GREATER SAGE-GROUSE RESPONSE TO COAL-BED NATURAL GAS

DEVELOPMENT AND WEST NILE VIRUS IN THE POWDER

RIVER BASIN, MONTANA AND WYOMING, USA.

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Greater Sage-grouse Response to Coal-bed Natural Gas Development and West Nile

Virus in the Powder River Basin, Montana and Wyoming, USA.

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  Understanding how population dynamics respond to landscape-scale disturbance and disease are crucial for effective wildlife management and conservation. Two new potential stressors on greater sage-grouse (*Centrocercus urophasianus*) populations in the Powder River Basin of Montana and Wyoming are coal-bed natural gas (CBNG) development and West Nile virus (WNv). I first examined how CBNG development, habitat, and other landscape features influenced trends in the abundance of displaying males and the status of sage-grouse leks. Second, I used rates of WNv-induced mortality and seroprevalence from radio-marked birds to estimate rates of WNv infection. Third, I studied the influence of female characteristics, season, and environmental variables on nest, brood, and female survival. I then used population models to estimate potential impacts of WNv on population growth. From 2001-2005, numbers of males on leks in CBNG fields declined more rapidly than leks outside CBNG. Of leks active in 1997 or later, only 38% within CBNG remained active by 2004-2005, compared to 84% of leks outside CBNG. By 2005, leks in CBNG had 46% fewer males per active lek than leks outside CBNG. Persistence of 110 leks was positively influenced by proportion sagebrush habitat within 6.4 km of the lek and negatively affected by CBNG development at multiple scales. Prohibiting CBNG development within 0.4 km of sage-grouse leks is inadequate to ensure lek persistence. From 2003-2005, minimum WNv-related mortality rates from 1 July-15 September ranged from 2.4-13.3% and maximum possible rates ranged from 8.2-28.9%. In spring 2005 and 2006, 10.3% and 1.8% respectively, of newly-captured females tested seropositive for neutralizing antibodies to WNv. Annual WNv infection rates were lower in habitats without CBNG development. Summer mortality from WNv occurred every year, decreased annual female survival rates by 0-27% per year, and reduced estimates of population growth by 7-10% per year. Changes in epizootiology of WNv and in distribution and management of surface water from CBNG development will play an important role in long-term impacts of WNv on greater sage-grouse populations in the Powder River Basin. Management should focus on eliminating man-made water sources that support breeding mosquitos known to vector the virus.

DEDICATION

  I dedicate this work to my parents, Ann Lincoln, Dan Shadoan, John Walker, and Linda Walker and to my wonderful family, near and far, both geographically and genetically, who offered support, unconditional love, patience, and understanding as I disappeared for years to study birds. Being surrounded by incredible people made me cherish my experience in Montana, especially Ty and Kristina Smucker, Dalit Ucitel and Greg Guscio, Alex Trillo, Jenny and Brian Woolf, Kathy Griffin, Cindy and Jeff Gilbert, Erick and Ann Greene, and Rob Domenech. Thank you for your friendship and many fine adventures. A dear friend, Jeanne Johnson, applied glue at regular intervals and taught me the skills to navigate in rough seas.

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TABLE OF CONTENTS

List of Tables

List of Figures

CHAPTER 1. INTRODUCTION

Widespread concern over declines in greater sage-grouse (*Centrocercus urophasianus*) abundance and distribution have led to extensive research and management efforts to understand and reverse population declines. Recently, energy development and West Nile virus have emerged as two new potential stressors on sage-grouse populations. My dissertation research was originally designed to evaluate impacts of CBNG development on greater sage-grouse demography. However, the emergence of WNv as an additional stressor on sage-grouse populations in the PRB (Naugle et al. 2004, 2005; Walker et al. 2004) and the apparent causal link between CBNG and WNv mortality (Zou et al. 2006, Doherty 2007) has generated the need to investigate potential consequences of both coal-bed natural gas and WNv mortality on sage-grouse populations.

In Chapter 2, I examine how CBNG development, habitat, and other landscape features influenced trends in the abundance of displaying males in the PRB between 2001-2005 and the status of sage-grouse leks between 1997-2005. I then use these results to estimate approximate threshold densities of CBNG development and the size of lek buffers required to maintain various levels of population persistence. A condensed version of this chapter was published in the Journal of Wildlife Management in 2007 (Walker et al. 2007*a*). In Chapter 3, I use data on WNv-induced mortality and seroprevalence from the PRB to estimate rates of WNv infection from 2003-2006. A condensed version of this chapter was published in the journal Avian Diseases in 2007 (Walker et al. 2007*b*). In Chapter 4, I use data from radio-marked females in three

1

regions of the PRB from 2003-2006 to generate age-specific estimates of nest, brood, and adult female survival for use in population models in Chapter 5 and to study the influence of female characteristics, season, and environmental variables on nest, brood, and female survival. These analyses also form the foundation for future research on how local and landscape habitat and infrastructure variables influence key vital rates after controlling for other factors. In Chapter 5, I use age-specific demographic estimates from the PRB to parameterize a life-stage simulation analysis model to examine potential consequences of WNv mortality for population growth under different scenarios. Chapter 5 also forms the basis for a separate manuscript reviewing the ecology of WNv in sagebrush habitat, impacts on greater sage-grouse demography, and potential range-wide consequences of WNv for sage-grouse populations (Walker and Naugle 2008).

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CHAPTER 2. GREATER SAGE-GROUSE POPULATION RESPONSE TO ENERGY

DEVELOPMENT AND HABITAT LOSS

Abstract: Modification of landscapes due to energy development may alter both habitat use and vital rates of sensitive wildlife species. Greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of Wyoming and Montana have experienced widespread, rapid changes to habitat due to recent coal-bed natural gas (CBNG) development. We analyzed lek-count, habitat, and infrastructure data to assess how CBNG development and other landscape features influenced trends in the numbers of male sage-grouse observed and persistence of leks in the PRB. From 2001-2005, the numbers of males observed on leks in CBNG fields declined more rapidly than leks outside of CBNG. Of leks active in 1997 or later, only 38% within CBNG fields remained active by 2004-2005, compared to 84% of leks outside CBNG fields. By 2005, leks in CBNG fields had 46% fewer males per active lek than leks outside of CBNG. Persistence of 110 leks was positively influenced by the proportion of sagebrush habitat within 6.4 km of the lek. After controlling for habitat, we found support for negative effects of CBNG development within 0.8 km and 3.2 km of the lek and for a time lag between CBNG development and lek disappearance. Current stipulations that prohibit development within 0.4 km of sage-grouse leks on federal lands are inadequate to ensure lek persistence and may result in impacts to breeding populations over larger areas. Seasonal restrictions on drilling and construction do not address impacts caused by loss of sagebrush and incursion of infrastructure that can affect populations over longer periods of time. Development thresholds suggest that the current density of development

is several times greater than that which allows sage-grouse breeding populations to persist. Increased spatial restrictions on CBNG development, rapid implementation of more effective mitigation measures, or both may be required to reduce impacts of CBNG development on sage-grouse populations in the PRB.

Large-scale modification of habitat associated with energy development may alter habitat use or vital rates of sensitive wildlife species. Populations in developed areas may decline if animals avoid specific features of infrastructure such as roads or power lines (Trombulak and Frissell 2000, Nelleman et al. 2001, 2003) or if energy development negatively affects survival or reproduction (Holloran 2005, Aldridge and Boyce 2007). For example, mortality caused by collisions with vehicles and power lines reduces adult and juvenile survival in a variety of wildlife species (reviewed in Bevanger 1998 and Trombulak and Frissell 2000). Indirect effects of energy development on populations are also possible due to changes in predator or parasite communities (Knight and Kawashima 1993, Steenhof et al. 1993, Daszak et al. 2000) or changes in vegetation structure and composition associated with disturbance (Trombulak and Frissell 2000, Gelbard and Belnap 2003). Negative impacts may be exacerbated if features of

development that attract animals (e.g., ponds) simultaneously reduce survival and thereby function as ecological traps (Gates and Gysel 1978).

Rapidly expanding coal-bed natural gas (CBNG) development is a concern for conservation of greater sage-grouse (*Centrocercus urophasianus*) in the Powder River Basin (PRB) of northeastern Wyoming and southeastern Montana. The PRB supports an important regional population, with over 500 leks documented between 1967-2005 (Connelly et al. 2004). In the past decade, the PRB has also experienced rapidly increasing CBNG development, with impacts on wildlife habitat projected to occur over an area of approximately 24,000 km^2 (Bureau of Land Management 2003*a, b*). Coal-bed natural gas development typically requires construction of 2-7 km of roads and 7-22 km of power lines per km^2, depending on well density, as well as an extensive network of compressor stations, pipelines, and ponds (Bureau of Land Management 2003*b*). Approximately 10% of surface lands and 75% of mineral reserves in the PRB are federally owned and administered by the Bureau of Land Management (BLM) (Bureau of Land Management 2003*a, b*). Over 50,000 CBNG wells have been authorized for development on federal mineral reserves in northeastern Wyoming, at a density of 1 well per 16-32 ha, and as many as 18,000 wells are anticipated in southeastern Montana (Bureau of Land Management 2003*a, b*). According to data from the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation, by the beginning of 2005, approximately 28,000 CBNG wells had been drilled on federal (~31%), state (~11%), and private (~58%) mineral holdings in the PRB. Mitigation for sage-grouse on BLM lands typically includes lease stipulations prohibiting surface infrastructure within 0.4 km of sage-grouse leks as well as restrictions on timing of

drilling and construction within 3.2 km of documented leks during the 15 March - 15 June breeding season and within crucial winter habitat from 1 December - 31 March (Montana only) (Bureau of Land Management 2003*a, b*). These restrictions can be modified or waived by BLM, or additional conditions of approval applied, on a case-by-case basis. In contrast, most state and private minerals have been developed with few or no requirements to mitigate impacts on wildlife.

Coal-bed natural gas development and its associated infrastructure may affect sage-grouse populations via several different mechanisms, and these mechanisms can operate at different scales. For example, males and females may abandon leks if repeatedly disturbed by raptors perching on power lines near leks (Ellis 1984), by vehicle traffic on nearby roads (Lyon and Anderson 2003), or by noise and human activity associated with energy development during the breeding season (Braun et al. 2002, Holloran 2005, Kaiser 2006). Collisions with nearby power lines and vehicles and increased predation by raptors may also increase mortality of birds at leks (Connelly et al. 2000*a*, 2000*b*). Alternatively, roads and power lines may indirectly affect lek persistence by altering productivity or survival of local populations at other times of the year. For example, mortality associated with power lines and roads occurs year-round (Patterson 1952, Beck et al. 2006, Aldridge and Boyce 2007). Ponds created during CBNG development may facilitate the spread of mosquitos that transmit West Nile virus (WNv), thereby increasing mortality in late summer (Walker et al. 2004, Zou et al. 2006, Walker et al. 2007). Loss and degradation of sagebrush habitat may also reduce carrying capacity of local breeding populations (Braun 1998, Connelly et al. 2000*b*, Crawford et al. 2004). Alternatively, birds may simply avoid otherwise suitable habitat if the density

of roads, power lines, or energy development increases above a certain threshold (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Doherty et al. 2008).

Understanding how energy development affects sage-grouse populations also requires that we control for other landscape features that affect population size and persistence, including the extent of suitable habitat. Sage-grouse are closely tied to sagebrush habitats throughout their annual cycle, and variation in the amount of sagebrush habitat available for foraging and nesting is likely to influence the size of breeding populations and persistence of leks (Ellis et al. 1989, Schroeder et al. 1999, Leonard et al. 2000, Smith et al. 2005). For this reason, it is crucial to quantify and separate effects of habitat loss from those of energy development.

To assess how CBNG development and habitat loss influence sage-grouse populations in the PRB, we conducted 2 analyses based on region-wide lek-count data. First, we analyzed counts of the numbers of males displaying on leks (hereafter, "lek counts") to assess whether trends in the number of males counted and proportion of active and inactive leks differed between areas with and without CBNG development. Lek counts are widely used for monitoring sage-grouse populations, and at present, are the only data suitable for examining trends in population size and distribution at this scale (Connelly et al. 2003, 2004). Second, we used logistic regression to model lek status (i.e., active or inactive) in relation to landscape features hypothesized to influence sage-grouse demographics and habitat use at 3 spatial scales. The objectives of the lek-status analysis were first, to identify the scale at which habitat and non-CBNG landscape features influence lek persistence and second, to evaluate and compare effects of CBNG

development at different scales with those of non-CBNG landscape features after controlling for habitat.

Study Area

We analyzed data from sage-grouse leks within an approximately 50,000-km^2 area of northeastern Wyoming and southeastern Montana (Figure 1). This area included all areas with existing or predicted CBNG development in the PRB (Bureau of Land Management 2003a, b) as well as surrounding areas without CBNG. Land use in this region was primarily cattle ranching with limited dry-land and irrigated tillage agriculture. Natural vegetation consisted of sagebrush-steppe and mixed-grass prairie interspersed with occasional stands of conifers. Sagebrush-steppe was dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory of native and non-native grasses and forbs. Plains silver sagebrush (*A. cana cana*) and black greasewood (*Sarcobatus vermiculatus*) co-occurred with Wyoming big sagebrush in drainage bottoms.

Methods

Lek-count trend analyses

Lek-count data. We used sage-grouse lek-count data in public databases maintained by Wyoming Game and Fish Department and Montana Department of Fish, Wildlife, and Parks as the foundation for analyses. We augmented databases with lek counts provided by consultants and by the BLM's Miles City field office for 37 leks (36 in Montana, 1 in Wyoming) known to have been counted but for which data were missing. We checked for and, when possible, corrected errors in the database after consultation with database managers and regional biologists for each state. We excluded

records with obvious errors, surveys in which lek status was not determined, leks without supporting count data, and duplicate leks prior to analysis.

Coal-bed natural gas development. We obtained data on the type, location, status, drilling date, completion date, and abandonment date of wells from public databases maintained by the Wyoming Oil and Gas Conservation Commission and Montana Board of Oil and Gas Conservation. Because wells are highly correlated with other features of development, such as roads, power lines, and ponds (D. E. Naugle, University of Montana, unpublished data), using locations of wells is a reliable way to measure the extent of CBNG development. We retained only those wells that were clearly in the ground, associated with energy development (gas, oil, stratification test, disposal, injection, monitoring, and water source wells), and likely to have infrastructure. We excluded wells that were plugged and abandoned, wells waiting on permit approval, wells drilled or completed in 2005 or later, and those with status reported as dry hole, expired permit, permit denied, unknown, or no report. We included wells in analyses starting in the year in which they were drilled or completed (i.e., started producing). For active wells without drilling or completion dates, we estimated start year based on approval and completion dates of wells in the immediate vicinity and in the same unit lease. Wells with current status reported as dormant, temporarily abandoned, or permanently abandoned were included until the year they were first reported abandoned. Because capped (i.e., "shut-in") wells may or may not have associated infrastructure, we included capped wells only in years in which they were surrounded by, or within 1 km of, a producing gas field.

We estimated the extent of CBNG development around each lek in each year. We first approximated the area affected by CBNG development by creating a 350-m buffer around all well locations using ArcInfo 8.2 (ESRI, Inc., Redlands, CA) and dissolving boundaries where buffers overlapped. We then estimated the proportion area within 3.2 km of the lek center covered by the buffer around wells. At current well density (1 well per 32-64 ha), a 350-m buffer around wells estimates the extent of CBNG development more accurately than larger or smaller buffer sizes. This metric is less sensitive to variation in spacing of wells than measures such as well density and therefore more accurate for estimating the total area affected by CBNG development.

Trends in lek counts. We examined lek-count data from 1988-2005. We categorized a lek as in CBNG if ≥40% of the area within 3.2 km was developed or if ≥25% was developed and ≥1 well was within 350 m of the lek center. We categorized a lek as outside CBNG if <40% of the area within 3.2 km was developed and no wells were within 350 m of the lek center. However, because few leks in CBNG were counted in consecutive years prior to 2001, we analyzed trends in lek-counts only from 2001-2005. We calculated the rate of increase in the number of males counted on leks for each year-to-year transition by summing count data across leks within each category according to their stage of development at the end of the first year of each year-to-year transition (Connelly et al. 2004). We summed data across leks to reduce the influence of geographic variation in detectability and used the maximum annual count for each lek to reduce the influence of within-year variation in detectability on the estimated rate of increase. Data for each transition were derived only from leks counted in both years and known to be active in at least 1 of the 2 years of the transition. We estimated mean rates

of increase in CBNG versus outside CBNG fields based on the slope of a linear regression of interval length versus rate of increase (Morris and Doak 2002). Wells completed between January and March (i.e., before lek counts were conducted) in the second year of each transition may have caused us to underestimate the amount of CBNG development around leks at the time counts were conducted. However, if CBNG development negatively affects populations, this would cause the difference between trends in lek-count data in CBNG and outside CBNG to be underestimated and produce a conservative estimate of impacts.

Timing of lek disappearance. If CBNG development negatively affects lek persistence, most leks in CBNG fields that became inactive should have done so following CBNG development. To explore this prediction, we examined the timing of lek disappearance in relation to when a lek was first considered in a CBNG field (i.e., $\geq$40% development within 3.2 km or $\geq$25% development and wells within 350 m of the lek center).

Development threshold. We estimated an approximate threshold density of CBNG development at which sage-grouse leks will remain active by calculating well densities around active leks affected by CBNG. This required assumptions about the scale and extent of CBNG around a lek at which development begins to affect lek persistence. Models with effects of CBNG within 3.2 km were strongly supported (see *Results*, below), whereas those with CBNG within 6.4 km received considerably less support. Thus, for this analysis, we conservatively assumed that only CBNG within 3.2 km would affect lek persistence. Impacts of 40% CBNG development at the 3.2-km scale were pronounced (see *Results*, below), so it is also reasonable to assume that CBNG

affects male lek attendance before development reached 40%. We used data on males

per active lek to identify the approximate extent of development within 3.2 km at which

male lek attendance begins to decline. We did this by comparing the number of males

per lek at active leks with no CBNG versus those with CBNG over a range of increasing

development. We varied the lower limit of development from 0.01% to 37.5% (in

intervals of 2.5%) and the maximum was held constant at 92% (the highest observed

value for any lek). We then calculated well densities around active leks that exceeded the

identified cut-off values. Because wells are often drilled in groups into different coal

seams from the same well pad, we then converted well densities into well-pad densities

based on an average of 1.43 wells per pad (Bureau of Land Management 2003*b*).

Lek-status analysis

   Definition of leks. We defined a lek as a site where multiple males were

documented displaying on multiple visits within a single year or over multiple years. We

defined a lek complex as multiple leks located <2.5 km from the largest and most

regularly attended lek in the complex (Connelly et al. 2004). We defined an initial set of

lek complexes based on those known prior to 1990. Leks discovered in 1990 or later

were considered separate complexes, even if they occurred <2.5 km from leks discovered

in previous years. This was done to avoid problems with the location of already-defined

leks and lek complexes shifting as new leks were discovered or if new leks formed in

response to nearby CBNG development. Leks newly discovered in the same year within

2.5 km of each other were grouped in the same lek complex. We used lek complexes as

the sample unit for calculating proportion of active and inactive leks and in the lek-status

analysis, but because "lek complex" can refer either to multiple leks or to a single lek, hereafter we refer to both simply as a "lek".

Lek status. We determined the final status of leks by examining count data from 2004-2005. We considered a lek active if ≥ 1 male was counted in 2004 or 2005, whichever was the last year surveyed. To minimize problems with non-detection of males, we considered a lek inactive only if: 1) at least 3 consecutive ground or air visits in the last year surveyed failed to detect males, or 2) if surveys in the last 3 consecutive years the lek was checked (2002-2004 or 2003-2005) failed to detect males. We classified the status of leks that were not surveyed or were inadequately surveyed in 2004 or 2005 as unknown. Survey effort in the PRB increased 5-fold from 1997-2005, and included systematic aerial searches for new leks and repeated air and ground counts of known leks within and adjacent to CBNG fields. Therefore, it is unlikely that leks shifted to nearby sites without being detected. Many leks in the PRB disappeared during a region-wide population decline in 1991-1995 (Connelly et al. 2004), well before most CBNG development in the PRB began. To eliminate leks that became inactive for reasons other than CBNG, we calculated proportions of active and inactive leks in CBNG and outside CBNG based only on leks active in 1997 or later.

Scale. We calculated landscape metrics at 3 distances around each lek: 0.8 km (201 ha), 3.2 km (3,217 ha), and 6.4 km (12,868 ha). The 0.8-km scale was selected to represent processes that impact breeding birds at or near leks, while avoiding problems with spatial error in lek locations. The 6.4-km scale reflects processes that occur at larger scales around the lek, such as loss of nesting habitat, demographic impacts on local breeding populations, or landscape-scale avoidance of CBNG fields. The 3.2-km scale is

that at which state and federal agencies apply mitigation for CBNG impacts (e.g., timing restrictions), and it is important to determine the appropriateness of managing at a 3.2-km scale versus at smaller or larger scales.

Habitat variables. Each model in our analysis represented a distinct hypothesis, or combination of hypotheses, regarding how landscape features influence lek persistence. We included 2 types of habitat variables in the analysis, the proportion of sagebrush habitat and the proportion of tillage agriculture in the landscape around each lek. Because the scale at which habitat most strongly influenced lek persistence was unknown, we considered habitat variables at all 3 scales. We calculated the amount of sagebrush habitat and tillage agriculture around each lek at each scale using ArcInfo 8.2 based on classified SPOT-5 satellite imagery taken in August 2003 over an approximately 15,700 km^2 area of the PRB. We restricted the lek-status analysis to leks within the SPOT-5 satellite imagery because the only other type of classified imagery available for this region (Thematic Mapper at 30-m resolution) is unreliable for measuring the extent of sagebrush habitat (Moynahan 2004). Areas with tillage agriculture were visually identified from the imagery and manually digitized. Classification accuracy was 83% for sagebrush habitat (i.e., sagebrush-steppe and sagebrush-dominated grassland). We excluded 20 leks for which >10% of classified habitat data were unavailable due to cloud cover or proximity to the edge of the imagery.

Road, power line, and CBNG variables. We hypothesized that infrastructure can affect lek persistence in 3 ways and included different variables to examine each hypothesis. Roads, power lines, and CBNG development may affect lek persistence in proportion to their extent on the landscape. Alternatively, the effects of roads and power

lines may depend their distance from the lek, in which case they are expected to drop off rapidly as distance increases. Coal-bed natural gas development may also influence lek status depending on how long the lek has been in a CBNG field. If CBNG increases mortality, it may be several years before local breeding populations are reduced to the point that males no longer attend the lek (Holloran 2005). Avoidance of leks in CBNG fields by young birds (Kaiser 2006) combined with high site fidelity of adults to breeding areas (Schroeder et al. 1999) would also result in a time lag between full CBNG development and lek disappearance.

We used TIGER/Line® 1995 public-domain road layers for Wyoming and Montana (U.S. Census Bureau 1995) to estimate the proportion of each buffer around each lek within 350 m of a road at each of the 3 scales. We used 1995 data, rather than a more recent version, to represent roads that existed on the landscape prior to CBNG development. We obtained autumn 2005 GIS coverages of power lines directly from utility companies and used this layer to estimate the proportion of each buffer around each lek within 350 m of a power line at each scale. Year-specific power line coverages were not available, so this variable includes both CBNG and non-CNBG power lines. We estimated the extent of CBNG development around each lek at each scale by calculating the proportion of the total buffer area around the lek center covered by a dissolved 350-m buffer around well locations. If a lek was a complex, we first placed a buffer around all lek centers in the complex then dissolved the intersections to create a single buffer. We selected a 350-m buffer around roads, power lines, and CBNG wells for 2 reasons. First, quantitative estimates of the distance at which infrastructure affects habitat use or vital rates of sage-grouse were not available, and 350 m is a reasonable

distance over which to expect impacts to occur, such as increased risk of predation near power lines or increased risk of vehicle collisions near roads. Second, we also wished to maintain a consistent relationship between well, road, and power line variables and the amount of area affected by each feature. We measured how long a lek was in a CBNG field as the number of years prior to 2005 during which the lek had ≥40% CBNG development within 3.2 km or ≥25% CBNG within 3.2 km and ≥ 1 well within 350 m of the lek center.

Analyses. We used a hierarchical analysis framework to evaluate how landscape features influenced lek status (i.e., active or inactive). Our first goal was to identify the scale at which habitat, roads, and power lines affected lek persistence. Our second goal was to evaluate and compare effects of CBNG development at different scales with those of roads and power lines after controlling for habitat. In both cases, we used an information-theoretic approach (Burnham and Anderson 2002) to select the most parsimonious model from a set of plausible candidate models. All analyses were conducted using logistic regression in R (version 2.3.1, R Development Core Team 2006). We used a logit-link function to bound persistence estimates within a (0,1) interval. Almost all CBNG development within the extent of the SPOT-5 imagery occurred after 1997, so we restricted our analysis to leks known to have been active in 1997 or later to eliminate those that disappeared for reasons other than CBNG development. We also excluded 4 leks known to have been destroyed by coal mining.

To identify the most relevant scale(s) for each landscape variable, we first allowed univariate models at different scales to compete. Variables assessed for scale effects included: (1) proportion sagebrush habitat, (2) proportion tillage agriculture, (3)

proportion area affected by power lines, and (4) proportion area affected by non-CBNG

roads. We then used the scale for each variable that best predicted lek status to construct

the final set of candidate models. We also included models with squared distance to

nearest road and squared distance to nearest power line in the final model set. To assess

different possible mechanisms of CBNG impacts, we evaluated models with the extent of

CBNG development or the number of years since the lek was classified as in a CBNG

field. To assess the scale at which CBNG impacts occur, we included models with the

extent of CBNG effects at all 3 scales. We also included models with interactions

between habitat and CBNG metrics to evaluate whether effects of CBNG development

are amelioriated by the amount of sagebrush habitat around the lek. To avoid problems

with multicollinearity, we did not allow models with correlated variables (i.e., $r > |0.7|$) in

the final model set.

We judged models based on Akaike's Information Criterion adjusted for small

sample size (AIC_c), and examined beta coefficients and associated standard errors in all

models to determine the direction and magnitude of effects. We estimated overdispersion

by dividing the residual deviance of the global model by the deviance degrees of

freedom. Goodness-of-fit testing was conducted in R following methods described in

Hosmer et al. (1997). We used parametric bootstrapping (Efron and Tibshirani 1993) to

obtain means, standard errors, and 95% confidence limits for persistence estimates

because coefficients of variation for most beta estimates were large (Zhou 2002). Due to

model uncertainty, we used model averaging to obtain unconditional parameter estimates

and variances (Burnham and Anderson 2002). We compared the relative importance of

habitat, CBNG, and infrastructure in determining lek persistence by summing Akaike

weights across all models containing each class of variable (Burnham and Anderson 2002). We also calculated evidence ratios to compare the likelihood of the best approximating habitat-plus-CBNG, habitat-plus-infrastructure, and habitat-only models.

To assess whether a known West Nile virus outbreak or habitat loss associated with tillage agriculture disproportionately influenced model selection and interpretation, we also reanalyzed the dataset after removing specific leks. The first analysis excluded 4 leks near Spotted Horse, Wyoming known to have disappeared after 2003 likely due to WNv-related mortality (Walker et al. 2004). The second analysis excluded 20 leks that had ≥5% agriculture at 1 or more of the 3 scales examined.

To evaluate the effectiveness of the stipulation for no surface infrastructure within 0.4 km of a lek, we examined the estimated probability of lek persistence without development versus that under full CBNG development with a 0.4-km buffer. We also used models with effects of CBNG within 3.2 km and CBNG within 6.4 km to estimate the probability of lek persistence over a range of lek buffer sizes from 0.4 to 6.4 km. This second analysis assumes that effects of CBNG only occur within the maximum distance specified under each model. We excluded data based on model with effects of CBNG within 0.8 km because effects of CBNG were apparent at both larger scales.

Results

Trends in lek counts. From 2001-2005, lek-count indices in CBNG fields declined by 82%, at a rate of 35% per year (mean rate of increase in CBNG = 0.65, 95% CI: 0.34-1.25) whereas indices outside CBNG declined by only 12%, at a rate of 3% per year (mean rate of increase outside CBNG = 0.97, 95% CI: 0.50-1.87) (Figure 2). The

mean number of males per active lek was similar between leks in CBNG and outside CBNG in 2001, but averaged 46% ± 8% (mean ± SE; range 33-55%) lower for leks in CBNG from 2002-2005 (Figure 3).

Lek status. Among leks active in 1997 or later, fewer leks remained active by 2004-2005 in CBNG fields (38%) than outside CBNG fields (84%) (Table 1). Of the 10 remaining active leks in CBNG fields, all were classified as being in CBNG in 2000 or later.

Timing of lek disappearance. Of 12 leks in CBNG fields monitored intensively enough to determine the year when they disappeared, 12 became inactive after or in the same year that development occurred (Figure 4). The average time between full CBNG development and lek disappearance was 4.1 ± 0.9 years (mean ± SE).

Development thresholds. Values for males per active lek and well-pad density were positively skewed, so we examined both median and mean values. Median values for males per active lek began to diverge once CBNG development exceeded 2.5% within 3.2 km. In contrast, mean values for leks with CBNG were approximately 2 males per lek lower even at the minimum level of development. After accounting for this initial difference, mean values for males per active lek began to diverge once CBNG development exceeded 7.5%. We approximated development thresholds using both values. A total of 67 active leks had >2.5% CBNG development within 3.2 km. Median density around these leks was 1 well pad per 305 ha (mean ± SE; 171 ± 31 ha). A total of 55 active leks had >7.5% CBNG development within 3.2 km. Median density around these leks was 1 well pad per 229 ha (mean ± SE; 146 ± 26 ha).

Lek-status analysis. We analyzed data from 110 leks of known status within the SPOT-5 imagery that were confirmed active in 1997 or later. Proportion sagebrush habitat and proportion tillage agriculture best explained lek persistence at the 6.4-km scale (Table 2). Proportion power lines also best explained lek persistence at the 6.4-km scale (although power line effects at the 3.2-km scale were also supported), whereas proportion roads best explained lek persistence at the 3.2-km scale.

The final model set consisted of 19 models: 2 models based on habitat only (i.e., sagebrush, sagebrush plus tillage agriculture), 4 models with habitat plus power line variables, 4 models with habitat plus road variables, and 9 models with habitat plus CBNG variables (Table 3). Goodness-of-fit testing using the global model revealed no evidence of lack of fit ($P = 0.49$). Our estimate of the variance inflation factor based on the global model ($\hat{c} = 0.96$) indicated no evidence of overdispersion.

Despite substantial model uncertainty, the top 8 of 19 models all included a moderate to strong positive effect of sagebrush habitat on lek persistence and a strong negative effect of CBNG development, measured either as proportion CBNG development within 0.8 km, proportion CBNG development within 3.2 km, or number of years in a CBNG field. These 8 models were well supported, with a combined Akaike weight of 0.96. Five of the 8 models were within 2 ΔAIC_c units of the best approximating model, whereas all habitat-plus-infrastructure and habitat-only models showed considerably less support (> 6 ΔAIC_c units lower). Evidence ratios indicate that the best habitat-plus-CBNG model was 28 times more likely to explain patterns of lek persistence than the best habitat-plus-infrastructure model and 50 times more likely than the best habitat-only model. Models 1 and 2 both included a negative effect of proportion

CBNG development within 0.8 km. Models with negative effects of number of years in CBNG (model 3) and proportion CBNG development within 3.2 km (model 4) also had considerable support. Although regression coefficients suggested that CBNG within 6.4 km also had a negative impact on lek persistence (Table 4), models with CBNG at 6.4 km showed considerably less support (~5-7 ΔAIC_c units lower). Tillage agriculture appeared in 1 well-supported model (model 2), and the coefficient suggested that tillage agriculture had a strong negative effect on lek persistence. However, this effect was poorly estimated, and the same model without tillage agriculture (model 1) was more parsimonious. Models containing effects of roads unrelated to CBNG development received little or no support in our analysis. Regression coefficients suggested negative effects of proximity to power lines and of proportion power line development within 6.4 km, but models with power line effects were only weakly supported (~6-8 ΔAIC_c units lower). Coefficients for interaction terms did not support an interaction between habitat and CBNG variables. The best approximating model accurately predicted the status of 79% of 79 active leks and 47% of 31 inactive leks. The summed Akaike weight for CBNG variables (0.97) was nearly identical to that of sagebrush habitat (1.00) and greater than that for the effects of tillage agriculture (0.26), power lines (0.02) or non-CBNG roads (0.01). Unconditional, model-averaged estimates and 95% confidence limits for beta estimates and odds ratios show that loss of sagebrush habitat and addition of CBNG development had effects of similar magnitude (Table 4).

The model-averaged estimate for the effect of CBNG within 0.8 km was close to those of the best approximating model (model 1, $\beta_{CBNG\ 0.8\ km}$ = -3.91 ± 1.11 SE) (Table 4). Thus, we illustrate the effects CBNG within 0.8 km on lek persistence using estimates

from that model (Figure 5a). We also illustrate results from model 3, which indicated

that leks disappeared, on average, within 3-4 years of full CBNG development (Figure

5b). The current 0.4-km stipulation for no surface infrastructure leaves 75% of the

landscape within 0.8 km and 98% of the landscape within 3.2 km open to CBNG

development. In an average landscape around a lek in our analysis (i.e., 74% sagebrush

habitat, 26% other land cover types), 75% CBNG development within 0.8 km would drop

the probability of lek persistence from 86% to 24% (Figure 5a). Similarly, 98% CBNG

development within 3.2 km would drop the average probability of lek persistence from

87% to 5%. Lek persistence was projected to increase with larger no-surface-

infrastructure buffers around leks. Background rates of lek persistence in areas without

CBNG development were ~85%. The estimated minimum buffer size required to

maintain average lek persistence at >50% (i.e., to allow a 35% drop in average lek

persistence) ranged from 2.6-5.2 km (Figure 6 *a, b*). In contrast, maintaining average lek

persistence at >75% is estimated to require a 3.0-6.0 km lek buffer (Figure 6 *a, b*).

Similar results are illustrated by models with varying levels of CBNG development and

different sizes of NSO buffers around leks (Figure 7 *a, b*).

   Secondary analyses. Analysis of reduced datasets did not meaningfully change

model fit, model selection, or interpretation, nor did it alter the magnitude or direction of

estimated CBNG effects. After excluding leks affected by WNv, the top 8 of 19 models

and all 3 models within 2 ΔAIC_c units included a positive effect of sagebrush within 6.4

km and a negative effect of CBNG development. Model-averaged estimates of CBNG

effects were similar to those from the original analysis ($\beta_{Sagebrush\ 6.4\ km}$ = 3.96 ± 1.97 SE;

$\beta_{CBNG\ 0.8\ km}$ = -3.48 ± 1.15 SE; $\beta_{CBNG\ 3.2\ km}$ = -4.39 ± 1.52 SE; $\beta_{CBNG\ 6.4\ km}$ = -4.57 ± 2.06

SE; $\beta_{\text{Years in CBNG}} = -1.30 \pm 0.61$ SE). After excluding leks with $\geq 5\%$ tillage agriculture, the top 4 of 11 models and 4 of 5 models within 2 ΔAIC_c units included a positive effect of sagebrush within 6.4 km and a negative effect of CBNG development. Estimates of CBNG effects were again similar to the original model-averaged values ($\beta_{\text{Sagebrush 6.4 km}} = 4.03 \pm 2.29$ SE; $\beta_{\text{CBNG 0.8 km}} = -3.34 \pm 1.41$ SE; $\beta_{\text{CBNG 3.2 km}} = -4.83 \pm 2.06$ SE; $\beta_{\text{CBNG 6.4 km}} = -4.76 \pm 3.21$ SE; $\beta_{\text{Years in CBNG}} = -2.44 \pm 1.25$ SE).

Discussion

Coal-bed natural gas development appeared to have severe negative effects on sage-grouse breeding populations as indexed by male lek attendance and lek persistence. Although the small number of transitions (n = 4) in the trend analysis limited our ability to detect differences between trends, effect sizes were nonetheless large and suggest more rapidly declining breeding populations in CBNG fields. Effects of CBNG development explained lek persistence better than effects of power lines, pre-existing roads, WNv mortality, or tillage agriculture, even after controlling for availability of sagebrush habitat. Approximate development thresholds suggest that the current density of development may be several times greater than that which allows sage-grouse leks and their associated breeding populations, to persist. Strong support for models with negative effects of CBNG at both the 0.8-km and 3.2-km scales indicate that the current restriction on surface infrastructure within 0.4 km is insufficient to protect breeding populations. Support for a lag time between full CBNG development and lek disappearance indicates that monitoring effects of a landscape-level change like CBNG may require several years before changes in lek status are detected.

In our study, non-CBNG roads did not appear to influence lek persistence, even though vehicle collisions and disturbance of leks near roads can have negative impacts on sage-grouse (Lyon and Anderson 2003, Holloran 2005). This may be because most roads in the PRB prior to CBNG development were rarely-traveled dirt tracks rather than the shaled, all-weather roads associated with CBNG development. Alternatively, negative impacts of roads may have been masked by the tendency for male sage-grouse to be attracted to roadways as display sites, for leks near roads to have higher detectability, or because areas in which males display (e.g., broad ridgetops, valley bottoms) are also good for building roads (Schroeder et al. 1999, Rowland 2004). Although models with power line effects were only weakly supported, coefficients nonetheless suggested that power lines (including those associated with CBNG) had a negative effect on lek persistence. Because CBNG development requires construction of both roads and power lines, impacts of CBNG could involve impacts from both features. West Nile virus also has contributed to local lek extirpations in the PRB (Walker et al. 2004). However, unless CBNG development facilitates the spread of WNv into sage-grouse habitat, impacts of the virus should be similar in areas with and without CBNG. Thus, the impact of WNv by itself cannot explain declining breeding populations in CBNG. Rather, increased WNv-related mortality may be an indirect effect of CBNG development (Zou et al. 2006). Other indirect effects, such as increased livestock grazing due to newly-available CBNG water, or changes in predator abundance caused by addition of ponds or power lines, may also indirectly influence sage-grouse populations.

Although CBNG development and loss of sagebrush habitat both contributed to declines in lek persistence, much more of the landscape in the PRB has potential for

CBNG than for tillage agriculture, suggesting that CBNG will have a greater impact on populations at the regional scale. In our analyses, we were unable to distinguish between conversion of sagebrush to cropland that would have occurred in the absence of CBNG development and that which occurred because CBNG water became available for irrigation following development. Although sage-grouse sometimes use agricultural fields during brood-rearing (Schroeder et al. 1999, Connelly et al. 2000b), large-scale conversion of sagebrush habitat to irrigated cropland in conjunction with CBNG development would clearly be detrimental to populations (Leonard et al. 2000, Smith et al. 2005), particularly because birds in agricultural areas likely experience elevated mortality due to pesticides and WNv (Connelly et al. 2000b, Doherty 2007).

Accumulated evidence across studies suggests that sage-grouse populations typically decline following energy development (Braun 1986, Remington and Braun 1991, Braun et al. 2002, Holloran 2005), but our study is the first to quantify and separate effects of energy development from those of habitat loss. Our results are similar to those of Holloran (2005), who found that "natural gas field development within 3-5 km of an active greater sage-grouse lek will lead to dramatic declines in breeding populations," that leks heavily impacted by development typically became inactive within 3-4 years, and that energy development within 6.2 km of leks can decrease male attendance. As in other parts of their range, sage-grouse populations in the PRB likely have declined due to cumulative impacts of habitat loss caused by anthropogenic change and other unknown population stressors (Crawford et al. 2004, Connelly et al. 2004). New threats, such as WNv, have also emerged (Naugle et al. 2004, Walker et al. 2007). Nonetheless, our analysis indicates that energy development has contributed to recent population declines

in the PRB. More importantly, the scale of future development in the PRB suggests that, without more effective mitigation, CBNG will continue to impact populations over an even larger area.

