APPENDIX K

POPULATION VIABILITY ANALYSIS REPORT (Miller et al. 2006)

Brian Maxfield

Population Viability Analysis for the Greater Sage-grouse (*Centrocercus urophasianus*) in Colorado

PRELIMINARY REPORT

Report prepared by:
Philip S. Miller
IUCN / SSC Conservation Breeding Specialist Group

In collaboration with

Members of the
Colorado Greater Sage-grouse
Conservation Plan Steering Committee

Preliminary Population Viability Analysis for the Greater Sage-grouse (*Centrocercus urophasianus*) in Colorado

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and
Colorado Greater Sage-grouse Conservation Plan Steering Committee Members

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Introduction

Dependent exclusively on sagebrush ecosystems that define the ecology of much of western North America, the greater sage-grouse (*Centrocercus urophasianus*) was once distributed across twelve states of the western United States and three provinces of Canada. Greater sage-grouse currently occupy 700,000 km^2, or 56%, of their potential pre-settlement range, which once covered approximately 1,200,000 km^2 (Connelly et al. 2004). The species is now lost from Nebraska and Alberta, and other peripheral populations are at increasing risk of extirpation. As a result of these declines, petitions have been filed to list the species under the United States Endangered Species Act.

In Colorado, greater sage-grouse occupy significant tracts of sagebrush habitat in the northwestern region of the state. Authors of the Colorado Greater Sage-grouse Conservation Plan (CCP) have identified six largely discrete regions where birds are found. In five of these areas local working groups have formed, comprised of concerned citizens, researchers, and managers dedicated to developing grouse conservation strategies at the local level. As in many other western states, there is concern over a variety of human activities – new housing development, oil and natural gas exploration, livestock grazing, surface mining, and hunting – that may unintentionally result in significant negative impacts to local sage-grouse populations. These impacts might possibly destabilize the integrity of the sagebrush habitat or the populations themselves to an extent where the risk of local extinction is greatly increased. Therefore, it is critical that the potential impact of these activities is evaluated using sound scientific methodologies, and the results of these analyses are incorporated into the evolving statewide species conservation strategies.

Population viability analysis, or PVA, can be an extremely useful tool for investigating current and future risk of Colorado greater sage-grouse population decline or extinction. The need for and consequences of alternative management strategies can be modeled to suggest which practices may be the most effective in managing sage-grouse populations in its wild habitat. *VORTEX*, a simulation software package written for population viability analysis, was used here as a vehicle to study the interaction of a number of greater sage-grouse life history and population parameters, to explore which demographic parameters may be the most sensitive to alternative management practices, and to test the effects of selected management scenarios.

The *VORTEX* package is a simulation of the effects of a number of different natural and human-mediated forces – some, by definition, acting unpredictably from year to year – on the health and integrity of wildlife populations. *VORTEX* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or random variables that follow specified distributions. The package simulates a population by recreating the essential series of events that describe the typical life cycles of sexually reproducing organisms.

PVA methodologies such as the *VORTEX* system are not intended to give absolute and accurate “answers” for what the future will bring for a given wildlife species or population. This limitation arises simply from two fundamental facts about the natural world: it is inherently unpredictable in its detailed behavior; and we will never fully understand its precise mechanics. Consequently, many researchers have cautioned against the exclusive use of absolute results from a PVA in order to promote specific management actions for threatened populations (e.g., Ludwig 1999; Beissinger and McCullough 2002; Reed et al. 2002; Ellner et al. 2002; Lotts et al. 2004). Instead, the true value of an analysis of this type lies in the assembly and critical analysis of the available information on the species and its ecology, and in the ability to compare the quantitative metrics of population performance that emerge from a suite of simulations, with each simulation representing a specific scenario and its inherent assumptions about the available data and a proposed method of population and/or landscape management. Interpretation of this type of output depends strongly upon our knowledge of greater sage-grouse biology in its habitat, the environmental conditions affecting the species, and possible future changes in these conditions.

The *VORTEX* system for conducting population viability analysis is a flexible and accessible tool that can be adapted to a wide variety of species types and life histories as the situation warrants. The program has been used around the world in both teaching and research applications and is a trusted method for assisting in the definition of practical wildlife management methodologies. For a more detailed explanation of *VORTEX* and its use in population viability analysis, refer to Appendix I, Lacy (2000) and Miller and Lacy (2003).

Specifically, we were interested in using this preliminary analysis to address the following questions:

- Can we build a series of simulation models with sufficient detail and precision that can accurately describe the dynamics of greater sage-grouse populations distributed across Colorado?
- What are the primary demographic factors that drive growth of greater sage-grouse populations in Colorado?
- How vulnerable are small, fragmented populations of greater sage-grouse in Colorado to extinction under current management conditions? How small must a population become to increase its risk of extinction to an unacceptable level?
- What are the predicted impacts of current and potential future levels of housing development on selected greater sage-grouse populations in Colorado?
- What are the predicted impacts of current and potential future levels of mining and other surface activities on selected greater sage-grouse populations in Colorado?
- What are the predicted impacts of current and potential future levels of hunting on selected greater sage-grouse populations in Colorado?
- What are the predicted impacts of current and potential future levels of petroleum and natural gas development on selected greater sage-grouse populations in Colorado?
- Can reproductive mitigation improve the viability of greater sage-grouse populations in Colorado in the face of other anthropogenic processes?

Baseline Input Parameters for Stochastic Population Viability Simulations

Much of the data discussed below are gleaned from Zablan et al. (2003), the radio telemetry studies on greater sage-grouse of Hausleitner (2003) and Thompson (unpublished) in Moffat County, Colorado and Peterson (1980) in North Park, Colorado.

Breeding System: The greater sage-grouse is a polygynous lek-breeding species. In *VORTEX*, a set of adult females are therefore randomly selected each year to breed with a given male. Breeding success of adult males within a give year is often dependent on the success of that male in the previous year. This was not specifically simulated in this analysis as this aspect of the breeding biology is unlikely to have a noticeable demographic impact on future population performance.

Age of First Reproduction: *VORTEX* considers the age of first reproduction as the age at which the first clutch of eggs is laid, not simply the onset of sexual maturity. Female sage-grouse can lay their first clutch at one year of age, while males are much more likely to be two years old at the time of egg-laying. Because of the very low probability of breeding success among yearling males, we elected to ignore this possibility in our models.

Age of Reproductive Senescence: In its simplest form, *VORTEX* assumes that animals can reproduce (at the normal rate) throughout their adult life. There are no real data available on senescence in sage-grouse, so we made a reasonable estimate of the maximum age possible for this species as 10 years. In reality, surpassing this age in our models is unlikely given observed mortality rates (see below).

Offspring Production: Based on the depth of our knowledge of sage-grouse life history, we have defined reproduction in these models as the production of newly-hatched chicks by a given female, roughly early May – June. Field data have been collected on the rates of nest initiation and success among both yearling and adult females. Of those that are initially unsuccessful in nesting, additional data exist on the rates of renesting success. With these data in hand, we can calculate the proportion of females that successfully reproduce in a given year through the following equation:

P(♀) = [(first nest initiation)(first nest success)] +
[(first nest initiation)(first nest NO success)(second nest initiation)(second nest success)]

Radio telemetry data from Hausleitner (2003) and Thompson (unpublished) in Moffat County allow us to derive estimates of these important parameters:

	Nest initiation	Nest success	Renest initiation	Renest success
Adults	0.93	0.50	0.16	0.75
Yearlings	0.83	0.39	0.22	0.57

Taken together, these data means that, on average, 38.7% of greater sage-grouse yearlings successfully reproduce in a given year, and 52.1% of adults are likewise successful. These results were combined in an equation used within *VORTEX* to describe the relationship between the average percentage of adult females breeding each year and their age.

Annual environmental variation in female reproductive success is modeled in *VORTEX* by specifying a standard deviation (SD) for the proportion of adult females that successfully lay a clutch of eggs within a given year. Wing receipt data from greater sage-grouse populations suggest that annual variability in reproductive success among yearling females is about 8%, while slightly lower among older birds (SD = 6%).

The maximum number of eggs per clutch has been set at 9, based on data collected by Griner (1939) in greater sage-grouse populations in eastern Utah. Given that an adult female lays a clutch of eggs, the distribution of clutch size was set as follows:

Number of eggs	%
1	1.0
2	1.0
3	1.0
4	1.0
5	5.5
6	27.3
7	35.0
8	25.0
9	3.2

This distribution yields an average clutch size of 6.75 eggs. The overall population-level sex ratio among eggs is assumed to be 50%.

Density-Dependent Reproduction: *VORTEX* can model density dependence with an equation that specifies the proportion of adult females that reproduce as a function of the total population size. In addition to including a more typical reduction in breeding in high-density populations, the user can also model an Allee effect: a decrease in the proportion of females that bread at low population density due, for example, to difficulty in finding mates that are widely dispersed across the landscape.

While a significant source of debate among species experts, there are no current field data to support density dependence in reproduction in greater sage-grouse populations. Consequently, this option was not included in the models presented here.

Male Breeding Pool: In many species, some adult males may be socially restricted from breeding despite being physiologically capable. This can be modeled in *VORTEX* by specifying a portion of the total pool of adult males that may be considered "available" for breeding each year. Observational data suggests that as few as 10% of the adult males are actually participating in the displays on leks within a given population segment, and this value was used in our baseline population analysis. Other researchers think this value may be much higher, approaching as high as 33%.

Mortality: *VORTEX* defines mortality as the annual rate of age-specific death from year x to $x + 1$; in the language of life-table analysis, this is equivalent to $q(x)$. Juvenile rates were composed of data estimated from hatching to 1 September (Northwestern Colorado: Thompson, unpublished), then 1 September to 30 March (Idaho: Beck et al., in press). Yearling and adult rates are largely based on data collected in North Park by Zablan et al. (2003), with additional data provided by Hausleitner (2003).

Age Class	% Mortality (SD)	
	Females	Males
0 – 1	75.7 (5.0)	74.5 (5.0)
1 – 2	24.0 (4.0)	36.5 (3.0)
2 - +	42.0 (4.0)	63.0 (1.0)

Inbreeding Depression: *VORTEX* includes the ability to model the detrimental effects of inbreeding, most directly through reduced survival of offspring through their first year. Because of the complete absence of information on the effects of inbreeding on the demography of greater sage-grouse, the group concluded that this option should not be included in our models.

Initial Population Size: A total of six discrete populations of greater sage-grouse were considered in this analysis. These populations are listed below, with their estimated numbers based on observed spring breeding counts of males on leks and a presumed 2:1 female:male ratio.

Population	**Breeding Males***	**Total Population**
Piceance / Parachute / Roan	186	1,104
Meeker / White River	28	153
North Park	1,234	6,731
Middle Park	290	1,581
Northern Eagle / Southern Routt Counties	104	567
Eagle	11	60
Routt	93	507
Northwestern Colorado	2,387	13,023
Zone 1	153	834
Zone 2	28	153
Zone 3A	534	2,913
Zone 3B	625	3,408
Zone 3C	139	759
Zone 4A	217	1,185
Zone 4B	76	414
Zone 5	294	1,605
Zone 6	304	1,659
Zone 7	17	93

* Average value, 2001 - 2005
** Total N = (0.55)(Breeding males) + 2(0.55)(Breeding males)

Note that the Northern Eagle / Southern Routt Counties and Northwestern Colorado regions are actually composed of metapopulations – that is, aggregates of subpopulations that are linked together through differential rates of dispersal. See below for a detailed discussion of additional metapopulation parameters.

VORTEX distributes the specified initial population among age-sex classes according to a stable age distribution that is characteristic of the mortality and reproductive schedules described previously.

Carrying Capacity: The carrying capacity, K, for a given habitat patch defines an upper limit for the population size, above which additional mortality is imposed randomly across all age classes in order to return the population to the value set for K.

The estimation of a carrying capacity is a very difficult process. The approach taken in this analysis involved identifying the most reasonable estimated high male lek count in a given region and, by applying the same transformation used to calculate current population size, determining total local carrying capacity. These results are given in the table below.

Population	Max. Breeding Males*	Total K
Piceance / Parachute / Roan	285	1554
Meeker / White River	--	300
North Park	1521	8296
Middle Park	327	1784
Northern Eagle / Southern Routt Counties	307	1673
Eagle	79	429
Routt	228	1244
Northwestern Colorado	2,387	18,170
Zone 1	268	1462
Zone 2	129	704
Zone 3A	570	3109
Zone 3B	667	3638
Zone 3C	153	835
Zone 4A	486	2651
Zone 4B	--	414
Zone 5	565	3082
Zone 6	400	2182
Zone 7	--	93

Metapopulation Parameters: For the Northern Eagle / Southern Routt Counties and Northwestern Colorado populations, additional data on dispersal was required. Field observations indicate that dispersing birds are predominantly composed of yearlings; as a result, we limited dispersal to only those birds aged 1 year. Moreover, while a small percentage of dispersing birds are observed to be male, the model assumes that only females disperse.

Largely in order to achieve a higher degree of model realism with respect to overall metapopulation dynamics, we derived a conditional function that limited the amount of dispersal into populations that were already approaching a given habitat's carrying capacity. Specifically, we prohibited dispersal into a given population when the recipient population was at least 80% saturated; in other words, under conditions when $N \geq 0.8K$.

Rates of dispersal – defined in *VORTEX* as the probability (expressed as a percentage) of an individual moving from one population to another, are given in the table below. Note that the rates between any two populations are not constrained to be symmetric, based on the available data. Source populations are listed as rows, while columns designate recipient populations.

Zone	1	2	3A	3B	3C	4A	4B	5	6	7
1	87	10	0	0	0	0	0	0	1	2
2	3	77	6	5	0	0	0	5	3	1
3A	1	2	69	10	10	0	0	5	3	0
3B	0	3	10	62	10	10	0	5	0	0
3C	0	1	15	15	60	0	4	5	0	0
4A	0	0	0	15	5	75	5	0	0	0
4B	0	0	0	0	3	3	93	1	0	0
5	0	3	5	5	5	0	3	74	5	0
6	1	3	3	0	0	0	0	3	87	3
7	1	1	0	0	0	0	0	0	1	97

Iterations and Years of Projection: All population projections (scenarios) were simulated 500 times. Each projection extends to 50 years, with demographic information obtained at annual intervals. All simulations were conducted using *VORTEX* version 9.60 (March 2006).

Table 1 below summarizes the baseline input dataset upon which all subsequent *VORTEX* models are based.

Table 1. Demographic input parameters for the baseline *VORTEX* Colorado greater sage-grouse models. See accompanying text for more information.

