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Research Article

Greater Sage-Grouse Population Trends Across Wyoming

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ABSTRACT The scale at which analyses are performed can have an effect on model results and often one scale does not accurately describe the ecological phenomena of interest (e.g., population trends) for wide-ranging species: yet, most ecological studies are performed at a single, arbitrary scale. To best determine local and regional trends for greater sage-grouse (*Centrocercus urophasianus*) in Wyoming, USA, we modeled density-independent and -dependent population growth across multiple spatial scales relevant to management and conservation (Core Areas [habitat encompassing approximately 83% of the sage-grouse population on ~24% of surface area in Wyoming], local Working Groups [7 regional areas for which groups of local experts are tasked with implementing Wyoming's statewide sage-grouse conservation plan at the local level], Core Area status (Core Area vs. Non-Core Area) by Working Groups, and Core Areas by Working Groups). Our goal was to determine the influence of fine-scale population trends (Core Areas) on larger-scale populations (Working Group Areas). We modeled the natural log of change in population size ($\bar{x}$ peak M lek counts) by time to calculate the finite rate of population growth (λ) for each population of interest from 1993 to 2015. We found that in general when Core Area status (Core Area vs. Non-Core Area) was investigated by Working Group Area, the 2 populations trended similarly and agreed with the overall trend of the Working Group Area. However, at the finer scale where Core Areas were analyzed separately, Core Areas within the same Working Group Area often trended differently and a few large Core Areas could influence the overall Working Group Area trend and mask trends occurring in smaller Core Areas. Relatively close fine-scale populations of sage-grouse can trend differently, indicating that large-scale trends may not accurately depict what is occurring across the landscape (e.g., local effects of gas and oil fields may be masked by increasing larger populations). Published 2017. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Centrocercus urophasianus*, density-dependent growth, density-independent growth, finite population growth rate, generalized linear model, greater sage-grouse, population viability analysis, Wyoming.

The scale at which analyses are performed can influence model outcomes because results will differ across scales (Bissonette 2017). There is no single scale to accurately and completely describe ecological phenomena (e.g., population trends) and therefore multiple spatial scales are required to accurately evaluate populations (Fuhlendorf et al. 2002, Bissonette 2017). For wide-ranging species, evaluating population trends at a single scale may result in an incomplete interpretation of population change (Fuhlendorf et al. 2002). Modeling population trends at multiple spatial scales also can facilitate the determination of the cause of population changes and be used to prioritize conservation strategies and research (Sadoul 1997, DeSante et al. 2001, Wallace et al. 2010). However, many studies are performed arbitrarily at single spatial scales and few researchers have evaluated the relationship between scale and population trends (Bissonette 1997, 2017; Fuhlendorf et al. 2002).

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) currently occupy roughly 56% of their historical range in western North America, which now includes portions of 11 states in the United States and 2 Canadian provinces but previously encompassed 15 states and 3 provinces (Connelly and Braun 1997, Schroeder et al. 2004). Range contraction has been linked to loss of habitat in the sagebrush (*Artemisia* spp.) ecosystem (Schroeder et al. 2004), for which sage-grouse are an obligate species (Beever and Aldridge 2011). Landscape changes of sagebrush ecosystems

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have been linked to livestock grazing (Beck and Mitchell 2000, Hayes and Holl 2003, Crawford et al. 2004), oil and gas development (Braun et al. 2002, Lyon and Anderson 2003, Holloran 2005), cultivation (Connelly et al. 2004), invasive plant species (e.g., cheatgrass [*Bromus tectorum*]; Wisdom et al. 2002, Knick et al. 2003, Connelly et al. 2004), and changes in fire regime (Connelly et al. 2000, 2004).

In addition to range contraction, sage-grouse populations generally have been declining range-wide since the 1920s (Braun 1998). Sage-grouse populations fluctuate over approximately 9- to 10-year cycles (Fedy and Aldridge 2011, Fedy and Doherty 2011), whereby periods of decline are followed by periods of increasing populations and vice versa (Rich 1985); however, subsequent population highs generally are lower than the preceding high level, resulting in an overall downward population trend (Braun 1998). The range-wide breeding population has declined 45–80% since the 1950s with the majority of declines occurring after 1980 (Braun 1998). Others have estimated breeding populations declined approximately 2% annually during 1965–2003 (Connelly et al. 2004). Of note, these studies occurred >13 years ago, and there is some uncertainty regarding more recent population trends. Population declines have resulted in sage-grouse populations in Canada being listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (Aldridge and Brigham 2003) and recently, the United States Fish and Wildlife Service (USFWS) considered listing sage-grouse under the Endangered Species Act but ruled sage-grouse were not warranted for protection (USFWS 2015). This ruling was based on unprecedented conservation efforts that were implemented in federal and state management plans written during the previous 5 years targeted at ameliorating population threats identified by the USFWS when they ruled that sage-grouse were warranted for listing in 2010 but precluded because of higher priority species (USFWS 2010).

The state of Wyoming contains approximately 37% of the remaining sage-grouse populations (Doherty et al. 2010). However, populations of sage-grouse in Wyoming are declining (Fedy and Aldridge 2011). Populations across the state declined 29–76% during 2007–2013, resulting in populations that represented approximately 4–25% of the size of the same populations in the 1970s and 1980s (Garton et al. 2011, 2015). Further, gas and oil development has caused lek abandonment and declines in breeding populations (Green et al. 2017), particularly in western and northeast Wyoming (Holloran 2005, Walker et al. 2007).

The period 2007–2013 appears to have encompassed the low end of the approximately 10-year cycle that perhaps ended in 2013, so population declines may have been exacerbated by the declining period in the population cycle. However, the last 3 decadal cycles have resulted in decreases in the magnitude of change between periods of highs and lows, resulting in an overall population decline and populations reaching the lowest range-wide estimate (48,641 males) since the 1960s when counting males on spring breeding grounds, or leks, began in earnest (Garton et al. 2011, 2015). This suggests populations should rebound, but low annual turnover and reproductive rates indicate population recovery may be slow (Connelly and Braun 1997). Furthermore, models forecasting future oil and gas, wind, and residential development in Wyoming project future population declines of 9–29% in Wyoming populations over long-term scenarios (Copeland et al. 2013), with measured declines of up to 15%/year estimated for current high-density developments (Green et al. 2017).

Sage-grouse are an indicator species of the overall health of sagebrush ecosystems (Connelly et al. 2004, Blomberg et al. 2013), which are one of the most imperiled ecosystems in North America (Noss et al. 1995). Bird species endemic to shrublands and grasslands are declining at quicker rates than any other species assemblage in North America (Knick et al. 2003). Sage-grouse may serve as an umbrella species, whereby management strategies for one species benefit co-occurring endemic species (Branton and Richardson 2011), such as passerine species (Rowland et al. 2006, Hanser and Knick 2011). Furthermore, recent evidence demonstrates that conservation of umbrella species results in higher species richness and abundance of co-occurring species when birds are the umbrella species (Branton and Richardson 2011). With sage-grouse populations decreasing, it is imperative to assess their population trends based on boundaries highlighting landscape changes and spatial variability of the populations.

Sage-grouse leks are traditional display areas where ≥ 2 male sage-grouse gather annually (or ≥ 2 years in the previous 5) in the spring to attract female mates and usually are located in open areas that are within or directly adjacent to sagebrush habitats (Connelly et al. 2011*b*). The consistent location of lek sites makes them ideal sites for population monitoring and counting males at leks (i.e., lek counts) has been used traditionally by state and provincial wildlife agencies as an index of population abundance (Walsh et al. 2004, Connelly et al. 2011*a*). Recently it has been questioned if lek counts are appropriate to use as accurate indicators of population trends (Walsh et al. 2004); however, Dahlgren et al. (2016) determined male lek counts were appropriate to use as an index of population change. Further, Blomberg et al. (2013) concluded lek counts were well suited for estimating population growth rates across multi-year intervals and multiple studies have used them in this way (Walker et al. 2007, Garton et al. 2011, Dahlgren et al. 2016, Monroe et al. 2016, Green et al. 2017).

Wyoming Game and Fish Department (WGFD) Working Group Areas (WGFD 2003) were established in 2003 to allow local working groups, comprised of up to 12 individuals knowledgeable in or from diverse areas such as agriculture, conservation, industry, and natural resource agencies, to implement Wyoming's statewide sage-grouse conservation plan at the local level (WGFD 2003). Wyoming Core Population Areas (Core Areas) are habitat designations encompassing approximately 83% of the sage-grouse population on approximately 24% of surface area in Wyoming; protection of these areas from disturbance is intended to maintain viable sage-grouse populations in Wyoming (State of Wyoming 2015). In 2008, the USFWS supported Wyoming's Core Population Areas strategy,

stating that it was a sound policy to conserve Wyoming's sage-grouse populations if implemented as written (USFWS 2015). The goal of the Core Area strategy was, " . . . to minimize future disturbance by co-locating proposed disturbances within areas already disturbed or naturally unsuitable" (State of Wyoming 2015).