It is unclear whether declines in lek attendance within CBNG fields were caused by impacts to breeding birds at the lek, reduced survival or productivity of birds in the surrounding area, avoidance of developed areas, or some combination thereof. We simultaneously observed greater support for CBNG models but decreasing magnitude of CBNG coefficients at smaller scales around leks, and model uncertainty precluded us from identifying the specific mechanism by which development causes impacts. Although sage-grouse appear to avoid areas with CBNG development in the PRB in winter (Doherty et al. 2008), birds may also avoid CBNG development in the spring and summer. Kaiser (2006) and Holloran et al. (2007) found that yearling females avoided nesting in portions of their natal areas with natural gas development, and yearling males were recruited to leks inside developed fields at lower rates, suggesting displacement to leks on the periphery. Birds breeding within gas fields may also show lower productivity (Lyon and Anderson 2003) or reduced survival compared to birds in natural habitats (Holloran 2005), either of which could result in reduced population growth (see Chapter 5). Experimental research using a before-after, control-impact design with radio-marked birds would be required to identify the relative importance of each mechanism in driving population declines within CBNG. Although this would allow us to identify mechanisms underlying declines, based on our findings and those of others (e.g., Holloran 2005, Aldridge and Boyce 2007, Doherty et al. 2008), such an experiment would likely be detrimental to the affected populations. Nonetheless, ongoing development provides an

opportunity to test mitigation measures in an adaptive management framework, with the ultimate goal of determining how to maintain robust sage-grouse populations in areas with CBNG development. The current pace and scale of CBNG development suggest that effective mitigation measures should be implemented quickly to prevent impacts from becoming more widespread.

Management implications

Our analysis indicates that maintaining extensive stands of sagebrush habitat over large areas (6.4 km or more) around leks is required for sage-grouse breeding populations to persist. This recommendation matches those of all major reviews on sage-grouse habitat requirements (Schroeder et al. 1999, Connelly et al. 2000*b*, Connelly et al. 2004, Crawford et al. 2004, Rowland 2004).

Our findings also refute the idea that prohibiting surface infrastructure within 0.4 km of the lek is sufficient to protect breeding populations, and indicate that increasing the size of no-development zones around leks would increase the probability of lek persistence. The buffer size required depends on the amount of suitable habitat around the lek and the level of impact deemed acceptable. For example, to maintain lek persistence at 50% would require a buffer size of at least 1.6-2.5 km (based on models with CBNG within 3.2 km and 6.4 km), an area 16-39 times larger than that provided by the current 0.4-km buffer. The need for larger buffer sizes is supported by several lines of reasoning. First, impacts from CBNG infrastructure (e.g., avoidance, collisions, increased raptor predation) can affect all seasonal habitats year-round (e.g., nesting, brood-rearing, summer, fall, and winter), not just birds attending leks during the breeding

season. Second, although timing restrictions likely reduce disturbance during the breeding season in the year the field is developed, they do not prevent impacts of infrastructure at other times of the year (e.g., winter; Doherty et al. 2008) or during the production phase, which may last several decades. Morevoer, based on lek-to-nest distances, a 0.4-km buffer is likely to protect <2% of all nesting females (Figure 1 *in* Holloran and Anderson 2005). Because leks in CBNG also have fewer males per lek, buffer sizes estimated solely from data on lek persistence may be too conservative. In practice, estimates of required buffer sizes may be less if buffers from adjacent leks overlap.

A new strategy may be necessary to maintain sage-grouse populations in regions with extensive CBNG development. I suggest a three-tier strategy of establishing core areas with little or no development, implementing more stringent on-site mitigation, and requiring off-site mitigation when on-site mitigation efforts fail. Protecting areas of undeveloped, high-quality sage-grouse habitat in the project area should be top priority. At present, there is little evidence that restrictions other than no surface occupancy allow sage-grouse to persist in CBNG landscapes, that former CBNG fields can or will be restored to a condition that meet year-round sage-grouse habitat requirements, or that populations can be easily reestablished in areas where they have been extirpated. Protected areas need only be maintained until gas production has ceased, until populations in former CBNG fields are reestablished, or until mitigation measures are identified that avoid major impacts to populations. Population goals in conservation plans for four of the five states (Wyoming, Colorado, North Dakota, and Montana) and two Canadian provinces (Alberta and Saskatchewan) experiencing oil and gas

development in the eastern half of the species' range all focus on maintaining the current

distiribution of greater sage-grouse and maintaining or increasing abundance (WGFD

2003, MFWP 2005, NDGFD 2005, CDOW 2007). Currently, 83% of federal minerals

within the eastern range of greater sage-grouse in the U.S. have already been leased with

current 0.4-km lek buffer and timing stipulations (Naugle et al. 2008). The severity of

impacts observed under current stipulations (Holloran 2005, Doherty et al. 2008, this

study) and the current pace and extent of leasing suggests that the potential for impacts

from oil and gas impacts throughout this species' eastern distribution is rapidly

increasing. Establishment of large core areas without energy development may be

required to maintain greater sage-grouse populations large and robust enough to meet

state and provincial population targets and that will continue to sustain historical land

uses, such as livestock grazing, hunting, and agriculture.

Improved mitigation within sage-grouse seasonal habitats may also allow

improved persistence of breeding populations. Previous research suggests that a more

effective mitigation strategy would include, at minimum, burying power lines (Connelly

et al. 2000*b*), minimizing road and well pad construction, vehicle traffic, and industrial

noise (Lyon and Anderson 2003, Holloran 2005), and managing CBNG-produced water

to prevent the spread of mosquitos that vector WNv (Zou et al. 2006, Doherty 2007,

Walker et al. 2007). Habitat improvement projects within CBNG fields may not improve

population persistence if such areas act as population sinks. Because sage-grouse use

large areas of mixed land ownership, a lack of regulation of CBNG in some areas may

undermine mitigation efforts on adjacent federal, state, or private lands. For that reason,

implementation of enhanced mitigation measures by operators regardless of mineral

ownership would be valuable, but will require broad-based support among stakeholders. Regardless, adaptive management will be required to to determine if and how robust sage-grouse populations can be maintained in CBNG fields. Off-site mitigation may be necessary if enhanced mitigation measures within CBNG fields cannot be implemented fast enough or broadly enough to meet overall population targets.

Successful conservation of sage-grouse populations in the PRB depends on the strategy adopted. Stakeholders must also establish acceptable population targets for areas with coal-bed natural gas development. The success or failure of conservation strategies for sage-grouse in the PRB may set a precedent for how impacts of are mitigated as energy development increases throughout the west.

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Figure 1. Distribution and status of active, inactive, and destroyed greater sage-grouse leks, coal-bed natural gas wells, and major highways in the Powder River Basin, Montana and Wyoming, U.S.A. The dashed line shows the extent of SPOT-5 satellite imagery. This map excludes leks that went inactive prior to 1997 and leks whose status in 2004-2005 was unknown. The status of leks within a lek complex are depicted separately. Dot sizes of active leks represent the final count of displaying males in 2004 or 2005, whichever was the last year surveyed: small = 1-25 males, medium = 26-50 males, large = 51-75 males.

Figure 2. Population indices based on male lek attendance for greater sage-grouse in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005 for: (a) all leks combined, and (b) leks categorized as in coal-bed natural gas fields or outside coal-bed natural gas fields on a year-by-year basis. Sample sizes in parentheses above each year-to-year transition indicate the number of leks available for calculating rates of increase for that transition.

Figure 3. Number of male sage-grouse per active lek in coal-bed natural gas (gray) and outside (black) coal-bed natural gas in the Powder River Basin, Montana and Wyoming, U.S.A., 2001-2005. Error bars represent 95% confidence intervals (error bars for leks outside CBNG are too small to be visible). Sample sizes in parentheses above each index indicate the number of active leks available for calculating males per active lek in each year.

Figure 4. Timing of greater sage-grouse lek disappearance relative to coal-bed natural

gas development in the Powder River Basin. Small dot = 1 lek, medium dot = 2 leks,

large dot = 3 leks. Twelve of 13 inactive leks in coal-bed natural gas fields for which the

year when the lek disappeared could be accurately determined became inactive after or in

the same year as development reached ≥40% within 3.2 km (or >25% development

within 3.2 km with ≥1 well within 350 m of the lek center).

Figure 5. Estimated lek persistence as a function of proportion sagebrush habitat within

6.4 km and either (a) proportion coal-bed natural gas (CBNG) development within 0.8

km or (b) number of years within a CBNG field for greater sage-grouse leks in the

Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Means and 95%

confidence intervals (dashed lines) are based on parametric bootstrapping. In (a), black

lines are estimated lek persistence with no CBNG development, and gray lines are

estimated lek persistence with 75% CBNG development within 0.8 km. Seventy-five

percent CBNG development within 0.8 km is equivalent to full development under the

Bureau of Land Management's current restriction on surface infrastructure within 0.4 km

of active sage-grouse leks. In (b), black lines are estimated lek persistence prior to

CBNG development, and gray lines are estimated lek persistence after 3 years in a

developed CBNG field (i.e., ≥40% CBNG within 3.2 km or ≥25% CBNG and ≥1 well

within 350 m of the lek center).

Figure 6. Estimated lek persistence as a function of the size of a no-surface-infrastructure buffer around leks for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Means and 95% confidence intervals (dashed lines) are based on model-averaged coefficients and standard errors presented in Table 4. All results are for leks in an average landscape (74% sagebrush habitat, 26% other cover types within 4 miles of the lek) and assume full coal-bed natural gas (CBNG) development outside the lek buffer (i.e., all areas outside the buffer are within 350 m of a CBNG well). Results in (a) assume that lek persistence is only affected by CBNG development within 3.2 km of the lek. Results in (b) assume that lek persistence is affected by CBNG development within 6.4 km of the lek. The minimum buffer size considered (0.4 km) is the Bureau of Land Management's current standard lease stipulation.

Figure 7. Estimated lek persistence as a function of the size of a no-surface-infrastructure buffer around leks and the extent of coal-bed natural gas development outside that buffer for greater sage-grouse leks in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Means and 95% confidence intervals (dashed lines) are based on model-averaged coefficients and standard errors presented in Table 4. All results are for leks in an average landscape (74% sagebrush habitat, 26% other cover types within 4 miles of the lek). Results in (a) assume that lek persistence is only affected by CBNG development within 3.2 km (2.0 mi.) of the lek. In (a), buffer sizes are 0.4 km (0.25 mi.; pale gray), 1.0 km (0.6 mi.; medium gray), and 1.6 km (1.0 mi.; dark gray). Results in (b) assume that lek persistence is affected by CBNG development within 6.4 km (4.0 mi.)

of the lek. In (b), buffer sizes are 1.0 km (0.6 mi.; pale gray), 1.6 km (1.0 mi.; medium gray), and 3.2 km (2.0 mi.; dark gray). The minimum buffer size considered in (a) was 0.4 km, which is the Bureau of Land Management's current standard lease stipulation.

Table 1. Status of greater sage-grouse leks in the Powder River Basin, Montana and

Wyoming, U.S.A as of 2004-2005 including only leks active in 1997 or later. See text for

definitions of active and inactive leks and for how leks were categorized as in coal-bed

natural gas development (In CBNG) vs. outside coal-bed natural gas (Outside CBNG).

Lek complexes were considered as a single lek.

Lek status	In CBNG		Outside CBNG	
	No.	%[a]	No.	%[a]
Active	10	38	211	84
Inactive	16	62	39	16
Unknown	1		43	
Total active + inactive	26		250	

[a] Percentages are based on the total number of active + inactive leks only.

Table 2. Univariate model selection summary for different classes of landscape variables influencing greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Models within each class are listed in order of decreasing maximum log-likelihood (LL).

Model[a]	LL	K	n	ΔAIC_c	w_i	Estimate	SE
Sagebrush							
6.4 km	-60.05	2	110	0.00	0.70	5.20	1.68
3.2 km	-60.95	2	110	1.81	0.28	4.38	1.53
0.8 km	-63.43	2	110	6.77	0.02	2.26	1.15
Tillage Agriculture							
6.4 km	-55.52	2	110	0.00	0.79	-20.98	6.02
3.2 km	-56.83	2	110	2.63	0.21	-19.31	6.30
0.8 km	-60.92	2	110	10.81	0.00	-10.44	4.59
Power Lines							
6.4 km	-58.69	2	110	0.00	0.52	-6.06	1.76
3.2 km	-58.81	2	110	0.24	0.46	-4.92	1.43
0.8 km	-62.12	2	110	6.84	0.02	-2.51	0.99
Roads							
3.2 km	-64.59	2	110	0.00	0.50	-2.50	1.99
6.4 km	-65.20	2	110	1.21	0.27	-1.52	2.35
0.8 km	-65.41	2	110	1.63	0.22	-0.08	0.87

Table 3. Model selection summary for greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005. Maximum log-likelihood (LL), number of parameters (K), ΔAIC_c values, and AIC_c weights (w_i) listed for each model in order of increasing ΔAIC_c units, starting with the best approximating model. All models shown. The AIC_c value of the best approximating model in the analysis was 108.54.

No.	Model[a]	LL	K	n	ΔAIC_c	w_i
1	Sagebrush 6.4 + CBNG 0.8	-51.16	3	110	0.00	0.24
2	Sagebrush 6.4 + Agriculture 6.4 + CBNG 0.8	-50.48	4	110	0.80	0.16
3	Sagebrush 6.4 + Years in CBNG	-51.56	3	110	0.80	0.16
4	Sagebrush 6.4 + CBNG 3.2	-51.70	3	110	1.09	0.14
5	Sagebrush 6.4 * CBNG 0.8	-50.98	4	110	1.81	0.10
6	Sagebrush 6.4 * Years in CBNG	-51.32	4	110	2.48	0.07
7	Sagebrush 6.4 + Agriculture 6.4 + CBNG 3.2	-51.52	4	110	2.88	0.06
8	Sagebrush 6.4 + CBNG 6.4	-53.69	3	110	5.07	0.02
9	Sagebrush 6.4 + Agriculture 6.4 + Dist. Power Line^2	-53.39	4	110	6.63	0.01
10	Sagebrush 6.4 + Agriculture 6.4 + CBNG 6.4	-53.48	4	110	6.81	0.01
11	Sagebrush 6.4 + Agriculture 6.4	-55.08	3	110	7.84	0.00
12	Sagebrush 6.4 + Power Lines 6.4	-55.08	3	110	7.84	0.00
13	Sagebrush 6.4 + Agriculture 6.4 + Power Lines 6.4	-54.07	4	110	7.99	0.00
14	Sagebrush 6.4 + Agriculture 6.4 + Dist. Road^2	-54.47	4	110	8.78	0.00
15	Sagebrush 6.4 + Agriculture 6.4 + Roads 3.2	-54.49	4	110	8.83	0.00
16	Sagebrush 6.4 + Dist. Power Line^2	-57.36	3	110	12.41	0.00

17	Sagebrush 6.4	-60.05	2	110	15.67	0.00
18	Sagebrush 6.4 + Roads 3.2	-59.39	3	110	16.46	0.00
19	Sagebrush 6.4 + Dist. Road^2	-59.46	3	110	16.62	0.00

[a] CBNG = coal-bed natural gas development. Numbers refer to the radius (km) around the lek at which the variable was measured.

Table 4. Model-averaged estimates of regression coefficients (β) and standard errors (SE), odds ratios, and lower (LCL) and upper (UCL) 95% confidence limits on odds ratios for effects of landscape variables on greater sage-grouse lek persistence in the Powder River Basin, Montana and Wyoming, U.S.A., 1997-2005.

Variable[a]	β	SE	Odds Ratio	Odds Ratio LCL	Odds Ratio UCL
Intercept	-1.25	1.40	-	-	-
Sagebrush	4.06	2.03	58.241	1.083	3131.682
Agriculture	-8.76	8.73	1.57×10^{-4}	5.81×10^{-12}	4.22×10^{3}
CBNG 0.8 km	-3.67	1. 18	0.026	0.003	0.257
CBNG 3.2 km	-4.72	1.50	0.009	0.001	0.169
CBNG 6.4 km	-5.11	2.04	0.006	0.0001	0.328
Years in CBNG[b]	-1.41	0.58	0.244	0.078	0.761

[a] CBNG = coal-bed natural gas development.

[b] The estimated regression coefficient for Years in CBNG could only be derived from one model.

Study area
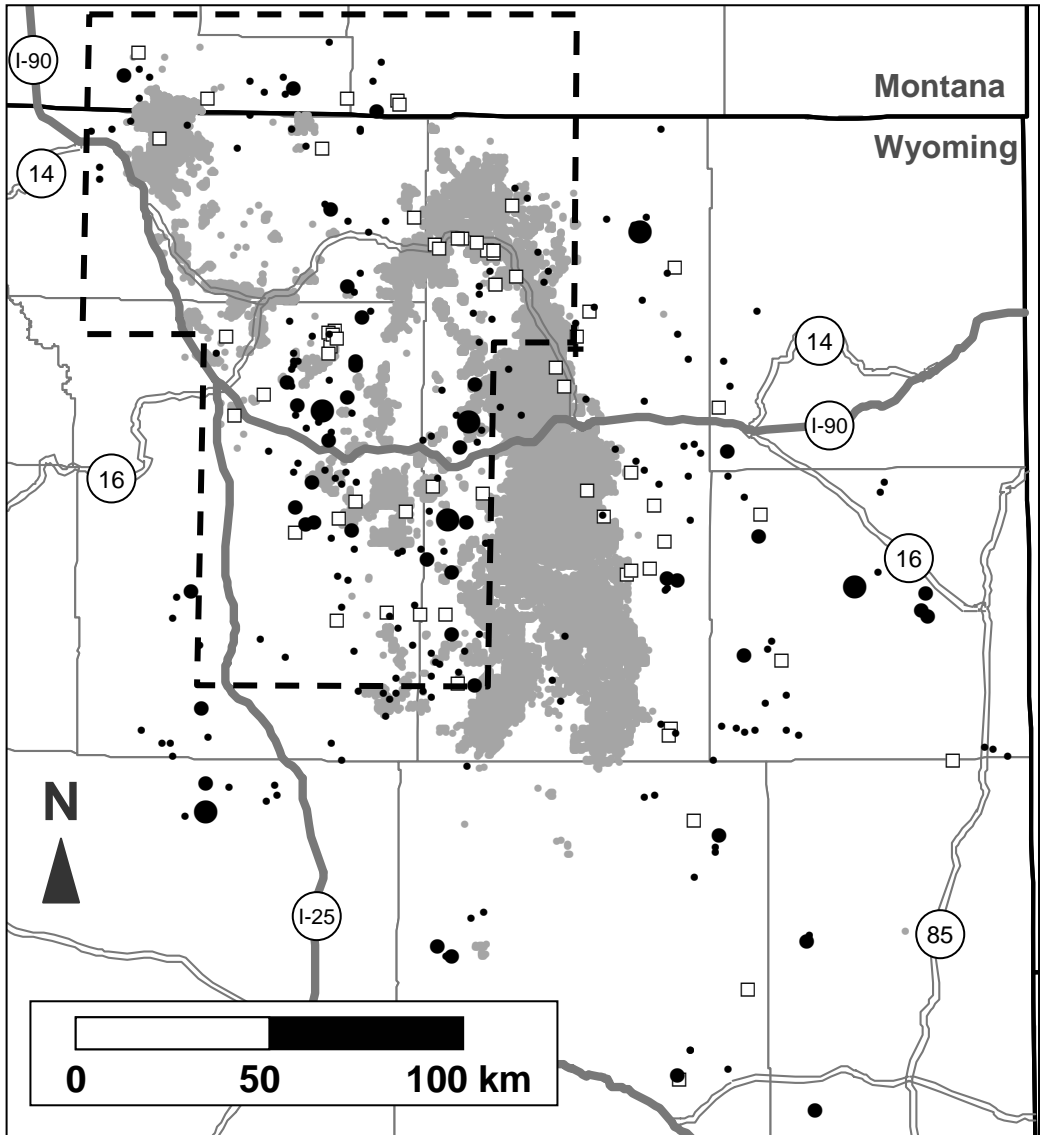
Boundary of SPOT-5 satellite imagery

● Coal-bed natural gas wells

□ Inactive lek

✚ Destroyed lek

Active lek:
- Small (1-25 males)
- Medium (26-50 males)
- Large (51-75 males)

Montana

Wyoming

I-90
14
16
I-25
14
I-90
16
85

N

0   50   100 km

Figure 2

Figure 3

Figure 4

Figure 5

a

Estimated lek persistence (y-axis)

Black = no CBNG

Gray = CBNG
with 0.4 km
buffer

Proportion sagebrush within 6.4 km (x-axis)

b

Estimated lek persistence (y-axis)

Black = no CBNG

Gray = after 3 yrs in CBNG

Proportion sagebrush within 6.4 km (x-axis)

Figure 6.

a

b

Figure 7.

a

Estimated lek persistence

Proportion CBNG within 3.2 km but outside buffer

b

Estimated lek persistence

Proportion CBNG within 6.4 km but outside buffer
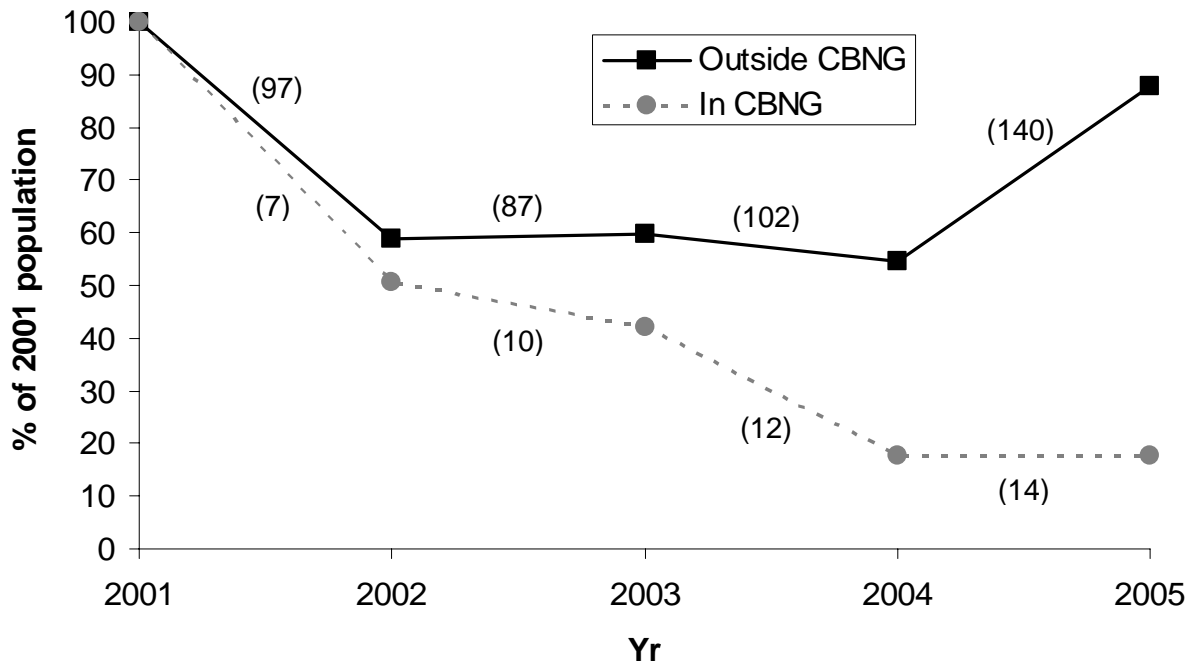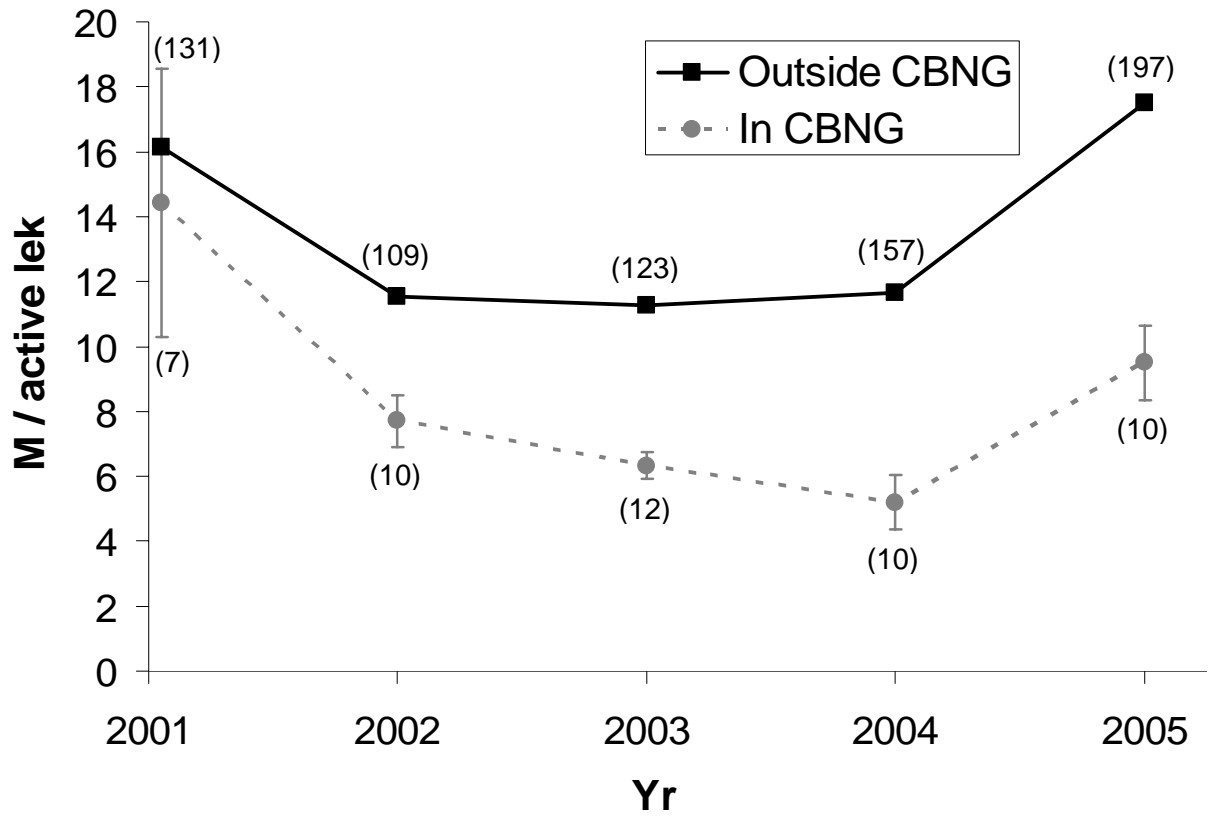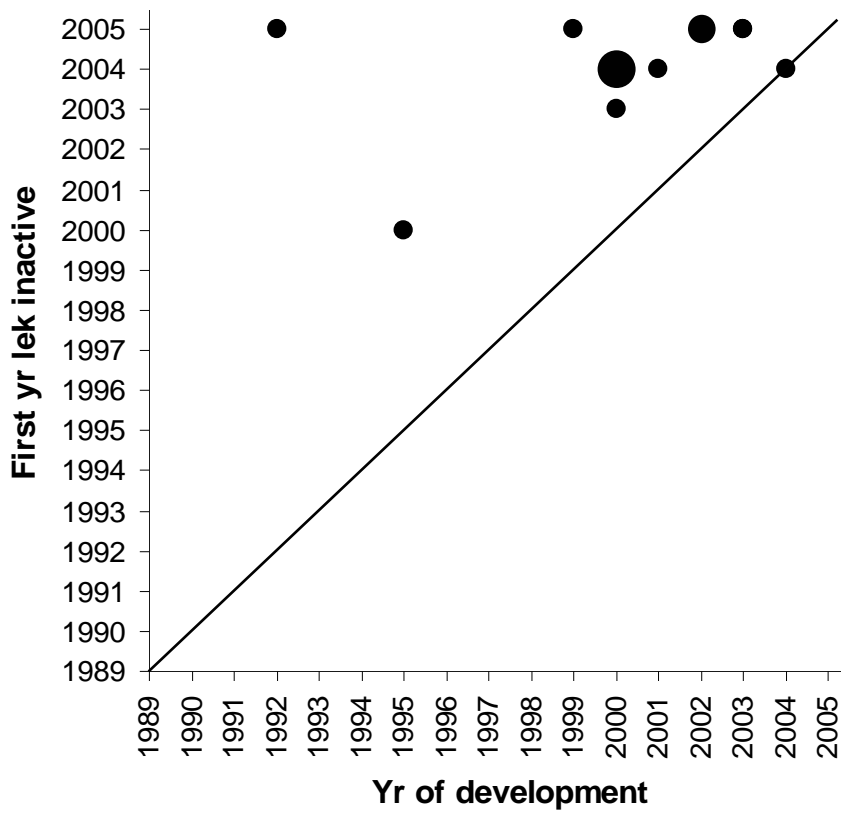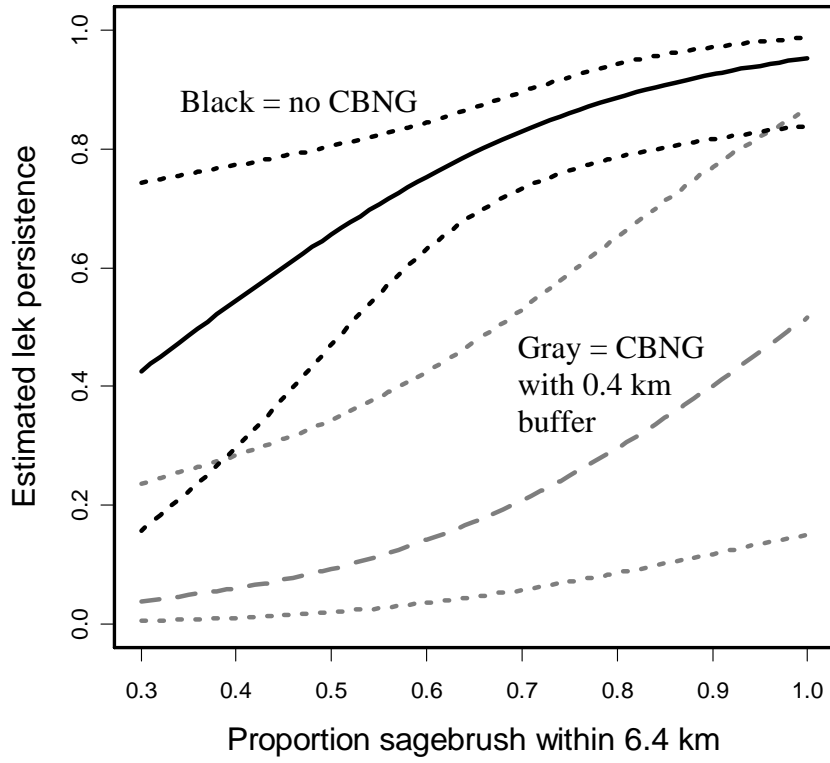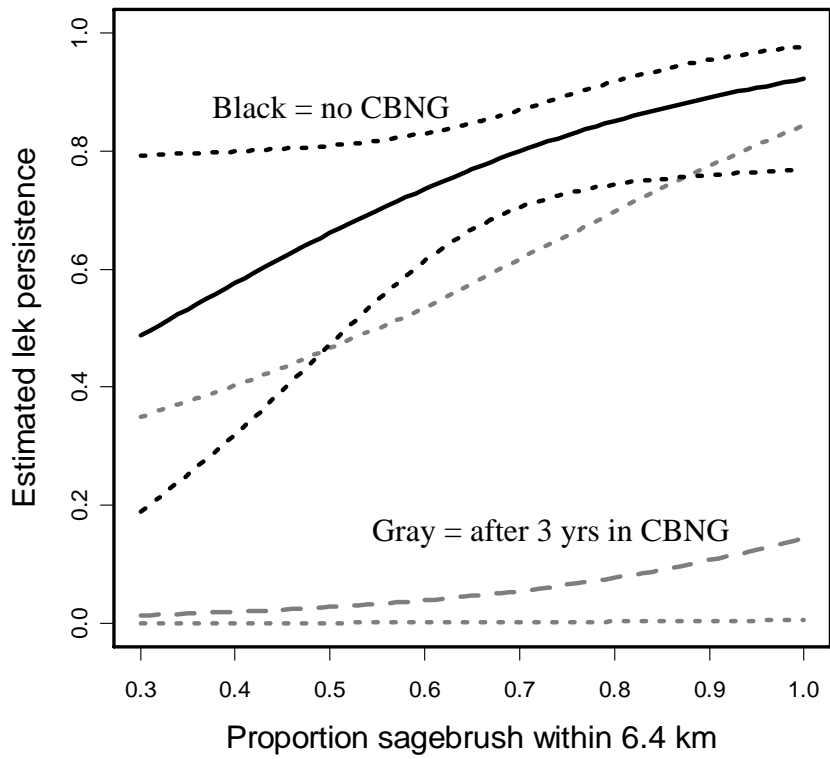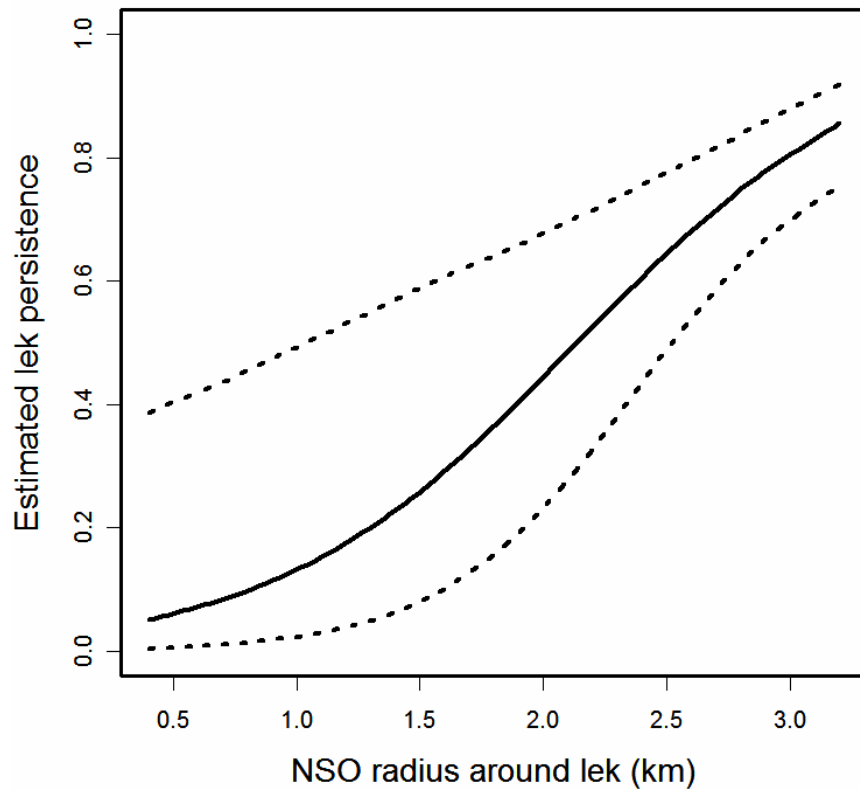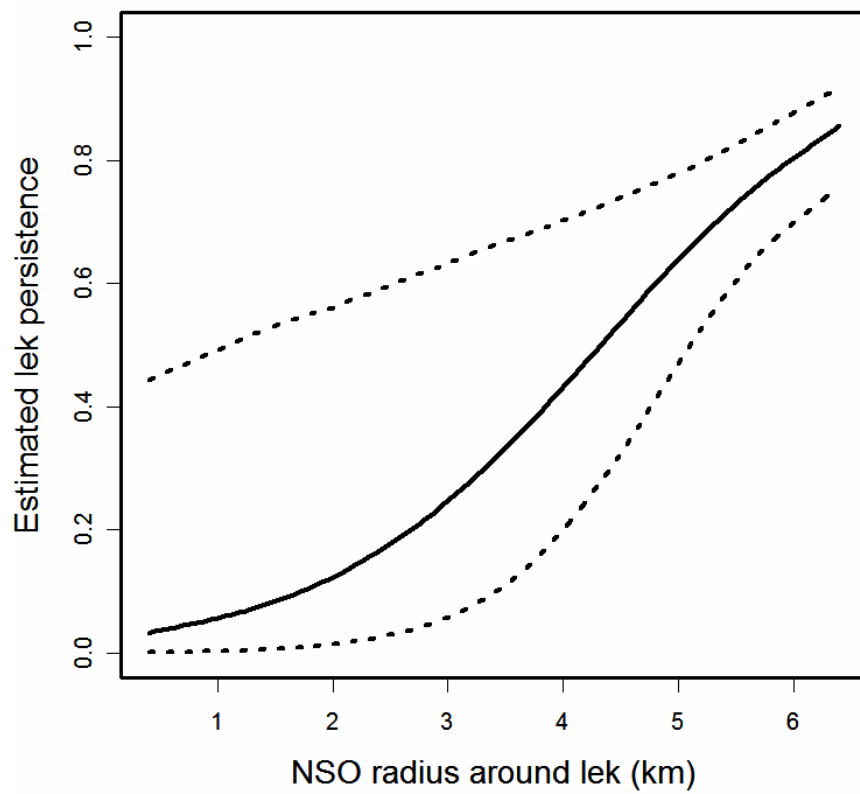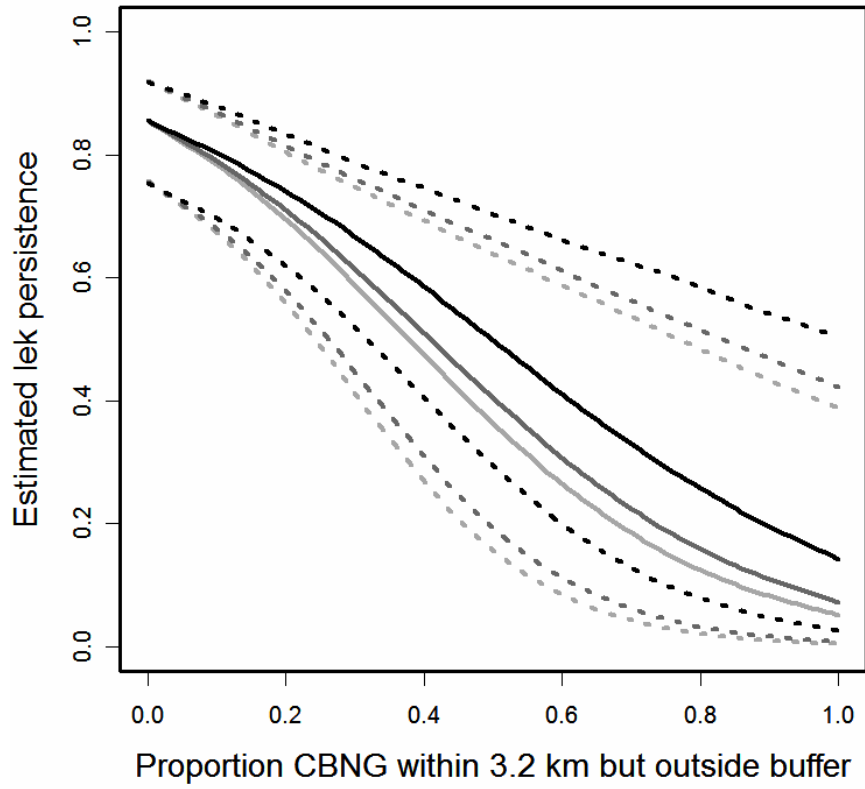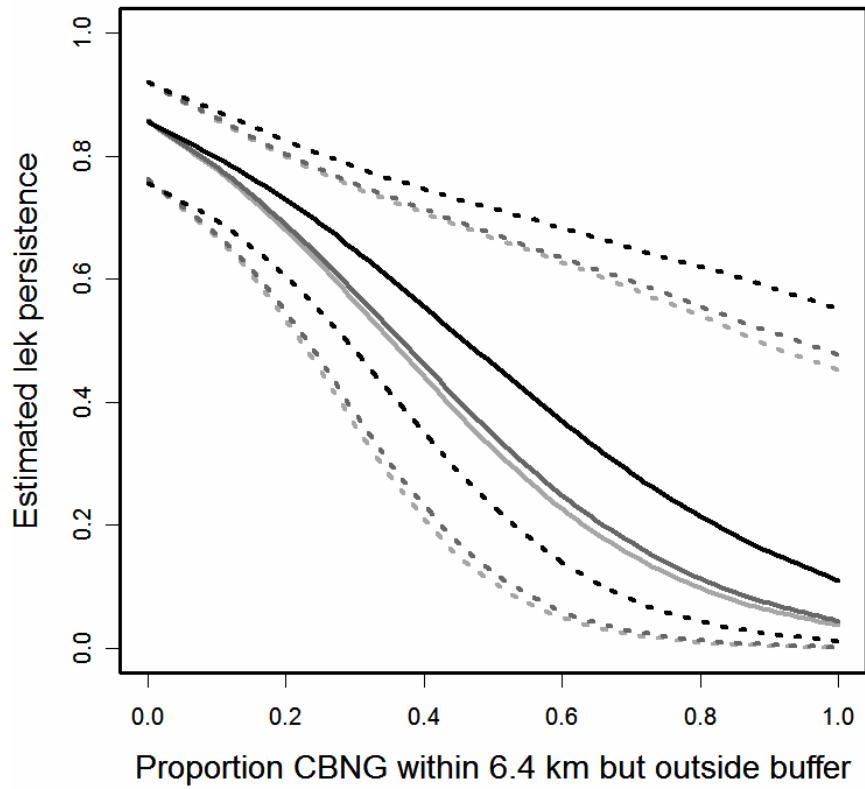
CHAPTER 3. WEST NILE VIRUS AND GREATER SAGE-GROUSE: ESTIMATING INFECTION RATE IN A WILD BIRD POPULATION

Abstract. Understanding impacts of disease on wild bird populations requires knowing not only mortality rate following infection, but also the proportion of the population that is infected. Greater sage-grouse (*Centrocercus urophasianus*) in western North America are known to have a high mortality rate following infection with West Nile virus (WNv), but actual infection rates in wild populations remain unknown. We used rates of WNv-related mortality and seroprevalence from radio-marked females to estimate infection rates in a wild greater sage-grouse population in the Powder River Basin (PRB) of Montana and Wyoming from 2003-2005. Minimum WNv-related mortality rates ranged from 2.4-13.3% among years and maximum possible rates ranged from 8.2-28.9%. All live-captured birds in 2003 and 2004 tested seronegative. In spring 2005 and spring 2006, 10.3% and 1.8% respectively, of newly-captured females tested seropositive for neutralizing antibodies to WNv. These are the first documented cases of sage-grouse surviving infection with WNv. Low to moderate WNv-related mortality in summer followed by low seroprevalence the following spring in all years indicates that annual infection rates were between 4-29%. This suggests that most sage-grouse in the PRB have not yet been exposed and remain susceptible. Impacts of WNv in the PRB in the near future will likely depend more on annual variation in temperature and changes in vector distribution than on the spread of resistance. Until the epizootiology of WNv in sagebrush-steppe ecosystems is better understood, we suggest that management to reduce impacts of WNv focus on eliminating man-made water sources that support breeding

mosquitos known to vector the virus. Our findings also underscore problems with using

seroprevalence as a surrogate for infection rate and for identifying competent hosts in

highly susceptible species.

