) which were similar to measures in earlier studies (Garton et al. 2011:369) and imply that the Columbia Basin SMZ effectively fluctuates independently of the remaining portions of the metapopulation. Most of the highest correlations in population changes amongst SMZs were associated with the Snake River Plain which was utilized as the primary SMZ to generate correlated rates for other zones. Movements were modeled using the same approach developed in earlier work (Garton et al. 2011:367) with the modification that Colorado Parks and Wildlife’s failure to participate required dropping those potential movements and connections (Table 9). The Columbia Basin SMZ population was effectively independent of other SMZs. Parametric bootstraps to forecast individual SMZ population persistence and overall persistence of the metapopulation consisting of all the populations produced more extreme forecasts (Table 7) in which probability of declining below effective population sizes of 50 in either short of long term approach 0, excepting the already low Columbia Basin, while long term (100 year) probabilities of declining below effective population sizes of 500 were 100% or close to it. The metapopulation model forecasts virtually no chance of the entire metapopulation declining below effective population sizes of 50 or 500 in either short- or long-term periods.

Discussion

All previously published analyses of sage-grouse populations have documented decreases throughout the species' range (Connelly and Braun 1997, Connelly et al. 2004, Schroeder et al. 2004, WAFWA 2008, Garton et al. 2011). Our results support these findings and provide compelling evidence that most populations have continued to decline over the last 6 years reaching a low in 2013 below 50,000 males attending leks range-wide, an 8 fold decline from the late 1960s. Moreover, our findings compliment conclusions of a recent USFWS report (U.S. Fish and Wildlife Service 2013) and other recent research that document ongoing threats to sage-grouse populations.

Great Plains Management Zone

This zone contains four sage-grouse populations (Garton et al. 2011), including the Dakotas, Northern Montana, Powder River Basin, and Yellowstone Watershed populations. Sage-grouse populations within the Great Plains management zone declined by two-thirds in the last 6 years with the entire management zone most likely declining below effective population sizes of both 50 and 500 within 30 years and with 90% certainty within 100 years. Individual populations all declined more than 50% in the last 6 years with both the Dakotas and Powder River Basin declining more than 70% raising a concern that they may be dropping into an extinction vortex. Even the largest population within the Yellowstone watershed fell by two-thirds with parametric bootstraps implying that every population except Northern Montana is virtually certain to go extinct (96% to 100% probabilities) unless recent patterns of decline change.

The Dakotas population is strongly influenced by energy development; moreover conversion of native rangeland to cropland is a major threat to the persistence of this sage-grouse population. Overall, this population is small and at high risk (U.S. Fish and Wildlife Service 2013). Additionally, Taylor et al. (2012) reported that sage-grouse viability in the Powder River Basin is impacted by multiple stressors including West Nile virus and energy development. Their research suggested that if development continues, future viability of sage-grouse populations in northeast Wyoming will be compromised. The expanding threat of energy development across the Powder River Basin and declining sage-grouse numbers makes this overall an at-risk population (U.S. Fish and Wildlife Service 2013). Finally, cropland conversion continues to take place in the Yellowstone Watershed and this population is potentially at risk (U.S. Fish and Wildlife Service 2013).

Wyoming Basin Management Zone

The Wyoming Basin management zone, containing the largest population of sage-grouse in the United States, has declined 60% in the last 6 years from almost 50,000 males attending leks in 2007 to less than 20,000 in 2013. Nevertheless the likelihood of the management zone population declining below effective population sizes of 50 or 500 are all less than 50% except for a three-quarters chance of declining below an effective population size of 500 in 100 years.

Here again we wonder about the role of drought in addition to fires and expanding oil and gas development on sage-grouse habitat as primary drivers behind these precipitous declines. Primary threats to sage-grouse populations in this zone are energy development and transfer, drought, and sagebrush eradication programs (U.S. Fish and Wildlife Service 2013). Sage-grouse population declines near energy developments in this area have been well documented (Lyon 2000; Holloran 2005; Holloran and Anderson 2005; Kaiser 2006). Residential development has also been identified as a threat (U.S. Fish and Wildlife Service 2013).

Southern Great Basin Management Zone

The Southern Great Basin is one of two major management zones showing the least precipitous population declines of only one-third. This management zone includes populations in California, Nevada, and Utah. A large portion of this zone is managed by the Bureau of Land Management. However, large areas of sagebrush habitat are at considerable risk due to wildfire, cheatgrass (*Bromus tectorum*) invasion, drought, and conifer expansion (U.S. Fish and Wildlife Service 2013) and many areas have burned over the last 10 years. Some of the historic habitat available to sage-grouse within this zone has transitioned to pinyon-juniper woodlands. The area of pinyon-juniper woodlands has increased approximately 10-fold throughout the western United States since the late 1800s (Miller and Tausch 2001).

Snake River Plain Management Zone

The Snake River Plain is the other major management zone showing relatively small population declines of only one-third. This zone contains one of the largest landscapes of connected sage-grouse habitat, and supports the largest sage-grouse population outside of the Wyoming Basin (Garton et al. 2011, U.S. Fish and Wildlife Service 2013). However, the Southern Great Basin and Snake River Plain combined represent a decline of almost 9,000 less males attending leks across the region over the last six years. Three small populations representing less than 500 males counted on leks in Sanpete-Emory Counties, Utah, Mono Lake, California-Nevada and Red-rock Lakes, Montana showed increases in males counted. In contrast, most of the remaining populations within these two zones had moderate declines except Toole-Juab Counties, Utah and Weiser, Idaho which may be dropping into extinction vortices. However every population is so low that its long-term probability of persistence is low except for the Snake-Salmon-Beaverhead population in Idaho which has high probability of persistence over both long- and short-term periods. The Snake River Plain Zone contains a large amount of land managed by BLM and USFS. Within some areas, wildfires and invasive species have continued to reduce the quality of habitat. The mountain Valley portions of this population appear to have relatively stable habitats (U.S. Fish and Wildlife Service 2013). Thus far, energy development is very limited and there are few wild horses.

The Northern Great Basin population of the Snake River Plain SMZ represents a large sage-grouse population in Oregon, Idaho, Nevada, and Utah. Wildfires and invasive species have reduced the quality and quantity of habitat in many portions of this area. The Murphy Fire Complex in Idaho and Nevada recently burned about 600,000 acres of habitat. The 2012 Long Draw fire in Oregon affected 582,000 acres. Since 2000, over 800,000 acres of sagebrush habitats have burned in the Nevada portion of this zone. In conjunction with fire, invasive weeds are also one of the greatest risks (U.S. Fish and Wildlife Service 2013). Other threats in this region include mining development, renewable energy development, transmission, and juniper encroachment at higher elevations (U.S. Fish and Wildlife Service 2013). West Nile virus has also been consistently detected in this region and in 2006 the population was subjected to the largest known West Nile virus mortality event involving sage-grouse in Oregon (U.S. Fish and Wildlife Service 2013).

Northern Great Basin Management Zone

BLM lands comprise a major portion of sagebrush landscapes in the Northern Great Basin (62%) followed by private (21%). This zone has experienced a 65% decline over the last six years with a 9.9% chance of falling below effective population size of 50 and a 72.2% chance of falling below effective population size of 500. These populations are subject to a broad suite of threats, including juniper encroachment, invasive weeds, renewable energy development, transmission lines, roads, OHV recreation, and residential development (U.S. Fish and Wildlife Service 2013). The central Oregon population within this zone is estimated to have only 53 percent of historic sagebrush habitat (U.S. Fish and Wildlife Service 2013) and its extinction appears likely. The Western Great Basin population within this zone is shared among southeastern Oregon, northeastern California and northwestern Nevada. Invasive weeds, fire, and juniper encroachment (particularly on the western edge) represent the greatest risks to this population (U.S. Fish and Wildlife Service 2013). In 2012, the Rush Fire burned more than 313,000 acres of key sage-grouse habitat in California and Nevada. Most of the largest leks and important nesting habitats were within the fire perimeter (U.S. Fish and Wildlife Service 2013). The Western Great Basin population has declined by 69% over the last 6 years and appears to be experiencing an extinction vortex.

Columbia Basin Management Zone

This zone contains two extant populations, Moses Coulee and Yakima Training Center. The Moses Coulee population has been maintaining its population for about the last 30 years, largely due to the Conservation Reserve Program. Major issues in Moses Coulee are the lack of habitat stability due to the abundant private land, habitat fragmentation, and dependence on farm programs (U.S. Fish and Wildlife Service 2013). The Yakima population is much smaller than Moses Coulee, but occurs mostly on public land. A substantial amount of the sage-grouse habitat on the area has been negatively affected by military activities and resulting wildfires. Despite efforts to manage wildfire risks, wildfires have continued to reduce the quantity of habitat for this population (U.S. Fish and Wildlife Service 2013). This zone declined by 6% over the last year and has an 82% chance of falling below effective populations sizes of 50 and 500. Extinction is probable for both the Moses Coulee and Yakima populations.

Colorado Plateau Management Zone

This management zone contains two populations; Parachute-Piceance Basin and Meeker-White River Colorado. Risks to sage-grouse in the zone include small size of existing populations, energy development and associated infrastructure, as well as pinyon-juniper. The USFWS considers these populations to be at high risk but no current data were provided by Colorado so population analyses were not possible.

Sage-grouse and Cycles

The range-wide and SMZ population reconstructions suggest that the dynamics of sage-grouse may be another example of the widely reported 10-year cycle in wildlife populations (Keith 1987, Blasius et al. 1999, Watson et al. 2000, Krebs et al. 2001) that are widely believed to result from time delays in the dynamics of herbivores and their interactions with their plant resources and/or predator populations. Blasius et al. (1999) found from a model based on a spatial lattice of patches that only small amounts of local migration are required to induce broad-scale phase synchronization with all patches locking onto the same collective rhythm. This phase synchronization leads to emergence of complex chaotic travelling wave synchronization which may be crucial to species persistence. Watson et al. (2000) found similar approximately 10-year cycles in Rock Ptarmigan (*Lagopus mutus*) and Red Grouse (*Lagopus lagopus scoticus*) synchronous over landscapes in Scotland that were successfully modeled without plant or predator community interactions from one-year lagged weather events combined with fourth-order delayed density dependence with emigration critical to synchrony across regions.

The figures plotting population reconstruction estimates suggest that every SMZ population is apparently at the bottom of an approximately 10-year cycle. What does this mean in terms of future sage-grouse population trends? In 3-4 years these populations could increase again or the cycle may be disappearing and the precipitous drops since 2007 may be the start of a complete population collapse. Biologists from Idaho, Oregon, Nevada, Utah and Wyoming felt that 2013 was a particularly bad year for lek counts as it followed multiple years of poor productivity due to the multi-year drought along with the associated wildfires.

Modeling Population Dynamics

With 6 more years of data every single SMZ population analysis picked the Gompertz model with a one year time lag and annually-declining carrying capacity as the best or second best model (Appendix 2). Zeng et al. (1998) demonstrated the power of the stochastic growth models we applied in detecting density dependence, complex dynamics and time lags. Lande et al. (2002) demonstrated that interpreting the coefficients of delayed density dependence are quite complex involving the negative elasticity of population growth rate per generation with respect to change in population size. Brook and Bradshaw (2006) found that Gompertz density dependent models were most frequently selected in a similar multi-model inferential analysis across 1198 species including birds, mammals, fish, insects and invertebrates. A similar comprehensive analysis was conducted for Lesser Prairie-Chicken populations throughout this species range. Garton et al. (In press) accumulated and analyzed counts of mostly males from 504 individual leks and 28 lek routes conducted from 1964 to 2012 (Garton et al. In press) and found a similar 57% decline in range-wide estimates of abundance from 80,000 in 2008 to 34,000 in 2012. Three of four ecoregional populations (analogous to SMZs for sage-grouse) showed precipitous declines with only the most northern population remaining approximately stable during that period. Even that population which has been supported by habitat improvements under the CRP program may now be at risk because of major cut-backs in funding for CRP in the region and conversion of habitat into corn fields.

The Powder River population in Wyoming represents one of the large populations early in the data set that has declined most dramatically within the last 6 years (-76%). In 2013 it reached a low of approximately 1600 males attending leks, a figure roughly 4% of the estimates in 1970-1990. Dave Naugle and his students have documented the impact of a “perfect storm” of habitat loss and disturbances through energy development combined with impacts of added water sources spreading West Nile Virus (Naugle, et al. 2004, 2005 Walker, et al. 2004, 2007a) in this population that portends serious negative consequences for sage-grouse populations experiencing expanded energy development throughout the multistate region containing minable energy sources (Doherty et al. 2008, Naugle, et al. 2011, Walker et al. 2007b).

Evidence for Stabilized or Increasing Populations

Every management zone and almost all populations have declined substantially except the sage-grouse population in Washington which exhibited a relatively small overall decline associated with reasonably stable populations in north-central Washington that was likely the result of more extensive development and use of CRP lands (Schroeder and Vander Haegen 2011). In contrast, the Yakima population continued a long-term decline. Beck et al. (2012) advocated eliminating sagebrush control management actions in sagebrush communities until new studies can demonstrate their positive consequences for sage-grouse and other wildlife species yet these still persist (Connelly 2014).

Given continued populations declines and ongoing loss of habitat quality and quantity in every SMZ, the conclusion seems pretty straightforward that current policies and programs are accomplishing little. Claims to the contrary notwithstanding (Connelly 2014), our analyses suggest it is far too early to proclaim various conservation programs are “successful”. However, it is possible that it is still too early to detect effects of habitat improvement and that efforts cast in an experimental framework with random assignment of treatments and controls will demonstrate substantial positive effects in the future. Connelly (2014) noted that current sage-grouse conservation efforts appear to be getting sage-grouse conservation “nowhere fast”, largely because of bureaucratic approaches and continued reliance on rhetoric and dogma. Similarly, Braun (2014) stated conservation plans overall in Colorado have been ineffective. Copeland et al. (2013) predicted that the core area policy of Wyoming plus a targeted $250 million easement investment could reduce possible population losses to 9–15% (95% CI: 3–32%), decreasing anticipated losses by roughly half statewide and nearly two-thirds within core areas. However, this finding apparently means the population will continue to decline, just at a slower rate. Many conservation efforts (e.g., fence marking, conifer control, enhanced fire protection) have recently been put in place. It may be too early to detect effects and this population analysis should be repeated at approximately 5-year intervals to broadly assess success of conservation efforts. Treating the entire sage-grouse population as a single metapopulation suggests that loss of the entire species across this enormous range is extremely unlikely over the short term though loss of individual populations is very likely. Overall persistence of the species into the far distant future is not assured or even likely without maintenance of the essential connectivity amongst populations and without substantial changes in the current trajectories of the populations occupying this broad region.

Management Implications

Studies of widely distributed species reinforce the extreme importance of collaborative studies across multiple land ownerships, political entities, and spatial scales in assessing the cumulative effects of myriad factors impacting natural communities and their key wildlife components. Failure of Colorado Parks and Wildlife to support this collaborative effort has placed substantial barriers to successful completion of a solid population assessment. Likewise no single governmental or private entity has the financial resources to devote to critical large-scale experimental research to evaluate the causal factors determining persistence of landscape species such as sage-grouse but multiple organizations, together, might succeed in developing solid understanding of the causal pathways required to maintain productive sage-steppe communities while simultaneously supporting productive rural communities in the landscape. Regular assessment of the status and prospects for landscape species such as sage-grouse will provide an invaluable assessment of the success of conservation actions throughout the region. Application of classic adaptive management would move this process forward substantially but is nowhere in evidence at present.

The total number of sage-grouse estimated by summing across all 27 populations with sufficient data to analyze but excluding Colorado leks, indicate a minimum total of 98,740 males in 2007 declined 55% to a total of 44,209 males in 2013. Overall, our results combined with findings from other recent studies suggest sage-grouse populations that are quite small or exposed to continuing severe threats (wildfire, energy development) are faring poorly. The evidence is clear that these populations continue to decline in spite of various conservation efforts. Populations occupying landscapes where wildfire is relatively rare and energy development limited have fared better over the last 6 years but nowhere have we found evidence that any larger populations are stable to increasing. Conservation efforts that emphasize protecting remaining habitats over broad landscapes are necessary to insure sage-grouse persistence on these lands.

Acknowledgements

We thank first the myriad state and federal biologists and volunteers that spent countless early morning hours counting male sage-grouse at leks and compiling these data for use in monitoring sage-grouse populations across the region. We especially thank biologists (Scott Gardner, Don Kemner, Adam Messer, Shawn Espinosa, Aaron Robinson, Dave Budeau, Jackie Cupples, Travis Runia, Avery Cook, Mike Schroeder and Tom Christiansen) in every state except Colorado who provided results of lek surveys from 2007 to 2013. Courtney Conway, J. Michael Scott and Dale Goble provided invaluable counsel on treatment of missing data from Colorado. Michael A. Schroeder and Clait E. Braun provided critical reviews of the manuscript to Pew Charitable Trusts that substantially improved the report.

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List of Tables

Appendices

Table 1. Summary of estimated minimum male population attending leks in each population

Sage-Grouse Population	Estimated Minimum No. Males 2007	SE	No. Males 2013	SE	Change
I Great Plains Management Zone					
Dakotas	1,112	307	311	55	-72%
Northern Montana	3,615	573	1,667	165	-54%
Powder River Basin	6,804	919	1,651	155	-76%
Yellowstone Watershed	8,747	949	3,045	196	-65%
II Wyoming Basin Management Zone					
Jackson Hole	133	82	136	44	2%
Wyoming Basin	43,040	2,727	15,767	644	-63%
III Southern Great Basin Management Zone					
Mono Lake, Californai-Nevada	435	266	543	157	25%
South Mono Lake, California	282	161	264	102	-6%
Northeast Interior Utah	412	192	241	71	-42%
Sanpete-Emery Counties, Utah	24	26	48	19	100%
South-Central Utah	1,501	570	737	208	-51%
Summit-Morgan Counties, Utah	87	67	65	19	-25%
Toole-Juab Counties, Utah	257	237	57	18	-78%
Southern Great Basin	5,087	691	3,388	259	-33%
IV Snake River Plain Management Zone					
Baker, Oregon	137	92	49	18	-64%

Bannack, Montana	219	81	177	35	-19%
Red Rocks Lake, Montana	260	202	357	113	37%
East Central Idaho	179	NA	86	35	-52%
Snake-Salmon-Beaverhead, Idaho	8,734	1,157	6,126	229	-30%
Northern Great Basin	9,927	1,144	6,580	376	-34%
Weiser, Idaho	153	73	51	15	-67%
V Northern Great Basin Management Zone					
Central Oregon	829	222	559	95	-33%
Klamath-Oregon-California	11	NA	0	0	-100%
Northwest-Interior Nevada	117	102	79	29	-32%
Western Great Basin	6,327	1,345	1,934	212	-69%
VI Columbia Basin Management Zone					
Moses-Coulee, Washington	230	84	202	39	-12%
Yakima, Washington	81	50	89	36	10%
VII Colorado Plateau Management Zone	NA	NA	NA	NA	NA
Total Across All Zones except CO	98,740		44,209		

Table 2. Summary of estimated minimum male population attending leks in each Sage-Grouse Management Zone

	Estimated Minimum				
Sage-Grouse Management Zone	No. Males	SE	No. Males	SE	Change
	2007		2013		
I Great Plains	20,016	1,462	6,674	312	-67%
II Wyoming Basin[1]	54,282	2,636	20,006	646	-63%
III Southern Great Basin	8,202	1,085	5,485	38	-34%
IV Snake River Plain	19,510	1,404	13,371	550	-32%
V Northern Great Basin	7,429	1,312	2,573	468	-65%
VI Columbia Basin	310	98	291	56	-6%
VII Colorado Plateau[1]	241	52	241	NA	NA
Total Across All Zones except CO	98,616	3,736	44,297	1,019	-55%
Total Across All Zones	109,990		48,641		-56%

[1] Missing estimates for Colorado portions of range replaced by last available estimates from 2007.

Table 3. Information Theoretic Measures of Best Models Across All SMZs

Model	K	Total AICc	ΔAICc
EGPE	3	-911.2	47.6
Period	4	-885.5	73.3
Gompertz	4	-894	64.8
Ricker	4	-894	64.8
Gompertz + Year	5	-910.6	48.2
Ricker + Year	5	-905.8	53
Gompertz + Period	5	-893.5	65.3
Ricker + Period	5	-891	67.8
Gompertz + Year, Period	6	-900.7	58.1
Ricker + Year, Period	6	-894	64.8
Gompertz t-1	4	-907.6	51.2
Ricker t-1	4	-906.5	52.3
Gompertz t-1 + year	5	-958.8	0
Ricker t-1 + Year	5	-941	17.8
Gomperz t-1 + Period	5	-929.1	29.7
Ricker t-1 + Period	5	-921	37.8
Gomperz t-1 + Year,Period	6	-951	7.8
Ricker t-1 + Year,Period	6	-930	28.8
Gompertz t-2	4	-903.4	55.4
Ricker t-2	4	-901.4	57.4
Gompertz t-2 + Year	5	-935.5	23.3
Ricker t-2 + Year	5	-918.2	40.6
Gomperz t-2+ Period	5	-918.8	40
Ricker t-2+ Period	5	-909.6	49.2
Gomperz t-2 + Year,Period	6	-926.5	32.3
Ricker t-2 + Year,Period	6	-907.9	50.9

Table 4. Estimated minimum number of males counted at leks in 2013 compared to estimated carrying capacities for individual populations in 2013, 2043 and 2113.