We assessed population trends of sage-grouse in Wyoming by incorporating lek count data across 23 years (1993–2015) into a population viability analysis (PVA) with density-independent (Dennis et al. 1991) and -dependent (Garton et al. 2011) population models to calculate the finite rate of population growth (λ) within multiple management delineations. We hypothesized that management-defined populations declined ($\lambda < 1.0$) during the study period and the trend in λ would differ for populations evaluated at multiple spatial scales (i.e., Core Areas by Working Group Area and Core Area status by Working Group Area). We investigated population trends across multiple spatial scales to determine the influence of fine-scale population trends (Core Areas) on larger-scale populations (Working Group Areas) and to determine if population trends of leks located within Core Areas varied from leks located outside of Core Areas.

STUDY AREA

Our study region encompassed the Wyoming distribution of current sage-grouse range (Christiansen and Whitford 2015) located within sagebrush communities, which covered approximately 150,000 km^2, or roughly 66% of the state (Beetle and Johnson 1982). Within Wyoming, the sagebrush-steppe communities are dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*; Cagney et al. 2010). Wyoming is semiarid and generally has long, cold winters and short, cool summers with the majority of precipitation occurring in spring and early summer. Average maximum temperature in lower basins in July ranged between 29°C and 35°C and average minimum temperature in January ranged between −12°C and −20°C depending on the region (Western Regional Climate Center [WRCC] 2016). Precipitation varies widely by elevation, topography, and region, but usually the majority falls in the mountains, whereas surrounding basins remain much drier (WRCC 2016). Elevation at evaluated lek sites averaged 1,824 m and ranged from 1,093–2,535 m. The sage-grouse range was divided into 7 Working Group Areas distributed throughout the state, which were designated to help implement Wyoming's Greater Sage-Grouse Conservation Plan based on recommendations from local working groups (WGFD 2003). A portion of the range was further divided into 27 Core Areas where disturbance was limited by special protections for these leks as part of the conservation efforts to help prevent listing sage-grouse as threatened or endangered (State of Wyoming 2015). Core Area boundaries were separate from and could overlap with Working Group Area boundaries (Fig. 1).

METHODS

We used the Wyoming statewide lek count database maintained and provided by the WGFD for all analyses. The WGFD and partnering agencies conducted lek counts with protocols approved by WGFD (Christiansen 2012). The database records date back to 1948, but we restricted counts to 1993–2015 because the number of leks counted annually was insufficient for analyses prior to 1993; the results of analyses were resilient to changing the starting and ending years to 1995 and 2013, respectively, showing the choice in years did not significantly influence results (Table S1, available online in Supporting Information). We restricted the dates of counts to 1 March–31 May to maximize probability of detecting peak male lek counts (Fedy and Aldridge 2011) and timing of counts to 30 minutes pre-sunrise to 90 minutes post-sunrise to maximize the number of leks included in analyses and increase precision of trend estimates (Monroe et al. 2016). We also removed records that indicated weather conditions with wind speeds ≥16 km/hour or where precipitation occurred to ensure all counts followed standardized lek count procedures (Christiansen 2012, Monroe et al. 2016). We calculated the peak male lek count for all leks annually and then averaged the peak male lek count across each population of interest, resulting in 1 average lek count per year (Monroe et al. 2016) to allow modeling of annual change in population size of count data (Morris and Doak 2002). We added 0.5 to all average lek counts to allow inclusion of mean counts of zero in analyses (Geissler and Noon 1981, Collins 1990, Monroe et al. 2016).

We investigated population trends of sage-grouse in Wyoming within multiple management delineations: Wyoming Game and Fish Department (WGFD) Working Group Areas (WGFD 2003), Wyoming Core Population Areas (Core Areas; State of Wyoming 2015), Core Areas by Working Group Area, and Core Area status (leks located within Core Areas [Core Areas] vs. leks located outside of Core Areas [Non-Core Areas]) by Working Group Area. For Core Areas by Working Group Area and Core Area status by Working Group Area groupings, where Core Areas were located in >1 Working Group Area, we assigned leks to the specific Working Group Area in which they were located.

Statistical Analyses

Population viability analysis is a collection of methods that has been used to quantitatively assess and forecast the most likely future status of a population or a group of related populations (Morris et al. 1999). Dennis et al. (1991) developed a simple linear regression-based method to perform PVAs and calculate population growth rates and extinction probabilities from time series data of population abundance, including count data. Some have criticized methods developed by Dennis et al. (1991) for the use of count data in PVAs (e.g., Holmes 2001). However, criticisms have focused on the use of regression models for the calculation of the probability of extinction or mean time to extinction, rather than the calculation of population growth rates (Ludwig 1999, Fieberg and Ellner 2000, Reed et al. 2002, Wilcox and Possingham 2002). Holmes (2001) argued that population growth rate is a more useful risk metric than the probability of extinction. Furthermore, the model in Dennis et al. (1991) has received broad support (Morris et al. 1999, Morris and Doak 2002) and has been

used widely to perform PVAs for a variety of species (Nicholls et al. 1996, Gerber et al. 1999, Schultz and Hammond 2003, Walker et al. 2007, Blomberg et al. 2013).

We regressed the natural logarithm (log) of annual change in population size $\left(\log\left(\frac{N_{t+1}}{N_t}\right)\right)$ against time, to estimate the intrinsic per capita rate of growth (r; Dennis et al. 1991, Morris and Doak 2002) assuming density-independent growth (exponential model), where r was the slope of the regression line. We employed a transformation for unequal variances as an independent variable (x_i) in all models (Morris and Doak 2002):

$$x_i = \sqrt{t_{i+1} - t_i},$$

where t_i is time in years. The dependent variable was (Morris and Doak 2002)

$$y_i = \frac{\left(\log\left(\frac{N_{t+1}}{N_t}\right)\right)}{\sqrt{t_{i+1} - t_i}}.$$

We also modeled r with Ricker (Ricker 1954, Dennis and Taper 1994) and Gompertz (Jacobson et al. 2004) growth models assuming density-dependent growth and using the same dependent variable as for the exponential model. We specified the Ricker form as

$$N_{t+1} = N_t exp\,(r + bN_t + \varepsilon_t),$$

where r is the estimated rate of population change, b is the slope estimate for density dependence, and ε_t is annual error (Dennis and Taper 1994, Morris and Doak 2002). Similarly, the Gompertz form (Jacobson et al. 2004) is specified as

$$N_{t+1} = N_t exp\,(r + b\log(N_t) + \varepsilon_t).$$

The Ricker model assumes a constant linear decrease of r as the population size (N_t) increases. The Gompertz model, however, assumes a linear decrease in r as $\log(N_t)$ increases, resulting in a stronger density-dependent response to a change in population size. We used the glm function in program R (R Version 3.2.5, www.r-project.org, accessed