Keywords: *Centrocercus urophasianus*, coal-bed natural gas, energy development,

flavivirus, greater sage-grouse, infection rate, sagebrush-steppe, West Nile virus.

Assessing risks posed by emerging infectious disease is an important part of

conservation planning and management for avian species of concern (6, 9, 20). Human

modifications to wildlife habitat often facilitate the spread of infectious diseases (6, 8,

20), and disease outbreaks may undermine efforts to maintain viable or harvestable

populations (21, 26, 35, 39).

Predicting impacts of emerging infectious disease and identifying suitable strategies

to control its spread requires knowing both the prevalence of disease and the mortality

rate of infected individuals (16, 17). Mortality rate is typically estimated by

experimentally infecting wild-caught animals in the laboratory (e.g., 4, 16). Ideally,

prevalence (i.e., exposure) would be measured by infection rate, defined as the proportion

of the population that is exposed to the pathogen during an outbreak and becomes

infected. Unfortunately, infection rates in wild populations are difficult to estimate (17,

18, 21). For that reason, most studies instead report seroprevalence as a surrogate for

infection rate (e.g., 1, 2, 9, 11, 19, 28, 33). Drawing inferences regarding exposure based

solely on seroprevalence assumes a linear relationship between the two. However,

because seroprevalence estimates exclude infected individuals that die prior to sampling,

seroprevalence may underestimate infection rate in susceptible species with high disease-related mortality (13, 17). Estimates of host competence that rely on seroprevalence suffer from the same problem. If infected hosts die soon after transmitting the virus, measures of seroprevalence after the outbreak will underestimate true disease prevalence and the importance of that host in the transmission cycle. Thus, to fully understand the prevalence, impacts, and epizootiology of disease in wild bird populations requires that we estimate not only mortality rate and seroprevalence, but also actual disease-related mortality, which in turn allows estimation of infection rates.

Knowing infection rate is also crucial for identifying potential strategies for mitigating disease impacts to susceptible species. If infection rates are low, it suggests that exposure is uncommon, and that it may be possible to further reduce exposure by managing vectors, alternative hosts, or both. In contrast, if infection rates are uniformly high, then focusing on other management strategies, such as vaccination, may be more effective.

The recent spread of West Nile virus (WNv) in North America represents an important potential stressor on native bird populations, including greater sage-grouse (*Centrocercus urophasianus*) (hereafter "sage-grouse"). Sage-grouse are gallinaceous birds native to western semi-arid sagebrush (*Artemisia* spp.) habitats (30). Previously widespread, the species has been extirpated over almost half of its original range due to loss, fragmentation, and degradation of sagebrush habitat (5, 15, 29). The species' conservation status has precipitated a coordinated effort to assess risks to populations and implement conservation and management actions to mitigate those risks (5). West Nile virus was first detected in dead sage-grouse in 2002. By 2003, WNv-related mortality

had reduced late-summer survival of adult females by 25% (22) and resulted in near-extirpation of a local breeding population in northeastern Wyoming (36). In summer 2004, survival was 10% lower (86%) at sites across the species' range with confirmed WNv mortalities than at sites without (96%) (23). The extreme susceptibility of sage-grouse was confirmed in 2004 when, in separate laboratory trials, all non-vaccinated birds (n=44) experimentally infected with WNv died within 6-8 days, regardless of dosage (4, T. Cornish, unpublished data). As of fall 2006, sage-grouse mortalities positive for WNv have been confirmed in 11 of 13 states and provinces where the species still occurs (23, 34). Despite concern over impacts of WNv on sage-grouse, actual prevalence of the virus in wild populations remains unknown.

Recent reviews of West Nile virus (WNv) have identified a lack of data on infection rates from wild populations as a major hindrance to understanding impacts of this recently-arrived pathogen on North American birds (21, 26). To better understand the prevalence and potential impacts of WNv on sage-grouse, we used rates of WNv-related mortality and seroprevalence from radio-marked females to retrospectively estimate annual WNv infection rates in a wild population from 2003-2005. We also examine implications of low infection rates for managing WNv risk in sage-grouse conservation and management strategies.

Materials and Methods

Female sage-grouse were captured and radio-marked from 2003-2006 as part of a study assessing impacts of coal-bed natural gas development on sage-grouse populations in the Powder River Basin (PRB) of southeastern Montana and northeastern Wyoming,

USA (elevation 1000-1400m). Study sites primarily consisted of semi-arid sagebrush-steppe and shortgrass prairie interspersed with mesic shrubland, greasewood (*Sarcobatus vermiculatus*) bottomlands, irrigated and dry-land crops, riparian woodland, and conifer forest. Dominant plant species in sagebrush-steppe included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and Plains silver sagebrush (*A. cana cana*) with an understory of native and exotic grasses and forbs.

We monitored radio-marked females every 2-4 days during the peak WNv transmission period (1 July - 15 September) in each year (36). Dead birds that yielded testable carcasses (i.e., carcasses with brain, wing or leg bones, internal organs, or spinal column present) underwent complete necropsies and microscopic examination of tissues by histopathology at the Wyoming State Veterinary Laboratory (Laramie, WY). Each carcass was tested for WNv using real-time polymerase chain reaction (31) and immunohistochemistry (14). Select cases positive for WNv were confirmed by isolation of the virus from one or more tissues (brain, heart, kidney, or bone marrow) in Vero cell cultures (32).

We used a Kaplan-Meier product limit estimator with staggered-entry design to estimate mortality in each year from 2003-2005 (38). Because 40% of 50 mortalities over the three years did not yield testable carcasses, mortality estimates based only on carcasses that tested positive for WNv infection may have underestimated actual WNv-related mortality. For that reason, we calculated both minimum WNv-related mortality based on mortalities confirmed positive for WNv and maximum possible WNv-related mortality based on total mortalities minus those confirmed negative for WNv. The maximum possible estimate included mortalities for which no carcass (e.g., only a radio-

transmitter) was recovered, the carcass was not testable (e.g., too decomposed), or if tests were inconclusive. Individuals captured after 1 July were left-censored on the date of capture, and individuals that disappeared prior to 15 September (i.e., fate unknown) were right-censored on the last date they were located (38). We estimated dates of mortality as the mid-point between last date observed alive and the first date observed dead. In some cases, we estimated timing of mortality more accurately from the condition of the carcass.

To determine whether sage-grouse survived infection with the virus, we collected blood samples from live-captured birds in August-September 2003 (n = 55), March-April 2004 (n = 66), August-October 2004 (n = 46), March-April 2005 (n = 58), and March-April 2006 (n = 109). Blood samples were refrigerated, centrifuged, and serum decanted within 12 hours of capture, then frozen until testing. Serum samples were tested for neutralizing antibodies to WNv using a micro plaque reduction neutralization test (PRNT) (37). All samples positive for WNv were also tested for St. Louis encephalitis virus, the only other flavivirus in this region known to cross-react serologically with WNv (3). We report seroprevalence as the proportion of females that tested positive (PRNT titer 1:100) for antibodies to WNv and calculated 95% confidence intervals using logistic regression.

We used rates of WNv-related mortality during the WNv season and observed seroprevalence the following spring to calculate infection rates in each year from 2003-2005. We based our calculations on the mathematical model of Komar et al. (17), who showed that infection rate, I, can be expressed in terms of post-epizootic seroprevalence, S, and mortality rate following WNv infection, M, as follows:

$$I = S / [1 - M + (S * M)] \qquad (1)$$

Because mortality rate, M, can be expressed as WNv-related mortality, ΔP, divided by infection rate (i.e., $M = \Delta P / I$), substituting for M and rearranging the equation allowed us to calculate infection rate from WNv-related mortality rate and post-epizootic seroprevalence:

$$I = \Delta P + S - (S * \Delta P) \qquad (2)$$

Because WNv-related mortality reduces post-epizootic population size and inflates the seroprevalence estimate, the $S*\Delta P$ term in Equation 2 is used to adjust the post-epizootic seroprevalence estimate to reflect seroprevalence based on population size prior to, rather than following, the outbreak. Our method assumes: (1) that additional WNv-related mortality did not occur between the end of the WNv transmission period and when serum samples were collected the following spring, and (2) that birds seropositive in spring were infected the previous summer. Coal-bed natural gas development may facilitate the spread of WNv by increasing the amount of surface water available to support breeding mosquitos (40). To better understand background rates of WNv mortality and infection in the absence of coal-bed natural gas development, we estimated rates with and without data from birds in or near areas with extensive coal-bed natural gas development.

To assess the accuracy of seroprevalence as a measure of actual infection rates, we also examined the relationship between infection rate and post-epizootic seroprevalence over a range of observed susceptibilities across species (4, 16).

Results

Estimated minimum WNv-related mortality was low in all years, ranging from 2.4% in 2005 to 13.3% in 2003 (Table 1). Maximum possible WNv-related mortality was low to moderate, ranging from 8.2% to 28.9% (Table 1). WNv-related mortality was higher in 2003, the 6th warmest summer on record in the PRB, than in 2004 and 2005, the 86th and 41st warmest, respectively (24). Rates of WNv mortality and infection were substantially lower for 2003 and slightly lower for 2004 when data from birds in areas with extensive coal-bed natural gas development were removed (Table 2).

All serum samples through fall 2004 (n = 167) tested negative for WNv. In spring 2005, six of 58 (10.3%) females captured tested seropositive. In spring 2006, two of 109 (1.8%) females tested seropositive. All females seropositive for WNv tested negative for St. Louis encephalitis virus (PRNT titers <1:10). Of the six seropositive females in 2005, four were yearlings (i.e., hatched in 2004) and two were adults (i.e., hatched in 2003 or earlier). Of the two seropositive females in 2006, one was a yearling (i.e., hatched in 2005), and one was an adult (i.e., hatched in 2004 or earlier). All birds were of normal mass for their age (mean ± SE; adult: 1.64 ± 0.05 kg, n =3; yearling: 1.44 ± 0.04 kg, n = 5) and exhibited no overt signs of WNv-related disease at capture (e.g., morbidity, ataxia, tilted head, drooping wings, or impaired flight) (4, 18, 36). Seropositive females also initiated nests at the same time as other hens and had normal clutch sizes. The presence of neutralizing antibodies to WNv in yearlings captured in spring indicates that antibodies were detectable for at least 5 months following exposure. Seropositive females were distributed across six leks at four different study sites. Microsatellite analyses demonstrated that none of the eight females were related and thus can be considered

independent replicates for seroprevalence calculations (K. L. Bush, University of Alberta, unpublished data).

Estimates of both minimum and maximum possible infection rates in the PRB were low to moderate in all three years (Table 1). Estimates of minimum infection rate ranged from 4.2-13.6% and maximum possible infection rate from 9.9%-28.9%. Infection rates were higher in 2003 than in 2004 or 2005. Sample sizes were insufficient to provide precise estimates of mortality, seroprevalence, or infection rate on a site-by-site basis.

In this study, seroprevalence estimates underestimated infection rate by a small amount in all three years of the study (Table 1). However, the relationship between infection rate and post-epizootic seroprevalence was increasingly non-linear with increasing susceptibility, and the difference between the two metrics for susceptible species was largest at intermediate infection rates (Figure 1).

Discussion

This study presents the first empirically-derived estimate of actual WNv infection rate reported for any wild bird population. In this study, estimates of seroprevalence and infection rate were similar. However, this is to be expected when infection rates and seroprevalence are both low (Figure 1). Because of the extreme susceptibility of sage-grouse, had actual infection rates been higher, the difference between observed seroprevalence and estimated infection rates would likely have been much greater. For susceptible species, seroprevalence may substantially underestimate both the prevalence and impacts of disease and confound inferences regarding exposure (e.g., habitat- or species-specific exposure rates). For example, in Rock Pigeons (*Columba livia*), which

63

are largely resistant to WNv (16), seroprevalence likely provides a reliable measure of exposure (e.g., 1; Figure 1). In contrast, for susceptible species (e.g., corvids, sage-grouse, American White Pelican [*Pelecanus erythrorhyncos*], and Ring-billed Gull [*Larus delawarensis*]; [4, 16, 18]), the value of seroprevalence data for making inferences about infection rates in the absence of information on mortality is suspect (Figure 1). Inferences regarding exposure in species with unknown susceptibility – including the vast majority of Nearctic and Neotropical species – may also be called into question. Despite low observed seroprevalence, sage-grouse are also considered competent amplifying hosts for WNv (4). The duration of infectious viremia in captive sage-grouse (3-5 days) was comparable to other avian species considered competent reservoirs, such as corvids, blackbirds, and raptors (16). Together, these findings underscore problems inherent with using seroprevalence as a surrogate for infection rate and for identifying competent hosts in the absence of data on disease-related mortality.

The discovery of WNv-specific antibodies in live sage-grouse also represents the first documented evidence that individuals of this species can survive WNv infection. Seropositive birds in our study likely survived because they successfully mounted an immune response to infection. However, it is also possible that seropositive birds acquired antibodies via passive vertical transmission from their mothers (12, 33). Although we observed no overt evidence of sub-lethal effects, if overwinter survival of infected birds was reduced compared to their uninfected counterparts, we may have underestimated infection rates.

How WNv will affect sage-grouse populations in the PRB in the future is unclear. Over the next decade, we suspect that impacts will depend less on resistance to disease

than on variation in temperature (23, 27, 41) and changes in vector distribution (40).

First, resistance appears to be neither widespread nor common. Low infection rates

indicate that most sage-grouse in the PRB probably have not been exposed to WNv and

remain susceptible. Second, temperature strongly affects physiological and ecological

processes that influence WNv transmission (7, 27, 41), and outbreaks are typically

associated with prolonged periods of above-average temperature and drought (10). In our

study, timing and extent of mortality across years were consistent with this hypothesis,

with lower mortality rates and later peaks of mortality in years with lower June-August

temperatures (2004-2005) (23). Third, construction of ponds associated with coal-bed

natural gas development increased larval mosquito habitat by 75% from 1999-2004 over

a 21,000-km^2 area of the PRB (40). Coal-bed natural gas development is anticipated to

continue in the PRB for the next 10-15 years in occupied sage-grouse habitats.

Estimates of both seroprevalence and infection rate in our study were generally lower

than seroprevalence estimates for many species in suburban, forested, farmland, urban, or

wetland sites in other parts of the U.S. (e.g., 1, 2, 11, 17, 28, 33) but similar to those in

desert regions of California (27). Due to seasonal drought in summer, sagebrush-steppe

may support fewer avian or mammalian hosts or fewer mosquito vectors than other, more

mesic habitats. Reservoir and amplifying hosts for WNv in this ecosystem remain

unknown and likely cannot be managed over large geographic scales. For this reason, we

suggest that management to reduce impacts of WNv in sage-grouse habitat focus on

eliminating mosquito breeding habitat in anthropogenic water sources, particularly coal-

bed natural gas ponds.

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Table 1. Mortality and West Nile virus (WNv) testing of radio-marked female sage-grouse during the peak WNv transmission period (1 July - 15 September) and seroprevalence the following spring in the Powder River Basin, 2003-2005, including birds from areas with extensive coal-bed natural gas development. Estimated minimum and maximum possible mortality (ΔP), seroprevalence (S), and minimum and maximum possible infection rates (I) given as mean (95% CI). Two typographical errors were discovered after publication of Walker et al. (2007). The lower confidence limit in 2004 was 0.110, not 0.011, and the number of females monitored in 2003 was 59, not 46.

Yr	No. sites	No. females	No. deaths	No. tested	+/- tests	Median date WNV deaths	ΔP (min)	ΔP (max)	S	I (min)	I (max)
2003	3	59	15	10	6/4	8/03 (7/24-8/05)	0.133 (0.048-0.219)	0.289 (0.178-0.399)	0.000 (-)	0.133[A] (0.048-0.219)	0.289[A] (0.178-0.399)
2004	6	118	17	9	4/5	8/23 (8/03-9/04)	0.037 (0.003-0.071)	0.094 (0.042-0.147)	0.103 (0.047-0.212)	0.136 (0.070-0.202)	0.187 (0.110-0.265)
2005	6	123	18	11	3/8	8/6 (7/28-8/07)	0.024 (0.000-0.053)	0.082 (0.033-0.132)	0.018 (0.005 – 0.070)	0.042 (0.011-0.074)	0.099 (0.047-0.150)

[A] Seroprevalence was 0.0 in fall 2003 and spring 2004, so the estimated infection rate in 2003 equaled estimated mortality.

Table 2. Mortality and West Nile virus (WNv) testing of radio-marked female sage-grouse during the peak WNv transmission period (1 July - 15 September) and seroprevalence the following spring in the Powder River Basin, 2003-2005, excluding birds from areas with extensive coal-bed natural gas development. This allows estimation of background infection rates in the absence of coal-bed natural gas development. Estimated minimum and maximum possible mortality (ΔP), seroprevalence (S), and minimum and maximum possible infection rates (I) given as mean (95% CI).

Yr	No. sites	No. females	No. deaths	No. tested	+ /- tests	ΔP (min)	ΔP (max)	S	I (min)	I (max)
2003	2	49	7	4	0/4	0.000 (-)	0.143 (0.047-0.239)	0.000 (-)	0.000[A] (-)	0.143[A] (0.047-0.239)
2004	4	110	14	7	2/5	0.020 (0.000-0.046)	0.081 (0.030-0.131)	0.103 (0.047-0.212)	0.121 (0.060-0.182)	0.175 (0.104-0.246)
2005	6	123	18	11	3/8	0.024 (0.000-0.053)	0.082 (0.033-0.132)	0.018 (0.005 – 0.070)	0.042 (0.011-0.074)	0.099 (0.047-0.150)

[A] Seroprevalence was 0.0 in fall 2003 and spring 2004, so the estimated infection rate in 2003 equaled estimated mortality.

Figure 1.

- 0.95 (AMCR, GRSG)
- 0.75 (BLJA)
- 0.55 (FICR, HOSP)
- 0.33 (COGR)
- 0.00 (EUST, ROPI)

Infection Rate (I)

Post-epizootic Seroprevalence (S)
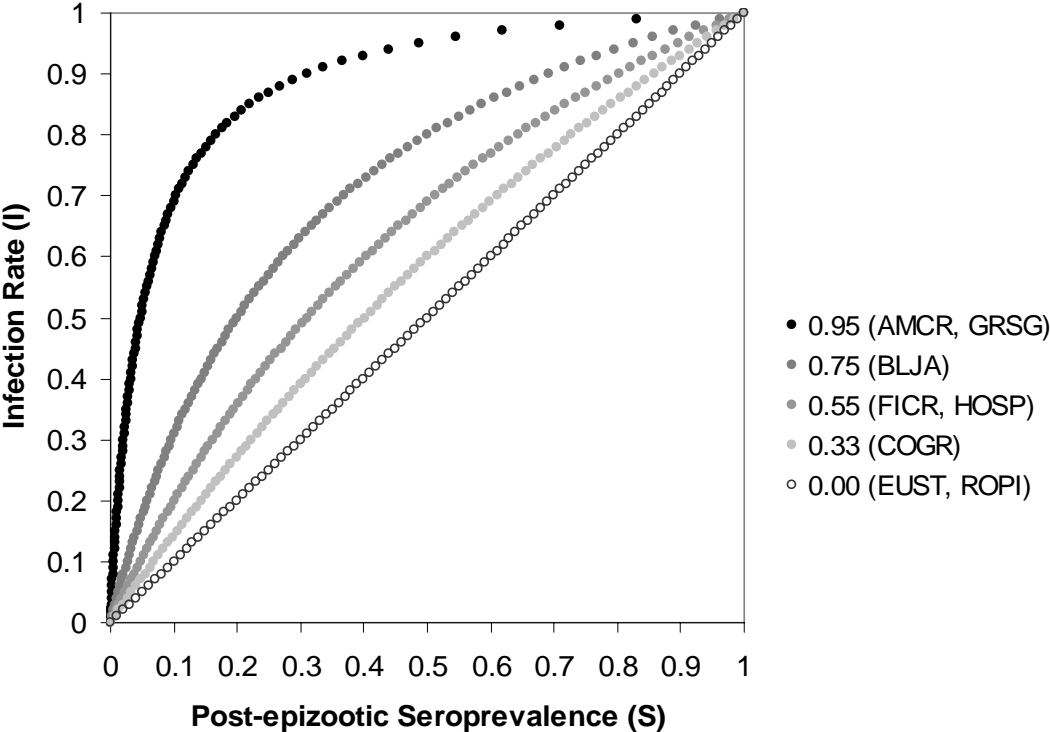
Figure 1. Predicted non-linear relationships between observed post-epizootic

seroprevalence (S) and actual infection rate (I) over a range of mortality rates following

infection (M) for representative species (4, 17). Abbreviations: AMCR = American Crow

(*Corvus brachyrhyncos*), GSGR = Greater Sage-grouse (*Centrocercus urophasianus*),

BLJA = Blue Jay (*Cyanocitta cristata*), FICR = Fish Crow (*Corvus ossifragus*), HOSP =

House Sparrow (*Passer domesticus*), COGR = Common Grackle (*Quiscalus quiscula*),

EUST = European Starling (*Sturnus vulgaris*), ROPI = Rock Pigeon (*Columba livia*).

Divergence between post-epizootic seroprevalence and infection rate increases with

susceptibility and is highest at intermediate infection rates.

Acknowledgements

CHAPTER 4. DEMOGRAPHICS OF GREATER SAGE-GROUSE IN THE POWDER

RIVER BASIN, 2003-2006.

Abstract: Obtaining reliable estimates of demographic rates and their variability over time and space is crucial for assessing and modeling the effects of potential stressors on long-term population growth for sensitive or declining wildlife species. We used maximum-likelihood methods to generate year and age-specific estimates of greater sage-grouse (*Centrocercus urophasianus*) nest, brood, and female survival rates in three regions of the Powder River Basin (Decker, MT; Buffalo, WY; Spotted Horse, WY)from 2003-2006. To assess the effect of West Nile virus (WNv) on female survival, we ran female survival analyses with and without WNv-related mortalities. We also compared maximum-likelihood estimates of nest success against values of apparent nest success and "quick" estimates of nest success derived from apparent nest success. We observed consistently high rates of nest initiation and hatching success. We also documented higher renesting rates and clutch sizes among adult females than among yearlings. Daily survival rates for nests were high during laying (0.993 ± 0.007) and higher for adult females than for yearlings. We also documented a pattern of higher daily nest survival rates earlier and later in the incubation period than in the middle. Spring precipitation the previous year had a positive effect on daily nest survival. Nest success and brood success showed parallel patterns within each region. Nest and brood success near Buffalo were lower in 2004 and high in 2005 and 2006; nest and brood success near Decker were higher in 2003 and 2004 than in 2005 and 2006. We observed the highest estimates of nest success ever reported for this species (95%) near Buffalo in 2006. Nest success

estimates obtained using the "quick" method were generally comparable with estimates derived from maximum-likelihood estimators, suggesting that the "quick" method is useful for correcting previously published estimates of apparent nest success. Parallel patterns of nest and brood survival suggest that these vital rates are influenced by similar suites of predators, or in similar ways by annual environmental (e.g., precipitation), habitat (e.g., grass height), or ecological conditions (e.g., predator abundance). Female survival was lowest in the Spotted Horse region in 2003 due to an outbreak of WNv and consistently lower in the Buffalo region than near Decker. We observed the lowest estimate of annual adult female survival (35%) ever reported for this species near Buffalo in 2005. Unexplained variation in nest, brood, and female survival across regions suggest that further investigation of local- or landscape-level habitat and anthropogenic features influencing sage-grouse and their major predators is warranted. On average, WNv-related mortality during the summer reduced annual female survival by 5% (range = 0-27%). Mortality due to WNv was an important new source of mortality in the Powder River Basin. The potential for detrimental effects of WNv on sage-grouse populations caused by landscape-level increases in anthropogenic water sources (e.g., coal-bed natural gas ponds) needs to be considered in resource management plans.

Obtaining reliable estimates of demographic rates and their variability over time and space is important for assessing and modeling the effects of potential stressors on

long-term population growth. All studies of greater sage-grouse published prior to 2003

reported demographic rates based on capture-recapture data (Zablan et al. 2003) or using

traditional metrics such as apparent nest success and apparent survival. A "quick"

method of estimating daily nest survival (Johnson and Klett 1985) has also been used to

study regional patterns of nest success in sage-grouse (Holloran et al. 2005). However,

numerous advances have been made in analysis techniques for demographic rates,

particularly in the application of group- and time-specific covariates to survival data

(Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004), and these techniques have

provided new insights into sage-grouse ecology and management (Hausleitner 2003,

Moynahan 2004, Aldridge 2005, Holloran 2005, Sika 2006). Due to potential

discrepancies between nest success estimates obtained from different estimation methods

(Moynahan et al. 2006*a*), it is also important to test whether estimates of apparent nest

success can even be used in population modeling. Assessing the role of potential

stressors such as West Nile virus (WNv) on long-term population growth also requires

estimating the effect of that stressor on vital rates, after controlling for the effects of other

important factors.

The objectives of this study were to: (1) generate robust year and age-specific

estimates of greater sage-grouse nest, brood, and annual female survival based on

maximum-likelihood methods in three regions of the Powder River Basin from 2003-

2006; (2) compare estimates of nest success obtained from maximum-likelihood methods

versus traditional metrics such as apparent nest success and those calculated using

Johnson and Klett's (1985) "quick" method; (3) assess the influence of WNv-related

mortality on annual female survival; and (4) assess how variation in nest and brood age,

female reproductive status, and precipitation influence vital rate estimates. Our estimates

rates also provide baseline data for future comparisons of how vital rates change as coal-

bed natural gas development expands into previously undeveloped landscapes in the

Powder River Basin.

Study Area

We conducted research in three regions of the Powder River Basin in southeastern

Montana and northeastern Wyoming: (1) three sites near Decker, Montana (Bighorn Co.)

from 2003-2006, (2) six sites near Buffalo, Wyoming (Johnson Co.) from 2004-2006, and

(3) one site near Spotted Horse, Wyoming (Campbell Co.) in 2003-2004 (Figure 1). We

studied the Spotted Horse site only in 2003-2004 because sage-grouse populations in the

area were largely extirpated by an outbreak of WNv in summer 2003 (Walker et al.

2004).

These three regions vary in elevation from 1100-1600 m. They experience cold,

dry winters, cool, wet springs, and hot, dry conditions in summer and fall. Average

annual precipitation varies from 11-15 in with most precipitation coming in the form of

winter snow (19-57 in annually) and rain in April - June (Western Regional Climate

Center, Reno, Nevada, USA). Natural landscapes consisted of rolling uplands with

sagebrush-steppe, mixed-grass prairie, and badlands, occasional stands of conifers, and

valleys with alkali bottoms, riparian shrubs, and woodland. Sagebrush-steppe was

dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an

understory of native and non-native grasses and forbs. Plains silver sagebrush (*A. cana*

cana) and black greasewood (*Sarcobatus vermiculatus*) co-occurred with Wyoming big

sagebrush in alkali bottoms. Land use was primarily cattle ranching with limited dry-land and irrigated tillage agriculture. The Spotted Horse region had widespread coal-bed natural gas development and large blocks of non-native pasture and tillage agriculture during 2003-2004. In the other two regions, the extent of coal-bed natural gas development expanded during the course of the study (Figure 1).

Sage-grouse inhabited areas of sagebrush-steppe from October-June. From July-September, birds used sagebrush-steppe, mixed-grass prairie, and areas with irrigated and dryland agriculture. Sage-grouse in the Decker region were largely non-migratory, showing average movements between breeding, summering, and wintering areas of <5 km. Many females in the Buffalo region were migratory, moving up to 30 km between nesting, summer, and winter areas (Doherty et al. 2008). Too few birds remained alive in the Spotted Horse region to draw conclusions about migratory status.

Methods

Field Methods

We captured and radio-marked females by rocket-netting (Giesen et al. 1982), spotlighting and hoop-netting (Wakkinen et al. 1992), and running modified walk-in traps (Schroeder and Braun 1991) on or near leks from mid-March through early April in each year. In the Decker and Spotted Horse regions, we also captured females by spotlighting and hoop-netting in brood-rearing areas in July-August and in sagebrush habitats in September and October. Upon capture, females were fitted with 21.6-g necklace-style radio collars with a 4-hour mortality switch (Model A4060, Advanced Telemetry Systems, Inc., Isanti, Minnesota) and address label. They were then banded with a size

20, individually-numbered, inscribed aluminum band (National Band and Tag Co., Newport, KY), aged by primary feather color, shape, and wear as juvenile, yearling, or adult (Eng 1995, Crunden 1963) and sexed by plumage, size, and tarsus length.

Nest monitoring. We used radio-telemetry to track marked females to nests during the nesting period (i.e., early April through the end of June). When we found a nest, we recorded its location using a hand-held global positioning system unit (eTrex Legend model, Garmin International, New York, New York) and monitored its status every 2-6 d until the eggs hatched or failed. The incubation period (i.e., the time between when the last egg is laid until hatch) for greater sage-grouse is 25-29 d (Schroeder et al. 1999). To eliminate the possibility of predators using markers to locate nests, we left no markers of any type. In 2003, we initially flushed females from the nest on the first visit to determine clutch size, but found that it increased the probability of nest abandonment. Thus, for the remainder of 2003, and in 2004-2006, we eliminated this problem by locating nesting females visually without flushing them. In many cases, mimicking the mooing sounds and slow, loud movement of cows while tracking females allowed close approach to nests and prevented females from flushing. Following the initial visit, we monitored the status of nests from a distance of 10-30 m using binoculars or by triangulating females to known nest locations using radio telemetry from 20-50 m away. If a hen was off the nest at the time of the visit, we checked the nest contents to determine nest status. Estimating clutch size is required to measure hatching success and apparent chick survival. In 2003-2005, we obtained a minimum estimate of clutch size based on the number of eggs counted following depredation or hatch. However, the number of eggs counted after hatch was sometimes less than that number counted and confirmed

prior to hatch. Therefore, in 2006, we conducted clutch counts by flushing the hen from the nest 21-24 d after the estimated incubation start date. Flushing females late in incubation caused no nest abandonment.

We considered a nest successful if ≥1 egg hatched; hatched eggs were identified by detached egg membranes (Klebenow 1969). One nest with an infertile clutch incubated for 54 d was considered successful. Nests were classified as unsuccessful if they were depredated, naturally abandoned, if the hen died during incubation. Because nest contents are not always reliable indicators of nest fate in sage-grouse (Coates 2007), if the nest appeared to have been depredated close to the predicted hatching date or if nest fate was unknown, we searched for evidence of chicks with radio-collared females for at least 3 visits following nest termination.

Although sage-grouse females generally do not begin incubation until the clutch is complete (Schroeder et al. 1999), they sometimes are found on nests during laying (Moynahan et al. 2006*a*). For nests that hatched, we estimated incubation start date by backdating 28 d from the estimated (or known) hatch date. Unless the hatch date was known more accurately, we estimated actual hatch date as the midpoint of the interval between visits before and after the nest hatched. For nests that did not hatch, we assumed that incubation started at the midpoint of the interval immediately preceding the first of two consecutive nest visits in which the hen was on the nest. We tested the validity of this assumption by comparing predicted hatch dates using the midpoint method against actual hatch dates of successful nests. Because the difference between predicted and actual hatch dates for successful nests averaged only 0.21 ± 0.15 d (mean $\pm$ SE; n = 219), estimates of incubation start date, and therefore nest age, were minimally biased. For

unsuccessful nests in which the female was already on the nest the first time she was located, we approximated incubation start date based on when the nest was depredated if it had been active for >21 d. Incubation start dates for some unsuccessful nests were classified as unknown. We estimated clutch initiation dates by subtracting the estimated number of days laying from the estimated incubation start date. Number of days laying was calculated as clutch size multiplied by a laying rate of 1.5 d per egg (Schroeder et al. 1999). When clutch size was unknown, we calculated initiation dates using the median clutch size for known-aged birds for each attempt (i.e., 8 for first nests of adults, 7 for renests of adults, 7 for first nests of yearlings, and 6 for renests of yearlings).

 Brood monitoring and survival. We monitored females with broods every 3-5 d until 35 d post-hatch. On each visit, we attempted to determine whether or not she had a brood by approaching the hen, searching for chicks, and observing hen behavior. We classified a hen as having a brood if chicks were observed or heard near the hen, if the hen gave a wing-dragging or flutter-hopping display, walked or ran away from the observer while vocalizing rather than flying, or aggressively approached the observer. At approximately 35 d post-hatch, we conducted both a night-time spotlight count and a day-time flush count to determine whether the brood survived and how many chicks survived to 35 d. Chicks typically roost in the immediate vicinity of the hen at night, which increases detectability by 40% over day-time flush counts (B. Walker, unpublished data). We chose 35 d post-hatch as a cut-off because most chick mortality has already occurred by this age (Burkepile et al. 2002, Huwer 2004, Aldridge 2005, Gregg et al. 2007), chicks younger than 25 d old are difficult to detect roosting underneath the hen, and most females with broods have not yet congregated in flocks. We classified broods as having

survived to 35 d if ≥1 chick was found with the hen on either the spotlight count or flush

count and the hen had not been seen with other adults prior to 35 d. Brood survival was

classified as unknown if the brood hen could not be followed for the full 35-d period or if

the brood hen was found in a flock with other adults and juveniles prior to 35 d post-

hatch. We considered a brood to have failed if the female flew long distance before

chicks were 10 d old or if she was located in an adult-only flock prior to 35 d post-hatch.

Female survival. We attempted to monitor female survival every 2-5 d from

April through mid-September in each year from 2003-2006, every 45 d during fall-winter

2003-2004, 2004-2005, and 2005-2006, and approximately every 90 d during fall-winter

2006-2007. From April-September, most checks were visits by ground crews, whereas

most checks during fall and winter were from the air. We attempted to locate and

confirm mortality of radio-marked females as soon as practicable following detection of a

mortality signal. Because aging radio-transmitters began to malfunction after reaching 2-

3 times their guaranteed battery life (i.e., they produced weak, irregular signals or

unpredictably switched back and forth between mortality and live mode), we right

censored these individuals the last time their status as alive or dead was visually

confirmed after unusual signals were first noted. To eliminate potential bias due to

capture-related stress or injury, we censored the first interval following capture.

Analyses

Nest initiation, renesting rate, clutch size, and hatching success. We estimated

age-specific nest initiation rates as the proportion of females found on a nest divided by

the number of females alive and adequately monitored during the nesting period (i.e.,

early April through the last known clutch completion date for first nests) in that year for each age class (yearling vs. adult). We considered females to have been adequately monitored if they were visually located at least once every 7 d during the nesting period. We estimated renesting rate as the proportion of females found on a second nest divided by the number of females alive and adequately monitored from the failure of their first nest through the end of the renesting period in any given year for each age class. We estimated clutch size only from clutches in which clutch size was confirmed. Because of our nest-monitoring protocol, we were not always able to obtain accurate clutch count data for nests depredated prior to the clutch count or hatching date. We measured age-specific hatching success as the total number of successfully hatched eggs in all nests divided by the total number of eggs laid in nests with known clutch size for each age class. We calculated standard errors for nest initiation, renesting rate, and hatching success as the square root of the theoretical variance of a proportion ($\sigma^2 = pq/n$), where p = proportion that nested, renested, or hatched, $q = 1 - p$, and n = number of sample units included in the analysis.

Apparent nest, brood, and female survival. We calculated apparent nest success as the number of successful nests divided by the total number of nests of known fate. Similarly, we calculated apparent brood success as the number of successful broods divided by the total number of broods of known fate and apparent chick survival as the total maximum number of chicks counted on the 35-d spotlight or flush count divided by the total number of chicks that hatched among broods of known fate. Brood fate was considered unknown if females with chicks flocked with other females prior to 35-day chick counts or if hens died when chicks were 15-35 d of age. Many brood females in

the Buffalo region were not monitored throughout the 35-d brood-rearing period because they crossed onto inaccessible property or could not be relocated. Therefore, estimates of apparent brood success and apparent chick survival are based on only a subset of broods in the brood-survival analysis. Broods were assumed to have failed if hens died when chicks were ≤ 15 d of age.

"Quick" estimates of daily nest survival. We used the "quick" method of Johnson and Klett (1985) to generate estimates of nest success for yearling and adult females in each region in each year. This method uses information about the average nest age when first discovered (*f*) and length of the incubation period (*h*) to estimate an approximate daily nest survival rate (*S*) as the (*h-f*) root of apparent nest success. From that, an approximate value for nest success is calculated as S^h. Because nests of radio-marked sage-grouse are typically discovered on the first visit after the start of incubation, we estimated average nest age when nests were discovered as one-half the length of the average monitoring interval in each year. In our study, these intervals were 5 d in 2003 and 3-4 d from 2004-2006.

Nest, brood, and female spring-summer daily survival rates. We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate sets of *a priori* candidate models describing variation in daily survival rate (DSR) of nests, of broods, and of females during the spring-summer season. We evaluated relative support for each candidate model using the generalized linear model method described by Rotella et al. (2004) in Statistical Analysis Software (SAS), version 9.1. For most models, we used the logit link to avoid convergence problems and constrain estimates to a (0, 1) interval (Rotella et al. 2004). However, we used the sine link in female survival models where

100% survival among a subset of individuals caused problems with convergence. This method allows staggered entry and right-censoring, variation in interval lengths between visits, and makes no assumptions about when nest failure, brood failure, or death of the female occur during an interval (Rotella et al. 2004). The method assumes: (1) homogenous DSRs within a set of covariate conditions; (2) fates are correctly classified; (3) visits do not influence survival; (4) fates are independent; (5) all visits in which fate is determined are recorded; (6) checks are conducted independently of fate, and (7) all nests, broods, and females are correctly aged (Dinsmore et al. 2002, Rotella et al. 2004). In each analysis, we assessed relative support for each model in the model set by comparing Akaike Information Criterion values adjusted for small sample size (AIC_c) and AIC_c weights (Burnham and Anderson 2002). To assess support for different variables, we examined maximum-likelihood estimates of coefficients and associated standard errors for each model. Due to model uncertainty, we used model-averaging to obtain unconditional estimates and standard errors for regression coefficients. We used the ESTIMATE command within SAS PROC NLMIXED to calculate nest success as the product of all DSRs for specific models of interest over a 28-d incubation period for nests, a 35-d period for broods, and over the spring-summer period for females (Rotella et al. 2004). These commands generate an approximate standard error for nest and brood success based on the Delta method (Seber 1982, Billingsley 1986). Tests for goodness-of-fit and overdispersion are not yet available for these types of models (Rotella et al. 2007). We estimated annual female survival as the product of spring-summer and fall-winter survival rates. Season lengths for spring-summer and fall-winter varied slightly among years depending on nesting phenology. Because we wished to make inferences

regarding natural processes that influence nest failure, especially predation, we considered a nesting interval successful if the nest was intact at the end of the interval and the female was alive or had been killed while away from the nest. If the female was killed by a predator while on the nest, we classified the nest as having failed. To estimate what female survival would have been in the absence of WNv mortality, we ran the analysis again after removing all females known to have died from WNv. This may underestimate the effect of WNv because only 40% of mortalities during the WNv season yielded testable carcasses (Walker et al. 2004).