	Estimated Males		Estimated Carrying Capacity of Minimum No. of Males					
Sage-Grouse Population	2013	SE	2013	SE	2043	SE	2113	SE
I Great Plains Management Zone								
Dakotas	311	55	280	79	97	31	45	18
Northern Montana	1,667	165	4,353	1,394	3,714	1,123	3,380	992
Powder River Basin	1,651	155	2,273	618	240	78	36	24
Yellowstone Watershed	3,045	106	3,087	14,671	241	1,138	136	644
II Wyoming Basin Management Zone								
Jackson Hole	NA	NA	NA	NA	NA	NA	NA	NA
Wyoming Basin	15,767	644	16,078	4,983	6,158	2,021	2,209	913
III Southern Great Basin Management Zone								
Mono Lake, Californai-Nevada	543	157	330	120	576	216	4,059	1,679
South Mono Lake, California	264	102	258	84	275	92	336	118
Northeast Interior Utah	NA	NA	NA	NA	NA	NA	NA	NA
Sanpete-Emery Counties, Utah	NA	NA	NA	NA	NA	NA	NA	NA
South-Central Utah	737	208	944	248	802	209	680	177
Summit-Morgan Counties, Utah	NA	NA	NA	NA	NA	NA	NA	NA
Toole-Juab Counties, Utah	NA	NA	NA	NA	NA	NA	NA	NA
Southern Great Basin	3,388	259	2,702	962	1,417	551	543	268
IV Snake River Plain Management Zone								
Baker, Oregon	NA	NA	NA	NA	NA	NA	NA	NA
Bannack, Montana	177	35	146	40	109	30	86	25

Red Rocks Lake, Montana	NA	NA	NA	NA	NA	NA	NA	NA
East Central Idaho	NA	NA	NA	NA	NA	NA	NA	NA
Snake-Salmon-Beaverhead, Idaho	6,126	229	5,727	1,823	5,074	1,539	4,719	1,394
Northern Great Basin	6,580	376	6,214	1,566	1,664	425	77	20
Weiser, Idaho	NA	NA	NA	NA	NA	NA	NA	NA
V Northern Great Basin Management Zone								
Central Oregon	559	95	509	178	148	58	28	17
Klamath-Oregon-California	NA	NA	NA	NA	NA	NA	NA	NA
Northwest-Interior Nevada	79	29						
Western Great Basin	1,934	212	2,548	812	701	228	40	15
VI Columbia Basin Management Zone								
Moses-Coulee, Washington	202	39	172	50	107	35	77	28
Yakima, Washington	NA	NA	NA	NA	NA	NA	NA	NA
VII Colorado Plateau Management Zone	NA	NA	NA	NA	NA	NA	NA	NA
Total Across All Populations* except CO	43,030		43,349		21,084		16,416	

*(> 25 leks counted)

Table 5. Estimated minimum number of males counted at leks in each management zone in 2013 compared to estimated carrying capacities in 2013, 2043 and 2113.

	Estimated Males		Estimated Carrying Capacity of Minimum No. of Males					
Sage-Grouse Management Zone	2013	SE	2013	SE	2043	SE	2113	SE
I Great Plains	6,674	312	3,798	1,378	1,444	546	481	193
II Wyoming Basin	15,903	646	15,541	4,536	6,784	2,135	2,248	918
III Southern Great Basin	5,485	38	4,862	1,514	3,722	1,175	2,649	875
IV Snake River Plain	13,371	550	13,275	4,008	6,420	2,083	2,330	1,111
V Northern Great Basin	2,573	468	2,796	835	1,027	330	382	152
VI Columbia Basin	291	56	233	70	120	39	64	24
VII Colorado Plateau	NA	NA	NA	NA	NA	NA	NA	NA
Total Across All Zones except CO	44,297	1,019	40,505	6,444	19,517	3,269	8,154	1,704

Table 6. Summary Presentation of results of parametric bootstraps to forecast probability (percentage) of populations falling below counts (N) of 20 and 200 and effective population sizes (Ne) of 50 and 500.

	30-year				100-year			
Sage-Grouse Population	N< 20	N< 200	Ne< 50	Ne< 500	N< 20	N< 200	Ne< 50	Ne< 500
I Great Plains Management Zone								
Dakotas	21.5	73.1	35.4	100.0	69.1	77.1	72.4	100.0
Northern Montana	2.7	6.2	5.6	11.5	16.7	24.0	7.2	13.7
Powder River Basin	2.9	77.6	5.8	99.0	98.7	98.9	98.8	99.3
Yellowstone Watershed	15.6	68.6	54.5	74.9	89.5	95.6	89.5	96.0
II Wyoming Basin Management Zone								
Jackson Hole	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Wyoming Basin	0.1	14.4	4.7	20.3	20.7	21.4	21.0	74.9
III Southern Great Basin Management Zone								
Mono Lake, Californai-Nevada	0.1	65.2	7.7	100.0	0.3	67.1	21.5	100.0
South Mono Lake, California	0.3	87.5	7.9	100.0	0.8	88.8	21.3	100.0
Northeast Interior Utah	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Sanpete-Emery Counties, Utah	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
South-Central Utah	0.1	8.2	0.9	100.0	17.9	36.9	18.7	100.0
Summit-Morgan Counties, Utah	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Toole-Juab Counties, Utah	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Southern Great Basin	0.1	2.6	1.3	36.8	3.3	77.0	10.4	90.5
IV Snake River Plain Management Zone								
Baker, Oregon	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Bannack, Montana	6.6	100.0	37.2	100.0	34.8	100.0	47.9	100.0
Red Rocks Lake, Montana	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

East Central Idaho	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Snake-Salmon-Beaverhead, Idaho	0.4	5.3	3.3	6.7	16.1	18.6	16.5	20.7
Northern Great Basin	9.9	13.6	12.6	46.7	35.3	90.2	72.2	92.3
Weiser, Idaho	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
V Northern Great Basin Management Zone								
Central Oregon	2.7	49.7	3.4	100.0	50.1	51.2	50.5	100.0
Klamath-Oregon-California	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Northwest-Interior Nevada								
Western Great Basin	13.1	13.2	13.1	78.1	54.6	99.9	96.2	99.9
VI Columbia Basin Management Zone								
Moses-Coulee, Washington	13.1	13.2	13.1	78.1	54.6	99.9	96.2	99.9
Yakima, Washington								
VII Colorado Plateau Management Zone	n/a		n/a		n/a		n/a	n/a
Average Across All Zones except CO	6	37	14	68	33	68	46	85

Table 7. Probabilities of extinction with standard errors (SE) estimated by parametric bootstraps across all models weighted by the probability that each models is the correct (best) model within the set of 26 models and the probability of extinction under a metapopulation model based on the best stochastic growth model across all SMZs incorporating movement between SMZ populations and correlated environmental perturbations amongst SMZ populations.

	Time	Probability (as %) for each SMZ individually (SE)				Probability Under Metapopulation	
Sage-Grouse Management Zone	Horizon	N<20	N<200	Ne<50	Ne<500	Ne<50	Ne<500
I Great Plains	30 yr	39.6 (7.6)	54.5 (9.9)	52.6 (9.6)	55.2 (9.9)	0%	0%
	100 yr	55.1 (9.9)	74.5 (6.5)	55.6 (9.8)	92.6 (5.1)	0%	100%
II Wyoming Basin	30 yr	0.1 (0)	14.2 (5.5)	4.1 (1.6)	21.4 (8.1)	0%	0%
	100 yr	21.8 (8.2)	22.5 (8.2)	22.2 (8.2)	76.2 (8.0)	0%	78%
III Southern Great Basin	30 yr	0 (0)	0 (0)	0 (0)	0.3 (0.2)	0%	0%
	100 yr	9.9 (6.0)	10.4 (6.1)	10.1 (6.0)	25.3 (6.3)	0%	91%
IV Snake River Plain	30 yr	0.5 (0.6)	2.6 (3.1)	2.1 (2.6)	4.5 (3.7)	0%	0%
	100 yr	10.1 (6.0)	20.6 (6.4)	6.5 (4.9)	46.7 (7.3)	0%	100%
V Northern Great Basin	30 yr	9.9 (5.3)	13.6 (6.7)	12.6 (6.5)	46.7 (7.3)	0%	2%
	100 yr	35.3 (8.1)	90.2 (5.7)	72.2 (6.2)	92.3 (4.9)	25%	100%
VI Columbia Basin	30 yr	11.8 (6.1)	85.2 (6.0)	42 (6.1)	100 (0)	85%	100%
	100 yr	77.7 (8.0)	90.5 (5.3)	80.2 (7.5)	100 (0)	100%	100%
VII Colorado Plateau		NA	NA	NA	NA	NA	NA
Range-wide Population						0%	0%

Table 8. Correlations in residuals among sage-grouse management zones from predictions of the overall best AICc Gompertz type model of density dependence in annual rates of change with 1-year time lag and declining trend in carrying capacity through time.

	Great Plains	Wyoming Basin	Southern Great Basin	Snake River Plain	Northern Great Basin	Columbia Basin
Great Plains	1	0.51	0.126	0.375	0.051	0.163
Wyoming Basin		1	0.299	0.348	0.083	0.061
Southern Great Basin			1	0.604	0.573	0.219
Snake River Plain				1	0.407	0.281
Northern Great Basin					1	0.278

Table 9. Dispersal rates among sage-grouse management zones representing the proportion of the population dispersing to another management zone each year.

	Wyoming Basin	Southern Great Basin	Snake River Plain	Northern Great Basin
Great Plains	0.050			
Wyoming Basin		0.020	0.011	
Southern Great Basin			0.024	0.004
Snake River Plain				0.035

Connections between management zones not presented are assumed to be zero.
Taken from Garton et al. 2011:367 Table 15.71.

Appendix 1. Top models of annual rates of change with estimates of carrying capacity in 2013, 2043 and 2113 for Populations.

Populations	Best Models	a	$b_1 lnNt$	$b_2 Nt$	$b_2 lnN_{t-1}$	$b_3 lnN_{t-2}$	c(period)	d(year)	S	r^2	K_{2013}	K_{2043}	K_{2113}
I Great Plains Management Zone													
Dakotas	Gompertz + Year	35.8948	-0.3942					-0.0167	0.256	0.189	323	91	5
Northern Montana	Gompertz t-1 + Period	2.8591			-0.3347		0.3066		0.1847	0.352	5127	5127	5127
Powder River Basin	Gompertz t-1 + year	67.1015			-0.396			-0.0318	0.2769	0.317	2436	219	1
Yellowstone Watershed	Ricker + Year	32.4125		-6E-05				-0.016	0.218	0.364	3393	0	0
II Wyoming Basin Management Zone													
Jackson Hole	NA$^+$												
Wyoming Basin	Gompertz t-1 + year	23.619			-0.2946			-0.0103	0.1485	0.246	17913	6275	543
III Southern Great Basin Management Zone													
Mono Lake, Californai-Nevada	Gompertz	3.1176	-0.5521						0.465	0.267	283	283	283
South Mono Lake, California	Gompertz	2.491	-0.4528						0.3431	0.228	245	245	245
Northeast Interior Utah	NA$^+$												
Sanpete-Emery Counties, Utah	NA$^+$												
South-Central Utah	Gompertz	2.2129	-0.3196						0.2779	0.186	1016	1016	1016
Summit-Morgan Counties, Utah	NA$^+$												
Toole-Juab Counties, Utah	NA$^+$												
Southern Great Basin	Gompertz t-2 + Year	28.088				-0.4317		-0.0123	0.1853	0.357	2229	948	129
IV Snake River Plain Management Zone													
Baker, Oregon	NA$^+$												
Bannack, Montana	Gompertz + Period	1.651	-0.3144				0.2848		0.1959	0.172	191	191	191

Red Rocks Lake, Montana	NA⁺										
East Central Idaho	NA⁺										
Snake-Salmon-Beaverhead, Idaho	Gompertz t-1 + Period	3.0269		-0.3423	0.2949		0.1794	0.371	6925	6925	6925
Northern Great Basin	Gompertz t-1 + year	49.0596		-0.5015		-0.0222	0.1251	0.514	6099	1616	73
Weiser, Idaho	NA⁺										
V Northern Great Basin Management Zone											
Central Oregon	Gompertz + Year, Period	60.8892	-0.5485		-0.1821	-0.0286	0.1881	0.321	423	89	2
Klamath-Oregon-California	NA⁺										
Northwest-Interior Nevada	NA⁺										
Western Great Basin	Gompertz t-1 + Year,Period	2.5868		-0.3036	0.251		0.2602	0.241	5016	5016	5016
VI Columbia Basin Management Zone											
Moses-Coulee, Washington	Gompertz t-1 + year	27.7956		-0.3647		-0.0129	0.2795	0.199	150	52	4
Yakima, Washington	NA⁺										
VII Colorado Plateau Management Zone	NA*										

*NA - Not Available because Colorado Parks and Wildlife Denied 4 requests to participate in this study.

NA⁺ - Not Estimated because fewer than 26 leks counted

Appendix 2. Top models of annual rates of change with estimates of carrying capacity in 2013, 2043 and 2113 for SMZs.

Sage-Grouse

Management Zone	Best Models	a	$lnNt$	b_1Nt	b_2lnN_{t-1}	c(period)	d(year)	S	r^2	K_{2013}	K_{2043}	K_{2113}
I Great Plains	Ricker + Year	30.2053	.	-1.7E-05	.	.	-0.015	0.2082	0.239	616	0	0
	Gompertz t-1 + year	31.6958	.	.	-0.3949	.	-0.014	0.2103	0.223	7317	2526	211
II Wyoming Basin	Gompertz t-1 + year	23.5212	.	.	-0.2978	.	-0.0102	0.1479	0.247	22825	8169	743
III Southern Great Basin	Gompertz t-1 + year	15.2114	.	.	-0.3777	.	-0.006	0.1299	0.339	4008	2488	818
IV Snake River Plain	Gomperz t-1 + Year,Period	25.4738	.	.	-0.4124	0.1566	-0.0107	0.1319	0.448	13919	6391	1039
	Gompertz t-1 + year	35.0669	.	.	-0.407	.	-0.0155	0.1367	0.393	13324	4250	296
V Northern Great Basin	Gompertz t-1 + year	27.4378	.	.	-0.33	.	-0.0123	0.1947	0.221	3344	1093	80
	Gomperz t-1 + Year,Period	40.9475	.	.	-0.367	-0.1634	-0.0189	0.1926	0.256	2716	579	16
VI Columbia Basin	Gompertz t-1 + year	27.8921	.	.	-0.3956	.	-0.0128	0.209	0.208	216	82	8
	Gompertz + Year	26.9596	-0.3979	.	.	.	-0.0123	0.2102	0.199	252	100	11
VII Colorado Plateau	NA*											

*NA - Not Available because Colorado Parks and Wildlife denied 4 requests to participate in this study.

Figure 1. Greater sage-grouse populations and management zones in western North America.