Model Input Parameter	Baseline Value
Breeding System	Polygynous
Age of first reproduction (♀ / ♂)	1 / 2
Maximum age of reproduction	10
Annual % adult females reproducing	38.7 (Yrl) / 52.1% (Ad)
Density dependent reproduction?	No
Maximum clutch size	9
Mean clutch size†	6.75
Overall offspring sex ratio	0.5
Adult males in breeding pool	10%
% annual mortality, ♀ / ♂ (SD)	
0 – 1	75.7 / 74.5 (5.0)
1 – 2	24.0 / 36.5 (3.0)
2 – +	42.0 / 63.0 (4.0 / 1.0)
Initial population size / carrying capacity	
Piceance / Parachute / Roan	1,104 / 1,554
Meeker / White River	153 / 300
North Park	6,731 / 8,296
Middle Park	1,581 / 1,784
Northern Eagle / Southern Routt Counties	567 / 1,673
Eagle	60 / 429
Routt	507 / 1,244
Northwestern Colorado	13,023 / 18,170
Zone 1	834 / 1,462
Zone 2	153 / 704
Zone 3A	2,913 / 3,109
Zone 3B	3,408 / 3,638
Zone 3C	759 / 835
Zone 4A	1,185 / 2,651
Zone 4B	414 / 414
Zone 5	1,605 / 3,082
Zone 6	1,659 / 2,182
Zone 7	93 / 93

† Exact probability distribution of individual clutch size specified in input file.

Definitions of Simulation Modeling Results

Results reported for selected modeling scenarios include:

$\underline{r_s}$ (SD) – The mean rate of stochastic population growth or decline (standard deviation) demonstrated by the simulated populations, averaged across years and iterations, for all simulated populations that are not extinct. This population growth rate is calculated each year of the simulation, prior to any truncation of the population size due to the population exceeding the carrying capacity.

$\underline{P(E)_{50}}$ – Probability of population extinction after 50 years, determined by the proportion of 500 iterations within that given scenario that have gone extinct within the given time frame. "Extinction" is defined in the *VORTEX* model as the lack of either sex.

$\underline{N_{50}}$ (SD) – Mean (standard deviation) population size at the end of the simulation, averaged across all simulated populations, including those that are extinct.

$\underline{GD_{50}}$ – The gene diversity or expected heterozygosity of the extant populations, expressed as a percent of the initial gene diversity of the population. Fitness of individuals usually declines proportionately with gene diversity.

Baseline Model Validation through Retrospective Population Analysis

An important component of population viability analysis involves testing our baseline simulation models against historical population census data. In this approach, we set the model's initial population size with a value based on historical data and then project the model forward to the present day, comparing the predicted trajectory with the real trajectory determined from field census counts. A reasonable fit between the observed and predicted curves gives considerable credibility to the simulation's mechanics and, therefore, instills much more confidence in the relative results from models that predict future responses of greater sage-grouse populations to human activities on the landscape.

The results of these retrospective analyses for each population are shown in Figure 1. With the exception of the Meeker / White River population, all other simulation models appear to accurately predict the true population census within a reasonable degree of uncertainty. Given this general degree of accuracy, the disparity between predicted population size and field census counts in the Meeker / White River analysis is likely not an error in the simulation model but instead probably reflects the small number of leks included in the field census, the difficulty in conducting detailed studies in the area, and the short time period over which the census was conducted. Therefore, the overall conclusion from this retrospective analysis is that our simulation model of Colorado greater sage-grouse population dynamics can be used with acceptable confidence in predicting the relative outcomes of alternative management scenarios for the species.

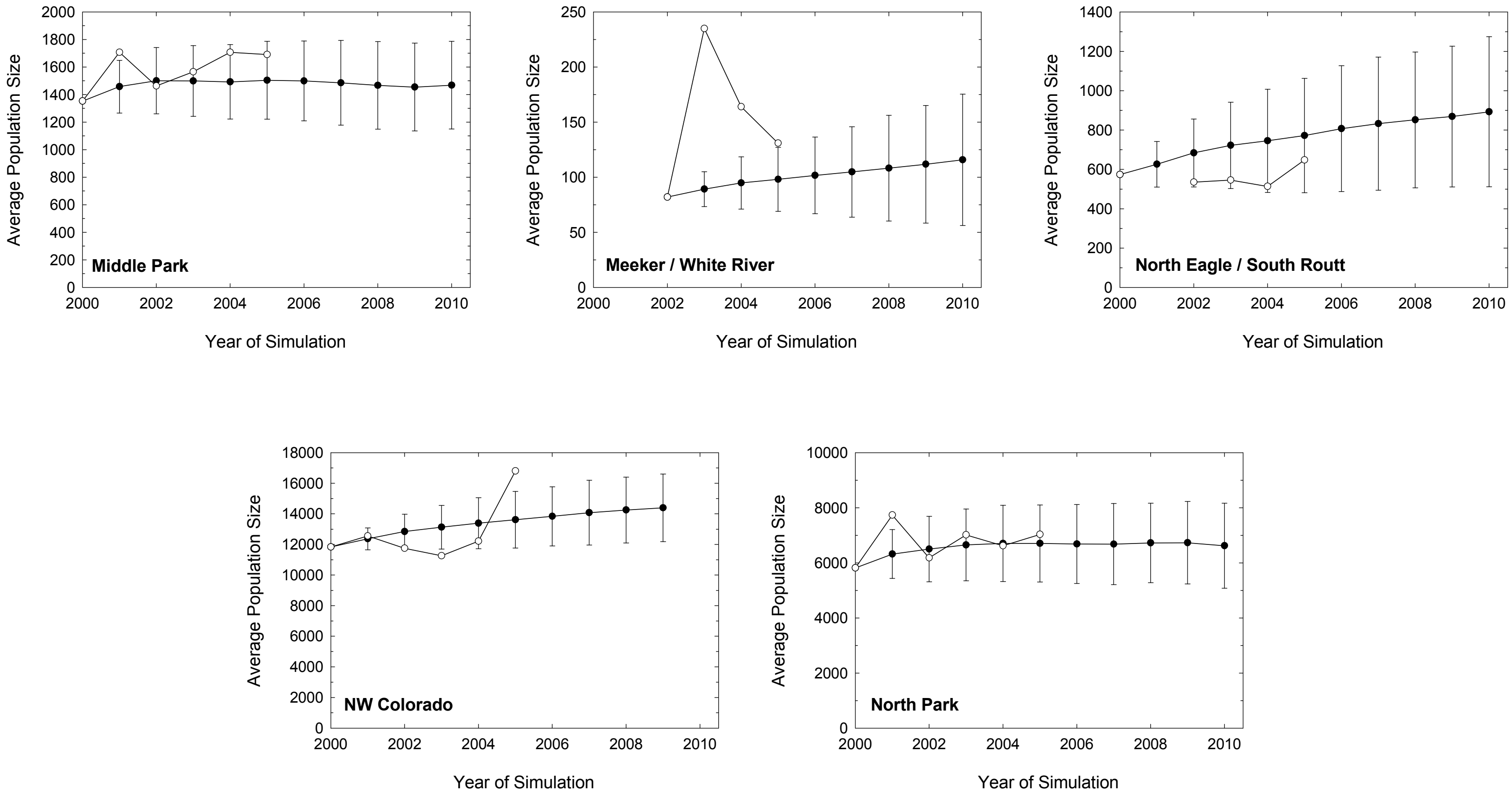


Figure 1. Retrospective projections for simulated greater sage-grouse populations in Colorado. Filled symbols indicate population sizes predicted using the PVA platform *Vortex*, while open symbols give "true" population size estimates derived from field counts. Analysis of the Piceance / Parachute / Roan population is not included here as field census data do not exist. See accompanying text for additional details on model construction and interpretation.

Baseline Model Projections

Table 2 and Figure 2 give the results of fifty-year projections for each of the six regional greater sage-grouse populations considered here. With the exception of Meeker / White River, each population displays long-term population growth values between 0.025 and 0.030, with no risk of extinction over the 50-year timeframe of the simulation. Consistent with the general theoretical expectations of small population biology, the Meeker / White River population shows a lower growth rate and a non-zero (albeit small) risk of extinction. This is a simple demonstration of the demographic instability inherent in smaller populations, as the underlying rates of mortality and reproduction are identical among all simulated populations studied here.

Table 2. Greater sage-grouse PVA: fifty-year projections of baseline models for each regional population. See text for additional information on model construction and parameterization.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Middle Park				
Baseline	0.022 (0.138)	0.000	1370 (400)	0.9531
Meeker / White River				
Baseline	0.019 (0.160)	0.016	208 (83)	0.6619
North Eagle / South Routt				
Baseline	0.031 (0.167)	0.000	988 (471)	0.8980
Piceance / Parachute / Roan				
Baseline	0.025 (0.139)	0.000	1202 (342)	0.9422
Northwest Colorado				
Baseline	0.030 (0.081)	0.000	15739 (1872)	0.9956
North Park				
Baseline	0.025 (0.135)	0.000	6582 (1794)	0.9903

Note that despite the robust levels of growth displayed for each population, the Middle Park and North Park simulated populations show a slightly negative trend in population size over the timeframe of the simulations presented here. This is a consequence of the rather "hard" demographic boundary imposed by *VORTEX* in the form of a carrying capacity, *K*. In the model's structure, if a given population is larger than the specified carrying capacity, animals within the population are removed randomly across all age-sex classes until the size is below *K*. When populations are close to this capacity, this reflective nature of carrying capacity in the model tends to drive a population away from K until a new equilibrium is reached at a level that is somewhere below the specified capacity. While the trajectories shown here may not be completely accurate in the long-term, they do suffice as informative baseline projections from which robust comparative analyses can be made in the risk analyses to follow.

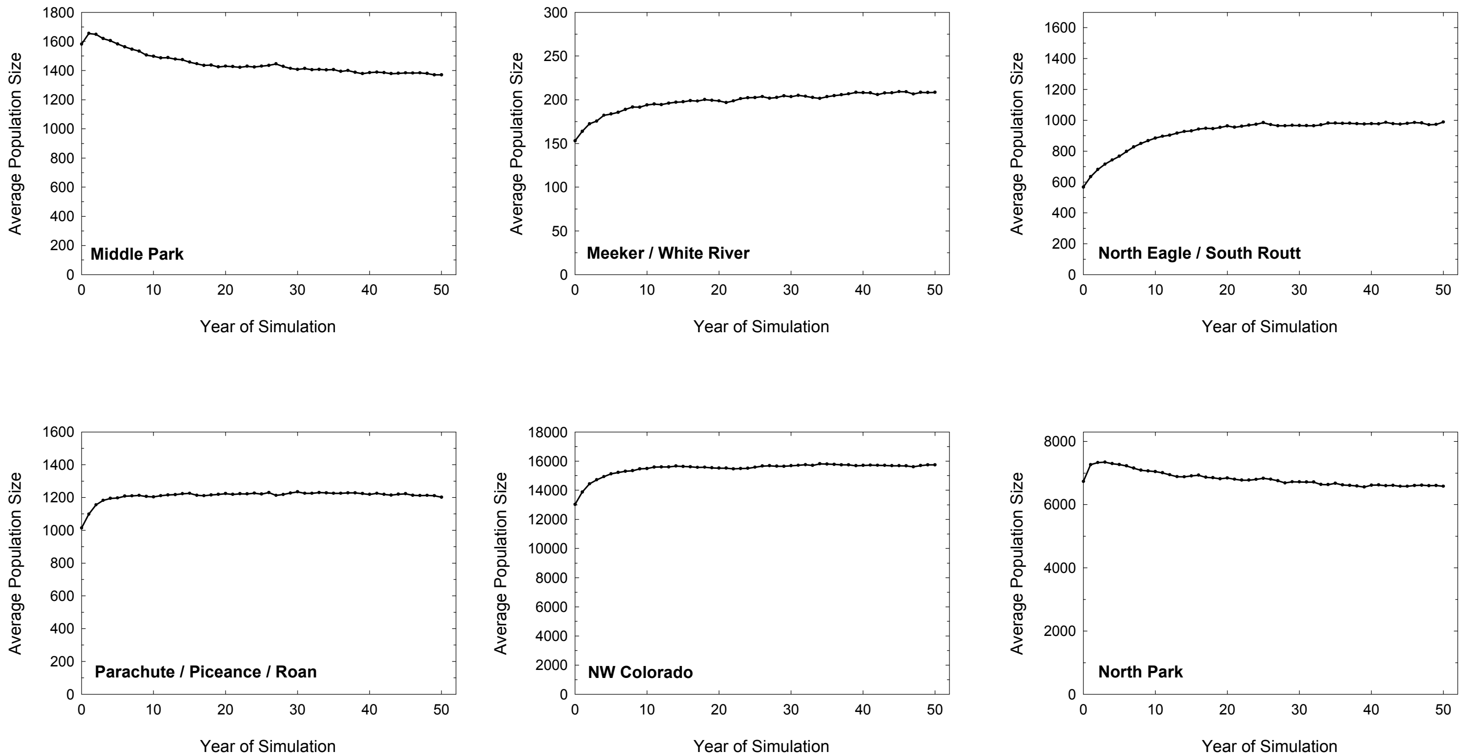


Figure 2. Fifty-year prospective projections for each of the six regional populations of greater sage-grouse in Colorado. See accompanying text for additional details on model construction and interpretation.

Demographic Sensitivity Analysis

During the development of the baseline input dataset, it quickly became apparent that a number of demographic characteristics of greater sage-grouse populations were being estimated with varying levels of uncertainty. This type of measurement uncertainty, which is distinctly different from the annual variability in demographic rates due to extrinsic environmental stochasticity and other factors, impairs our ability to generate precise predictions of population dynamics with any degree of confidence. Nevertheless, an analysis of the sensitivity of our models to this measurement uncertainty can be an invaluable aid in identifying priorities for detailed research and/or management projects targeting specific elements of the species' population biology and ecology.

To conduct this demographic sensitivity analysis, we identify a selected set of parameters from Table 1 whose estimate we see as considerably uncertain. We then develop proportional minimum and maximum values for these parameters (see Table 3).

Table 3. Uncertain input parameters and their stated ranges for use in demographic sensitivity analysis for the Colorado population of greater sage-grouse. Highlighted rows indicate those demographic parameters that show the highest sensitivity, *S*, as listed in the far right-hand column of the table. See accompanying text for more information.