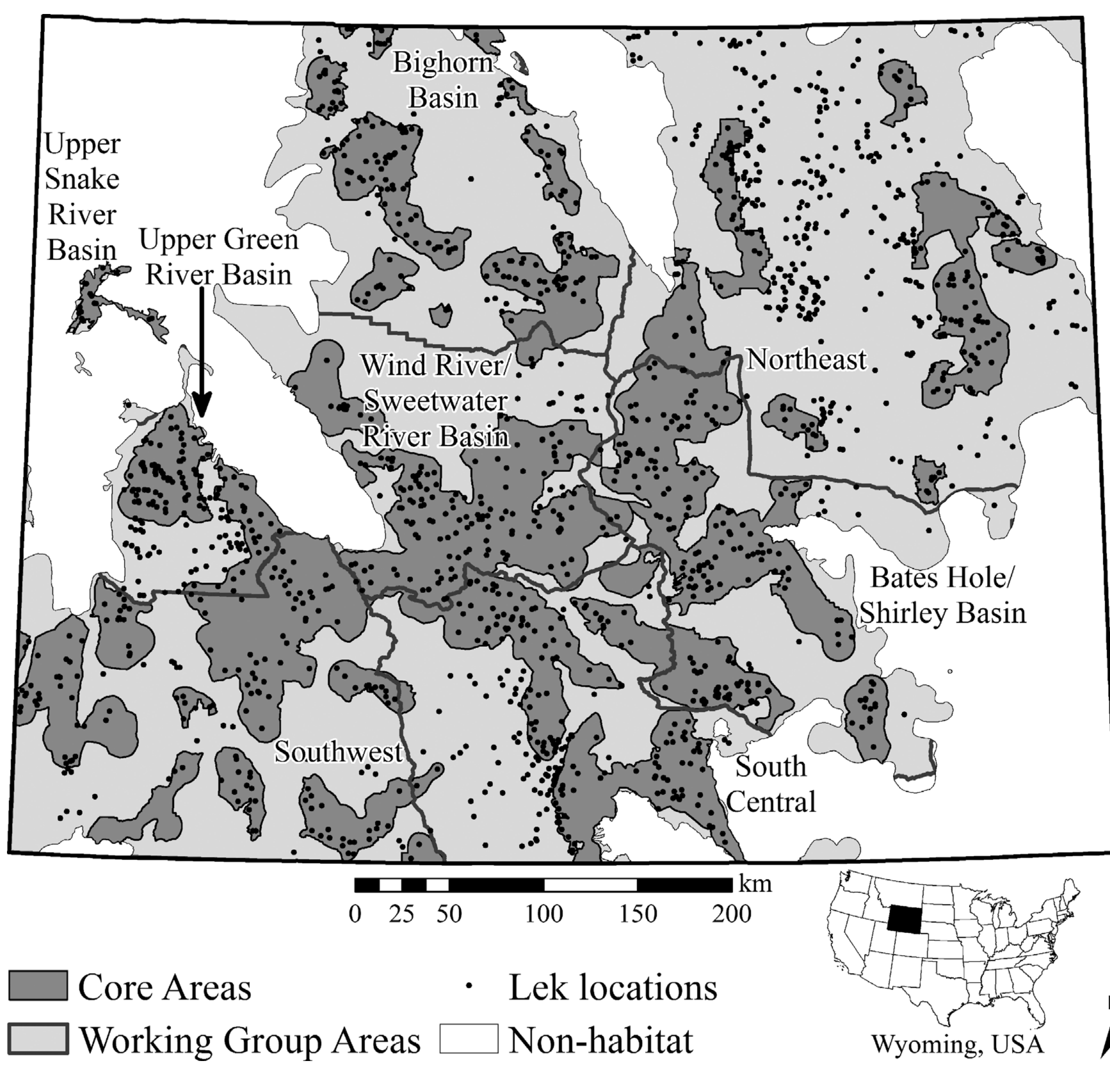

Figure 1. Core Population Areas (Core Areas), Wyoming Game and Fish Department Working Group Areas (labeled), and lek locations used in population viability analyses for greater sage-grouse, Wyoming, USA, 1993–2015.

25 Apr 2016) to perform all modeling; the exponential model structure was based on the popbio package code (Version 2.4.3, https://cran.r-project.org/web/packages/popbio/index.html, accessed 25 Apr 2016) following methods previously described (Monroe et al. 2016). The Ricker and Gompertz model structures were based on R code provided by D. F. Doak (University of Colorado, personal communication) and took the model forms as shown above. We then transformed r into λ based on the conversion $\lambda = e^r$ (Case 2000, Mills 2013).

Sage-grouse populations in Wyoming cycle every 6–9 years (Fedy and Aldridge 2011, Fedy and Doherty 2011); to account for these cycles, we attempted to de-trend the data by adding 2 different interval effect terms (see below) separately to each of the 3 models (exponential, Ricker, and Gompertz). We evaluated 9 models for every population with adequate data by applying the 3 base models and the 3 models with each of the 2 interval effects separately. The 2 interval effect terms were based on the cycles present in our reduced lek count data (1993–2015). We defined cycles using a generalized additive model (GAM; Hastie and Tibshirani 1990, Fewster et al. 2000, Wood 2006, Fedy and Aldridge 2011) employed with the gam function of the mgcv package (Version 1.8-9, https://cran.r-project.org/web/packages/mgcv/index.html, accessed 03 Mar 2016) in program R. We determined years when the annual rate of change in the abundance index (Fewster et al. 2000) experienced a statistically significant upturn or downturn, defined as change points, with the GAM analysis following methods previously described (Fig. 2; Fedy and Aldridge 2011). We selected the years that marked the end of a trend in the cycle (top of peaks and bottom of valleys) from the change points (inflection points) to define intervals. The years 2000 and 2006 marked the start of declining and the end of increasing intervals (peaks) and the years 1996, 2003, and 2013 marked the start of increasing and the end of declining intervals (valleys; Fig. 2). We categorized years into numbered intervals (1–6) with the inflection point years marking the start of the numbered intervals; we added the interval effect to models as a categorical covariate termed numbered interval. Similarly, we categorized each year into increasing or decreasing intervals based on trends in the abundance index between inflection points; we added this interval effect as a covariate termed trend interval. We set the inflection point years as the intercept (reference condition) in the glm to facilitate comparison of increasing and decreasing intervals to the inflection points. For both interval effects models (numbered and trend), we calculated the overall growth rate (r) by averaging growth rates across all intervals (Mills 2013).

Non-consecutive years of average peak male counts were not permissible with the interval effect models because we could not include a transformation to account for the unequal variances associated with varying interval lengths, which violates the assumption of equal variances required for regression analysis (Morris and Doak 2002, Stubben and Milligan 2007). Furthermore, >1 year of data per interval was required to run the glm function and model selection

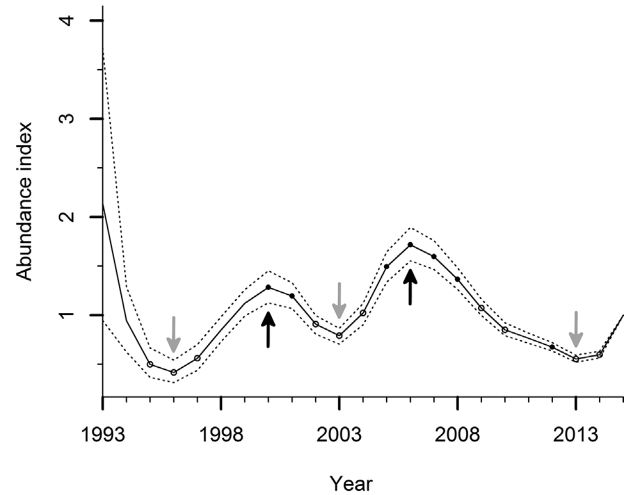

Figure 2. Overall lek trend model estimating abundance index from generalized additive modeling of lek count data used in population viability analyses for greater sage-grouse, Wyoming, USA, 1993–2015. We used the lek trend to define years where there were significant upturns (hollow circles) or downturns (black circles) in population cycles, defined as change points. Then we selected the years that marked the end of a trend in the cycle (inflection points) from the change points to define intervals. Peak years (black arrows) marked the start of declining and the end of increasing intervals and valley years (gray arrows) marked the start of increasing and the end of declining intervals. Dashed lines represent the 95% confidence interval.

analysis (details below). After calculating $\left(\frac{N_{t+1}}{N_t}\right)$, we removed values that were based on years (t) separated by time lengths >1 to ensure equal length of time between consecutive years; afterwards, we removed intervals (specific trend or numbered intervals) that contained <2 years of change in population size data. If the removal criteria resulted in <2 levels for the trend interval or numbered interval effects, then we did not perform that specific analysis. If processing resulted in <2 levels for the trend interval and number interval effects, then we removed the interval effect models from analysis for that population and analyzed only the 3 base models with the original dataset prior to processing to maximize the number of years of data used in analysis.

We used Akaike's Information Criterion (AIC) corrected for small sample sizes (AIC_c) to select the top model for each population (Working Group Areas, Core Areas, Core Areas by Working Group Area, and Core Area Status by Working Group Area; Burnham and Anderson 2010); we calculated AIC_c values with the AICcmodavg R package (Version 2.0-4, https://cran.r-project.org/web/packages/AICcmodavg/index.html, accessed 13 Apr 2016). For populations with >1 supported model based on the difference in AIC_c value from the lowest AIC_c value ($\Delta AIC_c < 2.0$; Burnham and Anderson 2010), we used 10-fold cross-validation folded to the maximum number of years of annual change in population size data up to 10 years to calculate the bias-corrected prediction error for each model (James et al. 2013). We calculated the 10-fold cross-validation bias corrected prediction error with the boot R package (Version 1.3-18,

https://cran.r-project.org/web/packages/boot/index.html, accessed 25 Apr 2016). We selected the top models with the lowest prediction error using the competing models with $\Delta AIC_c < 2.0$. We included our R code used to perform PVA in the supplemental material (Table S2, available online in Supporting Information).

RESULTS

We analyzed data from 1,556 of Wyoming's 2,418 documented leks after narrowing the lek count database to appropriate records (Fig. 1). We used 33,078 count records after excluding counts conducted under unsuitable conditions. Two Core Areas, Bear River located within the Southwest Working Group Area and Thermopolis located within the Bighorn Basin Working Group Area, lacked sufficient data to analyze Core Area-specific trends. We combined lek count data for the Thermopolis Core Area with other Core Areas for analysis based on Core Status by Working Group Area.

Seven of the 8 Working Group Area top models included the trend interval covariate. The Ricker and Gompertz trend interval models were identified as the top model of 3 different Working Group Areas each, whereas the exponential trend interval model was identified as a top model for the seventh population (Table S3, available online in Supporting Information). The exponential model was the top model for the eighth population (Table S3). Population trend analyses for the Working Group Areas showed that $\lambda < 1.0$ for 6 out of 8 populations and λ was different from 1.0 based on 95% confidence intervals for 5 of those 6 areas (Table 1). The 2 populations with an increasing trend, but with confidence intervals overlapping 1.0, were in the northwest part of the state (Upper Snake River Basin and Bighorn Basin), whereas the 2 populations in the southeast part of the state (Bates Hole-Shirley Basin and South Central) declined at a small but significant rate (0.7% annual decline each; 95% CI = 0.986 to <1.000; Fig. 3). The remaining populations declined between 4.5% and 29.6% annually (Fig. 3).