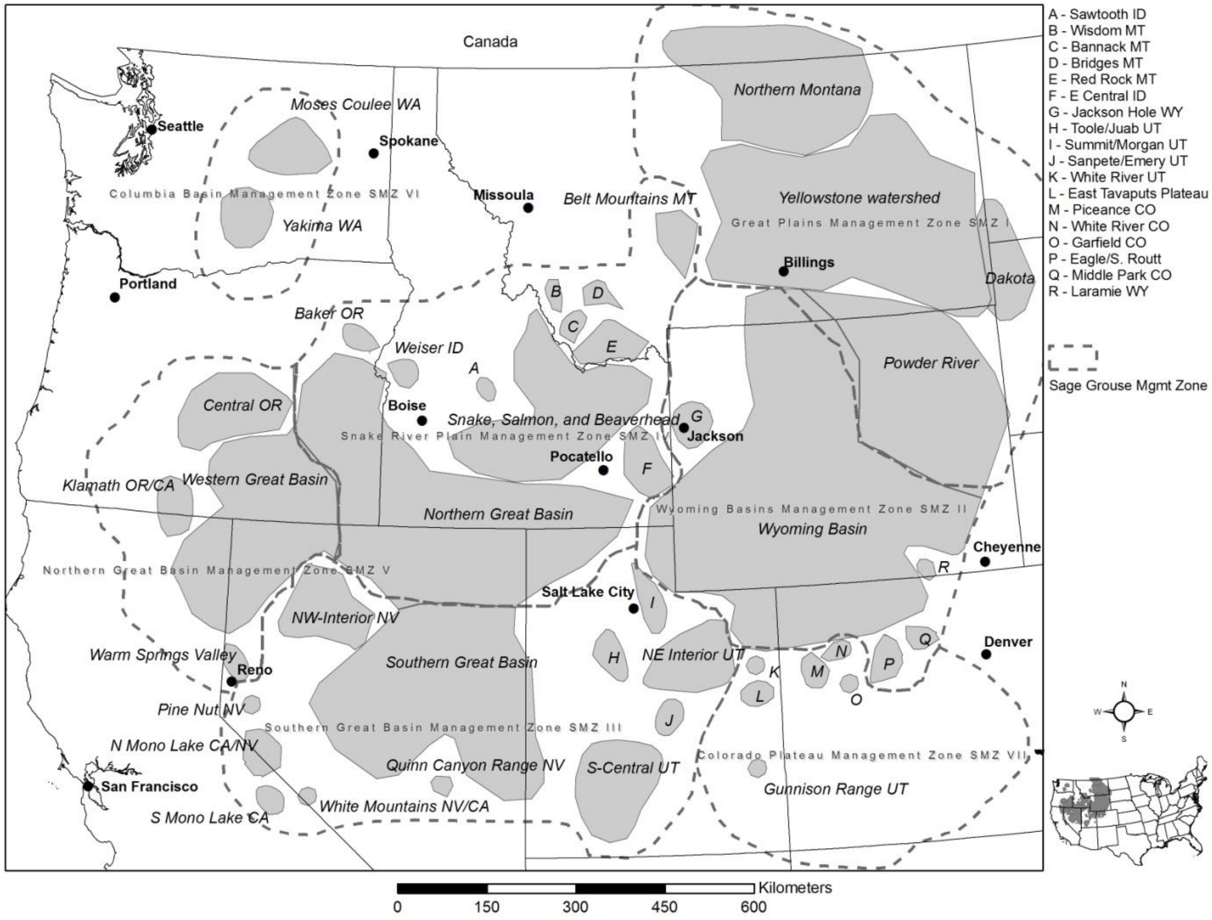
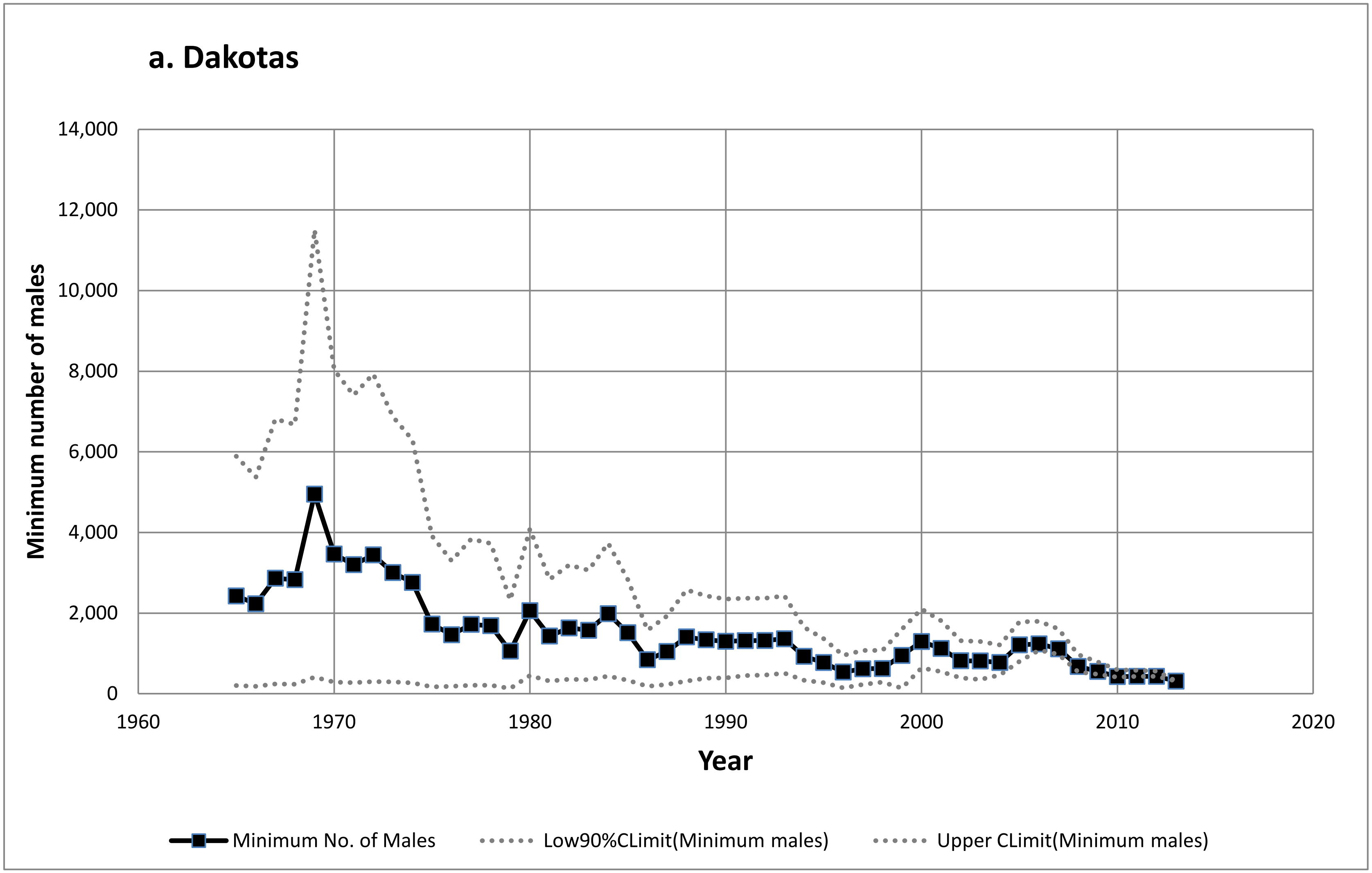
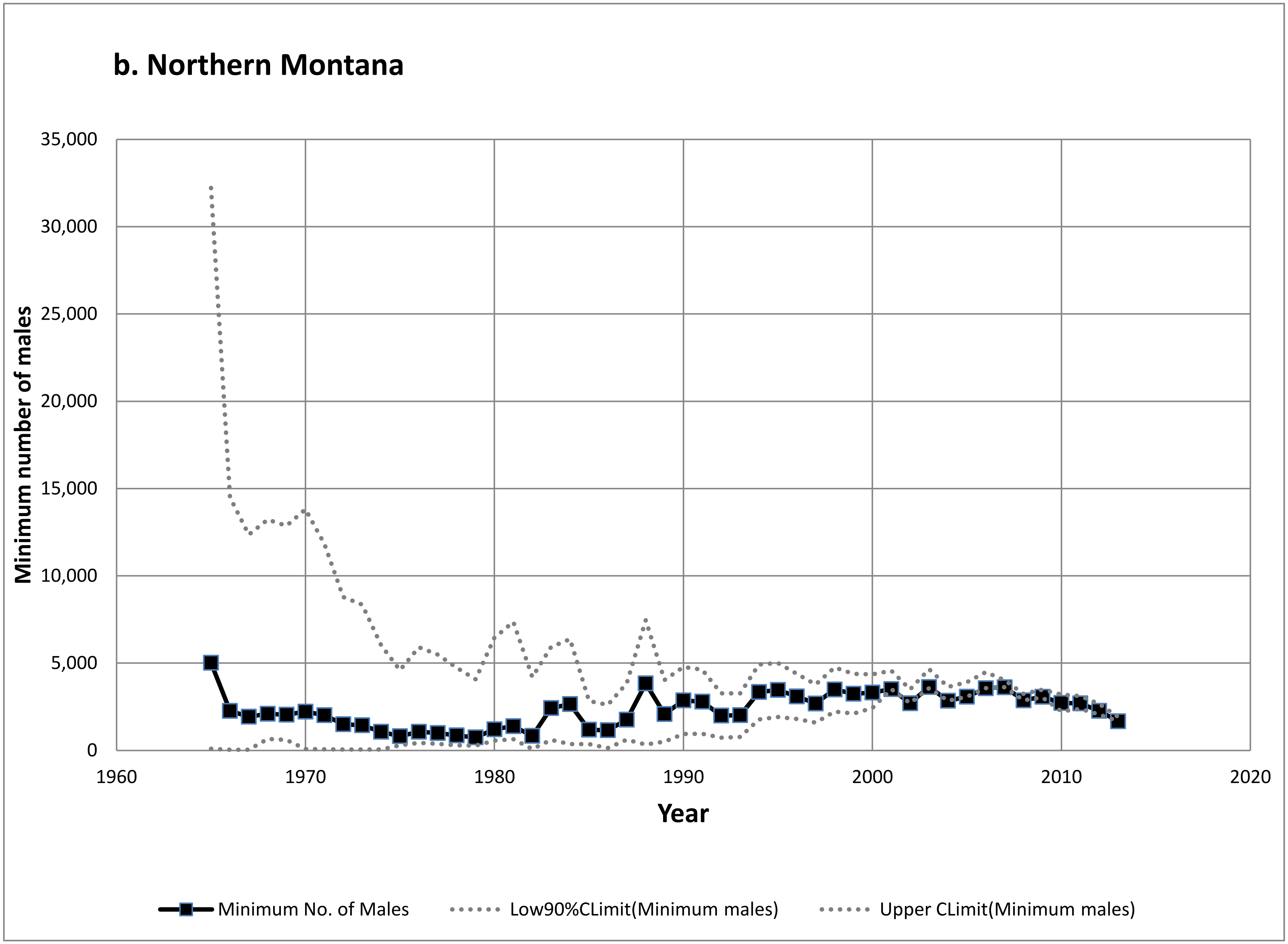
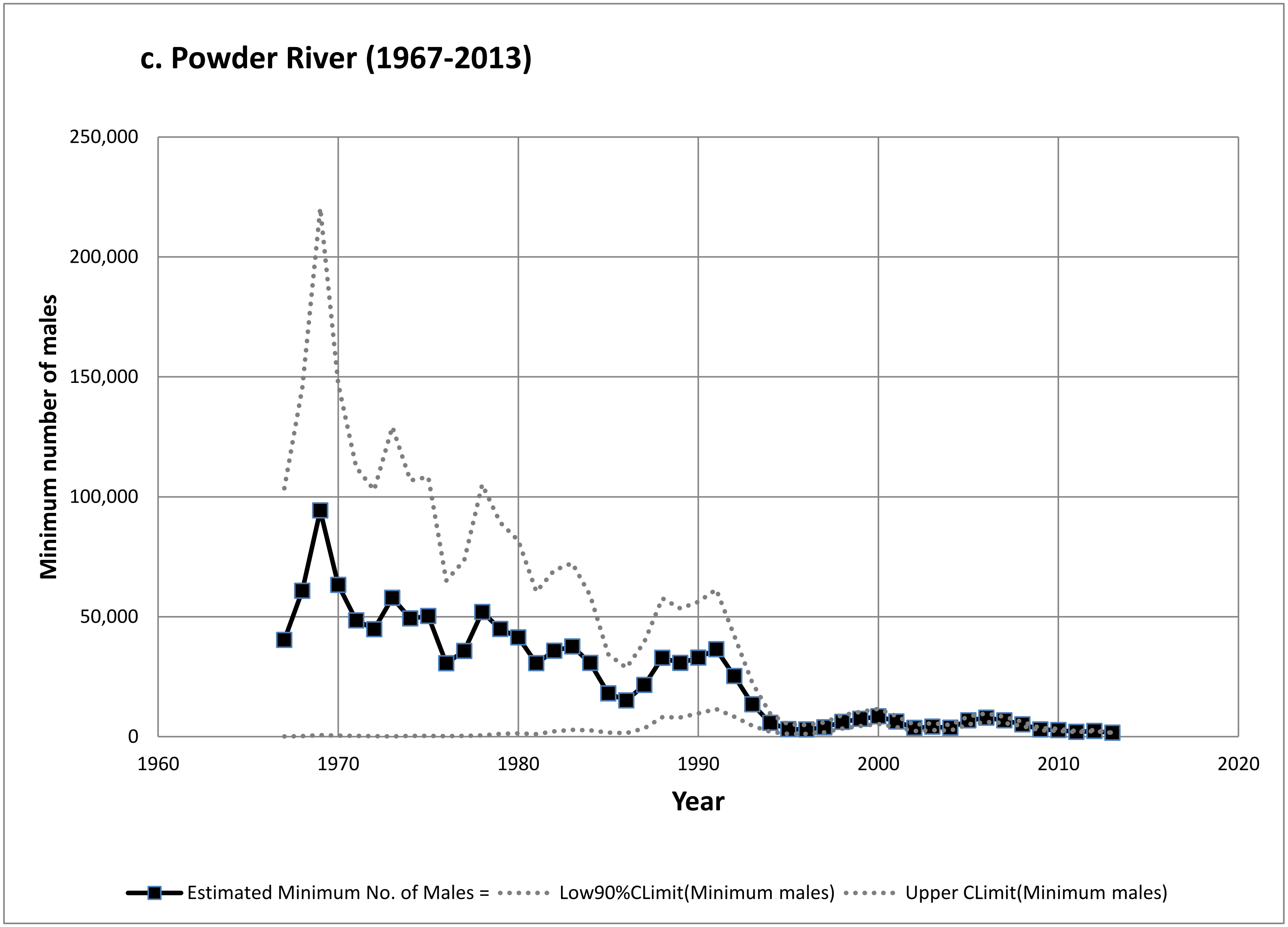
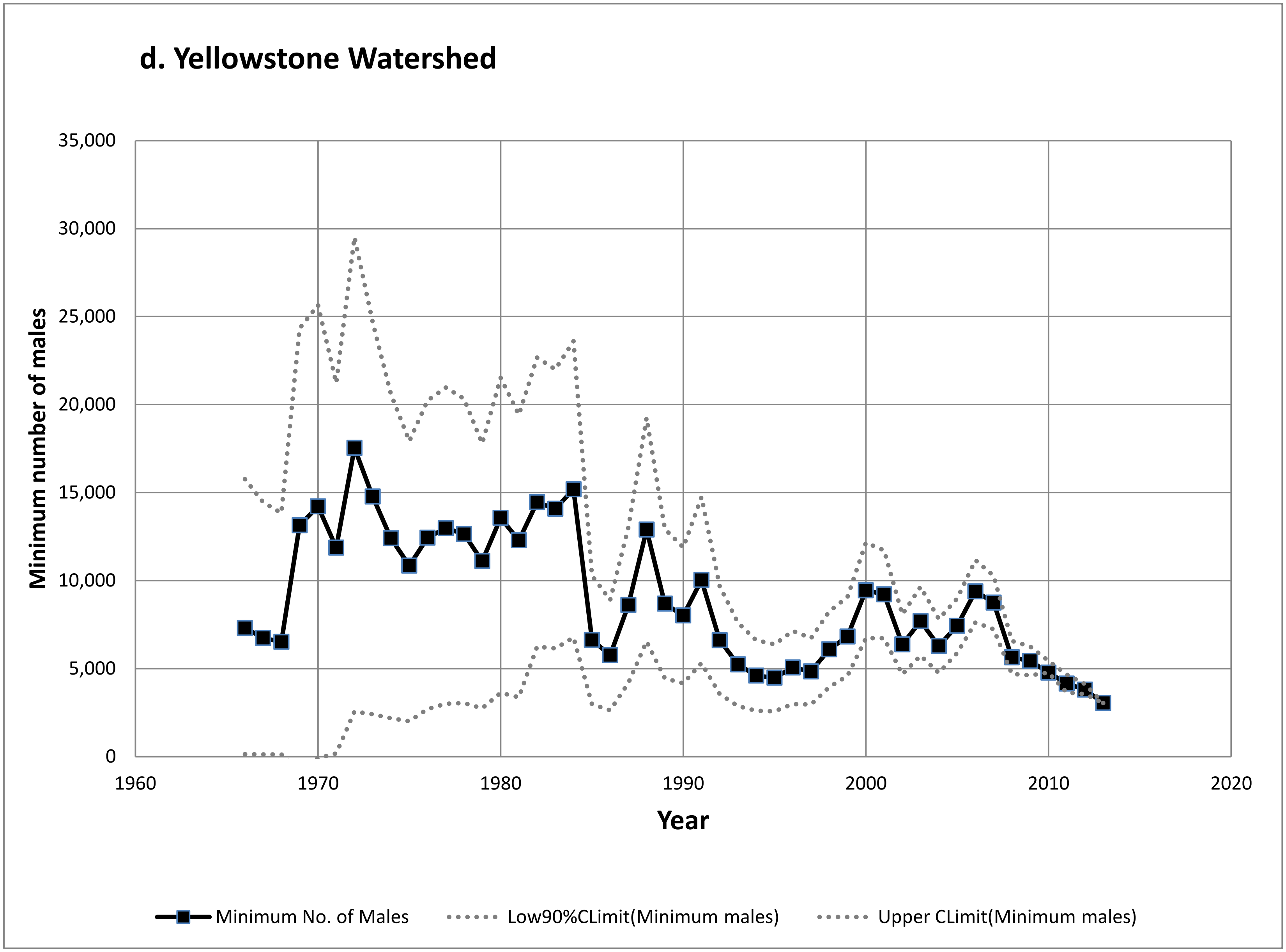


Figure 2. Population reconstructions for Great Plains populations and Management Zone I: a. Dakotas b. Northern Montana c. Powder River Basin d. Yellowstone Watershed e. Great Plains Management Zone I.


a. Dakotas
Minimum number of males
14,000
12,000
10,000
8,000
6,000
4,000
2,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


b. Northern Montana
Minimum number of males
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


c. Powder River (1967-2013)
Minimum number of males
250,000
200,000
150,000
100,000
50,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


d. Yellowstone Watershed
Minimum number of males
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

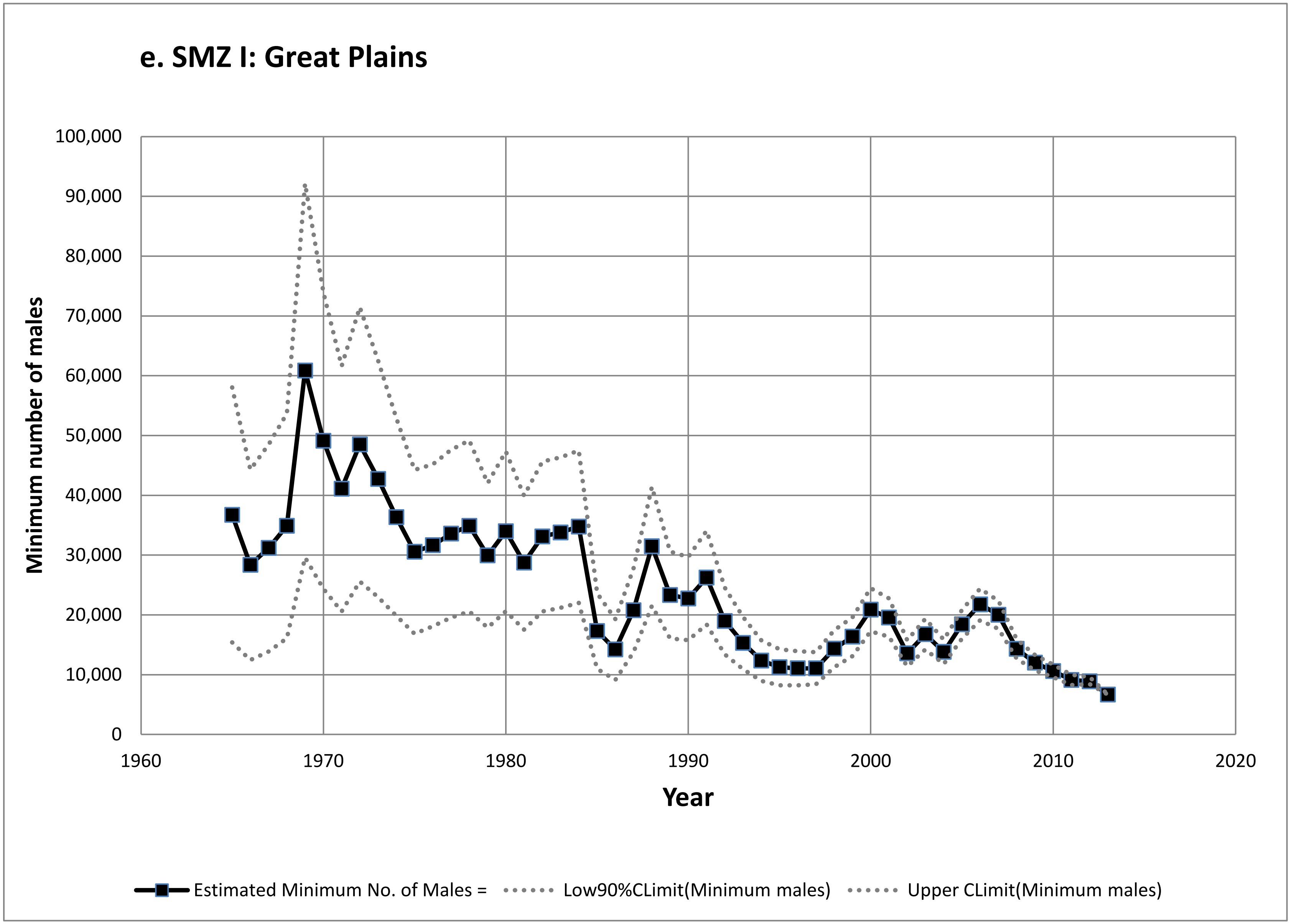
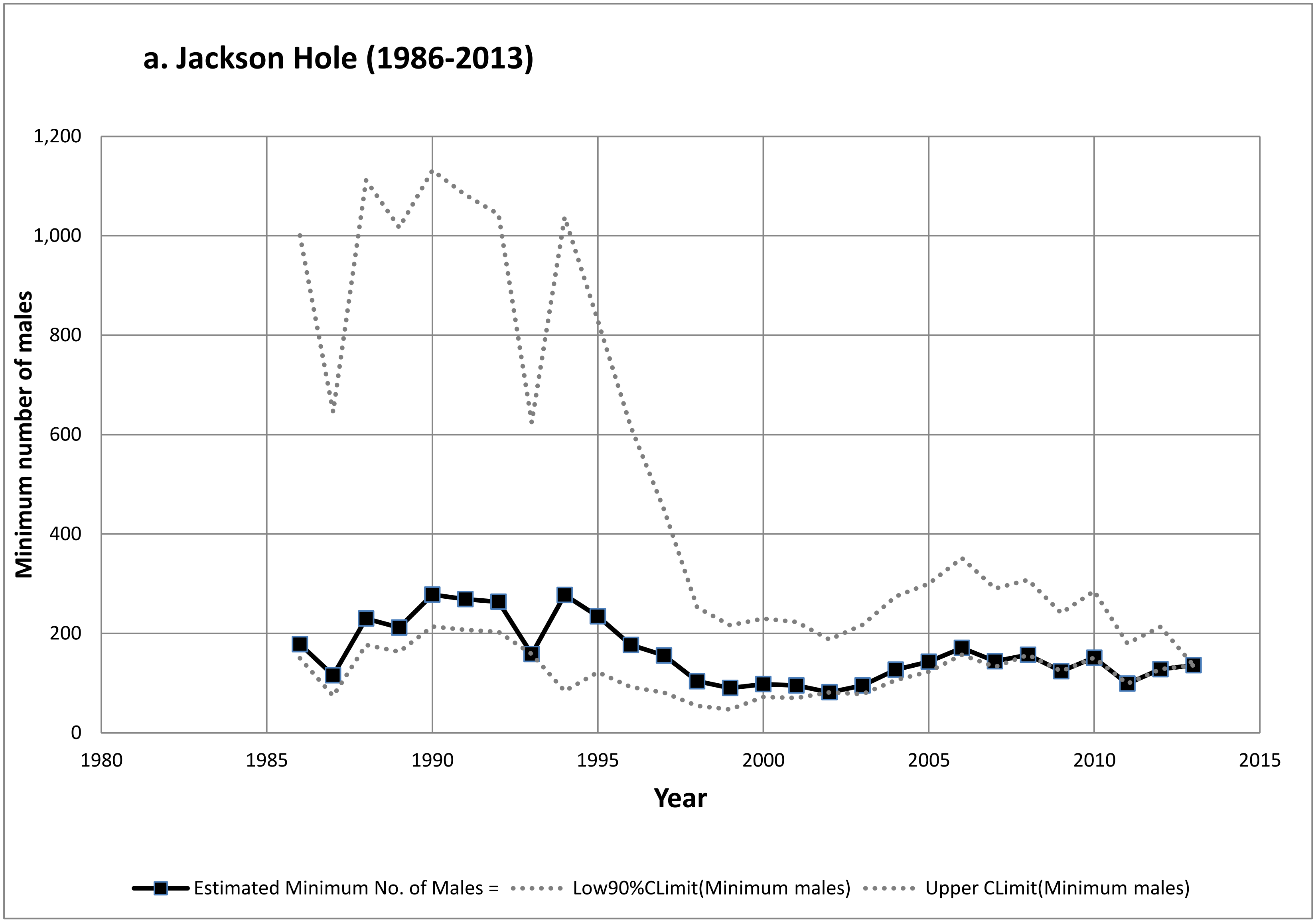
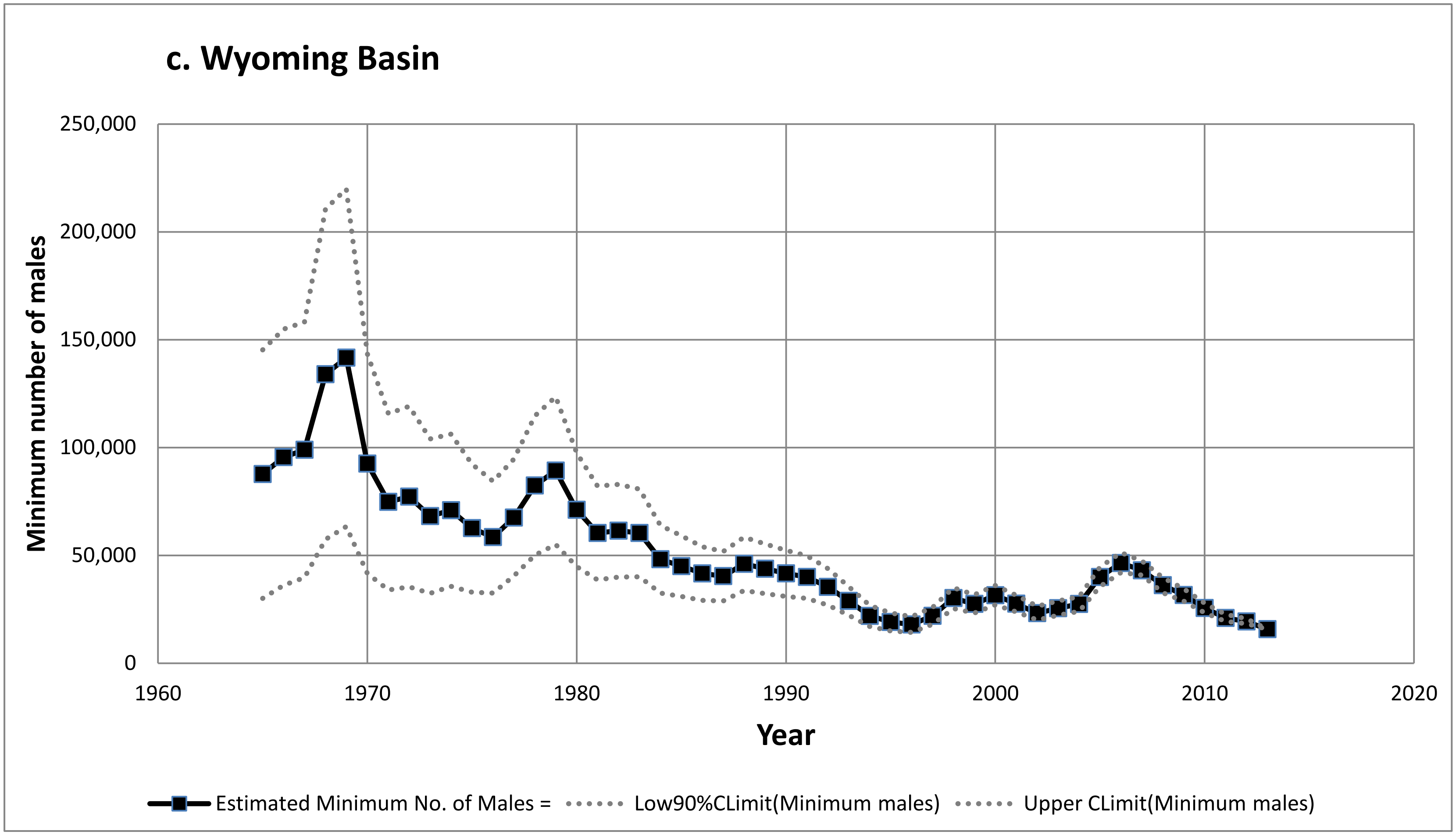

e. SMZ I: Great Plains
Minimum number of males
100,000
90,000
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 3. Population reconstructions for Wyoming Basins populations and Management Zone II: a. Jackson Hole, Wyoming; b. Middle Park, Colorado; c. Wyoming Basins; d. Management Zone II.