	Estimate			
Model Parameter	Minimum	Baseline	Maximum	*S*
Maximum Age	9	10	11	-0.01269
% Yearling Females Reproducing	34.83	38.7	42.57	-0.11957
% Adult Females Reproducing	46.89	52.1	57.31	-0.27038
Clutch Size	6.08	6.75	7.43	-0.39531
% Female Chick Mortality	68.13	75.7	83.27	1.273304
% Male Chick Mortality	67.05	74.5	81.95	-0.00098
% Yearling Female Mortality	21.6	24.0	26.4	0.080039
% Yearling Male Mortality	32.85	36.5	40.15	0.000976
% Adult Female Mortality	37.8	42.0	46.2	0.253294
% Adult Male Mortality	56.7	63.0	69.3	0.006833

For each of these parameters we construct two simulations, with a given parameter set at its prescribed minimum or maximum value, with all other parameters remaining at their baseline value. With the ten parameters identified above, and recognizing that the aggregate set of baseline values constitute our single baseline model, the table above allows us to construct a total of 20 additional, alternative models whose performance (defined, for example, in terms of average population growth rate) can be compared to that of our starting baseline model.

For the entire suite of sensitivity analysis models, we will consider a generic population of 6,700 individuals and a carrying capacity of 13,500 individuals. This population is large enough to be relatively immune from excessive demographic uncertainty that is characteristic of small populations. Furthermore, carrying capacity is large enough to allow for significant population growth and to observe proper demographic dynamics.

The proportional sensitivity of a given simulation model, S, is given by

$$S = [(\lambda_{Min} - \lambda_{Max}) / (0.2^* \lambda_{Base})]$$

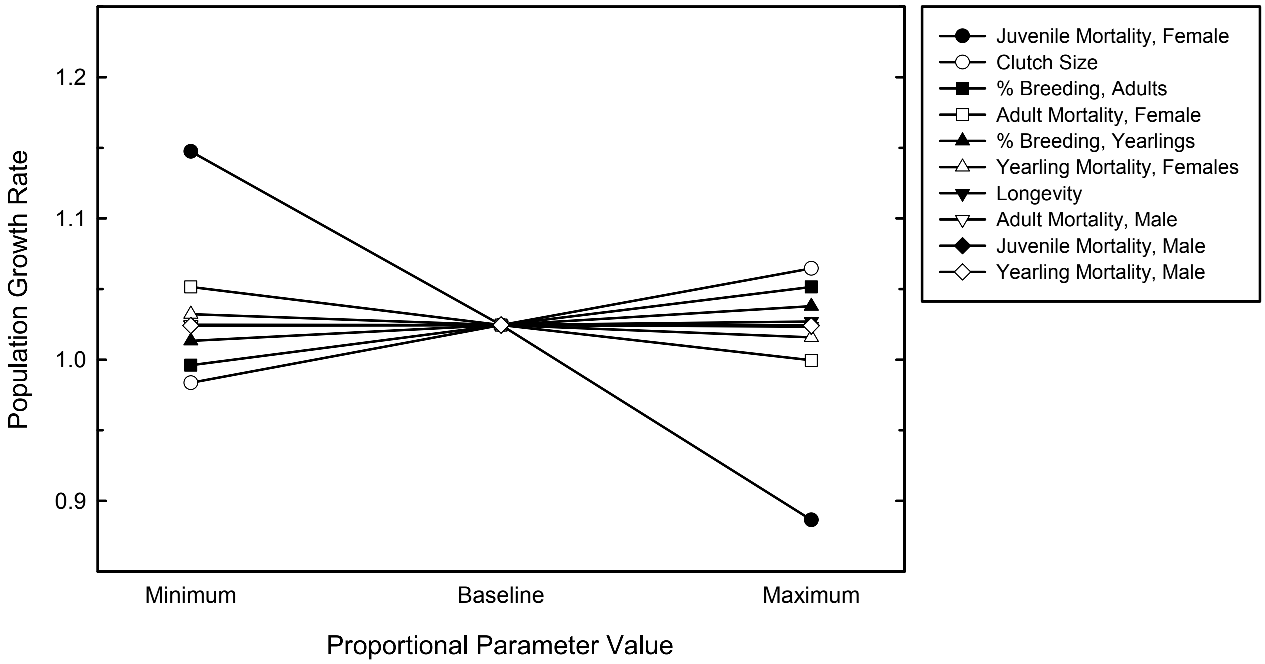
Where $\lambda = e^r$ is the annual rate of population growth calculated from the simulation and subscripts *Min*, *Max* and *Base* refer to simulations that include the minimum, maximum, and baseline values of the appropriate parameter, respectively. Using this formulation, model parameters with large S values show strong differences in λ when values are manipulated (modified from Heppell et al., 2000).

The results of the sensitivity analysis are shown in tabular form in Table 4 and graphically in Figure 3. Those lines with the steepest slope – namely, juvenile (chick) female mortality, clutch size, and adult female mortality – show the greatest degree of response in terms of population growth rate to changes in those parameters and, hence, the greatest sensitivity. These parameters can then be targeted in subsequent field activities for more detailed research and / or demographic management.

Table 4. Greater Sage-grouse PVA. Output from demographic sensitivity analysis models. See text for additional information on model construction and parameterization.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Baseline	0.024 (0.134)	0.000	10181 (3044)	0.9926
Maximum Age – Minimum	0.024 (0.135)	0.000	10230 (3218)	0.9923
Maximum Age – Maximum	0.027 (0.135)	0.000	10505 (2874)	0.9929
% Yearlings Breeding – Minimum	0.013 (0.136)	0.000	8987 (3578)	0.9914
% Yearlings Breeding – Maximum	0.037 (0.136)	0.000	11412 (2361)	0.9932
% Adult Females Breeding – Minimum	-0.004 (0.136)	0.000	5913 (3598)	0.9865
% Adult Females Breeding – Maximum	0.050 (0.135)	0.000	12077 (1837)	0.9940
Litter Size – Minimum	-0.017 (0.133)	0.000	3822 (2927)	0.9828
Litter Size – Maximum	0.063 (0.139)	0.000	112360 (1646)	0.9940
Juvenile Female Mortality – Minimum	0.138 (0.134)	0.000	13310 (564.8)	0.9933
Juvenile Female Mortality – Maximum	-0.120 (0.175)	0.226	41 (73)	0.7415
Juvenile Male Mortality – Minimum	0.024 (0.126)	0.000	10289 (3012)	0.9933
Juvenile Male Mortality – Maximum	0.024 (0.147)	0.000	10172 (3095)	0.9909
Yearling Female Mortality – Minimum	0.032 (0.136)	0.000	11132 (2625)	0.9929
Yearling Female Mortality – Maximum	0.016 (0.137)	0.000	9149 (3472)	0.9917
Yearling Male Mortality – Minimum	0.024 (0.134)	0.000	10291 (3029)	0.9928
Yearling Male Mortality – Maximum	0.024 (0.137)	0.000	10126 (3169)	0.9922
Adult Female Mortality – Minimum	0.050 (0.134)	0.000	12077 (1826)	0.9940
Adult Female Mortality – Maximum	0.000 (0.136)	0.000	6420 (3707)	0.9880
Adult Male Mortality – Minimum	0.024 (0.132)	0.000	10365 (3135)	0.9932
Adult Male Mortality – Maximum	0.023 (0.139)	0.000	10198 (3116)	0.9915

Figure 3. Demographic sensitivity analysis of a generic Colorado greater sage-grouse population. Those curves with the steepest slope indicate the model parameters with the greatest overall sensitivity. See accompanying text for additional information on model construction.



Simulating the Impacts of Human Activity on Sage-grouse Population Dynamics

Once the baseline demographic parameters are established, additional work must be devoted to determining the mechanisms through which specific human activities within greater sage-grouse habitat – namely housing development, surface mining, harvest, oil and natural gas development, and mitigation of reproductive success – may influence the bird's population dynamics in the future. Each individual activity is discussed in detail below.

Risk Analysis I: Impacts of Habitat – Centric Activities (Housing and Surface Mining) on Greater Sage-grouse Population Dynamics

Housing Development: Model Input

Regions considered: Meeker/White River; Middle Park; Northern Eagle / Southern Routt Counties

The primary assumption in our analysis is that the construction of new homes will reduce the amount of suitable sagebrush habitat available to sage-grouse. This can be modeled in *VORTEX* through a gradual reduction in habitat carrying capacity, K.

Human population projections through 2020, and associated estimates of average household size, were used to estimate the increase in new housing units across each affected region. Additional data on sagebrush habitat distribution were used to estimate the proportion of individual land parcels of different size classes that would occur within habitat considered optimal for greater sage-grouse. Using these estimates, two different levels of housing intensity were developed: Level 1, where only land parcels less than 40 acres in size were considered; and Level 2, where parcels up to 320 acres were considered to impact sagebrush habitat.

Region	% Reduction in K, 50 Years Level 1	Level 2
Meeker / White River	3.4%	23.5%
Middle Park	8.2	31.2
Northern Eagle / Southern Routt Counties		
Eagle	8.0	85.2
Routt	6.7	57.3

These reductions in carrying capacity are implemented in *VORTEX* as a linear decline in K over 50 years. For example, a Level 1 reduction in carrying capacity for Middle Park would result in a total reduction in K of 8.2%, from 1,784 to 1,638.

Surface Mining: Model Input
Regions considered: Middle Park, Northern Eagle / Southern Routt Counties, Northwestern Colorado, Piceance / Parachute / Roan

As with new housing development, the primary assumption in our analysis here is that surface mining for gravel, oil shale and similar resources will reduce the amount of suitable sagebrush habitat available to Sage-grouse. This can be modeled in *VORTEX* through a gradual reduction in habitat carrying capacity, K.

GIS analysis methods were used to identify sage-grouse habitat areas that could be targeted for surface mining activities, and linear rates of habitat carrying capacity loss were calculated over the 50-year period of the PVA model. Two levels of activity were considered, with increasing extent of disturbance to sage-grouse habitat (see table below). Low levels of activity in the Meeker / White River region were initially considered, then removed from the analysis due to their negligible impact. Detailed analysis of the Northwestern Colorado region indicates that mining activity is relevant only for zones 3C, 4B, 5, and 6.

Region	% Reduction in K, 50 Years Level 1	Level 2
Middle Park	15.0	26.0
Northern Eagle / Southern Routt Counties		
Eagle	17.0	35.0
Routt	17.0	35.0
Northwestern Colorado		
3C	6.0	10.0
4B	6.0	10.0
5	6.0	10.0
6	6.0	10.0
Piceance / Parachute / Roan	11.0	40.0

Results of Housing and Surface Mining Risk Analysis

Table 5 and Figure 4 show the combined results of the housing and surface activities analysis for the affected populations: Meeker / White River, Middle Park, Northern Eagle / Southern Routt Counties, and

Piceance / Parachute / Roan (the extent of sagebrush habitat loss was so small in the Northwestern Colorado region as to be essentially negligible). All four regions show some degree of greater sage-grouse population decline in the presence of the activities, with the lowest level seen in Meeker / White River and the greatest level of decline in Northern Eagle / Southern Routt Counties. In Middle Park, the relative contributions of housing and surface mining to population decline appear to be roughly equal as evidenced by the gradual increase in the magnitude of the decline from scenarios in which both housing and surface activities are at a low level (H1 – M1) to when both are at a high level (H2 – M2). On the other hand, in the Northern Eagle / Southern Routt Counties region the impacts of housing appear to be more severe since the high-level H2 housing scenarios show a more precipitous population decline. Interestingly, this appears to be at least partly linked to the more rapid decline seen in the much smaller Eagle subpopulation, which then contributes to the overall greater instability of the larger metapopulation. In addition, the high-level housing scenarios included a significant rate of habitat decline, with more than 85% of available greater sage-grouse habitat being lost over the time period of the simulation. This magnitude of decline, when combined with the small population sizes and their inherent demographic instability, works to put the larger metapopulation at a marked risk of extinction if conditions of habitat alteration reach predicted levels.

The extent of sagebrush habitat loss was so small in the Northwestern Colorado region as to be essentially negligible. As a result, this activity had no measurable impact on the predicted dynamics of a simulated Northwestern Colorado population. These results are not graphically depicted here.

Table 5. Greater sage-grouse PVA. Output from analysis of habitat – centric activities models. See text for additional information on model construction and parameterization.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Middle Park				
Baseline	0.022 (0.138)	0.000	1370 (400)	0.9531
Housing 1 – Mining 1	0.025 (0.139)	0.000	1122 (273)	0.9502
Housing 1 – Mining 2	0.025 (0.139)	0.000	979 (214)	0.9462
Housing 2 – Mining 1	0.023 (0.139)	0.000	802 (175)	0.9427
Housing 2 – Mining 2	0.023 (0.140)	0.000	667 (121)	0.9366
Meeker / White River				
Baseline	0.019 (0.160)	0.016	208 (83)	0.6619
Housing 2	0.021 (0.160)	0.022	198 (84)	0.6718
Northern Eagle / Southern Routt Counties				
Baseline	0.031 (0.167)	0.000	988 (471)	0.8980
Housing 1 – Mining 1	0.030 (0.168)	0.000	276 (55)	0.8156
Housing 1 – Mining 2	0.031 (0.168)	0.000	646 (261)	0.8921
Housing 2 – Mining 1	0.030 (0.172)	0.000	255 (82)	0.8217
Housing 2 – Mining 2	0.024 (0.177)	0.014	87 (19)	0.7854
Piceance / Parachute / Roan				
Baseline	0.025 (0.139)	0.000	1202 (342)	0.9422
Mining 1	0.025 (0.139)	0.000	1084 (296)	0.9404
Mining 2	0.023 (0.141)	0.000	778 (176)	0.9329

It may be important to note that the overall risks of population extinction under these habitat modification scenarios are perhaps an underestimate of the true risks. All of our modeling scenarios do not include significant levels of density dependence in either reproduction or mortality, other than the rather harsh “truncation” form of density dependence imposed when a simulated population exceeds the stated carrying capacity. The decision to exclude it from the modeling effort was based on the fact that specific data on the mode of action of density dependence is not available for greater sage-grouse. In these models, population growth continues at a relative constant average rate until K is exceeded, at which time individuals from the population are randomly removed across all age-sex classes until the population returns to a value at or slightly below K. In other words, the growth rate can remain high, even when the population is at K and the population has been reduced to relatively small numbers through the activity of something like housing development or surface mining activities. Some biologists may argue a contrary view – where the underlying intrinsic population growth declines to near 0.0 when the population reaches carrying capacity. This reduction in growth can lead to accompanying increases in demographic instability over time, especially when the population has been reduced to a small remnant as we are seeing in the Northern Eagle / Southern Routt Counties complex. Reduced average growth rates and instability in these rates can conspire to increase risk of further population decline and perhaps even extinction.