Fall-winter female survival rates. Due to relatively high fall-winter survival rates and long intervals between visits (45-90 d), maximum-likelihood methods failed to converge. Therefore, we estimated fall-winter female survival rates over the entire fall-winter period using Kaplan-Meier analysis (Winterstein et al. 2001) rather than estimating daily or monthly survival rates. Kaplan-Meier analysis allows staggered entry and right-censoring. We assumed that females died at the midpoint of the interval prior to detecting a mortality.

Observer effects. To meet assumption (3) in the nest-survival analysis, we excluded 14 nests (nine in 2003, three in 2005, and two in 2006) that were abandoned due to research activities. Also, brood fate could not be determined on all visits. Therefore, to meet assumption (2) in the brood-survival analysis, we eliminated from the analysis all visits in which brood fate could not be determined.

Hypotheses. Each of the candidate models in the model set represented a specific hypothesis for how female characteristics, season, and environmental variables, either alone or in combination, influenced daily nest, brood, and female survival. In the nest-

survival analysis, we constructed models as combinations of *Nest age*, *Hen age*, *Nest attempt*, *Julian date*, *Previous spring precipitation*, *Previous spring drought index*, *Region*, and *Year*. In the brood-survival analysis, we constructed models using *Brood age*, *Hen age*, *Nest attempt*, *Julian date*, *Spring precipitation*, *Region*, and *Year*. For the female survival analysis, we constructed models with effects of *Hen age*, *Nesting status, Brooding status, WNv season*, *Region*, and *Year*. We outline the biological hypotheses for running models with each of these variables below.

Nest age. Daily survival rate (DSR) of nests may increase with nest age for two reasons. Increasing grass and forb growth around nests over time (Hausleitner et al. 2005) may decrease the detectability of nests to predators and lead to a pattern of increasing DSR with nest age (Holloran et al. 2005, Moynahan et al. 2006*a*). Increasing nest survival with nest age may also result from heterogeneity among nests in detectability to predators because easily detected nests are likely to be depredated earlier (Klett and Johnson 1982, Martin et al. 2000, Dinsmore et al. 2002). To control for this phenomenon, we first examined the influence of *Nest age* on DSR. Because the relationship between DSR and Nest age may be non-linear, we also considered a model with both *Nest age* and *Nest age + Nest age^2*. We defined nest age as the number of days since the estimated start of incubation. Because females spend most of their time off the nest during laying (Schroeder et al. 1999), a behavior that may decrease detectability of nests and influence estimates of DSR, we estimated DSR during laying and during incubation separately.

Brood age. We hypothesized that DSR of broods would increase with brood age for the same reasons as nest age. In addition, broods become more mobile with age and

begin to fly at ~15 d (Schroeder et al. 1999). To allow for either linear or nonlinear responses of DSR to brood age, we considered models with *Brood age* and with *Brood age + Brood age²*. We defined brood age as the number of days elapsed since the estimated hatch date.

Hen age. Age of breeding females influences reproductive effort and reproductive success in a broad array of bird species, including sage-grouse, with older birds often having higher nest survival than younger birds (e.g., Holloran 1999, Hausleitner 2003). Older, more experienced females may be better able to select safe nest and brood-rearing locations than naïve breeders (i.e., yearlings). Alternatively, because nesting may put females at greater risk, females that place nests and raise broods in safe locations may simply be more likely to survive their first breeding season and be recruited into the adult age class. Yearlings also spend more time off the nest, and leave the nest more frequently during the day than adults, which may expose nests to greater predation from diurnal predators, such as common ravens (*Corvus corax*) (Coates 2007). Thus, we hypothesized that older females would have a higher DSR than yearlings for nests and broods. In contrast, female survival in sage-grouse generally declines with increasing age (Zablan et al. 2003, Hagen et al. 2005), possibly due to trade-offs caused by greater reproductive effort. Zablan et al. (2003) estimated annual survival for yearlings as 0.72-0.75, compared with 0.57-0.61 for adults. Thus, we anticipated lower survival among adult females than among yearlings. We also estimated age-specific nest and brood survival estimates to produce estimates that could be included in age-structured population models.

Season effects. Previous studies of sage-grouse have documented that late-season nests have higher survival than early-season nests (Sveum 1995, Popham 2000, Moynahan et al. 2006*a*, Sika 2006). Although this pattern has not been documented for broods, both later nests and later broods may also show higher survival because of changes in predator abundance, shifts in predator foraging strategies, increasing abundance of alternative prey over the course of the nesting season, or because increased grass cover decreases predation risk later in the season (Schroeder et al. 1999). To examine the hypothesis that nest and brood DSR increases over the course of the season, we compared the predictive value of two different variables: (a) *Nest attempt* included as a categorical nest- or brood-specific covariate, and (b) *Julian date* as a time-specific covariate. We predicted that nest and brood survival would be higher for second nesting attempts and nesting attempts later in the season. To allow for the possibility of a non-linear relationship between DSR and Julian date in the nest-survival analyses, we also included models with *Julian date + Julian date^2*. Another possibility is that brood survival could decrease over the course of the season (after controlling for brood age), especially in dry years when a lack of precipitation dries up mesic sites on which broods depend for insects and forbs or forces females and their broods to concentrate in what suitable brood-rearing habitat remains (Moynahan 2004). Thus, brood survival may decrease with increasing Julian date, or perhaps only in dry years. To examine this possibility, we considered models with a *Julian date * Spring precipitation* interaction in the brood-survival analysis.

Precipitation. We considered three variables describing different mechanisms for how precipitation affects DSR of nests. Seven nests were known to have failed due to

flooding and mudslides following a major snowstorm in mid-May 2005. To control for this phenomenon, we included an effect of extreme precipitation events in all models. We also compared the effect of winter plus spring precipitation versus winter plus spring precipitation the previous year. Grass and forb growth in sagebrush-steppe habitat are largely controlled by winter and spring precipitation, with greater herbaceous production in wetter years (Skinner et al. 2002). Increased grass and forb growth is typically preferred by females for nesting and brood-rearing (Hagen et al. 2007) and is commonly associated with higher nest success (Schroeder et al. 1999; Connelly et al. 2000, 2004). Thus, above-average spring precipitation may lead to increased nest survival (Holloran et al. 2005, also see Martin 2007). However, because birds often begin nesting in April before most new grass and forb growth has occurred, residual cover from the previous year may be more important (Schultz 2004, Holloran et al. 2005). In the Powder River Basin, birds nest from early April through mid-June. Thus, we measured the influence of spring precipitation on nest DSR by including normalized February-May precipitation in the current year and normalized February-July precipitation in the previous year. In contrast, because broods appear well after grass and forb growth has started, brood survival should depend on current year precipitation rather than residual grass cover. Thus, we only considered current spring precipitation in brood survival models. We calculated percent normal precipitation for each region in each year of our study (2003-2006) by dividing precipitation totals for each time period (Feb-May and Feb-July) by the long-term averages for those same periods based on precipitation data from 1957-2006 (Western Regional Climate Center, Reno, Nevada, USA). For the Decker region, we used precipitation data from the Sheridan Field Station, WY weather station (no.

488160). For the Buffalo region, we used data from the Buffalo, WY station (no.

481165). For the Spotted Horse region, we used precipitation data from the Clearmont,

WY station (no. 481816).

Reproductive status. We hypothesized that female survival may depend on current or

previous reproductive effort. Breeding-survival trade-offs are common in birds (Martin

1995, Clark and Martin 2008). In sage-grouse, nesting females are sometimes depredated

while on nests (Schroeder et al. 1999), and previous studies have documented lower

survival among nesting vs. non-nesting females (Sika 2006, *contra* Moynahan et al.

2006*b*). Females also actively defend young broods against predators with conspicuous

and potential risky behaviors such as wing-dragging displays and active aggression

(Schroeder et al. 1999). The tendency of brooding females to seek out wet meadows with

high forb and insect abundance in mid-summer may also expose them to higher predation

or mosquitos that vector WNv. Finally, residual effects of breeding may decrease

subsequent survival if individuals that bred are in poorer body condition and

consequently spend more time foraging than being vigilant. To test these ideas, we

included two different reproductive effort terms in the female survival analysis. We

coded intervals during the breeding season according to whether a female was or was not

incubating a nest (*OnNest*) and whether a female was or was not with a brood younger

than 35 d old (*WBrood*), with the expectation that nesting and brood-rearing females

would have lower survival than non-breeding females.

Region. Nest, brood, and female survival may vary geographically due to ecological

differences between study regions that we did not or could not measure (e.g., predator

communities, grazing pressure), differences in life-history strategies (i.e., resident vs.

migratory populations), or differences in land use that influence risk of mortality (e.g.,

extent of coal-bed natural gas development, agricultural development, roads and

powerlines, etc.) (Connelly et al. 2000, Zou et al. 2006*a*, Walker et al. 2007*a*).

Therefore, we included a dummy-coded, group-level covariate for *region* to account for

geographical variation unexplained by differences in other variables.

West Nile virus. We included a WNv variable in the female survival analysis. Sage-

grouse are highly susceptible to WNv (Clark et al. 2006). The *WNv* variable denotes

whether each day during the interval was, or was not, during the WNv transmission

period for that region in that year based on temperature. West Nile virus transmission is

regulated on an annual basis by temperature and the availability of suitable breeding

areas for mosquitos (Reisen et al. 2006, Zou et al. 2006*a*). Zou et al. (2006*b*) developed a

degree-day model to predict WNv transmission events based on temperature. However,

the model underpredicted WNv transmission in our area because temperatures at the

weather stations were lower than those at our study sites. Therefore, we revised the

model to be more inclusive based on the earliest and latest confirmed WNv-related

mortalities at our study sites (i.e., only a 64 degree-day threshold required for WNv

transmission), then estimated the WNv transmission period in each year at each site using

the revised criterion. We do not suggest that only 64 degree-days are required for within-

host WNv amplification and transmission, only that a 64 degree-day threshold at the

closest weather stations (10-40 miles away) coincided with WNv transmission events on

our study sites. We included a *WNv*Region* interaction to allow the severity of WNv

mortality to vary among regions because of greater availability of surface water from

coal-bed natural gas development and irrigated agriculture in the Spotted Horse and

Buffalo regions than near Decker (Walker et al. 2004, Zou et al. 2006*a*, Doherty 2007).

We also included models with a *WNv*WBrood* interaction to test whether females with broods were more vulnerable during the WNv transmission season than because broods typically require more mesic habitats in late summer than non-brooding females.

Year. Nest, brood, and female survival in sage-grouse can vary dramatically on an annual basis (Schroeder et al. 1999; Moynahan et al. 2006 *a*, *b*). Therefore, we included an effect of *Year* to account for annual variation in nest, brood, and female survival unexplained by other year-specific covariates (e.g., precipitation).

Results

Nest initiation, renesting rate, clutch size, and hatching success. Females typically began laying in late March or early April (Table 1). The latest date a nest was initiated in any year was 2 June. Nest initiation rates were consistently high (range = 0.89-1.00) across all sites, years, and age classes (Table 2 *a*). In almost all cases, the only females not found on nests were those that were not adequately monitored during the nesting season. Adults and yearlings showed similar rates of nest initiation rate (0.99 ± 0.008 SE for adults vs. 0.97 ± 0.013 SE for yearlings). Renesting rate was higher for adults (0.54 ± 0.054 SE) than for yearlings (0.19 ± 0.049 SE) (Table 2 *a, b*). Renesting rates were lower for both adults and yearlings in 2004. Over the course of four years, one of 14 adult females whose second nest failed attempted a third nest, whereas no yearling females attempted a third nest. Mean clutch size of first nests was consistently higher than that of renests, and clutch size was consistently higher for adults than for yearlings (Table 3). Observed clutch size varied from as many as 14 eggs (in an adult's first nest)

to only 2 eggs (in a yearling's renest). Hatching success was uniformly high, varying from 0.87-1.00 across all regions, years, and age classes (Table 3). There was no obvious relationship between hatching success and hen age or between hatching success and nest attempt (Table 3).

Apparent nest success and causes of nest failure. Apparent nest success varied by region and year from 0.46 to 0.85 (Table 4). Fifteen nests (ten in 2003, three in 2005, and two in 2006) were abandoned after the hen was flushed from the nest by observers during laying or early in incubation. Seventy-eight percent of 175 nests that failed due to natural causes were depredated (Table 5). Nest predators could not be identified in most cases, but mammals, birds, and snakes were all known to have depredated nests based on sign at nests. A major snowstorm on 11-12 May 2005 caused seven females to abandon first nests due to drifting snow, flooding, and mudslides (Table 5). Natural abandonment was otherwise uncommon; only three other nests were abandoned, all for unknown reasons. Mortality of females during incubation was the cause of failure for approximately 11% of 175 nests that failed due to natural causes (Table 5). Of these, only seven female were killed while on the nest. In these cases, the nest was also depredated. In contrast, 11 females were killed during the incubation period while away from their nests, which remained intact. The cause of failure for 10 nests was unknown. Quick estimates of nest success for each region, year, and age class were similar to maximum-likelihood estimates, except when sample sizes were low (Table 6).

Hatching dates, apparent brood success, and apparent chick survival. Almost one-quarter of females with broods in the Buffalo region could not be monitored for 35-d post-hatch because they crossed onto inaccessible property or moved long-distance and

could not be relocated, so the fate of many broods and chicks was unknown (Table 7). Therefore, inferences regarding brood and chick survival are based on only a subset of those broods that hatched. We did not monitor broods in Spotted Horse in 2004 because the only nest monitored at that site in 2004 failed. Hatching dates across regions ranged from 9 May through 3 July (Table 7). Apparent brood success ranged from 0.66-0.93 and was similar among regions (Table 7). Apparent chick survival ranged from 0.33-0.55 (Table 7), and was lowest in 2004 (0.33-0.38), highest in 2005 (0.51-0.55), and intermediate in 2006 (0.40-0.48).

Causes of female mortality. We could not determine cause of death for 40% of 217 hens that died during the study (Table 8). Among the remaining mortalities, suspected proximate causes of death, in order from most common to least common, included predation (104), infection with WNv (19), collisions with vehicles and power lines (4), other diseases (2), and legal harvest (1) (Table 8).

Daily nest survival during laying. We estimated DSR during laying using data from 34 nests found prior to the start of incubation. Only one nest failed during this period. Due to small sample size, we estimated survival from a constant-survival model only. Daily survival rate during laying was estimated as 0.993 ± 0.007 (mean $\pm$ SE). Assuming females 2 eggs every 3 days (Schroeder et al. 1999), we estimated nest success for a 12-d laying period as 0.916 ± 0.08 (mean $\pm$ SE). Thus, we estimated that approximately 8% of nests were depredated during laying.

Daily nest survival during incubation. We included 428 nests from 289 individual females in the nest-survival analysis (Table 9). All eight models for DSR of nests with model weight >0.01 (i.e., those within 5 AICc units of the best-approximating

model) included a *Region* by *Year* interaction (Table 10). Because coefficients for *Region*Year* effects in the top 6 models were similar, we illustrate them using results from the best-approximating model (Figure 2). Daily nest survival estimates from the Decker region were higher than in Spotted Horse in 2003 and similar to those near Buffalo in 2004, but much lower than near Buffalo in 2005 and 2006 (Figure 2). *Hen age* was in four of six models within 2.8 AIC units of the best approximating model (Table 10). As predicted, daily nest survival was higher among adults than among yearlings (Figure 3). A seasonal effect was also strongly supported, with all models within 2.2 AIC units including a positive effect of either *Julian date* or *Nest attempt*. As predicted, nests initiated earlier in the season (i.e., first nests) had lower survival than those initiated later (i.e., renests) (Figure 3). Previous spring precipitation had a positive effect on DSR in all cases (model-averaged ß ± SE = 0.79 ± 0.28), but compared to models with unspecified region and year effects, those with precipitation terms received essentially no support (>19 AIC_c units lower). The *Region*Year* interaction in the top model masks the effects of previous spring precipitation because these effects are confounded (i.e., previous spring precipitation is both region- and year-specific). Current spring precipitation showed no relationship with daily nest survival. The effects of *Nest age* were unexpected; nests had higher survival early and late during the incubation period rather than simply increasing with *Nest age* (Figure 4). A *Region*Year*Hen age+Nest attempt* model was used to produce estimates of nest success for comparison with other methods and for use in population modeling (Figure 5, Table 6).

 Daily brood survival. We included 246 broods from 206 individual females in the brood-survival analysis (Table 9). As predicted, brood survival increased with brood age

(Figure 6). All models for DSR of broods within 8 AICc units of the best-approximating

model included an effect of *Region* (Table 11), and estimates indicated higher brood

survival in the Buffalo region than near Decker (Figure 6). Brood survival was also

higher in Spotted Horse, but the effect was imprecisely estimated (Figure 6). The

second-best approximating model ($\Delta AIC_c = 0.40$) included a *Region*Year* interaction.

Results from this model suggest that the Buffalo region experienced intermediate brood

survival in 2004 (0.68) and high brood survival in 2005 (0.92) and 2006 (0.93) (Figure

7). In the Decker region, brood survival was intermediate in 2003 (0.63), high in 2004

(0.84), intermediate in 2005 (0.67) and 2006 (0.52), whereas the only estimate for

Spotted Horse suggested high brood survival in 2003 (0.82) (Figure 7). Effects of spring

precipitation and hen age on brood survival were positive in all models but were

imprecisely estimated. There were no obvious effects of year, Julian date, or spring

drought indices on brood survival.

       Daily spring-summer female survival. We censored four females that incurred

potentially life-threatening injuries during rocket-net captures (e.g., internal bleeding) and

six females that were never relocated following capture prior to analyses. In total, we

included 343 individuals in the spring-summer female survival analysis (Table 9). All

five models within 2 ΔAIC units of the best approximating model included a

Region*WNV interaction (Table 12). Results from these models highlight the extremely

low survival rates documented as a result of WNv mortality in Spotted Horse in 2003

(Figure 8). Model coefficients also suggest lower survival during 2003, during the WNv

season, and in the Buffalo region, but all effects were imprecisely estimated. The top

model also included a weak positive effect on DSR of being with a young brood, but

because hens only have young broods for short periods of time (<35d), the influence on season-long survival was minimal (Figure 7). There was no clear relationship between DSR and hen age or whether the hen was on a nest.

Re-running the analysis without the 19 confirmed WNv mortalities resulted in a top model with *Region + Year* effects, plus a positive but poorly estimated effect of having a young brood (Table 12). Results from this model indicate that, even in the absence of WNv impacts, female survival was lower near Buffalo than near Decker or Spotted Horse. A *Region*Year*Hen age* model was used to produce region-, year-, and age-specific estimates (Figure 9, Table 13).

Fall-winter female survival. We included 233 individuals in the fall-winter Kaplan-Meier female survival analysis (Table 9). Fall-winter survival for both age classes in the Buffalo region averaged lower in 2005-2006 than in other years. Juvenile survival near Decker in 2003-2004 and 2004-2005 was comparable with that of yearlings and adults. All yearlings near Decker in 2005-2006 and all adults near Buffalo in 2004-2005 survived the fall and winter. High fall-winter survival in Spotted Horse may be an artifact of small sample sizes (n = 1-4) in both years.

Annual female survival. Mortality associated with WNv reduced survival estimates in Spotted Horse in 2003 and in the Buffalo region in 2004 (Table 15). Effects of WNv mortality on survival were not detected in our sample of marked birds near Decker in 2003 or 2005, despite the documented outbreak near Spotted Horse. Effects of WNv on survival were detected in all years (2004-2006) near Buffalo.

Discussion

Nest initiation, renesting rate, clutch size, and hatching success. High nest

initiation rates in this study (0.97-0.99) contrast with substantially lower rates reported in

several other parts of their range, particularly for yearlings (Wallestad and Pyrah 1974,

Connelly et al. 1993, Heath et al. 1998, Lyon and Anderson 2003, Moynahan et al.

2006*a*, Sika 2006, Robinson 2007), but are consistent with high initiation rates reported

over 4 years in Washington (Schroeder 1997). In some cases, this discrepancy may be

due to other studies not monitoring birds early enough during the season (Connelly et al.

1993) or intensively enough during the nesting season (Lyon and Anderson 2003, Sika

2006) and therefore, having a higher likelihood of missing nests during laying or early in

incubation. However, it may also be due to natural annual or geographic variation in

environmental conditions that influenced pre-laying forage quality, body condition, or

both (Barnett and Crawford 1994, Gregg et al. 2006). Estimates of nest initiation,

including those reported here, are typically biased low because nests depredated during

laying or during the first few days of incubation likely go undetected. Similarly, nests of

females killed during laying or early incubation may also have gone undetected. Higher

observed renesting rates among adults match findings from several previous studies

(Sveum 1995, Heath et al. 1997, Moynahan et al. 2006*a*, Sika 2006, Gregg et al. 2006),

suggesting that yearling reproductive effort is somehow constrained by developmental,

physiological, or evolutionary factors.

　　　Similar year-to-year patterns in renesting rates between two geographically

disjunct regions suggests that ecological processes occurring over large scales, such as

regional precipitation patterns, drive annual variation in renesting rate. Renesting was

low in 2004 in both the Decker and Buffalo regions, the only year with below-average winter-spring precipitation during the course of our study, yet higher in all other years (except when precluded by high first nest survival). Studies of radio-marked greater sage-grouse farther north in Montana also documented low renesting rates in years with below-average winter-spring precipitation (2001 and 2004) and higher renesting rates in wetter years with greater grass and forb production (2002 and 2005) (except when high survival of first nests precluded renesting) (Moynahan 2004, Sika 2006).

Clutch sizes in this study were consistent with range-wide estimates for this species, but we documented individual cases of larger clutch size (14 eggs; first nest) and smaller clutch size (2; renest) than previously reported (Schroeder et al. 1999, Connelly et al. 2004). As in other studies, our data also indicate that, on average, adults lay ~0.5 more eggs per clutch than yearlings (Petersen 1980, Moynahan 2004, Sika 2006) and that clutch sizes of first nests average ~1.5 eggs larger than renests (Moynahan 2004, Sika 2006). Hatching success in the Powder River Basin (0.92) was within the normal range for the species (0.76-0.99) (Schroeder et al. 1999).

Nest and brood survival. Our estimate of DSR during laying (0.993) was generally higher than estimates of DSR during incubation – with the exception of the Buffalo region in 2005 and 2006 – and higher than DSRs reported during incubation in other studies (~0.96-0.97, Moynahan 2004, Fig. 3; ~0.96-0.98, Sika 2006). This supports the hypothesis that nests generally are at lower risk of predation during laying than during incubation, perhaps due to reduced scent or activity at the nest. Like waterfowl, some female sage-grouse also sometimes cover their nests with feathers and dried grass prior to clutch completion (unpub. data), a behavior that may reduce detectability to predators.

Estimates of daily nest survival in our study (~0.963-0.979) were comparable to those reported previously by Moynahan et al. (2006*a*) and Sika (2006), again with the exception of Buffalo in 2005 (0.988) and 2006 (0.996). Our estimate of nest success for first nests of adults over a 28-day period in Buffalo in 2006 (0.945) was the highest ever reported for this species.

Estimates of daily brood survival are difficult to compare with studies that estimated survival over shorter or longer time periods (e.g., 28 d, 30 d, 56 d) because DSR increased with brood age (this study, Moynahan 2004). Estimates of annual brood success to 35 d in our study (mean = 0.75, range = 0.52-0.93 across sites and years) were comparable with estimates to 35 d reported from Alberta based on radio-marked chicks (0.63; Aldridge 2005) but generally higher than those reported from central Montana based on day-time flush counts (~0.21-0.76; Moynahan 2004). Our estimates were similar to those from south-central Montana that were based on a combination of day-time flush counts and night-time spotlight counts (0.71-0.84; Sika 2006). Our estimates of brood survival to 35 d near Buffalo in 2005 (0.92) and 2006 (0.93) are the two highest ever reported for this species. Holloran (2005) also reported relatively high rates of brood survival (0.48-0.73) for broods 45-90 d of age (i.e., from hatch through 15 August).

Estimates of apparent chick survival are tentative because we were unable to follow all broods to 35 d and unable to estimate detectability. Estimates are likely biased low due to undercounting of chicks and because we were unable to conduct night-time counts on all brood hens. In contrast, values for apparent chick survival may overestimate true values due to non-independence of fates among chicks within a brood (Aldridge 2005). Our estimates of chick survival (range 0.33-0.55) were generally higher

than those reported from previous studies using radio-marked chicks. Burkepile et al. (2002) reported 21-32% survival of chicks marked with 1.0 g transmitters to 28 d. Aldridge (2005, Figure 3-1) reported ~35% chick survival to 35 d, not accounting for non-independent fates. Brood mixing is unlikely to have influenced estimates because brood switching is relatively uncommon during early brood-rearing (<1% ; Gregg et al. 2007). Apparent chick survival was lowest in both regions in 2004 (0.33-0.38), the only drought year during our study. This matches the findings of Moynahan (2004), who found that very few chicks survived to 30 d during a severe summer drought in 2001. However, due to uncertainty in our estimates of chick survival, we were unable to test whether chick survival parallels that of brood survival within each region over time.

Parallel, but opposite patterns of nest and brood survival within each region across years during our study suggest that substantial overlap occurs in nest and brood predators [American badger (*Taxidea taxus*), coyote (*Canis latrans*), weasels, common raven (*Corvus corax*), and snakes)], that nest and brood survival are both influenced by ecological processes that mediate predation, or both. For example, environmental conditions that promote high nest survival, such as high previous spring precipitation and greater residual grass cover, may also promote high brood survival. Predation was the major cause of nest failure in our study, and it is typically the major cause of nest and brood failure for this species range-wide (Schroeder et al. 1999).

Causes of mortality and female survival. As in most other studies, the proximate cause of most mortality was predation. However, the second most important documented cause of mortality (approximately 9% of all mortalities) was WNv, which reinforces the idea that the virus is a significant new source of mortality in susceptible populations.

Documentation of only one legally harvested sage-grouse indicates that hunting was not a major mortality factor in our study area from 2003-2006. This finding is consistent with a concurrent study that found little support for harvest as a major source of mortality further north in Montana in 2004-2005 (Sika 2006). Unlike other studies, no deaths were reported from stock tank drowning (Sika 2006) or poisoning (Blus et al. 1989).

The positive effect of having a young brood on female survival was contrary to our prediction that defending a brood increases risk for females. However, because it resulted in only a marginal increase in season-long survival, this effect may not be biologically meaningful. It is possible that females with broods could experience higher survival if predation risk diminishes as group size increases, particularly if surrounding individuals (chicks) are more vulnerable to predators (Pulliam 1973). Females capable of successfully raising broods may also be of higher quality or in better condition.

Sources of mortality and female survival. Effects of WNv led to substantially lower estimates of female spring-summer survival, and effects of WNv on survival were apparent for adults and yearlings, in all three regions, and in all four years of the study. Overall, WNv mortality reduced annual survival of females by 4.7% (range 0-21%) for yearlings and 5.2% (range 0-27%) for adults. The WNv outbreak near Spotted Horse in 2003 resulted in the lowest estimate of spring-summer survival for adult females ever reported for this species (0.13 ± 0.09 SE) (Walker et al. 2004). Annual female survival rates in the Buffalo and Decker regions were reduced by similar amounts due to WNv-related mortality, although pending WNv test results on 4 birds may increase our estimate of WNv-related mortality from Buffalo in 2006. Other sage-grouse studies have also

documented substantial negative effects of WNv on survival rates in late summer (Naugle et al. 2004, 2005; Moynahan et al. 2006*b*, Sika 2006, Kaczor 2008).

Our study reinforced previous studies showing higher survival in fall-winter than in spring-summer (Moynahan et al. 2006*b*). However, moderate spring-summer survival in Buffalo in 2005 (0.58± 0.08 SE) combined with low fall-winter survival (0.61 ± 0.02 SE) led to the lowest region- and year-specific estimate of annual survival ever reported for this species, excluding those attributed to outbreaks of WNv (Walker et al. 2004, Moynahan et al. 2006*b*). However, the cause of low fall-winter survival remains unknown. The winter of 2005-2006 was mild, with above average temperatures and below average snowfall (Western Regional Climate Center data, Reno, NV), and fall-winter survival rates in the Decker region were relatively high in 2005 (1.00 for 16 yearlings, 0.77 ± 0.01 SE for 40 adults). The pattern is also inconsistent with a reproductive trade-off hypothesis. Females in the Buffalo region had high reproductive effort and high nest and brood success in both 2005 and 2006, yet fall-winter survival was only lower in 2005-2006. We were unable to assess impacts of snow depth or winter storm events on overwinter female survival, even though these factors likely are important (Moynahan et al. 2006*b*). All of our fall-winter survival estimates came from years with mild winters and no unusual snowfall or temperature events that would have restricted access to sagebrush for forage or cover. Residual effects of WNv infection from the previous summer could have been one factor reducing overwinter survival of infected individuals in 2005-2006, but estimated infection rates in summer 2005 were relatively low (<10%) (Walker et al. 2007*b*).

The best-approximating models of nest, brood, and female survival rates all showed a large effect of region. However, patterns of nest, brood, and female survival within each region were clearly different, with higher female survival in the Decker region (even after excluding WNv-related mortalities) and higher nest and brood survival in the Buffalo region. Vital rates in the Decker region were close to range-wide averages, whereas in the Buffalo region, nest survival was the highest ever reported and female survival was one the lowest ever reported. This raises the question of which ecological processes are influencing vital rates in dramatically different ways near Buffalo. Data on local-scale vegetation characteristics and landscape-scale habitat and land-use patterns may help explain additional annual and geographic variation in vital rates. Data on how nest, brood, and adult predators are responding to anthropogenic changes associated with energy development would also be valuable, but may be logistically difficult to obtain at scales appropriate for studies of sage-grouse.

Management Implications

Minimal differences between quick and maximum-likelihood estimates of nest success with sample sizes >10 suggests that the "quick" method of estimating nest success is a valuable tool for adjusting previously published data on apparent nest success. Increased monitoring effort (i.e., decreased monitoring intervals) during the nesting period will result in improved estimates of nest initiation and renesting rates, and may reveal that sage-grouse initiate nests at higher rates than previously suspected. Parallel increases and decreases in annual renesting rates across regions and across studies suggest that renesting effort is strongly influenced by large-scale ecological

processes (e.g., regional precipitation patterns) that may be beyond the control of wildlife managers. Parallel patterns of annual nest and brood success within regions across years suggest that nest and brood predators of this species either show substantial overlap in the Powder River Basin, or that predation on nests and broods is influenced in similar ways by temporal variation in precipitation or understory productivity. Our finding of a positive effect of previous spring precipitation is consistent with previous recommendations to maintain residual grass cover as a way to improve habitat for nesting females and increase nest success (Connelly et al. 2000, Holloran et al. 2005, Hagen et al. 2007). Higher renesting rates, larger clutch sizes, and higher nest success among adult females, in combination with higher success of renests, underscores the importance of adult females for population growth. Management to improve spring-summer survival of adult females at both a local and a landscape scale would likely be more beneficial demographically than managing habitat for other life stages (e.g., broods). Management to reduce habitat for sage-grouse predators (e.g., powerlines for raptors) may also be beneficial, as predators were the main source of mortality for all life stages. Our findings suggest that reducing mortality due to WNv, particularly from anthropogenic sources (e.g., irrigated fields, coal-bed natural gas ponds, stock tanks and impoundments), is an important management concern in the Powder River Basin. The persistent, and in some cases, severe negative effects of WNv on sage-grouse in our study indicate that habitat "improvements" that create surface water in sage-grouse summer habitat may instead be detrimental to sage-grouse populations.

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Table 1. Timing of clutch initiation and clutch completion for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Values presented as mean (range).

| | Clutch initiation date | | | | Clutch completion date | | | |
| | AD | | YR | | AD | | YR | |
Region - Year	1st nests	Re-nests[a]	1st nests	Re-nests	1st nests	Re-nests[a]	1st nests	Re-nests
Decker - 2003	4/11 (4/06-4/23)	5/11 (4/25-5/27)	4/16 (4/06-5/08)	5/09 (4/30-5/15)	4/24 (4/18-5/03)	5/21 (5/06-6/04)	4/28 (4/21-5/19)	5/18 (5/08-5/26)
Decker - 2004	4/08 (3/30-5/01)	4/29	4/10 (4/02-4/22)	-	4/20 (4/11-5/12)	5/10	4/20 (4/13-5/03)	-
Decker - 2005	4/14 (3/28-5/04)	5/14 (4/25-5/27)	4/19 (4/04-5/06)	5/16	4/25 (4/09-5/16)	5/24 (5/07-6/05)	4/29 (4/15-5/12)	5/24
Decker - 2006	4/12 (4/04-4/29)	5/7 (5/01-5/17)	4/18 (4/09-4/26)	5/03 (4/25-5/10)	4/24 (4/15-5/10)	5/16 (5/12-5/27)	4/29 (4/21-5/06)	5/12 (5/06-5/19)
Buffalo - 2004	4/5 (3/29-4/14)	4/29	4/12 (4/02-4/27)	-	4/18 (4/11-4/26)	5/10	4/23 (4/16-5/04)	-

Table 1 (cont.). Timing of clutch initiation and clutch completion for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Values presented as mean (range).

| | Clutch initiation date | | | | Clutch completion date | | | |
| | AD | | YR | | AD | | YR | |
Region - Year	1st nests	Re-nests[a]	1st nests	Re-nests	1st nests	Re-nests[a]	1st nests	Re-nests
Buffalo - 2005	4/10 (3/31-5/03)	5/07 (4/30-5/20)	4/18 (4/04-5/03)	5/15 (5/14-5/17)	4/23 (4/12-5/15)	5/17 (5/11-5/26)	4/29 (4/16-5/18)	5/22 (5/20-5/25)
Buffalo - 2006	4/12 (4/08-4/23)	5/02	4/15 (4/06-5/01)	4/12	4/23 (4/19-5/05)	5/13	4/26 (4/18-5/12)	4/23
SH - 2003	4/20 (4/11-4/26)	5/07 (5/03-5/11)	4/20 (4/14-4/30)	-	5/03 (4/25-5/11)	5/14 (5/06-5/22)	5/02 (4/26-5/11)	-

[a] One successful third nest is included in adult renests from the Decker region in 2005.
[b] Totals also include hatched nests from breeding females of undetermined age (i.e., after-hatching-year birds).

Table 2a. Nest initiation rates ± SE, renesting rates ± SE, and second renesting rates ± SE for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Sample size is in parentheses.

Region – Year	Nest initiation rate			Renesting rate			Second renesting rate		
	AD	YR	All	AD	YR	All	AD	YR	All
Decker - 2003	1.00 ± 0.00 (20)	0.89 ± 0.07 (19)	0.95 ± 0.04 (40)	0.67 ± 0.14 (12)	0.56 ± 0.17 (9)	0.62 ± 0.11 (21)	0.00 ± 0.00 (1)	0.00 ± 0.00 (3)	0.00 ± 0.00 (4)
Decker - 2004	0.94 ± 0.04 (31)	0.94 ± 0.05 (18)	0.94 ± 0.03 (49)	0.09 ± 0.09 (11)	0.00 ± 0.00 (8)	0.05 ± 0.051 (19)	0.00 ± 0.00 (1)	-	0.00 ± 0.00 (1)
Decker - 2005	0.98 ± 0.02 (53)	1.00 ± 0.00 (15)	0.99 ± 0.02 (68)	0.58 ± 0.10 (26)	0.10 ± 0.10 (10)	0.44 ± 0.08 (36)	0.33 ± 0.22 (3)	0.00 ± 0.00 (1)	0.25 ± 0.18 (4)
Decker - 2006	1.00 ± 0.00 (47)	1.00 ± 0.00 (21)	1.00 ± 0.00 (68)	0.56 ± 0.18 (18)	0.33 ± 0.16 (9)	0.48 ± 0.10 (27)	0.00 ± 0.00 (3)	0.00 ± 0.00 (2)	0.00 ± 0.00 (5)
Decker - TOTAL	0.98 ± 0.01 (151)	0.96 ± 0.02 (73)	0.97 ± 0.01 (225)	0.51 ± 0.06 (67)	0.25 ± 0.07 (36)	0.42 ± 0.05 (103)	0.13 ± 0.12 (8)	0.00 ± 0.00 (6)	0.07 ± 0.07 (14)
Buffalo - 2004	1.00 ± 0.00 (12)	1.00 ± 0.00 (35)	1.00 ± 0.00 (48)	0.50 ± 0.35 (2)	0.00 ± 0.00 (15)	0.06 ± 0.06 (17)	0.00 ± 0.00 (1)	-	0.00 ± 0.00 (1)

Table 2a (cont.). Nest initiation rates ± SE, renesting rates ± SE, and second renesting rates ± SE for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Sample size is in parentheses.

Region – Year	Nest initiation rate			Renesting rate			Second renesting rate		
	AD	YR	All	AD	YR	All	AD	YR	All
Buffalo - 2005	1.00 ± 0.00	0.94 ± 0.04	0.97 ± 0.02	0.80 ± 0.13	0.33 ± 0.19	0.63 ± 0.12	0.00 ± 0.00	-	0.00 ± 0.00
	(36)	(31)	(68)	(10)	(6)	(16)	(1)		(1)
Buffalo - 2006	1.00 ± 0.00	0.98 ± 0.03	0.98 ± 0.02	0.50 ± 0.36	0.25 ± 0.22	0.33 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	(21)	(40)	(61)	(2)	(4)	(6)	(3)	(2)	(5)
Buffalo - TOTAL	1.00 ± 0.00	0.97 ± 0.02	0.98 ± 0.01	0.71 ± 0.12	0.12 ± 0.07	0.33 ± 0.08	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	(69)	(106)	(177)	(14)	(25)	(39)	(5)	(2)	(7)
SH - 2003	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	0.50 ± 0.25	0.00 ± 0.00	0.29 ± 0.17	0.00 ± 0.00	-	0.00 ± 0.00
	(8)	(4)	(12)	(4)	(3)	(7)	(1)		(1)
TOTAL	0.99 ± 0.01	0.97 ± 0.01	0.98 ± 0.01	0.54 ± 0.05	0.19 ± 0.05	0.39 ± 0.04	0.07 ± 0.07	0.00 ± 0.00	0.05 ± 0.04
	(228)	(173)	(414)	(85)	(64)	(149)	(14)	(8)	(22)

Table 2b. Renesting rates ± SE (proportion of females that had an unsuccessful first nest and survived detected on a second nest) for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003, excluding birds that abandoned nests due to investigator disturbance. Sample size is in parentheses.