a. Jackson Hole (1986-2013)
Minimum number of males
1,200
1,000
800
600
400
200
0
1980
1985
1990
1995
2000
2005
2010
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

NO UPDATED COLORADO DATA YET


c. Wyoming Basin
Minimum number of males
250,000
200,000
150,000
100,000
50,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

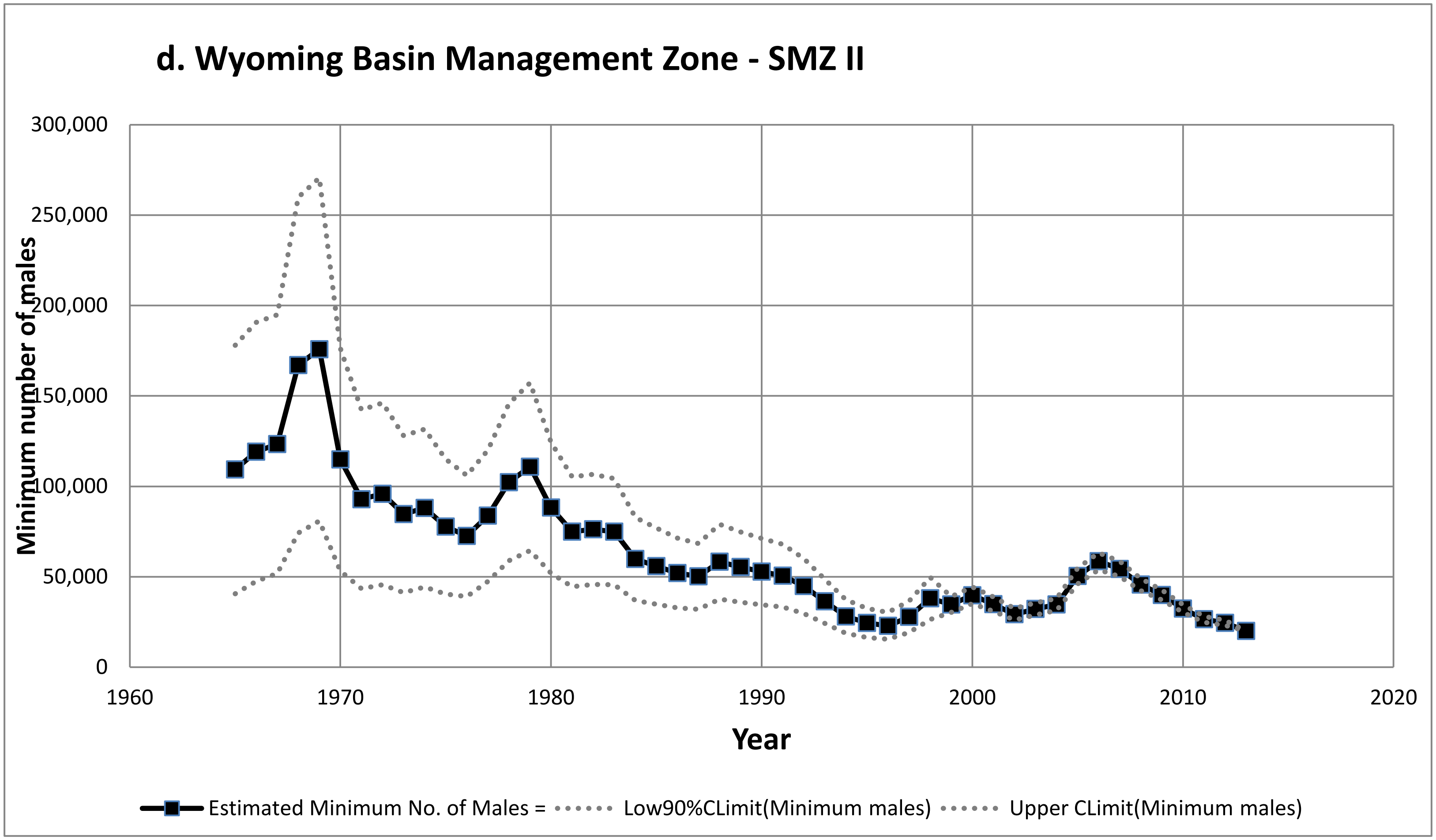
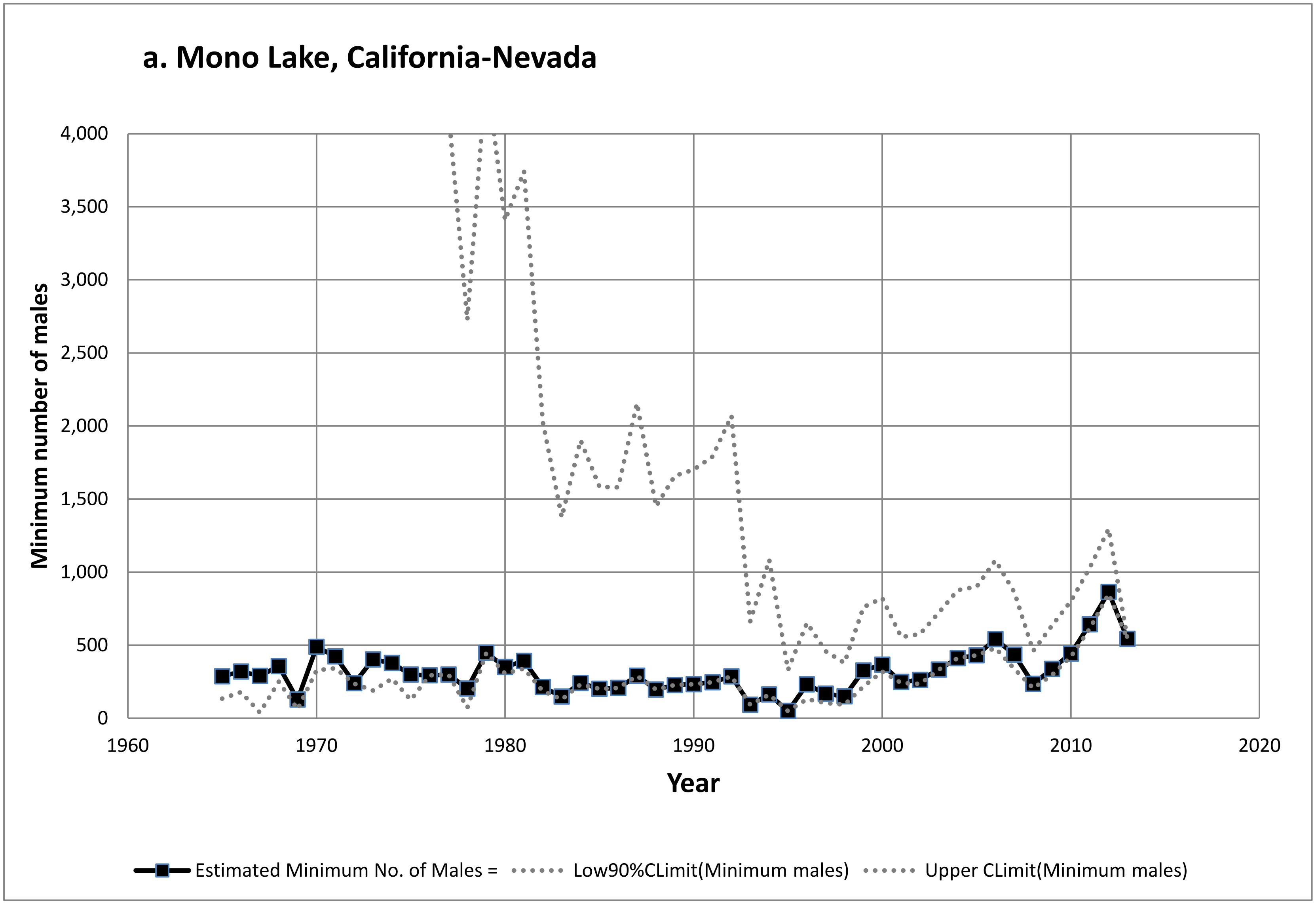
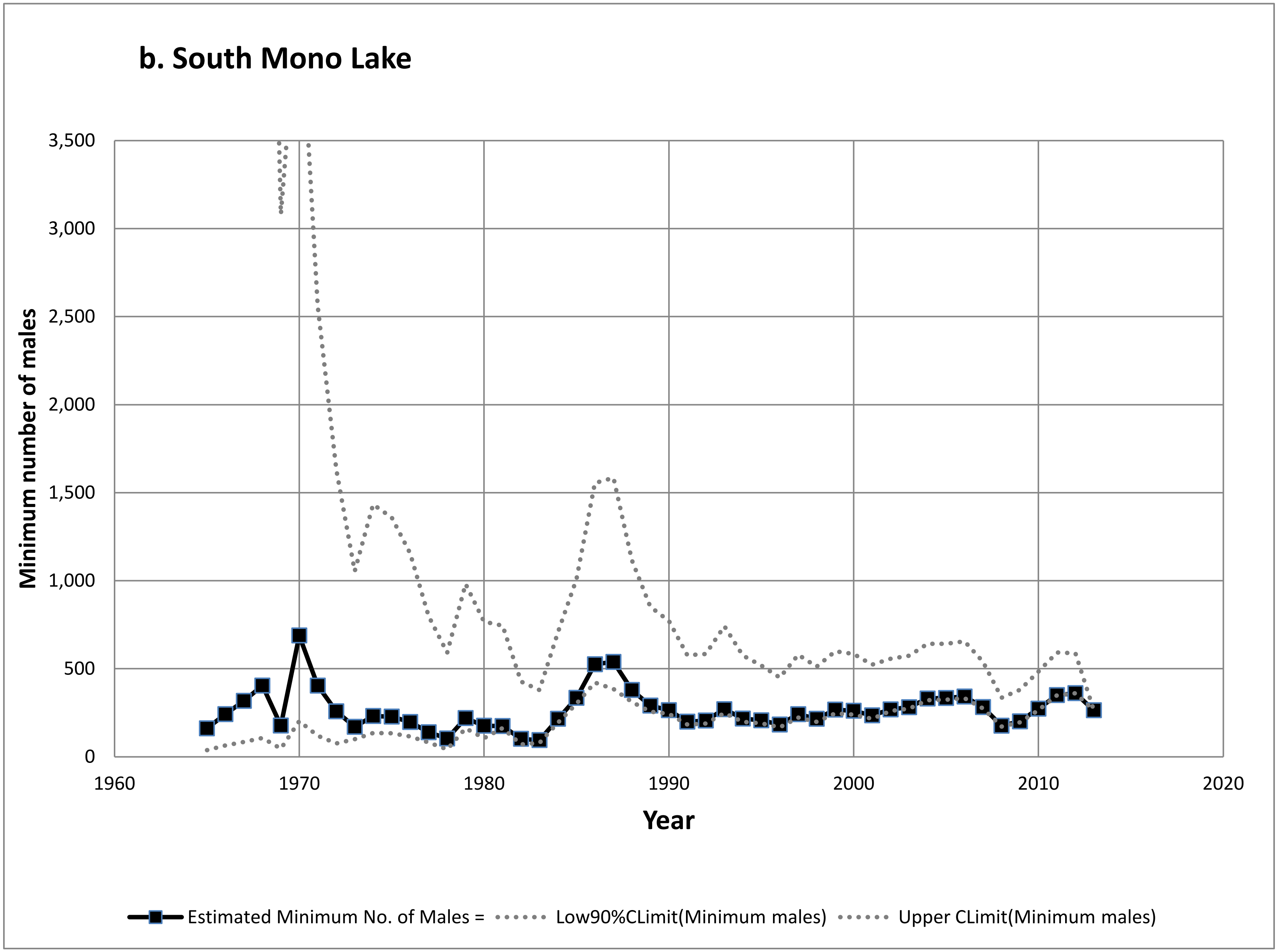
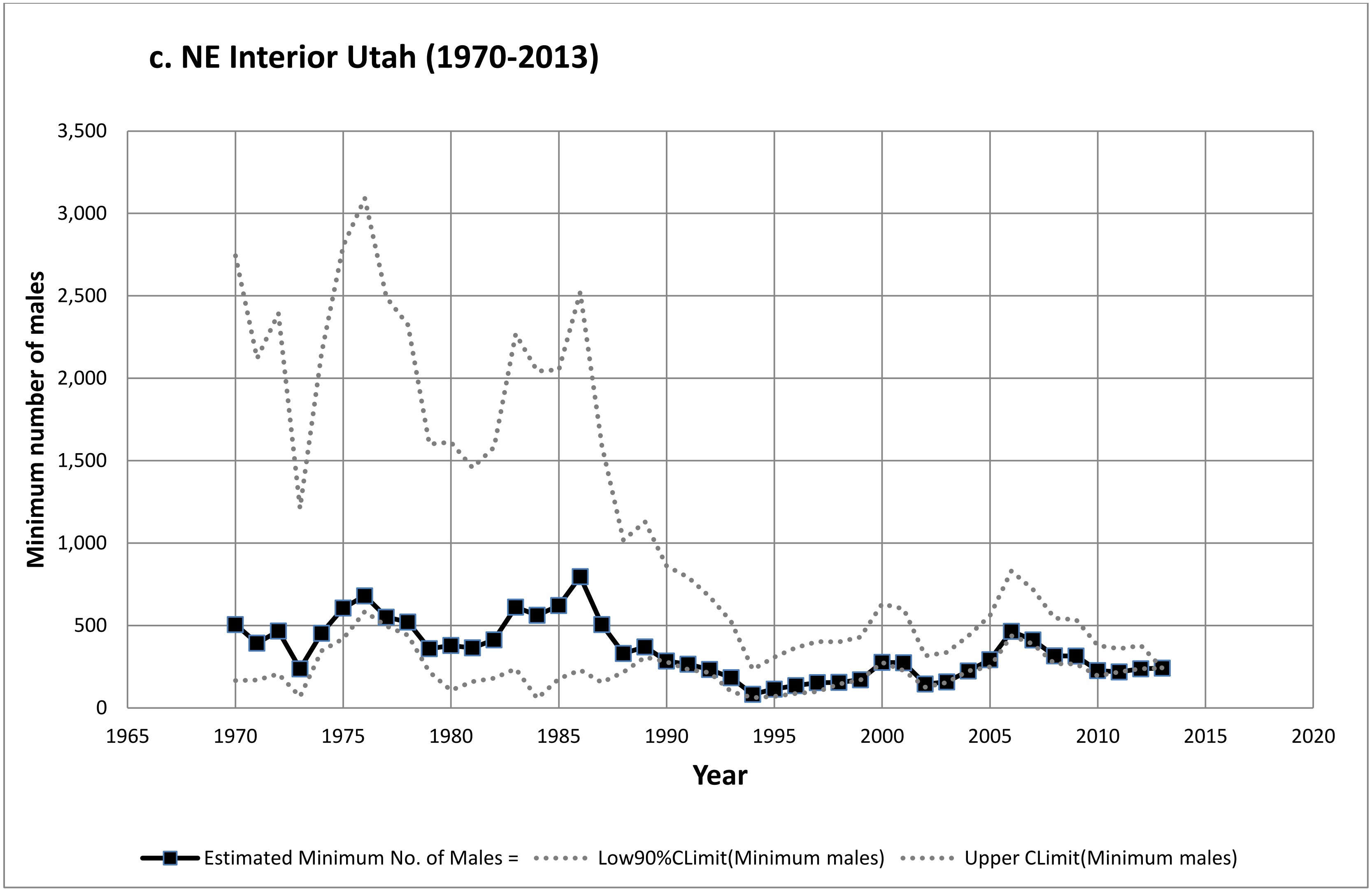
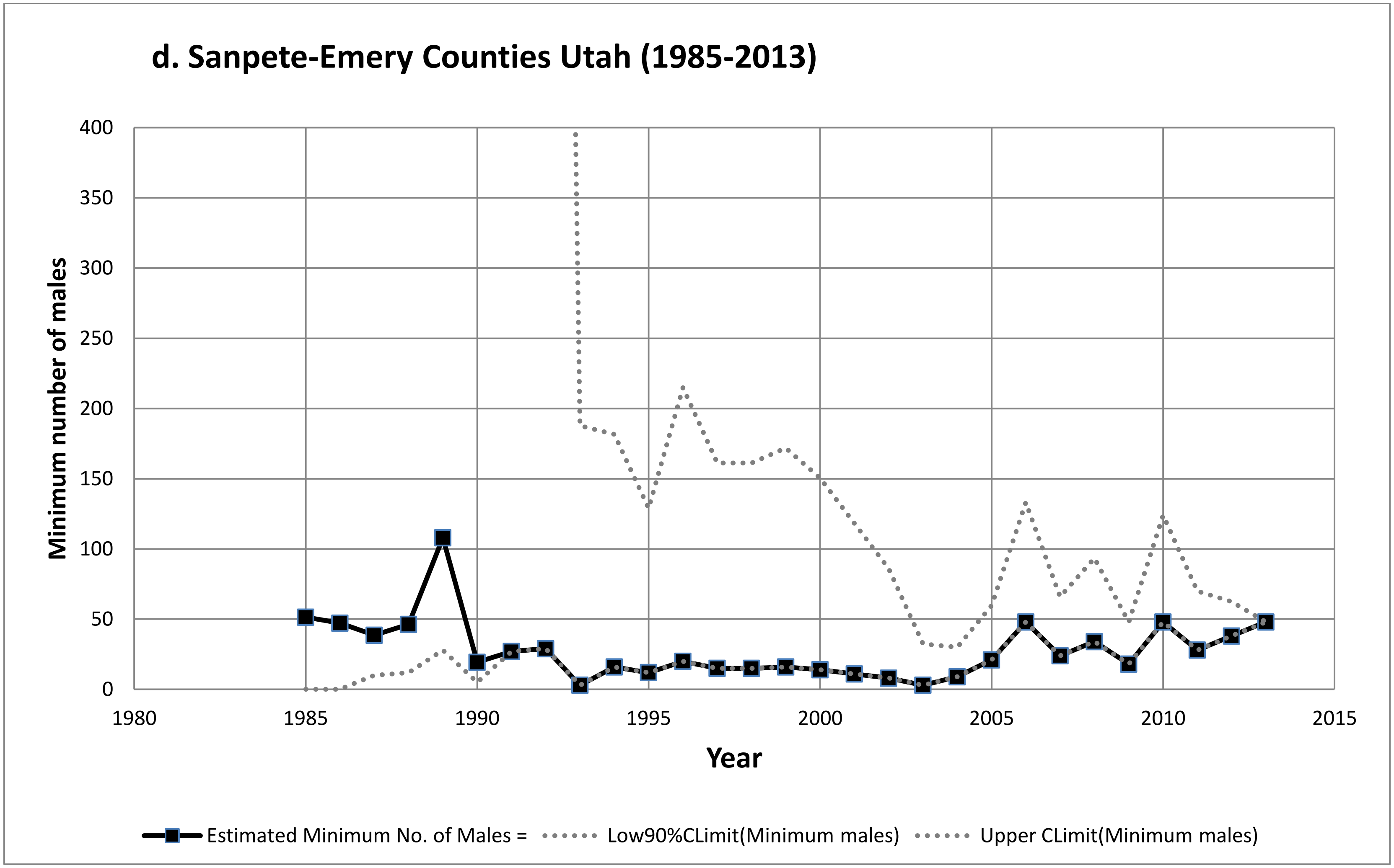

d. Wyoming Basin Management Zone - SMZ II
Minimum number of males
300,000
250,000
200,000
150,000
100,000
50,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

