



Population Ecology

# Demography of Greater Prairie-Chickens: Regional Variation in Vital Rates, Sensitivity Values, and Population Dynamics

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**ABSTRACT** Intensification of rangeland management has coincided with population declines among obligate grassland species in the largest remaining tallgrass prairie in North America, although causes of declines remain unknown. We modeled population dynamics and conducted sensitivity analyses from demographic data collected for an obligate grassland bird that is an indicator species for tallgrass prairie, the greater prairie-chicken (*Tympanuchus cupido*), during a 4-year study in east-central Kansas, USA. We examined components of reproductive effort and success, juvenile survival, and annual adult female survival for 3 populations of prairie-chickens across an ecological gradient of human landscape alteration and land use. We observed regional differences in reproductive performance, survivorship, and population dynamics. All 3 populations of prairie-chickens were projected to decline steeply given observed vital rates, but rates of decline differed across a gradient of landscape alteration, with the greatest declines in fragmented landscapes. Elasticity values, variance-scaled sensitivities, and contribution values from a random-effects life-table response experiment all showed that the finite rate of population change was more sensitive to changes in adult survival than other demographic parameters in our declining populations. The rate of population change was also sensitive to nest survival at the most fragmented and least intensively grazed study site; suggesting that patterns of landscape fragmentation and land use may be affecting the relative influences of underlying vital rates on rates of population growth. Our model results indicate that 1) populations of prairie-chickens in eastern Kansas are unlikely to be viable without gains from immigration, 2) rates of population decline vary among areas under different land management practices, 3) human land-use patterns may affect the relative influences of vital rates on population trajectories, and 4) anthropogenic effects on population demography may influence the regional life-history strategies of a short-lived game bird. © 2012 The Wildlife Society.

**KEY WORDS** contributions, elasticity, land use and land cover change (LULCC), Leslie matrix, life-table response experiment (LTRE), population viability, prospective analysis, variance-scaled sensitivities.

Intensification of agricultural practices has had negative impacts on grassland and farmland birds worldwide (Vickery et al. 1999, Donald et al. 2001, Kleijn et al. 2010). In North America, declines of grassland bird populations have been steeper and more widespread than any other guild of birds because of land use and land cover change in native prairies (Knopf 1994, Peterjohn and Sauer 1999). More than 95% of the American tallgrass prairie has been lost to cultivation and much of the remaining habitat is intensively managed for livestock production (Samson and Knopf 1994, Vickery et al. 1999). Grassland birds coevolved with large

grazing animals and periodic fire, but modern practices for management of grasslands for livestock production are the most significant ecological driver for native species in intact grasslands (Fuhlendorf and Engle 2001). For example, hay-cutting in grasslands can be beneficial or detrimental to the productivity of grassland songbirds, depending on timing of mowing and relative condition of the surrounding landscape (Perlut et al. 2008, With et al. 2008). Interactions between grazing and fire frequency of native prairies influence demography, abundance, and diversity of grassland birds (Powell 2006, 2008; With et al. 2008), as well as the probabilities of site colonization and local extinction (McNew et al. 2012).

The Flint Hills of eastern Kansas is an ecologically important ecoregion that contains the largest remaining tracts of intact tallgrass prairie in North America. In the past 30 years, rangeland management practices have shifted from periodic burning and year-round grazing by cow-calf herds to more intensive annual spring burning combined with intensive early stocking of steers during the first half of the summer

Received: 20 April 2011; Accepted: 2 November 2011;  
Published: 1 March 2012

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growing season (Smith and Owensby 1978). Intensification of rangeland management has coincided with population declines among obligate grassland species (Robbins et al. 2002, Reinking 2005, Powell 2008), which appear to be due to reduced demographic performance among animals that require residual vegetative cover for concealment (Wilgers and Horne 2006, With et al. 2008).

The greater prairie-chicken (*Tympanuchus cupido* L.; hereafter prairie-chicken) is an obligate grassland bird and an indicator species for unfragmented grasslands in the tallgrass prairie ecosystem (Poiani et al. 2001, Winter et al. 2006). Ongoing range contractions and declines in population numbers of prairie-chickens have paralleled continental losses of native tallgrass prairie, and the species currently occupies only a fraction of their original range prior to European settlement (Schroeder and Robb 1993, Johnsgard 2002). Eastern Kansas is a core area for prairie-chickens because large tracts of grasslands remain relatively intact (Johnsgard 2002). However, state monitoring programs suggest that populations of prairie-chickens in the region have been declining for the last 30 years (Rodgers 2009). Little is known about the vital population processes of prairie-chickens in this region, or the demographic mechanisms linking land use and land cover change to population declines. Vital rates of prairie-chickens have been studied among populations in fragmented habitats at margins of the species range (Svedarsky 1988, McKee et al. 1998, Ryan et al. 1998), but few demographic data are available for core populations in their extant range (Robel 1970, Horak 1985, Augustine and Sandercock 2010).

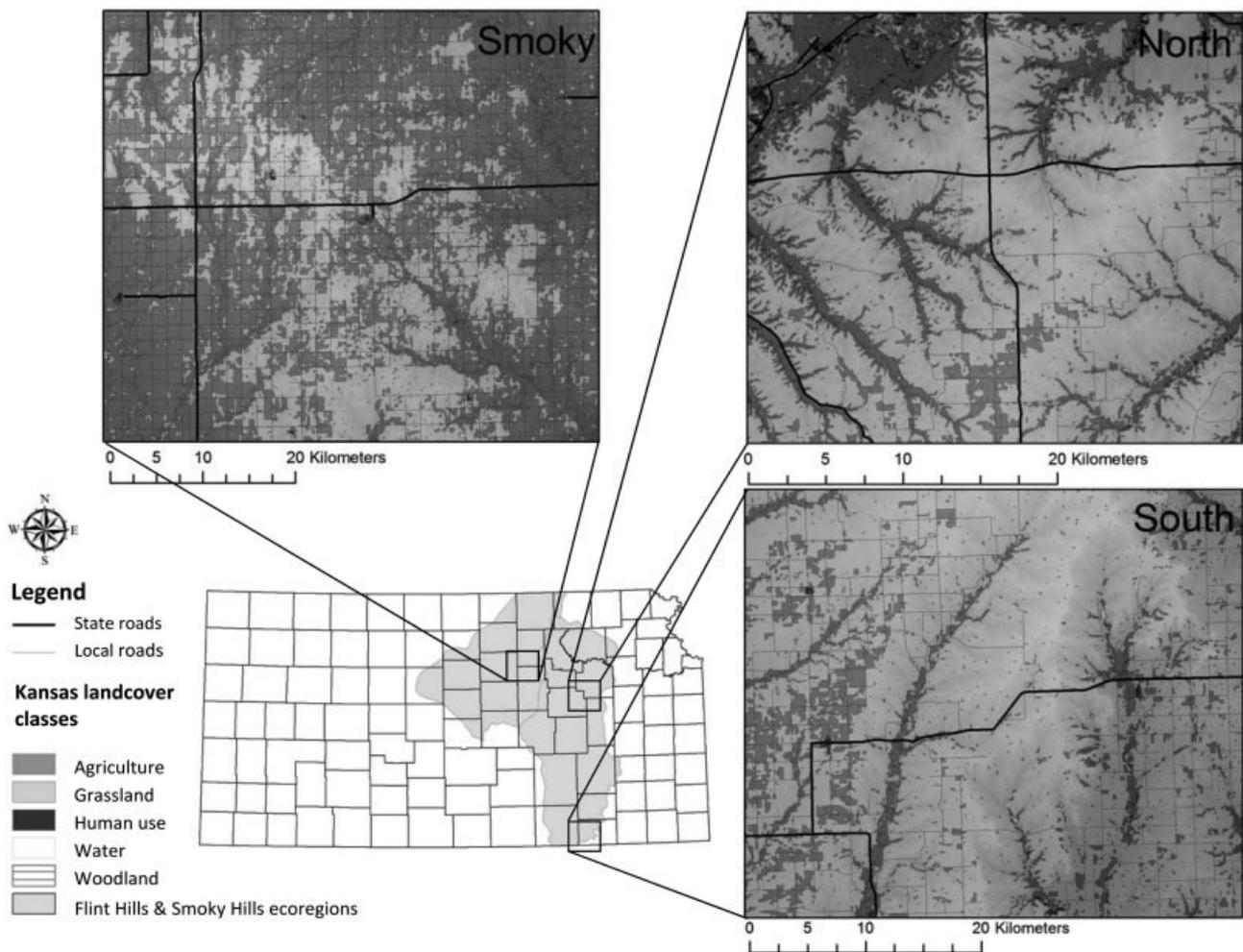
Conservation efforts for prairie-chickens require baseline data representing vital rates and their respective influence on population dynamics in native and managed habitats. Prairie-chickens occupy habitats ranging from contiguous and intensively-grazed rangeland in the southern Flint Hills to fragmented and lightly-grazed grasslands in the Smoky Hills (McNew et al. 2011*b*). Nest survival and adult survival appear to be reduced by increases in landscape fragmentation and the frequency of prescribed burns (Robbins et al. 2002, Patten et al. 2007, McNew et al. 2011*a*). Nest survival of prairie-chickens in the Flint Hills has been higher in the past (35%; Robel 1970) than the most recent estimates (8%; Augustine and Sandercock 2010). Tradeoffs among life-history traits and density-dependence can buffer populations against perturbations, but we do not know how anthropogenic change has affected population growth rates or viability of prairie-chickens at the core of their extant distribution, or which vital rates are driving regional population dynamics. Wisdom and Mills (1997) introduced life-stage simulation analyses (LSA) as a demographic technique for exploring the influence of simulated variation in vital rates on the variance of population change ( $\lambda$ ) with input variables taken from a suite of population studies of prairie-chickens. In a retrospective analysis, the authors concluded that a composite measure of fecundity (nest survival and brood survival) explained the greatest amount of variation in the simulated rate of population change. On the other hand, prospective population models for other species of upland gamebirds

have sometimes identified juvenile or adult survival as vital rates with the greatest potential impact on  $\lambda$  (Sandercock et al. 2005, Hagen et al. 2009). Given regional differences in life-history traits and environmental conditions within the range of prairie-chickens, a single set of management recommendations may not be adequate for stabilizing or increasing population numbers.

