

Spatial Variation in Lesser Prairie-Chicken Demography: A Sensitivity Analysis of Population Dynamics and Management Alternatives

CHRISTIAN A. HAGEN,^{1,2} *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

BRETT K. SANDERCOCK, *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

JAMES C. PITMAN,³ *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

ROBERT J. ROBEL, *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*

ROGER D. APPLGATE,⁴ *Research and Survey Office, Kansas Department of Wildlife and Parks, Emporia, KS 66801, USA*

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ABSTRACT The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is currently considered a candidate for protection under the Endangered Species Act. To identify potential limiting factors for lesser prairie-chicken populations, we developed an age-based matrix model of lesser prairie-chicken population dynamics to compare the relative importance of components of reproduction and survival, and determine if various management alternatives stabilize or increase rates of population change. We based our analyses on an intensive 6-year population study from which demographic rates were estimated for each age class in Kansas. We used deterministic models and elasticity values to identify parameters predicted to have the greatest effect on the rate of population change (λ) at 2 study sites. Last, we used life-stage simulation analysis to simulate various management alternatives. Lambda was <1 for both populations (site 1: $\lambda = 0.54$, site 2: $\lambda = 0.74$). However, we found differences in sensitivity to nest success and chick survival between populations. The results of the simulated management scenarios complemented the lower-level elasticity analysis and indicated the relative importance of female survival during the breeding season compared with winter. If management practices are only capable of targeting a single demographic rate, changes to either nest success or chick survival had the greater impact on λ at site 1 and 2, respectively. Management that simultaneously manipulated both nest success and chick survival was predicted to have a greater effect on λ than changes in survival of adult females. In practice, our demographic analyses indicate that effective management should be based on habitat conservation measures to increase components of fecundity. (JOURNAL OF WILDLIFE MANAGEMENT 73(8):000-000; 2009)

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Understanding variation in life-history traits and their relationship to seasonal habitats is critical to species conservation and management. As with most grouse, population dynamics of lesser prairie-chicken (*Tympanuchus pallidicinctus*) are likely driven by interaction between predation rates and the amount of available escape cover (i.e., the cover-predator complex; Bergerud 1988, Sandercock et al. 2005). Dense cover to conceal incubating females during nesting and moderate cover with abundant forbs and insects for rapid growth of chicks are characteristic of the life-history requirements of most grouse species. Recent work from southwest Kansas, USA, indicated that lesser prairie-chickens that nested in areas of dense nesting cover, (i.e., primarily sand sagebrush [*Artemisia filifolia*] and taller warm-season grasses) had increased likelihood of successfully hatching a nest (Pitman et al. 2005). However, more open-canopy habitats had greater invertebrate biomass and yielded heavier chicks that had greater survival until first breeding (Hagen et al. 2006, Pitman et al. 2006a). Adult females that occupied areas with denser cover were more

successful in hatching nests and had higher annual survival than females in areas with less cover (Hagen et al. 2007b). Similar survival patterns of lesser prairie-chickens were evident in Oklahoma and New Mexico, USA (Patten et al. 2005).

We modeled population dynamics and conducted sensitivity analyses of lesser prairie-chickens using a synthesis of field data from a 6-year study that examined ecological factors of nest success, chick survival, and annual adult survival in Kansas (Hagen et al. 2005a, b, 2007a, b; Pitman et al. 2005, 2006a). The work from southwestern Kansas suggested that ecological variability between the 2 study sites (Table 1) was related to variation in reproductive rates and survival. The primary differences between study areas were in concealment cover and invertebrate biomass (important chick forage) in sand sagebrush communities (Pitman et al. 2005; Hagen et al. 2006, 2007b). We synthesized demographic rates estimated from this larger body of work, applied them to age-based matrix models, and simulated potential management practices to better understand which life-history traits could most effectively be managed.

First, we assessed the population status of lesser prairie-chicken by estimating the finite rate of population change (λ) and its respective confidence intervals to determine whether populations were sustaining ($\lambda \geq 1.0$) or predicted to decline ($\lambda < 1.0$). Second, we conducted sensitivity

¹ E-mail: christian.a.hagen@state.or.us

² Present address: Oregon Department of Fish and Wildlife, 61374 Parrrell Road, Bend, OR 97702, USA

³ Present address: Research and Survey Office, Kansas Department of Wildlife and Parks, Emporia, KS 66801, USA

⁴ Present address: Tennessee Wildlife Agency, P.O. Box 40747, Nashville, TN 37204, USA

Table 1. Ecological characteristics of 2 study sites for lesser prairie-chicken in Finney County, Kansas, USA, 1998–2003.