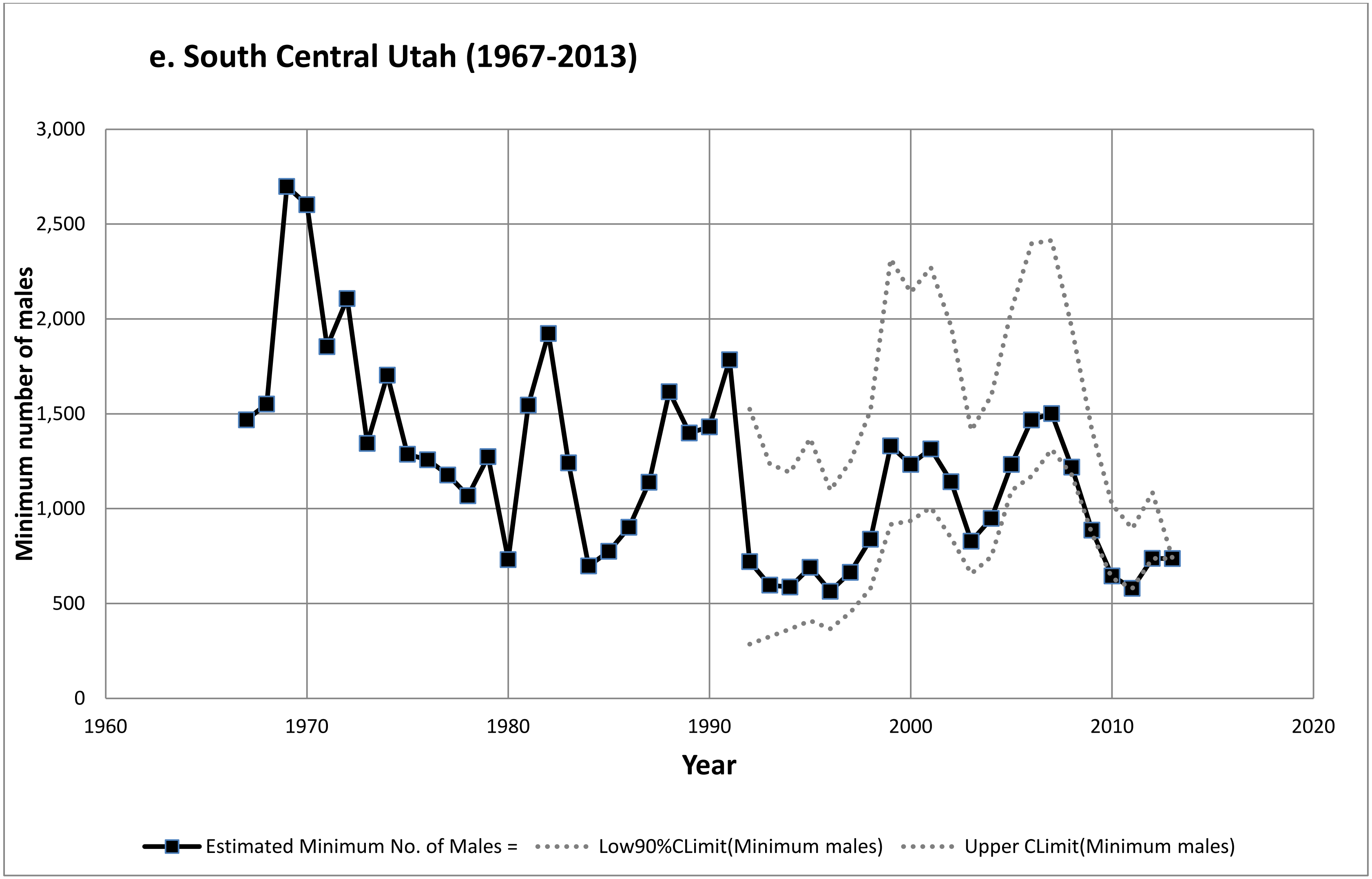
Figure 4. Population reconstructions for Southern Great Basin populations and Management Zone III: a. Mono Lake, California-Nevada; b. South Mono Lake; c. Northeast Interior, Utah; d. Sanpete-Emery; e. South-central Utah; f. Summit-Morgan, g. Toole-Juab Utah; h. Southern Great Basin; i. Management Zone III.

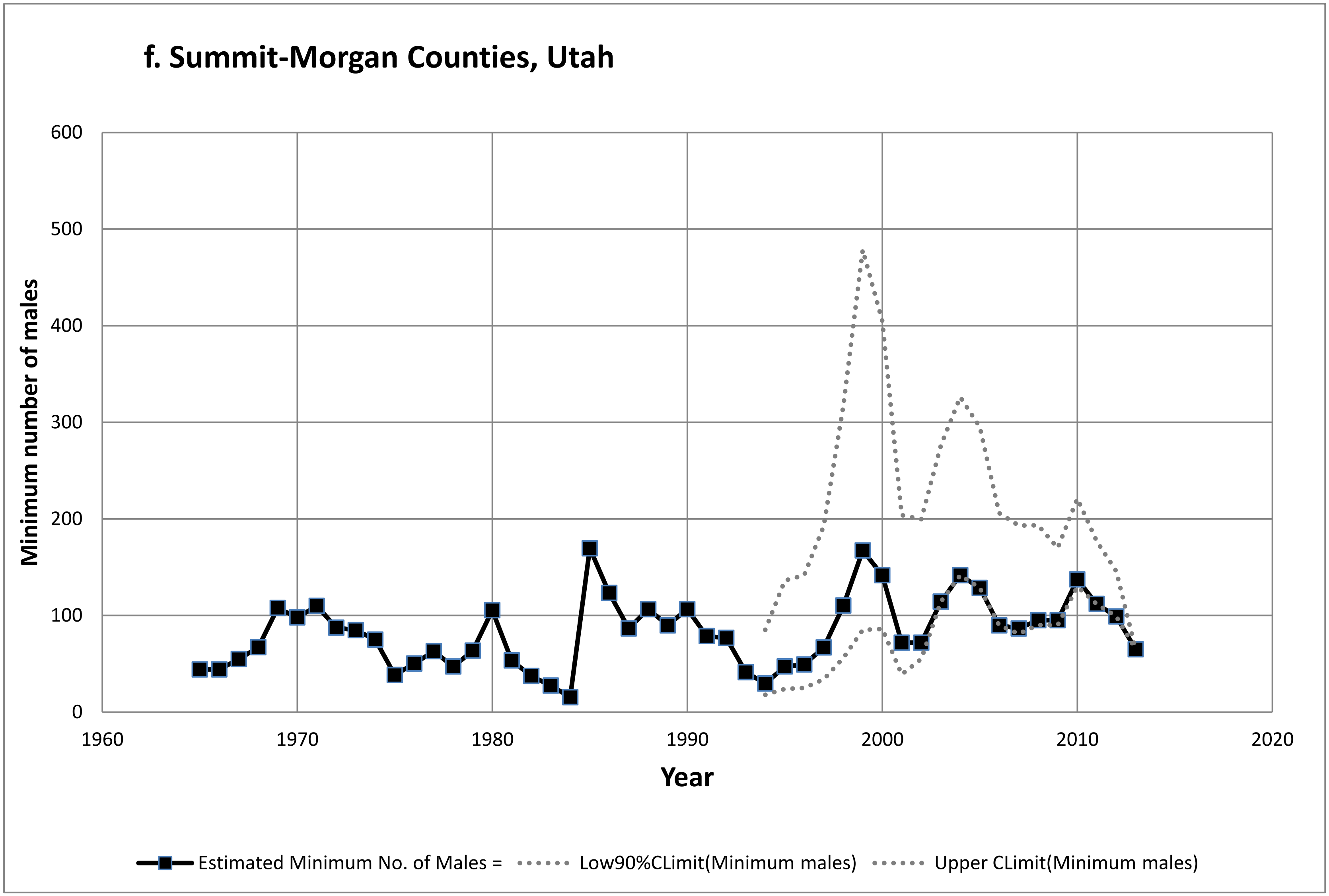

a. Mono Lake, California-Nevada
Minimum number of males
4,000
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

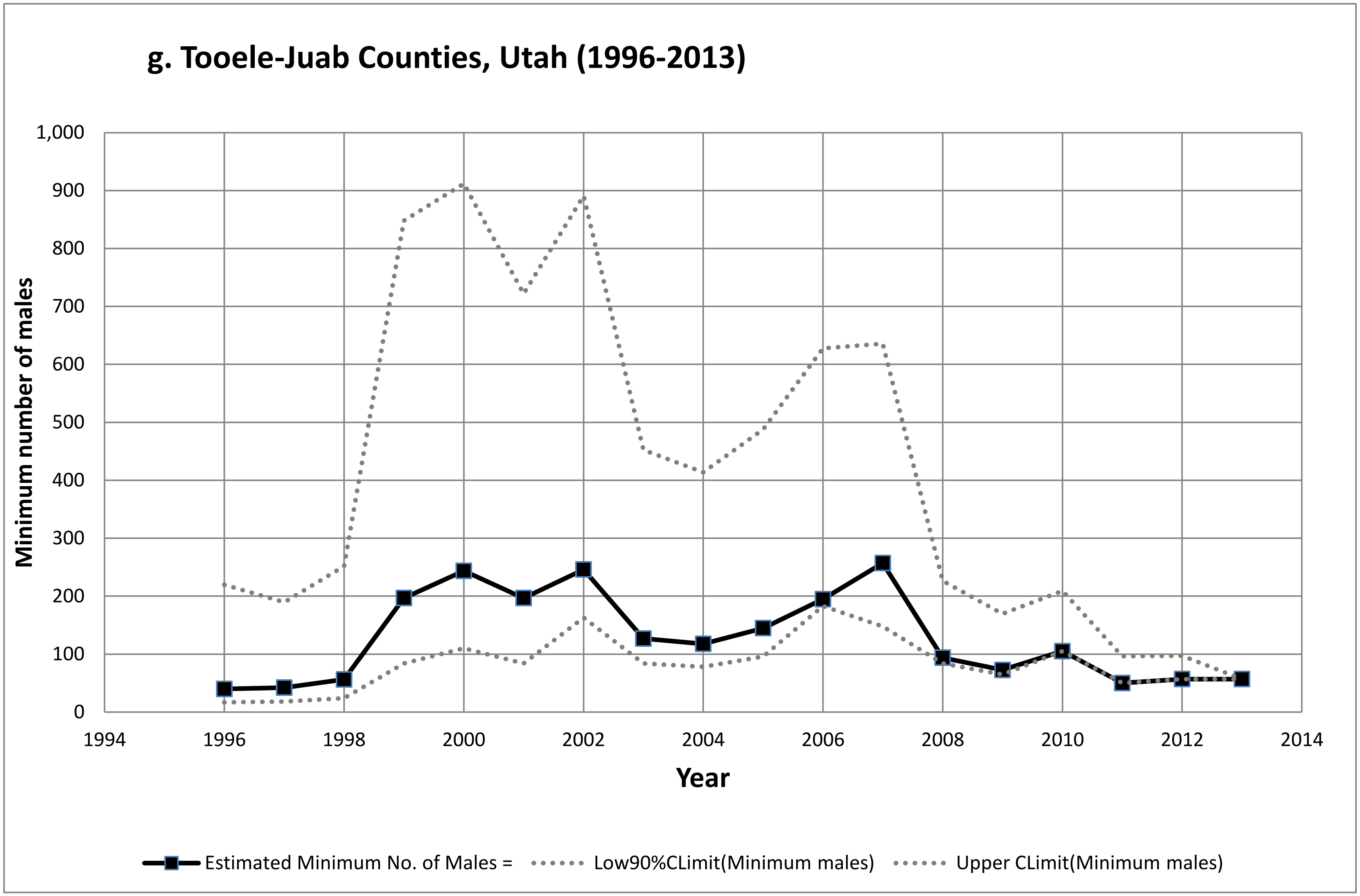

b. South Mono Lake
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

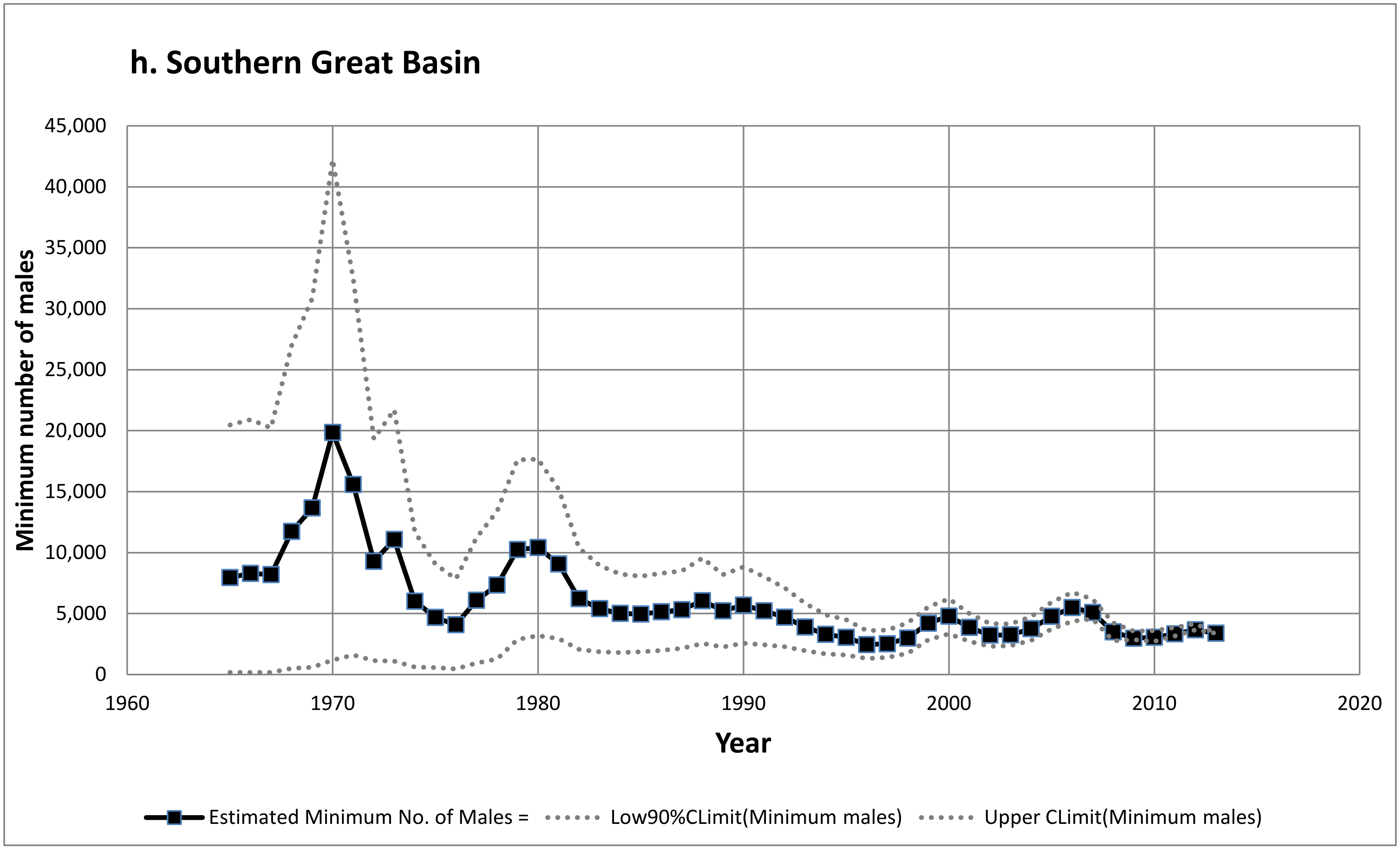

c. NE Interior Utah (1970-2013)
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


d. Sanpete-Emery Counties Utah (1985-2013)
Minimum number of males
400
350
300
250
200
150
100
50
0
1980
1985
1990
1995
2000
2005
2010
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


e. South Central Utah (1967-2013)
3,000
2,500
2,000
1,500
1,000
500
0
Minimum number of males
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


f. Summit-Morgan Counties, Utah
Minimum number of males
600
500
400
300
200
100
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


g. Tooele-Juab Counties, Utah (1996-2013)
Minimum number of males
1,000
900
800
700
600
500
400
300
200
100
0
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


h. Southern Great Basin
Minimum number of males
45,000
40,000
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

