Viability and Conservation of an Exploited Sage Grouse Population

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Abstract: *We analyzed the viability of the Sage Grouse (*Centrocercus urophasianus*) population of North Park, Colorado, to evaluate its supposed decline due to hunting pressure and habitat degradation. Demographic data from 23 years of surveys were used to parameterize a post-breeding, female-based projection matrix with three life stages: juveniles, yearlings, and adults. The population was found to be approximately stable or in decline only if immigration and apparent surveying errors were factored from the data set. Adult and juvenile survival and adult and juvenile reproduction, respectively, were identified as the most limiting demographic factors. Empirical evidence from designed experiments with Sage Grouse has shown that these demographic factors respond markedly to habitat manipulations, especially brush manipulation. Several plausible management scenarios were evaluated with 100-year population projections generated through Monte Carlo simulation (1000 iterations), sampling from a normal probability distribution entraining the observed variability in each demographic parameter (95% confidence limits). Habitat manipulations to achieve moderate levels (~15% canopy cover) of sagebrush (*Artemisia tridentata*) are recommended. Regression analyses with power tests showed correspondence between hunting mortality and total mortality for juveniles and adults. Provided that habitat manipulations improve the survival of juveniles and adults, population viability may be conserved without reducing harvest by hunters.*

Viabilidad y Conservación de una Población Explotada de *Centrocercus urophasianus*

Resumen: *Analizamos la viabilidad de la población de *Centrocercus urophasianus* en el Parque Norte, Colorado, para evaluar su supuesto declive ocasionado por presiones por caza y degradación del hábitat. Datos demográficos de 23 años de estudios fueron utilizados para parametrizar una matriz de proyección posterior a la estación reproductiva, basada en hembras y con tres estadios de vida: juveniles, organismos de un año y adultos. La población se encontró en una situación aproximadamente estable o en declive unicamente si la inmigración y errores aparentes de muestreo fueran eliminados de la base de datos. La supervivencia de juveniles y adultos y la reproducción de adultos y juveniles respectivamente, fueron identificados como los factores demográficos más limitantes. Evidencias empíricas de experimentos diseñados con la especie han demostrado que estos factores demográficos responden marcadamente a manipulaciones del hábitat, especialmente a la manipulación por fricción. Diversos escenarios plausibles de manejo fueron evaluados con proyecciones poblacionales de 100 años mediante simulaciones Monte Carlo (1000 repeticiones), muestreos de una distribución de probabilidad normal incorporando la variabilidad observada en cada parámetro demográfico (95% limites de confianza). Se recomienda la manipulación del hábitat para alcanzar niveles moderados (~15% cobertura de dosel) de salvia arbustiva (*Artemisia tridentata*). Análisis de regresión con pruebas de poder mostraron correspondencia entre la mortalidad por caza y la mortalidad total de juveniles y adultos. Pensando que las manipulaciones al hábitat mejorarían la supervivencia de juveniles y adultos, la viabilidad poblacional podría ser conservada sin reducir la cosecha por cazadores.*

Introduction

Sage Grouse (*Centrocercus urophasianus*) are endemic to the sagebrush (*Artemisia* spp.) steppes of western North America and were once a highly valued gamebird in California, Colorado, Idaho, Nevada, North Dakota, Montana, Oregon, South Dakota, Utah, Washington, and Wyoming (Braun et al. 1977; Autenrieth 1981; Ritchie et al. 1994). Sage Grouse depend on sagebrush for food and cover and are extremely sensitive to fragmentation of large tracts of sagebrush rangeland (Schneegas 1967; Martin 1970; Braun et al. 1977). Sagebrush removal programs, overgrazing by cattle of herbaceous forage shared by Sage Grouse, and general encroachment of civilization into rangeland have been associated with drastic reductions in or elimination of many Sage Grouse populations (Schneegas 1967; Klebenow 1970; Braun et al. 1977; Swenson et al. 1987; Ritchie et al. 1994). Today, Sage Grouse are locally threatened, endangered, or extinct over much of their former range. Sage Grouse have been extirpated in Arizona, Kansas, Nebraska, New Mexico, Oklahoma, and British Columbia, and they are no longer hunted in Saskatchewan and South Dakota. The viability of populations is generally uncertain, due in part to a lack of appropriate long-term data and analyses.