Region - Year	AD	YR	Combined
Decker - 2003	0.50 ± 0.18 (8)	0.33 ± 0.19 (6)	0.43 ± 0.13 (14)
Decker - 2004	0.09 ± 0.087 (11)	0.00 ± 0.00 (8)	0.05 ± 0.051 (19)
Decker - 2005	0.58 ± 0.097 (26)	0.10 ± 0.095 (10)	0.44 ± 0.083 (36)
Decker - 2006	0.56 ± 0.18 (18)	0.25 ± 0.15 (8)	0.46 ± 0.098 (26)
Decker - TOTAL	0.48 ± 0.063 (63)	0.16 ± 0.064 (32)	0.37 ± 0.050 (95)
Buffalo - 2004	0.50 ± 0.35 (2)	0.00 ± 0.00 (15)	0.06 ± 0.06 (17)
Buffalo - 2005	0.78 ± 0.14 (9)	0.20 ± 0.18 (5)	0.57 ± 0.13 (14)
Buffalo - 2006	0.50 ± 0.36 (2)	0.00 ± 0.00 (3)	0.20 ± 0.18 (5)
Buffalo - TOTAL	0.69 ± 0.13 (13)	0.04 ± 0.043 (23)	0.28 ± 0.075 (36)
SH - 2003	0.50 ± 0.25 (4)	0.00 ± 0.00 (2)	0.33 ± 0.19 (6)
TOTAL	0.51 ± 0.056 (80)	0.11 ± 0.041 (57)	0.34 ± 0.041 (137)

Table 3. Clutch size and hatching success for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Clutch size values presented as mean ± SE (except where n = 1). Hatching success data presented as a proportion (no. eggs hatched in successful nests of known clutch size / no. eggs laid in successful nests with known clutch size).

| Region - Year | Clutch size | | | | Hatching success | | | |
| | AD | | YR | | AD | | YR | |
	1st nests	Re-nests	1st nests	Re-nests[a]	1st nests	Re-nests	1st nests	Re-nests
Decker - 2003	8.68 ± 0.21	6.63 ± 0.65	8.31 ± 0.26	6.00 ± 0.58	0.79 (62/69)[b]	0.90 (27/30)	0.92 (57/62)	0.77 (10/13)
Decker - 2004	8.00 ± 0.20	-	7.33 ± 0.29	-	0.97 (125/129)	-	0.97 (34/35)	-
Decker - 2005	7.75 ± 0.25	6.53 ± 0.27	6.67 ± 0.60	5.00	0.88 (153/174)	0.93 (64/69)	0.95 (21/22)	-
Decker - 2006	8.37 ± 0.21	6.30 ± 0.40	8.08 ± 0.40	6.50 ± 0.50	0.97 (161/166)	0.88 (35/40)	0.97 (86/89)	1.0 (7/7)

Table 3 (cont.). Clutch size and hatching success for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Clutch size values presented as mean ± SE (except where n = 1). Hatching success data presented as a proportion (no. eggs hatched in successful nests of known clutch size / no. eggs laid in successful nests with known clutch size).

| | Clutch size | | | | Hatching success | | | |
| | AD | | YR | | AD | | YR | |
Region - Year	1st nests	Re-nests	1st nests	Re-nests[a]	1st nests	Re-nests	1st nests	Re-nests
Buffalo - 2004	8.56 ± 0.41	-	7.40 ± 0.38	-	0.90 (64/71)	-	0.95 (74/78)	-
Buffalo - 2005	8.55 ± 0.37	6.50 ± 0.56	7.50 ± 0.39	4.00	0.93 (148/159)	0.8 (28/35)	0.86 (112/130)	0.89 (8/9)
Buffalo - 2006	7.00 ± 0.29	7.00	7.13 ± 0.18	7.00	0.89 (119/133)	1.0 (7/7)	0.93 (200/214)	1.0 (7/7)
SH - 2003	8.67 ± 0.42	4.50 ± 2.50	8.33 ± 0.33	-	0.94 (32/34)	1.0 (2/2)	0.75 (6/8)	-

[a] Sample size n =1 for yearling renests with known clutch size for Decker in 2005 and Buffalo in 2005.
[b] This estimate includes data from one nest that was incubated for 50+ days in which all 9 eggs failed to hatch.

Table 4. Apparent nest success and number and fate for nests of adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003. Apparent nest success is presented as a proportion (successful nests/total nests).

Region - Year	AD		YR		Combined
	1st nests	Re-nests[a]	1st nests	Re-nests	Annual total
Decker - 2003	0.38	0.88	0.41	0.40	0.47
	(8/21)	(7/8)	(7/17)	(2/5)	(24/51)
Decker - 2004	0.62	0.00	0.41		0.53
	(18/29)	(0/1)	(7/17)	-	(25/47)
Decker - 2005	0.45	0.69	0.27	0.00	0.46
	(23/51)	(11/16)	(4/15)	(0/1)	(38/83)
Decker - 2006	0.48	0.60	0.60	0.33	0.52
	(21/44)	(6/10)	(12/20)	(1/3)	(40/77)
Decker - TOTAL	0.48	0.69	0.43	0.33	0.49
	(70/145)	(24/35)	(30/69)	(3/9)	(127/258)
Buffalo - 2004	0.75	0.00	0.50		0.56[b]
	(9/12)	(0/1)	(17/34)	-	(27/48)

Table 4 (cont.). Apparent nest success and number and fate for nests of adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse, WY in 2003. Apparent nest success is presented as a proportion (successful nests/total nests).

| Region - Year | AD | | YR | | Combined |
	1st nests	Re-nests[a]	1st nests	Re-nests	Annual total
Buffalo - 2005	0.64	0.88	0.69	1.00	0.70[b]
	(23/36)	(7/8)	(20/29)	(2/2)	(53/76)
Buffalo - 2006	0.95	1.00	0.79	1.00	0.85
	(19/20)	(1/1)	(31/39)	(1/1)	(52/61)
Buffalo - TOTAL	0.75	0.80	0.67	1.00	0.71[b]
	(51/68)	(8/10)	(68/102)	(3/3)	(132/185)
Spotted Horse - 2003	0.50	0.50	0.25	-	0.43
	(4/8)	(1/2)	(1/4)		(6/14)
TOTAL	0.57	0.70	0.57	0.50	0.57[b]
	(125/220)	(33/47)	(99/175)	(6/12)	(265/457)

[a] One successful third nest from the Decker region in 2005 is included in renests.
[b] Totals include successful nests of unknown-aged females (i.e., after-hatching-year) near Buffalo in 2004 (n=1) and 2005 (n=1).

Table 5. Apparent proximate cause of failure for nests of adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003.

| Region - Year | No. failed nests / total nests | Cause of nest failure | | | | | | |
| | | | | | ♀ killed | | | |
		Predation	Weather	Abandoned	on / off nest	Research	Did not hatch	Unknown
Decker - 2003	27 / 51	10	0	0	1 / 2	9	1	4
Decker - 2004	22 / 47	18	0	1	0 / 2	0	0	1
Decker - 2005	45 / 83	31	7	1	2 / 3	1	0	0
Decker - 2006	37 / 77	28	0	1	1 / 3	1	0	3
Decker - TOTAL	131 / 258	87	7	3	4 / 10	11	1	8
Buffalo - 2004	21 / 48	21	0	0	0	0	0	0
Buffalo - 2005	23 / 76	19	1	0	0	2	0	1
Buffalo - 2006	9 / 61	3	0	0	3 / 1	1	1	0
Buffalo - TOTAL	53 / 185	43	1	0	3 / 1	3	1	1
SH - 2003	8 / 14	6	0	0	0	1	0	1
TOTAL	192/457	136	8	3	7, 11	15	2	10

Table 6. Comparison of "quick" estimates of nest success and nest success estimated from maximum-likelihood estimates of daily survival rate based on a *Region*Year*Hen age + Nest attempt* model for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. "Quick" nest success estimates (Johnson and Klett 1985) are for the incubation period only.

Region - Year	"Quick" estimate				Maximum-likelihood estimate (mean ± SE)				Absolute Difference			
	AD		YR		AD		YR		AD		YR	
	1st nests	Re-nests[a]	1st nests	Re-nests	1st nests	Re-nests[a]	1st nests	Renests	1st nests	Re-nests[a]	1st nests	Re-nests
Decker - 2003	0.35	0.86	0.38	0.37	0.72 ±0.11	0.82 ±0.08	0.48 ±0.15	0.65 ±0.13	-0.37	0.04	-0.10	-0.28
Decker - 2004	0.60	0.00[b]	0.39	-	0.61 ±0.09	-	0.55 ±0.12	-	-0.01	-	-0.16	-
Decker - 2005	0.43	0.67	0.24	0.00[b]	0.47 ±0.07	0.64 ±0.08	0.29 ±0.11	-	-0.03	0.03	-0.05	-0.47[b]
Decker - 2006	0.45	0.58	0.58	0.31[b]	0.52 ±0.08	0.68 ±0.09	0.51 ±0.12	0.67 ±0.11	-0.07	-0.10	0.07	-0.36[b]

Table 6 (cont.). Comparison of "quick" estimates of nest success and nest success estimated from maximum-likelihood estimates of daily survival rate based on a *Region*Year*Hen age + Nest attempt* model for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. "Quick" nest success estimates (Johnson and Klett 1985) are for the incubation period only.

Region - Year	"Quick" estimate				Maximum-likelihood estimate (mean ± SE)				Absolute difference			
	AD		YR		AD		YR		AD		YR	
	1st nests	Re-nests[a]	1st nests	Re-nests	1st nests	Re-nests[a]	1st nests	Re-nests	1st nests	Re-nests[a]	1st nests	Re-nests
Buffalo - 2004	0.74	0.00[b]	0.48	-	0.72 ±0.14	-	0.49 ±0.09	-	0.02	-	-0.01	-
Buffalo - 2005	0.62	0.88[b]	0.67	1.00[b]	0.69 ±0.08	0.80 ±0.07	0.79 ±0.08	0.87 ±0.06	-0.07	0.07[b]	-0.12	0.13[b]
Buffalo - 2006	0.95	1.00[b]	0.78	1.00[b]	0.95 ±0.05	0.97 ±0.03	0.88 ±0.06	0.92 ±0.04	0.00	-0.03	-0.10	0.08[b]
SH - 2003	0.47[b]	0.47[b]	0.22[b]	-	0.56 ± 0.19	0.71 ±0.15	0.28 ±0.25	-	-0.09[b]	-0.24[b]	-0.06[b]	-

[a] One successful third nest from the Decker region in 2005 is included in renests.
[b] Values are based on sample sizes of nests ≤ 9.

Table 7. Earliest and latest hatching dates, apparent brood survival, number and fate of broods, apparent chick survival, and minimum no. chicks surviving to 35d for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Brood data presented as no. successful broods / no. broods of known fate / no. broods of unknown fate. Chick data presented as no. chicks that survived to 35d / no. chicks hatched in broods of known fate / no. chicks hatched in broods of unknown fate.

Region - Year	Hatching date			Apparent brood success			Apparent chick survival		
	AD	YR	All	AD	YR	All[a]	AD	YR	All[b]
Decker - 2003	5/15-7/03	5/19-6/25	5/15-7/03	0.71 (10/14/1)	0.56 (5/9/0)	0.67 (16/24/1)	0.54 (54/100/3)	0.28 (19/67/0)	0.43 (75/174/3)
Decker - 2004	5/11-6/10	5/13-5/28	5/11-6/10	0.89 (16/18/0)	1.00 (6/6/1)	0.91 (21/23/2)	0.32 (40/125/6)	0.58 (22/38/5)	0.38 (62/163/11)
Decker - 2005	5/10-7/03	5/18-6/12	5/10-7/03	0.77 (24/31/4)	1.00 (4/4/0)	0.80 (28/35/4)	0.47 (93/197/27)	0.78 (18/23/0)	0.50 (111/220/27)
Decker - 2006	5/13-6/23	5/20-6/03	5/13-6/23	0.81 (17/21/6)	0.75 (8/12/0)	0.76 (25/33/6)	0.42 (61/145/30)	0.38 (33/88/0)	0.40 (94/233/30)

Table 7 (cont.). Earliest and latest hatching dates, apparent brood survival, number and fate of broods, apparent chick survival, and minimum no. chicks surviving to 35d for adult (AD) and yearling (YR) female sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003. Brood data presented as no. successful broods / no. broods of known fate / no. broods of unknown fate. Chick data presented as no. chicks that survived to 35d / no. chicks hatched in broods of known fate / no. chicks hatched in broods of unknown fate.

Region - Year	Hatching date			Apparent brood survival			Apparent chick survival		
	AD	YR	All	AD	YR	All[a]	AD	YR	All[b]
Buffalo - 2004	5/09-5/24	5/14-5/29	5/09-5/29	0.88	0.58	0.71	0.41	0.26	0.33
				(7/8/1)	(7/12/5)	(15/21/6)	(29/70/0)	(20/78/30)	(51/156/30)
Buffalo - 2005	5/10-6/23	5/14-6/20	5/10-6/23	0.96	0.95	0.96	0.51	0.63	0.55
				(27/28/3)	(18/19/3)	(46/48/6)	(84/164/Unk)	(67/107/13+)	(152/277/21+)
Buffalo - 2006	5/19-6/06	5/16-6/06	5/16-6/06	0.88	0.92	0.91	0.43	0.50	0.48
				(7/8/12)	(22/24/8)	(29/32/20)	(24/56/70)	(78/155/48)	(102/211/118)
SH - 2003	5/23-6/08	5/31	5/23-6/08	0.80	1.00	0.83	0.54	0.50	0.54
				(4/5/0)	(1/1/0)	(5/6/0)	(19/35/0)	(3/6/0)	(22/41/0)

[a] Totals also include broods from females of undetermined age (i.e., after-hatching-year).
[b] Totals also include chicks from females of undetermined age (i.e., after-hatching-year).

Table 8. Suspected cause of death of radio-collared female sage-grouse near Decker, MT from 2003-2007, Buffalo, WY from 2004-2007, and Spotted Horse (SH), WY in 2003-2004.

Region - Year	No. mortalities	Suspected proximate cause of death								
		Raptor kill	Mammal kill	Unknown predator	WNv	Vehicle collision	Powerline collision	Other disease	Legal harvest	Unknown
Decker 2003-2004	21	1	0	13	0	0	1	0	0	6
Decker 2004-2005	27	4	1	10	3[a]	0	0	0	0	9
Decker 2005-2006	24	3	2	5	0	0	0	1[b]	0	13
Decker 2006-2007	34	1	0	13	3	0	0	1[c]	0	16
Buffalo 2004-2005	23	8	4	6	1	0	0	0	1	3
Buffalo 2005-2006	39	7	4	9	3	2	0	0	0	14
Buffalo 2006-2007	39	3	0	7	3[d]	0	0	1	0	25[d]
SH 2003-2004	10	1	0	2	6	0	1	0	0	1
All regions - all years	217	28	11	65	19[d]	2	2	2	1	87[d]

[a] Two of the three mortalities positive for West Nile virus near Decker in 2004 occurred in alfalfa fields irrigated with water from coal-bed natural gas development.
[b] Aspergillosus.
[c] Metastatic mineralization of the kidney reported, cause unknown.
[d] Four mortalities listed here as unknown cause of death may have died from West Nile virus and are currently being tested at the Wyoming State Veterinary Laboratory.

Table 9. Sample sizes for nest, brood, and female survival analyses and interval lengths (d) for female survival analyses in three regions of the Powder River Basin, 2003-2006. Spring-summer survival was measured from the beginning of nesting (30 Mar - 6 Apr, depending on the year) to 10 Sept. Fall-winter survival was measured from 10 Sept to the beginning of nesting the following spring.

| Region - Year | No. nests | No. broods | Spring-summer | | | Fall-winter | | | |
			No. yearlings	No. adults	Interval length (d)	No. juveniles	No. yearlings	No. adults	Interval length (d)
Decker 2003	40	25	21	27	160	13	15	22	202
Decker 2004	46	25	31	42	164	11	19	35	208
Decker 2005	82	36	16	60	157	0	16	40	206
Decker 2006	73	36	26	50	159	0	18	26	202
Buffalo 2004	46	23	39	12	166	0	28	8	199
Buffalo 2005	72	52	34	40	166	0	23	23	208
Buffalo 2006	58	43	52	23	157	0	25	14	208
SH 2003	11	6	4	10	162	0	2	1	203
SH 2004	0	0	1	4	162	0	1	3	203
All regions - all years	428	246	219	254		24	147	172	
No. individuals	289	206	343 (spring-summer)			233 (fall-winter)			

Table 10. *A priori* models of daily survival rate for greater sage-grouse nests in the Powder River Basin, 2003-2006. Models are ranked by ΔAIC_c values.

No.	Model[1]	K	AIC_c	ΔAIC_c	w_i
1	Region*Year+Hen Age+Julian Date	13	1020.046	0.000	0.333
2	Region*Year+Hen Age+Attempt	13	1021.552	1.506	0.157
3	Region*Year+Julian Date	12	1021.887	1.841	0.132
4	Region*Year+Attempt	12	1022.155	2.109	0.116
5	Region*Year+Hen Age	12	1022.651	2.606	0.090
6	Region*Year+Hen Age+Julian Date+Julian Date^2	14	1022.833	2.787	0.083
7	Region*Year	11	1023.990	3.944	0.046
8	Region*Year+Julian Date+Julian Date^2	13	1025.051	5.006	0.027
9	Region+Year+Hen Age+Julian Date	11	1029.546	9.500	0.003
10	Region*Year*Hen Age+Julian Date	20	1029.962	9.916	0.002
11	Region+Year+Hen Age+Attempt	11	1030.545	10.499	0.002
12	Region+Year+Hen Age	10	1030.915	10.869	0.001
13	Region*Year*Hen Age+Attempt	20	1031.201	11.155	0.001
14	Region+Year+Attempt	10	1031.403	11.358	0.001
15	Region+Year+Julian Date	10	1031.462	11.417	0.001
16	Region+Year*Hen Age+Julian Date	14	1031.880	11.834	0.001

17	Region*Year*Hen Age	19	1032.220	12.174	0.001
18	Region+Year*Hen Age+Attempt	14	1032.746	12.701	0.001
19	Region+Year+Hen Age+Julian Date+Julian Date^2	12	1032.882	12.836	0.001
20	Region*Year*Hen Age+Julian Date+Julian Date^2	21	1032.956	12.910	0.001
21	Region+Year*Hen Age	13	1033.316	13.270	0.000
22	Region+Year*Hen Age+Julian Date+Julian Date^2	15	1035.146	15.100	0.000
23	Region+Year+Julian Date+Julian Date^2	11	1035.284	15.239	0.000
24	Julian Date+Julian Date^2+PrevSprPrecip	7	1038.522	18.477	0.000
25	Hen Age+Julian Date+Julian Date^2+PrevSprPrecip	8	1040.175	20.129	0.000
26	Julian Date+PrevSprPrecip	6	1040.673	20.627	0.000
27	Attempt+PrevSprPrecip	6	1040.951	20.905	0.000
28	Attempt*PrevSprPrecip	7	1041.604	21.558	0.000
29	Hen Age+Julian Date+PrevSprPrecip	7	1041.771	21.726	0.000
30	Julian Date*PrevSprPrecip	7	1042.259	22.213	0.000
31	Hen Age+Attempt+PrevSprPrecip	7	1042.495	22.449	0.000
32	Hen Age+Attempt*PrevSprPrecip	8	1043.110	23.064	0.000
33	Hen Age+PrevSprPrecip	6	1043.389	23.343	0.000
34	Hen Age+Julian Date*PrevSprPrecip	8	1043.396	23.350	0.000
35	NestAge+NestAge^2+ExtremePrecip	4	1044.653	24.608	0.000

36	Hen Age+Julian Date+Julian Date^2	7	1045.364	25.319	0.000
37	Julian Date+Julian Date^2+SprPrecip	7	1045.388	25.342	0.000
38	Hen Age+Julian Date	6	1045.954	25.908	0.000
39	Attempt*SprPrecip	7	1046.154	26.108	0.000
40	Julian Date+SprPrecip	6	1046.177	26.131	0.000
41	Attempt+SprPrecip	6	1046.316	26.270	0.000
42	Hen Age+Attempt	6	1046.355	26.309	0.000
43	Hen Age+Julian Date+Julian Date^2+SprPrecip	8	1047.361	27.315	0.000
44	Julian Date*SprPrecip	7	1047.500	27.454	0.000
45	Hen Age+Julian Date+SprPrecip	7	1047.924	27.878	0.000
46	Hen Age+SprPrecip	6	1048.049	28.003	0.000
47	Hen Age+Attempt*SprPrecip	8	1048.088	28.042	0.000
48	Hen Age+Attempt+SprPrecip	7	1048.242	28.197	0.000
49	Hen Age+Julian Date*SprPrecip	8	1049.254	29.208	0.000

[1] All models include effects of *nest age + nest age^2* and *extreme precipitation*.

Table 11. *A priori* models of daily survival rate for greater sage-grouse broods in the Powder River Basin, 2003-2006. Models are ranked by ΔAIC$_c$ values.

No.	Model	K	AIC$_c$	ΔAIC$_c$	w_i
1	Brood Age+Region	4	304.106	0.000	0.225
2	Brood Age+Region*Year	9	304.509	0.403	0.184
3	Brood Age+Region+Hen Age	5	304.820	0.714	0.157
4	Brood Age+Region*Year+Hen Age	10	305.480	1.374	0.113
5	Brood Age+Region+Julian Date	5	306.061	1.955	0.085
6	Brood Age+Region*Year+Julian Date	10	306.494	2.388	0.068
7	Brood Age+Region+Hen Age+Julian Date	6	306.745	2.639	0.060
8	Brood Age+Region*Year+Hen Age+Julian Date	11	307.464	3.358	0.042
9	Brood Age+Region+Year	7	309.365	5.259	0.016
10	Brood Age+Region+Year+Hen Age	8	310.427	6.321	0.010
11	Brood Age+Region+Year+Julian Date	8	311.148	7.042	0.007
12	Brood Age+Region+Year*Julian Date	11	311.647	7.542	0.005
13	Brood Age+Region+Year+Hen Age+Julian Date	9	312.203	8.097	0.004
14	Brood Age	2	312.264	8.159	0.004
15	Brood Age+Region+Year*Julian Date+Hen Age	12	312.302	8.197	0.004
16	Brood Age+SprPrecip	3	313.017	8.911	0.003

17	Brood Age+Julian Date	3	313.972	9.867	0.002
18	Brood Age+Julian Date+SprPrecip	4	314.163	10.057	0.001
19	Brood Age+SprPMDI	3	314.211	10.105	0.001
20	Brood Age+Hen Age	3	314.265	10.159	0.001
21	Brood Age+Hen Age+SprPrecip	4	314.980	10.874	0.001
22	Brood Age+Region+Year*Hen Age	11	315.073	10.967	0.001
23	Global	12	315.261	11.156	0.001
24	Brood Age+Julian Date+SprPMDI	4	315.755	11.649	0.001
25	Brood Age+Hen Age+Julian Date	4	315.975	11.869	0.001
26	Brood Age+Julian Date*SprPrecip	5	316.094	11.988	0.001
27	Brood Age+Hen Age+Julian Date+SprPrecip	5	316.127	12.021	0.001
28	Brood Age+Year	5	316.169	12.063	0.001
29	Brood Age+Hen Age+SprPMDI	4	316.209	12.103	0.001
30	Brood Age+Hen Age*SprPrecip	5	316.627	12.521	0.000
31	Brood Age+Region+Year*Hen Age+Julian Date	12	316.924	12.818	0.000
32	Brood Age+Julian Date*SprPMDI	5	317.356	13.250	0.000
33	Brood Age+Hen Age*SprPMDI	5	317.732	13.626	0.000
34	Brood Age+Hen Age+Julian Date+SprPMDI	5	317.754	13.648	0.000
35	Brood Age+Year+Julian Date	6	317.823	13.717	0.000

36	Brood Age+Hen Age*SprPrecip+Julian Date	6	317.832	13.726	0.000
37	Brood Age+Julian Date*SprPrecip+Hen Age	6	318.058	13.953	0.000
38	Brood Age+Year+Hen Age	6	318.168	14.062	0.000
39	Brood Age+Year*Julian Date	9	318.767	14.661	0.000
40	Brood Age+Julian Date*SprPMDI+Hen Age	6	319.352	15.246	0.000
41	Brood Age+Hen Age*SprPMDI+Julian Date	6	319.364	15.258	0.000
42	Brood Age+Year+Hen Age+Julian Date	7	319.820	15.714	0.000
43	Brood Age+Year*Julian Date+Hen Age	10	320.773	16.667	0.000
44	Brood Age+Year*Hen Age	9	321.354	17.248	0.000
45	Brood Age+Year*Hen Age+Julian Date	10	323.106	19.000	0.000

Table 12. *A priori* models of daily spring-summer female survival rate for greater sage-grouse in the Powder River Basin, spring 2003 - spring 2007. Models are ranked by ΔAIC_c values.

No.	Model	K	AIC_c	ΔAIC_c	w_i
1	Region*WNV+Year+With Brood	10	1611.503	0.000	0.221
2	Region*WNV+Year	9	1611.997	0.494	0.173
3	Region*WNV+Year+On Nest	10	1612.730	1.227	0.120
4	Region*WNV+Year+Hen Age+With Brood	11	1612.975	1.472	0.106
5	Region*WNV+Year+Hen Age	10	1613.595	2.091	0.078
6	Region+Year+With Brood+WNV	8	1614.247	2.744	0.056
7	Region*WNV+Year+Hen Age+On Nest	11	1614.391	2.887	0.052
8	Region+Year+WNV	7	1615.007	3.504	0.038
9	Region+Year+On Nest+WNV	8	1615.582	4.079	0.029
10	Region+Year+With Brood*WNV	9	1615.800	4.297	0.026
11	Region+Year+Hen Age+With Brood+WNV	9	1615.867	4.363	0.025
12	Region+Year+Hen Age+WNV	8	1616.739	5.235	0.016
13	Global	10	1617.267	5.764	0.012
14	Region+Year+Hen Age+On Nest+WNV	9	1617.366	5.862	0.012
15	Region+Year+Hen Age+With Brood*WNV	10	1617.427	5.924	0.011

16	Region*Hen Age+Year+With Brood+WNV	11	1618.077	6.574	0.008
17	Region*Hen Age+Year+WNV	10	1619.003	7.500	0.005
18	Region*Hen Age+Year+With Brood*WNV	12	1619.638	8.134	0.004
19	Region*Hen Age+Year+On Nest+WNV	11	1619.660	8.157	0.004
20	Region+Year+With Brood	7	1621.341	9.838	0.002
21	Region+Year+Hen Age+With Brood	8	1623.057	11.553	0.001
22	Region+Year	6	1623.579	12.075	0.001
23	Region*Year	10	1623.943	12.439	0.000
24	Region+Year+Hen Age	7	1625.413	13.909	0.000
25	Region*Hen Age+Year+With Brood	10	1625.503	14.000	0.000
26	Region+Year+On Nest	7	1625.542	14.039	0.000
27	Region*Year+Hen Age+On Nest	12	1626.598	15.094	0.000
28	Region*Year*Hen Age	20	1627.251	15.748	0.000
29	Region+Year+Hen Age+On Nest	8	1627.367	15.864	0.000
30	Region*Hen Age+Year	9	1627.938	16.435	0.000
31	Region*Hen Age+Year+On Nest	10	1629.882	18.378	0.000
32	Region*Year+With Brood	11	1670.830	59.327	0.000
33	Region*Year+On Nest	11	1677.943	66.439	0.000
34	Region*Year*Hen Age+On Nest+WNV	22	1720.185	108.682	0.000

35	Region*Year+Hen Age	11	1734.204	122.701	0.000
36	Region*Year*Hen Age+On Nest	21	1734.731	123.227	0.000
37	Region*Year*Hen Age+With Brood*WNV	23	1758.631	147.127	0.000
38	Region*Year*Hen Age+WNV	21	1770.376	158.873	0.000
39	Region*Year+Hen Age+With Brood	12	1782.309	170.806	0.000
40	Region*Year*Hen Age+With Brood+WNV	22	1785.598	174.095	0.000
41	Region*Year+Hen Age+WNV	12	1794.996	183.492	0.000
42	Region*Year+Hen Age+With Brood*WNV	14	1811.092	199.588	0.000
43	Region*Year+Hen Age+On Nest+WNV	13	1823.341	211.838	0.000
44	Region*Year+Hen Age+With Brood+WNV	13	1841.026	229.522	0.000

Table 13. *A priori* models of daily spring-summer female survival rate for greater sage-grouse in the Powder River Basin, spring 2003 - spring 2007, excluding mortalities confirmed positive for West Nile virus. Models are ranked by ΔAIC_c values.

No.	Model[1]	K	AIC_c	ΔAIC_c	w_i
1	Region+Year+With Brood	7	1454.115	0.000	0.312
2	Region+Year	6	1455.091	0.976	0.192
3	Region+Year+Hen Age+With Brood	8	1455.488	1.373	0.157
4	Region+Year+Hen Age	7	1456.617	2.502	0.089
5	Region+Year+On Nest	7	1456.762	2.647	0.083
6	Global	9	1457.452	3.337	0.059
7	Region+Year+Hen Age+On Nest	8	1458.329	4.214	0.038
8	Region*Hen Age+Year+With Brood	10	1458.972	4.857	0.028
9	Region*Year	10	1459.626	5.511	0.020
10	Region*Hen Age+Year	9	1460.129	6.014	0.015
11	Region*Hen Age+Year+On Nest	10	1461.857	7.741	0.007
12	Region*Year*Hen Age+On Nest	21	1466.915	12.800	0.001
13	Region*Year*Hen Age	20	1468.292	14.177	0.000
14	Region*Year+With Brood	11	1500.477	46.362	0.000
15	Region*Year*Hen Age+With Brood	21	1509.824	55.708	0.000

16	Region*Year+On Nest	11	1517.646	63.531	0.000
17	Region*Year+Hen Age	11	1549.517	95.402	0.000
18	Region*Year+Hen Age+On Nest	12	1568.049	113.933	0.000
19	Region*Year+Hen Age+With Brood	12	1605.581	151.466	0.000

Table 14. Spring-summer survival estimates ± SE for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003-2004, including and excluding mortalities confirmed positive for West Nile virus.

	Survival (including WNv)		Survival (excluding WNv)	
Region - Year	AD	YR	AD	YR
Decker - 2003	0.680 ± 0.099	0.593 ± 0.117	0.680 ± 0.099	0.593 ± 0.117
Decker - 2004	0.808 ± 0.065	0.580 ± 0.100	0.808 ± 0.065	0.682 ± 0.099
Decker - 2005	0.732 ± 0.061	1.000	0.732 ± 0.061	1.000
Decker - 2006	0.637 ± 0.070	0.731 ± 0.087	0.671 ± 0.069	0.764 ± 0.084
Buffalo - 2004	0.447 ± 0.216	0.644 ± 0.082	0.593 ± 0.231	0.668 ± 0.081
Buffalo - 2005	0.582 ± 0.079	0.639 ± 0.086	0.627 ± 0.078	0.671 ± 0.085
Buffalo - 2006	0.696 ± 0.103	0.589 ± 0.076	0.696 ± 0.103	0.647 ± 0.075
SH - 2003	0.125 ± 0.087	0.482 ± 0.249	0.392 ± 0.184	0.693 ± 0.254
SH - 2004	1.000	1.000	1.000	1.000

Table 15. Annual survival estimates for adult (AD) and yearling (YR) female greater sage-grouse near Decker, MT from 2003-2006, near Buffalo, WY from 2004-2006, and near Spotted Horse (SH), WY in 2003-2004, including and excluding mortalities confirmed positive for West Nile virus.

Region - Year	Annual survival (including WNv)		Annual survival (excluding WNv)	
	AD	YR	AD	YR
Decker - 2003	0.588	0.514	0.587	0.514
Decker - 2004	0.740	0.519	0.740	0.610
Decker - 2005	0.562	1.000	0.562	1.000
Decker - 2006	0.563	0.606	0.594	0.634
Buffalo - 2004	0.447	0.575	0.593	0.596
Buffalo - 2005	0.354	0.472	0.381	0.496
Buffalo - 2006	0.596	0.519	0.596	0.569
SH - 2003	0.125	0.482	0.392	0.693
SH - 2004	1.000	1.000	1.000	1.000

Figure 1. Expansion of coal-bed natural gas development in the Powder River Basin from 1997-2005. Approximate boundaries of study sites with radio-marked greater sage-grouse in the Powder River Basin, 2003-2006 are outlined with black dashed lines. Study regions are labeled in bold. Gray dots represent active coal-bed natural gas wells. County names are in small font.

Figure 2. Daily survival rate (DSR) of nests (with 95% CIs) in three regions of the Powder River Basin, 2003-2006. SH = Spotted Horse.

Figure 3. Daily survival rate (DSR) of nests (with 95% CIs) in relation to date and hen age based on nests in three regions of the Powder River Basin, 2003-2006.

Figure 4. Estimated daily survival rate (DSR) of nests during incubation (with 95% CIs) as nest age increases based on nesting data from three regions of the Powder River Basin, 2003-2006. We illustrate the effect with data from nests in the Decker region in 2003 that began incubation on May 12, the average date of clutch completion in that region in that year in that region.

Figure 5. Estimated nest success (with 95% CIs) in three regions of the Powder River Basin, 2003-2006 for first nests and renests of (a) yearlings and (b) adults based on a *Region*Year*Hen age + Attempt* model. SH = Spotted Horse.

Figure 6. Daily survival rate (DSR) of broods (with 95% CIs) in three regions of the Powder River Basin, 2003-2006. Point estimates start at brood age of 1 d and are shown

for every other day through 35 d. Point estimates and CIs are offset for clarity. SH =

Spotted Horse.

Figure 7. Estimated brood success (with 95% CIs) in three regions of the Powder River

Basin, 2003-2006 based on a *Region*Year* model.

Figure 8. Estimated spring-summer survival (with 95% CIs) for greater sage-grouse

females without broods (i.e., non-nesting females and females with unsuccessful nests)

and those that raised broods to 35 d in three regions of the Powder River Basin, 2003-

2006, based on the best-approximating model (*Region*WNv+Year+WBrood*).

Figure 9. Spring-summer survival (with 95% CIs) for (a) yearling and (b) adult females

in three regions of the Powder River Basin from 2003-2007, based on a

Region*Year*Hen age model. Estimates presented include (white bars) or exclude (gray

bars) mortalities confirmed positive for West Nile virus. SH = Spotted Horse.

Figure 10. Fall-winter juvenile, yearling, and adult female survival (with 95% CIs) in

three regions of the Powder River Basin from 2003 - 2006. Estimates refer to survival

from fall to the following spring (e.g., 2003 means fall 2003 - spring 2004). Survival

data on juveniles were only collected in the Decker region in fall-winter 2003-2004 and

2004-2005. Survival estimates for Spotted Horse were based on only 2 individuals in

2003-2004 and 4 individuals in 2004-2005.