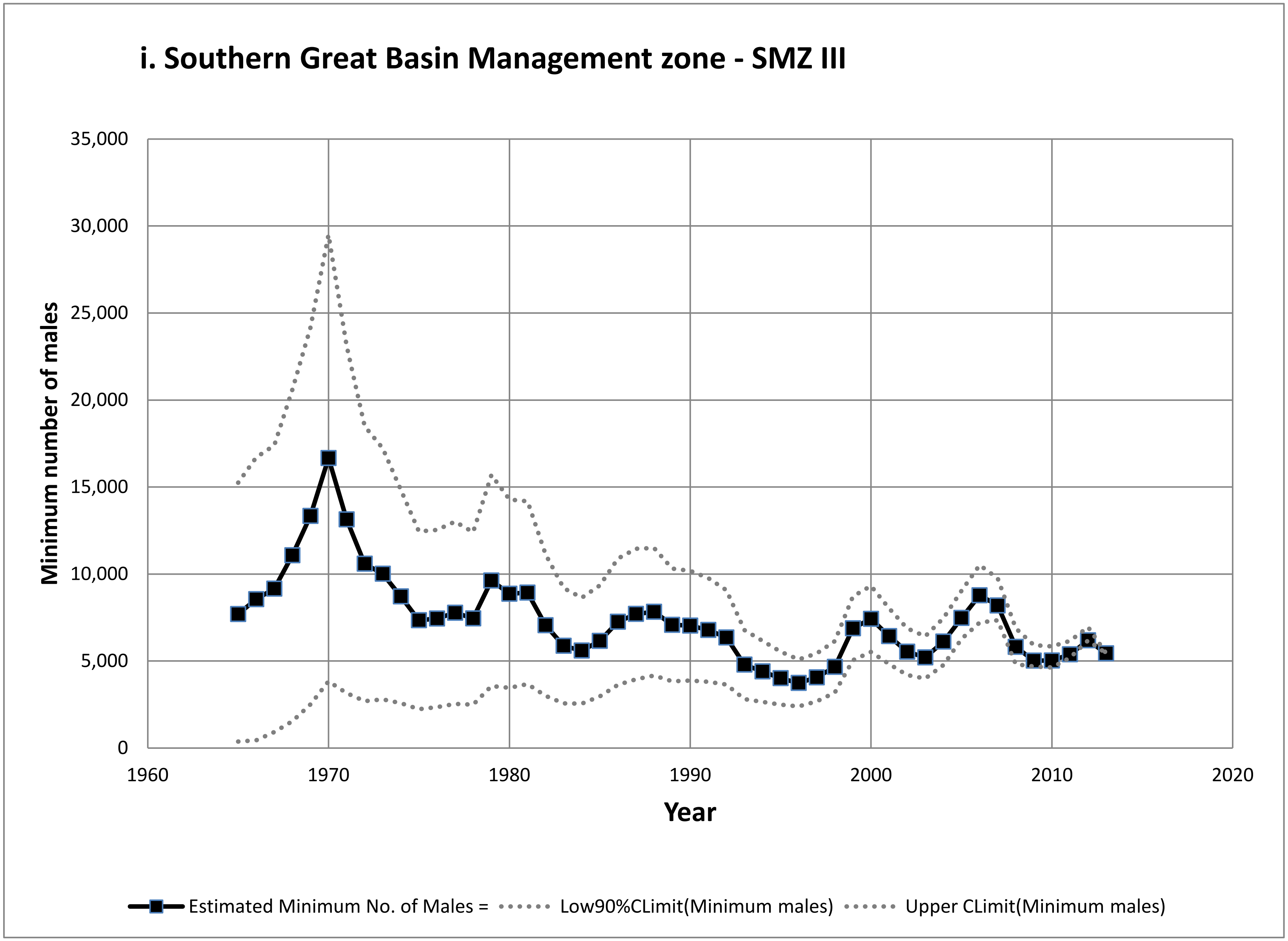
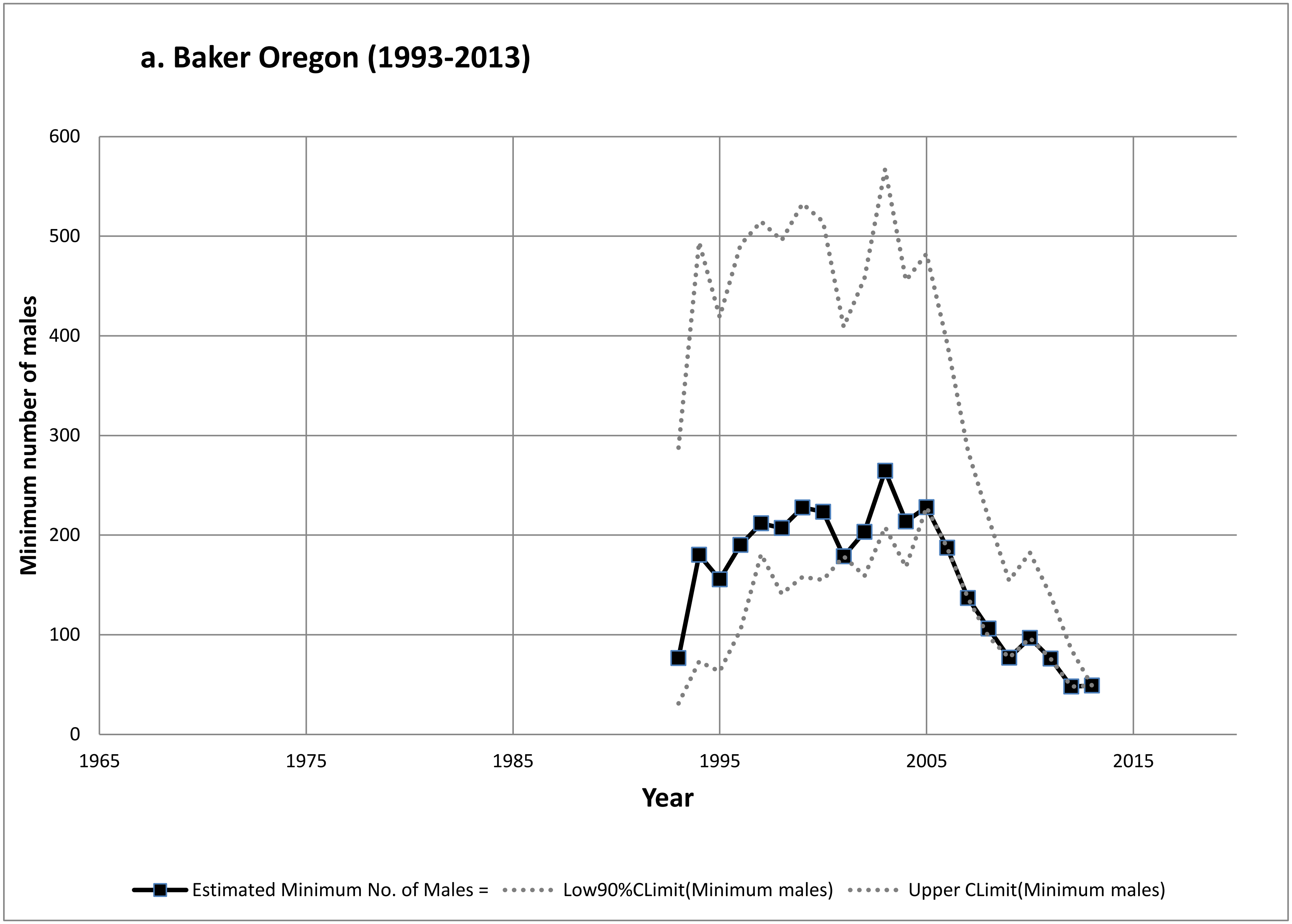
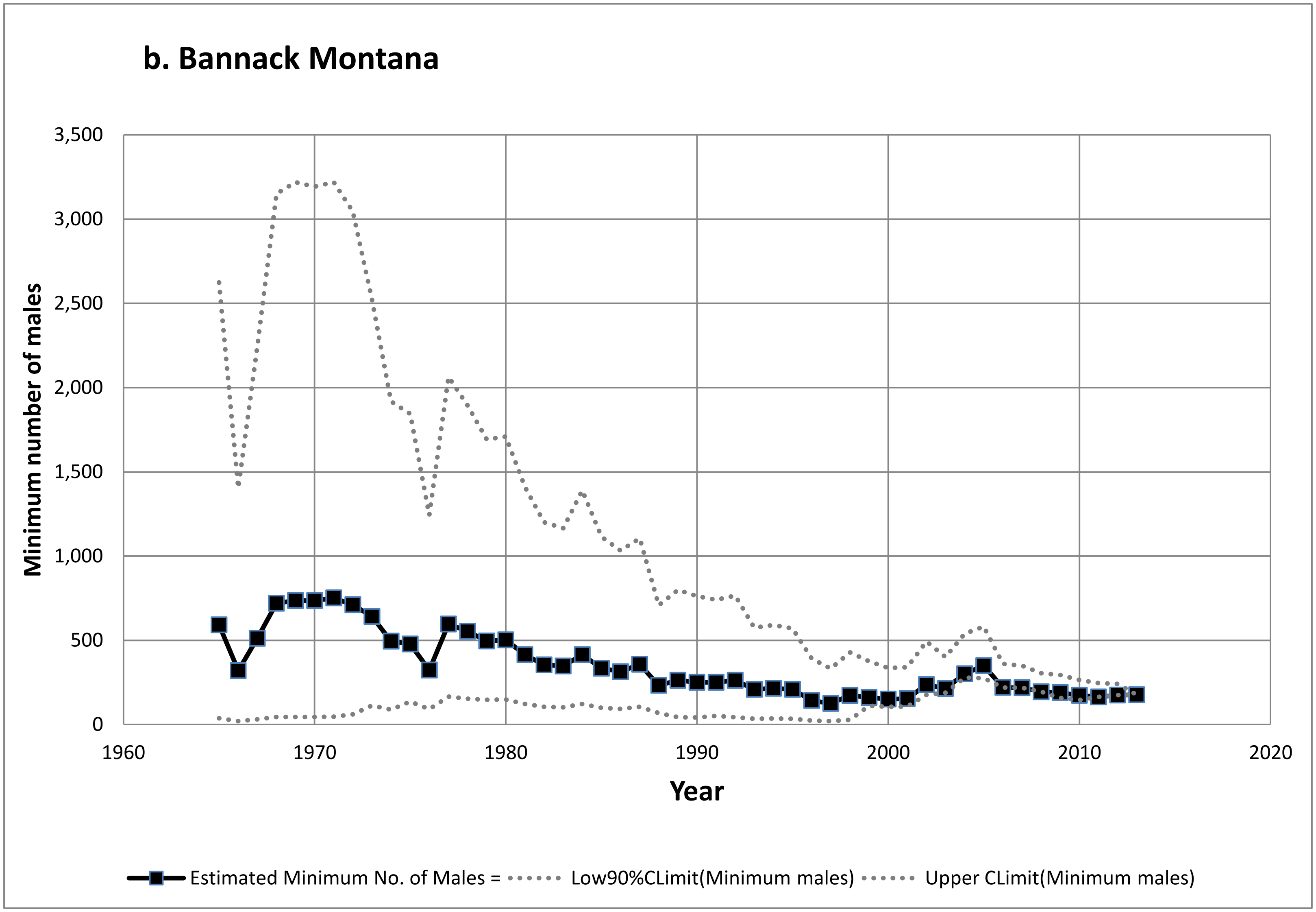
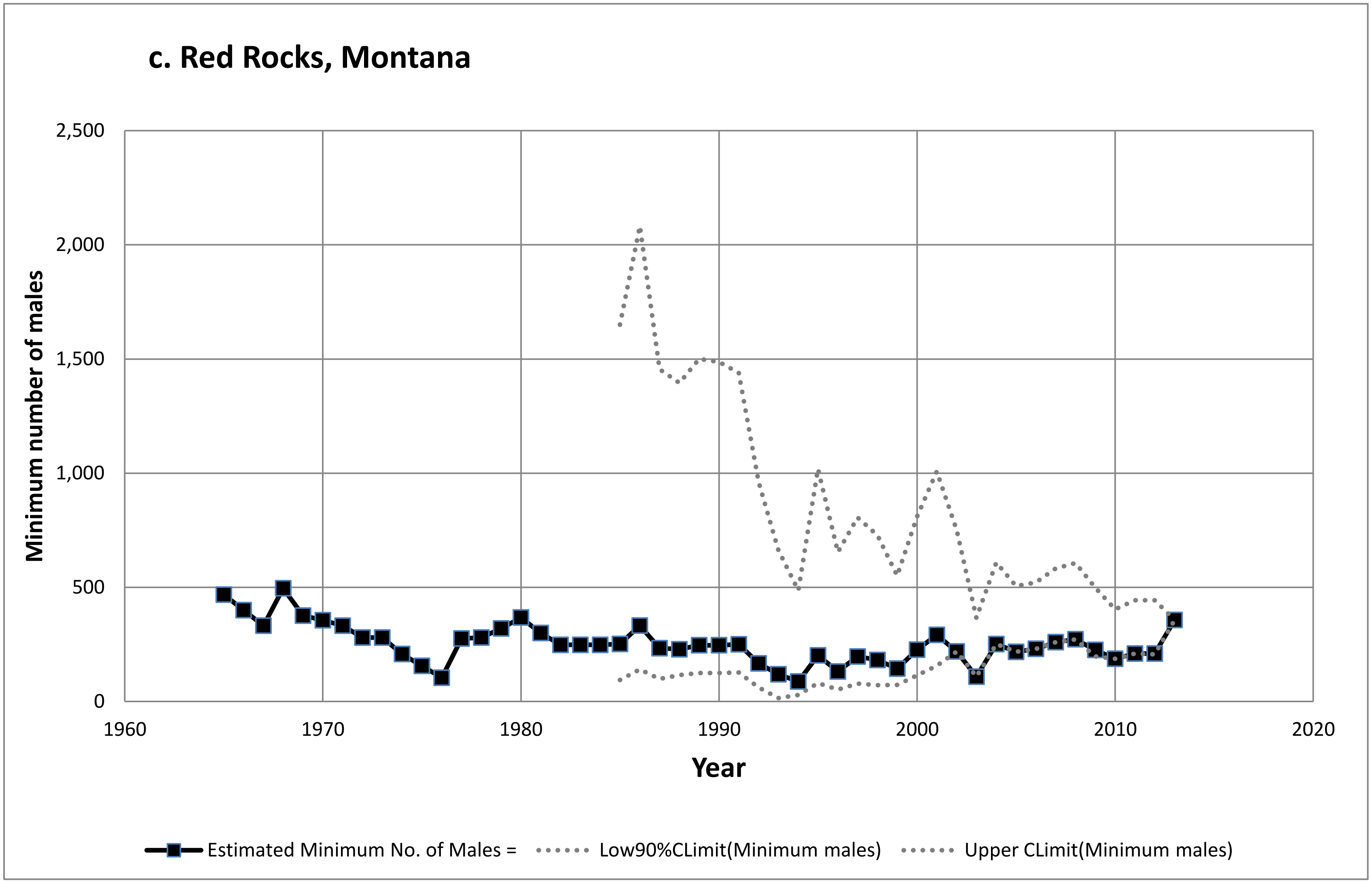
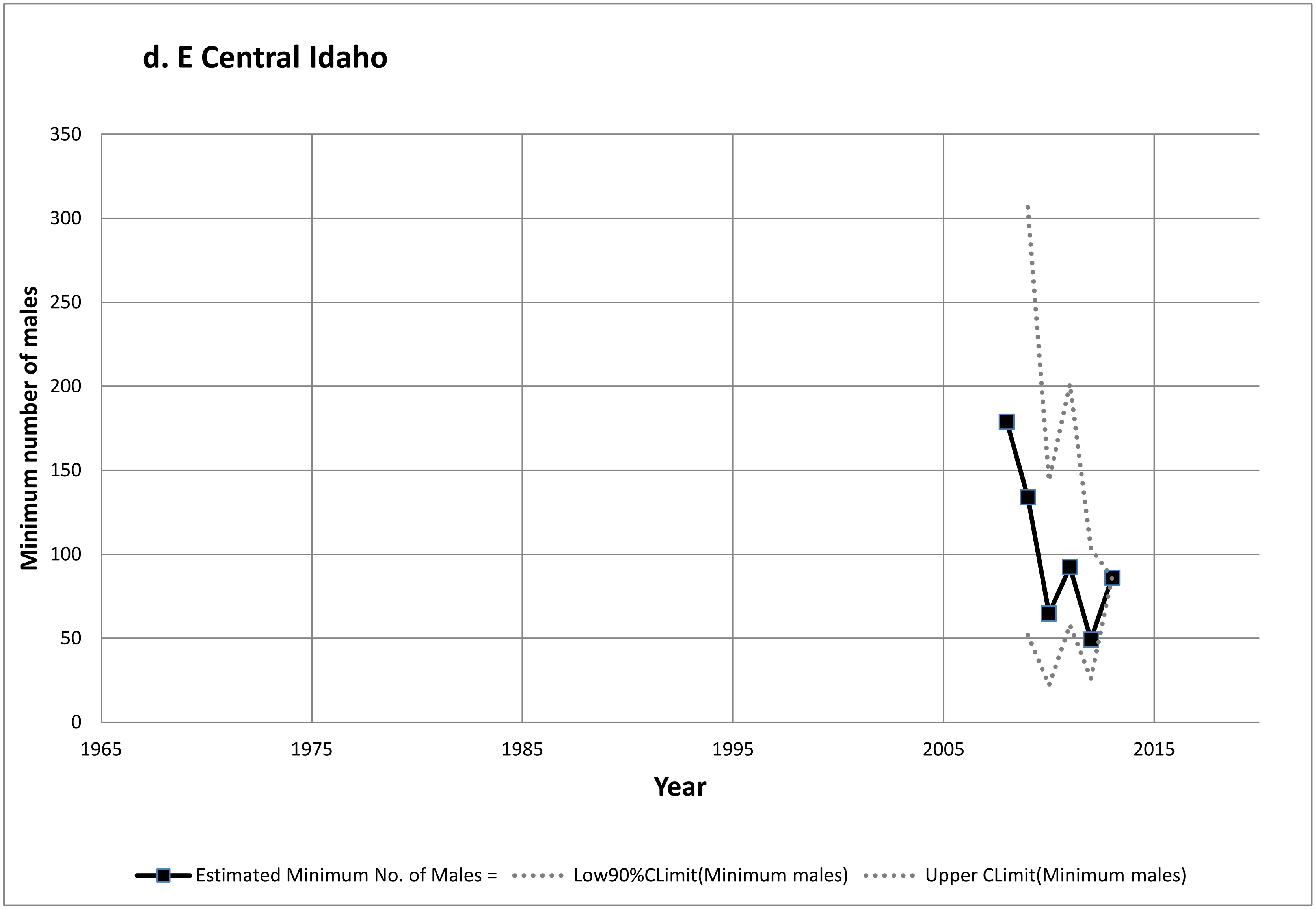

i. Southern Great Basin Management zone - SMZ III
Minimum number of males
35,000
30,000
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 5. Population reconstructions for Snake River Plain populations and Management Zone IV: a. Baker, Oregon; b. Bannack, Montana; c. Red Rocks, Montana; d. East-central Idaho; e. Snake-Salmon-Beaverhead; f. Northern Great Basin; g. Weiser Idaho; h. Management Zone IV.

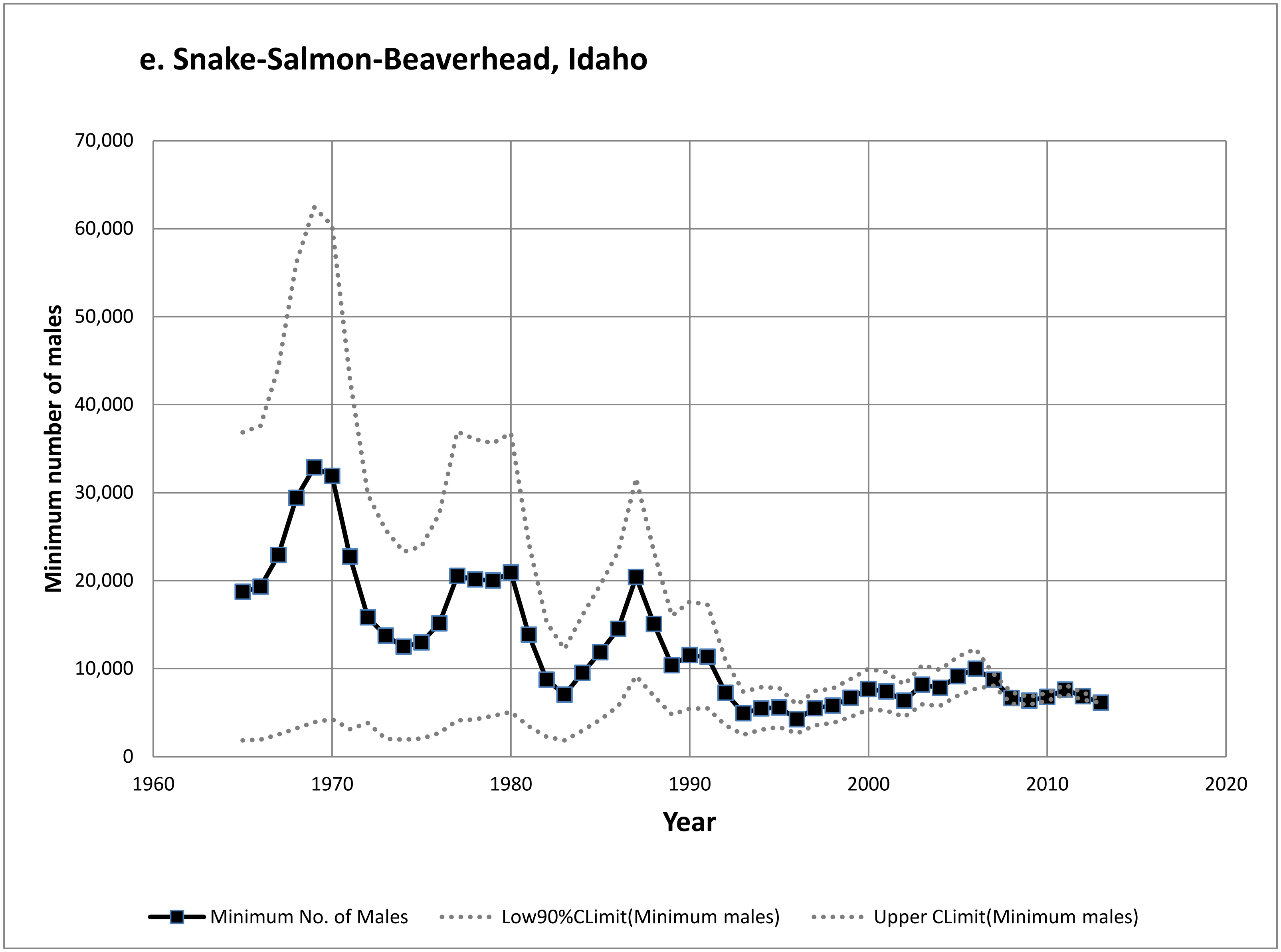

a. Baker Oregon (1993-2013)
Minimum number of males
600
500
400
300
200
100
0
1965
1975
1985
1995
2005
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

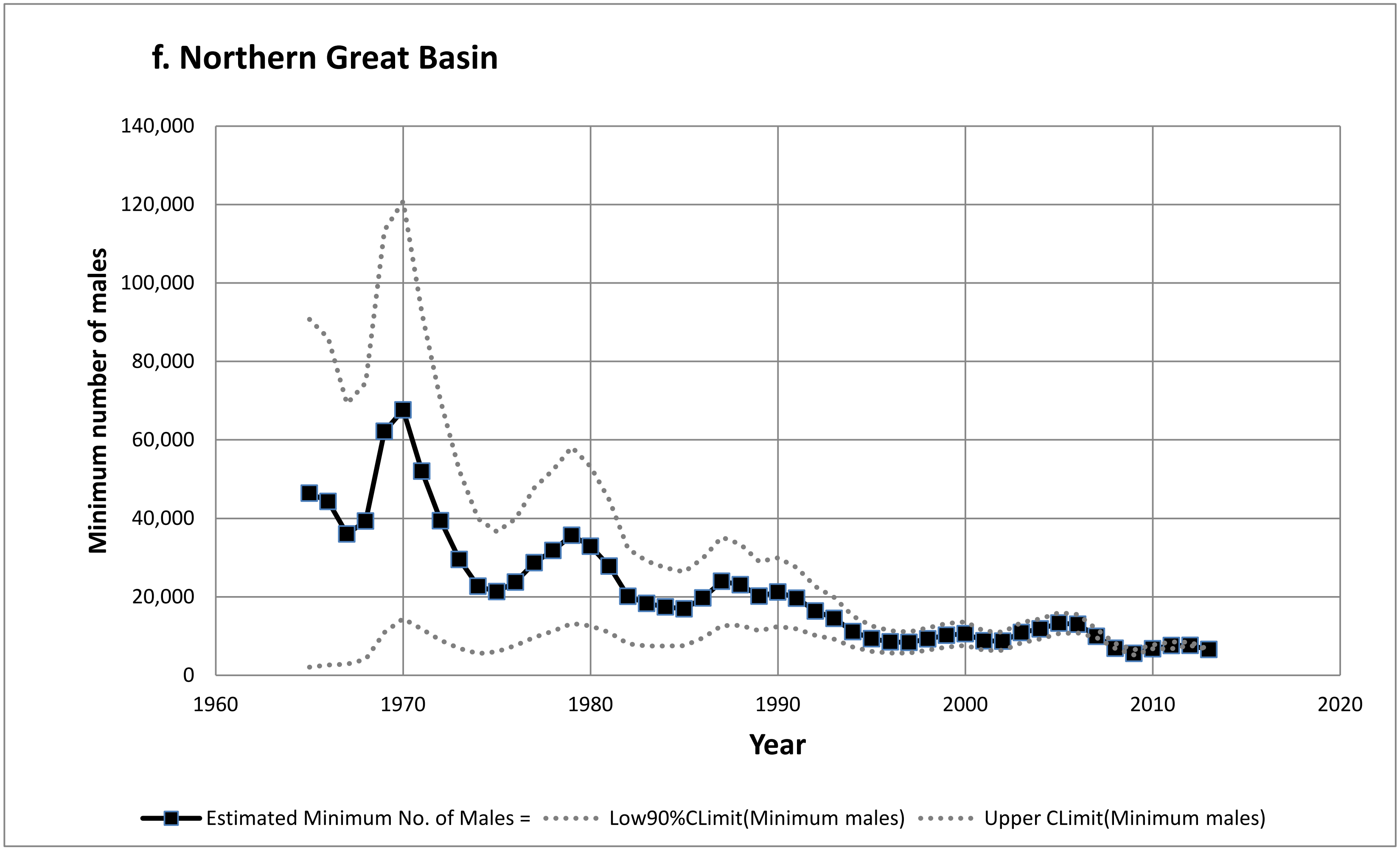

b. Bannack Montana
Minimum number of males
3,500
3,000
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