Variable	Site 1			Site 2			Source ^a
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	
Shrub density (plants/ha)	3,611	689	10 ^b	4,206	697	15	1
Shrub cover (%)	6.51	0.90	113 ^c	9.40	7.74	113	2,3,4
Grass cover (%)	41.73	2.37	113	32.88	2.21	113	2,3,4
Forb cover (%)	13.01	0.91	113	9.25	0.84	113	2,3,4
Visual obstruction reading (VOR; dm)	1.72	0.11	113	2.07	0.10	113	2,3,4
Grass height (cm)	12.78	0.72	91 ^d	20.11	0.98	83	4
Invertebrate biomass (g)	4.27	0.89	4 ^e	2.12	0.85	12	2
Raptor predation (proportion)	0.15	0.04	101	0.09	0.04	45	3,4
Mammalian predation (proportion)	0.47	0.05	101	0.56	0.07	45	3,4

^a Sources: 1) Hagen 2003, 2) Hagen et al. 2005^b, 3) Hagen et al. 2007^b, 4) Pitman et al. 2005.

^b Sample sizes for shrub density were based on estimates calculated per pasture with ≥ 35 locations used to estimate density within a pasture.

^c Sample size for shrub, grass, and forb cover and VOR resulted from pooling random locations from 3 studies to estimate means for each variable.

^d Sample sizes for grass height were obtained from random points only for the yr 2000–2002, the only period these data were collected.

^e Sample sizes for invertebrate biomass were based on repeated measures ($n = 42$ and $n = 29$) of 4 and 12 broods at sites 1 and 2, respectively.

analyses to identify which life-history stages would have the greatest effect on the finite rate of population change. Specifically, we combined prospective (e.g., elasticity and variance-scaled sensitivity) and retrospective techniques (life-stage simulation analyses) to examine specific management strategies that were aimed at improving population status through enhancing habitat conditions during the reproductive period (i.e., increases in nest success, chick survival, and female survival) or by reducing mortality of breeding age birds during winter (legal harvest period).

STUDY AREA

The study region comprised 2 approximately 5,000-ha fragments of native sand sagebrush prairie near Garden City, Finney County, Kansas (Hagen et al. 2005^a, ^b; Pitman et al. 2005). We conducted work at site 1 (37°52'N, 100°59'W) from 1998 to 2003. During 2000–2003, we expanded our trapping and monitoring efforts to include site 2 (37°51'N, 100°46'W). Prior to the 1970s, these 2 sites were part of a contiguous sand sagebrush grassland (Waddell and Hanzlick 1978). The development of center-pivot irrigation systems led to the conversion of 150,000 ha of sand sagebrush to irrigated cropland (Robel et

al. 2004). Native vegetation in the prairie fragments was primarily sand sagebrush, yucca (*Yucca* spp.), love grass (*Eragrostis trichodes*), bluestem (*Andropogon* spp.), and big sandreed (*Calamovilfa gigantea*). Soils were in the choppy sands range site category, and topography was generally flat to rolling hills and dunes (Hulett et al. 1988). Native rangelands were grazed seasonally by domestic livestock.

METHODS

This study was a synthesis of existing data from a 6-year study, and field methods and parameter estimation are described elsewhere (Pitman et al. 2005, 2006^a, ^b, ^c; Hagen et al. 2006, 2007^b). We estimated 7 demographic parameters for lesser prairie-chickens. An additional 2 parameters were treated as constants: 1) to account for the assumed 1:1 sex ratio (0.5) at hatch and 2) egg hatchability (i.e., $1 - [\text{the proportion of infertile and unhatched embryos/total clutch size}]$) at 0.93 (SE = 0.01).

Clutch size (CLUTCH) was the total number of eggs laid in the nest. Partial clutch loss during incubation occurred in 30% of successful nests, with a median of 2 eggs lost.

We estimated apparent nest success (NEST) as the proportion of nests hatching ≥ 1 egg. Mayfield estimates

Table 2. Estimates ($\hat{\theta} \pm \text{SE}$) of demographic parameters of yearling and adult lesser prairie-chickens radiomarked in Finney County, Kansas, USA, 1998–2003.