Population viability analysis (PVA) can help to refine the management of challenging species such as Sage Grouse. A PVA is a type of risk assessment designed to project the likelihood of a population's persistence—or, more directly, its extinction—under particular conditions. The conditions incorporated into the projection model for a population include demographic parameters, primarily the reproduction and survival of particular cohorts or sex and age classes (Boyce 1992; Gotelli 1995). Conventionally, estimates of demographic traits are used to parameterize Leslie's linear projection matrix, and computer simulation programs are used to make the projections. Variations on the classic Leslie matrix can be derived for linear population projection even for species with complex life cycles (Crouse et al. 1987; Pascual & Adkison 1994). Environmental influences on demographic parameters can be strong. Stochasticity in the environment can cause significant variability in the demographic parameters used to construct the projection matrix (Boyce 1992; Nantel et al. 1996). To model these effects, estimates of the variance in matrix elements are used to create distributions of respective parameter estimates, and a simulator repeatedly samples from these distributions to project the population over time for a stochastic environment. Sensitivity analysis of the respective matrix elements detects which demographic factors are most limiting to population growth (Crouse et al. 1987). Elasticity analysis demonstrates the comparative impacts of equivalent changes to the different elements on the overall population (Silvertown et al. 1996). By using sensitivity and elasticity analyses to iden-

tify prime demographic classes to target for manipulation and population projections to demonstrate persistence under differing conditions, managers can evaluate the likely effectiveness of proposed conservation strategies without haphazardly causing an extinction through in situ experimentation. Depending on the quality of the data used to parameterize the projection matrix, PVA can be highly useful for improving the management of declining species.

Colorado presents particularly good prospects for examining the Sage Grouse dilemma because much of its sagebrush rangeland has been altered, but enough habitat and birds remain to facilitate wildlife population studies (Lovell et al. 1985; Hupp & Braun 1991; Braun 1995). Colorado's largest remaining hunted Sage Grouse population occupies the greater North Park Valley of the Platte River. This population has experienced substantial fluctuations because of habitat alteration and possibly hunting pressure. The North Park population is also distinctive in that spring population surveys and autumn hunter-harvest monitoring have been conducted every year since 1973, generating what is likely the most comprehensive long-term Sage Grouse demography data set in existence.

Concerns have been acknowledged (Braun 1995) that the overall trend for the North Park population, like other Sage Grouse populations, is toward decline. Until now, however, the available demographic data have not been used for PVA. Regulated hunting has been encouraged, with varying harvest intensity among years. Hunting has been considered a source of compensatory mortality, and bag limits and season lengths have been liberalized in recent years to promote hunting opportunity (Braun & Beck 1996).

We present a PVA for the North Park Sage Grouse flock. Our objectives were to identify the overall population trend, predict population dynamics for the next century, identify the demographic parameters most influential on population growth, and suggest important considerations regarding habitat quality for future management. We consider the likely impacts of hunting and habitat degradation on the viability of this population.

Methods

Population Surveys

There are 27 active lekking areas within the North Park area. Visual counts of birds were made at each lek from a distance of 400 m or less with spotting scopes and binoculars during repeated daily sessions throughout April and May from 1973 to 1995. Both males and females were counted, but overall abundance estimates were based on counts of males because female attendance at leks is irregular. The presence of yearling males was

noted when possible. Peak male attendance at a lek was taken as the estimate of cock abundance at that site for that season. Peak counts were combined to derive an overall cock population estimate each year. It was assumed that all males present were observed at a given lek during the peak count (Emmons & Braun 1984; Braun & Beck 1996).

Hunter harvest data were collected (Braun & Beck 1985) in two ways. Check stations were operated during estimated peak recreational days (at least the first weekend of the season) at major highway points leading from the North Park management unit. Hunter cooperation was mandatory and enforced. One wing was collected from each bird examined at the stations. Wings were also collected from volunteer wing collection stations along highways throughout each season, when check stations were not operated.

Ratios of adults to yearlings to juveniles for each sex and sex ratios for each of the three stages (age classes) were determined through laboratory analysis of wings collected from hunters (Beck et al. 1975). Nesting success for adult females and yearling females was estimated by determining the proportion of females in each stage (adults, yearlings) with primary feather molt patterns indicating nesting activity in Sage Grouse (C.E.B., unpublished data). The relative nesting success for each stage was scaled to overall per capita female juvenile production to obtain an estimate of the number of female juveniles produced per capita for yearlings and adults, assuming equivalent average brood sizes between stages. Brood size is the number of juveniles per female in the autumn population. Differences in realized fecundity between adults and yearlings were from nesting success alone.

Calculating Additional Demographic Parameters

Because survival was not measured directly (radiotelemetry was not a part of this study), derivation of survival estimates was based on stage-specific abundance estimates between years. Sex ratios for adults and yearlings obtained from harvest data were multiplied by cock count data to estimate the abundance of females of each age class in the population the previous spring. This approach assumes that stage (age class) and sex ratios do not change from breeding until the start of the next hunting season, that all classes of birds are proportionally exploited by hunters, and that winter survival is not sex-biased.