In this study, we estimated demographic rates for 3 populations of prairie-chickens, synthesized rates in a stage-based matrix model to estimate regional rates of population change, and used the tools of matrix models to evaluate the influence of vital rates on finite rates of population change. First, we estimated the components of fecundity and survival based on monitoring of radio-marked females. Second, we determined the population status of prairie-chickens by estimating the finite rate of population change to assess whether populations were viable ( $\lambda \geq 1.0$ ) or projected to decline ( $\lambda < 1.0$ ). Third, we conducted prospective elasticity and variance-scaled sensitivity (VSS) analyses to identify the vital rates predicted to have the greatest influence on  $\lambda$  for 3 populations under different ecological conditions. Last, we conducted a retrospective analysis based on the methods of a random effects life-table response experiment (LTRE) to examine the relative contribution of vital rates to the observed variation in population growth rates among the 3 populations in different landscapes. We hypothesized that land use and land cover change may affect the population viability of prairie-chickens. Specifically, we predicted that reproductive output, survivorship, and the finite rate of population change would be negatively affected by fragmentation of grasslands and management practices based on annual burning and intensive grazing regimes. Our goal was to develop management recommendations that would improve demographic performance of prairie-chickens as a key component of conservation efforts for prairie grouse.

## STUDY AREAS

Our field study was conducted at 3 sites in 2 ecoregions: 2 sites located in the southern and northern Flint Hills of eastern Kansas (South and North, respectively) and 1 site in the Smoky Hills of northcentral Kansas (Smoky; Fig. 1). The 3 study areas were >100 km apart and differed in patterns of grassland fragmentation, as well as rangeland management practices (McNew et al. 2011*a, b*). The South site (635 km<sup>2</sup>) was the most intact grassland landscape with a landcover of 90% grassland and 3% cropland, a mean grassland patch size of 185 ha, and a road density of 0.32 km of roads per km<sup>2</sup>. The majority of the site was managed with range management practices of annual spring burning and intensive early stocking with cattle (1 head per 0.8 ha for 90 days) with pastures stocked in late March–early April (Smith and Owensby 1978, Hagen et al. 2009). The North site (533 km<sup>2</sup>) had an intermediate landcover of 81% grassland and 10% cropland, a mean grassland patch size of 51 ha, and a road density of 0.57 km/km<sup>2</sup>. Annual spring burning was common and lands were managed with a mixture of intensive early stocking with cattle and season-long stock grazing



**Figure 1.** Locations and landscape composition of the Southern Flint Hills (South), Northern Flint Hills (North), and Smoky Hills (Smoky) greater prairie-chicken demography sites in east-central Kansas, USA, 2006–2009.

(1 head per 1.6 ha for 180 days). The Smoky site (1,295 km<sup>2</sup>) was a more fragmented landscape with land-cover of 53% grassland and 38% cropland, a mean grassland patch size of 15 ha, and a greater road density of 1.4 km/km<sup>2</sup>. Native grass pastures at the Smoky site were burned infrequently at fire return intervals  $\geq 2$  years, grazed at low to moderate intensity (1 head per  $>2$  ha for 180 days), and stocked with cattle 1 month later in the season (*ca.* 1 May) than the other 2 study sites. Cultivated crops at all 3 sites included wheat, sorghum, soybeans, and corn.

## METHODS

### Capture and Monitoring of Prairie-Chickens

We used standardized field methods at all 3 study sites in our 4-year study. We captured prairie-chickens with walk-in traps and drop-nets at lek sites during March–April of 2006–2009 (Silvy et al. 1990, Schroeder and Braun 1991). We sexed captured birds reliably by pinnae length, coloration, and other plumage characteristics (Henderson et al. 1967). We determined age-class as yearling or adult from the shape, coloration, and wear of the outermost 2 primaries (numbers 9 and 10; Schroeder and Robb 1993).

We individually marked all captured prairie-chickens with a numbered metal leg band and 3 colored leg bands. We fitted females with 11-g necklace-style very high frequency (VHF) radio transmitters equipped with mortality switches and an expected battery life of 12 months (Model RI-2B, Holohil Systems Ltd., Ontario, Canada). We monitored radio-marked females  $\geq 3$  times per week during the breeding, nesting, and brood-rearing seasons (Mar–Aug) and weekly during the post-breeding and winter periods (Sep–Feb). Once a female localized in an area for 3 successive days, we located the nest by tracking the female with portable radio receivers and handheld antennas (Model R2000, Advanced Telemetry Systems, Isanti, MN). We flushed the female once in early incubation to count eggs, determine stage of incubation, and record nest location with a handheld Global Positioning System (GPS) in Universal Transverse Mercator (UTM) coordinates. To minimize disturbance, we monitored females with nests daily at distances  $\geq 100$  m by triangulation of the radio signal until we determined that the female was no longer attending the nest. We revisited nests and classified nest fate as successful by presence of pipped eggshells ( $\geq 1$  chick produced), or as failed if nest contents were destroyed by predators or other causes.

For broods that successfully hatched, we conducted systematic brood flushes within 1 hour of sunrise at 14, 24, 34, and 60 days post-hatch by radio-tracking the brood female (Fields et al. 2006, Pitman et al. 2006a). If the female was flushed with a brood, we carefully searched the area to be sure we detected all fledglings and recorded the maximum number of young. If we did not observe young, we conducted a second flush count 2 days later to confirm presence or absence of a brood.

We used dipnets and spotlights to capture  $\geq 25$ -day-old juveniles by locating radio-marked females at night. We collected 20  $\mu$ L of blood, recorded morphometrics, and attached radio-transmitters to their backs with surgical sutures (Burkpile et al. 2002). The 3-g transmitters (modified model A4300, Advanced Telemetry Systems, Isanti, MN) were  $< 5\%$  of juvenile mass and had an expected battery life of 400 days. We used field evidence at locations where we recovered transmitters to determine whether adults and juveniles died or if the transmitter was dropped (Hagen et al. 2007). Field methods were approved by Kansas State University's Institutional Animal Care and Use Committee (Protocol numbers 2474 and 2781).

### Estimation of Demographic Parameters

We estimated 10 demographic parameters for prairie-chickens in Kansas.

*Nesting propensity.*—We calculated the probability of nesting (NEST) as the proportion of radio-marked females that attempted at least 1 nest. We calculated renesting rates (RENEST) as the percentage of radio-marked females that initiated a second nest conditional upon loss of the first nest. We considered a female unavailable for renesting if she was killed while incubating a first nest or if we were unable to relocate her during the renesting period. Estimates of NEST and RENESEST calculated as the number of nests found divided by the number of females available for nesting are likely biased low because nests may fail before discovery. Therefore, we estimated the number of nests and renests using estimates of daily survival rates for each study site and nesting attempt (see below) using a Horvitz–Thomson estimator (Dinsmore et al. 2002, Fondell et al. 2006). The number of expected nests always exceeded the number of available radio-marked females for all sites and all years (results not shown). Thus, we set NEST and RENESEST equal to 1.0; indicating that all females initiated first nesting attempts and if the first attempt failed, all females laid a replacement clutch.

*Nest and brood survival.*—Nest survival (NSURV) was the proportion of nests that produced  $\geq 1$  hatched chick, whereas brood survival (BSURV) was the proportion of hatched clutches that produced  $\geq 1$  24-day-old chick. We used the nest survival model in Program MARK (ver. 6.0, White and Burnham 1999) to generate maximum likelihood estimates of daily nest survival corrected for exposure before discovery, as well as daily brood survival from hatch to 24 days of age. We used multiple model selection and inference based on minimization of Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ) to evaluate the influence of 4 factors

on daily nest survival: nesting attempt (first or reneest), female age, year, and study site (Burnham and Anderson 2002). Successful nests were uncommon and we combined nesting attempts to explore the effects of 3 factors on daily brood survival: female age-class (yearling, adult), year, and study site. We used the most parsimonious model to estimate daily survival probabilities, and then extrapolated the overall nest survival probability as the product of daily survival probabilities (e.g., 37-day exposure period). We calculated brood survival as the estimate of daily brood survival raised to the 24th power. Corrections for overdispersion are not possible with the nest survival model because the global models are saturated and  $\hat{c}$  is not identifiable (Dinsmore et al. 2002). We calculated variances of extrapolated nest survival using the delta method (Powell 2007).