Figure 11. Estimated annual survival of (a) yearling and (b) adult females in three regions of the Powder River Basin, 2003 - 2006 based on a *Region*Year*Hen age* model. Estimates presented include (white bars) or exclude (gray bars) mortalities confirmed positive for West Nile virus. Estimates refer to survival from fall in that year through the following spring. Survival estimates for Spotted Horse were based on only 2 individuals in 2003-2004 and 4 individuals in 2004-2005.
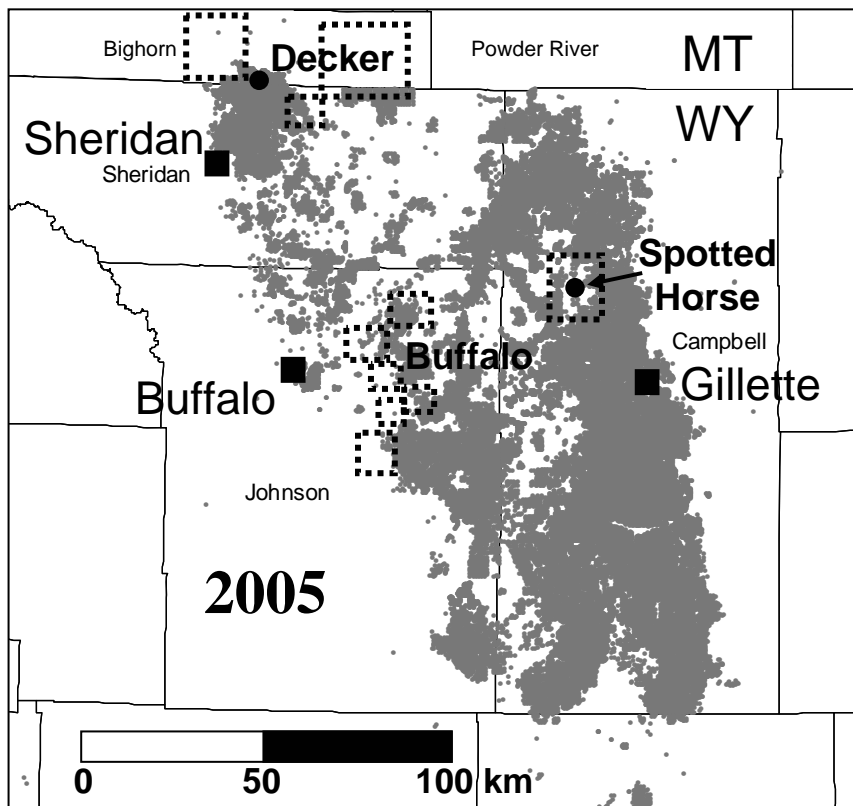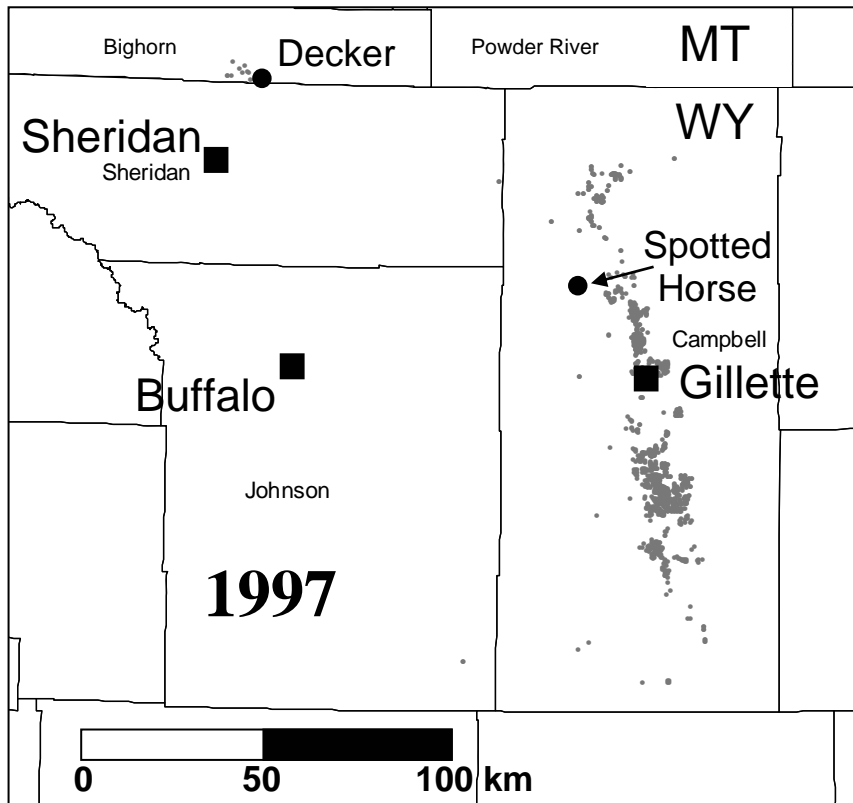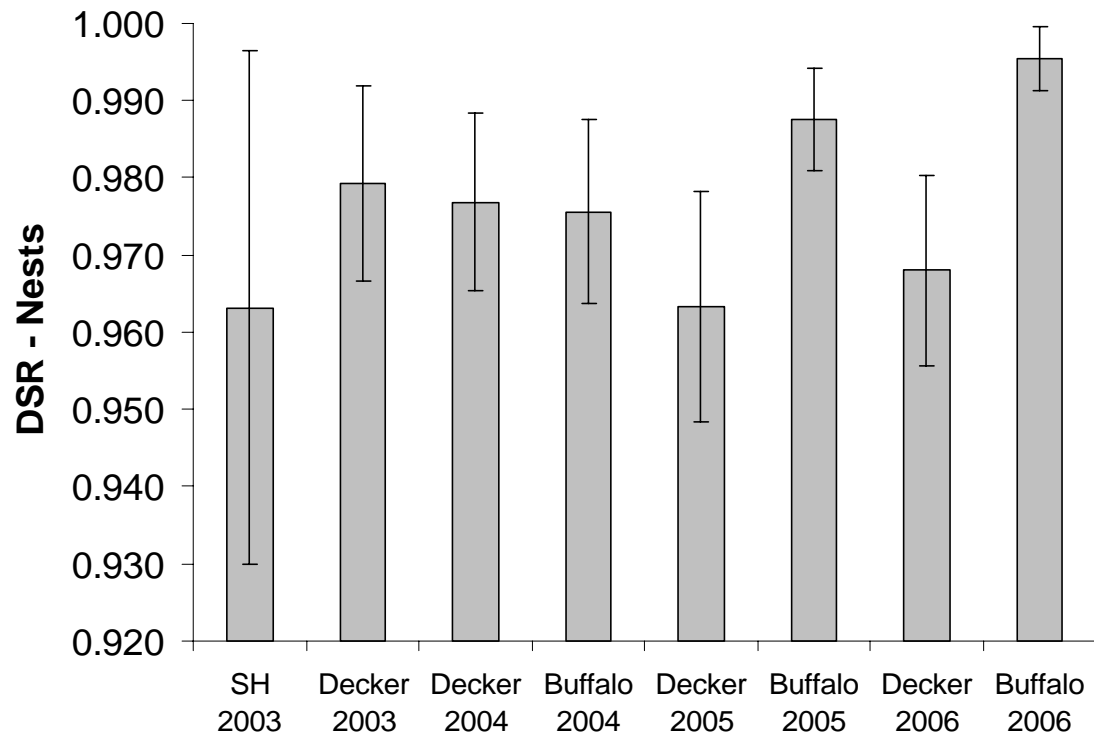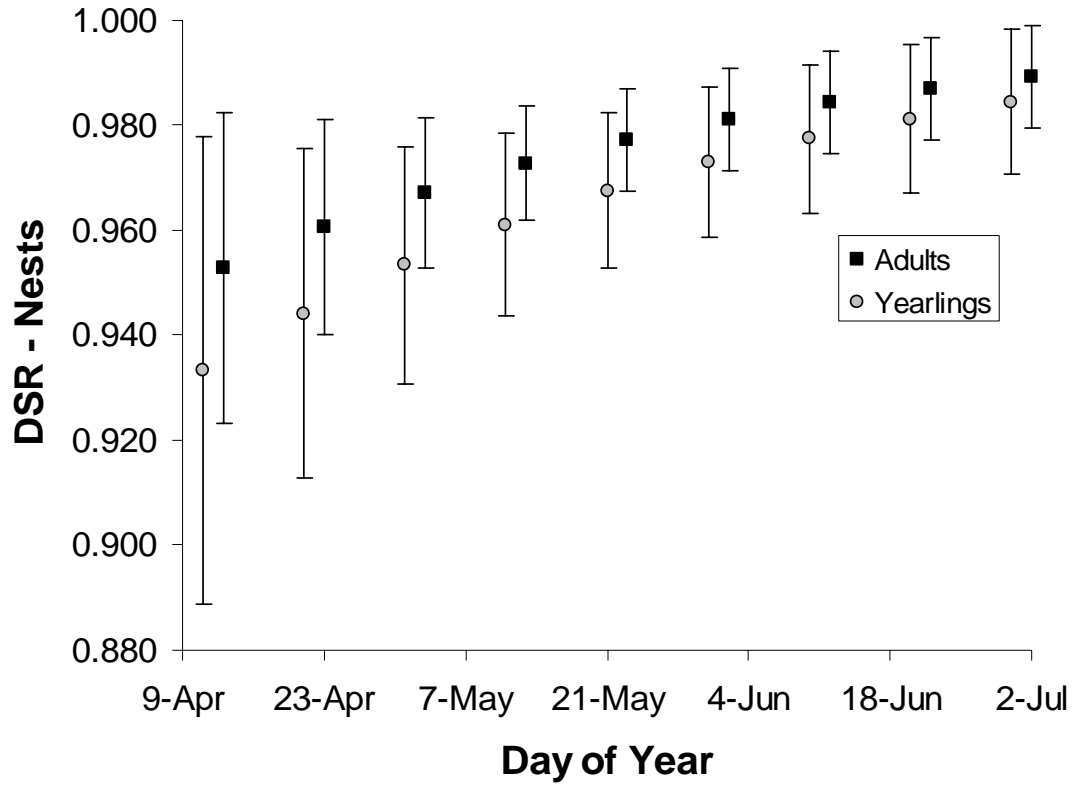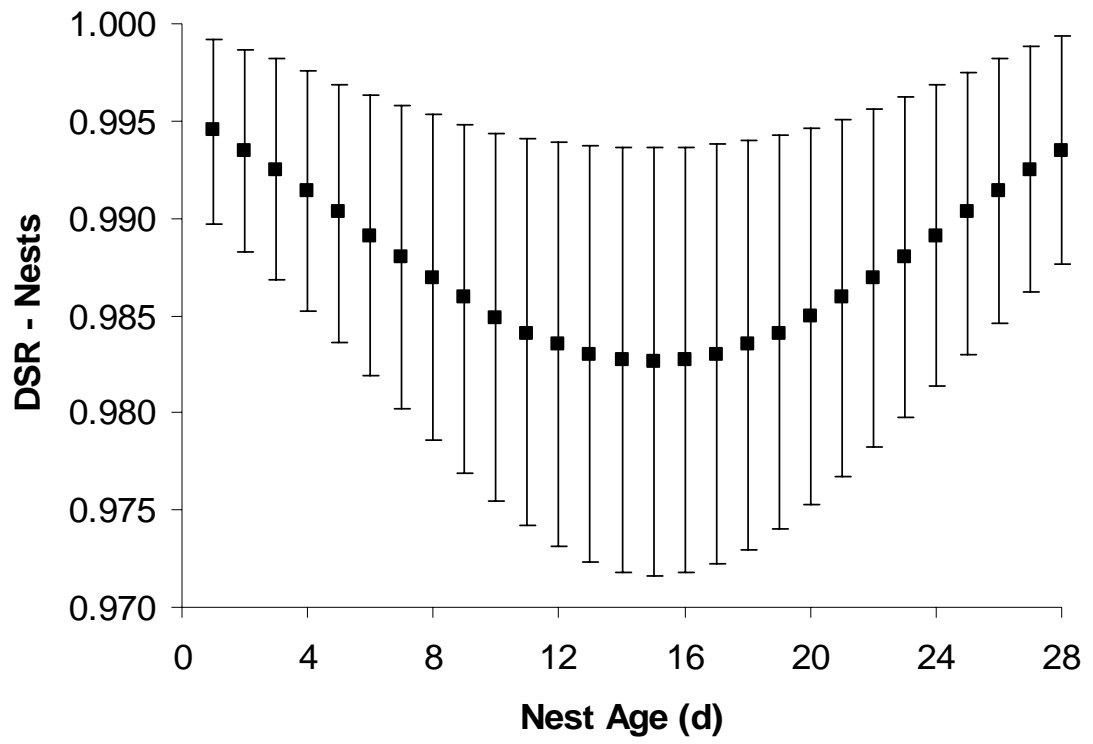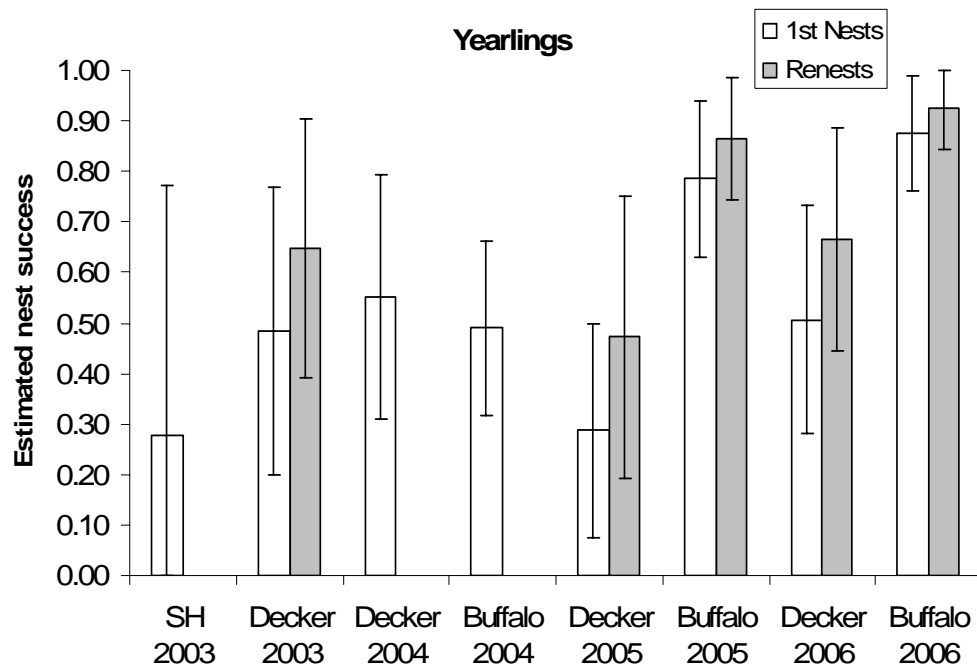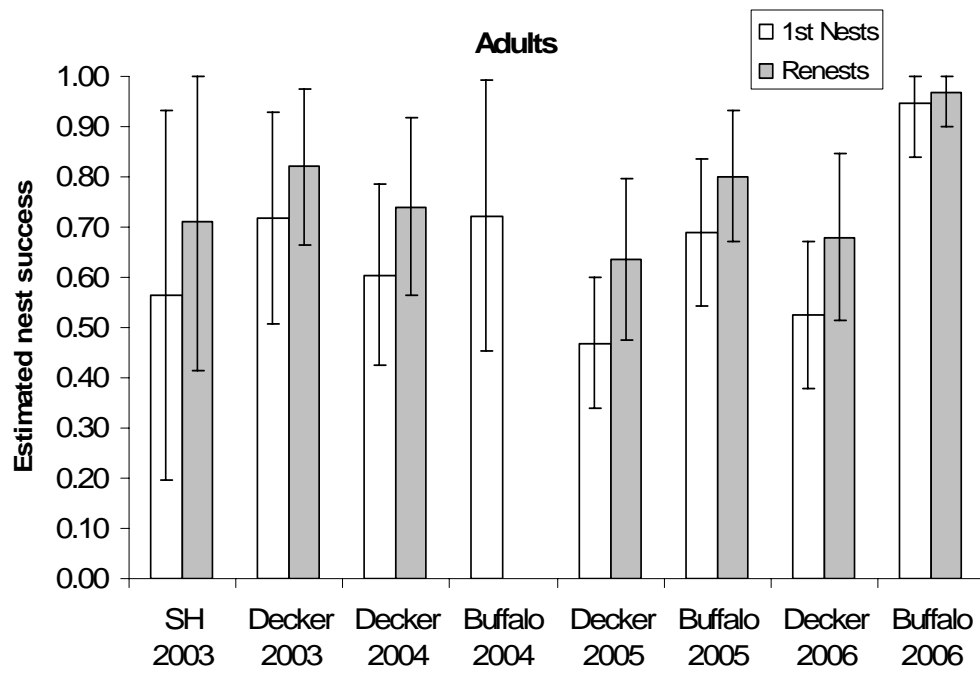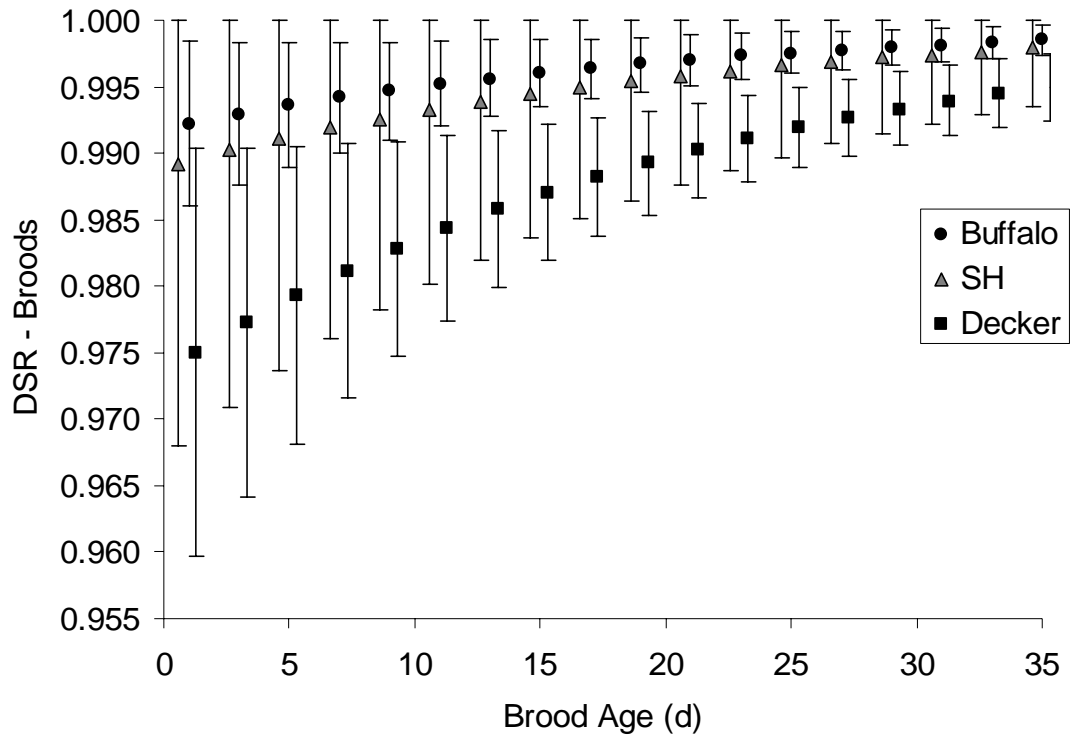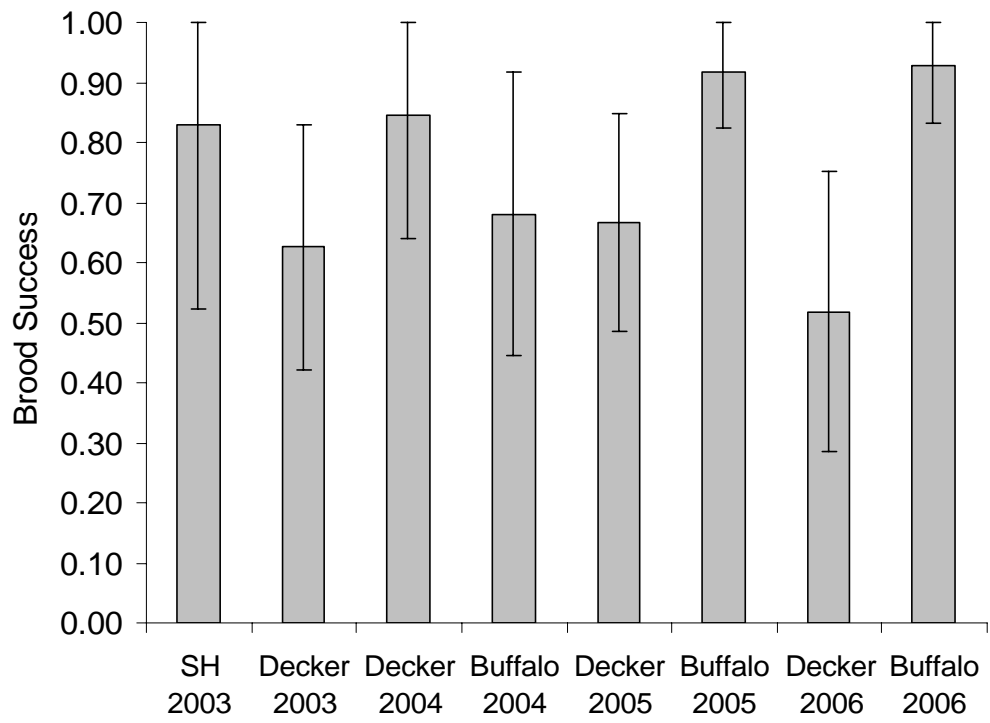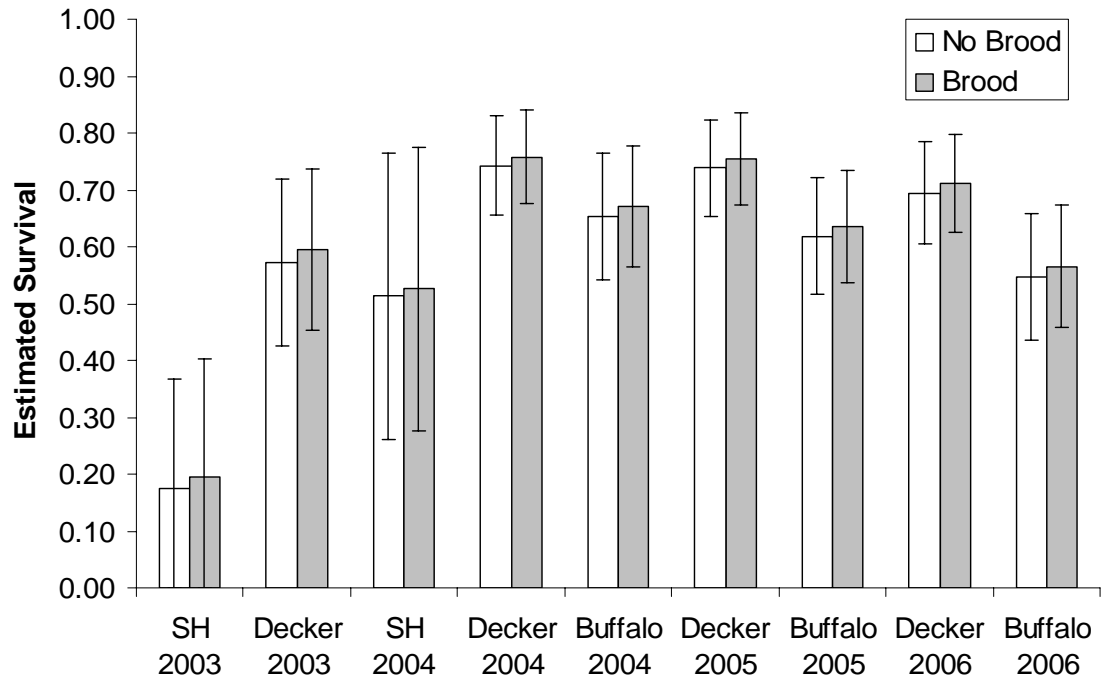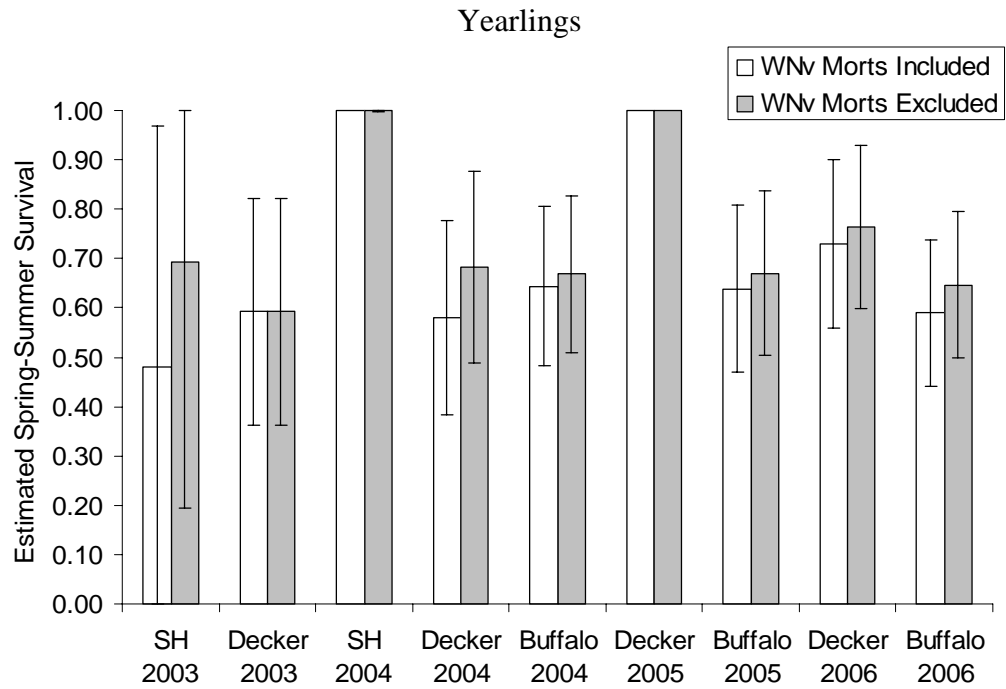
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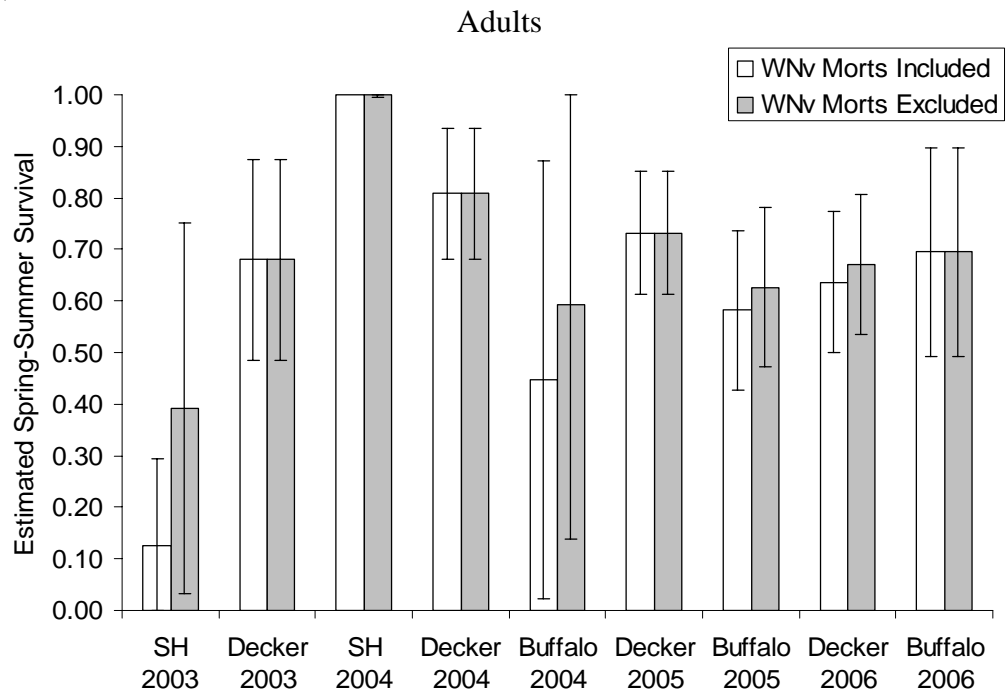Figure 3.

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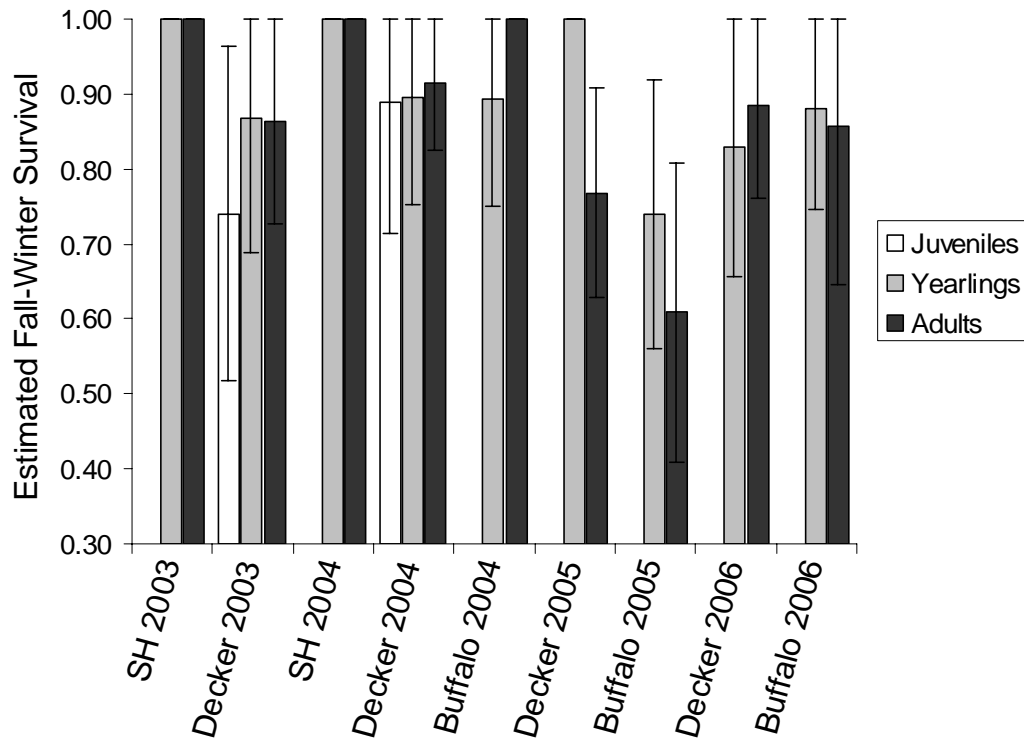
Figure 5.

(a)

(b)

Figure 6.

Figure 7.

Figure 8.

Figure 9.

(a)

(b)

Figure 10.

Figure 11.

(a)

Yearlings

(b)

Adults
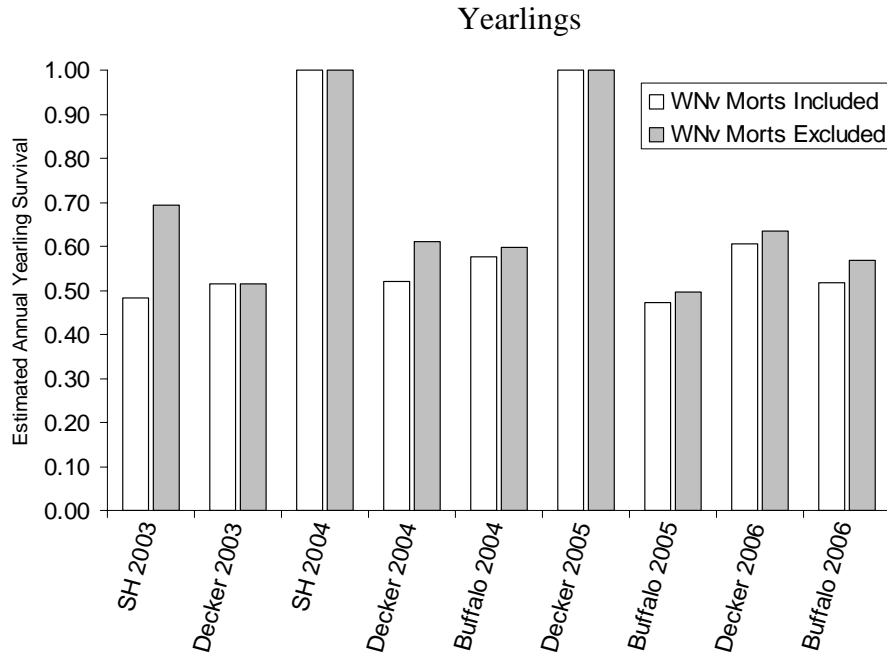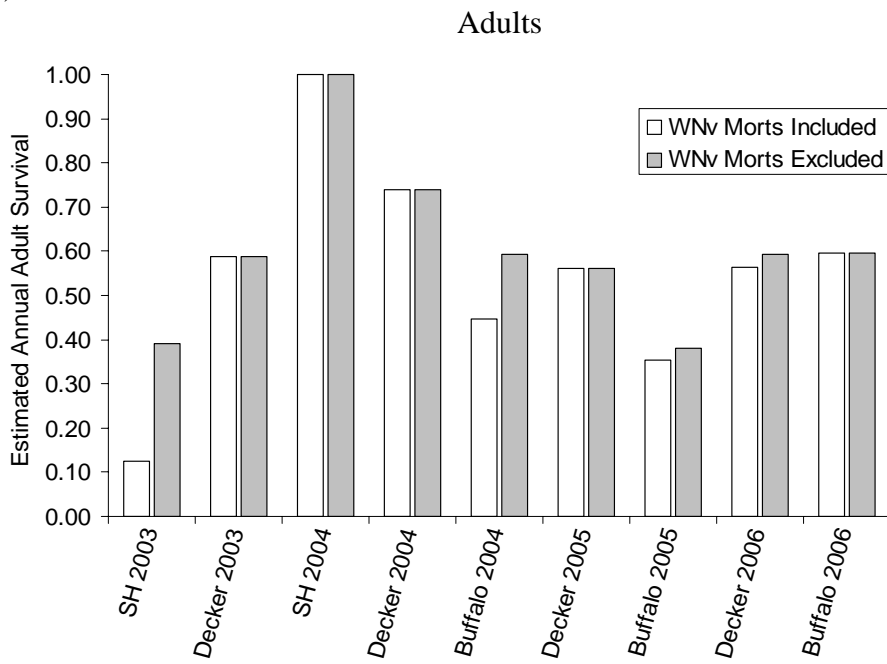
CHAPTER 5. IMPACTS OF WEST NILE VIRUS ON POPULATION GROWTH OF GREATER SAGE-GROUSE.

Abstract. A new concern for conservation of greater sage-grouse (*Centrocercus urophasianus*) in western North America is the arrival and spread of West Nile virus (Flaviviridae, *Flavivirus*) (WNv). Since 2003, declines in late-summer survival due to WNv-related mortality and mortality events have been reported in 11 of the 13 states within the species' current range, and laboratory studies have documented 100% mortality following infection. However potential long-term effects of WNv on populations have not been investigated. We used life-stage simulation analysis models and empirical data on WNv-related mortality and infection rates from radio-marked sage-grouse to explore potential impacts of WNv on population growth in the Powder River Basin of northeastern Wyoming and southeastern Montana, USA from 2003-2006. Observed levels of mortality indicate that WNv reduced estimates of population growth (i.e., finite rate of increase, λ) by -0.073 to -0.103 per year. Simulated impacts based on current estimates of WNv infection rate suggested an average decline in λ of -0.073 to -0.075 due to WNv. Because of low annual infection rates, resistance to WNv disease was projected to increase gradually over time (assuming no changes in virulence). Severe outbreaks of WNv may result in increased resistance in the population, but may also simultaneously reduce local abundance below thresholds for population persistence. Residual or sublethal (i.e., carryover) effects of WNv infection in surviving individuals have the potential to hinder the evolution of resistance. Presently, carryover effects appear to have little influence on population growth because so few individuals survive

infection, but they may become relevant if infection rates or the proportion of resistant birds in the population increases. Changes in the virulence or epizootiology of WNv and in the distribution and management of surface water from coal-bed natural gas development will play an important role in long-term impacts on greater sage-grouse populations in the Powder River Basin.

Keywords: *Centrocercus urophasianus*, demographics, flavivirus, greater sage-grouse, population model, life-stage simulation analysis, Powder River Basin, sagebrush, vital rates, West Nile virus.

Emerging infectious diseases can act as important new sources of mortality for populations of sensitive and declining wildlife species. A major new concern for conservation of North American birds, including greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse"), in North America is the arrival and spread of West Nile virus (WNv; Flaviviridae, *Flavivirus*) (McLean 2006, Koenig et al. 2007, LaDeau et al. 2007). Recent studies have documented declines in sage-grouse survival attributable to WNv in wild (Naugle et al. 2004, 2005; Walker et al. 2004, 2007*b*) and laboratory populations (Clark et al. 2006). West Nile virus first arrived within the current range of sage-grouse in 2002 (Kilpatrick et al. 2007), and WNv-related mortality in sage-grouse was documented that year (Naugle et al. 2004). In 2003, WNv-related mortality reduced late-summer survival rate of females by ~25% across much of the eastern half of the species' range (Naugle et al. 2004), and resulted in near-extirpation of a local breeding population in northeastern Wyoming by spring 2004 (Walker et al. 2004). From

2004-2007, annual WNv-related mortality and localized severe mortality events have
been reported throughout the species' range. By the end of 2007, WNv-positive
mortalities had been documented in 11 of the 13 states and provinces where the species
still occurs, with the exception of Washington and Saskatchewan (U. S. Geological
Survey 2006; Walker 2006; Walker et al. 2007*b*). In northeastern Wyoming and
southeastern Montana, WNv-related mortality during the summer resulted in an average
decline in annual female survival of 5% (range 0-27%) from 2003-2006 (Chapter 4).
Overall, estimates of WNv-related mortality among breeding-aged females during the
summer WNv transmission period across the species' range varied from 0-71% (Walker
et al. 2004, Naugle et al. 2005, USGS 2006, Kaczor 2008).

The spread and prevalence of resistance to WNv-induced disease over time also
has important implications for effects of the virus on populations. West Nile virus is now
considered the predominant endemic arthropod-borne disease in North America (Gubler
2007, Kramer et al. 2008), and it has been a persistent source of mortality in sage-grouse
since 2003 (Walker 2006, Walker et al. 2007*b*). However, managing WNv risk for sage-
grouse is a daunting task because of the scale at which reservoir and amplifying hosts
(Kato et al. 2008), mosquito vectors (Doherty 2007), and sage-grouse are distributed
during the summer transmission period (Connelly et al. 2000). For that reason, most
wildlife managers must simply hope that resistance to disease will increase over time. To
date, the combination of high mortality rates during severe WNv outbreaks, 100%
mortality among experimentally infected birds from both eastern and western portions of
the species' range, and low seroprevalence among survivors (0-10%), suggest that
resistance to WNv-induced disease in sage-grouse generally is low (Naugle et al. 2004,

2005; Walker et al. 2004, 2007*b*; Clark et al. 2006). The first cases of sage-grouse

surviving WNv infection were documented in 2005 and 2006 in northeastern Wyoming

(Walker et al. 2007*b*), but live, seropositive birds have not yet been reported from other

parts of the species' range. Exposure to the virus could increase resistance to WNv-

induced disease over time at the population level and improve the likelihood of long-term

population persistence, but changes in resistance depend on annual infection rates and the

fitness of individuals that survive infection compared to uninfected birds.

Sublethal or residual (i.e., "carryover") effects of WNv infection may also be

important in determining population-level impacts of the virus. As in other birds (e.g.,

raptors; Nemeth et al. 2006*a, b*) and in mammals (e.g., humans, horses; Hayes et al.

2005, Hayes and Gubler 2006), sage-grouse that survive WNv infection may nonetheless

suffer persistent symptoms (Clark et al. 2006). In other species, non-lethal cases of WNv

infection often result in chronic symptoms (e.g., reduced mobility, weakness,

disorientation, muscle pain, etc.) and lengthy recovery periods (Marra et al. 2004, Hayes

et al. 2005; Nemeth et al. 2006*a, b*). These symptoms in turn, may decrease nutritional or

body condition of individuals and influence fall-winter survival, reproductive effort, or

both following infection. In sage-grouse, nutritional condition prior to the breeding

season is positively correlated with reproductive effort and success (Dunbar et al. 2005,

Gregg et al. 2006). Carryover effects of WNv infection on sage-grouse have not been

studied because low infection rates and high mortality have left few infected survivors for

observation (Walker et al. 2007*b*). However, carryover effects might substantially

influence population growth if the proportion of infected survivors increases over time.

Understanding the consequences of increased risk of WNv on populations due to

changes in land use is also crucial for projecting potential impacts of the virus. Anthropogenic changes may increase disease risk by directly or indirectly altering the abundance and habitat use of vectors, reservoirs, and hosts during the transmission period (McSweegan 1996). Of particular concern in the Powder River Basin are ponds associated with coal-bed natural gas (CBNG) development that increase the availability and distribution of larval habitat for mosquitos that vector WNv (Zou et al. 2006*a*, Doherty 2007) and increases in irrigated cropland and water impoundments for livestock due to increased availability of CBNG water. Additional water sources may simultaneously attract sage-grouse in late summer (Connelly and Doughty 1989, Schroeder et al. 1999, Connelly et al. 2000), concentrate potential WNv reservoirs and amplifying hosts, and increase mosquito abundance (Doherty 2007).

Understanding impacts of WNv on populations requires incorporating variation in all of these factors – mortality, resistance to disease, carryover effects, and anthropogenic changes to landscapes – into demographic models. Matrix models, in particular, are valuable for understanding how the influence of impacts on vital rates translates into consequences of potential stressors for population growth. Life-stage simulation analysis in particular, allows consideration of changes in both the mean and variance of specific vital rates on changes in population growth (Wisdom et al. 2000, Reed et al. 2002). However, assumptions associated with matrix models (e.g., populations at stable age distribution) suggest that such models are best used to identify changes in population growth rate under different scenarios, rather than absolute values for growth rates (Reed et al. 2002).

Overall, several lines of evidence suggest that WNv could be an important new stressor on sage-grouse populations, but the potential for long-term population-level effects of WNv has not been explored. We used population projection models, degree-day models for predicting WNv risk (Zou et al. 2006*b*), and empirical data on WNv-related mortality rates from radio-marked females to explore potential impacts of WNv on population growth in the Powder River Basin of northeastern Wyoming and southeastern Montana. We used stage-specific vital rates to parameterize a life-stage simulation analysis model to predict long-term population growth under eight different scenarios: (1) no WNv mortality, (2) observed WNv mortality; (3) simulated current WNv mortality; (4) simulated current WNv mortality with increasing resistance to WNv-induced disease over time; (5) simulated current WNv mortality with increasing resistance to disease and carryover effects on infected survivors; (6) simulated elevated WNv mortality due to expansion of CBNG development; (7) simulated elevated WNv mortality with increasing resistance; and (8) simulated elevated WNv mortality with increasing resistance and carryover effects.

Methods

Analyses. We conducted both analytical sensitivity and elasticity analyses and life-stage simulation analysis to test the importance of mean vital rate values and their variability in predicting λ for the Powder River Basin (Mills et al. 1999, Wisdom et al. 2000,. We then generated and compared means for λ for each impact scenario based on 1000 simulations in MATLAB (version R2007a, The Mathworks, Inc., Natick, Massachusetts, USA).

166

Correlation among vital rates. We used correlations between vital rates to generate sets of correlated random vital rates for simulations (Box 8.6 in Morris and Doak 2002). We conducted analyses both with and without correlations to see how correlation structure influenced estimates of λ and interpretation of sensitivities, elasticities, and r^2 values. Incorporating correlation structure is important for generating realistic combinations of vital rates for simulations that are representative of typical values for the population of interest (Wisdom et al. 2000, Mills and Lindberg 2002, Morris and Doak 2002). Estimating correlations among vital rates requires estimates of each vital rate over multiple years, preferably for as many years as there are vital rates (Morris and Doak 2002). We were unable to generate a meaningful correlation matrix from the Powder River Basin data due to the short time-frame of the study (2003-2006) and because not all vital rates were estimated in all years. Instead, we assigned pairs of vital rates a correlation coefficient of none (0.00), low (0.25), moderate (0.50), or high (0.75) based on whether published data indicated that both vital rates were regulated by the same biological mechanism(s) (Appendix A). We also examined correlation coefficients between vital rates in the range-wide data to check for evidence for or against hypothesized correlations. We then tested to make sure the final correlation matrix was valid (i.e., positive semi-definite) (Box 8.8 in Morris and Doak 2002).

Sampling vs. process variance. Total variance in survival and productivity estimates is comprised of an unknown mix of temporal, spatial, and sampling variation. Because variance can strongly influence population model results and interpretation (Wisdom et al. 2000), sampling variance must be removed from total variance to obtain an estimate of actual spatial and temporal (i.e., process) variance in each vital rate.

167

Because sampling variance was unlikely to be equal across years or across studies, we

used the variance discounting method of White (2000) to remove sampling variance from

total variance estimates for Powder River Basin and range-wide data. In that analysis,

estimates of variance for binomially-distributed vital rates in each year were estimated

from the theoretical variance of a proportion ($\sigma^2 = pq/n$), where p = proportion that

survived, $q = 1 - p$, and n = number of sample units included in the analysis.

  Model structure. We used a two-stage, female-based life-cycle model to

summarize stage-specific rates of fertility and survival (Figure 1). We used vital rates for

each stage to calculate fertility and survival estimates for parameterizing a 2 x 2 stage-

specific population projection model (i.e., Lefkovitch matrix model) based on a pre-

breeding, birth-pulse census and a one-year projection interval, with birds "censused" on

~1 April just prior to the initiation of nesting. The two stages are yearlings (YR) and

older adults (AD). Stage-specific survival and fecundity values were considered the

same for all individuals within each stage. Female sage-grouse commonly breed as

yearlings, so yearling females were allowed to reproduce in the model. Variables in the

projection matrix included:

  f_{yr}: fertility of yearlings (no. female juveniles produced per yearling female),

  f_{ad}: fertility of adults (no. female juveniles produced per adult female),

  s_{yr}: annual survival of yearlings from the start of the breeding season (~1 April) in

    their second calendar year through the start of the breeding season in their third

    calendar year,

  s_{ad}: annual survival of adults from the start of the breeding season (~1 April) through

    the start of the breeding season in following calendar year.

Vital Rates. Whenever possible, we used mean vital rates and their associated

variances from the Powder River Basin (Chapter 4) in the projection model. However,

because vital rates vary both temporarily and spatially, a 4-year study is insufficient to

adequately characterize means and variances. Moreover, data were not available for all

vital rates in all years (e.g., juvenile survival, renest success). Therefore, we also

summarized year- and site-specific estimates of vital rates from published and

unpublished literature sources from across the species' range for comparison (Appendix

B). In the range-wide data, estimates based on combined data from several years were

treated as a single estimate for that study location. Estimates from the same study

location in the same year were included only once, even if they appeared in more than

one publication. We excluded data that did not use reliable methods for obtaining or

estimating vital rates and those with sample sizes <10 (Appendix B). When data from the

Powder River Basin were unavailable or too sparse to reliably estimate means or

variances, we used range-wide means, variances, or both. We also used range-wide data

to establish upper and lower bounds and to identify appropriate sampling distributions for

each vital rate.