For the Core Area populations, the 3 basic models without interval covariates comprised the top models for 19 out of 32 populations; the 3 trend interval models comprised the top models for 11 of the populations, and the top model for the Sage Core Area population was the Gompertz numbered interval model (Table S4, available online in Supporting Information). Analyses for 24 of 31 Core Area populations and the statewide Non-Core Area population showed that $\lambda < 1.0$ and of those, λ differed from 1.0 for 15 Core Area populations and the Non-Core Area population based on 95% confidence intervals (Table 2). The remaining 7 Core Area population trends were increasing ($\lambda > 1.0$), but 95% confidence intervals overlapped 1.0. These increasing populations were scattered throughout the northeast, northwest, and southwest portions of the state (Fig. 4). The most severely declining Core Areas ($\lambda < 0.95$) were located in the western half of the state (Fig. 4), including the largest, Greater South Pass. The next 2 largest Core Areas located in central and south-central Wyoming, Natrona, and South Rawlins, were declining as well ($\lambda = 0.990$ and 0.987, respectively; Fig. 4), with 95% confidence intervals that did not overlap 1.0 (Table 2), albeit at a less severe rate.

The 3 basic models without interval effects encompassed the top model for 27 of 46 Core Area and Non-Core Area populations grouped by Working Group Areas (Table S5, available online in Supporting Information). The 3 trend interval models comprised the top models for 17 of the remaining populations and the exponential numbered interval and Gompertz numbered interval models were the top model for one population each (Table S5). Thirty-three populations were declining ($\lambda < 1.0$), including 21 for which λ differed from 1.0 (Table 3). The remaining 13 populations were increasing; however, λ differed from 1.0 for only 1 population (Table 3). At least 1 Core Area population declined severely ($\lambda < 0.95$) within each Working Group Area except for the Upper Snake River Basin Working Group Area (Fig. 5). The Non-Core Area populations were declining in 6 of the remaining 7 Working Group Areas (Fig. 5). There was $\geq$1 Core Area population that increased in 6 of 8 Working Group Areas as well (Fig. 5). All populations in the Bates Hole-Shirley Basin Working Group (5) and the Upper Green River Basin (3) were declining, whereas both populations in the Upper Snake River Basin (Non-Core Areas and Jackson Core Area) were increasing (Fig. 5). The remaining Working Groups (Bighorn Basin, Northeast, South Central, and Southwest) contained increasing and decreasing Core Area populations (Fig. 5).

The top model for 10 of the Core Area Status populations (Core Area vs. Non-Core Area) grouped by Working Group Areas was one of the 3 trend interval effects models, whereas one of the basic models was the top model for the remaining

Table 1. Top models selected for population viability analyses of lek count data for greater sage-grouse populations, Wyoming, USA, 1993–2015, grouped based on Working Group Areas. Not all populations contained data from the full range of years investigated; we present the range and total number of years of lek count data analyzed. For each population, we present the finite rate of population growth (λ) and 95% confidence intervals.

Population	Years	No. years	Model	λ	λ 95% CI
Bates Hole–Shirley Basin	1997–2015	18	Ricker trend interval	0.993	0.986–<1.000
Bighorn Basin	2003–2015	12	Exponential trend interval	1.061	0.823–1.368
Northeast	1998–2015	17	Ricker trend interval	0.955	0.933–0.978
South Central	1996–2015	19	Ricker trend interval	0.993	0.986–<1.000
Southwest	1993–2015	22	Gompertz trend interval	0.704	0.560–0.883
Upper Green River Basin	1997–2015	18	Gompertz trend interval	0.741	0.524–1.047
Upper Snake River Basin	2003–2015	8	Exponential	1.078	0.853–1.360
Wind River–Sweetwater River Basin	1993–2015	22	Gompertz trend interval	0.771	0.628–0.947

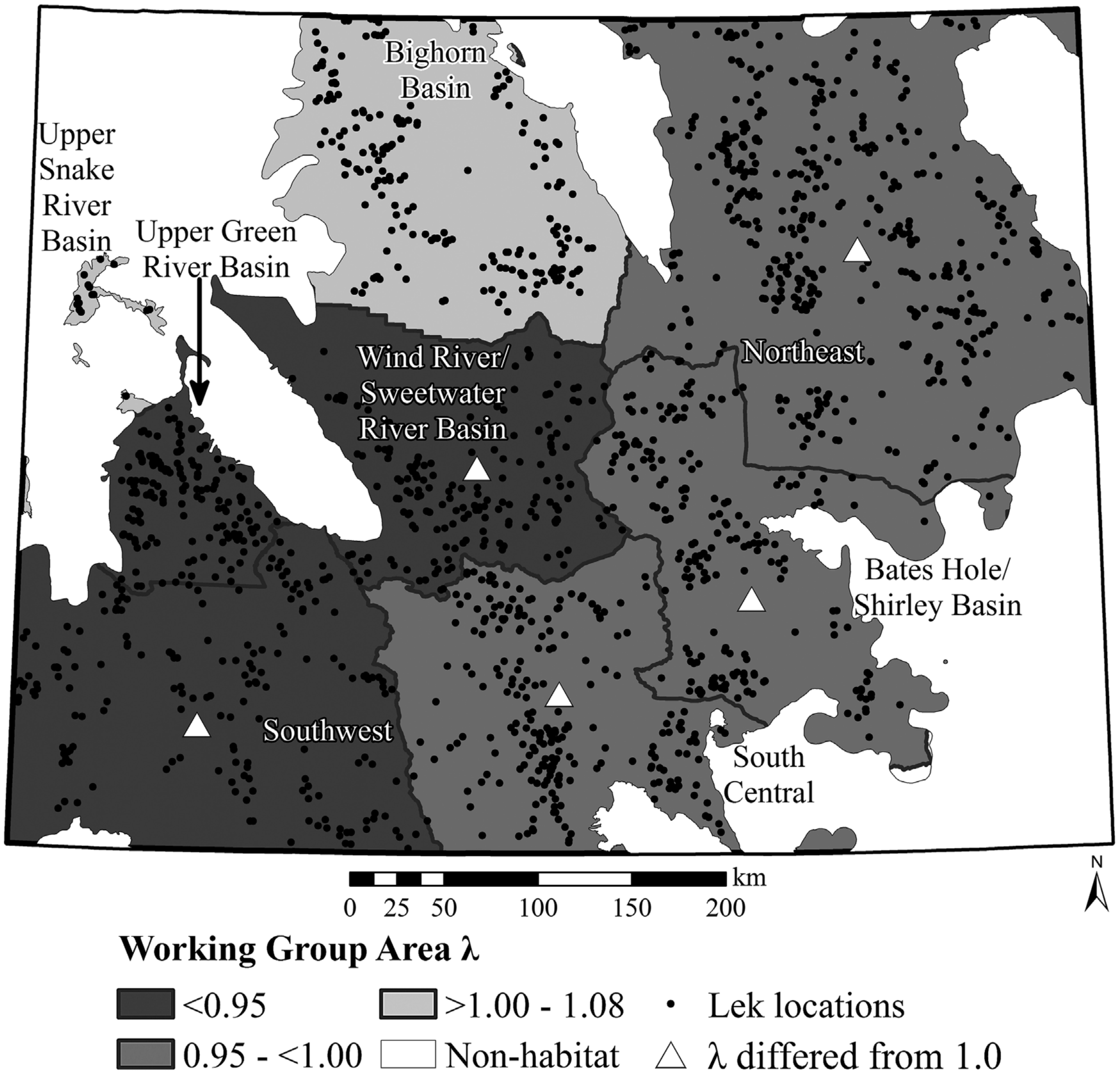

Figure 3. Finite rate of population growth (λ) of greater sage-grouse populations by Wyoming Game and Fish Department Working Group Area (labeled), Wyoming, USA, 1993–2015. We used lek count data to calculate population growth rate with population viability analyses.

6 populations (Table S6, available online in Supporting Information). Eleven of the Core Area Status populations were declining, of which λ differed from 1.0 for 7 populations, and the remaining 5 populations were increasing (Table 4). The trend in λ was similar between Core Area and Non-Core Area populations for 7 of 8 Working Group Areas (i.e., Core Area and Non-Core Area populations both increased or decreased); populations declined in 5 of those 7 Working Group Areas (Fig. 6). The Core Area population was declining and the Non-Core Area population was increasing in the remaining Working Group Area, the Wind River-Sweetwater River Basin (Fig. 6). Similar to the Working Group Area analysis, the Core Area and Non-Core Area populations in the northwest (Bighorn Basin and Upper Snake River Basin) were increasing, and the most severely declining populations ($\lambda < 0.95$) occurred in the southwest, central (except for Non-Core Areas in Wind River-Sweetwater River Basin, which were increasing), and northeast regions (Fig. 6). The Bates Hole-Shirley Basin population declined at a slow rate (0.993) when analyzed as a whole (Table 1), but when analyzed separately by Core Area status, both the Core Area and Non-Core Areas were declining rapidly (0.828 and 0.731, respectively; Table 4), though the 95% confidence intervals for the λ estimate of the Non-Core Area population overlapped 1.0, likely because of small sample of leks counted per year. This discrepancy was likely due to the Ricker trend interval being the top model for the Working Group Area, whereas the Gompertz trend interval and Gompertz were the top models for the Core Area and Non-Core Areas. We provide further details below why the Gompertz model results in lower λ estimates, but briefly it is due to the stronger density-dependent effect (thus more extreme λ estimates) with the Gompertz model compared to the Ricker model. Similar to the South Central Working Group Area results (0.993; Table 1), the South Central Core Area population declined very slightly (0.995), but the Non-Core Area population was declining more rapidly (0.966; Table 4, Fig. 6).