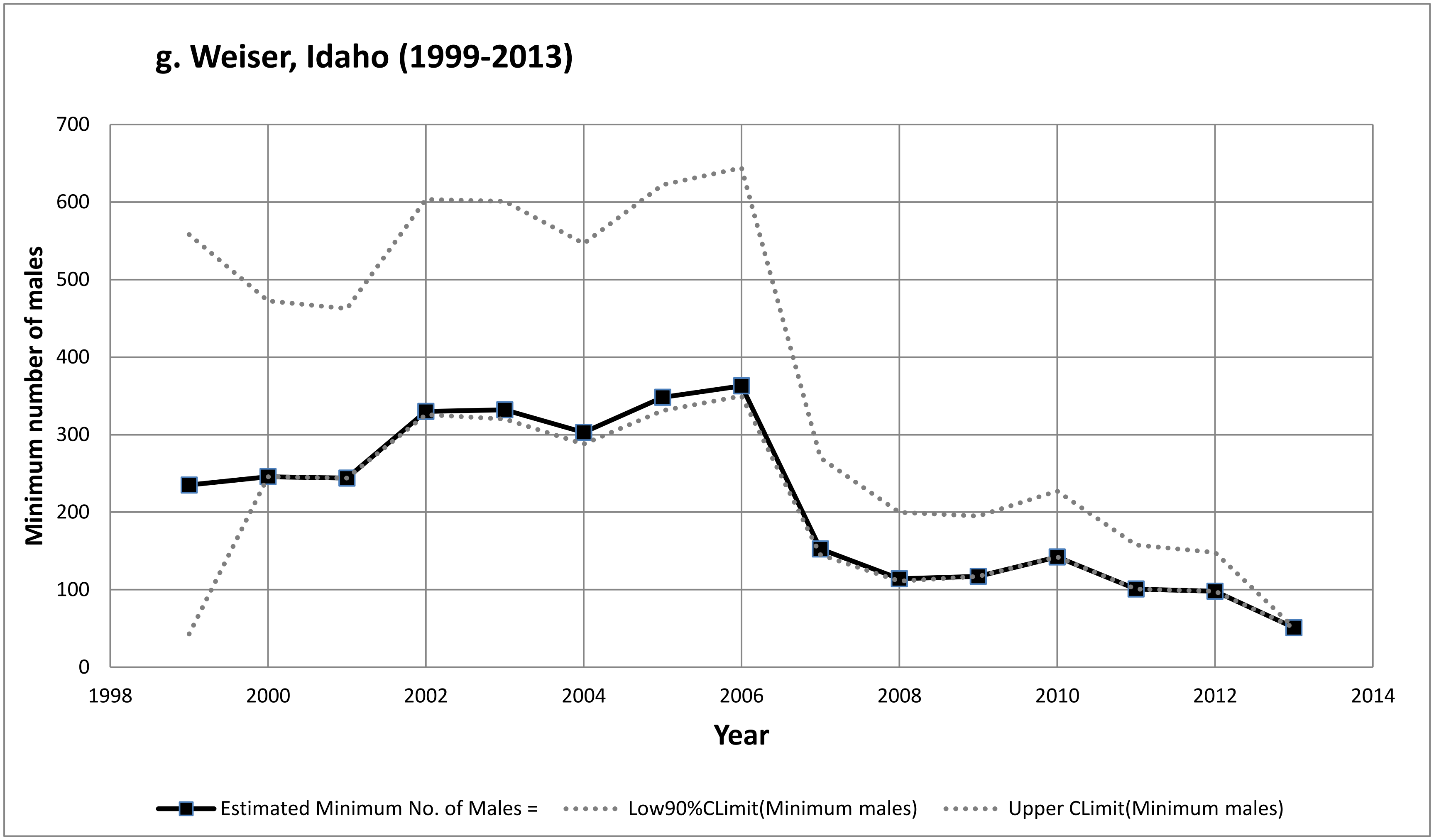

c. Red Rocks, Montana
Minimum number of males
2,500
2,000
1,500
1,000
500
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)



d. E Central Idaho
Minimum number of males
350
300
250
200
150
100
50
0
1965
1975
1985
1995
2005
2015
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


e. Snake-Salmon-Beaverhead, Idaho
Minimum number of males
0
10,000
20,000
30,000
40,000
50,000
60,000
70,000
1960
1970
1980
1990
2000
2010
2020
Year
Minimum No. of Males
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


f. Northern Great Basin
Minimum number of males
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


g. Weiser, Idaho (1999-2013)
Minimum number of males
700
600
500
400
300
200
100
0
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

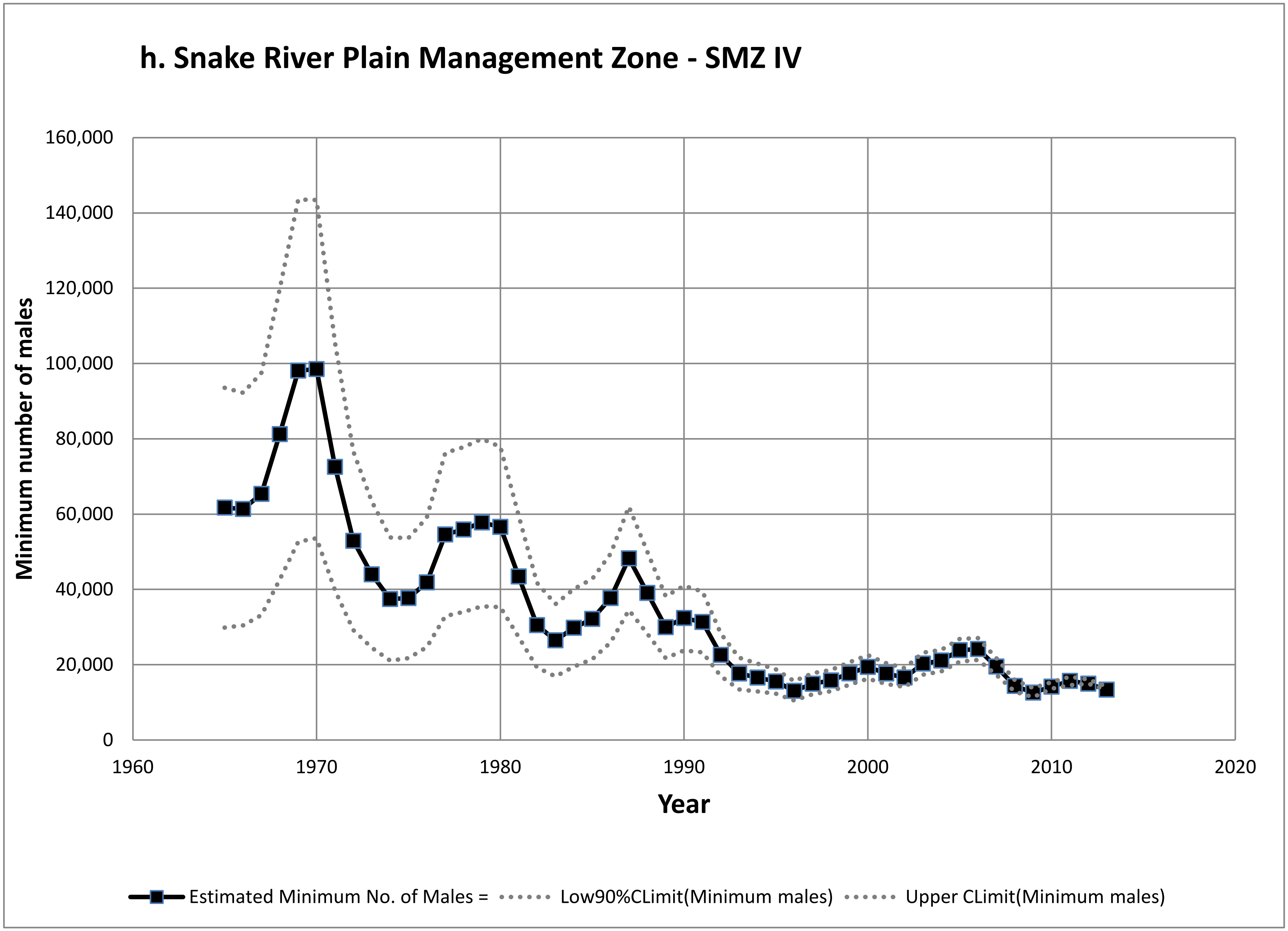
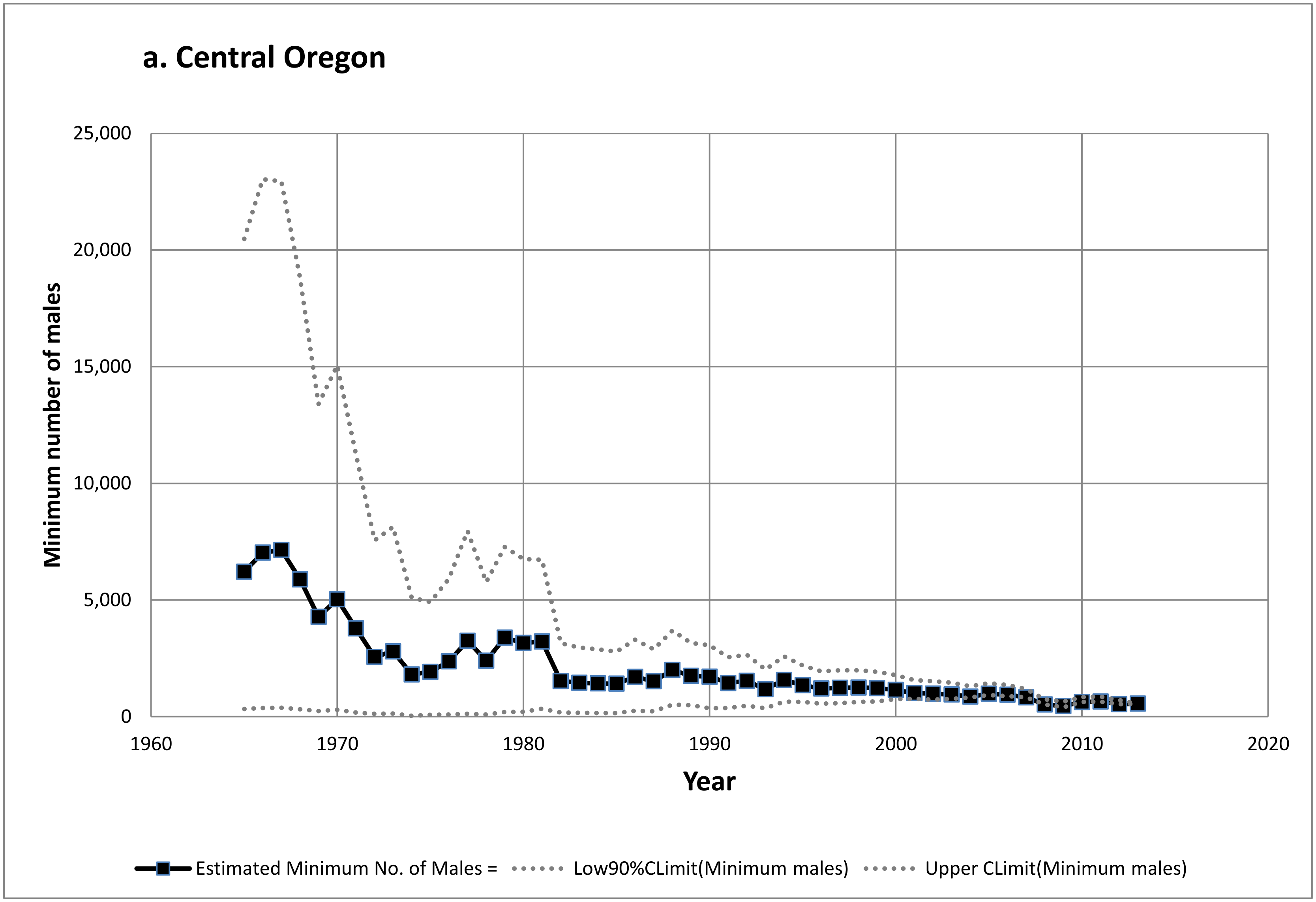
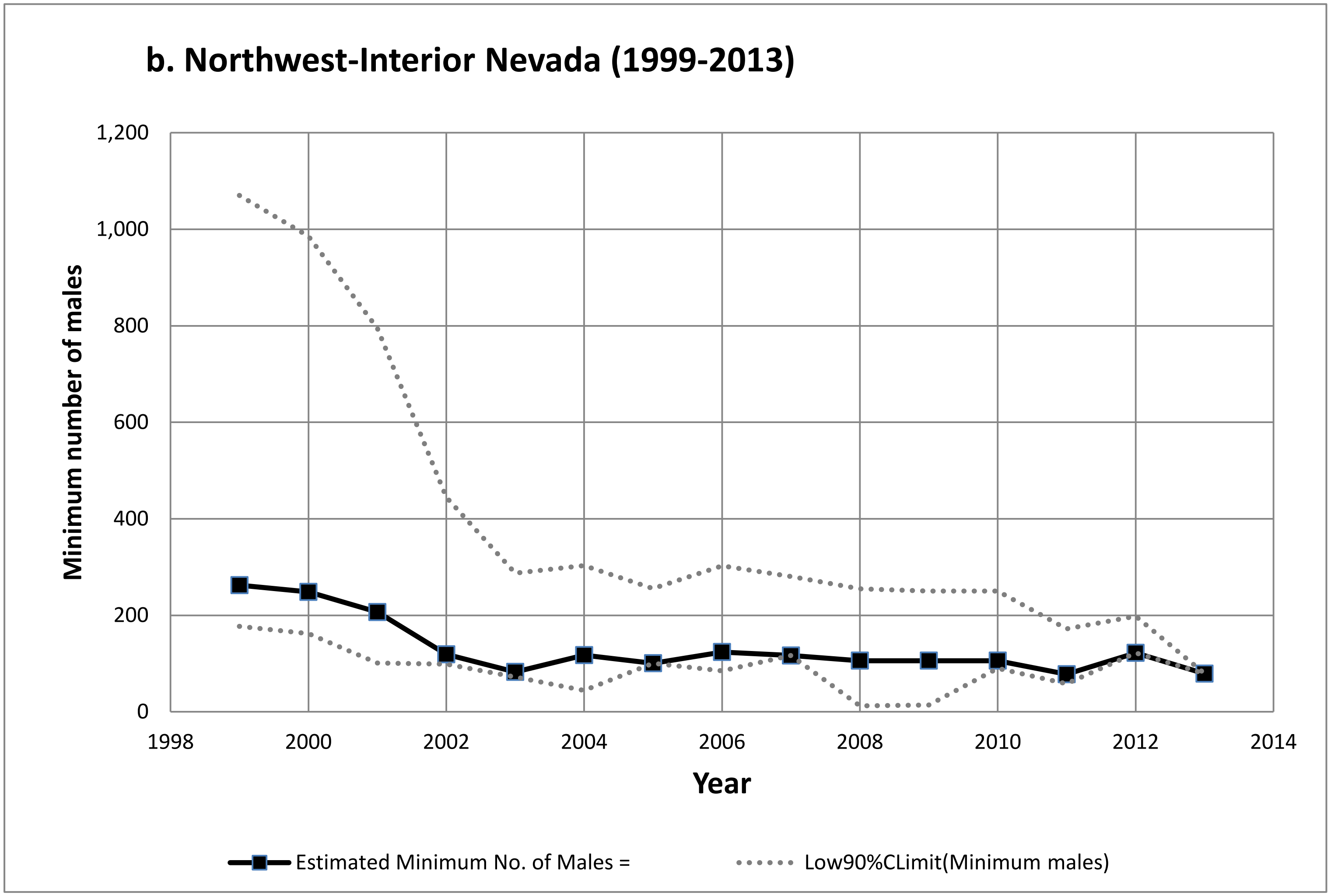
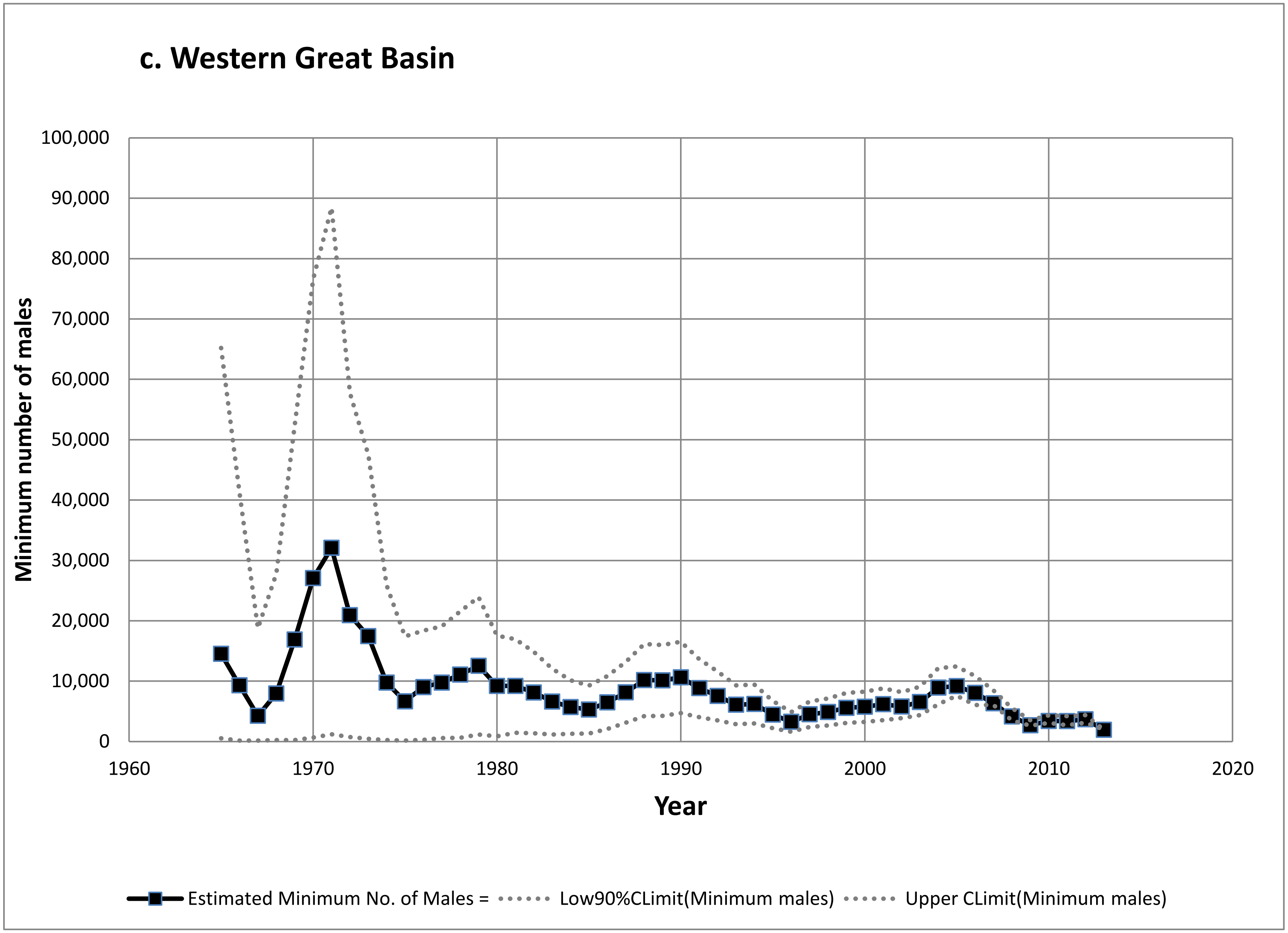

h. Snake River Plain Management Zone - SMZ IV
160,000
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
Minimum number of males
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 6. Population reconstructions for Northern Great Basin populations and Management Zone V: a. Central Oregon. b. Northwest-Interior Nevada; c. Western Great Basin Core; d. Management Zone V.


a. Central Oregon
Minimum number of males
25,000
20,000
15,000
10,000
5,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)


b. Northwest-Interior Nevada (1999-2013)
Minimum number of males
1,200
1,000
800
600
400
200
0
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)


c. Western Great Basin
Minimum number of males
100,000
90,000
80,000
70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