Therefore, the absence of density dependence in this system may result in an artificially high level of apparent stability and, consequently, population security. This characteristic of our simulations may perhaps be investigated in more detail and evaluated for its robustness at a later date. In the meantime, we can conclude that the reduction of available sagebrush habitat through housing development and surface mining activities can greatly reduce the size of associated greater sage-grouse populations.

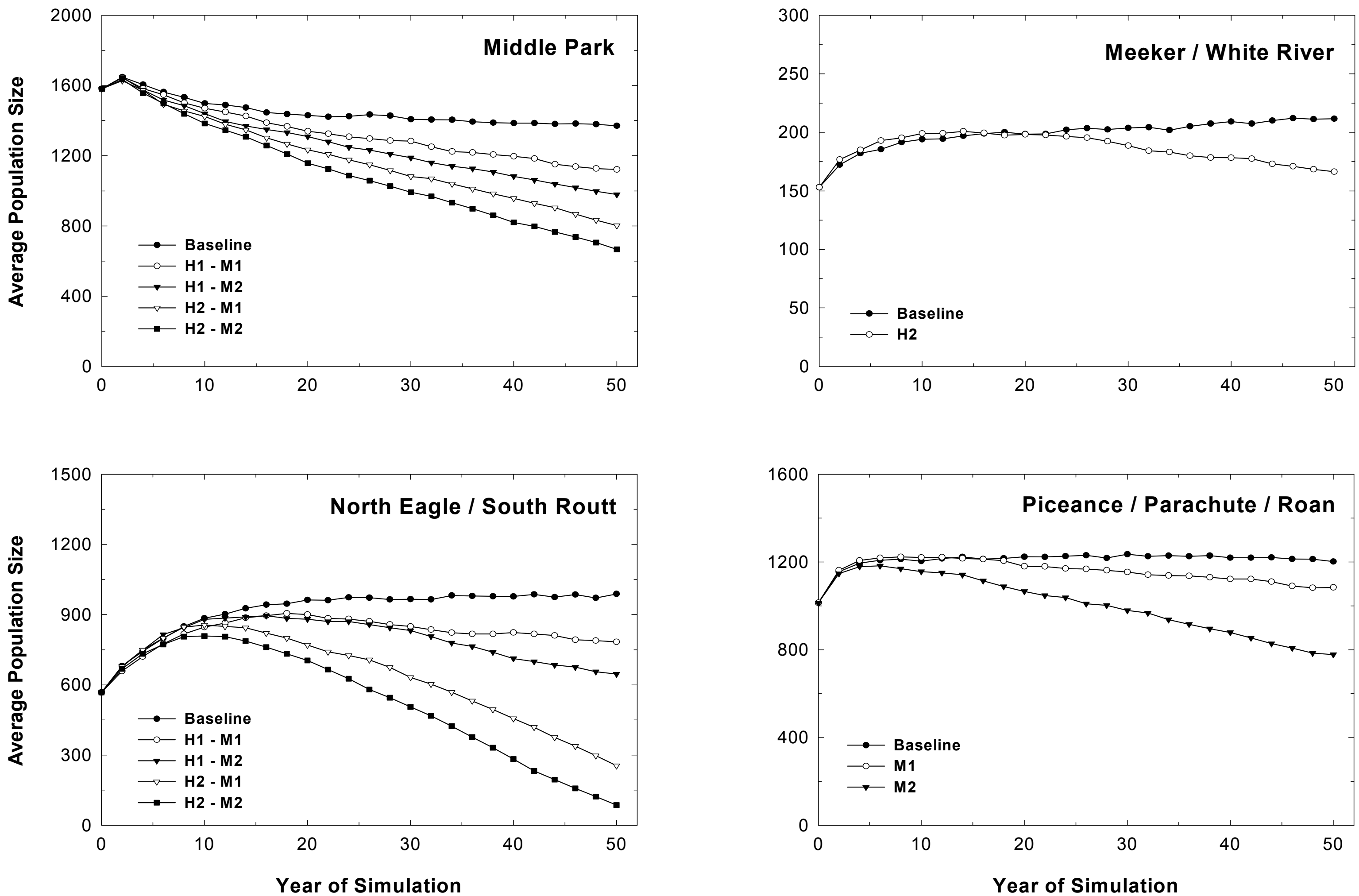


Figure 4. Average projected size of simulated greater sage-grouse populations in the presence of habitat – centric human activities (housing development = H, surface mining = M). Numerical designations “1” and “2” refer to low or high levels of development ntensity, respectively, as described in the section on model inputs. See accompanying text for additional information on model construction and results

Risk Analysis II: Impacts of Local Harvest/ Hunting on Greater Sage-grouse Population Dynamics

Harvest: Model Input

Region considered: North Park

The primary assumption in an analysis of harvest is that such a process will directly impact the mortality rates of affected age-sex classes. Detailed data on harvest composition (based on wing receipts) are available from Jackson County (North Park) dating back to 1970. These data were used in conjunction with high male lek count data in the same area to derive an estimate of the percentage of the total sage-grouse population that was harvested by hunters during the time period 2000 – 2004. From 2000 to 2003, the average harvest was approximately 3.3% of the estimated total population, while in 2004 the harvest increased dramatically to nearly 15% of the population. Moreover, additional analysis indicates that the average composition of the harvest from 1974 to 1998 does not appear to deviate significantly from the age-sex structure of the wild population. In other words, there appears to be little evidence to suggest a noticeable bias in the age or sex of the birds that are harvested.

Based on these historic data, the potential impacts of long-term additional hunting-based mortality was investigated by adding 1%, 2%, 4%, or 8% mortality to all age-sex classes of greater sage-grouse during each year of the simulation. Note that an often vigorous debate exists on the mechanism of hunting mortality in game species such as greater sage-grouse. For many species, hunting mortality is typically thought to be *compensatory*; in other words, hunting is a method for removing individuals from a population that would otherwise die from other natural causes, so that the actual hunting mortality does not impose an additional burden on the population. For other species, hunting may largely act in an *additive* fashion, thereby increasing the overall mortality rate of affected cohorts above that observed in an unaffected population. As is the case with most natural phenomenon, the "truth" for greater sage-grouse likely falls between these two extremes. The hunting models described here do not by definition ascribe to a specific level of compensation and/or additivity, but instead merely serve as a tool to stimulate discussion of hypotheses and associated assumptions.

Results of Harvest Risk Analysis

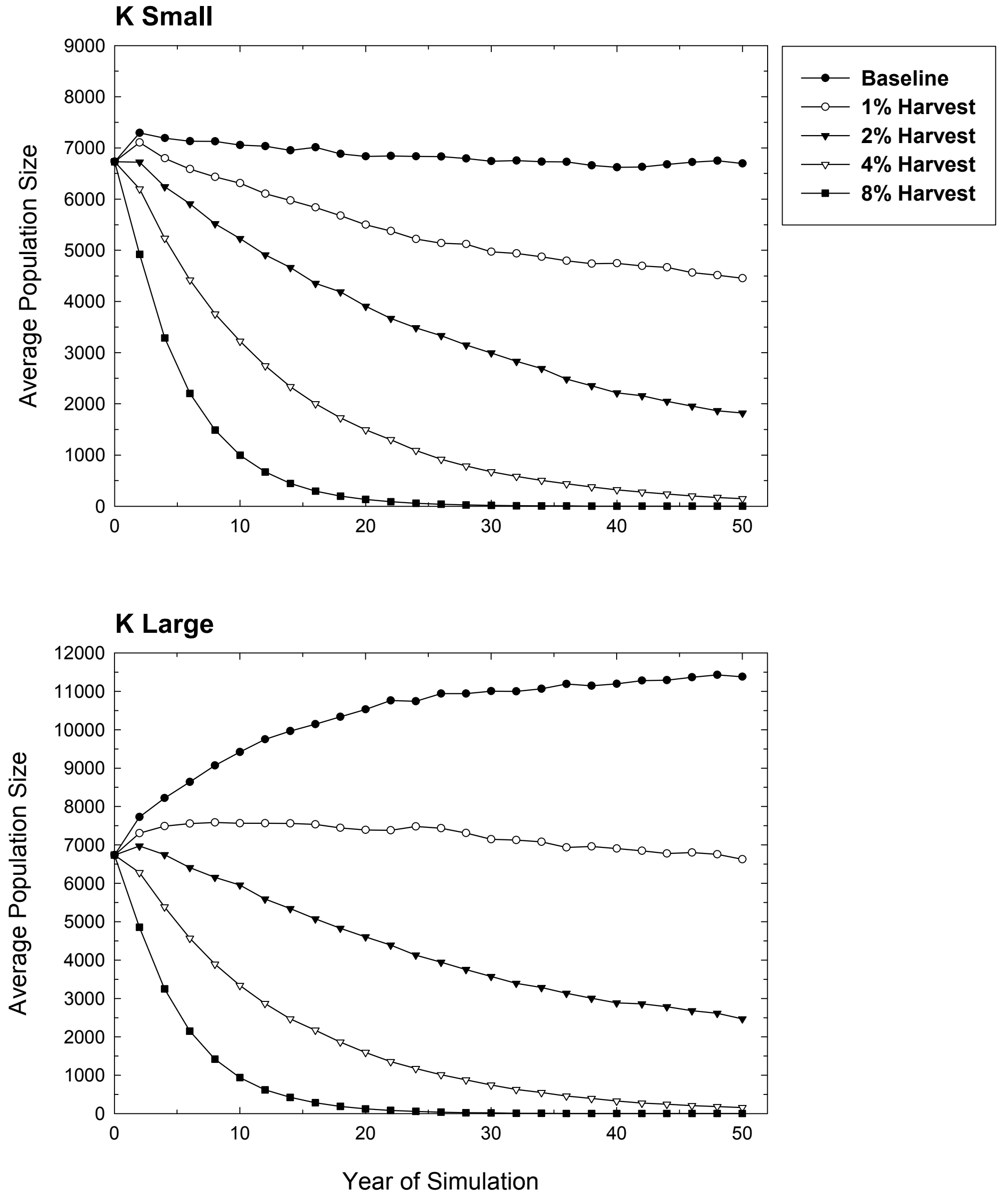
Table 6 and Figure 5 present the results of our harvest analysis on a simulated North Park population of greater sage-grouse. Note that even the imposition of an additional 1% increase in mortality across all age-sex classes can lead to a qualitative change in the growth character of our simulated population – from one that increases at approximately 2.5% per year to one that declines at 0.1 to 0.2% per year.

Table 6. Greater sage-grouse PVA. Output from North Park harvest models. See text for additional information on model construction and parameterization.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
K Small				
Baseline	0.026 (0.136)	0.000	6697 (1634)	0.9903
1% Harvest	-0.001 (0.139)	0.000	4454 (2253)	0.9855
2% Harvest	-0.030 (0.143)	0.000	1820 (1482)	0.9700
4% Harvest	-0.089 (0.163)	0.030	147 (242)	00.8253
8% Harvest	-0.225 (0.233)	0.996	1 (1)	0.1814
K Large				
Baseline	0.024 (0.135)	0.000	11379 (3272)	0.9929
1% Harvest	-0.002 (0.139)	0.000	6624 (4140)	0.9876
2% Harvest	-0.029 (0.144)	0.000	2467 (2649)	0.9718
4% Harvest	-0.089 (0.164)	0.032	156 (208	0.8286
8% Harvest	-0.224 (0.236)	0.994	1 (1)	0.5887

It is clear from these analyses that even a seemingly small increase in mortality – if applied equally to all age-sex classes at the same time – can have dramatic effects on the growth potential and long-term viability of affected populations.

Figure 5. Average projected size of simulated North Park greater sage-grouse populations under different levels of harvest. Harvest is defined here as the identified percentage increase in annual mortality rates across all age classes of both sexes. The top panel shows population projections in the presence of a restrictive carrying capacity, set as 8300 individuals, while the bottom panel shows the same projections when that restrictive carrying capacity is lifted, thereby allowing essentially unrestricted population growth throughout the duration of the simulation. See accompanying text for more information on model construction and results.



It may be argued that the marked declines in population size seen in all harvest scenarios is at least partially caused by the restrictions imposed by the addition of a carrying capacity in our North Park population models. This carrying capacity, estimated to be about 8300 individuals, might be low enough to drive populations to decline as they encounter the restriction to grow beyond the ceiling. To further investigate this hypothesis, a second set of models was developed that effectively removed this restrictive ceiling by increasing carrying capacity K from 8300 to 15,000 individuals. As seen in the bottom panel of

Figure 4, the removal of this restriction allowed the baseline (unharvested) population to nearly double in size over the 50 years of the simulation. However, the harvested populations showed a nearly identical trajectory in the presence of added mortality: significant decrease in growth potential and, in the most extreme cases, rapid population decline to extinction. Therefore, the imposition of a carrying capacity does not seem to be a major factor in predicting how a simulated greater sage-grouse population will respond to additional hunting-based mortality.

A very important assumption in these analyses is that our simulated harvest represents, effectively, 100% additive mortality on top on natural mortality acting on the population. In other words, we are assuming that all those birds that are removed from the population through harvest would have otherwise survived during the year, and many of them would have reproduced. We are therefore simulating the most extreme harvest scenario, in contrast to one where there is some level of compensatory mortality that would serve to reduce the overall magnitude of added mortality on the population. There is considerable controversy on the degree of compensatory v. additive mortality in game species such as greater sage-grouse (see Johnson and Braun 1999 for a review of this topic); while the controversy rages, the analyses presented here provide more general cautionary insights into the sensitivity of sage-grouse populations to slight increases in mortality rates – particular of juvenile and adult females.

Risk Analysis III: Impacts of Oil and Natural Gas Development on Greater Sage-grouse Population Dynamics

Oil and Natural Gas: Initial Model Input

Regions considered: North Park, Northwestern Colorado, Piceance / Parachute / Roan

Scientific evaluation of the effects of oil and gas development on greater sage-grouse in Colorado does not currently exist. Until such research can be completed, we must rely on recent studies from Holloran (2005) and Lyon and Anderson (2003) conducted in Wyoming.