The average number of years of data for populations for which the exponential model was the top model was 7.650 years (95% CI = 6.015–9.285), which was shorter than all other models, including the other 2 basic models (Gompertz: $\bar{x} = 13.391$, 95% CI = 11.562–15.221; Ricker: $\bar{x} = 14.000$, 95% CI = 13.031–14.969). In all cases, the average number of years for populations where the basic model was the top model were shorter than for populations where the equivalent model included the trend interval covariate (exponential trend interval: $\bar{x} = 15.000$, 95% CI = 13.654–16.346; Gompertz trend interval: $\bar{x} = 18.684$, 95% CI = 17.630–19.738; Ricker trend interval: $\bar{x} = 17.111$, 95% CI = 16.474–17.748). Within populations for which trend interval models were the top selected, the average number of years analyzed was significantly shorter for exponential trend intervals compared to Gompertz trend interval populations and nearly significantly shorter than Ricker trend interval populations. We found that 12 years was the shortest lek count data timeframe that resulted in λ values that differed from 1.0 across all models. The Gompertz model resulted in the lowest λ estimates of the 3 model forms, ranging from 0.207–0.731 for top selected models. The exponential model resulted in the widest range in λ estimates (0.753–1.509), whereas the Ricker model was the narrowest (0.948–0.984). The exponential model was the most common model form for populations with <10 years of data and was the top model for 16 of such populations and the Gompertz model was the top model for the remaining 2 populations.

DISCUSSION

We found that in general when we investigated Core Area status (Core Area vs. Non-Core Area) by Working Group Area, the 2 populations tended to trend in the same direction and agreed with the overall trend of the Working Group Area. However, at the finer scale where we analyzed Core Areas separately within Working Group Areas, in most instances, Core Areas within the same Working Group Area trended differently (5 out of 8 Working Groups). For example, the overall trend of the Bates Hole-Shirley Basin Working Group Area was stable (λ = 0.993), as was the largest Core Area within its boundary, Natrona (λ = 0.992). However, the remaining 3 Core Areas were all declining (λ range: 0.570–0.970) as was the Non-Core Area population (λ = 0.970). In this Working Group Area, the Natrona Core Area was driving the overall population trend and masking the population declines occurring in other Core Areas. Furthermore, the Bighorn Basin Working Group overall trend was increasing slightly (λ = 1.061) and the overall Core Area population trend was increasing slightly as well (λ = 1.059) when we investigated by Core Area status.

Table 2. Top models selected for population viability analyses of lek count data for greater sage-grouse statewide populations in Wyoming, USA, 1993–2015, grouped based on Core Areas. Not all populations contained data from the full range of years investigated; we present the range and total number of years of lek count data analyzed. For each population, we identify the top model form selected for population estimation, and present the finite rate of population growth (λ) and 95% confidence intervals.

Population	Years	No. years	Model	λ	λ 95% CI
All Non-Core Areas	1996–2015	19	Gompertz trend interval	0.327	0.264–0.406
Blacks Fork	1996–2015	19	Ricker trend interval	0.992	0.986–0.998
Buffalo	2000–2015	15	Gompertz	0.465	0.311–0.696
Continental Divide	1993–2015	20	Exponential trend interval	1.156	0.783–1.707
Crowheart	1996–2015	14	Gompertz	0.384	0.307–0.480
Daniel	1997–2015	18	Ricker	0.984	0.974–0.995
Douglas	2000–2015	15	Exponential	0.972	0.690–1.369
Elk Basin East	2003–2013	8	Exponential	1.039	0.805–1.341
Elk Basin West	2003–2015	12	Exponential	1.038	0.409–2.633
Fontenelle	2003–2015	12	Ricker	0.982	0.965–1.000
Grass Creek	2003–2015	12	Gompertz	0.397	0.219–0.719
Greater South Pass	1994–2015	21	Gompertz trend interval	0.828	0.687–0.998
Hanna	1997–2015	18	Gompertz trend interval	0.735	0.531–1.017
Heart Mountain	2003–2015	12	Gompertz	0.324	0.167–0.627
Hyattville	2003–2015	12	Ricker	0.979	0.951–1.009
Jackson	2003–2015	8	Exponential	1.080	0.817–1.427
Little Mountain	2006–2015	4	Exponential	0.894	0.504–1.584
Natrona	1998–2015	17	Ricker trend interval	0.990	0.983–0.997
Newcastle	2000–2015	15	Exponential trend interval	1.225	0.664–2.260
North Gillette	2003–2015	12	Gompertz	0.469	0.256–0.861
North Glenrock	2003–2015	12	Gompertz	0.505	0.283–0.902
North Laramie	1998–2015	15	Ricker	0.970	0.956–0.984
Oregon Basin	2003–2015	12	Gompertz	0.610	0.359–1.037
Powder	2009–2012	3	Gompertz	0.207	0.040–1.082
Sage	1997–2015	18	Gompertz numbered interval	0.366	0.318–0.421
Salt Wells	2000–2015	15	Gompertz trend interval	0.627	0.452–0.870
Seedskadee	2007–2013	6	Exponential	0.802	0.558–1.154
Shell	2007–2013	6	Exponential	0.753	0.539–1.052
South Rawlins	1998–2015	15	Ricker trend interval	0.987	0.979–0.995
Thunder Basin	2000–2015	15	Exponential trend interval	1.102	0.824–1.474
Uinta	2003–2015	12	Exponential trend interval	1.035	0.688–1.556
Washakie	2003–2015	12	Exponential trend interval	0.964	0.653–1.422

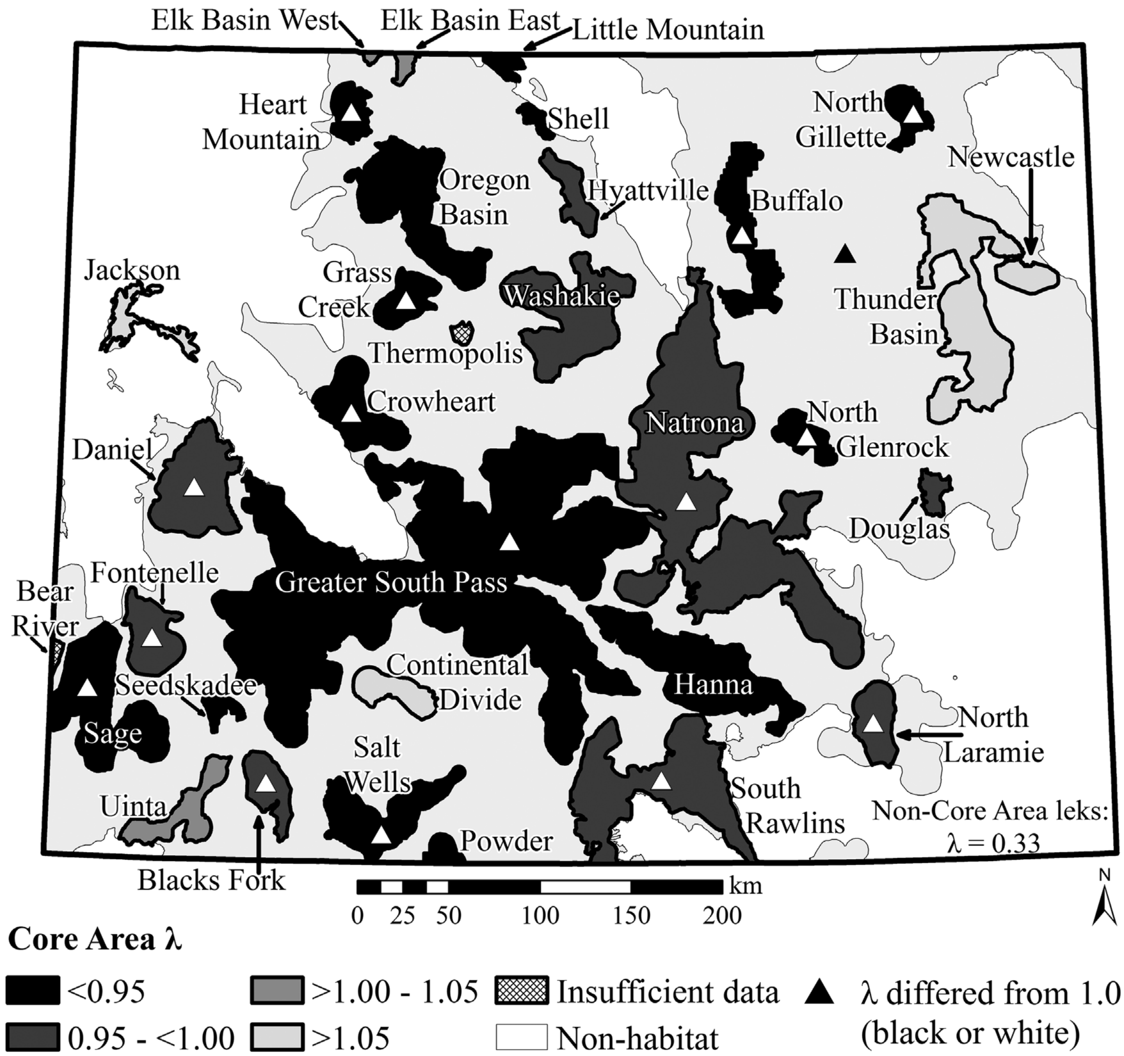

Figure 4. Finite rate of population growth (λ) of greater sage-grouse populations by Wyoming Core Population Areas (Core Areas), Wyoming, USA, 1993–2015. We used lek count data to calculate population growth rate with population viability analyses.