*Clutch size, egg and chick success.*—Total clutch laid (TCL) was determined for each nest by counting the number of eggs after the onset of incubation. Egg success, or chicks produced per egg laid (C/E), was conditional upon nest survival and calculated by dividing the total number of eggs laid in successful clutches by the total number that hatched. We calculated chick success, or fledglings produced per chick hatched (F/C), for successful broods as the proportion of hatched chicks that survived until 24 days of age. We pooled data across study sites when estimating chick success because sample sizes of successful broods were small. We calculated sampling and process variances of egg success and chick success using procedures described by White (2000).

We derived fecundity ( $F_j$ ), or the number of female chicks produced per female, from 7 reproductive parameters as follows assuming a 1:1 sex ratio of chicks at hatch:

$$F_j = [(NEST \times TCL_1 \times NSURV_1) + (1 - NSURV_1) \times RENESEST_1 \times TCL_2 \times NSURV_2] \times C/E \times BSURV \times F/C \times 0.5$$

where subscripts 1 and 2 denote parameter estimates for first nests and renests, respectively, and subscript  $j$  denotes age-class (yearling, adult).

*Juvenile and female survival.*—We monitored radio-marked prairie-chickens weekly during a 4-year period between March 2006 and February 2010 until death, transmitter failure, or until birds left the study area and could not be located for 1 month. We estimated monthly survival of juveniles and females at each study site with the nest survival procedure, a general model for known-fate data in Program MARK 6.0 (Hartke et al. 2006, Mong and Sandercock 2007). We evaluated survival of juveniles ( $S_j$ ) for an 8-month period from 24 days of age until recruitment into the breeding population the following spring (Aug to Feb) but evaluated female survival ( $S_Y$  = survival of yearling females,  $S_A$  = survival of adult females) for a 12-month period (Mar to Feb). We based multiple model selection and inference on minimization of  $AIC_c$  and evaluated the influence of study site and female age-class (female survival only) on monthly survival (Burnham and Anderson 2002). We pooled years of study for independent analyses of juvenile and female

survival. In both cases, we used the most parsimonious model to derive monthly survival probabilities, and then estimated the 8-month survival rate of juveniles and the annual survival rates of females as the product of consecutive monthly survival rates at each study site.

### Prospective Analysis

*Population model.*—To describe the population dynamics of prairie-chicken populations, we developed a deterministic matrix model for each of the 3 study areas using demographic data collected during the study. For each population, we synthesized vital rates for 3 age-classes of female prairie-chickens: juveniles (J; <10 months old), yearlings (Y; ≥11 and <22 months old), and adults (A; ≥22 months old). We captured females during the spring lekking season before nesting and we used a pre-breeding birth-pulse model. Fecundity and annual survival generally differ between age-classes in prairie grouse (Robel 1970, Hartke et al. 2006, Hagen et al. 2007) and our pre-breeding 2-age-class matrix model took the form:

$$\mathbf{A} = \begin{bmatrix} F_Y S_J & F_A S_J \\ S_Y & S_A \end{bmatrix},$$

where  $F_i$  is the age-specific fecundity and  $S_i$  is the age-specific probability of survival.

*Analytical procedures.*—We used the functions of package POPBIO in program R (ver. 2.13, Stubben and Milligan 2007) to estimate the finite rate of population change ( $\lambda$ ), the stable age distribution ( $\mathbf{w}$ ), and the reproductive value ( $\mathbf{v}$ ) for our 3 populations of prairie-chickens (Caswell 2001). We used bootstrapping procedures to calculate 95% confidence intervals for fecundity estimates and matrix properties by taking random draws from a normal distribution for clutch size and beta distributions for probabilities. We drew random samples of vital rates for each model run from distributions based upon the total variance observed for each parameter rather than process variance only because 3 yearly estimates prevented us from decomposing total variance into estimates of process and sampling variances (White 2000). Our bootstrap distributions of population metrics based on total variance were broader than estimates based on process variance alone, and our inferences for site differences were conservative. Bootstrapped means were similar to observed means (<0.01), and confidence intervals derived from bootstrapping were unbiased and did not require adjustment (Caswell 2001). If the 95% confidence interval of a bootstrap distribution for  $\lambda$  included 1, we did not consider the rate of change significantly different than a stationary population. Likewise, we did not consider  $\lambda$  to differ among study populations if a mean was within the 95% confidence interval of the bootstrap distribution for another population, and vice versa.

*Sensitivity analysis.*—The sensitivities of  $\lambda$  with respect to changes in matrix elements ( $a_{ij}$ ) can be assessed for absolute (sensitivity =  $\partial\lambda/\partial a_{ij}$ ) or proportional changes (elasticity =  $\ln \partial\lambda/\ln \partial a_{ij}$ ). We calculated elasticities for the lower-level vital rates ( $x_{ij}$ ) that comprise yearling ( $F_Y$ ) and adult ( $F_A$ ) fecundity by taking the product of the sensitivity matrix and

the partial derivatives of the matrix elements with respect to each lower level parameter ( $\partial a_{ij}/\partial x$ ; Caswell 2001)

$$e_x = \frac{x}{\lambda} \frac{\partial\lambda}{\partial x} = \frac{x}{\lambda} \sum_{i,j} \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x},$$

Elasticities of lower-level vital rates do not sum to 1 like elasticities of matrix elements, but may be combined to determine the relative net effect of management actions on  $\lambda$  (Mills et al. 1999, Caswell 2000). Thus, we summed lower-level elasticities across age-classes and nesting attempts to evaluate the relative effectiveness of integrated management actions for improving  $\lambda$ . Elasticity values may covary with the variance of a vital rate (Pfister 1998), and we used VSSs to assess vital rate sensitivities (Link and Doherty 2002). We calculated the VSS for demographic parameters that were probabilities ( $x$ ) as:

$$\text{VSS}_x = \left( \frac{\sqrt{x(1-x)}}{\lambda} \right) \frac{\partial\lambda}{\partial x}.$$

Clutch size of prairie chickens was not a probability, and the appropriate variance-stabilizing transformation for a normal distribution is  $3\ln(x)$ . We used the transformation  $3\ln(\text{TCL})$  to facilitate comparison of VSS values for parameters on different scales, the normal distribution for clutch size, and binomial distribution for probabilities (W. A. Link, USGS Patuxent Wildlife Research Center, personal communication). We report both standard elasticities and VSSs for comparison.

### Retrospective Analysis

We used a random effects LTRE to evaluate how the variance in each vital rate and the covariance among vital rates contribute to the variance in  $\lambda$  among study sites (Brault and Caswell 1993, Caswell 2001). Differences in landscape or habitat conditions may be complex, affecting many demographic parameters simultaneously. Our LTRE decomposed treatment effects into contributions ( $c$ ) from each of the vital rates in the model by comparing each population's matrix to a reference population, in which vital rates were averaged over all 3 study sites. The effects of each study site on the variance of the finite rate of population change  $\text{Var}(\lambda)$  were decomposed for each demographic rate by the approximation:

$$\text{Var}(\lambda) \approx \sum_{i,j} \sum_{k,l} \text{Cov}(x_{ij}, x_{kl}) s_{ij} s_{kl},$$

where  $\text{Cov}(x_{ij}, x_{kl})$  is the variance-covariance matrix for pairs of vital rates  $x_{ij}$  and  $x_{kl}$ , and  $s_{ij}$  and  $s_{kl}$  are the lower-level sensitivities for a mean population matrix recast as column and row vectors, respectively (Brault and Caswell 1993, Caswell 1996). We calculated the mean matrix for the 3 study populations ( $\bar{\mathbf{A}}$ ) as:

$$\bar{\mathbf{A}} = (\mathbf{A}^{\text{South}} + \mathbf{A}^{\text{North}} + \mathbf{A}^{\text{Smoky}})/3$$

We conducted LTRE analyses using functions of the POPBIO package of program R.



**Table 2.** Candidate models and model statistics for daily nest survival ( $n = 286$  nests) of greater prairie-chickens at 3 sites in Kansas, USA, 2006–2009.

Model structure	Model statistics <sup>a</sup>				
	$K$	$-2 \log L$	$AIC_c$	$\Delta AIC_c$	$w_i$
Site + attempt	4	1,265.7	1,273.7	0.0	0.423
Site	3	1,269.2	1,275.2	1.5	0.206
Site + attempt + female age	5	1,265.4	1,275.5	1.8	0.179
Site + female age	4	1,268.9	1,277.0	3.3	0.085
Site + year	4	1,269.1	1,277.1	3.4	0.078
Constant	1	1,278.6	1,280.6	6.9	0.014
Year	2	1,277.3	1,281.3	7.6	0.010

<sup>a</sup> Model fit is described by the number of parameters ( $K$ ),  $-2 \log$  likelihood ( $-2 \log L$ ), Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ), and AIC weights ( $w_i$ ).

more than twice as high at the Smoky site (yearling:  $F = 0.21 \pm 0.05$ , adult:  $F = 0.23 \pm 0.05$ ) than either site in the Flint Hills, including the South (yearling and adults:  $F = 0.06 \pm 0.04$ ) and North sites (yearling:  $F = 0.09 \pm 0.04$ , adult:  $0.10 \pm 0.04$ ). Differences were not significant because 95% confidence intervals were overlapping in all cases (Table 1).