Essentially, Holloran identified two levels of demographic impact on sage-grouse populations in Wyoming, as a function of the density of wells within a 3-km (2-mile) distance from a lek. Holloran (2005) found that male lek attendance was affected by increasing oil and gas development: leks with 5-15 wells within 3km (2 miles) were lightly impacted, while those with >15 wells within 3km were heavily impacted. Since the PVA model assumes that only 10% of males breed, male activity reduction is not likely to strongly influence model performance. However, Holloran also found that annual survival of adult nesting females declined 20.4% (73.4% pretreatment to 53.0% post treatment) in development areas. He also found a 6.4% decline in annual survival (91.8% pretreatment to 85.4% post-treatment) for nesting yearling females. In addition, Lyon and Anderson (2003) found that female nest initiation rates declined in disturbed areas from 89% to 65%, a 24% decline.

In an attempt to estimate oil and gas impacts on greater sage-grouse, we increased adult female mortality by 20%, increased yearling female mortality by 6.4%, and decreased nest initiation by 24% where oil and gas development reaches Holloran's heavy impact criteria (>15 wells within 3km). Holloran used leks where well density was >5 as treatment leks. Leks with less than that level of development were used as controls, where impacts were assumed to be minimal. For our analysis, we raised this control level from 5 to 8 wells/lek. Considering only current infrastructure, North Park is already at 8 wells/lek. As North Park populations remain stable, we believe this upward adjustment in the bottom impact threshold is warranted and supported by current trend data in North Park. Impacts at levels of development between the control and 15 wells/lek were considered to be less than those above 15 wells/lek, though intermediate levels of demographic impacts to female sage-grouse were not reported by Holloran (2005) or Lyon and Anderson (2003). For development densities between our control level of 8 wells/lek and the high impact threshold of 15 wells/lek, we imposed a gradual increase in demographic impact, applying an annual increment of additional mortality and decreased nest initiation each year until the high threshold was reached. The heavy impact parameters were applied each year once the heavy impact threshold was crossed.

To cover a range of possible scenarios, we evaluated three levels of future development (1000, 5000, 20,000 additional wells) in addition to currently active wells. The first two scenarios (1000, 5000) were used for the North Park population (we eliminated 20,000 because forecasts indicate that even 5,000 was a very high estimate for this area), while all three were used for Northwestern Colorado and Piceance / Parachute / Roan. The future development scenarios for each population are intended to represent reasonable low, medium and high levels of potential development over the 50-year life of the PVA model. They do not represent published estimates of development but are selected only to provide a picture of what impacts might be at each level of development. We attempt to keep the scenarios plausible however, by comparing with estimates of foreseeable development for the three areas developed by BLM and others, especially in Northwestern Colorado and Piceance / Parachute / Roan. The medium and high levels in North Park substantially exceed current estimates (~100 wells in the next 20 years). We assumed that existing and new wells would operate through the full life of the model. Holloran (2005) found that existing facilities continued to impact populations after construction, so both existing and potential new wells were combined in each portion of this analysis.

To evaluate development intensity, we randomly plotted wells for each development scenario and then counted the number of wells (current and future) within each 3-km (2-mi) lek buffer. These counts were then averaged across each population or zone. Current active wells were plotted in a GIS within each of the three target populations. Well placement for the various scenarios was then added to the existing well layer. New wells were randomly placed within greater sage-grouse overall range in each population area in the North Park and Piceance / Parachute / Roan populations. In the Northwestern Colorado population, half of the wells were randomly placed in Zones 2 and 3b, both areas with substantial current oil and gas activity. The remaining wells were randomly placed in the remaining Zones, except Zone 7.

For the purposes of this PVA, we assumed that the density of new wells will increase linearly over time. We also assumed that sage-grouse demographic responses will also react linearly over time between the thresholds > 8 wells per lek and >15 wells/lek as described in the table above. The model assumes that impacts of development increase linearly from no impact below the control threshold (8 wells/lek) to the high impact measures once the high threshold is reached (15 wells/lek). That is, no impact is assessed from 0 to 8 wells, annually increasing impacts (heavy impact rates/number of years between control and high threshold) from 9 to 15 wells, and heavy impacts above 15 wells. Therefore, sage-grouse demographic rates will change linearly over time as well until the critical well density threshold is reached (15 wells/lek). Once the heavy impact development level is reached, heavy impact demographic parameters will continue to be applied throughout the remaining course of the 50-year simulation.

A representative set of "trajectories" for the three demographic rates affected is shown in Figure 5 below, considering only adult female mortality in the Piceance / Parachute / Roan region.

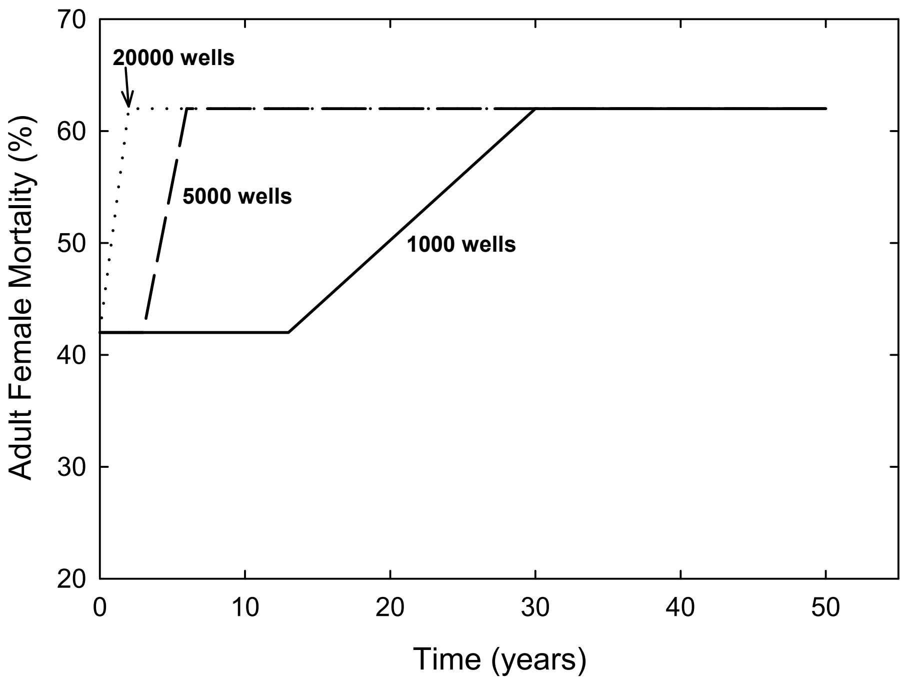


Figure 6. Simulated increase in adult female mortality of Greater sage-grouse in the Piceance / Parachute / Roan region under alternative scenarios of oil and natural gas well development in the region. As the total number of proposed wells increases, the time required to reach the "critical" threshold density of 15 wells / lek decreases, leading to a more rapid rise in mortality as wells are constructed. See text for additional information.

The year at which each threshold is reached under each development scenario was derived from the GIS well plots for each population and Northwestern Colorado zone. These threshold points are presented in Table 7. The body of the table indicates the number of years required to reach the appropriate threshold for each population and development scenario.

Table 7. Time thresholds for impacts from oil and natural gas well development on greater sage-grouse population demographics. The first value gives the number of years before an impact begins, while the second value indicates the number of years before maximum impact is reached. "—" indicates that the appropriate impact threshold is not reached within the 50-year span of the PVA model. See text for additional information on model parameterization.

	Proposed Well Density		
Region	1000	5000	20,000
North Park	1 / 20	1 / 4	
Piceance / Parachute / Roan	13 / 30	3 / 6	1 / 2
Northwestern		25 / 50	6 / 13
1	— / —	30 / —	8 / 20
2	— / —	15 / 30	4 / 8
3A	— / —	40 / —	10 / 20
3B	5 / 30	10 / 30	3 / 8
3C	— / —	20 / 50	5 / 13
4A	— / —	40 / —	10 / 20
4B	— / —	45 / —	11 / 20
5	— / —	40 / —	10 / 20
6	— / —	40 / —	10 / 20
7			

Oil and Natural Gas: Initial Risk Analysis Results

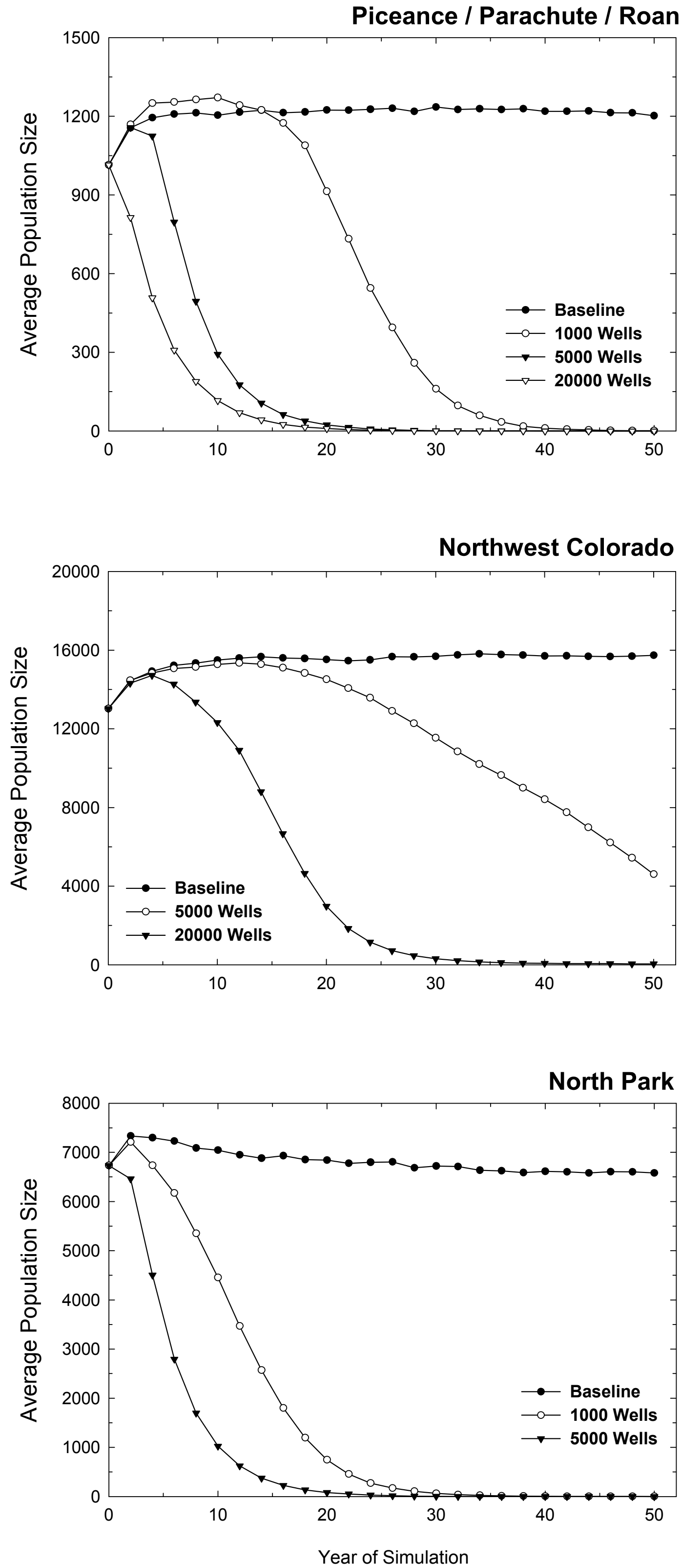
The results of our analysis of oil and natural gas development, and its impact on local populations of greater sage-grouse, are depicted in Table 8 and Figure 7. In all three regions where such development is either currently underway or to begin soon, our simulations suggest that the impact may be severe on the future viability of nearby greater sage-grouse populations. The onset of development leads to strongly negative population growth, rapid population decline and, in all cases but one (lower levels of development in Northwestern Colorado), nearly certain extinction of local grouse populations within 50 years.

This rather dramatic result is clearly the result of imposing strong demographic consequences on greater sage-grouse populations that live and breed near current or proposed oil and natural gas development areas. The data of Holloran (2005) indicate a marked reduction in survival and breeding success of greater sage-grouse in close proximity to oil and natural gas development areas; these data have been used essentially unmodified in this analysis, and clearly represent an unsustainable situation.

Table 8. Greater sage-grouse PVA. Output from initial oil and natural gas analysis models. See text for additional information on model construction and parameterization.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Piceance / Parachute / Roan				
Baseline	0.025 (0.139)	0.000	1202 (342)	0.9422
1000 Wells	-0.120 (0.245)	0.907	1 (2)	0.4616
5000 Wells	-0.220 (0.260)	1.000	—	—
20,000 Wells	-0.260 (0.257)	1.000	—	—
Northwestern Colorado				
Baseline	0.030 (0.081)	0.000	15739 (1872)	0.9956
5000 Wells	-0.011 (0.089)	0.000	4604 (1798)	0.9925
20,000 Wells	-0.011 (0.163)	0.072	48 (29)	0.5142
North Park				
Baseline	0.025 (0.135)	0.000	6582 (1794)	0.9903
1000 Wells	-0.191 (0.230)	0.988	1 (1)	0.4636
5000 Wells	-0.252 (0.238)	1.000	—	—

Figure 7. Average projected size of simulated greater sage-grouse populations in the presence of oil and natural gas development in selected regions of Colorado. See accompanying text for more information on model construction and results.



It is possible that the "raw" data presented in Holloran (2005) represent a worst-case scenario with respect to local greater sage-grouse population viability, for two primary reasons:

1. The natural gas fields Holloran studied were in the most intense development phase, where activity is at its highest and, consequently, impacts on local grouse populations may be most severe. Such development lasts a finite period of time – perhaps only 5 to 10 years – before the field transitions into a production phase where activity is reduced and subsequent impacts on local grouse populations may actually decline. The simulations presented here effectively assume that this development phase remains in effect throughout the 50-year duration of the simulation – thereby possibly over-estimating the long-term impact of the well field on sage-grouse dynamics.
2. Through environmental conditions beyond his control, Holloran actually collected data on the impacts of oil and natural gas field development on greater sage-grouse during a period of marked drought. While the detailed mechanisms of drought's impact on local grouse populations is not fully understood, it is possible that the measured effects in the presence of oil and natural gas development were compounded by the coincident drought – thereby leading to an overestimate of the true impacts of well-field development on local grouse populations.

Oil and Natural Gas: Revised Model Input
Regions considered: Northwestern, Piceance / Parachute / Roan

For several reasons we conducted a second, revised oil and natural gas development modeling exercise. First, the scenario we used in our initial analysis was oversimplified in comparison to actual well field development. That is, the amount of disturbance to sage-grouse can be expected to vary greatly over the process of oil or natural gas exploration, drilling, and production. The initial model data input were derived from the development phase, which creates the most disturbance for sage-grouse.