Rate (units)	Site 1						Site 2					
	Yearling			Ad			Yearling			Ad		
	<i>n</i>	$\hat{\theta}$	SE	<i>n</i>	$\hat{\theta}$	SE	<i>n</i>	$\hat{\theta}$	SE	<i>n</i>	$\hat{\theta}$	SE
CLUTCH ₁ (eggs)	33	11.9	0.32	43	12.5	0.29	25	11.7	0.36	41	12.2	0.23
CLUTCH ₂ (eggs)	6	8.0	0.60	8	7.6	0.52	8	8.3	0.52	8	7.1	0.52
NEST ₁ ^a (prob)	33	0.303	0.080	43	0.140	0.053	25	0.320	0.093	41	0.415	0.077
NEST ₂ (prob)	6	0.167	0.152	8	0.125	0.117	8	0.125	0.117	8	0.125	0.117
RENEST (prob)	39	0.223	0.055	51	0.157	0.051	33	0.242	0.075	49	0.163	0.053
CHICK (prob)	7	0.119	0.015	5	0.616	0.039	10	0.277	0.020	16	0.184	0.009
<i>P</i> ₀ (prob)	32	0.539	0.089 ^b	32	0.539	0.089 ^b	32	0.539	0.089 ^b	32	0.539	0.089 ^b
<i>S</i> _{breeding} (prob)	24	0.613	0.095	50	0.502	0.078	33	0.735	0.073	48	0.620	0.070
<i>S</i> _{nonbreeding} (prob)	24	0.911	0.040	50	0.874	0.048	33	0.944	0.026	48	0.913	0.034
<i>S</i> _{winter} (prob)	24	0.768	0.079	50	0.687	0.080	33	0.847	0.055	48	0.772	0.088

^a We calculated parameter estimates from field data gathered between 1998 and 2002, and we estimated seasonal female and juvenile survival from 2000 to 2003.

^b We pooled estimates of juvenile survival (*P*₀) across areas and female age classes due to sample sizes.

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or nest survival models were not needed because we found all nests early in incubation (<1–3 days) and monitored nests daily until failure or hatching.

Renesting (RENEST) was the probability of a female laying a replacement clutch, conditional on failure of a first nest (1–NEST₁). We calculated RENESEST as the number of females laying renests divided by total number of first nests. We monitored renests and determined fates as described above.

We derived chick survival for 34 days posthatch (CHICK) from daily survival rates of prefledging chicks using a modified Mayfield estimator applied to the change in brood size between flush counts (Pitman et al. 2006a).

The expected number of female chicks produced per female (F_j) was

$$F_j = [(CLUTCH_1 \times NEST_1) + (1 - NEST_1) \times (RENEST \times CLUTCH_2 \times NEST_2)] \times (0.93 \times 0.5 \times CHICK),$$

where subscripts 1 and 2 indicate parameter estimates associated with first nesting and renesting attempts, respectively, and subscript j denotes the age class (yearling [Y], adult [A]).

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Survival from independence at 34 days to first breeding (P_0) and survival of breeding age females (P_j) were estimated from radiomarked birds (Pitman et al. 2006a, Hagen et al. 2007b). However, we derived estimates of P_j from 3 biological periods (breeding [Mar–Jun, 4 months], non-breeding [Jul–Oct, 4 months], winter [Nov–Feb, 4 months]) to examine the importance of seasonal female survival to rates of population change. The probability of a female surviving from April to April was

$$P_j = (S_{\text{breeding}} \times S_{\text{nonbreeding}} \times S_{\text{winter}}),$$

where S indicates a 4-month survival estimate and subscript j denotes the age class (Y,A).

We constructed a deterministic female life-cycle model to summarize the age-structured variation in demographic rates for both populations. In our field work, we captured birds at leks in April, in effect a spring census. Thus, we developed our matrix model as a prebreeding birth-pulse model:

$$A = \begin{bmatrix} F_Y P_0 & F_A P_0 \\ P_Y & P_A \end{bmatrix}.$$

We derived the finite rate of population change (λ), stable age (\mathbf{w}), reproductive value (\mathbf{v}), and sensitivity analyses using algorithms of Caswell (2001) in MATLAB 6.5 software (Mathworks Inc. 2003). We calculated 95% confidence limits around the observed λ , using the parametric bootstrap method (Manly 1997, Ebert 1999, Fieberg and Ellner 2001). We generated bootstrapped λ values in 4 steps: 1) we resampled lower-level demographic rates from a probability distribution (i.e., beta-distributions for probabilities, and

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normal distributions for continuous variables), 2) we parameterized the projection matrix with each set of bootstrapped draws, 3) we calculated λ from the re-parameterized matrix, and 4) we repeated these steps 10,000 times. If $\lambda = 1$ was in the upper or lower 2.5% of the bootstrap distribution, then we rejected the null hypothesis of population stability. We followed the above procedure to estimate 95% confidence intervals for the other matrix properties.