*Juvenile survival.*—During 2007–2009, we radio-marked 23 juveniles from 11 broods ( $n = 5$  at North,  $n = 18$  at Smoky) and monitored the birds until death or until transmitters were shed. Because of low rates of nest and brood survival, we were unable to monitor any juveniles at the South site. The top model ( $\Delta AIC_c = 0$ ) indicated that monthly survival probabilities were similar between the 2 study sites. A model in which monthly survival rates varied between study sites was considered parsimonious ( $\Delta AIC_c = 1.9$ ; Table 4). However, the beta estimate for the effect of site did not differ significantly from 0 ( $\beta = 0.06$ , 95% CI:  $-0.02$ – $0.14$ ). Monthly juvenile survival estimated from the constant model was  $0.895 \pm 0.033$ , and extrapolated juvenile survival from 24 days of age to first breeding as yearlings across all sites was  $0.41 \pm 0.001$ .

*Yearling and adult survival.*—We monitored 279 radio-marked yearling and adult female prairie-chickens during the 3.8-year period from March 2006 to January 2010. Differences in female survival among study sites were strong-

**Table 3.** Candidate models and model statistics for daily brood survival to 24 days post-hatch of greater prairie-chickens ( $n = 66$  broods) at 3 sites in Kansas, USA, 2006–2009.

Model structure	Model statistics <sup>a</sup>				
	$K$	$-2 \log L$	$AIC_c$	$\Delta AIC_c$	$w_i$
Constant	1	86.5	88.5	0.0	0.416
Site	3	84.2	90.3	1.7	0.176
Year	2	86.4	90.4	1.9	0.162
Site + female age	4	83.9	91.9	3.4	0.076
Year + female age	3	86.0	92.1	3.5	0.071
Site + year	4	84.0	92.1	3.6	0.069
Site + female age + year	5	83.8	93.9	5.4	0.029

<sup>a</sup> Model fit is described by the number of parameters ( $K$ ),  $-2 \log$  likelihood ( $-2 \log L$ ), Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ), and AIC weights ( $w_i$ ).

**Table 4.** Candidate models and model statistics for monthly (Sep–Mar) survival of juvenile greater prairie-chickens ( $n = 23$ ) from 24 days of age to first breeding at the North and Smoky study sites in Kansas, USA, 2007–2009.

Model structure	Model statistics <sup>a</sup>				
	$K$	$-2 \log L$	$AIC_c$	$\Delta AIC_c$	$w_i$
Constant	1	57.7	59.7	0.0	0.421
Year	2	56.5	60.6	1.0	0.262
Site	2	57.5	61.6	1.9	0.160
Site + year	3	55.8	62.1	2.4	0.129
Month	7	49.7	65.2	5.5	0.027
Month $\times$ site	14	40.4	74.3	14.6	0.000

<sup>a</sup> Model fit is described by the number of parameters ( $K$ ),  $-2 \log$  likelihood ( $-2 \log L$ ), Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ), and AIC weights ( $w_i$ ).

ly supported by the data, and models with a site effect accounted for more than 90% of the relative support (Table 5). A model that included both study site and female age was parsimonious ( $\Delta AIC_c = 0.65$ ) and suggested higher survival among adults than yearlings (Table 1). Model-averaged estimates of annual survival were ranked opposite to the observed patterns for seasonal productivity. Female survival was lowest at the Smoky site (yearlings =  $0.34 \pm 0.001$ , adults =  $0.42 \pm 0.002$ ), intermediate at the North site (yearlings =  $0.42 \pm 0.001$ , adults =  $0.50 \pm 0.003$ ), and highest at the South site (yearlings =  $0.64 \pm 0.01$ , adults =  $0.71 \pm 0.01$ ; Table 1).

### Prospective Analyses

Finite rates of population change for the 3 populations were:  $\lambda_{\text{South}} = 0.76$  (95% CI =  $0.72$ – $0.81$ ),  $\lambda_{\text{North}} = 0.57$  (95% CI =  $0.53$ – $0.63$ ), and  $\lambda_{\text{Smoky}} = 0.53$  (95% CI =  $0.48$ – $0.59$ ). Thus, all populations were projected to decline but at different rates. Net reproductive rates ( $R_0$ ) were consistently  $< 1$ , and productivity was not adequate for female replacement. Stable-age distributions were skewed toward adults at all sites ( $\mathbf{w}_Y = 0.04$ – $0.17$ ,  $\mathbf{w}_A = 0.83$ – $0.96$ ), and reproductive values were greater for adults than yearlings for all populations ( $\mathbf{v}_Y = 1$ ,  $\mathbf{v}_A = 1.11$ – $1.22$ ). Damping ratios were high ( $\rho > 147$ ) and all populations would be expected to converge rapidly to a stable age distribution ( $t_{20} < 0.6$  yr).

**Table 5.** Candidate models and model statistics for monthly (Mar–Feb) survival of yearling and adult greater prairie-chickens ( $n = 279$ ) at 3 study sites in Kansas, USA, 2006–2009.

Model structure	Model statistics <sup>a</sup>				
	$K$	$-2 \log L$	$AIC_c$	$\Delta AIC_c$	$w_i$
Site	3	793.5	799.5	0.0	0.535
Site + female age	4	792.2	800.2	0.7	0.386
Time	46	209.4	803.9	4.8	0.060
Constant	1	805.5	807.5	8.0	0.010
Female age	2	803.7	807.7	8.2	0.009
Time $\times$ site	101	656.7	871.0	71.4	0.000

<sup>a</sup> Model fit is described by the number of parameters ( $K$ ),  $-2 \log$  likelihood ( $-2 \log L$ ), Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ), and AIC weights ( $w_i$ ).

**Table 6.** Asymptotic properties of projection matrices for 3 populations of greater prairie-chickens in Kansas, USA, 2006–2009.

Matrix properties <sup>a</sup>	South		North		Smoky	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
$\lambda$	0.76	0.72–0.81	0.57	0.53–0.63	0.53	0.48–0.59
$w_Y$	0.07	0.02–0.13	0.15	0.07–0.24	0.23	0.14–0.33
$w_A$	0.93	0.87–0.97	0.85	0.76–0.93	0.77	0.67–0.86
$v_Y$	1.00	1.00–1.00	1.00	1.00–1.00	1.00	1.00–1.00
$v_A$	1.11	1.03–1.19	1.18	1.07–1.28	1.2	1.07–1.32
$\rho$	299	15–1,552	190	11–981	147	9–756
$t_{20}$	0.53	0.42–1.11	0.57	0.43–1.25	0.60	0.45–1.36
$R_0$	0.12	0.04–0.25	0.08	0.03–0.16	0.09	0.04–0.15
$T$	7.92	6.21–10.2	4.64	4.08–5.46	3.88	3.61–4.27

<sup>a</sup>  $\lambda$  = finite rate of population change,  $w$  = stable age distribution for yearlings (Y) and adults (A),  $v$  = reproductive value,  $\rho$  = damping ratio,  $t_{20}$  = time to model convergence,  $R_0$  = net reproductive rate,  $T$  = generation time (years).

Generation times ranged from 4 years to 8 years and were ranked Smoky < North < South (Table 6).

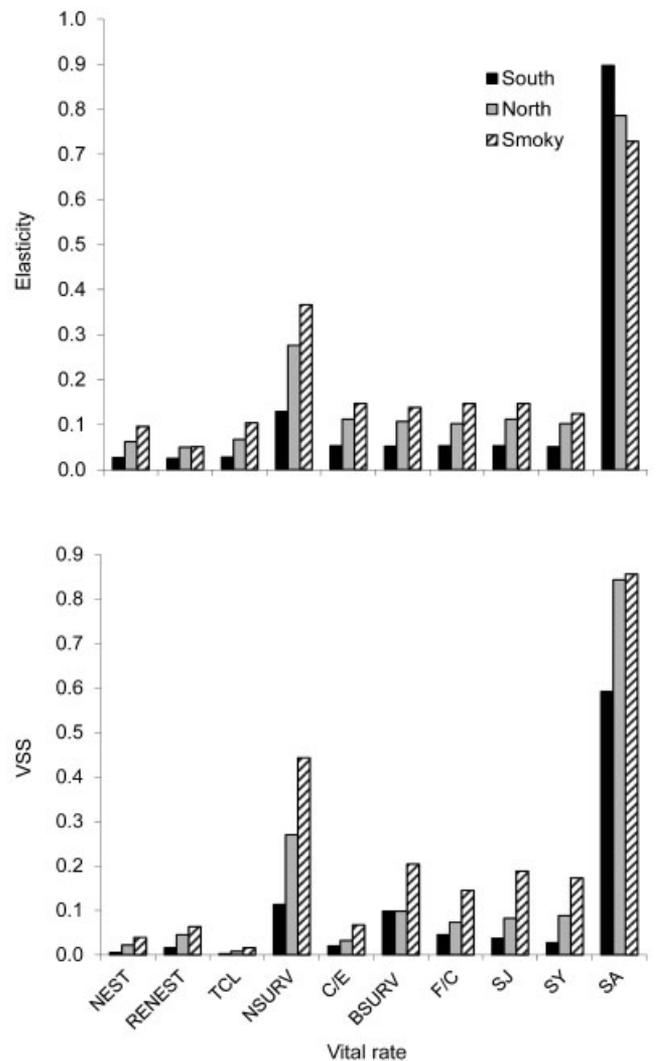
Elasticity values and VSSs for lower-level parameters indicated that  $\lambda$  would be most sensitive to future changes in adult survival ( $S_A$ ) in declining populations of prairie-chickens. Elasticities and VSSs were also congruent in ranking second the effect of nest survival (NSURV) of both stage-classes and all nesting attempts, especially at the Smoky site (Fig. 2). Other components of fecundity, such as nest initiation rates (NEST, RENEST) and clutch size (TCL) had lower elasticities and VSSs at all sites.