However, when we analyzed Core Area populations within the Bighorn Basin separately, 6 populations were declining. We also detected the reverse situation in the Northeast and Southwest Working Groups. These Working Groups were declining overall and within both Core Area and Non-Core Area populations when investigated by Core Area status. However, 2 Core Areas within the Northeast Working Group and 3 Core Areas within the Southwest Working Group were actually increasing. These examples highlight the ability of relatively close populations to experience different population trends, likely because of localized factors influencing trends at small scales.

We developed an effective methodology to perform a PVA at multiple spatial scales and varying lengths of time on a species with known population cycles that incorporated density-independent and density-dependent population growth. We handled population cycles by incorporating interval covariates into the standard density-independent and density-dependent models and the top models included interval effects for half of the populations investigated (48%). Populations with a longer number of years of data, and thus a greater potential to capture multiple 6–9-year cycles common in Wyoming (Fedy and Aldridge 2011), were more likely to have the top model contain the trend interval covariate based on average number of years of data by model structure. The numbered interval covariate was not as effective and was only the top model for 3 populations. In general, the large-scale populations (i.e., Working Group Areas) tended to have more years of data compared to small-scale populations (i.e., Core Areas), which increased the likelihood to include multiple cycles and thus likely increased the probability of the trend interval covariate to be included in the top model. It also is possible that the difference in top model selection across scales was due to the potential influences of those trends. At large spatial scales, broad pattern effects (e.g., climate) likely helped influence population trends. At smaller scales, local factors (e.g., gas and oil development) likely influenced population trends. The trend interval covariate may have explained broad-scale patterns such as climate, which is known to drive cyclic

Table 3. Top models selected for population viability analyses of lek count data for greater sage-grouse statewide populations in Wyoming, USA, 1993–2015, grouped based on Core Areas within each Working Group Area. Not all populations contained data from the full range of years investigated; we present the range and total number of years of lek count data analyzed. For each population we identify the top model form selected for population estimation, and present the finite rate of population growth (λ) and 95% confidence intervals.

Population	Years	No. years	Model	λ	λ 95% CI
Bates Hole-Shirley Basin – All Non-Core Areas	1998–2015	17	Exponential	0.970	0.798–1.179
Bates Hole-Shirley Basin – Greater South Pass	2008–2013	5	Exponential	0.834	0.431–1.614
Bates Hole-Shirley Basin – Hanna	1997–2015	18	Gompertz trend interval	0.570	0.346–0.940
Bates Hole-Shirley Basin – Natrona	2000–2015	15	Ricker trend interval	0.992	0.987–0.997
Bates Hole-Shirley Basin – North Laramie	1998–2015	15	Ricker	0.970	0.956–0.984
Bighorn Basin – All Non-Core Areas	2003–2015	12	Exponential trend interval	1.144	0.762–1.716
Bighorn Basin – Elk Basin East	2003–2013	8	Exponential	1.039	0.805–1.341
Bighorn Basin – Elk Basin West	2003–2015	12	Exponential	1.038	0.409–2.633
Bighorn Basin – Grass Creek	2003–2015	12	Gompertz	0.397	0.219–0.719
Bighorn Basin – Heart Mountain	2003–2015	12	Gompertz	0.324	0.167–0.627
Bighorn Basin – Hyattville	2003–2015	12	Ricker	0.979	0.951–1.009
Bighorn Basin – Little Mountain	2006–2015	4	Exponential	0.894	0.504–1.584
Bighorn Basin – Oregon Basin	2003–2015	12	Gompertz	0.610	0.359–1.037
Bighorn Basin – Shell	2007–2013	6	Exponential	0.753	0.539–1.052
Bighorn Basin – Washakie	2003–2015	12	Exponential numbered interval	1.114	0.845–1.470
Northeast – All Non-Core Areas	1998–2015	17	Gompertz trend interval	0.653	0.493–0.866
Northeast – Buffalo	2000–2015	15	Gompertz	0.465	0.311–0.696
Northeast – Douglas	2000–2015	15	Gompertz	0.652	0.420–1.012
Northeast – Natrona	2000–2015	13	Ricker	0.948	0.904–0.994
Northeast – Newcastle	2000–2015	15	Exponential trend interval	1.225	0.664–2.260
Northeast – North Gillette	2003–2015	12	Gompertz	0.469	0.256–0.861
Northeast – North Glenrock	2003–2015	12	Gompertz	0.505	0.283–0.902
Northeast – Thunder Basin	2000–2015	15	Exponential trend interval	1.102	0.824–1.474
South Central – All Non-Core Areas	1997–2015	18	Exponential trend interval	0.966	0.669–1.396
South Central – Greater South Pass	1998–2015	17	Exponential trend interval	1.090	0.808–1.469
South Central – Hanna	1998–2015	17	Ricker trend interval	0.995	0.989–1.001
South Central – South Rawlins	1998–2015	15	Gompertz trend interval	0.636	0.490–0.827
Southwest – All Non-Core Areas	1996–2015	19	Gompertz	0.427	0.322–0.567
Southwest – Blacks Fork	1996–2015	19	Gompertz trend interval	0.754	0.601–0.945
Southwest – Continental Divide	1993–2015	20	Exponential trend interval	1.156	0.783–1.707
Southwest – Fontenelle	2003–2015	12	Ricker	0.982	0.965–1.000
Southwest – Greater South Pass	1996–2015	19	Exponential trend interval	1.308	0.946–1.808
Southwest – Powder	2009–2012	3	Gompertz	0.207	0.040–1.082
Southwest – Sage	1997–2015	18	Gompertz numbered interval	0.366	0.318–0.421
Southwest – Salt Wells	2000–2015	15	Gompertz trend interval	0.626	0.453–0.866
Southwest – Seedskadee	2007–2013	6	Exponential	0.802	0.558–1.154
Southwest – Uinta	2003–2015	12	Exponential trend interval	1.035	0.688–1.556
Upper Green River Basin – All Non-Core Areas	1997–2015	18	Gompertz	0.354	0.223–0.561
Upper Green River Basin – Daniel	1997–2015	18	Gompertz	0.586	0.397–0.865
Upper Green River Basin – Greater South Pass	1997–2015	18	Gompertz trend interval	0.792	0.621–1.010
Upper Snake River Basin – All Non-Core Areas	2011–2015	4	Exponential	1.067	0.596–1.909
Upper Snake River Basin – Jackson	2003–2015	8	Exponential	1.080	0.817–1.427
Wind River-Sweetwater River Basin – All Non-Core Areas	2001–2015	14	Ricker	0.966	0.934–0.998
Wind River-Sweetwater River Basin – Crowheart	1996–2015	14	Gompertz	0.384	0.307–0.480
Wind River-Sweetwater River Basin – Greater South Pass	1994–2015	21	Gompertz trend interval	0.779	0.626–0.969
Wind River-Sweetwater River Basin – Washakie	2011–2015	4	Exponential	1.509	1.087–2.094

patterns (Kausrud et al. 2008), better than local factors. Certain caveats should be clear when comparing λ estimates across populations: 1) the model structure can affect the magnitude of λ (e.g., at the broadest scale [Working Group Areas] λ estimates were most similar by model structure, not population investigated; Table S7, available online in Supporting Information); 2) the number of years of data can affect which model was the top selected; and 3) many populations did not contain data for the whole study period, so comparisons are most appropriate to populations with similar time periods assessed. However, we think that our model selection methods (AIC_c followed by10-fold cross-validation) selected the best model structure that recovered the actual dynamics for each population as reflected in the count data. Therefore, λ estimates reflect population-specific dynamics occurring on the landscape and are not just the result of a model structure that happened to be selected as the top model. We think our methodologies are sound, and variation in models selected (model structure) across populations represent true variation in biological processes that are regulating individual populations.