The estimated spring abundances of females were multiplied by their respective estimated per capita fecundity to obtain an overall estimate of juvenile abundance for the start of each autumn. Abundance estimates for females and juveniles were combined to generate an estimate of total female population size for the start of autumn, assuming that female mortality over the summer was insignificant; an earlier radiotelemetry study (Dunn & Braun 1986) supports this assumption. Thus, estimates were obtained each year for the numbers of yearling (previous autumn's juveniles) and adult females present in spring and female juveniles present at the start of autumn. The number of new adult females (yearlings from the previous autumn) each spring was derived by subtracting the proportion of adult females from the upcoming autumn from the total adult female population, again assuming that summer mortality was insignificant and equivalent among cohorts. Annual survival was calculated by dividing the estimated abundances of "old" adult (>2 years) and newly recruited adult females in the upcoming year by their respective abundances and for juveniles by dividing yearling females in the following spring count by the current autumn's juvenile abundance. Thus, we used a three-stage, female-based, post-breeding model, which is supported by the observations of Connelly et al. (1993).

Population Viability Analysis

Survival and fecundity data for each of three age classes of females were derived from the aforementioned methods and used to parameterize the population projection matrix. MATLAB software (Janzow et al. 1992) was used to derive additional life history parameters from the matrix. The linear projection was of the standard form

$$\boldsymbol{n}_{(t+1)} = \mathbf{A}\boldsymbol{n}_{(t)},$$

where $\boldsymbol{n}_{(t+1)}$ is the projected population for time $t + 1$, $\mathbf{A}$ is the projection matrix, and $\boldsymbol{n}_{(t)}$ is the current population vector (Gotelli 1995). Lambda (λ = net rate of population change) was given as the dominant eigenvalue of the projection matrix $\mathbf{A}$; the right eigenvector $\boldsymbol{w}$, with elements converted into relative proportions, provided the stable age distribution

$$\mathbf{A}\boldsymbol{w} = \lambda\boldsymbol{w}.$$

The left eigenvector ($\boldsymbol{v}$) of the Leslie matrix, actually calculated in MATLAB as the right eigenvector ($\boldsymbol{w}$) of the inverse matrix $\mathbf{A}'$, scaled to λ, yielded the reproductive values for the three stages (Crouse et al. 1987). Sensitivity and elasticity matrices ($\mathbf{S}$ and $\mathbf{e}$) were generated as

$$\mathbf{S} = (a_{ij}/\lambda)((v_i w_j)/(\langle v, w \rangle))$$

$$\mathbf{e} = (a_{ij}/\lambda)(\partial\lambda/a_{ij}),$$

where a_{ij} refers to an element of $\mathbf{A}$ and $\langle \rangle$ denotes the scalar product (de Kroon et al. 1986; Crouse et al. 1987; Kalisz & McPeek 1992; Silvertown et al. 1996).

The parameterized projection matrix was used for population projections with Lotus @RISK software (Winston 1996). A distinct benefit of long-term data such as those for North Park is that annual variability in demographic parameters can be incorporated into population

projections. This variability can be caused by (1) demographic stochasticity arising from the random patterns in sequences of demographic events (births and deaths)—the same kind of "sampling error" evident in disproportional outcomes of independent coin flips—or (2) environmental stochasticity. Demographic stochasticity is swamped from large populations like North Park's in the same way outcomes of coin flips equalize with increasing sample size, so variability of parameters in our analysis reflects primarily environmental stochasticity (Gotelli 1995). Stochastic modeling increases the realism of the modeling processes, and thus the reliability of the projection results (Boyce 1992). In a sense, stochastic modeling indirectly accounts for complex ecosystem feedbacks into single-population dynamics as manifest in the history of demographic data. For this study the standard deviations for stage-based fecundity and survival estimates were entrained into Monte Carlo population projection with environmental stochasticity, assuming a normal probability distribution for environmental conditions, in @RISK. One-hundred-year projections were replicated with 1000 iterations. Total female population estimates for each year were truncated to integer values to avoid overestimating viability (Gotelli 1995).

We independently manipulated the most influential demographic parameters on population dynamics, as identified by sensitivity and elasticity analyses, at 5% and 10% increments for additional @RISK simulations. The different matrices are hereafter called "management scenarios" because management is implicit in changing the values of matrix elements. Estimates of likelihood of maintaining populations of differing sizes over the projection interval were compared between management scenarios to illustrate the likely relative impacts of those strategies on the future of the North Park Sage Grouse population. The relationship between hunting mortality and overall mortality for each stage and for the total population of females was examined with least-squares regression (Bonett 1994).