### Retrospective Analysis

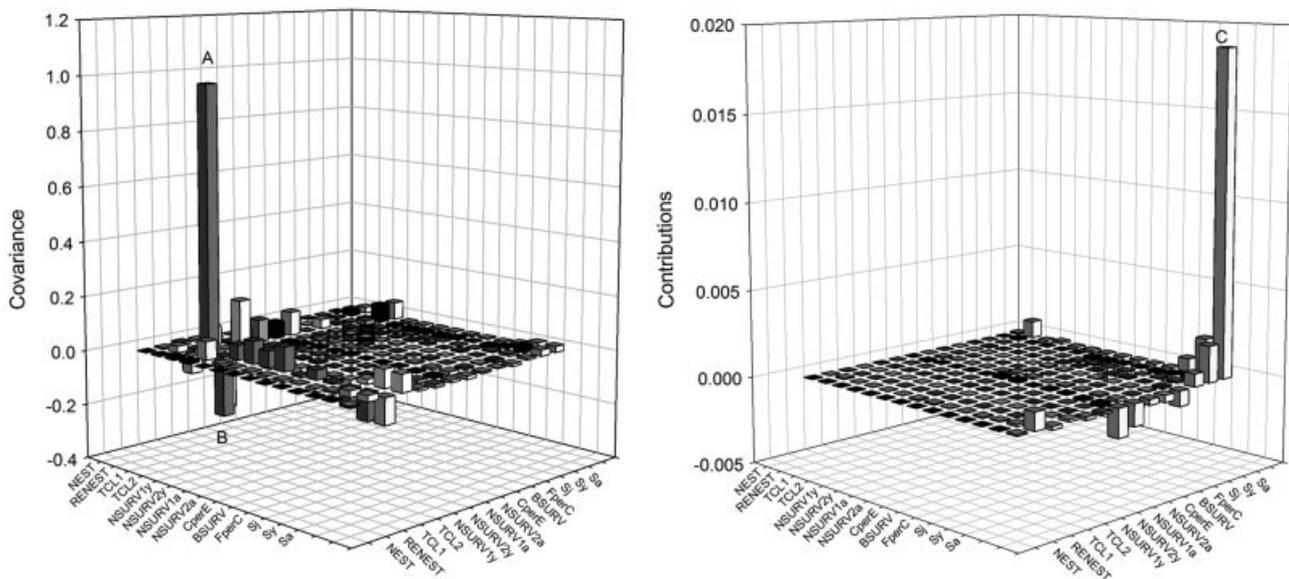
Using a mean matrix of all 3 populations as a reference population, the effect of study site on  $\lambda$  was calculated as the difference from the mean matrix:  $\lambda_{\text{South}} = 0.15$ ,  $\lambda_{\text{North}} = -0.05$ , and  $\lambda_{\text{Smoky}} = -0.10$ . The sum of the differences in lambda among the 3 populations,  $\text{Var}(\lambda) = 0.017$ , was a good approximation to the summed contributions of vital rates calculated with the random effects LTRE ( $\sum c = 0.017$ ). Variances and covariances were larger for clutch sizes ( $\text{TCL}_{1,2}$ ) than any other vital rate. However, contributions of adult survival accounted for most ( $\geq 52\%$ ) of variation in  $\lambda$  among the 3 sites (Fig. 3). Higher rates of fecundity at the Smoky site contributed little to the observed variance of  $\lambda$ . Thus, site differences in the annual survival of adult females were primarily responsible for regional variation in rates of population change among our 3 study areas in Kansas. Unexpectedly for an upland gamebird, site differences in components of fecundity had relatively little effect on the variance of population change.

## DISCUSSION

Our 4-year field study of 3 populations of prairie-chickens in Kansas provides the first evidence for the demographic mechanisms driving ongoing population declines in the core of the extant range of a sensitive grassland bird. Reproductive potential was consistently high in our 3 study populations: all females initiated a first clutch and nearly all birds renested if the first clutch was lost, clutch sizes were large ( $>12$  eggs in first nests), and hatchability of eggs was good if a nest survived incubation ( $\geq 0.80$ ). However, estimates of productivity were depressed by dismal rates of nest



**Figure 2.** Elasticities (above) and variance-scaled sensitivities (VSS; below) of demographic rates of 3 populations of greater prairie-chickens in Kansas, USA, 2006–2009. Management actions are expected to have similar effects on the stage-specific reproductive parameters, and elasticities and VSSs have been summed across female age classes and nesting attempts. NEST and RENEST = initiation rates of first and renests, TCL = clutch sizes, NSURV = nest survival probabilities, C/E = chicks hatched per eggs laid for successful nests, BSURV = brood survival probabilities, F/C = fledglings produced per chick hatched, SJ = 8-month survival of juveniles to recruitment, SY and SA = annual survival probabilities for yearling and adult females, respectively.



**Figure 3.** Left: Variance–covariance matrix for lower-level demographic rates from 3 populations of greater prairie-chickens in Kansas, USA, 2006–2009. Diagonal and off-diagonal entries are variances and covariances, respectively. Right: Contributions of the lower-level parameters to the variance in the finite rate of population change ( $\lambda$ ) among the 3 populations, estimated from a random effects life-table response experiment (LTRE). Important peaks are indicated by letter. A = variance in TCL1 (clutch size of first nests); B = negative covariance between TCL1 and TCL2 (clutch size of first nests and re-nests); C = contribution of variation in adult survival ( $S_a$ ) on the variation in  $\lambda$ .

(<0.30) and brood survival (<0.35), which included some of the lowest estimates ever reported for prairie-chicken populations. Females were vulnerable to predators while attending eggs and young, and survival rates of yearlings and adults were highly variable among study sites.

All populations were projected to decline but rates of decline differed among sites. Population change was most sensitive to changes in adult survival at all 3 sites, which confirms the strong influence of survival on population declines of upland game birds (Sandercock et al. 2008, Hagen et al. 2009). The relative influence of fecundity parameters differed among the study populations but our results were consistent among different analytical approaches for sensitivity analyses. Last, our data indicate that differences in the rates of population decline among study sites were largely due to variation in adult survival; which appeared to be mediated by anthropogenic alteration of prairie landscapes. Our results suggest that conservation actions aimed at recovering declining populations of prairie-chickens must consider local conditions rather than general management prescriptions applied across the entire range of the species.

### Demography

Despite high reproductive potential, low nest and brood survival resulted in depressed productivity, especially at the South and North sites in the intensively-managed Flint Hills ecoregion. Indeed, our estimates of nest survival (0.04–0.28) are among the lowest values ever reported for prairie-chickens, including an estimate of 0.32 for the endangered Attwater’s prairie-chicken in Texas (Peterson and Silvy 1996), and were well below the threshold of 0.50 recommended for maintaining stable population numbers

(Westemeier 1979). Estimates of nest survival for 22 studies of prairie-chickens averaged 0.49 (Bergerud and Gratson 1988), and indicated that nest survival should be higher among core populations than isolated populations at the peripheral margins of the species’ range. For example, reported nest survival ranged from 0.31 to 0.39 in the fragmented prairie of southwestern Missouri (McKee et al. 1998, Ryan et al. 1998) to a high of 0.80 in relatively contiguous grasslands of North and South Dakota (Svedarsky 1988, Norton 2005).

Brood survival to 24 days post-hatch ranged from 0.27 to 0.34 at our study sites and was lower than values reported for prairie-chickens in privately managed grasslands of southeast Nebraska (0.59; Matthews et al. 2011) or Ft. Pierre National Grasslands of South Dakota (0.83; Norton 2005). Our estimates of 24-day brood survival rate (0.06–0.23) were also about 50% lower than values reported for 60-day survival of lesser prairie-chicken broods in the sand sagebrush prairie (0.50; Pitman et al. 2006a) and short-grass prairie (0.53; Fields et al. 2006) of western Kansas. Survival of lesser prairie-chicken broods is influenced by habitat conditions, especially overhead cover, and differences in rangeland management of grasslands are likely responsible for regional differences in nest and brood survival (Fields et al. 2006, Pitman et al. 2006a).