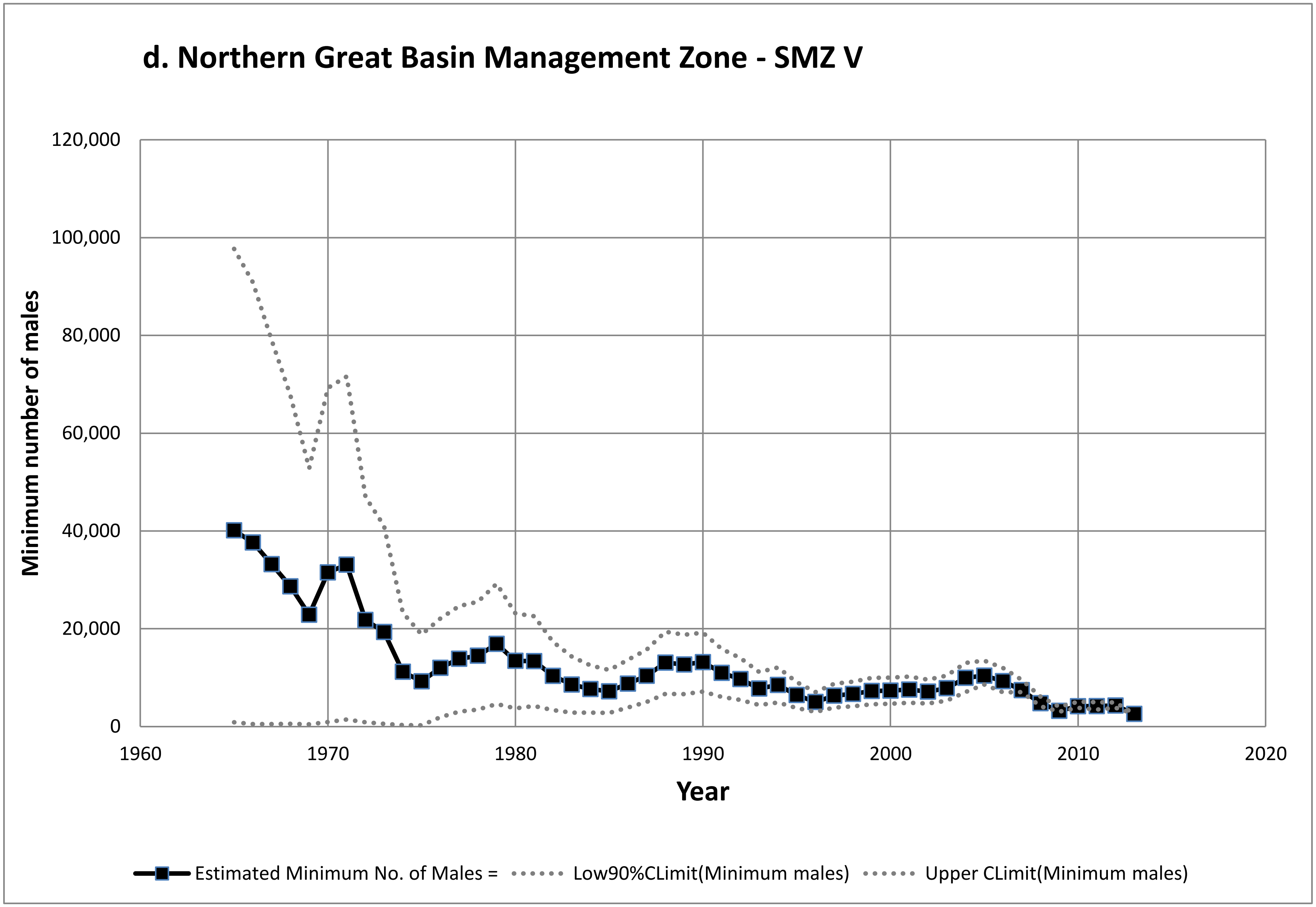
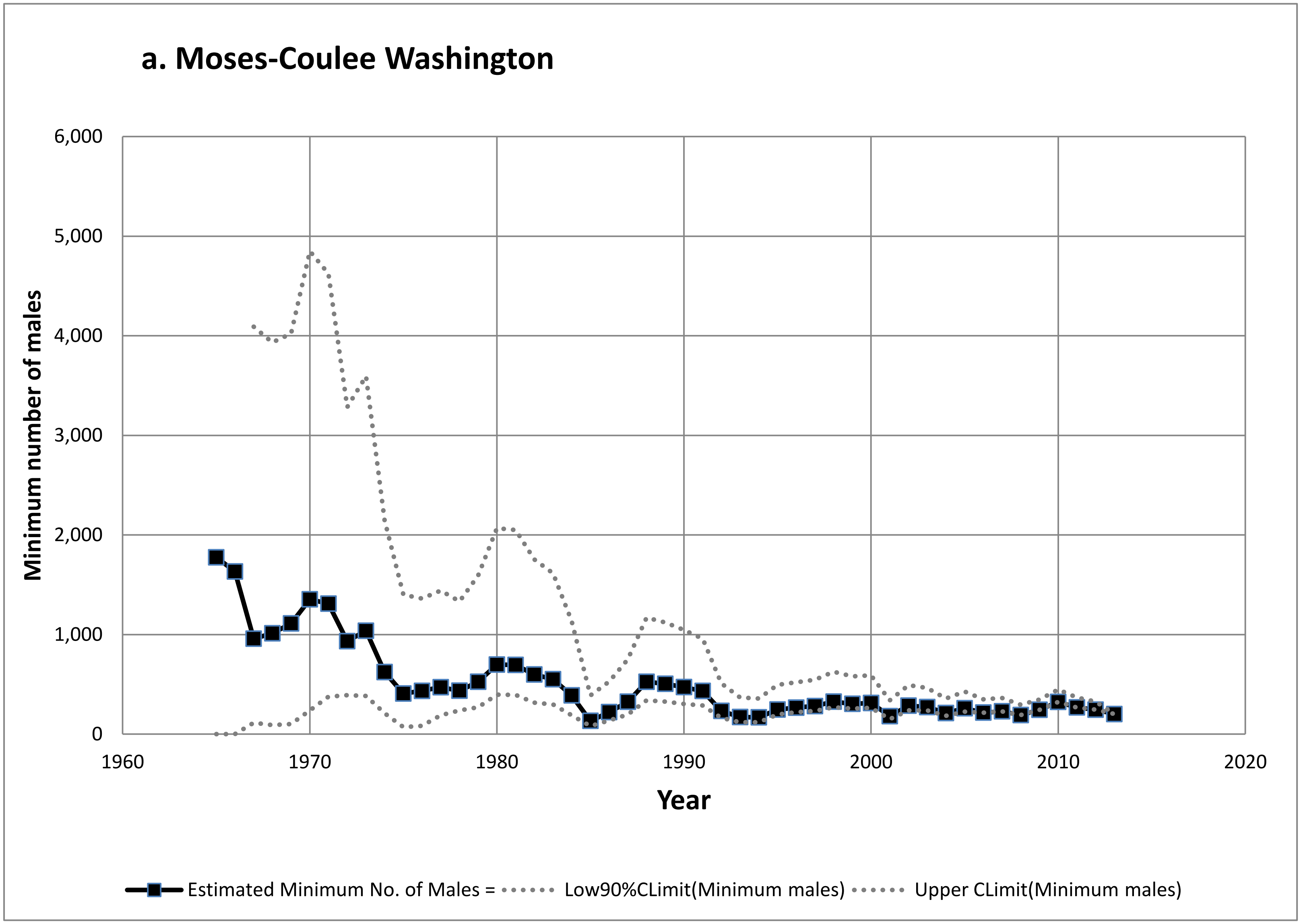
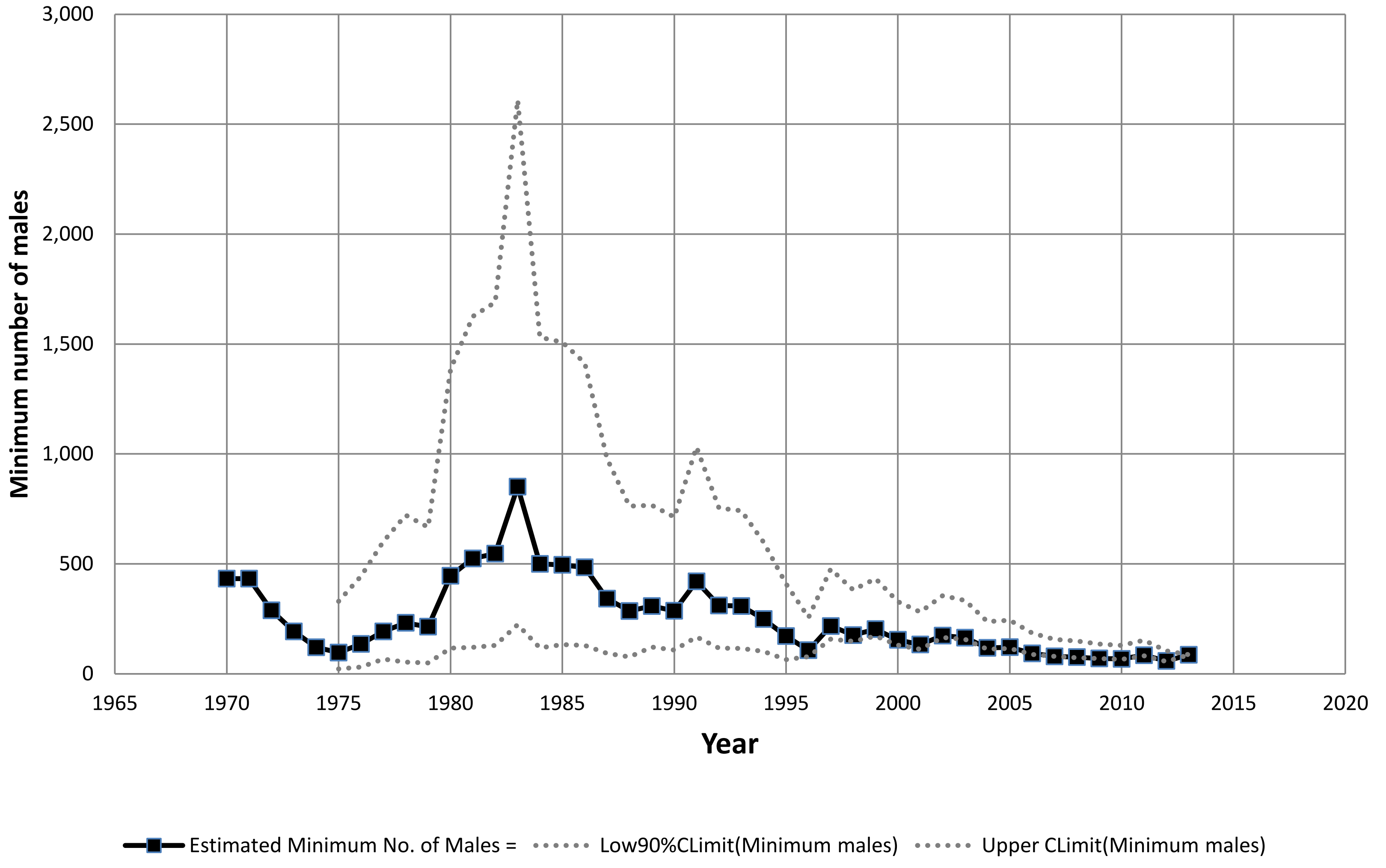
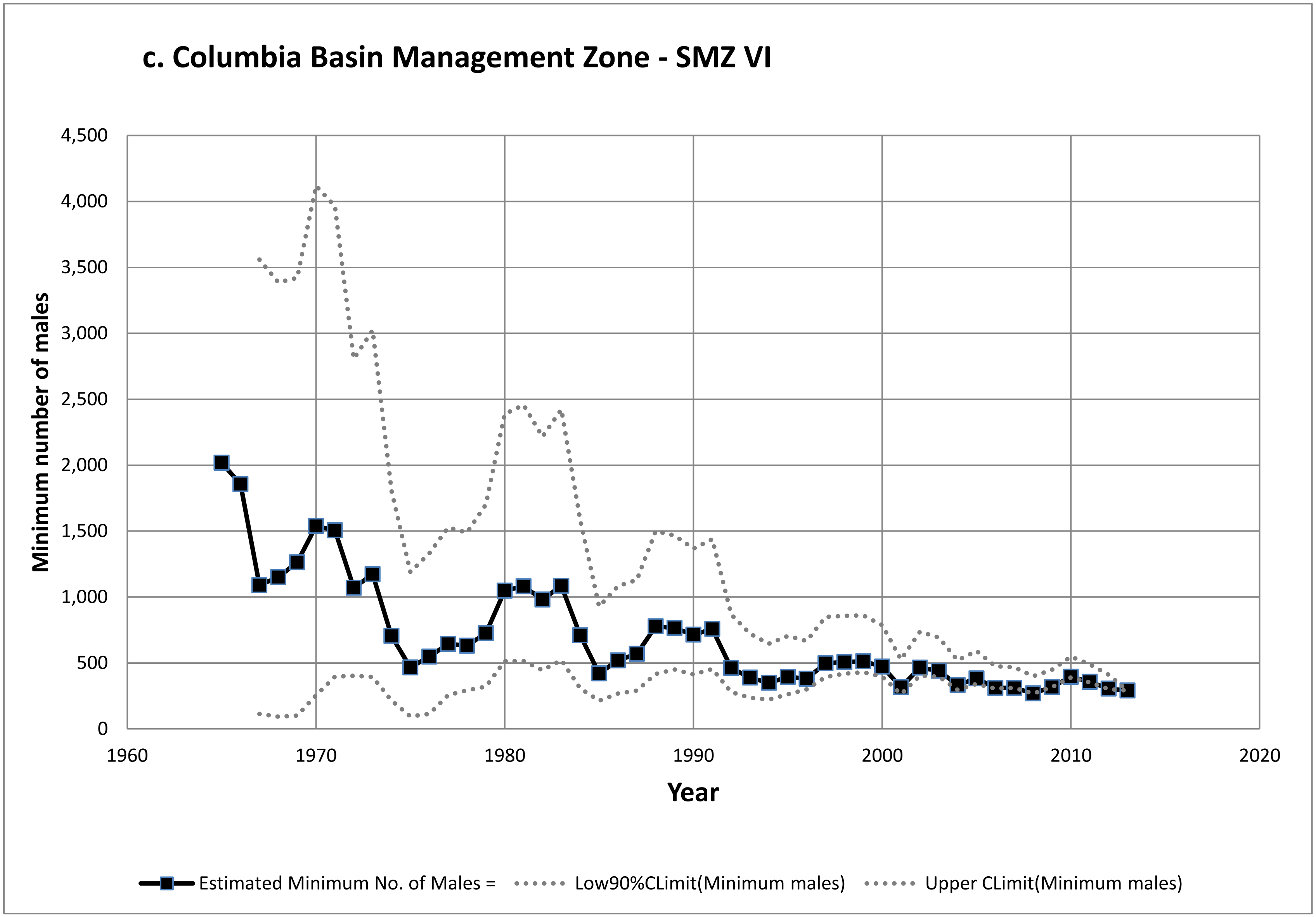

d. Northern Great Basin Management Zone - SMZ V
Minimum number of males
120,000
100,000
80,000
60,000
40,000
20,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)

Figure 7. Population reconstructions for Columbia Basin populations and Management Zone VI: a. Moses-Coulee, Washington. b. Yakima, Washington. c. Management Zone VI.


a. Moses-Coulee Washington
Minimum number of males
6,000
5,000
4,000
3,000
2,000
1,000
0
1960
1970
1980
1990
2000
2010
2020
Year
Estimated Minimum No. of Males =
Low90%CLimit(Minimum males)
Upper CLimit(Minimum males)



b. Yakima Washington (1970-2013)



c. Columbia Basin Management Zone - SMZ VI

Figure 8. Estimated minimum number of males attending leks from population reconstructions for each management zone and range-wide population of Greater Sage-Grouse from combining total estimates across all Sage-Grouse Management Zones I-VI for period 2007 to 2013. SMZ I –Great Plains = navy blue; SMZII Wyoming Basin =red; SMZIII Southern Great Basin=chartreuse; SMZIV Snake River Plain = black; SMZ V Northern Great Basin = pink; SMZ VI Columbia Basin = light blue; Range-wide = purple.

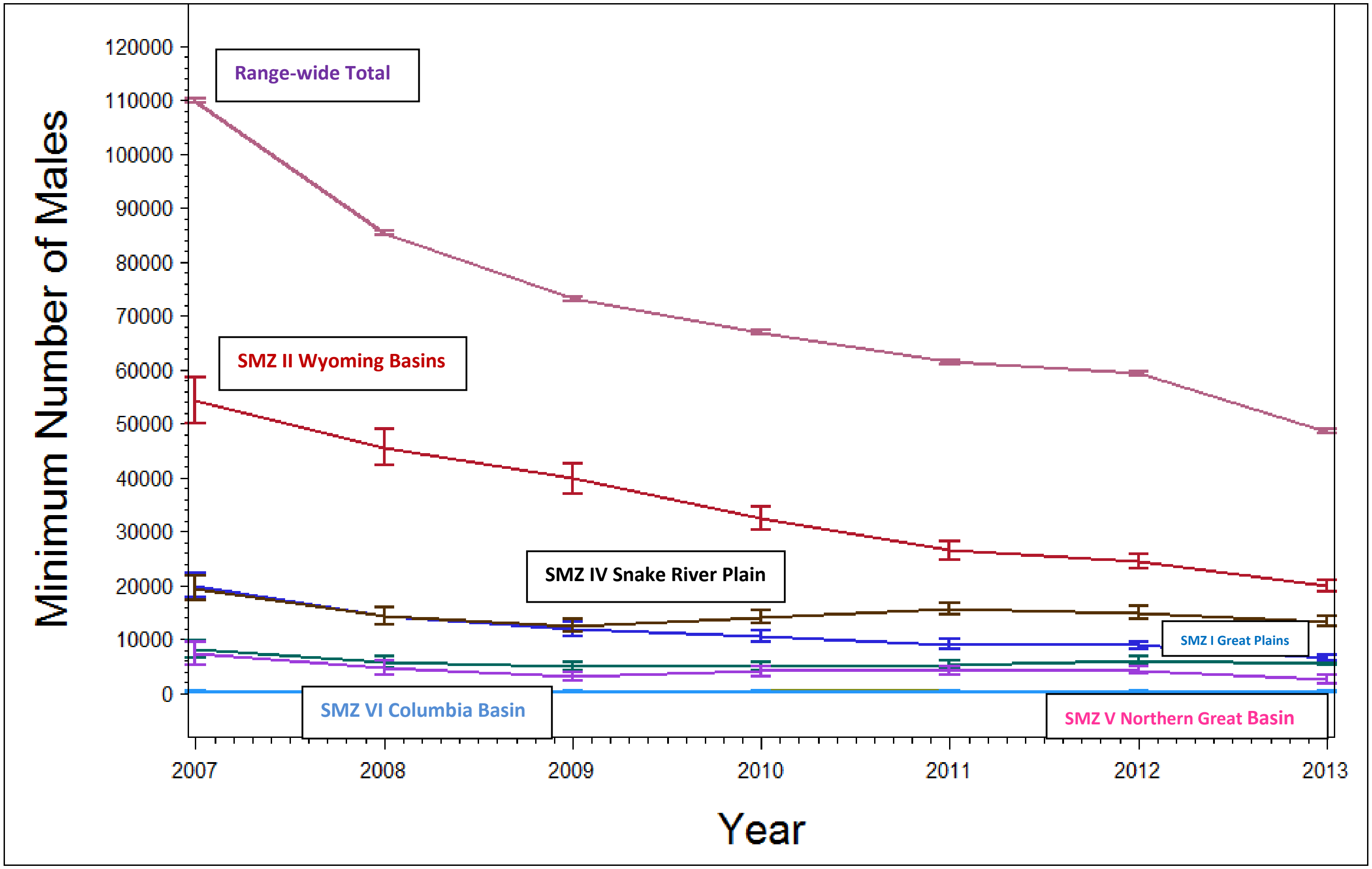


Figure 9. Population reconstruction for range-wide population of Greater Sage-Grouse from combining total estimates across all Sage-Grouse Management Zones I-VI.

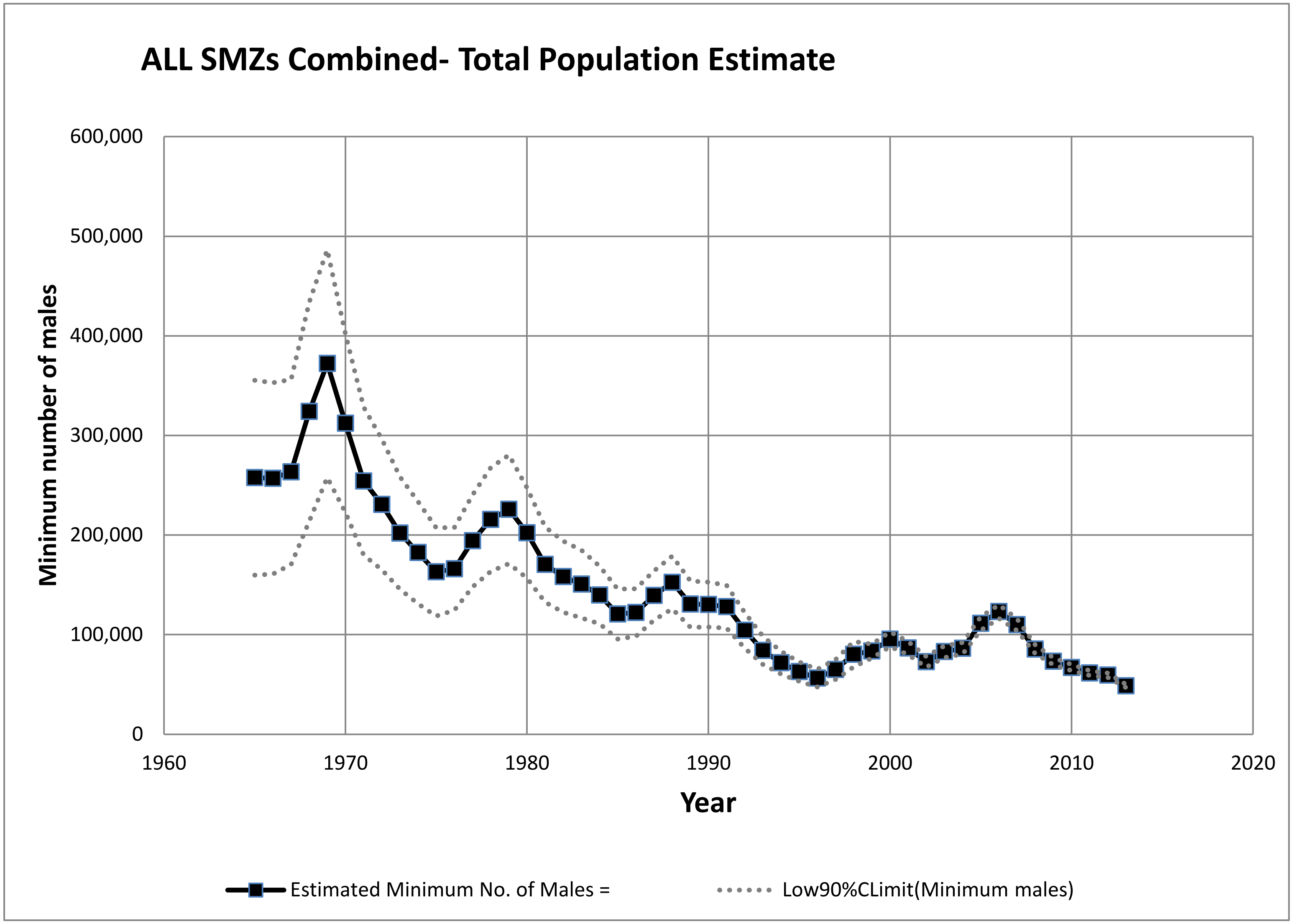


Figure 10. Validation of model predictions by comparing observed abundance in 2013 to forecasts of best models for 2013 estimated from mean rates of change forecast from 2007 to 2013. Note that predictions were tested from the 10 best models in Appendix 2 for all management zones except Colorado Plateau.