As mentioned above, model structure also affected the magnitude of λ values (Table S7). The Gompertz model resulted in the lowest λ values, whereas the exponential and Ricker values were similar in range. This was true for comparing top model results across populations and within population results. Pellet et al. (2006) used exponential, Gompertz, and Ricker models to model population growth

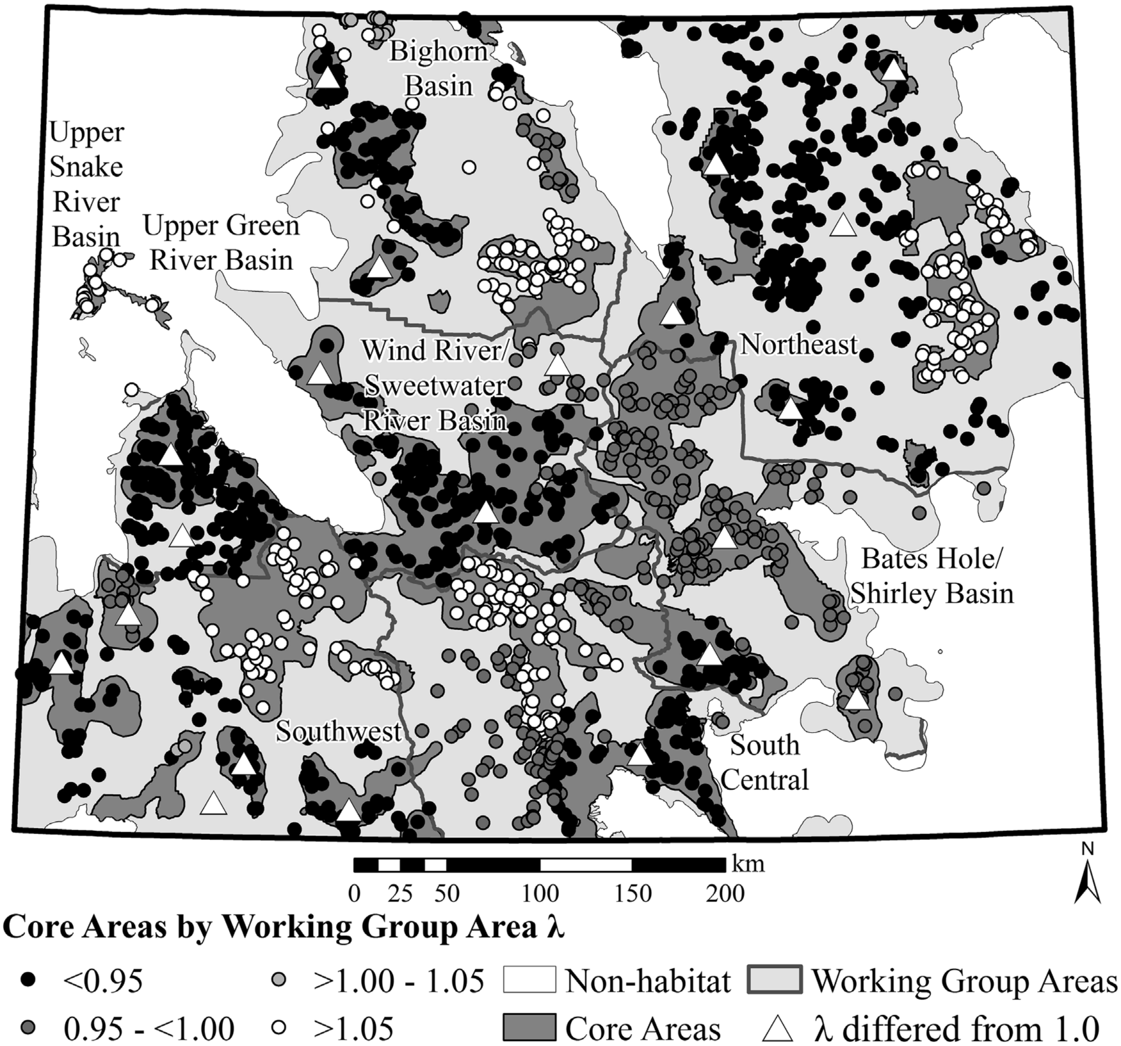

Figure 5. Finite rate of population growth (λ) of greater sage-grouse populations by Wyoming Core Population Areas (Core Areas) grouped by Wyoming Game and Fish Department Working Group Areas (labeled), Wyoming, USA, 1993–2015. We used lek count data to calculate population growth rate with population viability analyses.

Table 4. Top models selected for population viability analyses of lek count data for greater sage-grouse statewide populations in Wyoming, USA, 1993–2015, grouped based on Core Areas status (Core Area vs. Non-Core Area) within each Working Group Area. Not all populations contained data from the full range of years investigated; we present the range and total number of years of lek count data analyzed. For each population we identify the top model form selected for population estimation, and present the finite rate of population growth (λ) and 95% confidence intervals.

Population	Years	No. years	Model	λ	λ 95% CI
Bates Hole-Shirley Basin – Core Areas	1997–2015	18	Gompertz trend interval	0.828	0.687–0.997
Bates Hole-Shirley Basin – Non-Core Areas	1998–2015	17	Gompertz	0.731	0.504–1.059
Bighorn Basin – Core Areas	2003–2015	12	Exponential trend interval	1.059	0.814–1.378
Bighorn Basin – Non-Core Areas	2003–2015	12	Exponential trend interval	1.144	0.762–1.716
Northeast – Core Areas	1998–2015	17	Ricker	0.953	0.929–0.978
Northeast – Non-Core Areas	1998–2015	17	Gompertz trend interval	0.653	0.493–0.866
South Central – Core Areas	1998–2015	17	Ricker trend interval	0.995	0.988–1.002
South Central – Non-Core Areas	1997–2015	18	Exponential trend interval	0.966	0.669–1.396
Southwest – Core Areas	1993–2015	22	Gompertz trend interval	0.708	0.563–0.890
Southwest – Non-Core Areas	1996–2015	19	Gompertz	0.427	0.322–0.567
Upper Green River Basin – Core Areas	1997–2015	18	Gompertz trend interval	0.787	0.576–1.074
Upper Green River Basin – Non-Core Areas	1997–2015	18	Gompertz	0.354	0.223–0.561
Upper Snake River Basin – Core Areas	2003–2015	8	Exponential	1.080	0.817–1.427
Upper Snake River Basin – Non-Core Areas	2011–2015	4	Exponential	1.067	0.596–1.909
Wind River-Sweetwater River Basin – Core Areas	1993–2015	22	Gompertz trend interval	0.770	0.624–0.950
Wind River-Sweetwater River Basin – Non-Core Areas	2001–2015	14	Exponential trend interval	1.340	0.667–2.692

in European tree frogs (*Hyla arborea*) and growth rates were lowest for the Gompertz model as well; the growth rates calculated with the exponential and Ricker models were more similar with the exponential growth rate being higher. All growth rates of tree frogs showed declining population trends. However, Colchero et al. (2009) modeled population growth of an isolated desert bighorn sheep (*Ovis canadensis*) population with the same 3 models and reported that the Gompertz model resulted in the highest growth rate by far, whereas the exponential and Ricker models resulted in more similar growth rates once again, with the exponential growth rate being the lowest. In this case study on bighorn sheep, populations had increasing growth rates. It appears that the Ricker and exponential models tend to attenuate growth estimates toward stable growth, whereas the Gompertz model tends to estimate more extreme population growth rates. This is likely due to the stronger density-dependent effect at small population sizes caused by the way in which the model is implemented. There is a constant linear decrease in r as the natural logarithm of population size increases; therefore, the density-dependent effect becomes less pronounced as population sizes increase.

We are not able to make direct comparisons between our population trends and previous studies because we used different population delineations; however, we can formulate general comparisons. The Northeast Working Group Area overlapped most of the Powder River Basin population analyzed by Garton et al. (2011, 2015), who reported a 0.3% annual decline from 1965–2013. Our λ estimate of 0.955 for the Northeast population corresponded to a much larger annual decline of 4.5% from 1998–2015. The Powder River Basin population included leks in southeast Montana and the range of years analyzed differed between the studies; however, both studies indicate that this population has declined over the past several decades. Based on the weighted average of Working Group Area λ estimates, we indicated a 9.9% statewide annual decline. Three additional studies investigated Wyoming statewide trends based on lek count