Second, even though the data on which we based the model input (Holloran 2005) are from the phase of development when the most disturbance to sage-grouse can be expected to occur, sage-grouse populations in the area continue to exist and are not currently demonstrating a population "crash" as depicted in our model results (Figure 7). This suggests our model oversimplifies the relationship between GrSG populations and oil and gas development.

Third, oil and gas development and greater sage-grouse co-exist in several landscapes (including North Park), so we know that not all situations are as extreme as we initially modeled.

Fourth, the initial oil and natural gas modeling exercise showed dramatic impacts from oil and natural gas development (Figure 7). The results from this modeling exercise are not very instructive regarding the relative potential impacts of oil and gas development, because all model versions showed such extreme effects. Even if the extreme impacts are to be expected at one end of the impact "continuum", valuable information regarding management of greater sage-grouse and oil and gas development may be derived from exploring other areas of the impact continuum, before the impacts are so severe.

Therefore, it was decided to revise certain elements of the risk analysis pertaining to the impacts of oil and natural gas development. We constructed a more complicated, but hopefully more realistic model that accounts for changes in the level of disturbance to sage-grouse over the process of oil and gas well field development (termed "*Progressive Well Field Development and Mitigation"* analyses). Our revised models also allow us to explore how sage-grouse might respond to differing levels of disturbance (termed

"*Alternate Disturbance Levels*" analyses), and how best to manage for sage-grouse population viability in areas where oil and/or natural gas development is likely.

These additional analyses were specifically designed to help us address the following questions:

- How would the demographic behavior of our simulated populations of GrSG respond if we modify the oil and gas development model to more accurately reflect the progression of impacts, reclamation, and mitigation at and/or near individual well pad sites, throughout the oil and natural gas development process? We assume that reclamation and mitigation provide effective demographic responses in the population.
- To what extent will the demographic behavior of our simulated populations of greater sage-grouse change if we assume a less severe direct impact to GrSG demographics through oil and gas development, even in the absence of mitigation?

We focused on the Piceance / Parachute / Roan and Northwestern Colorado regions as they effectively represented what we believe to be, on a comparative scale, high-intensity and low-intensity development scenarios, respectively.

Description of Modified Input Parameters

Progressive Well Field Development and Mitigation (Region considered: Piceance / Parachute / Roan)- As displayed graphically in Figure 6, we originally assumed that once the maximum level of demographic disturbance due to well-field development was reached, this high level of disturbance would persist throughout the duration of the simulation. This demographic profile is repeated specifically for adult female mortality in (A) of Figure 8. However, it was recognized that a shift in activity from well-field development to production, in conjunction with a concerted effort in well-field reclamation by responsible authorities, could lead to a reduction in demographic disturbance in nearby greater sage-grouse populations. This recognition was then simulated through a more complex description of those demographic variables thought to be most acutely impacted by this activity, namely, yearling and adult female breeding success (% birds successfully breeding in a given year), and yearling and adult female mortality rates.

In order to describe these more complex demographic profiles, we have derived the following parameters that describe the general trajectories of breeding success and mortality over the duration of the simulations:

- R_0 The magnitude of change in the specified demographic variable following the onset of well-field development;
- T_1 The time period over which the specified demographic variable changes following the onset of well-field development;
- D The duration of time that the demographic disturbance is at a maximum, i.e., when well-field development is most intense;
- T_2 The time period over which the specified demographic variable changes (rebounds) following the shift in activity from well-field development to well-field production;
- R_1 The magnitude of change (rebound) in the specified demographic variable following the shift in activity from well-field development to well-field production.

In all initial simulations, we assume that well-field development results in an increase in demographic disturbance directly in accordance with the data from Holloran (2005). This is portrayed in Figure 8 by an increase in adult female mortality from the pre-development rate of 42% to the maximum rate of 62% – just as we assumed in our initial analyses. Therefore, R_0 = 20%. In all Piceance / Parachute / Roan simulations, we have estimated that a total of 16,000 wells (2,000 pads, 8 wells/pad) will be developed over the next decade. Moreover, we now assume that the beginning of demographic disturbance occurs when the well-pad density reaches 1 pad/km^2 within a 2-mile radius of an active lek, and reaches its maximum when the density reaches 2 pads/km^2 within the same radius. This translates into upper and lower disturbance triggers of 24 and 50 wells/lek, respectively. These new triggers are rather different from the thresholds identified in earlier PVA work (8 and 15 wells/lek), but are considered to be considerably more realistic and defensible.

Based on this assessment, we assume that the onset of demographic disturbance from this development begins at year 4 and reaches its maximum level at year 8; therefore, T_1 is set at 4 years. Duration *D* is plausibly set at either 5 or 10 years in order to explore the sensitivity of our models to variation in this variable. Return time T_2 is either set to the initial period T_1 or, more pessimistically, set to $2T_1$ to simulate a more difficult and longer effort required to mitigate well-field development in the shift to production. The demographic recovery/rebound (R_1) was set equal to R_0, or was considered incomplete (due, for example, to difficulties in returning the well-field landscape to a more undisturbed setting), in which case we set $R_1 = 0.5R_0$.

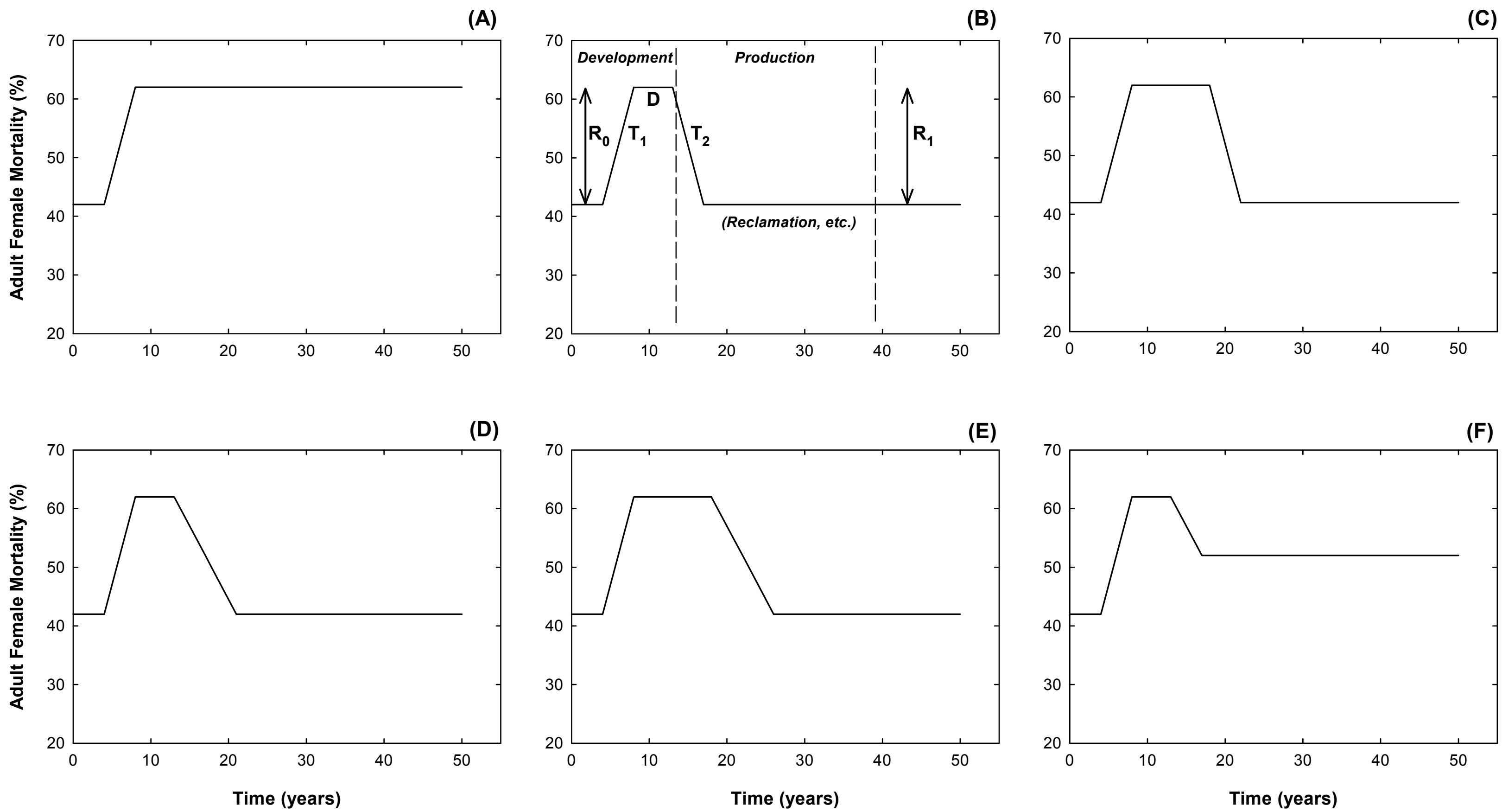


Figure 8. Revised oil and natural gas development risk analysis: generalized adult female greater sage-grouse mortality profiles associated with different timing and mitigation scenarios in *Progressive Well Field Development and Mitigation* analyses in the Piceance / Parachute / Roan region of Colorado. In (A), mitigation is absent and the maximum impacts of well development persist through the duration of the simulation. In (B), well development leads to a mortality increase to the maximum impact over time period T_1 (4 years), over which time the well density increases from 24 to 50 wells/2-mile radius of an active lek. The maximum impact persists for duration D (5 years), after which time the shift to well production and associated landscape reclamation lead to a reduction in impact over time period T_2 (4 years). Finally, the mortality rate declines by magnitude R_1, in this case equivalent to the original magnitude R_0, representing the onset of well development. (C) $T_1 = T_2 = 4$ years; $D = 10$ years. (D) $T_1 = 4$ years, $D = 5$ years, $T_2 = 8$ yeas. (E) $T_1 = 4$ years, $D = 10$ years, $T_2 = 8$ years. (B) through (E) are repeated as in (F), with only partial demographic recovery following reclamation as $R_1 = 0.5R_0$. See accompanying text for more details.

Upon inspection of Figure 8, we can see that (B) represents a "best-case" scenario – where duration D is short, return time T_2 is also short, and demographic recovery is full ($R_1 = R_0$). On the other end of the spectrum, (E) represents a "worst-case" scenario where duration and return times are long. Even more pessimistic is the corresponding scenario combining (E) and (F) – where duration and return times are long and recovery is only partial ($R_1 = 0.5R_0$). It is particularly interesting in this analysis to try to tease apart the relative contributions of these individual parameters to the demographic performance of an impacted greater sage-grouse population. In other words, if well-field mitigation and reclamation is to occur, what would be most beneficial to the long-term viability of associated sage-grouse populations – minimizing duration D, minimizing return time T_2, or maximizing the extent of demographic recovery R_1? Through a process akin to demographic sensitivity analysis, we can begin to shed some light on these questions in the context of designing optimal management strategies that strive for environmental responsibility and economic necessity.

Alternate Disturbance Levels (<u>Regions considered: Northwestern Colorado and Piceance / Parachute / Roan</u>) - To explore how sage-grouse might respond to varying levels of disturbance during development (and recognizing that the initial analysis was based on data from the most intensive disturbance period of well field development), a replicate set of models was constructed for Piceance / Parachute / Roan in which the impacts of oil and natural gas development were reduced by 50% relative to the original models constructed directly from Holloran's observations (Figure 9). Specifically, we increased adult female mortality by 10%, increased yearling female mortality by 3.2%, and decreased nest initiation by 12% when oil and gas development reaches the critical threshold of 50 wells/lek.

Oil and natural gas development in the Northwestern Colorado metapopulation is expected to be less intense than that currently expected in the Piceance / Parachute / Roan region. Specifically, we assume that 50% of the total level of development will occur in Zones 2 and 3B, lower levels occurring in Zones 3A and 3C, and the remainder taking place in the remaining Zones with the exception of Zone 7 where no activity is assumed to take place. Therefore, we included energy development only in Zones 2, 3A, 3B and 3C. Using the same quantitative triggers as used in PPR, we estimate that the lower well-density threshold will be reached in 26 years for Zones 2 and 3B, and in 44 years for Zones 3A and 3C (Figure 10). Maximum thresholds are reached at 50 years (end of the simulation) for Zones 2 and 3B, while the maximum is not reached within this time period for Zones 3A and 3C. Under this assumption, and given the 50-year time period for simulation in this analysis, we do not have the opportunity to investigate well-field mitigation as we did in the Piceance / Parachute / Roan analysis. Nevertheless, the Northwestern Colorado scenarios will provide a valuable contrast to the PPR analyses with respect to the impacts of differing levels of development on populations of considerably different sizes.