Demographic parameters from populations in variable environments have unusual statistical properties in that their variances can actually destabilize and inflate as more surveys are added to the data set (Boyce 1992). This can bias stochastic models toward overestimating extinction probability if data from truly exceptional years are included. For reliable stochastic modeling, the span of the data needs to be sufficient to stabilize the variance of the parameters, especially λ (Boyce 1992). Variances for the North Park demographic parameter estimates were plotted over time as a graphic diagnostic of sample adequacy.

Results

Life-history parameters with standard deviations were derived from analysis of field survey data (Table 1). Survival and fecundity estimates for yearlings and adults are similar, but the two stages were kept separate because (1) the three-stage model is already workably parsimonious, and (2) hunters may distinguish older from younger adult grouse, even in flight, suggesting some potential for future selective harvest. In the overall analysis, 4 years of survival and reproduction estimates were deleted from the data set, including 1977, 1984, 1986, and 1994. This decision was based on the derivation of annual survival estimates greater than 100%, in spite of known hunting losses. This was likely caused by unrecorded immigration or gross underestimation of spring abundances in those years. Emmons and Braun (1984) suggested that poor lek attendance caused by inclement weather in some years can lead to this type of measurement error. The spring counts from the outlier years were still used in calculating survivorship for preceding years; only survival values for years with survival greater than 100% for some stage were excluded from the final analysis. The rate of population change, λ, with exceptional years included was greater than 1.00, suggesting an increasing population. The tenably modified data set yielded a λ slightly below 1.00 (Fig. 1), indicating a generally decreasing population, which reflects the trend subjectively observed by field biologists (Braun & Beck 1996).

The stable age distribution was characterized by equal proportions of adults and juveniles, with relatively few yearlings. Reproductive values for yearlings and adults were equivalent (Table 1). The reproductive value represents the number of juveniles in the post-breeding population that females in the later stages are "worth." Accordingly, adult and yearling females were found to be approximately equal in importance as reproducers.

Previous estimates for minimum time span needed for demographic data to stabilize the variance of λ for bird

Table 1.   Life-history table for the North Park, Colorado, Sage Grouse population, based on 23 years of demographic data and a three-stage, female-based model.

Stage	Age (years)	Annual survival		Fecundity		Reproductive value	Stable age distribution
		$\overline{x}$	SE	$\overline{x}$	SE		
1	≤1	0.330	0.119	0.550	0.217	1.00	0.428
2	1–2	0.731	0.212	0.817	0.245	2.42	0.144
3	2+	0.733	0.213	0.817	0.245	2.43	0.428

$$
\begin{bmatrix}
m_0p_0 & m_1p_1 & m_2p_2 \\
(0.181) & (0.596) & (0.598) \\
\\
p_0 & 0 & 0 \\
(0.330) \\
\\
0 & p_1 & p_2 \\
& (0.731) & (0.733)
\end{bmatrix}
\qquad
\begin{bmatrix}
n_0 \\
\\
\\
n_1 \\
\\
\\
n_2
\end{bmatrix}
$$

$$\lambda = 0.9794$$

$$
\mathbf{S} \quad = \quad
\begin{bmatrix}
\underline{0.2357} & \underline{0.0794} & \underline{0.2355} \\
\underline{0.5704} & 0.1921 & 0.5698 \\
0.5727 & \underline{0.1929} & \underline{0.5722}
\end{bmatrix}
$$

$$
\mathbf{e} \quad = \quad
\begin{bmatrix}
0.0436 & 0.0483 & 0.1438 \\
0.1941 & -- & -- \\
-- & 0.1440 & 0.4282
\end{bmatrix}
$$

*Figure 1. Projection matrix, λ, sensitivity matrix (**S**) and elasticity matrix (**e**) for the North Park Sage Grouse population using a post-breeding model. For the projection matrix, m_x is realized per capita fecundity for stage x, p_x is annual survival for stage x, and n_x is estimated post-breeding abundance for stage x. Underlined elements of **S** correspond to non-zero elements of the original projection matrix. Progressively larger values for elements of **S** reflect the greater relative importance of the life-history parameter estimates with which they correspond. Larger values of **e** reflect the relative net effects of changing the corresponding projection matrix value by a given amount.*

populations ranged from 30 to 50 years (Thomas 1990; Boyce 1992). Variances for the North Park demographic elements and λ tended to stabilize with approximately 12 years of data (Fig. 2). Juvenile fecundity was an exception, showing a tremendous increase in the fourteenth year. Therefore, the span of the data set is probably sufficient to capture a suitable amount of environmental stochasticity to generate useful parameter estimates. Lambda was actually less variable in the data set containing the presumed measurement errors (final $\sigma^2 = 0.271$ for unmodified data set, $\sigma^2 = 0.297$ for modified data set), which likely makes our persistence probability estimates conservative.