Nest initiation rate ($INIT_1$) was defined as the proportion of females in each stage

(i.e., yearling or adult) that were adequately monitored during the nesting season and

initiated at least one nest (i.e., laid at least one egg). Renesting rate ($INIT_2$) is defined as

the proportion of females whose first nests were unsuccessful that survived, were

adequately monitored, and initiated a second nesting attempt. Second renesting rate

($INIT_3$) is defined as the proportion of females whose first and second nests were

unsuccessful that survived, were adequately monitored, and initiated a third nesting

attempt. Although rates of nest initiation and renesting are likely biased low because some nests fail before they can be discovered, no method exists to correct this bias.

Clutch size was defined as the number of female eggs laid in the nest. On average, adults lay ~0.5 eggs per clutch more than yearlings in first nests, and first nests (8.3) average ~1.5 eggs per clutch more than renests (Petersen 1980, Schroeder 1997, Moynahan 2004, Chapter 4). Due to a lack of data on third nests, we assumed that clutch sizes of third nests (adults only) averaged one egg fewer than second nests. Data on sex ratio at hatch were unavailable. Therefore, instead of including sex ratio as a separate vital rate with unknown mean and variance, we instead assumed an equal ratio of males to females at hatch and multiplied clutch size means by 0.5 to generate stage-specific estimates of clutch size for female eggs only ($CLUTCH_1$, $CLUTCH_2$, and $CLUTCH_3$).

Nest success ($SUCC_1$, $SUCC_2$) was defined as the probability of a nest surviving from laying through hatching. We considered a nest successful if ≥ 1 egg hatched. We used exponentiated estimates of daily survival rates (DSR) of nests to estimate region, year, and stage-specific nest success for first and second nesting attempts for each region and year in the Powder River Basin (Chapter 4) and then calculated mean values across regions and years. Data from second nesting attempts included one successful third nest of one female in 2005. Yearlings have never been recorded attempting a third nest (Appendix B), so third nests were excluded from yearling fertility calculations. For range-wide data, we estimated nest success during incubation by adjusting reported rates of apparent nest success using the "quick" method of Johnson and Klett (1985). Apparent nest success was defined as the proportion of nests that hatched at least one egg. The "quick" method uses the average age of when nests are found (*f*) and average

age of nests at hatch (h) to calculate an approximate daily nest survival rate (S) as the (h-f) root of apparent nest success. Nest success is then calculated as S^h. Nests of radio-marked female sage grouse are typically found during the first visit following the start of incubation (Schroeder et al. 1999, Chapter 4). Thus, we estimated the average age at which nests were found for each study as one-half the reported monitoring interval, where day 1 represented the first day of incubation (i.e., the date of clutch completion). Quick estimates of nest success during incubation were then multiplied by estimated nest success during laying, based on a daily survival estimate of 0.997 during laying (Chapter 4) and laying intervals that varied by age and nest attempt (10.5 d and 9 d for yearling first nests and renests and 12 d and 10.5 d for adult first nests and renests, respectively).

Hatchability (HATCH) was defined as the mean proportion of eggs that hatched across regions and years (i.e., no. of eggs in all clutches of known size divided by the no. of eggs that hatched from all clutches of known size). For range-wide data, there were no published estimates of differences in hatchability of eggs between yearlings and adults, between first nests and renests, or between male and female eggs, so we used the same value (0.923) in all calculations.

Chick survival (CHSURV) was defined as the proportion of chicks that survived from hatch to 35d based on a combination of night-time spotlight counts and day-time flush counts (i.e., apparent chick survival). We were unable to distinguish between male and female chicks, so we assumed that chick survival estimates were representative of females. Males are thought to survive at lower rates than females as juveniles (Swenson 1986), but data on sex-specific survival of chicks <35 d old are not available. Chick

survival estimates from range-wide data also did not distinguish males from females (e.g., Burkepile et al. 2002, Aldridge 2005, Gregg 2006, Gregg et al. 2007, Chapter 4).

Juvenile survival was defined as the proportion of females that survive from ~35 days old to the start of the breeding season (~1 April) in their second calendar year. Estimates of survival for juveniles produced by yearling vs. adult females were unavailable, so we used the same juvenile survival estimates in calculations for both stages. Because the interval length for juvenile survival depends on when the chick hatches, we used data on average hatch dates for first and subsequent nesting attempts to calculate the approximate interval length required for first nests (9.1 mo [$JUVSURV_{91}$]) and for renests (8.3 mo [$JUVSURV_{83}$]). In the Powder River Basin, estimates of juvenile survival were for the 6.67-month interval from 10 Sept through ~1 April. Data on juvenile survival from 35 d of age through 10 Sept were unavailable. Range-wide estimates of juvenile survival were only reported for 5-7 month long intervals (Sept-Nov through March). Because most chick mortality occurs prior to 35 d (Burkepile et al. 2002, Aldridge 2005, Gregg et al. 2007), we assumed that monthly survival rates for juveniles from 35 d of age to 10 Sept were similar to those over the fall and winter.

Fertility and survival calculations. Stage-specific fertility for yearlings (f_{yr}) was calculated as:

[$INIT_{1YR}$ x $FCLUTCH_{1YR}$ x $SUCC_{1YR}$ x HATCH x $CHSURV_{YR}$ x $JUVSURV_{91}$] +

[$INIT_{1YR}$ x (1-$SUCC_{1YR}$) x $INIT_{2YR}$ x $FCLUTCH_{2YR}$ x $SUCC_{2YR}$ x HATCH x $CHSURV_{YR}$ X

$JUVSURV_{83}$].

Stage-specific fertility (f_{yr}) for yearlings in the Powder River Basin averaged 0.569. Stage-specific fertility for adults (f_{ad}) was calculated as:

[$INIT_{1AD}$ x $FCLUTCH_{1AD}$ x $SUCC_{1AD}$ x HATCH x $CHSURV_{AD}$ x $JUVSURV_{91}$] +

172

$$[INIT_{1AD} \text{ x } (1\text{-}SUCC_{1AD}) \text{ x } INIT_{2AD} \text{ x } FCLUTCH_{2AD} \text{ x } SUCC_{2AD} \text{ x } HATCH \text{ x } CHSURV_{AD} \text{ x }$$
$$JUVSURV83] +$$

$$[INIT_{1AD} \text{ x } (1\text{-}SUCC_{1AD}) \text{ x } INIT_{2AD} \text{ x } (1\text{-}SUCC_{2AD}) \text{ x } INIT_{3AD} \text{ x } FCLUTCH_{3AD} \text{ x } SUCC_{2AD} \text{ x } HATCH$$
$$\text{x } CHSURV_{AD} \text{ x } JUVSURV_{83}].$$

Stage-specific fertility (f_{ad}) for adults in the Powder River Basin averaged 0.846.

Yearling survival (s_{yr}) was defined as the proportion of yearling (i.e., "second-year") females that survived from the start of the breeding season (~ 1 April) in their second calendar year (i.e., their first breeding season) to the start of the breeding season (~ 1 April) in their third calendar year. Yearling survival in the Powder River Basin averaged 0.639.

Adult survival (s_{ad}) was defined as the proportion of adult (i.e., "after-second-year") females that survived from the start of the breeding season (~1 April) to the start of the breeding season (~ 1 April) the following year. Adult survival in the Powder River Basin averaged 0.556. In the range-wide survival data, we excluded estimates from studies that estimated annual survival rates from poncho or wing-tagged birds, as those types of marks likely increase detectability to predators and bias survival estimates. We was unable to include data from studies that analyzed yearling and adult daily or monthly survival rates but failed to report stage-specific survival estimates.

WNv impact scenarios. Each scenario required adjusting juvenile, yearling, and adult survival rates to account for to WNv-related mortality. Most chicks reach the juvenile stage (i.e., > 35 d old) prior to the onset of WNv transmission season in early July (particularly in years with high success of first nests and low renesting rates), so we made no adjustments to chick survival estimates. This results in a conservative estimate of the impact of WNv. Mortality from WNv may reduce chick survival directly, and

173

non-independent chicks and juveniles whose mothers die of WNv may also experience higher mortality. Calculations for each scenario were as follows:

(1) *No impact.* We based estimated means and variances of juvenile survival and annual yearling and adult female survival on the Powder River Basin dataset that excluded WNv-related mortalities (Chapter 4).

(2) *Observed WNv mortality.* We based estimated means and variances of juvenile survival and annual yearling and adult female survival on the Powder River Basin dataset that included WNv-related mortalities (Chapter 4). Juveniles are confirmed to have died from WNv (Naugle et al. 2004, Aldridge 2005), but we had too few juveniles collared during the WNv season in each year to estimate WNv-related mortality. Because juveniles flock together with yearlings and adults during the summer, we assumed they would all experience similar exposure to WNv. Therefore, we used observed reductions in adult and yearling spring-summer survival due to WNv (mean 5.3%, range 0.0 - 26.7%) to adjust estimates of juvenile survival for each region in each year as follows:

$$\text{JUVSURV83}_{adj} = (\text{JUVSURV83}^{(0.12)})^{(6.67)} \times ((\text{JUVSURV83}^{(0.12)})^{(1.63)} \times (1\text{-WNv mortality rate}))$$
$$\text{JUVSURV91}_{adj} = (\text{JUVSURV91}^{(0.11)})^{(6.67)} \times ((\text{JUVSURV91}^{(0.12)})^{(2.43)} \times (1\text{-WNv mortality rate}))$$

We then calculated a mean and variance for juvenile survival from adjusted estimates.

(3) *Current WNv mortality.* In all remaining scenarios, we based estimated means and variances of juvenile, yearling, and adult survival on the Powder River Basin dataset that excluded WNv-related mortalities. We then simulated impacts of WNv using empirical data on infection rates, WNv-related mortality rates, and predicted WNv transmission events from the Powder River Basin to adjust juvenile, yearling, and survival rates in response to WNv mortality. West Nile virus infection rate is

regulated by temperature (Reisen et al. 2006, Zou et al. 2006*b*), distribution and

abundance of breeding sites for mosquito vectors (Zou et al. 2006*a, b*; Doherty 2007),

and distribution and abundance of infected reservoir and amplifying hosts (Kato et al.

2008). To estimate adjustments to survival rates due to WNv, we first examined

relationships between annual WNv severity predicted from temperature data (Western

Regional Climate Center, Reno, Nevada, USA) using a degree-day model (Zou et al.

2006*b*) and actual reductions in annual survival due to WNv mortality for each of the

three regions in the Powder River Basin from 2003-2006. However, these

relationships were inconsistent (Figure 2*a, b*), suggesting that temperature is not the

only predictor of WNv severity in the Powder River Basin (Zou et al. 2006*a*, Doherty

2007). Instead, we randomly selected infection rates from a stretched beta

distribution (mean = 0.07, SD = 0.0548, minimum = 0.005, maximum = 1.0; Box 8.3

in Morris and Doak 2002) so that median infection rates matched the midpoint

(~0.058) of observed annual minimum and maximum rates (Walker et al. 2007*b*).

This SD allows most years to have low rates of WNv infection (e.g., median 0.055)

and mortality (median 0.053). The relatively low SD produces some years with

extreme values for infection rate, but data from 10,000 simulations indicate that

values generally do not exceed ~0.50. This distribution resulted in a mean simulated

annual infection rate of 0.069, a median simulated annual infection rate of 0.055

(range 0.005-0.515), and a conservative distribution of infection rates (Figure 3). The

distribution of simulated infection rates contrasts with the distribution of annual

predicted number of WNv events according to the degree-day model of Zou et al.

(2006*b*) and a modified degree-day model based on actual dates of bird mortality

(Figure 4). Mortality due to WNv (M) was calculated from infection rate (I) and resistance to WNv-induced disease (R) as: $M = I - (I * R)$, which represents the proportion of the population infected minus the proportion infected but resistant. In this scenario, we maintained resistance constant at 0.04, the mean spring seroprevalence value measured over three years of study (Walker et al. 2007*b*).

(4) *Current WNv mortality with increasing resistance to WNv disease.* We assessed how an increase in resistance to WNv-induced disease would change population growth rate by calculating changes in the proportion of resistant individuals in the population under simulated vital rates and rates of WNv infection and WNv mortality. Because not all birds that are exposed to the virus become infected, we define "resistance" as the ability to survive exposure, infection, or both, and we assume the individuals with neutralizing antibodies to WNv were at minimum, exposed to the virus. Under this definition, resistant individuals may nonetheless experience sublethal or residual effects of WNv infection. We assumed that resistance to infection and disease was heritable and that all female offspring of a resistant female inherited traits that conferred resistance (i.e., heritability of resistance = 1). Seroprevalence data indicated that, on average, only 0.04 (range 0.00-0.10) of birds captured in spring had survived WNv infection from previous years (Walker et al. 2007*b*). Therefore, we used 0.04 as our starting value for resistance. We ran each simulation with 20 replicates to simulate responses within a reasonable management timeframe of 20 years, then ran the simulation 1000 times to generate means and standard deviations for λ over the 20-year period.

(5) *Current WNv mortality with resistance and carryover effects.* We assessed how

residual effects on overwinter survival and sublethal effects on reproductive effort

might influence population growth rate by calculating changes in the proportion of

resistant individuals in the population over time and by then reducing overwinter

survival by 5%, nest initiation by 5% (adults) or 10% (yearlings), renesting rate by

10% (adults) or 20% (yearlings), and all clutch sizes by ~1 egg (~0.5 female eggs) for

surviving infected individuals. We then ran each simulation with 20 replicates (i.e.,

20 years) and ran the simulation 100 times to generate means and SDs for λs over the

20-year period.

(6) *Elevated WNv mortality (with and without resistance and carryover effects).* We

estimated changes in population growth for a scenario in which average WNv-related

mortality increases due to the expansion of CBNG development. Coal-bed natural

gas development is increasing the number and distribution of surface water ponds

within sage-grouse habitat in the Powder River Basin (Zou et al. 2006*a*), and these

ponds support breeding populations of the mosquito *Culex tarsalis* (Doherty 2007), a

common, highly competent vector of WNv (Goddard et al. 2002, Turell et al. 2005).

Zou et al. (2006*a*) estimated that CBNG development increased larval habitat for *C.

tarsalis* by ~75% over a 21,000 km^2 area between 1999-2004. Coal-bed natural gas

ponds likely increase exposure of sage-grouse to WNv in areas that otherwise would

show low infection rates (Chapter 3, Walker et al. 2007*b*). In 2003, WNv mortality in

the Spotted Horse region, an area with abundant CBNG ponds (Doherty 2007), was

much higher (~75%) than in undeveloped areas near Decker (0%) (Walker et al.

2004), even though high summer temperatures predicted high rates of WNv

transmission throughout the Powder River Basin (Zou et al. 2006*b*). Furthermore, five of six WNv-positive mortalities at that time occurred next to CBNG ponds. In 2004, a year of relatively low and later WNv mortality, two of three WNv-positive mortalities in the Decker region occurred in alfalfa fields irrigated with water from CBNG development (Table 7, Chapter 4). Although mosquito control has been recommended for CBNG ponds (Doherty 2007, Walker et al. 2007*b*), there is no guarantee that control efforts will be consistently and appropriately implemented on all public and private lands. For this reason, we simulated elevated mortality due to CBNG by increasing the mean of the beta distribution used to estimate WNv infection rates (mean = 0.10, SD = 0.0548). This resulted in an average simulated annual WNv infection rate of 0.100 (range 0.007-0.380), a median simulated annual infection rate of 0.090, and average simulated annual WNv mortality of 0.096 (range 0.007-0.365). Although other, more complex CNBG scenarios are possible, an increase in average WNv-related mortality to ~10% throughout the Powder River Basin is plausible, and possibly too conservative, considering the established mechanistic links between CBNG, mosquitos, and WNv (Zou et al. 2006*a*, Doherty 2007, Walker et al. 2007*b*), the proximity of previous WNv-positive mortalities to CBNG water, the rapid spread and large scale of development (Walker et al. 2007*b*), and documented population declines in areas with CBNG development (Walker et al. 2004, 2007*a*).

Results

Vital rates and their importance in population growth. Vital rate means and

process variance from the Powder River Basin were similar to range-wide values, with a

few exceptions (Appendix B). Results of life-stage simulation analysis suggested that

different vital rates were important for λ than those based on analytical elasticity values

(Figure 5). Mean elasticity values suggested that rates of nest initiation, clutch size, and

hatchability had an equally important influence on λ as nest success, and chick, juvenile,

yearling, and adult survival. However, because nest initiation, clutch size, and

hatchability showed little variation in the Powder River Basin, life-stage simulation

analysis identified other vital rates with greater potential to influence λ (Figure 6). Vital

rates most important for population growth identified using life-stage simulation analysis

included nest success, chick survival, juvenile survival, yearling survival, and adult

survival, in that order (Figures 5, 6). Because vital rates require different management

strategies, we also grouped vital rates subject to similar management actions (Figure 5).

life-stage simulation analysis results for the Powder River Basin were similar to those

from range-wide data (Figure 6).

WNv impact scenarios. The addition of WNv mortality resulted in a reduction in

average estimated λ of -0.059 to -0.076 under scenarios with current mortality rates when

vital rates were correlated and from -0.075 to -0.103 when vital rates were uncorrelated

(Table 1). For the most part, excluding correlations among vital rates had only minor

effects on estimates of how WNv influences λ (Table 1) and did not change our overall

finding of substantially lower values for λ due to WNv mortality. Reductions in λ under

scenarios with observed WNv mortality versus simulated WNv mortality were the same

(-0.73), suggesting that the distribution we selected for simulating infection rates was representative of actual WNv mortality. Elevated levels of WNv mortality, as expected, resulted in substantially larger decreases in estimated λ, ranging from -0.085 to -0.119 for scenarios with correlated vital rates, and -0.97 to -0.115 to scenarios with uncorrelated vital rates. However, substantial annual variation in vital rates resulted in wide variation in simulated values for λ in all scenarios (Figure 7). Thus, population growth rates can vary substantially from year to year.

Resistance to WNv disease was projected to increase only slightly during the 20-year period we examined. Low WNv infection rates, and consequently, low WNv mortality in most years, resulted in too few individuals exposed to the virus to quickly select for increased resistance. Resistance was projected to increase from 0.04 (our starting value) to 0.151 (range 0.082 - 0.374) over 20 years under current estimates of infection rate (Figure 8 *a*, *b*) and to 0.245 (range 0.125 - 0.514) under scenarios with elevated mortality. Increased resistance reduced annual WNv mortality rates from an average of 0.067 to 0.060 after 20 years (Figure 9) under current infection rates and from 0.097 to 0.075 under elevated infection rates. Increased resistance also reduced average declines in λ due to WNv (Table 1).

Carryover effects on fall-winter survival and subsequent reproductive effort slightly eroded gains in resistance to WNv disease (Figure 8 *a* ,*b*) because infected individuals survived at lower rates and produced fewer offspring. Resistance estimates at year 20 in the presence of carryover effects was 0.126 (range 0.074 - 0.253) under current infection rates and 0.198 (range 0.104 - 0.391) under elevated infection rates. However, on average, carryover effects influenced < 1% of all individuals in the population in any

given year over the 20-year period we examined (Figure 10). Carryover effects were

projected to have only minor impacts on λ, and resulted in only slightly greater declines

in λ (-0.01 to -0.02) than resistance-only scenarios (Table 1).

Discussion

West Nile virus was a persistent new source of mortality in greater sage-grouse in

the Powder River Basin that has the potential to reduce annual population growth and

cause severe local population declines during outbreaks. Mortality from WNv resulted in

a reduction in λ, regardless of whether impacts were based on observed or simulated

WNv mortality rates. However, in any given year, declines in λ caused by WNv can be

masked by naturally large annual variation in vital rates. For that reason, changes in lek

counts are likely to detect only severe population reductions due to WNv (Walker et al.

2004), and monitoring impacts of low to moderate levels of WNv mortality on

populations will require tracking and testing of radio-marked individuals during the

transmission season (Walker et al. 2004). Without monitoring radio-marked individuals,

impacts of WNv mortality, and even severe outbreaks, may go undetected and lead to the

misperception among managers and policy-makers that WNv is no longer an issue for

greater sage-grouse in the Powder River Basin. Moreover, in the absence of radio-

marked birds, population declines due to severe or persistent WNv mortality may be

incorrectly attributed to other potential stressors (e.g., weather, range management) and

lead to inappropriate policy and management decisions.

In our study, mortalities from WNv were an order of magnitude more common

than power line collisions, vehicle collisions, or harvest (Chapter 4). However,

occasional severe local outbreaks of WNv throughout the species' range appear to have impacts of a magnitude similar to organophosphate pesticide poisoning (Blus et al. 1989) and intensive, active energy development (Holloran 2005, Walker et al. 2007*a*). Whether populations heavily impacted by WNv (e.g., Spotted Horse, Wyoming) (Walker et al. 2004) can recover to previous levels will not be known for several years.

Resistance to WNv disease in simulations increased relatively slowly over time, in part because annual infection rates were low in most areas in most years. Estimating change in resistance to disease over time is complicated by several factors, including the potential for competition among viral strains (Davis et al. 2005) and rapid selection for changes in virulence (Davis et al. 2004). Paradoxically, the phenomenon that would promote increased resistance – high rates of WNv infection – can also lead to large reductions in local population size, which in some cases, may be problematic for population persistence. A parallel is found in insects in agricultural systems, in which only massive mortality events (e.g., pesticide spraying) that select for resistant individuals are capable of promoting the rapid spread of pesticide resistance. Even so, low rates of WNv transmission and infection in undeveloped sage-grouse habitats have almost certainly prevented more severe outbreaks and local extirpations. Naturally high variation in population growth rates in this species may allow populations to rebound quickly from impacts of WNv if consecutive years have high survival, high productivity, or both as seen in portions of the Powder River Basin from 2003-2006. The impact of WNv during a string of low-survival or low-productivity years may be severe.

Carryover effects are unlikely to substantially influence population growth except under conditions of high infection rates or high levels of resistance. Because carryover

effects were simulated based on best guess estimates rather than empirical data, they may or may not represent realistic values. Even so, it appears that so few infected individuals typically survive infection, such that resistant infected birds constitute only a small fraction of the fall or spring population in any given year. Carryover effects of WNv infection may be more important in areas with high infection rates (i.e., high exposure) caused by differences in land use (e.g., irrigated agriculture, CBNG development; Zou et al. 2006 *a*, Doherty 2007, Walker 2007*b*) or they may become more important several decades from now if resistance to WNv increases within and among sage-grouse populations.

Our model for the Powder River Basin may over- or underestimate impacts of WNv on populations in the Powder River Basin. Sage-grouse mortalities from WNv have occurred as early as 14 June in the Powder River Basin, which overlaps with chick survival from renests (Chapter 4). If mortality due to WNv commonly occurs among late-hatched chicks <35 d of age, among brooding females, or both, the scenarios presented may have substantially underestimated WNv impacts. Positive or negative density-dependent effects not included in our model could also influence impacts of WNv on population growth. In sage-grouse, the potential for negative density-dependent effects on population growth has been recognized (Connelly et al. 2003, LaMontagne et al. 2002, Sedinger and Rotella 2005), but no empirical evidence exists to evaluate whether the phenomenon occurs. Negative density-dependence may allow populations to recover more quickly from annual effects of WNv mortality. Positive density-dependence may also be an issue. For example, survival and population growth may be inhibited if severe WNv outbreaks greatly reduce local abundance, or if population size is

already reduced by other stressors (e.g., habitat loss and fragmentation, fire, weeds; Connelly et al. 2004). Positive density-dependent effects may occur if smaller flock sizes result in reduced overwinter survival (Courchamp et al. 1999, Stephens and Sutherland 1999), or if reduced lek size due to WNv mortality is associated with reduced female attendance (Kokko 1997), increased emigration, or delayed or reduced reproductive effort. Considering both forms density-dependence may be valuable in viability analyses for specific populations of known population size and carrying capacity. Impacts of WNv will likely be less severe for sage-grouse populations that summer at higher elevations than those in the Powder River Basin (e.g., southwestern Montana, extreme northwestern Colorado, western Wyoming, etc.). Lower temperatures at high elevations shorten periods of mosquito activity, increase larval development times, and reduce rates of virus amplification (i.e., longer extrinsic incubation periods) (Reisen et al. 2006).

Managing WNv impacts. Potential management strategies to reduce impacts of WNv in the Powder River Basin and elsewhere are limited. First, we know too little about which hosts initiate and maintain WNv transmission cycles (Kato et al. 2008). Even when key hosts have been identified (e.g., American robin [*Turdus migratorius*]; Kilpatrick et al. 2006), they typically cannot be managed at appropriates scales within sage-grouse habitat. Thus, most management for WNv involves attempts to reduce mosquito populations. Man-made water sources known to support breeding *Culex tarsalis* in sage-grouse habitat include overflowing stock tanks, stock ponds (especially seep and overflow areas and muddy shorelines with hoof prints), irrigated agricultural fields, and ponds constructed for CBNG development (Zou et al. 2006*a*, Doherty 2007). New water sources can be constructed in ways that discourage breeding mosquitos (e.g.,

steep-sided bare edges, restricted livestock access points, overbuilding ponds to prevent backup of water into standing vegetation, fluctuating water levels, overflow prevention) (Doherty 2007). Mosquito populations may also be managed using biological controls such as mosquitofish [*Gambusia* sp.] or native fish species, using biological or chemical larvicides, or by spraying for adults, but only if such methods are consistently and appropriately implemented by qualified mosquito control personnel (Doherty 2007). Mosquito control programs appear effective for reducing WNv risk in other habitats (Gubler et al. 2000, Reisen and Brault 2007) but the costs and benefits of control need to be weighed against potential detrimental effects of widespread spraying (Marra et al. 2004). Requiring infectious disease impact statements as part of planned, large-scale changes in land use (e.g., energy development, grazing plans) (McSweegan 1996) may also improve coordinated management of WNv risk in sage-grouse summer habitat.

Analytical elasticity and life-stage simulation analysis suggest that several different vital rates could respond to improved range and land management to offset impacts of WNv on λ. Increasing forb abundance during the pre-laying period is anticipated to increase female nutritional condition and renesting rate (Dunbar et al. 2005, Gregg et al. 2006). Similarly, increasing grass and sagebrush height is likely to improve nest success. Greater sage-grouse females clearly prefer nests sites with taller sagebrush and grass (Hagen et al. 2007), and taller grass height around nests has been documented to increase nest success in several different parts of the species' range (Holloran and Anderson 2005, Rebholz 2007). Chick survival may be increased by increasing forb and grass cover (Dahlgren et al. 2006, Hagen et al. 2007). Although broods use areas with less sagebrush than is available, decreasing sagebrush height or cover via spraying,

185

burning, or mowing would likely decrease nest success and overwinter survival (Swenson et al. 1987, Leonard et al. 2000, Smith et al. 2005) and is not recommended. Increasing the size and extent of undeveloped sagebrush landscapes and the amount of tall sagebrush cover would likely simultaneously increase juvenile, yearling, and adult survival. Although no studies have clearly linked female survival to landscape-scale habitat conditions, wintering birds prefer areas with large expanses of sagebrush cover and areas away from energy development (Homer et al. 1993, Doherty et al. 2008) and breeding populations are more likely to persist in areas with higher proportions of sagebrush habitat within 6.4 km of leks (Walker et al. 2007*a*). Selection for wintering areas with greater exposed sagebrush cover and taller sagebrush (Connelly et al. 2000) also suggests a benefit of increasing mature sagebrush cover, particularly during severe winters (Moynahan et al. 2006). Removing roads and power lines in sage-grouse habitat would decrease mortality from power line collisions, vehicle collisions, and avian predators that nest and hunt from power lines (Knight and Kawashima 1993, Steenhof et al. 1993).

The emergence of WNv as a new stressor on greater sage-grouse populations highlights the current impasse in sage-grouse management and conservation. Historic stressors such as fires and invasive weeds continue to cause habitat loss and fragmentation, and new stressors such as West Nile virus and rapidly increasing energy development are known to cause population declines, yet potential solutions for offsetting those losses conflict with livestock grazing and energy production, two of the most culturally and economically important land uses within sage-grouse habitat.

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Table 1. Estimated average reduction in annual population growth (i.e., finite rate of increase, λ) under various West Nile virus (WNv) impact scenarios relative to no WNv mortality based on life-stage simulation analysis using vital rates for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, 2003-2006. Results are based on 1000 life-stage simulation analysis simulation replicates. Reductions in λ due to WNv mortality may be masked in any given year by annual fluctuations in vital rates influential for population growth (e.g., nest success, chick survival, juvenile survival, survival of breeding-aged females).

Scenario	Correlated $\Delta\lambda$	Uncorrelated $\Delta\lambda$
No WNv	0.000	0.000
Observed WNv	-0.073	-0.103
Current WNv	-0.073	-0.075
Current WNv - resistance	-0.059	-0.084
Current WNv - resistance and carryover effects	-0.076	-0.088
Elevated WNv	-0.119	-0.115
Elevated WNv - resistance	-0.085	-0.097
Elevated WNv - resistance and carryover effects	-0.097	-0.110

Figure 1. Life-cycle and stage-based projection matrix for a 2-stage, pre-breeding, birth-pulse model for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA. Stage 1 consists of yearlings (YR) and stage 2 consists of older adults (AD).

Figure 2. Relationships between predicted no. days with West Nile virus transmission events based on a degree-day model (Zou et al. 2006*b*) and absolute decreases in (a) spring-summer survival and (b) annual survival due to WNv-related mortality in three regions of the Powder River Basin, Montana and Wyoming, USA, 2003-2006.

Figure 3. An example of the distribution of simulated WNv infection rates for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA. Infection rates were simulated using a stretched beta distribution with mean = 0.07, SD = 0.055, min = 0.005, and max = 1.0. Median infection rate from this distribution = 0.055.

Figure 4. An example of the predicted distribution of the annual number of WNv transmission days based on temperature data from Sheridan Field Station, WY (station no. 488160) with (a) degree-day criteria based on a 14.3º temperature threshold for virus amplification within *Culex tarsalis* and 109 degree-day extrinsic incubation period for median virus transmission (Reisen et al. 2006, Zou et al. 2006*b*) and (b) degree-day criteria modified to match observed WNv mortalities in sage-grouse near Decker, MT.

Figure 5. Variance in population growth (i.e., finite rate of increase, λ) based on (a) mean elasticity values, (b) coefficients of determination in life-stage simulation analysis for each vital rate, and (c) for vital rates affected by different management strategies. All analyses are based on vital rates from the Powder River Basin, Montana and Wyoming, USA, 2003-2006. Simulated data included correlations between vital rates. Values in (a) are mean elasticity values standardized to 1. Values in (b) and (c) are coefficients of determination (r^2) standardized to 1. YR = yearling, AD = adult. Vital rates with a "1" refer to first nests, "2" refers to renests. See text for vital rate definitions.

Figure 6. Annual population growth (i.e., finite rate of increase, λ) regressed on (a, b) yearling nest success (first nests), (c, d) adult nest success (first nests), (e, f) survival of chicks from yearling females, (g, h) survival of chicks from adult females, (i, j) survival of juveniles from first nests, (k, l) survival of juveniles from second nests, (m, n) annual yearling survival, and (o, p) annual adult survival for female greater sage-grouse in the Powder River Basin, Montana and Wyoming, USA from 2003-2006 and for range-wide values. Relationships are based on 1000 replicates from life-stage simulation analysis. The left panel illustrates relationships based on Powder River Basin data; the right panel illustrates relationships based on range-wide data. All simulations included correlations between vital rates. Range-wide values in (f) and (h) are based on the same mean and variance.

Figure 7. Distribution of simulated annual population growth rates (i.e., finite rate of increase, λ) for female greater sage-grouse based on life-stage simulation analysis using

data on vital rates from the Powder River Basin, Montana and Wyoming, USA, 2003-

2006, assuming no WNv impacts. Values are based on 1,000 simulation replicates.

Figure 8. Projected change in resistance to WNv disease of greater sage-grouse females

(at the start of the breeding season) over a 20-year period based on simulated vital rates

from the Powder River Basin, 2003-2006 using life-stage simulation analysis. Error bars

represent 1 SD. All estimates are based on 1000 simulation replicates with an initial

value for resistance of 0.04 at year 1 (i.e., 4% of the initial population resistant to WNv

disease). Scenarios presented are for: (a) current WNv mortality with (black squares) and

without (hollow squares) carryover effects and (b) elevated WNv mortality with (black

squares) and without (hollow squares) carryover effects. Values are offset for clarity.

Figure 9. Distribution of WNv-related mortality among female greater sage-grouse (a) in

the 1st year of the simulation and (b) in the 20th year of the simulation with increasing

resistance over time based on simulated infection rates from the Powder River Basin,

2003-2006, assuming no carryover effects of WNv infection. Values are based on 1,000

simulation replicates.

Figure 10. Projected change in the proportion of WNv-infected resistant sage-grouse in

the spring population (i.e., at the start of the breeding season) over a 20-year period based

on simulated vital rates from the Powder River Basin, 2003-2006 using life-stage

simulation analysis. Error bars represent 1 SD. Estimates are based on 1000 simulation

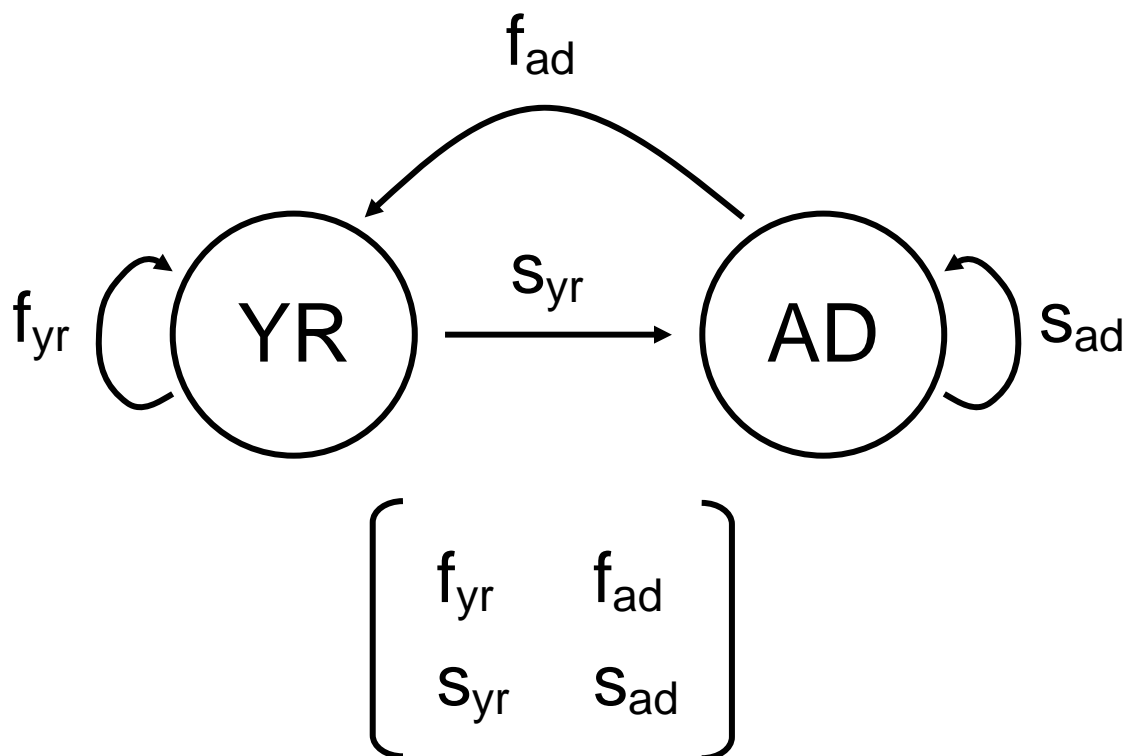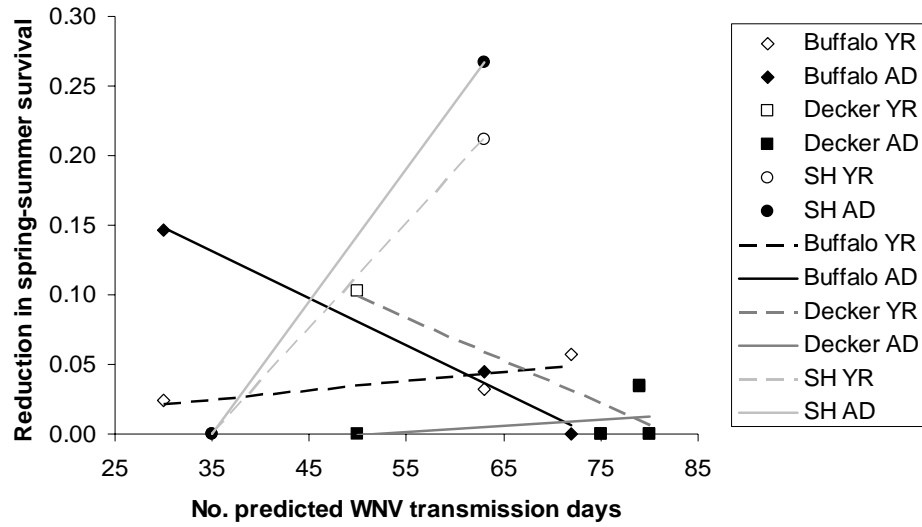replicates with an initial value for resistance of 0.04 at year 1.

Figure 1.

$$\begin{bmatrix} f_{yr} & f_{ad} \\ s_{yr} & s_{ad} \end{bmatrix}$$

Figure 2.

a.

b

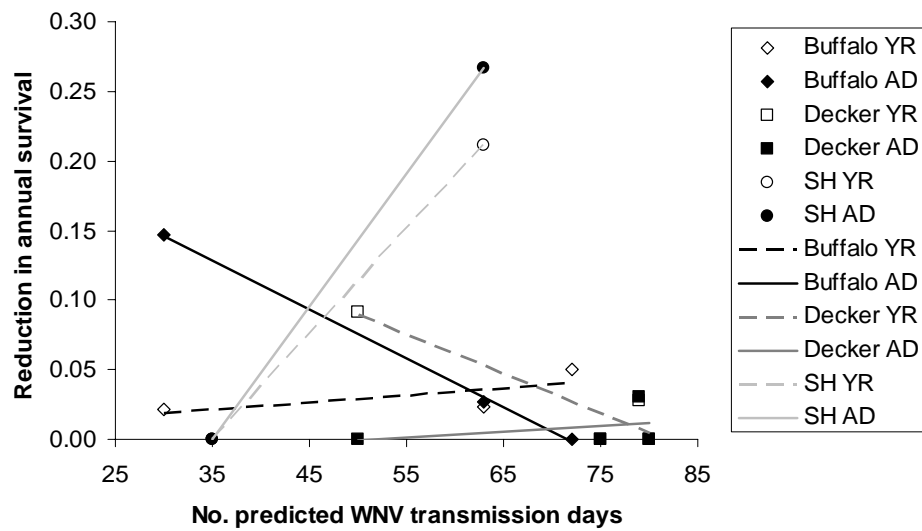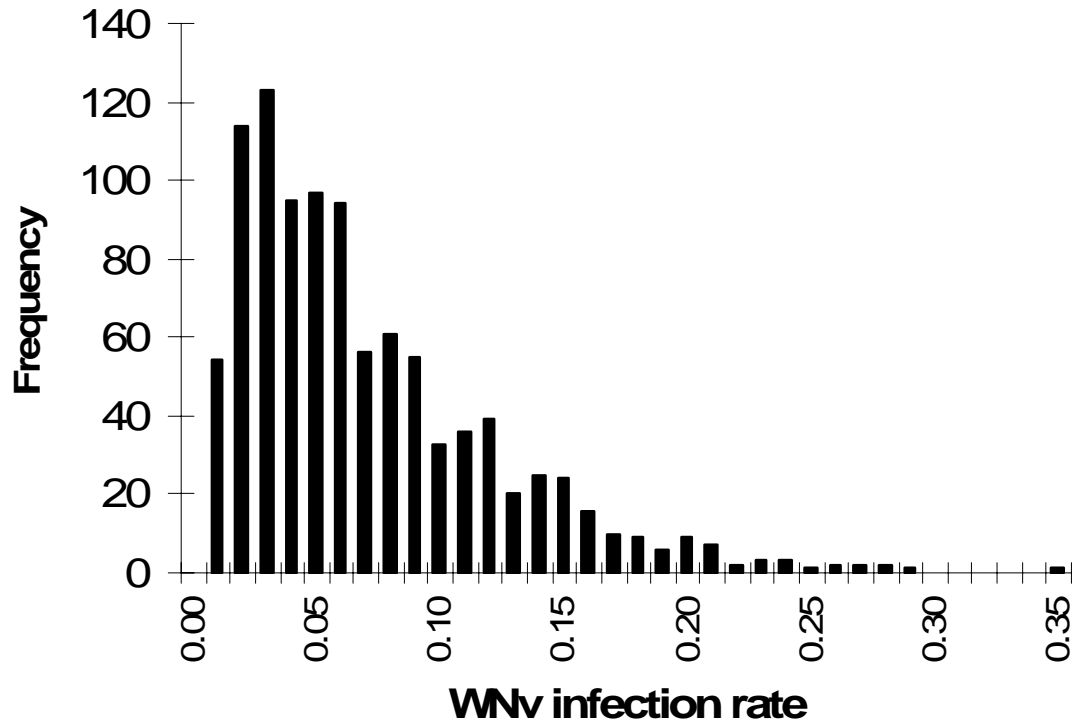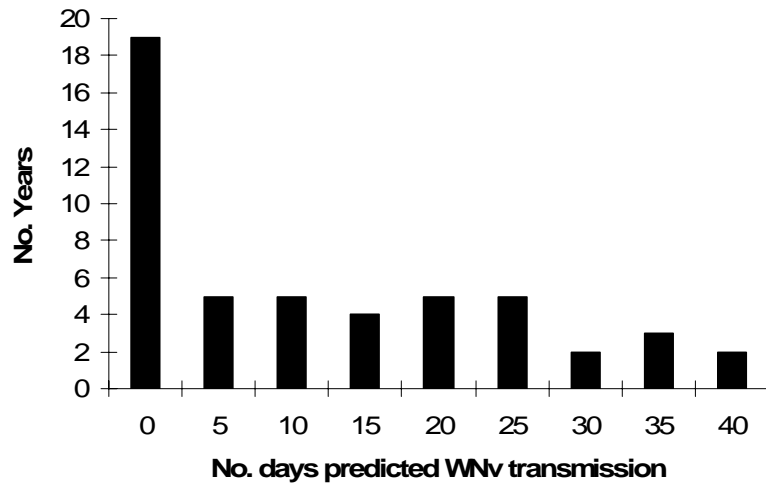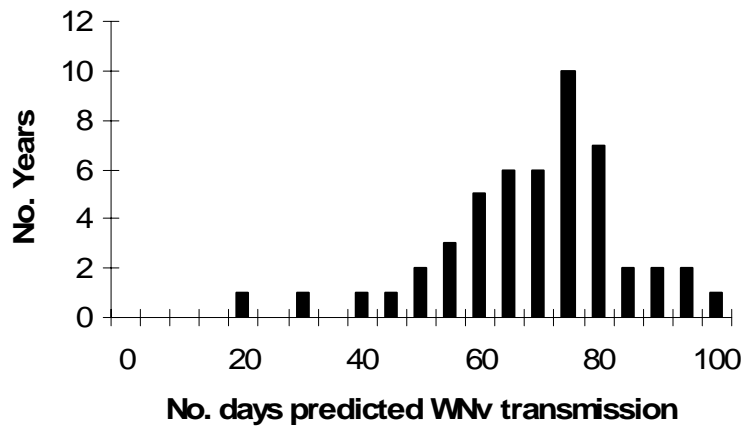Figure 3.