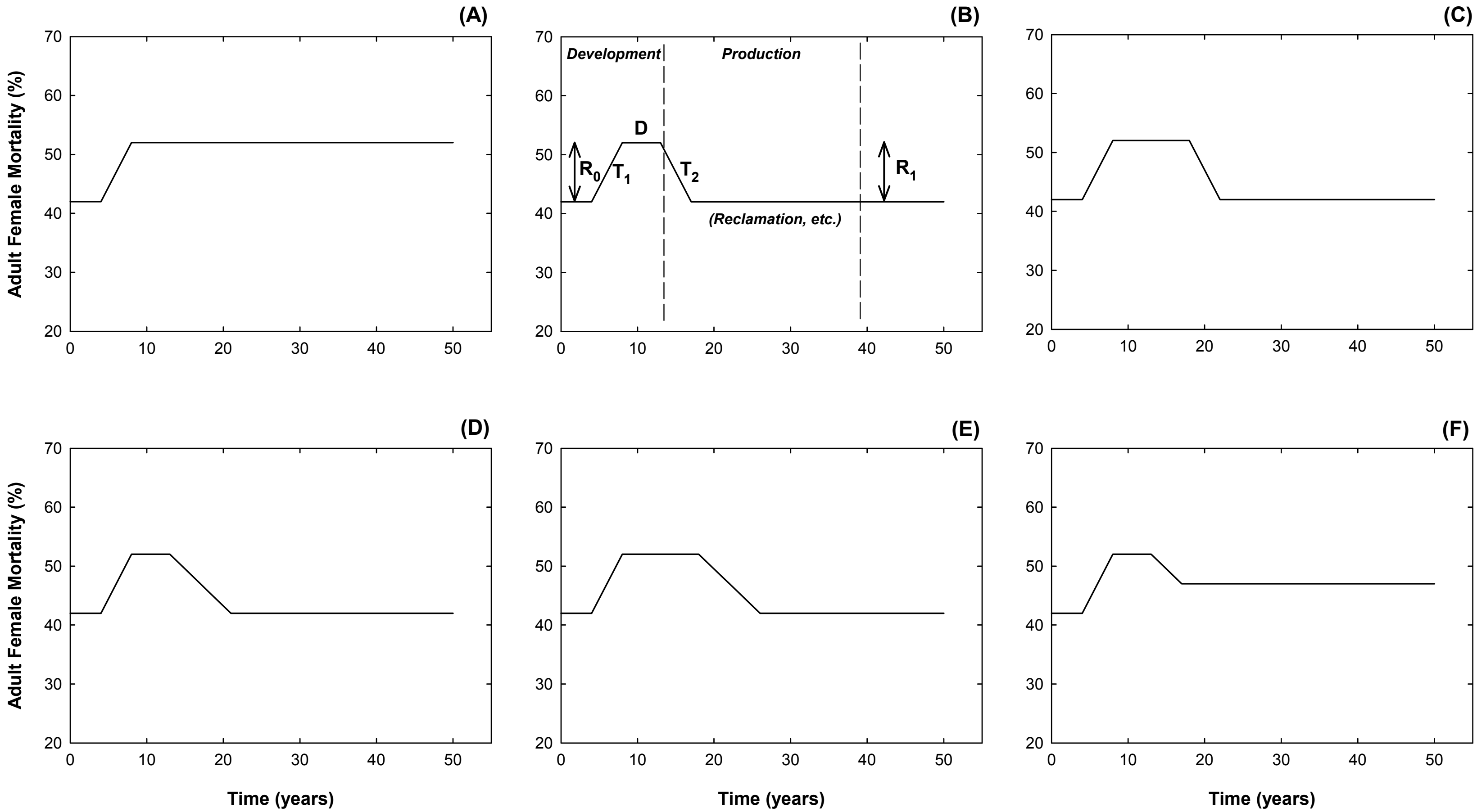


Figure 9. Revised oil and natural gas development risk analysis: *Alternate Disturbance Levels* applied to generalized adult greater sage-grouse female mortality profiles from *Progressive Well Field Development and Mitigation* analyses in the Piceance / Parachute / Roan region of Colorado. In contrast to the graphs given in Figure 8, base demographic impacts in the *Alternate Disturbance Levels* analysis are assumed to be 50% lower than those directly observed by Holloran (2005). In (A), mitigation is absent so the maximum impacts of well development persist through the duration of the simulation. In (B), well development leads to a mortality increase to the maximum impact over time period T_1 (4 years), over which time the well density increases from 24 to 50 wells/2-mile radius of an active lek. The maximum impact persists for duration D (5 years), after which time the shift to well production and associated landscape reclamation lead to a reduction in impact over time period T_2 (4 years). Finally, the mortality rate declines by magnitude R_1, in this case equivalent to the original magnitude R_0, representing the onset of well development. (C) T_1 = T_2 = 4 years; D = 10 years. (D) T_1 = 4 years, D = 5 years, T_2 = 8 yeas. (E) T_1 = 4 years, D = 10 years, T_2 = 8 years. (B) through (E) are repeated as in (F), with only partial demographic recovery following reclamation as $R_1 = 0.5R_0$. See accompanying text for more details.

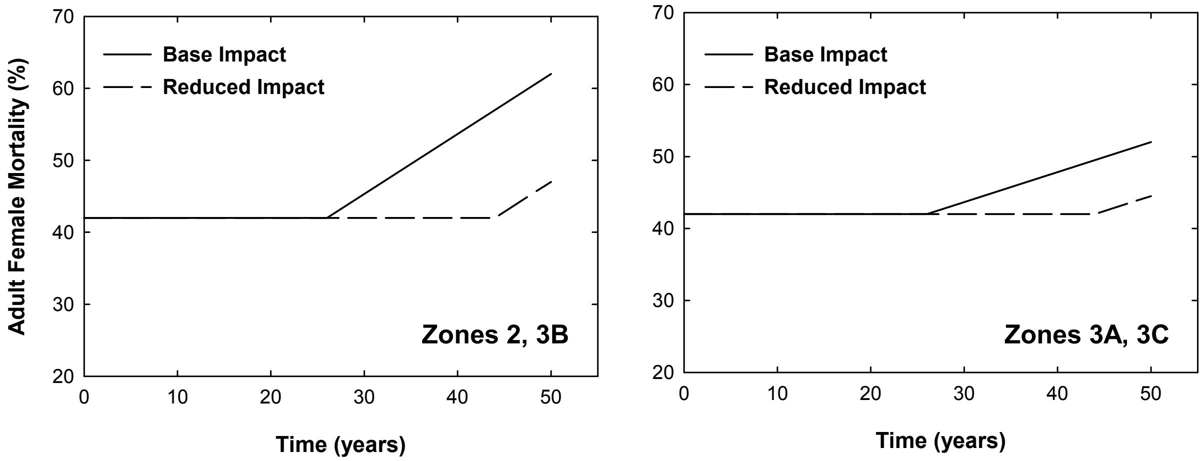


Figure 10. Revised oil and natural gas development risk analysis: *Alternate Disturbance Levels* applied to generalized adult greater sage-grouse female mortality profiles in selected subpopulations of the Northwestern Colorado region. Base demographic impacts are assumed to be directly taken from those observed by Holloran (2005), while in the *Alternate Disturbance Levels*, impacts are 50% less ("reduced impact") than those reported in Holloran (2005). Note that the maximum demographic disturbance levels seen in the Piceance / Parachute / Roan region are not reached before the end of the 50-year simulation for any Northwestern Colorado area, thereby making a detailed analysis of well-field mitigation impractical. See accompanying text for more details.

Oil and Natural Gas: Revised Risk Analysis Results

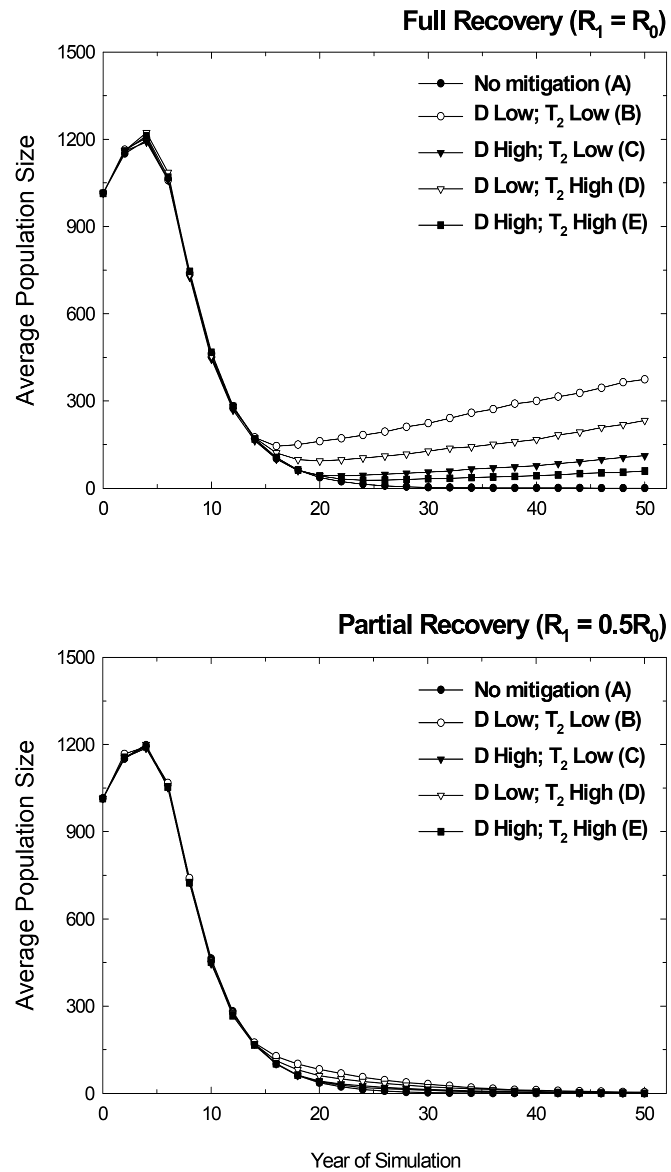
Progressive Well Field Development and Mitigation (Region considered: Piceance / Parachute / Roan)- The results of our basic well-field development and mitigation analysis are presented in Table 9 and Figures 11 and 12. As was seen in the initial analyses for this region, the simplified treatment of well-field development and production leads to an extremely rapid rate of population decline and extinction within 30 years of the onset of well-field construction (Figure 11, (A) line). When mitigation and reclamation are included in the simulations, and in particular under the assumption of full demographic recovery through this activity, extinction risks can decline significantly and growth rates (particularly in the time period following the onset of mitigation and reclamation) can become much more robust. For example, under the most optimistic conditions of well-field mitigation and reclamation (D and T_2 low, with full demographic recovery) population growth rates may remain highly negative for the first 15 to 20 years but can rebound to average more than 2.5% for the remaining 30 to 35 years of the simulation (Figure 11, (B) line).

Figures 11 and 12 can help us separate the relative contributions of each phase of well-field evolution and mitigation activities to the viability of impacted greater sage-grouse populations. The top panel of Figure 11 indicates that the largest extent of population recovery as determined by average population size occurs when duration D (the duration of the most intense disturbance) is low (B and D lines). This effect is seen even more dramatically when we use extinction probability as a measure of population performance (Figure 12). The greatest level of impact is demonstrated when the extent of demographic recovery, R_1, is incomplete (Table 9, $R_1 = 0.5R_0$). Under these conditions, growth rates remain highly negative and extinction probabilities remain very high, even if other aspects of well-field mitigation are pursued aggressively.

Table 9. Greater sage-grouse PVA.: output from the analysis of well-field development and mitigation options in Piceance / Parachute / Roan region. See Figure 8 and text for additional information on model construction and parameterization.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Full Recovery ($R_1 = R_0$)				
No mitigation	-0.205 (0.266)	1.000	—	—
D Low; T_2 Low	-0.033 (0.195)	0.058	374 (385)	0.6956
D High; T_2 Low	-0.081 (0.243)	0.366	112 (196)	0.5485
D Low; T_2 High	-0.049 (0.211)	0.132	233 (304)	0.6181
D High; T_2 High	-0.107 (0.256)	0.542	59 (137)	0.4951
Partial Recovery ($R_1 = 0.5R_0$)				
No mitigation	-0.205 (0.266)	1.000	—	—
D Low; T_2 Low	-0.139 (0.248)	0.838	4 (11)	0.4023
D High; T_2 Low	-0.164 (0.260)	0.924	1 (7)	0.3571
D Low; T_2 High	-0.145 (0.252)	0.852	4 (12)	0.4607
D High; T_2 High	-0.172 (0.263)	0.948	1 (4)	0.3835

Figure 11. Average projected size of simulated greater sage-grouse populations in the Piceance / Parachute / Roan region, in the presence of varying scenarios of oil and natural gas well-field development and mitigation. Total well development includes the construction of 16,000 wells spread over 2,000 well pads. Labels (B) – (E) refer to profiles identified in Figure 8. See Figure 8 and text (“*Progressive Well Field Development and Mitigation”)* for accompanying information on model construction and parameterization.



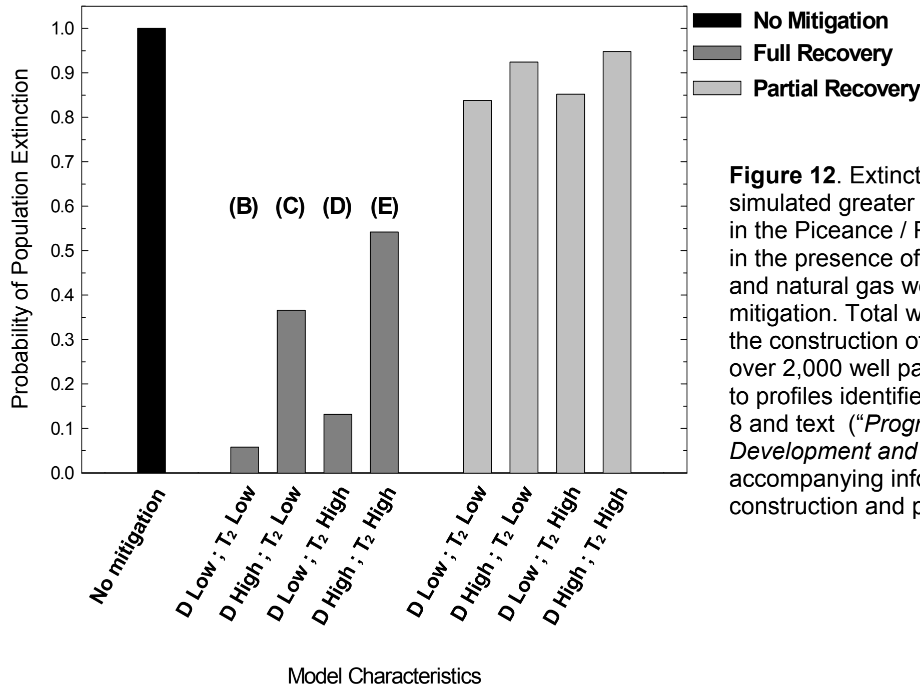


Figure 12. Extinction probabilities for simulated greater sage-grouse populations in the Piceance / Parachute / Roan region, in the presence of varying scenarios of oil and natural gas well-field development and mitigation. Total well development includes the construction of 16,000 wells spread over 2,000 well pads. Labels (B) – (E) refer to profiles identified in Figure 8. See Figure 8 and text (*"Progressive Well Field Development and Mitigation")* for accompanying information on model construction and parameterization.

Given this information, we may conclude that with respect to maintaining viability of greater sage-grouse populations in the presence of oil and natural gas extraction, the impacts of well-field development and production are most effectively mitigated by, in order of decreasing efficacy,

- Maximizing the extent of sage-grouse demographic recovery to near levels observed before the onset of well-field development ($R_1 = R_0$);
- Minimizing the time period of maximum demographic impact (D);
- Minimizing the time period over which demography recovery is achieved (T_s).

The relative feasibility of these activities on the ground is outside the expertise of this author. Nevertheless, it is hoped that this analysis can stimulate discussion among those parties both involved in the undertaking and concerned with the consequences of these activities so that effective protection of nearby greater sage-grouse populations can be achieved.