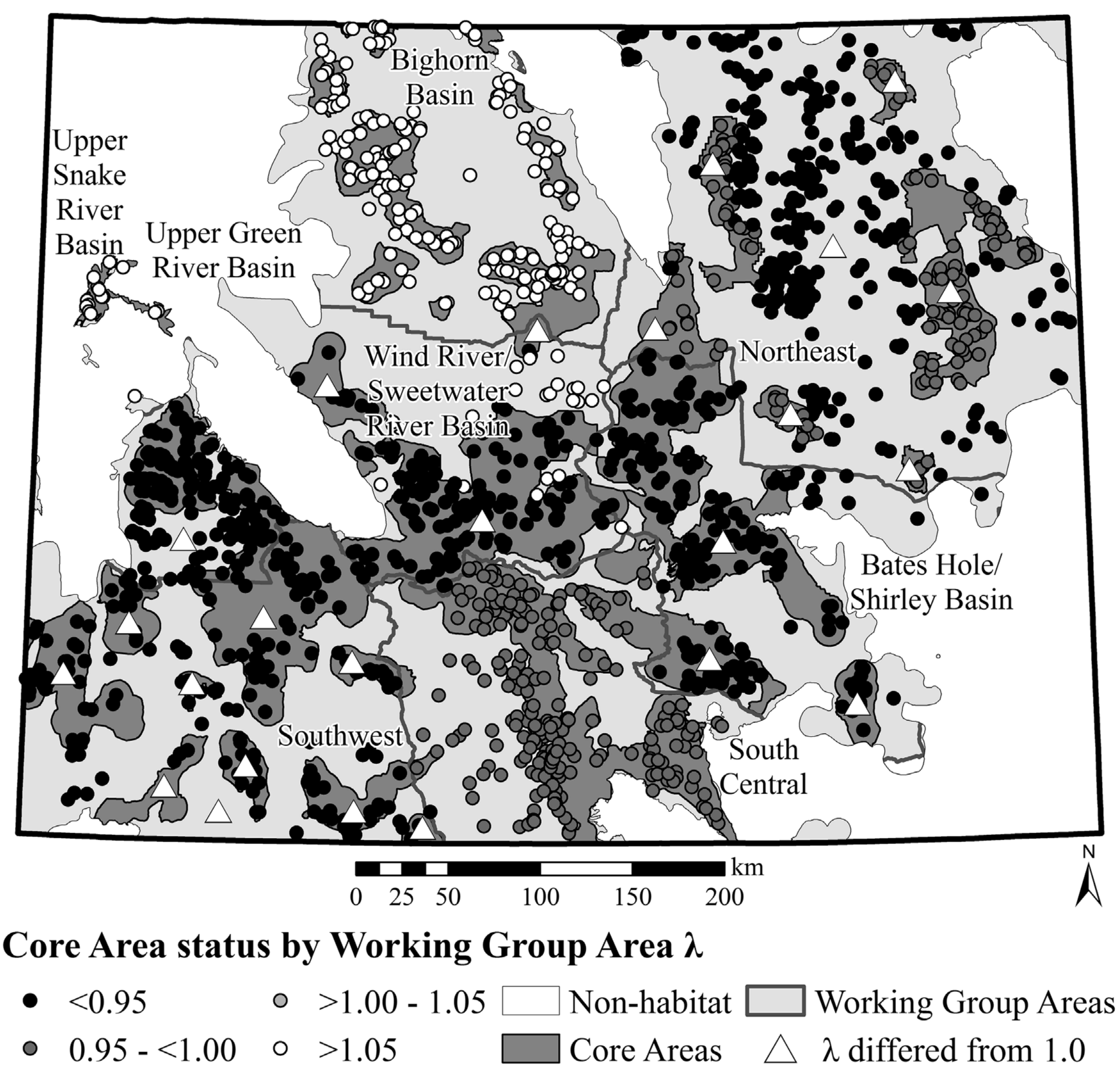

Figure 6. Finite rate of population growth (λ) of greater sage-grouse populations by Wyoming Core Population Area status (Core Area vs. Non-Core Area) grouped by Wyoming Game and Fish Department Working Group Areas (labeled), Wyoming, USA, 1993–2015. We used lek count data to calculate population growth rate with population viability analyses.

data. Green et al. (2017) documented annual statewide declines of 2.5% during 1984–2008, Monroe et al. (2017) reported annual statewide declines of 6.0% during 2004–2014, and Fedy and Aldridge (2011) reported an overall statewide population decline of 54% during 1968–2006, which averaged a 1.4% annual decline. All of these studies used different leks, time periods, and models in analyses, which partly explains the varying population growth estimates; however, taken together it is clear statewide sage-grouse populations in Wyoming have declined over the past several decades.

Walker et al. (2007) also investigated sage-grouse population trends in the Powder River Basin during 2001–2005. Leks were divided into those located within coal bed natural gas fields and those located outside gas fields. Again, comparisons are not direct because we investigated a longer time frame and we did not divide leks into groups based on gas fields. However, our 4.5% estimated annual decline closely resembled the non-gas field annual population decline of 3.0%; the gas field population declined 35% per year (Walker et al. 2007). Perhaps a better evaluation would be to compare non-gas field populations to Core Area populations within the Northeast Working Group because Core Area boundaries were developed to represent suitable habitat, from which disturbed lands were excluded (State of Wyoming 2015). Core Area populations within the Northeast Working Group declined similarly to the whole Working Group Area population at an annual decline of 4.7%, which again was similar to non-gas field populations reported by Walker et al. (2007).

Annual population trends also were estimated for gas field and non-gas field populations in western Wyoming within the Upper Green River Basin Working Group Area during 1998–2004 (Holloran 2005). Holloran (2005) documented a 21.3% annual decline for the gas field population and a 13.4% annual decline for the non-gas field population. We estimated a more drastic annual decline of 25.9% for the Working Group Area population, albeit over a longer period (1997–2015) and the 95% confidence intervals overlapped 1.0 slightly. We also estimated a 21.3% annual decline for Core Area populations within the Upper Green River Basin (presumably non-gas field populations) and a 64.6% annual decline for the Non-Core Area population; in this case the λ estimate comparisons do not match well. These population declines occurred during a rise in active gas and oil wells (by 4.4 times) located within the Upper Green River Basin Working Group Area over the same time period (Wyoming Oil and Gas Conservation Coalition, http://wogcc.state.wy.us, accessed 15 Oct 2015). Notably, the Core Areas and their associated protections were not developed until 2008 (State of Wyoming 2008), and our study period went back to 1997 for this population.

The general trend in λ was similar between Core Area and Non-Core Area populations for 7 out of 8 Working Group Areas (Fig. 6). Core Area and Non-Core Area populations were both increasing in the Bighorn Basin ($\lambda = 1.059$ and 1.144, respectively). For the Upper Green River Basin, Southwest, Bates Hole-Shirley Basin, and Northeast Working Group Areas, both Core Area and Non-Core Area populations were declining, with the Northeast Core Area population having the highest λ value of 0.955. The Core Area population in the South Central Working Group was stable ($\lambda = 0.995$), while the Non-Core Area population was declining more substantially ($\lambda = 0.966$); however, the 95% confidence intervals overlapped 1.0 for both populations. The one case where the 2 population trends diverged was in the Wind River-Sweetwater River Basin Working Group, in which the Core Area population was declining ($\lambda = 0.770$) and the Non-Core Area population was increasing ($\lambda = 1.340$). Although it is interesting to compare Core Area versus Non-Core Area trends, we did not intend this analysis to be an evaluation of the Core Area strategy as evidenced by our choice to investigate trends dating back to 1993. Also, by the nature of how Core Areas were established, in which approximately 83% of the sage-grouse population was encompassed in approximately 24% of the surface areas of the state (State of Wyoming 2015), they contained a larger sample size of leks counted compared to Non-Core Areas in all but the Northeast Working Group Area. The number of leks counted were still comparable between Core and Non-Core Areas in all but the Bates Hole-Shirley Basin, Bighorn Basin, and Upper Snake River Basin Working Groups, which contained <10 leks annually in Non-Core Areas. The Core Area delineations were a convenient scale at which to investigate population trends at a finer resolution than the Working Group Areas and management decisions are applied at both scales. Moving forward, using Core Areas will be an important approach to monitor sage-grouse population trends because Core Area populations are managed in a much more conservative manner than Non-Core Area populations to ensure the protection of this species in Wyoming (State of Wyoming 2015). Furthermore, it is concerning for sage-grouse management that the Core Area delineations were selected for protections because they were presumably the best and most stable populations in Wyoming even prior to the increased protections in 2008, and yet 77% of the Core Area populations were declining and 4 out of 7 of the remaining populations were merely stable.

When managing a species of concern, we should evaluate the possibility that adjacent populations could be experiencing different population trends to determine what local factors are influencing small-scale population trends and not assume that large-scale trends entirely account for what is occurring across the landscape. For example, a local population affected by a gas and oil field may be declining annually, but the larger-scale trend may mask the decline because the larger population, which is located in a region experiencing increased spring precipitation and thus higher chick survival, is increasing. To assist with determining population trends and influences on those trends across multiple spatial scales and how small-scale trends may be affecting large-scale populations, clustering leks based on biologically relevant landscape features and climatic conditions in a hierarchical, nested approach could be used to better define population boundaries.

MANAGEMENT IMPLICATIONS

Core Area and Working Group Area population delineations are relevant to Wyoming sage-grouse management because both are important in helping WGFD manage this species. Our approach of monitoring populations at different spatial scales using these boundaries will allow managers to focus efforts on small-scale populations (Core Areas or portions of Core Areas located within specific Working Group Areas) that are doing the poorest and influencing the larger-scale population trends downward. Focusing management efforts toward smaller-scale populations should be a more efficient use of time and resources to better assist with species protections and also could support further investigations into factors influencing population change. Conversely, determining the fine-scale populations that are stable or increasing through this analysis could assist managers with identifying which management strategies have been most effective. Those strategies could then be applied more broadly in other populations that are declining, where appropriate.

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