Sensitivity and elasticity analyses revealed that adult and juvenile survival were the demographic parameters most limiting to the population's growth, followed by
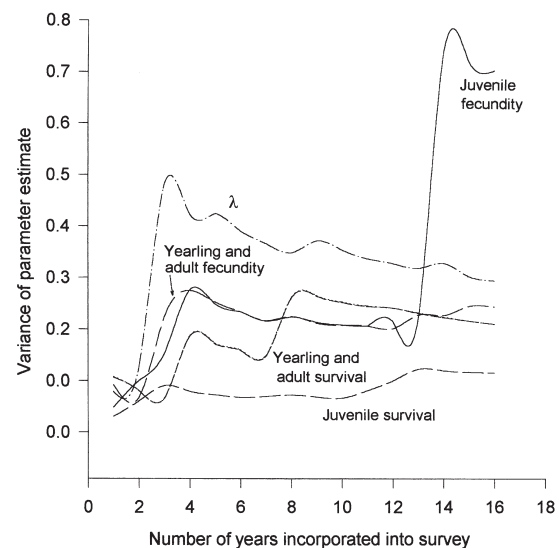

Figure 2. Variability of estimated demographic parameters as a function of sample size for the North Park, Colorado, Sage Grouse population.

adult and juvenile fecundity. These results reflect the importance of these two stages in the stable age distribution. Yearling survival was also important to population growth (Table 1; Fig. 1) and was included as a variable for manipulation in management scenario population projections.

Changes in adult survivorship produced the largest increases in lambda for each level of increase (5% and 10%; Figs. 3 & 4). At 10% improvement in survival of any
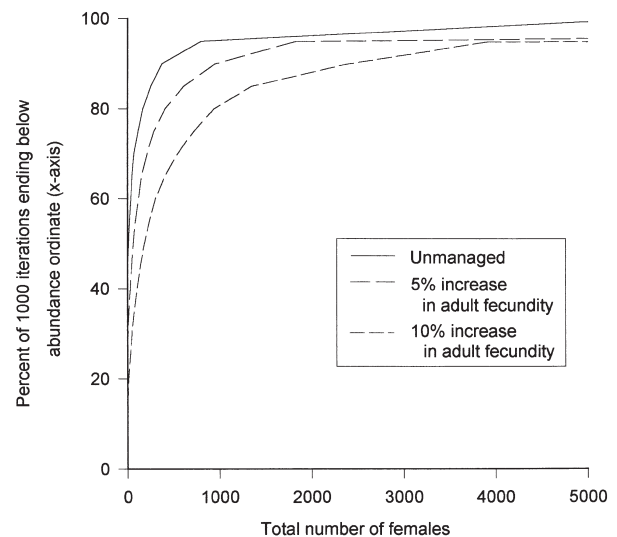

Figure 3. Stochastic, 100-year projection results for Monte Carlo simulations with 1000 iterations each. Extinction occurred for unmanaged and for 5% and 10% increases in adult fecundity in 45%, 25%, and 15% of iterations, respectively. Corresponding λ values are 0.979, 0.986, and 0.993.
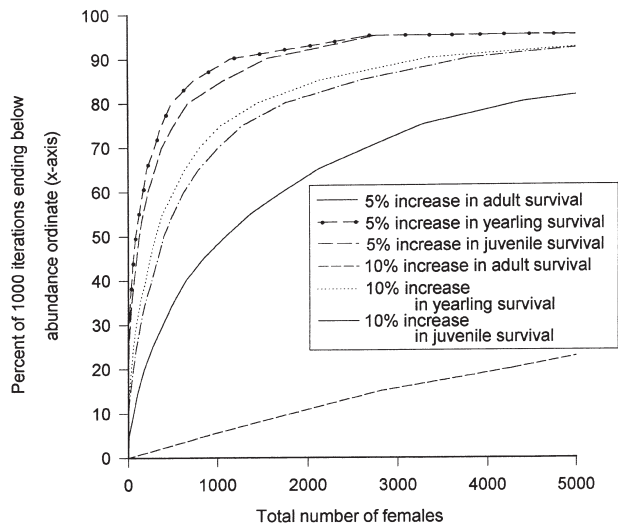
Figure 4. Stochastic, 100-year projection results for six additional Monte Carlo simulations with 1000 iterations each. Extinction occurred for 5% increases in adult, yearling, and juvenile survival and 10% increases in adult, yearling, and juvenile survival in 5%, 20%, 20%, 0%, 10%, and 10% of iterations, respectively. Corresponding λ values are 1.008, 0.989, 0.986, 1.036, 1.026, and 1.001.

stage class, λ exceeded 1.00 (Fig. 4). Conservation biologists typically target 95% probability of survival for the upcoming 100 years in designing management scenarios for finite populations such as Sage Grouse in North Park (Boyce 1992). The most conservative successful management scenario among the options we examined was a 5% increase in adult survival (Fig. 4), which resulted in a 3% increase in λ and doubled the population's time to extinction.