Our 3 study populations of prairie-chickens had markedly different demographic rates that covaried across an ecological gradient of grassland fragmentation and prescribed burning and grazing intensity. Rangeland management appears to be influencing reproductive success, whereas landscape composition and pattern accounts for variation in regional survival rates of prairie-chickens in Kansas. Nest and brood survival were depressed across Kansas, but were higher in the less

intensively grazed and more fragmented prairie of the Smoky Hills site than in the more contiguous and intensively-grazed Flint Hills sites. Our results are counterintuitive because nest survival is negatively affected by fragmentation in both prairie chickens and grassland songbirds (Ryan et al. 1998, Winter et al. 2000, Herkert et al. 2003). Nevertheless, low estimates of nest and brood survival in large unfragmented Kansas prairie are consistent with recent work by Augustine and Sandercock (2010) in the northern Flint Hills. Despite large tracts of contiguous tallgrass prairie in the Flint Hills, patterns of land ownership may be detrimental for conservation if landowners apply annual burning and intensive early stocking of cattle over large contiguous rangelands. The amount and quality of residual cover limits nest and brood survival for prairie-chickens (McKee et al. 1998, Pitman et al. 2005, Fields et al. 2006), and annual burning and intensive early cattle grazing both remove residual vegetation (Fuhlendorf and Engle 2001, With et al. 2008). Our data suggest that large-scale patterns of rangeland management are more limiting to nest and brood survival than the moderate levels of fragmentation caused by agriculture and roads.

In contrast to regional patterns of nest and brood survival, survival probabilities of juveniles, yearlings, and adults were lowest in the most fragmented and least intensively-grazed Smoky site and highest in the least fragmented and most intensively-grazed South site (Table 1). Our estimates of annual survival for females at the Smoky site were low ( $S_Y = 0.34$ ,  $S_A = 0.42$ ), but our estimates for the South site ( $S_Y = 0.64$ ,  $S_A = 0.71$ ) were among the highest values reported from field studies of prairie-chickens (41–56%, Hamerstrom and Hamerstrom 1973, Wisdom and Mills 1997, Augustine and Sandercock 2010). The North site had intermediate amounts of habitat fragmentation and grazing intensity, and the survival rates of prairie-chickens were intermediate as well. Higher rates of mortality at the Smoky site could be the result of higher predator densities in fragmented grasslands (A. J. Gregory, Kansas State University, unpublished data), a tradeoff between female survival and nest survival, or a combination of these factors. More than 90% of mortality events were due to predators, and higher predation rates at the Smoky site could also be due to the functional responses of predators to habitat fragmentation. Coyotes (*Canis latrans*) use edge habitats and roads for travel and foraging (Kuehl and Clark 2002, Tigas et al. 2002). Last, most losses occur during the summer while females are attending young (L. B. McNew, Kansas State University, unpublished data). High predation rates of females in fragmented areas with greater residual vegetation suggests that vertical structure may aid concealment of nests and lead to higher nest survival, but mortality rates of female grouse may be higher if they are unable to detect and elude approaching predators (Wiebe 1998, Hagen et al. 2007). Our results demonstrate that rangeland management and fragmentation drive variation in vital rates of prairie chickens, but future work is needed to better understand the proximate mechanisms and to devise management strategies that improve habitat conditions at scales relevant to conservation.

### Projected Population Declines

Finite rates of population change were consistently  $\lambda < 1$ ; indicating that all 3 populations are projected to decline without immigration. High damping ratios ( $\rho \geq 147$ ) and rapid convergence to a stable age distribution ( $t_{20} < 0.6$  yr) indicated that transient dynamics may not greatly influence population change and asymptotic matrix properties should describe current population demographics (Caswell 2001). All 3 populations had low net reproductive rates ( $R_0 \leq 0.12$ ) despite high reproductive effort. Higher adult survival and lower reproductive success at the South site resulted in an average generation time that was twice as high as the Smoky site, and a stable age distribution more heavily skewed toward adult females. Intermediate vital rates resulted in an intermediate demography of prairie-chickens at the North site. Projected annual population declines without immigration were 24%, 43%, and 47% at the South, North, and Smoky sites, respectively. Variation in local and large-scale habitat conditions and predation risk due to human land use may account for differences in rates of population decline.

Our deterministic matrix models treated our study populations as closed (Caswell 2001). In fact, our models were asymmetric because they did not include gains from immigration, but could have included losses to permanent emigration, which cannot be separated from mortality. Thus, projected rates of population change will not match observed population trends for a site if immigration rates are  $>0$ . Our results generally agree with an independent data set of annual lek surveys collected during our spring trapping efforts, as well as annual lek counts conducted for the entire region by the Kansas Department of Wildlife and Parks, which indicate 30–50% declines in lek attendance at our Flint Hill sites during the study period (Rodgers 2009, L. B. McNew, unpublished data). However, annual male lek attendance did not decline significantly over the study period at the Smoky site, which had the greatest projected population declines and the discrepancy requires explanation.

One possibility is that our estimates of demographic rates could have been biased low. Transmitters could be a handicap but females were captured at lek sites in advance of the nesting season, and previous work has also shown that estimates of survival from radio-marked juvenile and female prairie-chickens are not lower than birds that are banded only (Hagen et al. 2006, Pitman et al. 2006a). Disturbance was unlikely to negatively bias our estimates of nest survival because we only flushed females once in early incubation to determine clutch size and stage of incubation, and all monitoring was conducted at a distance by telemetry. All nest visits ( $\leq 2$  per nest) occurred under dry conditions with researchers wearing rubber boots and latex gloves to minimize scent. Females never abandoned clutches because of nest visits, and only 4 of 286 nests were abandoned during the entire study. Last, we conducted brood flushes soon after sunrise when chicks are brooded by females; resulting in high detection probabilities of broods and accurate estimates of brood survival. Estimates of nest initiation and re-nesting rates are typically biased low if complete detection of nests before failure is assumed (McPherson et al. 2003). However,

we estimated nest and renesting rates using the Horvitz–Thomson estimator that accounted for potential bias associated with failure before discovery (Dinsmore et al. 2002, Fondell et al. 2006).

An alternative explanation for discrepancies between lek counts and our model projections is that the Smoky site is a sink population maintained by immigration. The grassland-dominated landscapes on which prairie-chickens occur are highly fragmented in the Smoky Hills, which may lead to greater movements during natal or breeding dispersal. Preliminary genetic data suggest that prairie-chickens captured at the Smoky site and an adjacent Smoky Hill sub-population are functionally linked by a high number of migrants per generation (A. J. Gregory, unpublished data). Because of the size and configuration of suitable grassland habitat in a matrix of cultivated farmland, the population dynamics of prairie-chickens in the Smoky Hills may be best explained by a metapopulation dynamic structure. Our 4 years of demographic data demonstrate that local fecundity is not adequate to maintain population numbers but movements and connectivity could be critical for maintaining population viability.

### Vital Rate Sensitivities

High elasticities and VSSs for adult survival differed from conclusions of previous work on prairie-chickens where the finite rate of change ( $\lambda$ ) was more sensitive to changes in nest and chick survival (Wisdom and Mills 1997, Fefferman and Reed 2006, Hagen et al. 2009). Female prairie-chickens reach sexual maturity as yearlings, lay large clutches, and have a high propensity for nesting and renesting (McNew et al. 2011*b*). High reproductive potential and relatively short life expectancies ( $\leq 3$  yr; Robel and Ballard 1974, Schroeder and Robb 1993) suggest that fecundity should have the greatest influence on prairie-chicken population dynamics (Bergerud and Gratson 1988, Morrow et al. 1996, Sæther and Bakke 2000). However, changes in nest and chick survival had relatively little influence on changes in asymptotic  $\lambda$  for populations suffering high rates of reproductive failure, and suggest that management actions directed at improving adult survival would be more effective at mitigating population declines for all populations. Nevertheless,  $\lambda$  appeared to be less sensitive to adult survival and more sensitive to fecundity parameters at the Smoky site than the 2 Flint Hill sites (Fig. 2); suggesting that human land use patterns may affect not only vital rates themselves but the relative influences of vital rates on population dynamics.