We ranked prescriptions for potential management actions (e.g., habitat improvements, or harvest management) using sensitivity analyses. Elasticities (e_{ij}) of the matrix elements were scaled (ln) sensitivity values (s_{ij}) so that they summed to 1 (Caswell 2001):

$$e_{ij} = \frac{\partial(\ln \lambda)}{\partial(\ln a_{ij})} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}.$$

The matrix elements F_Y and F_A were comprised of several demographic variables, and we calculated the elasticity of these lower-level rates (x_i). The elasticity of λ to these parameters was evaluated by taking the partial derivatives of the matrix with respect to the lower-level parameters (Caswell 2001):

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

where e_x is the elasticity of λ to a proportional change in a lower-level parameter (x). Parameters with high elasticity often have low variance. We also used variance-scaled sensitivities (VSSs) as a measure of demographic rate elasticity because scaling associated with VSS allows for an evaluation of a given change in a demographic rate independent of the absolute value of the parameter (Link and Doherty 2002). Link and Doherty (2002) defined prospective analyses as the functional dependence of λ on lower-level rates (x_i). The relationship of the mean and variance for any random variable distributed on a unit interval suggests that VSSs based on the arcsine square-root transform are more appropriate for demographic probabilities (θ), where

$$VSS = \frac{\partial \ln \lambda}{\partial [2 \sin^{-1}(\sqrt{\theta})]} = \left(\frac{\sqrt{\theta(1-\theta)}}{\lambda} \right) \frac{\partial \lambda}{\partial \theta}$$

For continuous demographic rates (i.e., clutch size), we converted normal variables to proportions by

$$q(\theta) = \ln(\theta) / k_{\text{max}},$$

where θ = mean clutch size and k_{max} was the maximum clutch size observed for a specific age class and nesting attempt (Link and Doherty 2002). We reported both standard elasticities and VSSs for comparative purposes and highlighted the benefits of each approach.

We used a modified life-stage simulation analysis (LSA) approach (Mills et al. 1999), where we identified a specific management target for each demographic rate of interest. We examined the effect an absolute increase in a given rate had on λ . We selected the 4 most important demographic rates, as determined from ranking of the VSSs, for the perturbation analyses. The perturbation analysis simulated management practices that would presumably yield large changes in λ with respect to the targeted demographic rate (Mills et al. 1999). The lower-level VSSs indicated NEST₁, CHICK, P_0 , and $S_{Y,A\text{-breeding}}$ were the most important rates with respect to changes in λ , and we used these in the perturbation analyses. We assumed hypothetical management scenarios for NEST₁ and CHICK would respond the greatest to management of vegetative cover because residual cover and forb abundance are important to variation in these 2 demographic parameters (Buhnerkempe et al. 1984, Riley and Davis 1993). Manipulations to P_0 and $S_{Y,A}$ were possible surrogates for modifying hunting seasons for lesser prairie-chickens, as this is typical management for increasing annual survival of harvested populations.

Using a modified LSA requires that the mean of a given demographic rate increase by a fixed amount and simultaneously reduce variability in the rate (approx. 10% in our study). We conducted simulations for perturbations from a uniform distribution with its respective range for targeted demographic rates, and drew all other rates randomly from either a normal (e.g., CLUTCH_{*i,j*}) or beta distributions (e.g., probabilities; Wisdom et al. 2000). We simulated stochastic management scenarios by including an estimate of variance along with each demographic rate of management interest. For example, we set NEST and CHICK to have a probability of 0.4 and 0.5; we set P_0 to have a mean of 0.6 and 0.7 and a range of ± 0.05 and $S_{Y,A\text{-breeding}}$ $S_{Y,A\text{-winter}}$ to have a mean of 0.8 and 0.9 and a range of ± 0.05 . We constrained perturbations to the stated probabilities, as these rates were either comparable or at the upper limits of values reported for this species and congeners (Schroeder and Robb 1993, Hagen and Giesen 2005). We assessed the effectiveness of a proposed management action by the proportion of bootstrap replicates ($n = 5,000$) in a simulation where $\lambda \geq 1$. We assumed that most management actions for lesser prairie-chicken populations would affect all age classes in a similar manner. Thus, simulations for NEST and P_i were drawn from the same probability distribution for both yearling and adult females.

RESULTS

Habitat quality differed between the 2 study areas. Site 1 had less shrub cover (and density) and more grass cover but of lower stature species of grass than site 2 (Table 1). However, forb cover and invertebrate biomass were greater at site 1 than at site 2. Raptor predation of lesser prairie-chicken females was slightly higher at site 1, but mammalian predation was similar between the 2 sites.

The finite rate of population change differed between the 2 populations: $\lambda^{(1)} = 0.535$ (95% CI = 0.286–0.845) and $\lambda^{(2)} = 0.739$ (95% CI = 0.616–1.343). The 95% confidence

Table 3. Asymptotic properties of projection matrices for 2 populations of lesser prairie-chicken in southwestern Kansas, USA, 1998–2003: the finite rate of population change (λ), stable age-distribution ($w_{Y,A}$), reproductive value (v), damping ratio (ρ), time to convergence to stable age distribution (t_{20}), net reproductive rate (R_0), and generation time (T). We calculated point estimates from each population matrix, and bias-corrected 95% confidence intervals from bootstrap distributions ($n = 10,000$).