Discussion

The ultimate goal of PVA is to quantify population growth and compartmentalize the demographic factors contributing to the observed pattern. Thus, the decision to represent yearlings distinctly from adults in spite of similarities in fecundity and survival proved prudent. By separating yearlings from the adults, the importance of adult demographics was discerned more clearly. Thus, reproduction and survival of juveniles and adults—as opposed to yearlings—were identified as the demographic factors on which managers should focus most to improve viability for staving off extinction, improving harvest opportunities for hunters, or stabilizing the population against future disturbances.

It is logical to question the practicality of attempting to improve survival or fecundity. Identification of key population matrix elements does not automatically con-

fer management significance to those factors. If nothing can realistically be done to change a demographic parameter, management is at a dead end. Survival and realized fecundity values for Sage Grouse, however, have been shown to depend on habitat quality. All Sage Grouse avoid areas without sagebrush (Wallestad 1975; Braun et al. 1977; Johnson et al. 1996). Barnett and Crawford (1994) found that female nutrition during the pre-laying phase influences clutch size and that nutrition was best when preferred herbaceous forbs were abundant. Wallestad and Pyrah (1974) and Connelly et al. (1991) documented the preference of female Sage Grouse for forb-rich sagebrush habitat with sufficient sagebrush cover to reduce nest predation risks. Most predation of Sage Grouse is by rodents on eggs in the nest (Braun et al. 1977; Ritchie et al. 1994). DeLong et al. (1995) estimated that Sage Grouse nest success in Oregon was only 15%, with 96% of failures attributable to predation. Dense sagebrush stands (41% canopy cover) were associated with the lowest nest predation rates in Oregon, but only if residual grass cover was also heavy (19% canopy cover; Gregg et al. 1994). Drut et al. (1994) reported that 19–31% sagebrush cover, with 9–19% cover of forbs, was preferred by females with broods. Ritchie et al. (1994) found nest predation to be lowest in forb-rich stands with about 17% sagebrush canopy cover for protection. Johnson et al. (1996) found that Wyoming ground squirrels (*Spermophilus elegans*) were least abundant in forb-rich plant communities associated with about 15% sagebrush cover. Wyoming ground squirrels are an important nest predator in North Park. Therefore, habitat management that reduces ground squirrel abundance should influence potential and realized fecundity and the presence or absence of Sage Grouse. Based on previous research, about 15–20% canopy cover of sagebrush may be optimal nesting habitat for sites like North Park.

The habitat preferences of Sage Grouse can depend on season and sex. Males and females without broods apparently prefer denser sagebrush stands in summer than do females with broods (Ellis et al. 1989; Gregg et al. 1993). All Sage Grouse prefer dense sagebrush stands (25% or greater canopy cover) in winter (Homer et al. 1993), probably needing a minimum of 15% sagebrush cover (Wallestad 1975). Suitable winter habitat has been found to limit population growth where sagebrush control programs have drastically reduced sagebrush cover below these levels (Swenson et al. 1987).

The management scenarios we considered (Figs. 3 & 4) address the demographic factors most limiting to the population (Fig. 1). North Park, like most areas in traditional Sage Grouse range, has been affected by historic intensive grazing by cattle, road and utilities development, and direct habitat modification. Sage Grouse habitat improvement programs of brush management are highly feasible (Johnson et al. 1996). If forb production can be increased or maintained at high levels while ade-

quate sagebrush cover is maintained (15–20%), Sage Grouse survival and reproduction may increase. Any proposed "optimal" sagebrush cover level is hypothetical but has strong support in the literature (Martin 1970; Wallestad 1975; Drut et al. 1994; Ritchie et al. 1994; Johnson et al. 1996). The effects of sagebrush management can be dramatic: Ritchie et al. (1994) found that reducing decadent sagebrush to a level of 17% canopy cover resulted in a threefold decrease in predation on artificial Sage Grouse nests. Thus, the population manipulation scenarios presented (Figs. 3 & 4) are realistic endpoints for habitat outcomes. Efforts resulting in increased adult survival will be particularly useful in increasing the viability of the North Park population.