Elasticity values are a useful tool in conservation biology but have several caveats (de Kroon et al. 2000, Hagen et al. 2009). First, elasticity values assess proportional changes for a population at the asymptotic stable age distribution (de Kroon et al. 2000) and should not be used to make management prescriptions during transient dynamics if a population takes a long time to converge (Caswell 2001, Fefferman and Reed 2006). Our populations were predicted to converge to stable age distributions rapidly ( $t_{20} < 0.7$  yr); suggesting that elasticities should predict the impacts of management pre-

scriptions for short-term perturbations (Fefferman and Reed 2006). Second, elasticities covary with projected population growth rates (de Kroon et al. 2000); and the relative influence of vital rates depend on whether the population is increasing or decreasing. High elasticity values for adult survival are typical of gamebird populations with  $\lambda < 1$ , and highlight the influence of adult survival on declining populations (Sandercock et al. 2008). Third, elasticities may be related to the variances of their respective vital rates (Mills et al. 1999) and vital rates with high variances tend to have low elasticities (Pfister 1998). We addressed the functional relationship between the mean and variance of vital rates by calculating VSSs and comparing them to elasticities (Link and Doherty 2002, Hagen et al. 2009), but we found that the relative influence of vital rates on  $\lambda$  were generally unaffected by differences in observed variance among rates. Fourth, elasticities are derivatives that measure small changes around the mean values and may be less successful at predicting the impacts of large perturbations (Drechsler 1998, de Kroon et al. 2000). A combination of  $\lambda < 1$  and significantly depressed fecundities at all sites may explain why our elasticities suggest that management actions aimed at increasing adult survival would be most effective at increasing  $\lambda$ , whereas previous studies of stable populations have prescribed actions to increase reproductive success or juvenile survival parameters (Wisdom and Mills 1997, Fefferman and Reed 2006, Hagen et al. 2009). Last, elasticities identify key vital rates but field logistics and economics may constrain management actions (Mills et al. 1999, Link and Doherty 2002). High elasticity values for adult survival at the South site are less useful for conservation, because survival is already higher than most populations and improvements are unlikely to be possible. Therefore, elasticity analyses should not be the only tool used to evaluate potential management actions for declining populations (de Kroon et al. 2000, Ehrlén et al. 2001, Mills et al. 2001).

### Life-Table Response Experiment

Retrospective analyses, such as LTREs, describe how observed variation in the vital rates affects the observed variation in  $\lambda$  among populations (Caswell 1996, 2001). Many of the vital rates differed among our populations of prairie-chickens because of large differences in habitat conditions among study sites. By assessing the contributions of vital rates to differences in  $\lambda$ , we found that the effect of study site on the rate of population decline was primarily caused by site differences in adult survival. Indeed, differences in adult survival accounted for 52–68% of the variation in  $\lambda$  among study sites, and contributions were positive in the nearly unfragmented South site, whereas they were negative in the moderate to highly fragmented North and Smoky sites. Variation in predation rates among sites was positively associated with the degree of habitat fragmentation (McNew et al. 2011*a*), and variation in the regional rates of population declines may be better explained by patterns of landscape composition and fragmentation than by differences in range-land management practices of grasslands.

## MANAGEMENT IMPLICATIONS

Populations of prairie-chickens at our study sites in the Flint Hills and Smoky Hills of Kansas are not viable with current rates of low reproductive output. Results of sensitivity analyses suggest that management actions aimed at increasing adult survival will have the greatest benefit to declining populations. However, actions focused solely on improving adult survival rates are unlikely to be successful at stabilizing populations, especially in the annually burned and intensively grazed Flint Hills region, as adult survival is already near a biological maximum of 0.64–0.71 per year. At current low levels of nest and brood survival ( $<0.30$  and  $<0.34$ , respectively), adult survival would need to exceed 0.95 to offset population declines at our study sites in the Flint Hills. Management efforts aimed at increasing nest and brood survival are likely more realistic. Provided adult survival remains unchanged, probability of nest and brood survival would need to exceed 0.55 and 0.63 for populations to stabilize at the South and North sites, respectively. Moreover, these rates are likely overestimates because management actions that improve nest survival may enhance other vital rates as well (Pitman et al. 2006*b*). Reproductive performance might be improved in the Flint Hills by implementation of burning and grazing regimes that provide adequate residual vertical and overhead herbaceous cover for successful nesting and brood-rearing while preventing encroachment and fragmentation of native prairie by woody vegetation (McKee et al. 1998, Robbins et al. 2002, Patten et al. 2007). Rotational grassland management regimes such as patch-burn grazing may provide adequate nesting and brood rearing habitat without negatively affecting cattle production (Fuhlendorf et al. 2006, Rensink 2009), and future research should address the potential of patch-burn grazing for mitigating declines of prairie-chickens and other grassland birds in the Flint Hills.

Nest and brood survival were higher for the Smoky Hills population than the Flint Hills, but fecundity was still significantly less than levels required for a self-sustaining population. In addition, the population at the Smoky site experienced higher rates of predation on female prairie chickens than populations in the Flint Hills. At current levels of nest and brood survival, annual survival would need to exceed 0.92 for the Smoky population to stabilize. Alternately, nest and brood survival would need to exceed 0.80 for  $\lambda \geq 1$  at the Smoky site, given current survival rates of females ( $\leq 0.42$ ). Thus, mitigating population declines will likely be more difficult in areas suffering significant loss ( $>40\%$ ) and fragmentation of prairie than in low quality but contiguous prairies. Actions that improve both reproductive and survival rates simultaneously, such as predator removals or prairie restoration, will be required. Predator removals can benefit fecundity and adult survival of ground-nesting game birds (Garrettson and Rohwer 2001, Frey et al. 2003) but are expensive, time-consuming, and a short-term solution for relatively small areas (Côté and Sutherland 1997). Management actions aimed at reducing the negative impacts of edge effects by increasing the num-

ber, sizes, and proximity of tallgrass prairie fragments will likely be more effective at increasing vital rates, and improving long-term population viability. The effects of landscape composition and arrangement, rangeland management regimes, and their interaction on productivity and survival need to be quantified for more effective management of prairie-chickens and other sensitive species of grassland birds.

## ACKNOWLEDGMENTS

We thank the many field technicians who helped to collect field data. Funding and equipment were provided by a consortium of federal and state wildlife agencies, conservation groups, and wind energy partners under the National Wind Coordinating Collaborative including: National Renewable Energies Laboratory (DOE), U.S. Fish and Wildlife Service, Kansas Department of Wildlife and Parks, Kansas Cooperative Fish and Wildlife Research Unit, National Fish and Wildlife Foundation, Kansas and Oklahoma chapters of The Nature Conservancy, BP Alternative Energy, FPL Energy, Horizon Wind Energy, and Iberdrola Renewables. B. K. Sandercock and S. M. Wisely were supported by the Division of Biology at Kansas State University. A. J. Gregory was supported by a research fellowship from the NSF-funded GK-12 Program (DFE-0841414).

## LITERATURE CITED

- Augustine, J. K., and B. K. Sandercock. 2010. Demography of female greater prairie-chickens in unfragmented grasslands in Kansas. *Avian Conservation and Ecology* 6:2. <<http://dx.doi.org/10.5751/ACE-00429-060102>>.
- Bergerud, A. T., and M. W. Gratson. 1988. Adaptive strategies and population ecology of northern grouse. University of Minnesota, Minneapolis, USA.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444–1454.
- Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radiotransmitters to one-day-old sage grouse chicks. *Wildlife Society Bulletin* 30:93–96.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Caswell, H. 1996. Analysis of life table response experiments II. Alternative parameterizations for size- and stage-structured models. *Ecological Modelling* 88:73–82.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Côté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11:395–405.
- de Kroon, H., J. van Groenendael, and J. Ehrlén. 2000. Elasticities: A review of methods and model limitations. *Ecology* 81:607–618.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Donald, P. F., R. E. Green, and M. F. Heath. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London Series B Biological Sciences* 268:25–29.
- Drechsler, M. 1998. Sensitivity analysis of complex models. *Biological Conservation* 86:401–412.
- Ehrlén, J., J. van Groenendael, and H. de Kroon. 2001. Reliability of elasticity analysis: reply to Mills et al. *Conservation Biology* 15:278–280.