Matrix properties	Site 1		Site 2	
	\bar{x}	95% CI	\bar{x}	95% CI
λ	0.535	0.286–0.840	0.739	0.616–1.343
w_Y	0.352	0.092–0.565	0.339	0.167–0.568
w_A	0.648	0.435–0.909	0.661	0.432–0.832
v_Y	1.00	Non-estimable	1.00	Non-estimable
v_A	0.60	0.32–0.65	0.91	0.49–1.14
ρ	11.64	3.81–591.00	7.87	2.50–24.77
t_{20}	1.22	0.47–2.24	1.45	0.93–3.28
R_0	0.37	0.08–1.06	0.49	0.29–1.28
T	1.61	1.21–1.82	2.34	1.63–3.53

limits indicated that site 1 would be projected to decline without immigration, whereas site 2 was not significantly different from $\lambda = 1$. Damping ratios were high in both populations ($\rho > 7.87$) and both populations would be expected to converge rapidly to a stable age distribution ($t_{20} < 1.5$ yr; Table 3). Adults constituted the majority of the stable-age distribution vector (w) at site 1 (0.66) and site 2 (0.65). Adults at site 2 tended to have a higher reproductive value ($v = 0.91$) than adults at site 1 ($v = 0.60$), but both were lower than yearlings ($v = 1.00$; Table 3). A juvenile female from either study site had highly variable but poor prospects ($R_0 < 0.5$) to replace herself during the short generation time ($T < 2.4$ yr).

Elasticity values for the lower-level rates suggested that λ was most sensitive to future changes in 3 rates: P_0 and CHICK tied rank for first, survival for all 3 adult seasons ranked second at site 1, and survival for all 3 adult seasons ranked first and P_0 and CHICK tied rank for second at site 2 (Table 4). We ranked yearling survival estimates for ($\lambda^{(2)}$) and clutch size of yearling's first nests ($\lambda^{(1)}$) as third largest effect on rates of population change. Because NEST_{1j} was also part of the reneesting element in the matrix, its elasticity value was equal to CLUTCH_{1j}. Reneesting and other components of fecundity would contribute little to future changes in λ . Variance-scaled sensitivities enabled a closer examination of potential effects of each vital rate by combining sensitivities and their variance. Variance-scaled sensitivities indicated that changes in CHICK would have the single largest contribution to changes in λ at both sites (Table 4). Interestingly, VSSs ranked juvenile survival (P_0) as second and third at site 2 and 1, respectively. The VSSs rankings of future changes in S_{ij} were much lower than those resulting from the elasticity rankings. Furthermore, each seasonal survival rate had its own VSS value, which indicated that survival of adult females during the breeding season was the most influential survival rate of breeding-age birds.

Absolute increases in demographic parameters resulted in mixed effects on λ for each study site (Table 5). Generally, increases in one demographic rate had relatively small effects

Table 4. Elasticities (e_x) and variance-scaled sensitivities (VSSs) for lower-level demographic rates (x) of matrices for 2 populations of lesser prairie-chicken in southwestern Kansas, USA, 1998–2003. The top 3 ranked rates are in bold.

Rate	Site 1				Site 2			
	e_x	Rank	VSS	Rank	e_x	Rank	VSS	Rank
CLUTCH _{1Y}	0.239	3	0.003	15	0.097	5	0.001	16
CLUTCH _{1A}	0.213	6	0.003	16	0.256	4	0.004	15
NEST _{1Y}	0.234	4	0.355	4	0.095	5	0.139	8
NEST _{1A}	0.210	7	0.522	2	0.253	4	0.300	3
RENEST _Y	0.010	9	0.019	14	0.004	6	0.008	14
RENEST _A	0.015	8	0.035	12	0.004	7	0.010	13
CLUTCH _{2Y}	0.010	9	0.000	18	0.004	6	0.000	17
CLUTCH _{2A}	0.015	8	0.000	17	0.004	7	0.000	18
NEST _{2Y}	0.010	9	0.027	13	0.004	6	0.012	11
NEST _{2A}	0.015	8	0.040	11	0.004	7	0.011	12
CHICK	0.477	1	0.741	1	0.362	2	0.704	1
P_0	0.477	1	0.441	3	0.362	2	0.335	2
$S_{Y\text{-breeding}}$	0.228	5	0.181	7	0.260	3	0.156	7
$S_{Y\text{-nonbreeding}}$	0.228	5	0.071	10	0.260	3	0.063	10
$S_{Y\text{-winter}}$	0.228	5	0.125	9	0.260	3	0.111	9
$S_{A\text{-breeding}}$	0.295	2	0.294	5	0.378	1	0.296	4
$S_{A\text{-nonbreeding}}$	0.295	2	0.156	8	0.378	1	0.174	6
$S_{A\text{-winter}}$	0.295	2	0.199	6	0.378	1	0.205	5