Figure 4.

a.

b

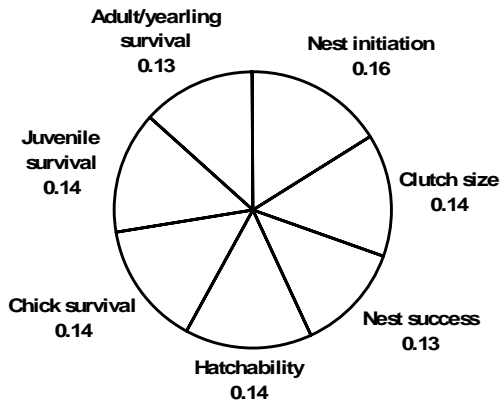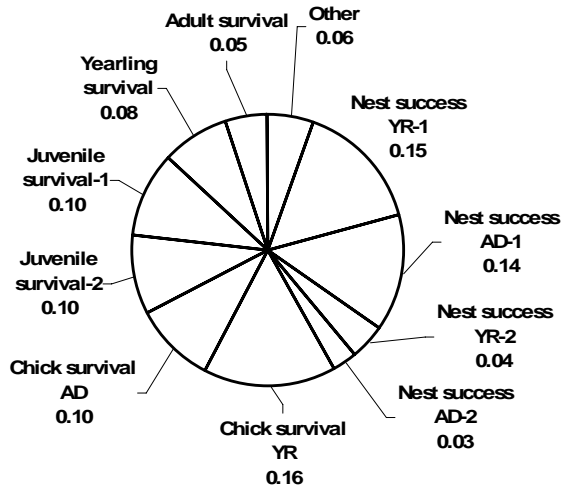Figure 5.

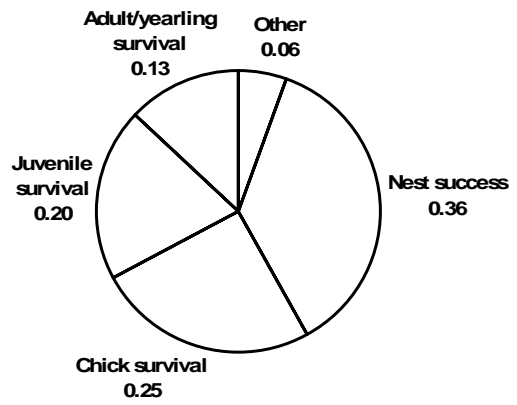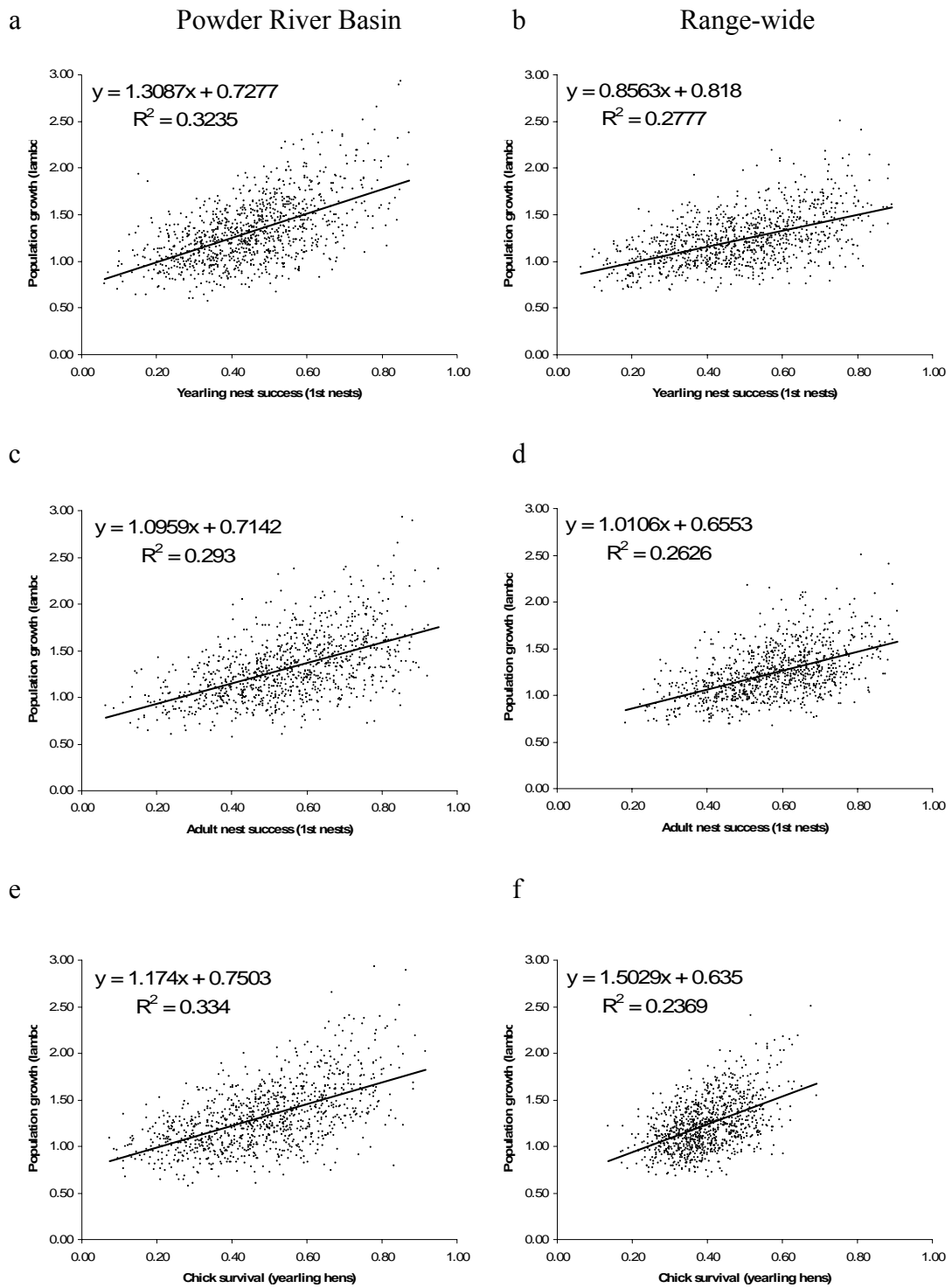a   Mean elasticity

b r^2 c r^2

Figure 6.

a   Powder River Basin   b   Range-wide
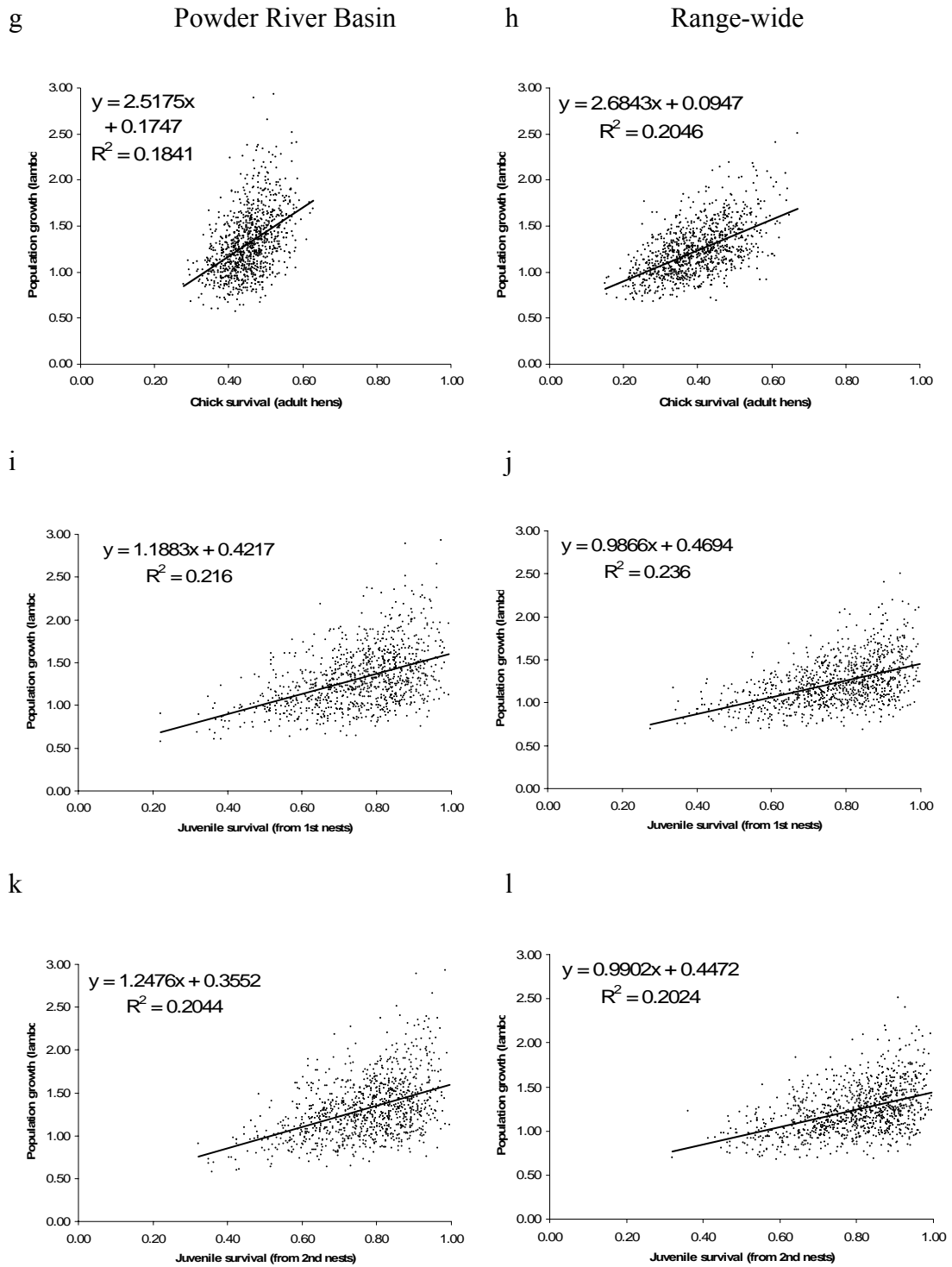

205

Figure 6 (cont.).
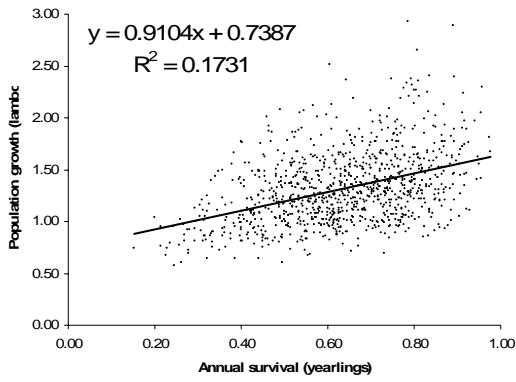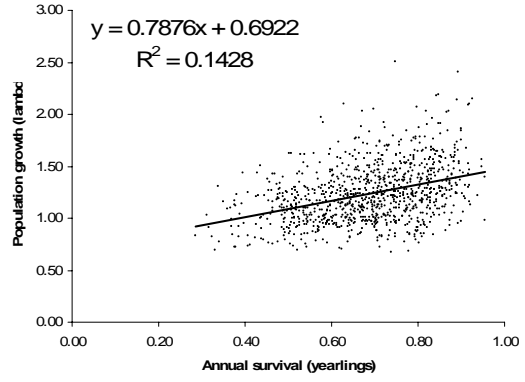
g   Powder River Basin   h   Range-wide

Figure 6 (cont.).

m   Powder River Basin   n   Range-wide
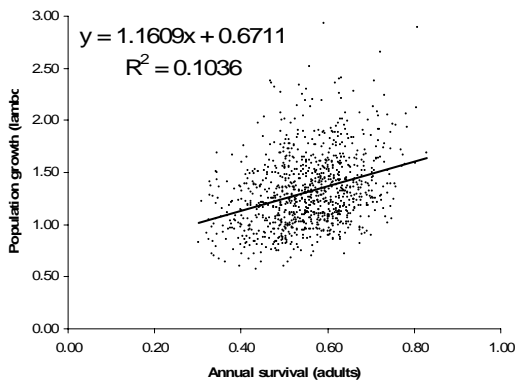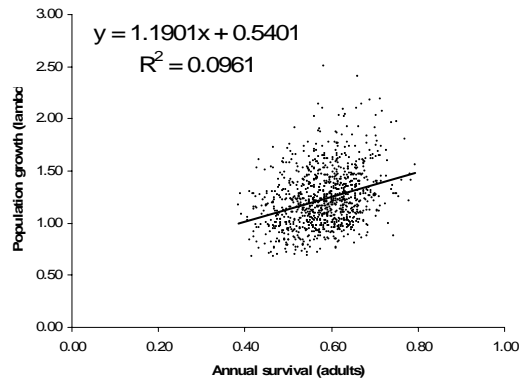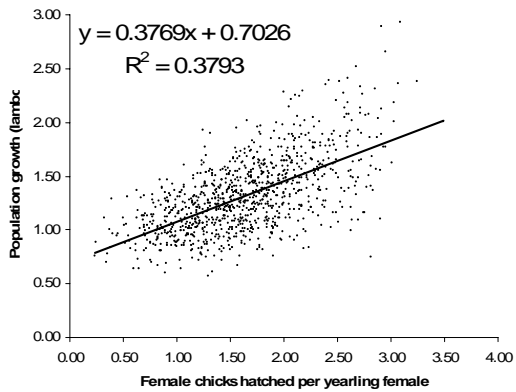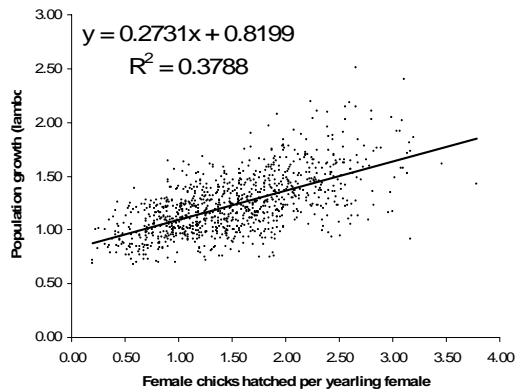
Figure 6 (cont.).
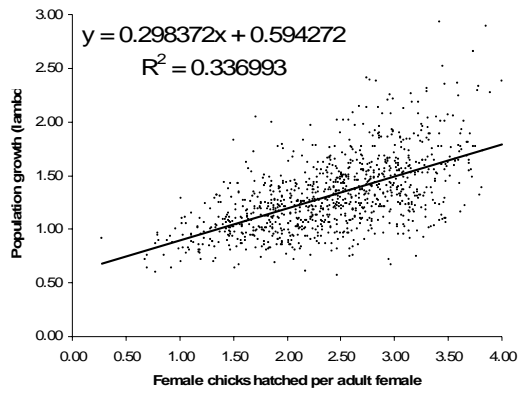
s   Powder River Basin   t   Range-wide
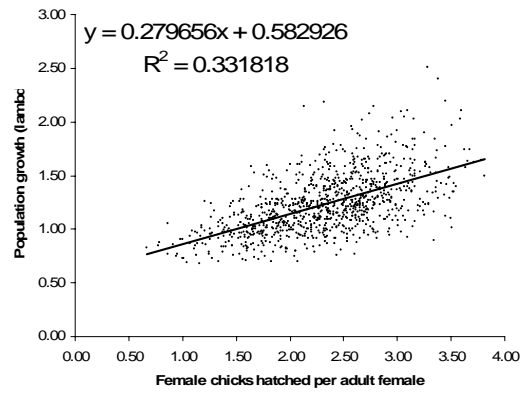
Figure 7.
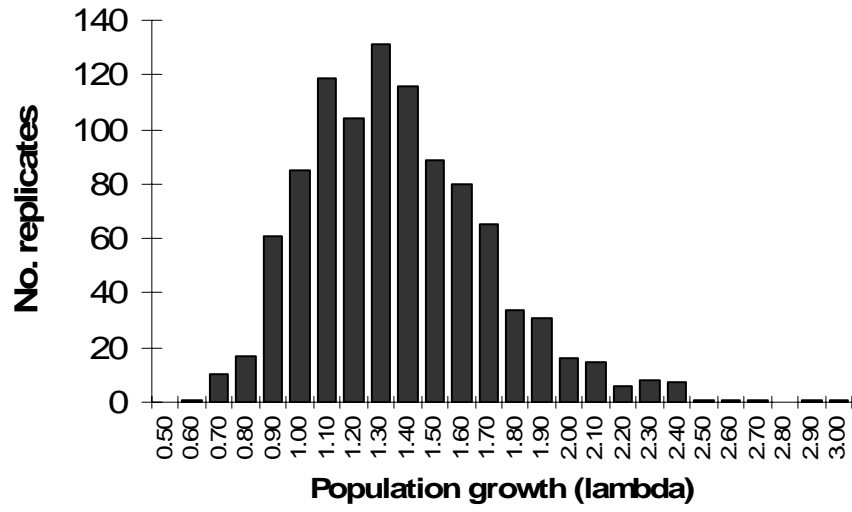
Figure 8.

a   Current WNv infection rates

b   Elevated WNv infection rates

Figure 9.

a   Year 1

b   Year 1

c   Year 20

d   Year 20

Figure 10.
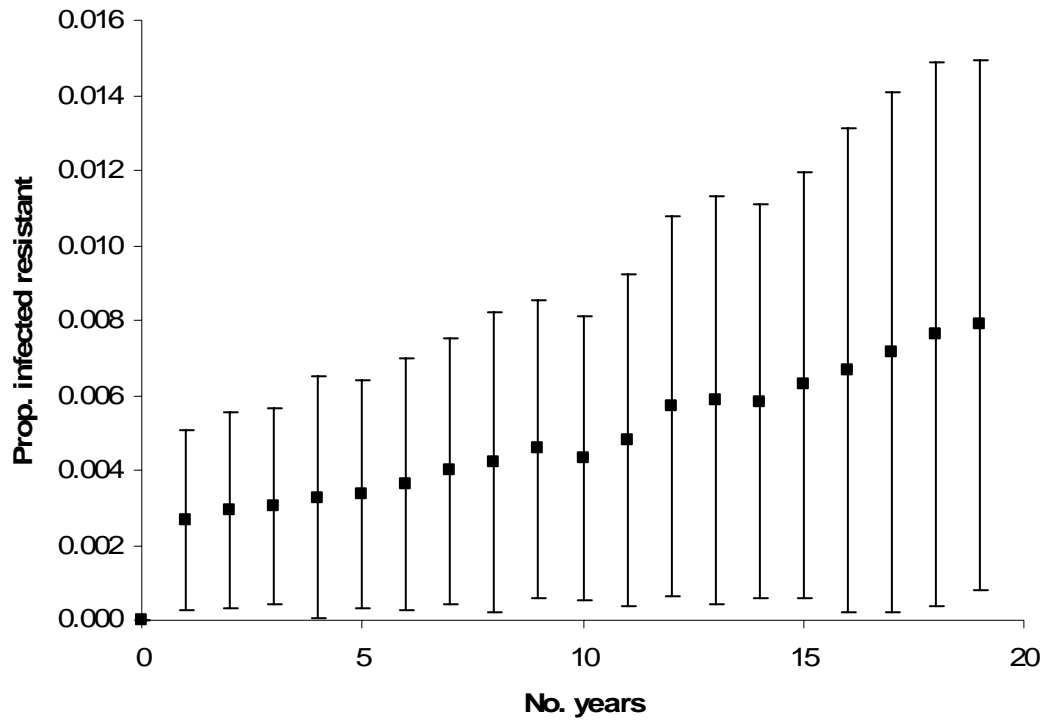
Appendix A. Correlation structure

Incorporating correlation structure is important for generating realistic combinations of vital rates for simulations that are representative of typical values for the population of interest (Mills and Lindberg 1999, Wisdom et al. 2000, Morris and Doak 2002). We assigned pairs of vital rates a correlation coefficient of none (0.00), low (0.25), moderate (0.50), or high (0.75) based on whether published data indicated that both vital rates were regulated by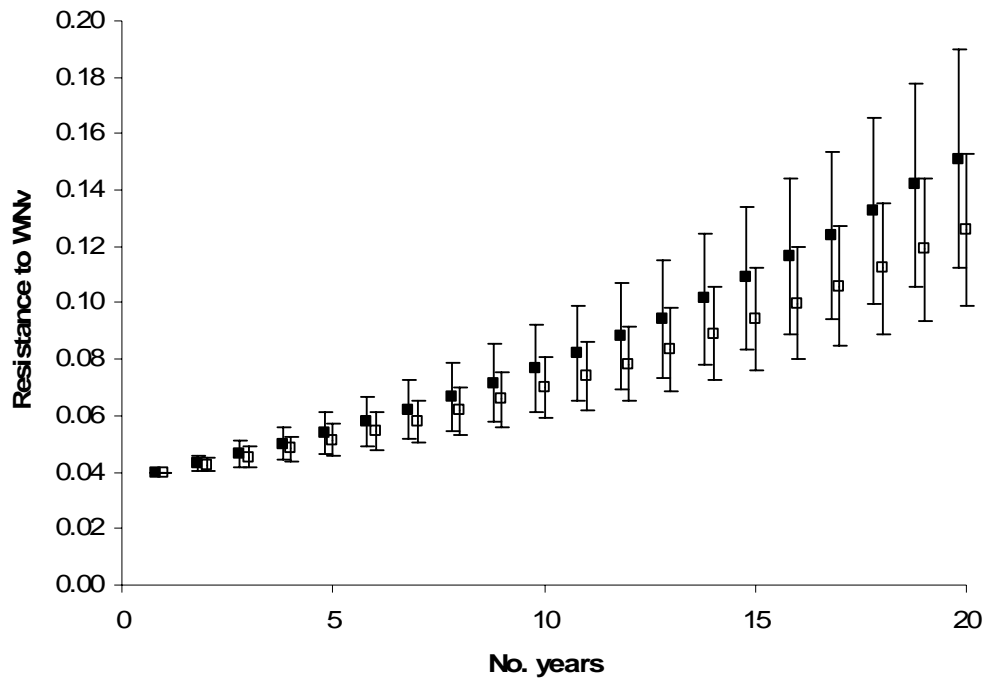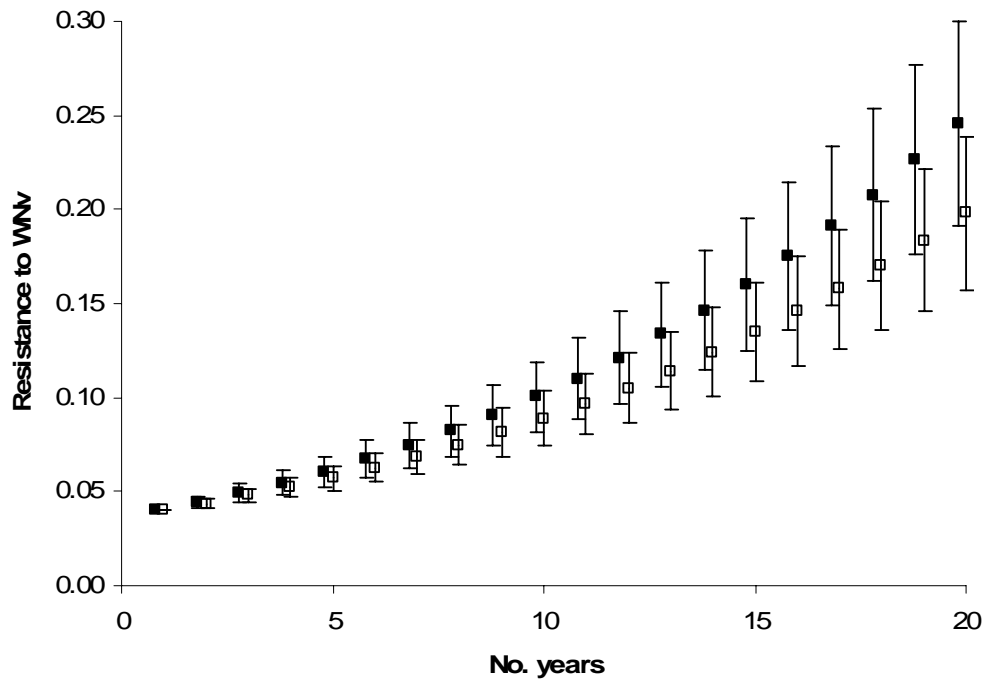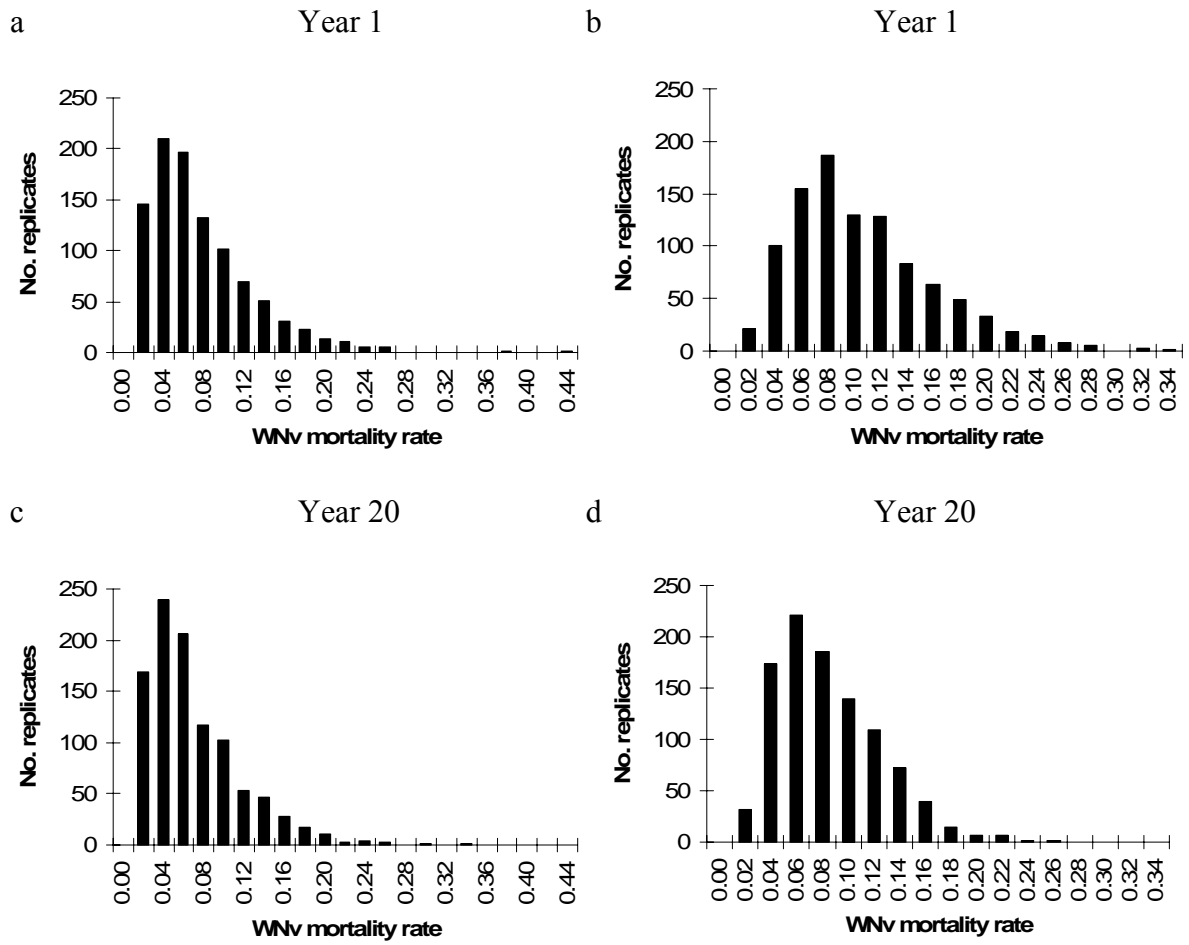 the same biological mechanism(s). We also examined correlation coefficients between vital rates in the Powder River Basin and range-wide vital-rate data to check for evidence for or against hypothesized correlations. Below are the biological justifications for each correlation.

Reproductive effort should be influenced by female nutritional condition during the pre-laying period. Yearling and adults occur in mixed flocks during the winter and early spring, so nutritional condition should be similar between stages, and initiation rates of yearlings and adults should be moderately correlated. Females may also adjust their reproductive effort if environmental cues such as residual grass height, winter and spring precipitation, or early spring forb abundance are reliable indicators of nest success or chick survival. Years in which reproductive effort is high suggests that rates of nest initiation and renesting should be at least weakly positively correlated as well. Renesting rates of yearlings and adults were moderately, positively correlated both in the Powder River Basin and range-wide. Clutch size is also a form of reproductive effort, and should show moderate, positive correlations among stages. The correlation should be weakly positive across nesting attempts because clutch sizes of renests vary more than those of

first nests. We also estimated weak positive correlations between clutch size and nest initiation and renesting rates within each stage and nesting attempt (i.e., renesting rates of yearlings weakly positively correlated with renest clutch sizes of yearlings).

Both yearling and adult nest success are strongly influenced by predator abundance (Schroeder et al. 1999), and yearlings and adults use the same habitats for nesting and initiate both first nests and renests at about the same time (Chapter 4). Yearling and adult nest success were moderately correlated ($r = 0.654$) both in the range-wide data and in the Powder River Basin data (0.704), so these were estimated to have at least a moderate correlation (0.50). The same logic applies to success of renesting attempts. We estimated a weak positive correlation between first nest success and chick survival because both may benefit from increased understory growth and cover (Hagen et al. 2007). In the Powder River Basin, years with higher nest success tracked years with higher brood success (Chapter 4).

Survival of chicks is regulated by availability of forbs and insects and understory cover, so chick survival of yearling and adult chicks should show at least a moderate positive correlation. Survival of juveniles from first nests and renests is, in essence, the same vital rate, so we assigned it a correlation of 0.9. Juvenile survival, yearling survival, and adult survival are all influenced by the same environmental conditions (e.g., snowstorms), parasite communities, and predator communities and should show at least a weak positive correlation. No negative correlations were identified that had a clear biological basis.

The estimated correlation matrix among variables used in all analyses along with variable definitions are shown below.

214

	I_{Y1}	I_{A1}	I_{Y2}	I_{A2}	I_{A3}	C_{Y1}	C_{Y2}	C_{A1}	C_{A2}	C_{A3}	N_{Y1}	N_{A1}	N_{Y2}	N_{A2}	H	S_{CY}	S_{CA}	S_{J83}	S_{J91}	S_Y	S_A
I_{Y1}	1	0.50	0.25	0.25	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I_{A1}	0.50	1	0.25	0.25	0	0	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0
I_{Y2}	0.25	0.25	1	0.50	0.25	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I_{A2}	0.25	0.25	0.50	1	0.50	0	0	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0
I_{A3}	0	0	0.25	0.50	1	0	0	0	0	0.25	0	0	0	0	0	0	0	0	0	0	0
C_{Y1}	0.25	0	0	0	0	1	0.25	0.50	0	0	0	0	0	0	0	0	0	0	0	0	0
C_{Y2}	0	0	0.25	0	0	0.25	1	0.25	0.25	0	0	0	0	0	0	0	0	0	0	0	0
C_{A1}	0	0.25	0	0	0	0.50	0.25	1	0.25	0	0	0	0	0	0	0	0	0	0	0	0
C_{A2}	0	0	0	0.25	0	0	0.25	0.25	1	0	0	0	0	0	0	0	0	0	0	0	0
C_{A3}	0	0	0	0	0.25	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
N_{Y1}	0	0	0	0	0	0	0	0	0	0	1	0.50	0.25	0.25	0	0.25	0.25	0	0	0	0
N_{A1}	0	0	0	0	0	0	0	0	0	0	0.50	1	0.25	0.25	0	0.25	0.25	0	0	0	0
N_{Y2}	0	0	0	0	0	0	0	0	0	0	0.25	0.25	1	0.50	0	0	0	0	0	0	0
N_{A2}	0	0	0	0	0	0	0	0	0	0	0.25	0.25	0.50	1	0	0	0	0	0	0	0

	I_{Y1}	I_{A1}	I_{Y2}	I_{A2}	I_{A3}	C_{Y1}	C_{Y2}	C_{A1}	C_{A2}	C_{A3}	N_{Y1}	N_{A1}	N_{Y2}	N_{A2}	H	S_{CY}	S_{CA}	S_{J83}	S_{J91}	S_Y	S_A
H	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
S_{CY}	0	0	0	0	0	0	0	0	0	0	0.25	0.25	0	0	0	1	0.50	0	0	0	0
S_{CA}	0	0	0	0	0	0	0	0	0	0	0.25	0.25	0	0	0	0.50	1	0	0	0	0
S_{J83}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.9	0.25	0.25
S_{J91}	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9	1	0.25	0.25
S_Y	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.25	0.25	1	0.25
S_A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.25	0.25	0.25	1

[a] Variables include. I_{Y1} = nest initiation rate of yearlings; I_{A1} = nest initiation rate of adults; I_{Y2} = renesting rate of yearlings; I_{A2} = renesting rate of adults; I_{A3} = second renesting rate of adults; C_{Y1} = clutch size (female eggs) of yearling first nests; C_{Y2} = clutch size (female eggs) of yearling renests; C_{A1} = clutch size (female eggs) of adult first nests; C_{A2} = clutch size (female eggs) of adult renests; C_{A3} = clutch size (female eggs) of adult second renests; N_{Y1} = nest success of yearling first nests; N_{A1} = nest success of adult first nests; N_{Y2} = nest success of yearling renests; N_{A2} = nest success of adult renests (and second nests); H = hatching success; S_{CY} = survival of chicks from yearling females from hatch to 35 d; S_{CA} = survival of chicks from adult females from hatch to 35 d; S_{J83} = survival of juveniles from 35 d of age to 10 September for renests; S_{J91} = survival of juveniles from 35 d of age to 10 September for first nests; S_Y = annual survival of yearlings; S_A = annual survival of adults.

Appendix B. Vital rate summary

Vital Rate[a]	Powder River Basin		Range-wide	
	Mean	Variance[b]	Mean	Variance[b]
$INIT_{YR1}$	0.982	0.0003	0.829	0.0166
$INIT_{AD1}$	0.990	0.0001	0.930	0.0038
$INIT_{YR2}$	0.151	0.0284	0.148	0.0368
$INIT_{AD2}$	0.460	0.0681	0.395	0.0599
$INIT_{AD3}$	0.042	0.0021	0.074	0.0051
$FCLUTCH_{YR1}$	3.74	0.0880	3.81	0.118
$FCLUTCH_{YR2}$	2.98	0.1460	3.29	0.316
$FCLUTCH_{AD1}$	4.10	0.0860	4.16	0.040
$FCLUTCH_{AD2}$	3.19	0.1930	3.52	0.200
$FCLUTCH_{AD3}$	2.69	0.1500	3.02	0.200[c]
$SUCC_{YR1}$	0.453	0.0226	0.481	0.0268
$SUCC_{AD1}$	0.555	0.0284	0.569	0.0183
$SUCC_{YR2}$	0.521	0.1739	0.540	0.1309
$SUCC_{AD2}$	0.618	0.0958	0.553	0.0623
HATCH	0.923	0.0005	0.921	0.0018
$CHSURV_{YR}$	0.488	0.0274	0.391[d]	0.0084[d]
$CHSURV_{AD}$	0.456	0.0033	0.391[d]	0.0084[d]
$JUVSURV_{83}$	0.776	0.0154[e]	0.799	0.0154
$JUVSURV_{91}$	0.757	0.0177[e]	0.782	0.0177
$SURV_{YR}$	0.639	0.0239	0.684	0.0182

SURV$_{AD}$	0.556	0.0082	0.582	0.0050

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[a] Variables defined as: INIT$_{YR1}$ = nest initiation rate of yearlings; INIT$_{AD1}$ = nest initiation rate of adults; INIT$_{YR2}$ = renesting rate of yearlings; INIT$_{AD2}$ = renesting rate of adults; INIT$_{AD3}$ = second renesting rate of adults; FCLUTCH$_{YR1}$ = clutch size (female eggs) of yearling first nests; FCLUTCH$_{YR2}$ = clutch size (female eggs) of yearling renests; FCLUTCH$_{AD1}$ = clutch size (female eggs) of adult first nests; FCLUTCH$_{AD2}$ = clutch size (female eggs) of adult renests; FCLUTCH$_{AD3}$ = clutch size (female eggs) of adult second renests; SUCC$_{YR1}$ = nest success of yearling first nests; SUCC$_{AD1}$ = nest success of adult first nests; SUCC$_{YR2}$ = nest success of yearling renests; SUCC$_{AD2}$ = nest success of adult renests (and second nests); HATCH = hatching success; CHSURV$_{YR}$ = survival of chicks from yearling females from hatch to 35 d; CHSURV$_{AD}$ = survival of chicks from adult females from hatch to 35 d; JUVSURV$_{83}$ = survival of juveniles from 35 d of age to 10 September for renests; JUVSURV$_{91}$ = survival of juveniles from 35 d of age to 10 September for first nests; SURV$_{YR}$ = annual survival of yearlings; SURV$_{AD}$ = annual survival of adults.

[b] Process variance estimated using the method of White (2000).

[c] Process variance for clutch size of second renests could not be estimated from range-wide data, so the value for clutch size of renests was used instead.

[d] Mean and process variance for chick survival of yearling and adult females were the same in range-wide data because most previous publications did not present chick survival estimates separately for each stage.

[e] Process variance for juvenile survival could not be estimated from Powder River Basin data, so values represent raw variance estimates from range-wide data.