- Fefferman, N. H., and J. M. Reed. 2006. A vital rate sensitivity analysis for nonstable age distributions and short-term planning. *Journal of Wildlife Management* 70:649–656.
- Fields, T. L., G. C. White, W. C. Gilgert, and R. D. Rodgers. 2006. Nest and brood survival of lesser prairie-chickens in west central Kansas. *Journal of Wildlife Management* 70:931–938.
- Fondell, T. F., J. B. Grand, D. A. Miller, and R. M. Anthony. 2006. Renesting by dusky Canada geese on the Copper River Delta, Alaska. *Journal of Wildlife Management* 70:955–964.
- Frey, S. N., S. Majors, M. R. Conover, T. A. Messmer, and D. L. Mitchell. 2003. Effect of predator control on ring-necked pheasant populations. *Wildlife Society Bulletin* 31:727–735.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625–632.
- Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie, Jr. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* 16:1706–1716.
- Garretson, P. R., and F. C. Rohwer. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. *Journal of Wildlife Management* 65:398–405.
- Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2007. Age-specific survival and probable causes of mortality in female lesser prairie-chickens. *Journal of Wildlife Management* 71:518–525.
- Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2006. Radiotelemetry survival estimates of lesser prairie-chickens in Kansas: are there transmitter biases? *Wildlife Society Bulletin* 34:1064–1069.
- Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of population dynamics and management alternatives. *Journal of Wildlife Management* 73:1325–1332.
- Hamerstrom, F., and F. Hamerstrom. 1973. The prairie chicken in Wisconsin: highlights of a 22-year study of counts, behavior, movements, turnover and habitat. Department of Natural Resources, Technical Bulletin No. 64, Madison, Wisconsin, USA.
- Hartke, K. M., J. B. Grand, G. R. Hepp, and T. H. Folk. 2006. Sources of variation in survival of breeding female wood ducks. *Condor* 108:201–210.
- Henderson, F. R., F. W. Brooks, R. E. Wood, and R. B. Dahlgren. 1967. Sexing of prairie grouse by crown feather patterns. *Journal of Wildlife Management* 31:764–769.
- Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, S. K. Sherrod, M. A. Jenkins, J. Faaborg, and S. K. Robinson. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. *Conservation Biology* 17:587–594.
- Horak, G. J. 1985. Kansas prairie chickens. Kansas Fish and Game Commission, Pratt, USA.
- Johnsgard, P. A. 2002. Grassland grouse and their conservation. Smithsonian Institute, Washington, D.C., USA.
- Kleijn, D., H. Schekkerman, W. J. Dimmers, R. J. M. Van Kats, D. Melman, and W. A. Teunissen. 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits *Limosa l. limosa* in the Netherlands. *Ibis* 152:475–486.
- Knopf, F. L. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15:247–257.
- Kuehl, A. K., and W. R. Clark. 2002. Predator activity related to landscape features in northern Iowa. *Journal of Wildlife Management* 66:1224–1234.
- Link, W. A., and P. A. Doherty. 2002. Scaling in sensitivity analysis. *Ecology* 83:3299–3305.
- Matthews, T. W., A. J. Tyre, J. S. Taylor, J. J. Lusk, and L. A. Powell. 2011. Habitat selection and brood survival of greater prairie-chickens. Pages 179–194 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. University of California Press, Berkeley, USA.
- McKee, G., M. R. Ryan, and L. M. Mechlin. 1998. Predicting greater prairie-chicken nest success from vegetation and landscape characteristics. *Journal of Wildlife Management* 62:314–321.
- McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2011a. Human mediated selection on life-history traits of greater prairie-chickens. Pages 255–266 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. University of California Press, Berkeley, USA.
- McNew, L. B., A. J. Gregory, S. M. Wisely, and B. K. Sandercock. 2011b. Reproductive biology of a southern population of greater prairie-chickens. Pages 209–221 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. University of California Press, Berkeley, USA.
- McNew, L. B., T. J. Prebyl, and B. K. Sandercock. 2012. Effects of rangeland management on the site occupancy dynamics of prairie-chickens in a protected prairie preserve. *Journal of Wildlife Management* 76:38–47.
- McPherson, R. J., T. W. Arnold, L. M. Armstrong, and C. J. Schwarz. 2003. Estimating the nest-success rate and the number of nests initiated by radiomarked mallards. *Journal of Wildlife Management* 67:843–851.
- Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* 13:815–829.
- Mills, L. S., D. F. Doak, and M. J. Wisdom. 2001. Elasticity analysis for conservation decision making: reply to Ehrlen et al. *Conservation Biology* 15:281–283.
- Mong, T. W., and B. K. Sandercock. 2007. Optimizing radio retention and minimizing radio impacts in a field study of upland sandpipers. *Journal of Wildlife Management* 71:971–980.
- Morrow, M. E., R. S. Adamcik, J. D. Friday, and L. B. McKinney. 1996. Factors affecting Attwater's prairie-chicken decline on the Attwater prairie chicken National Wildlife Refuge. *Wildlife Society Bulletin* 24:593–601.
- Norton, M. A. 2005. Reproductive success and brood habitat use of greater prairie chickens and sharp-tailed grouse on the Fort Pierre National Grassland of central South Dakota. Thesis, South Dakota State University, Brookings, USA.
- Patten, M. A., E. Shochat, D. H. Wolfe, and S. K. Sherrod. 2007. Lekking and nesting response of the greater prairie-chicken to burning of tallgrass prairie. *Proceedings of the Tall Timbers Fire Ecology Conference* 23:149–155.
- Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2008. Regional population viability of grassland songbirds: effects of agricultural management. *Biological Conservation* 141:3139–3151.
- Peterjohn, B. G., and J. R. Sauer. 1999. Population status of North American grassland birds from the North American Breeding Bird Survey, 1966–1996. *Studies in Avian Biology* 19:27–44.
- Peterson, M. J., and N. J. Silvy. 1996. Reproductive stages limiting productivity of the endangered Attwater's prairie-chicken. *Conservation Biology* 4:1264–1276.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America* 95:213–218.
- Pitman, J. C., C. A. Hagen, B. E. Jamison, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2006a. Survival of juvenile lesser prairie-chickens in Kansas. *Wildlife Society Bulletin* 34:675–681.
- Pitman, J. C., C. A. Hagen, B. E. Jamison, R. L. Robel, T. M. Loughin, and R. D. Applegate. 2006b. Nesting ecology of lesser prairie-chickens in sand sagebrush prairie of southwestern Kansas. *Wilson Journal of Ornithology* 118:23–35.
- Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. *Journal of Wildlife Management* 69:1259–1269.
- Poiani, K. A., M. D. Merrill, and K. A. Chapman. 2001. Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. *Conservation Biology* 15:513–522.
- Powell, A. F. L. A. 2006. Effects of prescribed burns and bison (*Bos bison*) grazing on breeding bird abundances in tallgrass prairie. *Auk* 123:183–197.

- Powell, A. F. L. A. 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. *Journal of Field Ornithology* 79:41–52.
- Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *Condor* 109:949–954.
- Reinking, D. L. 2005. Fire regimes and avian responses in the central tallgrass prairie. *Studies in Avian Biology* 30:116–126.
- Rensink, C. B. 2009. Impacts of patch-burn grazing on livestock and vegetation in the tallgrass prairie. Thesis, Kansas State University, Manhattan, USA.
- Robbins, M. B., A. T. Peterson, and M. A. Ortega-Huerta. 2002. Major negative impacts of early intensive cattle stocking on tallgrass prairies: the case of the greater prairie-chicken (*Tympanuchus cupido*). *North American Birds* 56:239–244.
- Robel, R. J. 1970. Possible role of behavior in regulating greater prairie-chickens. *Journal of Wildlife Management* 34:306–312.
- Robel, R. J., and W. B. Ballard. 1974. Lek social organization and reproductive success in the greater prairie-chicken. *American Zoologist* 14:121–128.
- Rodgers, R. 2009. Prairie-chicken lek surveys—2009. Performance Report, Statewide Wildlife Research and Surveys. Kansas Department of Wildlife and Parks, Pratt, USA.
- Ryan, M. R., J. L. W. Burger, D. P. Jones, and A. P. Wywiałowski. 1998. Breeding ecology of greater prairie-chickens (*Tympanuchus cupido*) in relation to prairie landscape configuration. *American Midland Naturalist* 140:111–121.
- Sæther, B. E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.
- Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *Bioscience* 44:418–421.
- Sandercock, B. K., W. E. Jensen, C. K. Williams, and R. D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. *Journal of Wildlife Management* 72:970–982.
- Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology* 86:2176–2186.
- Schroeder, M. A., and C. E. Braun. 1991. Walk-in funnel traps for capturing greater prairie-chickens on leks. *Journal of Field Ornithology* 62:378–385.
- Schroeder, M. A., and L. A. Robb. 1993. Greater prairie-chicken (*Tympanuchus cupido*). Account 36 in A. Poole, P. Stettenheim, and F. Gill, editors. *The birds of North America*. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Silvy, N. J., M. E. Morrow, E. Shanley, and R. D. Slack. 1990. An improved drop net for capturing wildlife. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 44:374–378.
- Smith, E. F., and C. E. Owensby. 1978. Intensive-early stocking and season-long stocking of Kansas Flint Hills range. *Journal of Range Management* 31:14–17.
- Stubben, C. J., and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22:11. <<http://www.jstatsoft.org/v22/i11>>.
- Svedarsky, W. D. 1988. Reproductive ecology of female greater prairie-chickens in Minnesota. Pages 193–267 in A. T. Bergerud and M. W. Gratson, editors. *Adaptive strategies and population ecology of northern grouse*. University of Minnesota Press, Minneapolis, USA.
- Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation* 108:299–306.
- Vickery, P. D., P. L. Tubaro, J. M. C. D. Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999. Conservation of grassland birds in the Western Hemisphere. *Studies in Avian Biology* 19:2–26.
- Westemeier, R. L. 1979. Factors affecting nest success of prairie-chickens in Illinois. *Proceedings of the Prairie Grouse Technical Council* 13: 9–15.
- White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, New York, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Wiebe, K. 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behaviour* 56:1137–1144.
- Wilgers, D. J., and E. A. Horne. 2006. Effects of different burn regimes on tallgrass prairie herpetofaunal species diversity and community composition in the Flint Hills, Kansas. *Journal of Herpetology* 40:73–84.
- Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. *Condor* 102:256–266.
- Winter, M., D. H. Johnson, and J. A. Shaffer. 2006. Does body size affect a bird's sensitivity to patch size and landscape structure? *Condor* 108: 808–816.
- Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chicken as an example. *Journal of Wildlife Management* 61:302–312.
- With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* 141:3152–3167.

Associate Editor: Gary White.