on λ , except for large increases in CHICK = 50%, P_0 = 70%, or $S_{A\text{-breeding}}$ at site 2 (Table 5). A management goal for nest success of 50% had the largest effect on $\lambda^{(1)}$. Increases in winter survival had minimal effect on λ at both sites, but increases in $S_{A\text{-breeding}}$ had a greater effect at site 2. Simulations of management actions that simultaneously achieved NEST + CHICK rates of 40% had 2.5–5.3 times the effect on $\lambda^{(1)}$ and $\lambda^{(2)}$, respectively, than did managing for high levels of female survival.

DISCUSSION

Our synthesis used empirical data from a 6-year field study and yielded several important results about demographic rates of lesser prairie-chickens: 1) our populations exhibited a life-history strategy of high productivity, 2) changes in nest success and chick survival may have had the largest impact on population growth rates, 3) female survival during breeding was more influential on population dynamics than

Table 5. Proportion of simulated population matrices ($n = 5,000$) for management objectives that resulted in $\lambda \geq 1$. We used a modified life-stage simulation analysis in which each demographic rate was targeted for management objectives of 40% and 50% for nesting and chick survival, 60% and 70% for annual juvenile survival, and 80% and 90% for seasonal survival of breeding age females for 2 populations of lesser prairie-chicken in southwestern Kansas, USA, 1998–2003.

Vital rate	Management objective (%)	Variance of objective (%)	Site	
			Site 1	Site 2
NEST	40	30–50	0.059	0.027
	50	40–60	0.149	0.071
CHICK	40	30–50	0.001	0.211
	50	40–60	0.020	0.454
NEST + CHICK	40	30–50	0.096	0.288
	50	40–60	0.581	0.817
P_0	60	50–70	0.019	0.058
	70	60–80	0.043	0.115
	80	75–85	0.013	0.058
S_{breeding}	90	85–95	0.027	0.144
	80	75–85	0.006	0.010
S_{winter}	90	85–95	0.007	0.029

winter mortality, and 4) the application of 3 different sensitivity analyses provided similar patterns but different levels of resolution in examining the importance of vital rates. We discuss the synthesis of our results with research conducted on habitat use and other aspects of these populations since 1997 (Hagen et al. 2005b, 2006, 2007b; Pitman et al. 2005, 2006a, c) and place them in the context of lesser prairie-chicken conservation.

The applicability of demographic models is limited by the quality of the data; thus, it is important to consider the potential limitations or biases of our demographic data. We are confident that our estimates of female and juvenile survival are unbiased because radiomarking does not affect adult survival (Hagen et al. 2006). High rates of censoring (>20%) can positively bias known-fate survival estimates when sample sizes are small (<50 animals; Tsai et al. 1999). Right-censoring of adults and yearlings in our study was approximately 30%, but right-censored lesser prairie-chickens from our study areas had similar survival to those with known fates (Hagen et al. 2006). Right-censoring of radiomarked juveniles was low (6.3%) and those estimates are likely accurate, albeit from a sample of 32 birds over 3 years. We are also confident in our estimates of nest success. Nest success in our study was similar to published estimates (Hagen and Giesen 2005), and females were flushed only once during incubation to determine clutch size (Pitman et al. 2006c). Westemeier et al. (1998) reported that flushing greater prairie-chicken (*Tympanuchus cupido*) females from nests resulted in 95% of those females returning to nests, and nest success was not negatively impacted. It is possible that estimates of CHICK may have been biased low because of our systematic flush-counts, if these counts negatively affected survival or if detection probabilities were low. However, >33% of all broods in our study suffered complete brood loss prior to the first flush at 14 days posthatch (Pitman et al. 2006b). Most flush-counts were conducted in the morning while chicks were being brooded by the female;

thus, detection probability was likely high. Once chicks reached 34 days of age, their mobility and independence increased, and they could readily mix with other broods.