The contribution of hunting losses to overall mortality (Table 2) should also be considered. If hunting mortality is additive to total mortality for a stage, there should be a detectable relationship between annual harvest intensity and overall losses of birds. Regression analysis can therefore provide some information about the importance of hunting mortality. In order to demonstrate that harvest is truly compensatory, however, the number of individuals lost to hunting must be shown to represent losses that would otherwise occur from other causes in the absence of hunting. That is, removal of hunting would shift the relative importance of various causes of mortality but would not affect overall mortality. Density dependence in mortality is the underlying cause of such compensation (Mackie et al. 1990; Ellison 1991); under density independence, hunting mortality is additive. Despite their importance to wildlife management, compensatory dynamics arising from density dependence are not well documented for game animals (Mackie et al. 1990). Evaluating density-dependent mortality and compensation for the North Park population would be possible with precise data on the sources and intensity of mortality as hunting mortality varies. For two reasons, we do not provide this definitive analysis. First, radio tracking was not part of this study but presents a potentially valuable direction for future research. Second, the high level of environmental stochasticity characterizing this system causes much variability in habitat and forage between years, meaning that carrying capacity varies

likewise. This complicates the assessment of density dependence. Thus, although our PVA accommodates stochasticity, our analysis of the effects of hunting are limited to weak inference through correlation.

Regression analysis of stage-based total mortality versus hunter harvest revealed that the total number of birds lost from the autumn population each year correlates to harvest intensity. This suggests, through retroduction, that hunting mortality at some threshold level may be additive within stages. Deaths from hunting explained a significant amount of variation in annual mortality for juveniles and yearlings and for the total population. No correlation was found between harvest of adults and total adult mortality, but a significant type II error probability ($p = 0.70$) indicates that this conclusion stems from sample inadequacy (Bonett 1994). These results provide sufficient basis to hypothesize that hunting losses may be additive. Given the sensitivity of population dynamics to survival, it may be prudent to decrease hunting experimentally in all or part of the management area for a few years to see if survival rates improve. If habitat improvements can be made that increase survival rates to a point where they no longer limit population growth, then reductions in hunting may not be beneficial. This is precisely the appropriate application of PVA: the elucidation of the most reasonable hypotheses to consider in designing management plans for a population (Lindenmayer et al. 1993; Pascual & Adkison 1994; Ratsirarson et al. 1996; Silvertown et al. 1996).

Population viability analysis remains the best available technology, albeit retroductive, for safely evaluating management options for sensitive or threatened populations. The reliability of our PVA is enhanced by the long time span and fine demographic detail of the North Park data set, which made it possible to model stochasticity and to examine relationships between harvest and overall mortality. Continuing the annual population surveys to track the key demographic elements and net rate of population change as they vary through time after manipulations will further refine knowledge about the viability of Sage Grouse in North Park.

Acknowledgments

Table 2. Relationships between hunting mortality and total mortality for demographic groups in North Park, Colorado, Sage Grouse population.*

Group	τ	Power (%)	Pearson's r	SE	p
Juveniles	7.394	>95	0.849	0.136	<0.0001
Yearlings	1.778	>95	0.660	0.194	0.0041
Adults	3.414	30.2	0.366	0.240	0.1484
Overall population	1.283	>95	0.949	0.081	<0.0001

*Results are from least-squares regression ($\alpha = 0.05$, n = 17, τ = estimated treatment effect) and power analysis ($\alpha,\beta = 0.05$).

Literature Cited

Autenrieth, R. E. 1981. Sage Grouse management in Idaho. Wildlife bulletin 9. Idaho Department of Fish and Game, Boise.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of Sage Grouse hens in Oregon. Journal of Range Management 47:114-118.

Beck, T. D. I., R. B. Gill, and C. E. Braun. 1975. Sex and age determination of Sage Grouse from wing characteristics. Colorado Division Game, Fish and Parks Information, Denver.

Bonett, D. G. 1994. Business statistics. Kendall Hunt, Dubuque, Iowa.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481-506.

Braun, C. E. 1995. Distribution and status of Sage Grouse in Colorado. Prairie Naturalist 27:1-9.

Braun, C. E., and T. D. I. Beck. 1985. Effects of changes in hunting regulations on Sage Grouse harvest and populations. Pages 335-343 in S. L. Beasom and S. F. Robertson, editors. Game harvest management. Proceedings of the third international symposium. Caesar Kleberg Research Institute, Kingsville, Texas.

Braun, C. E., and T. D. I. Beck. 1996. Effects of research on Sage Grouse management. Transactions of the North American Wildlife and Natural Resoures Conference 61:429-436.

Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of Sage Grouse habitats. Wildlife Society Bulletin 5:99-106.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage Grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55:521-524.

Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting by Sage Grouse in southeastern Idaho. Condor 95:1041-1043.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: the relative contributions of demographic parameters to population growth rate. Ecology 67:1427-1431.

DeLong, A. K., J. A. Crawford, and D. C. DeLong, Jr. 1995. Relationships between vegetational structure and predation of artificial Sage Grouse nests. Journal of Wildlife Management 59:88-92.