The projected stable age distributions (\mathbf{w}) should reflect the natural age distribution because damping ratios were high ($\rho \geq 11.6$) and convergence times were relatively short ($t_{20} \leq 1.5$ yr). A comparison between the observed age structure of the radiomarked females for both areas (yearling = 0.38, ad = 0.62) suggested a good fit of these matrix properties. Meeting the assumption of \mathbf{w} in the model is important especially when reproductive values (\mathbf{v}) are unequal in the population (Hoekman et al. 2002), as was the case in both of our populations. Both populations had short generation times ($T < 2.3$ yr) with low net reproductive rates ($R_0 < 0.5$), but the 95% confidence intervals for both R_0 estimates were highly variable and included 1, suggesting that populations had some likelihood of replacement over their short generation times.

Variance-scaled sensitivities enabled us to evaluate potential impacts of each lower-level rate using a metric that accounted for both sensitivity and inherent variability. The VSSs indicated that the effects of CHICK on λ was 1.7–2.1 times greater than any other rate at both sites. We concur with Peterson et al. (1998) that sensitivity to CHICK should have a greater population-level impact because total brood loss for a female results in no contribution of young that year. Total clutch loss of first nests may have a similar effect, but there is a probability of reneating based on stage at loss of first nest (Pitman et al. 2006b). The VSS of NEST₁ indicated that future changes in this rate had the second and third largest impact on λ at site 1 and 2, respectively. Because >30% of all female mortality occurs during the nesting season (Hagen et al. 2007b), we concluded that λ had a greater sensitivity to nest success of older birds. Thus, conservation measures that increase nest success will likely also increase female survival (Hagen et al. 2007b).

Our findings indicate a generalized life-history strategy for prairie chickens, a life-history strategy of boom-or-bust fecundity. Such a strategy may drive short-term dynamics in a short-lived high reproductive potential (Sæther and Bakke 2000). Survival (S) of radiomarked juveniles in our study is a known-fate estimate of marked individuals. However, at the population level, recruitment (or production) comprises 2 rates, juvenile survival and immigration from other habitat patches. Because natal dispersal of female lesser prairie-chicken often occurs just prior to the breeding season (Pitman et al. 2006c), new individuals could be added to the population without experiencing the extrinsic factors as juveniles residing on our study sites.

Several studies concluded that elasticity analyses alone were inadequate, but incorporating other complementary sensitivity indices may yield a more complete understanding of biological systems (Mills et al. 1999, Heppell et al. 2000, Link and Doherty 2002, Nichols and Hines 2002). The perturbation analysis and VSS ranks provided evidence that nesting and brood rearing aspects of the life history and breeding-season female survival were critical to maintaining

population stability for lesser prairie-chickens in southwest Kansas. Thus, increases in adult winter survival or juvenile survival by eliminating hunting (<3% of all mortality) would do little to stabilize these populations (Table 5). Hunting of a declining population can only be justified if hunting mortality is mostly compensatory to natural mortality. Harvest of willow ptarmigan (*Lagopus lagopus*) and greater sage-grouse (*Centrocercus urophasianus*) indicated that decreases in adult survivorship from hunting negatively affected population growth, especially in years with poor recruitment (Steen and Erikstad 1996, Johnson and Braun 1999). The markedly higher harvest rates (10–20%) in those studies likely had a larger effect on survival than the low harvest rates (2–5%) observed in our study (Hagen et al. 2007b).

Vegetation cover and structure and avian predation risks differed between sites, and these extrinsic factors were likely related to differences in demographic rates (Table 1). Sagebrush density, canopy cover, and grass height contributed to the concealment and success of nesting females (Pitman et al. 2005). Specifically, site 2 had 2 pastures with the highest densities of sagebrush plants (>9,000 plants/ha) and highest probability of nest success and female survival during incubation (Pitman et al. 2005). Additionally, annual survival was greater at site 2, which may have resulted from greater concealment or thermoregulatory properties of the habitat (Patten et al. 2005). Interestingly, a slightly larger proportion of lesser prairie-chicken mortalities were attributed to raptors at site 1 than site 2, providing some evidence that the greater concealment cover yielded increased female survival at site 2. Moderate stands of sagebrush (4,000–6,000 plants/ha) yielded the highest daily survival rate of chicks through 14 days posthatch (Pitman et al. 2006a) and greatest abundance of invertebrates (Hagen et al. 2005b). Habitat characteristics with greater forb cover were available at site 1 and the effect was evidenced by increased chick growth rates and survival at this study site (Hagen et al. 2005b, Pitman et al. 2006b). The interspersed (or lack thereof) of nesting and brood-rearing habitats suggested that the risk of using more open habitat may yield faster growth rates and improved survival. Thus, differences in chick survival and nest success on our study sites may have been explained in part by differences in optimal sagebrush density for these life-history stages.

Ascertaining the precise status of these populations was difficult given that both sampling and process variance were included in the parameter estimates. Our point estimates of λ 's projected 26–46% annual declines for the study populations without immigration, but only site 1 was significantly lower than a stable population. The confidence limits around λ in both populations suggested that λ was similar between areas. The λ values were <1 in these 2 fragmented populations and indicated that they must be maintained by immigration from other habitat patches. Lek survey routes through this region have detected declines similar to those reported in our analyses (Fig. 1B), but age-ratio data collected during our study support the idea that immigration is a potential mechanism for population

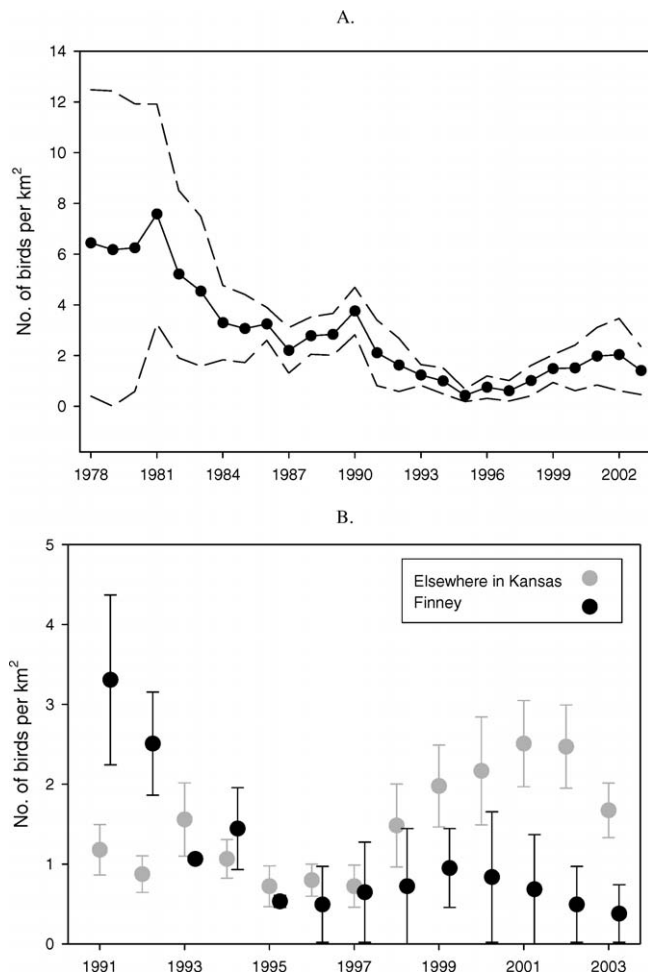


Figure 1. Population trends for lesser prairie-chicken populations (birds/km² and 95% CIs) in sand sagebrush prairie of Kansas, USA, as estimated from (A) 5 survey routes monitored consistently since 1978, and (B) more recent trends (1991–2003) of lesser prairie-chickens in Finney County, Kansas, as compared with the rest of the species range in Kansas. Both figures depict data recorded along systematic survey routes conducted by the Kansas Department of Wildlife and Parks.

stability. Our analyses were based on data from intensive field studies and complementary to the conclusions of literature reviews across large geographical regions (Peterson and Silvy 1996, Wisdom and Mills 1997, Peterson et al. 1998).

MANAGEMENT IMPLICATIONS

Management efforts aimed at increasing the quality or quantity of nesting and brood habitat will have the greatest benefits to lesser prairie-chicken populations. Specifically, vegetation should be managed to maximize reproductive output and female survival during the breeding period. For increasing nesting success, habitat management should include adequate sagebrush cover (>18%) and density (6,500–9,000 plants/ha), grass cover (>30%) and height (>25 cm; Pitman et al. 2005, Hagen et al. 2007b); typically these are later seral or successional habitats. However, an interspersed of earlier successional habitats with greater herbaceous cover (>15%) and less sagebrush cover (6–10%) and density (3,000–5,000 plants/ha) are needed to increase

chick growth rates and brood survival (Hagen et al. 2005a). The optimal extent of interspersed or juxtaposition of nesting and brood-rearing habitats needs to be quantified for more effective management. Additionally, if female survival during the breeding season is enhanced concurrent to increases in nesting success and brood survival, the largest positive effects on λ may be realized. Our study provides some initial insights as to the impacts of hunting on a declining species. Based on our population models, reduction or elimination of the hunting of lesser prairie-chickens may slightly increase annual survival but would have little overall effect on λ . However, our results may not be representative of harvest rates within the lesser prairie-chicken range of Kansas. The statewide harvest rate cannot be accurately estimated because current methods only allow for an estimate of total harvest. Thus, improvements in survey methodology of harvest and creating a band-recovery program are needed to assess the impacts of harvest to population stability on a statewide scale.

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