Drut, M. S., J. A. Crawford, and M. A. Gregg. 1994. Brood habitat use by Sage Grouse in Oregon. Great Basin Naturalist 54:170-176.

Dunn, P. O., and C. E. Braun. 1986. Summer habitat use by adult female and juvenile Sage Grouse. Journal of Wildlife Management 50:228-235.

Ellis, K. L., J. R. Parrish, J. R. Murphy, and G. H. Richins. 1989. Habitat use by breeding male Sage Grouse: a management approach. Great Basin Naturalist 49:404-407.

Ellison, L. N. 1991. Shooting and compensatory mortality in tetraonids. Ornis Scandinavica 22:229-240.

Emmons, S. R., and C. E. Braun. 1984. Lek attendance of male Sage Grouse. Journal of Wildlife Management 48:1023-1028.

Gotelli, N. J. 1995. A primer of ecology. Sinauer Associates, Sunderland, Massachussetts.

Gregg, M. A., J. A. Crawford, and M. S. Drut. 1993. Summer habitat use and selection by female Sage Grouse (*Centrocercus urophasianus*) in Oregon. Great Basin Naturalist 53:293-298.

Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of Sage Grouse nests in Oregon. Journal of Wildlife Management 58:162-166.

Homer, C. G., T. C. Edwards, Jr., R. D. Ramsey, and K. P. Price. 1993. Use of remote sensing methods in modelling Sage Grouse winter habitat. Journal of Wildlife Management 57:78-84.

Hupp, J. W., and C. E. Braun. 1991. Geographic variation among Sage Grouse in Colorado. Wilson Bulletin 103:255-261.

Janzow, P., J. Scordato, and K. Schiaparelli. 1992. The student edition of MATLAB. Prentice Hall, Englewood Cliffs, New Jersey.

Johnson, K. H., R. A. Olson, and T. D. Whitson. 1996. Composition and diversity of plant and small mammal communities in tebuthiuron-treated big sagebrush (*Artemisia tridentata*). Weed Technology 10:404-416.

Kalisz, S., and M. A. McPeek. 1992. Demography of an age-structured annual: resampled projection matrices, elasticity analyses, and seed bank effects. Ecology 73:1082-1093.

Klebenow, D. A. 1970. Sage Grouse versus sagebrush control in Idaho. Journal of Wildlife Management 23:396-400.

Lindenmayer, D. B., T. W. Clark, R. C. Lacey, and V. C. Thomas. 1993. Population viability analysis as a tool in wildlife conservation policy: with reference to Australia. Environmental Management 17:745-758.

Lovell, D. C., J. R. Choate, and S. J. Bissell. 1985. Succession of mammals in a disturbed area of the Great Plains. Southwestern Naturalist 30:335-342.

Mackie, R. J., K. L. Hamlin, D. F. Pac, G. L. Dusek, and A. K. Wood. 1990. Compensation in free-ranging deer populations. Transactions of the North American Wildlife and Natural Resources Conference 55:518-526.

Martin, N. S. 1970. Sagebrush control related to habitat and Sage Grouse occurrence. Journal of Wildlife Management 34:313-320.

Nantel, P., D. Gagnon, and A. Nault. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biology 10:608-621.

Pascual, M. A., and M. D. Adkison. 1994. The decline of the Steller Sea Lion in the Northeast Pacific: demography, harvest or environment? Ecological Applications 4:393-403.

Ratsirarson, J., J. A. Silander, Jr., and A. F. Richard. 1996. Conservation and management of a threatened Madagascar palm species, *Neodypsis decaryi*, Jumelle. Conservation Biology 10:40-52.

Ritchie, M. E., M. L. Wolfe, and R. Danvir. 1994. Predation of artificial Sage Grouse nests in treated and untreated sagebrush. Great Basin Naturalist 54:122-129.

Schneegas, E. R. 1967. Sage Grouse and sagebrush control. Transactions of the North American Wildlife and Natural Resources Conference 32:270-274.

Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conservation Biology 10:591-597.

Swenson, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease in Sage Grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. Biological Conservation 41:125-132.

Thomas, C. D. 1990. What do real population dynamics tell us about minimum viable population sizes? Conservation Biology 4:324-327.

Wallestad, R. 1975. Male Sage Grouse responses to sagebrush treatment. Journal of Wildlife Management 39:482-484.

Wallestad, R. O., and D. B. Pyrah. 1974. Movement and nesting of Sage Grouse hens in central Montana. Journal of Wildlife Management 38:630-633.

Winston, W. L. 1996. Simulation modeling using @RISK. Wadsworth, Florence, Kentucky.