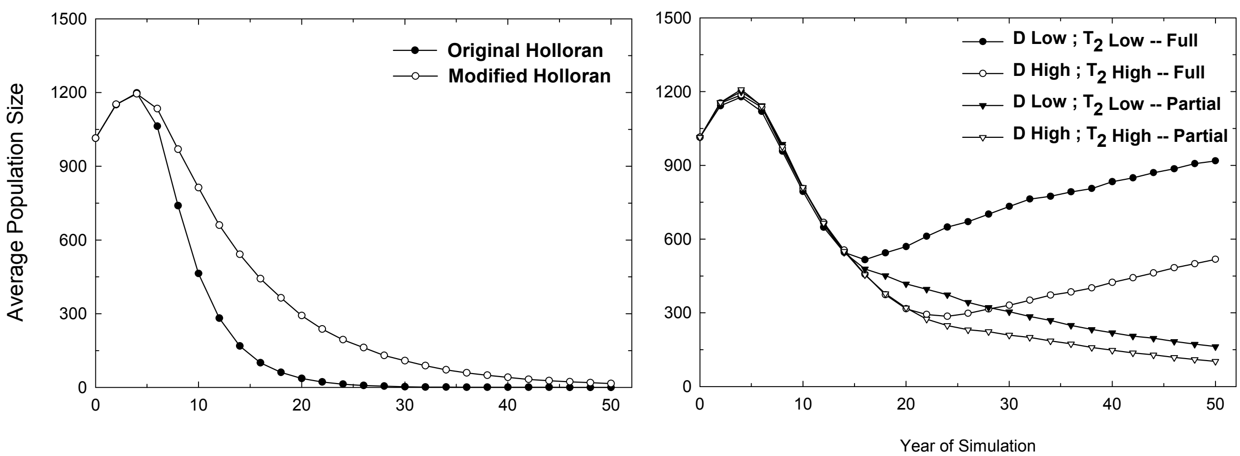
Alternate Disturbance Levels – Even when the demographic impacts are reduced by 50% from Holloran's (2005) original estimates, the simulated Piceance / Parachute / Roan population is heavily impacted by oil and natural gas development and production (Table 10 [first 2 rows of data], Figure 13 [left panel]). The initial population decline is less severe under the assumption of reduced demographic disturbance, and the population growth rate shows significant improvement over the original simulations, but the underlying growth rate remains highly negative and the ultimate outcome of the simulations are very similar.

Table 10. Greater sage-grouse PVA: output using revised assumptions of the impact of oil and natural gas

development. Data are the outcome of different well-field development and mitigation scenarios in Piceance / Parachute / Roan region (*Progressive Well Field Development and Mitigation*), where the base impacts of well-field development are reduced by 50% (*Alternate Disturbance Levels*) from the initial analyses that used the direct observations of Holloran (2005). See Figure 9 and text for additional information on model construction and parameterization.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Original impact (Holloran 2005)	-0.205 (0.139)	1.000	—	—
Modified impact (50% of original)	-0.102 (0.208)	0.478	15 (25)	0.5766
Mitigation Options (using modified impact from above)				
D Low; T_2 Low – Full Recovery	-0.001 (0.151)	0.000	918 (479)	0.8808
D High; T_2 High – Full Recovery	-0.020 (0.163)	0.006	517 (426)	0.7918
D Low; T_2 Low – Partial Recovery	-0.049 (0.167)	0.042	162 (188)	0.7525
D High; T_2 High – Partial Recovery	-0.058 (0.175)	0.080	102 (124)	0.6999

Figure 13. Average projected size of simulated greater sage-grouse populations in the Piceance / Parachute Roan region under revised assumptions of the impact of oil and natural gas development. The left panel illustrates *Alternate Disturbance Levels*: the original estimated impact compared with the modified impact (50% of the original). The right panel illustrates alternative scenarios of well-field development and mitigation, using the modified base impact level from the left panel. See Figures 8 and 9 and text for accompanying information on model construction and parameterization.



When oil and natural gas development occurs in selected Zones of the Northwestern Colorado region, overall greater sage-grouse metapopulation viability is high over the time period of the simulations presented here (Table 11, Figure 14). The consequences of the delayed onset of demographic disturbance following oil and natural gas development is clear in Figure 14, as is the lower overall impact of development under the *Alternate Disturbance Levels* analysis. As expected, the consequences of oil and natural gas activity begin to show themselves around year 30 of the simulation, in accordance with the onset of demographic disturbance in Zones 2 and 3B at year 26. While the disturbance does not lead to a measurable risk of metapopulation extinction in the 50-year timeframe of the simulations presented here, population size does indeed decline markedly in the latter portions of the simulation. Oil and natural gas development activity, it is clear, is predicted to have an impact in this region, with the possibility that the overall greater sage-grouse regional population may decline to levels below those currently estimated.

Table 11. Greater sage-grouse PVA: output using revised assumptions of the impact of oil and natural gas development. Data are the outcome of different well-field development and mitigation scenarios in the Northwestern Colorado region (*Progressive Well Field Development and Mitigation*), where the base impacts of well-field development are reduced by 50% (*Alternate Disturbance Levels*) from the initial analyses that used the direct observations of Holloran (2005). See Figure 9 and text for additional information on model construction and parameterization. Population size and extinction probability are given for the entire metapopulation. See text for additional information on model construction.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Original impact (Holloran 2005)				
No well development	0.030 (0.081)	0.000	15824 (1824)	0.9956
10,000 wells	0.016 (0.083)	0.000	10809 (2526)	0.9951
Modified impact (50% of original)				
No well development	0.030 (0.081)	0.000	15824 (1824)	0.9956
10,000 wells	0.022 (0.082)	0.000	13484 (2384)	0.9954

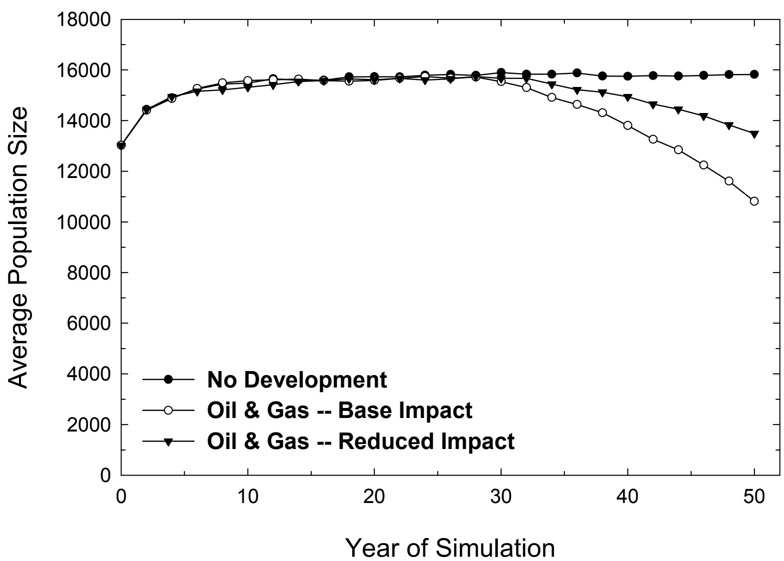


Figure 14. Average projected size of simulated greater sage-grouse populations in the Northwestern Colorado region, under revised assumptions of the base impact of oil and natural gas development. *Alternate Disturbance Levels* analysis is illustrated: the original estimated impact (base) compared with the reduced impact (50% of the original). See text for additional information on model construction.

The PVA analyses presented here may be seen as preliminary, particularly because they are based on data collected from Wyoming under a single development phase (Holloran 2005), and may be subject to refinement at a later date. Nevertheless it is important to recognize that in our models oil and natural gas development are expected to impact two important demographic parameters: adult female breeding success and mortality. Those two parameters are precisely the demographic parameters that appear to be primary drivers of population growth as determined in the sensitivity analysis of the PVA. Therefore, while the exact degree of impact is unknown at the present time, it remains quite likely that this type of activity, with its direct impacts on sage-grouse demographic rates, can have a much more severe impact on the stability and future viability of local sage-grouse populations than those activities such as housing development, which we believe act solely to reduce the quantity and/or quality of available sagebrush habitat.

Risk Analysis IV: An Assessment of Increasing Reproductive Success Through Reproductive Mitigation as a Greater Sage-grouse Management Tool

Reproductive Success Mitigation: Model Input
<u>Regions considered: All</u>

In addition to the anthropogenic activities in Risk Analyses I - III, our PVA model considers the impact that increasing reproductive success could have on improving greater sage-grouse population demographics. Mitigation activities that might increase sage-grouse reproductive success can include improving habitat quality and/or availability, population augmentation, or predator mitigation. It is important to consider that "predator mitigation" does not by necessity mean "predator control" in the typical sense. Mitigation can also be at least partially achieved through, for example, habitat modifications that make predation on nesting sage-grouse less likely.

The choice was made to simulate reproductive mitigation through improving reproductive success, since past research (e.g., Duebbert and Kantrud 1974; Garretson and Rohwer 2001) has demonstrated that such activity can be highly beneficial during the breeding season for waterfowl species. Unfortunately, analogous data do not exist for greater sage-grouse, and studies on European species have targeted adult survival.

In light of the data cited above, we elected to simulate three different levels of reproductive mitigation by increasing the percentage of breeding-age greater sage-grouse that successfully reproduce in a given year by 5%, 10%, or 15%. These values were added to the baseline measures for both yearlings and adults. For example, the baseline value of 38.7% of yearling females breeding was increased to 43.7%, 48.7%, and 53.7%. Reproductive mitigation was simulated in the large majority of models that included one or more human activities in order to evaluate its utility as a management action that could possibly ameliorate the negative impact of other activities on the landscape.

Reproductive Mitigation Results: (1) Housing and Surface Mining; (2) Harvest (3) Initial Oil and Natural Gas Development Model

The results of our reproductive mitigation models for housing, surface mining, and the initial oil and natural gas development analysis are shown in Table 12 and Figure 15. The efficacy of reproductive mitigation as a management tool for greater sage-grouse depends on the primary type of human activity that takes place within sage-grouse habitat, and on the underlying growth dynamics of the grouse populations. For example, in Middle Park where housing and surface activities are of primary concern and the current population is already thought to be close to its habitat carrying capacity, reproductive mitigation appears to have relatively little overall impact. This is because, as we have learned before, housing development and surface mining activities act to reduce carrying capacities, while leaving the underlying greater sage-grouse population demography unchanged (in the absence of density-dependent phenomena). The increase in reproductive success through various mitigation activities only serves to hasten the approach of the simulated population to carrying capacity, after which time the population's trajectory is constrained by the gradual decrease in available habitat.

In contrast, consider the case of Meeker / White River where the population has an opportunity to grow to a carrying capacity that is currently rather large compared to today's population size. In this instance, an increase in reproductive success through mitigation activities can have a dramatic effect on the growth potential of the simulated greater sage-grouse population. Over the first 20 years of the simulation, the population can increase in size by as much as about 50% compared to the baseline trajectory, in the absence of housing development and reproductive mitigation. At later stages of the simulation, the model's growth potential is ultimately constrained by the gradual reduction in habitat carrying capacity – but reproductive mitigation models still show final population sizes that are at least as large as the baseline model. Under these conditions, reproductive mitigation can have a considerable impact potential.

The effects of reproductive mitigation can be much more pronounced under moderate levels of harvest mortality, as demonstrated in North Park in Table 12 and Figure 15. When reproductive mitigation is strong, the population can grow to a level that is larger than that predicted in the baseline model where harvest is absent. Even under low levels of reproductive mitigation, the final size of the harvested population is nearly three times that of a population where reproductive mitigation is absent. Of course, under conditions of higher harvest mortality, the benefits gained from reproductive mitigation are not as pronounced. The practice of reproductive mitigation, however, is shown here to have significant potential to improve the viability of greater sage-grouse populations in the presence of certain types of detrimental human activities on the landscape.

When reproductive mitigation is assessed in the context of our initial assumptions around the impacts of oil and natural gas development, the situation remains much less optimistic. As exemplified by the Piceance / Parachute / Roan example given in Table 12 and Figure 15 the increase in reproductive success achieved through mitigation does not sufficiently compensate for the significant declines in survival and breeding success that result from oil and natural gas development. Overall population sizes may be considerably higher in the early stages of the simulation, particularly under assumed conditions of strong reproductive mitigation, but the general trend in population trend remains strongly negative, with high extinction risks by the end of the 50-year simulation.

Table 12. Greater sage-grouse PVA: output from analysis of reproductive mitigation models. “H2” and “M2” refer to high levels of habitat loss through housing and surface mining activities, respectively, in Middle Park and Meeker / White River. “20,000 Wells” refers to a given level of oil and natural gas activity in the Piceance / Parachute / Roan region (in the initial oil an gas risk analysis), and “2%” in North Park refers to specific level of harvest mortality through hunting. Reproductive mitigation is simulated through a 5%, 10% or 15% increase in the number of yearling and adult females that breed in a given year. See text for additional information on model construction and results.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Middle Park				
Baseline	0.022 (0.138)	0.000	1370 (400)	0.9351
Housing 2 – Mining 2	0.023 (0.140)	0.000	667 (121)	0.9366
Housing 1 – Mining 2 +5%	0.064 (0.140)	0.000	725 (71)	0.9410
Housing 2 – Mining 1 +10%	0.103 (0.140)	0.000	741 (50)	0.9408
Housing 2 – Mining 2 +15%	0.140 (0.142)	0.000	752 (38)	0.9374
Meeker / White River				
Baseline	0.019 (0.160)	0.016	208 (83)	0.6619
Housing 2	0.020 (0.162)	0.010	165 (62)	0.6347
Housing 2 +5%	0.061 (0.153)	0.000	208 (32)	0.6937
Housing 2 +10%	0.099 (0.154)	0.000	219 (22)	0.7024
Housing 2 +15%	0.139 (0.153)	0.000	224 (16)	0.7007
North Park				
Baseline	0.026 (0.136)	0.000	6697 (1634)	0.9903
2%	-0.030 (0.143)	0.000	1820 (1482)	0.9700
2% +5%	0.010 (0.145)	0.000	5379 (2208)	0.9870
2% +10%	0.048 (0.145)	0.000	7237 (1306)	0.9903
2% +15%	0.084 (0.148)	0.000	7829 (825)	0.9907
Piceance / Parachute / Roan				
Base line	0.025 (0.139)	0.000	1202 (342)	0.9422
20,000 Wells	-0.260 (0.257)	1.000	—	—
20,000 Wells +5%	-0.204 (0.251)	0.998	1 (2)	0.5559
20,000 Wells +10%	-0.152 (0.243)	0.916	1 (5)	0.3953
20,000 Wells +15%	-0.107 (0.216)	0.530	17 (44)	0.5612

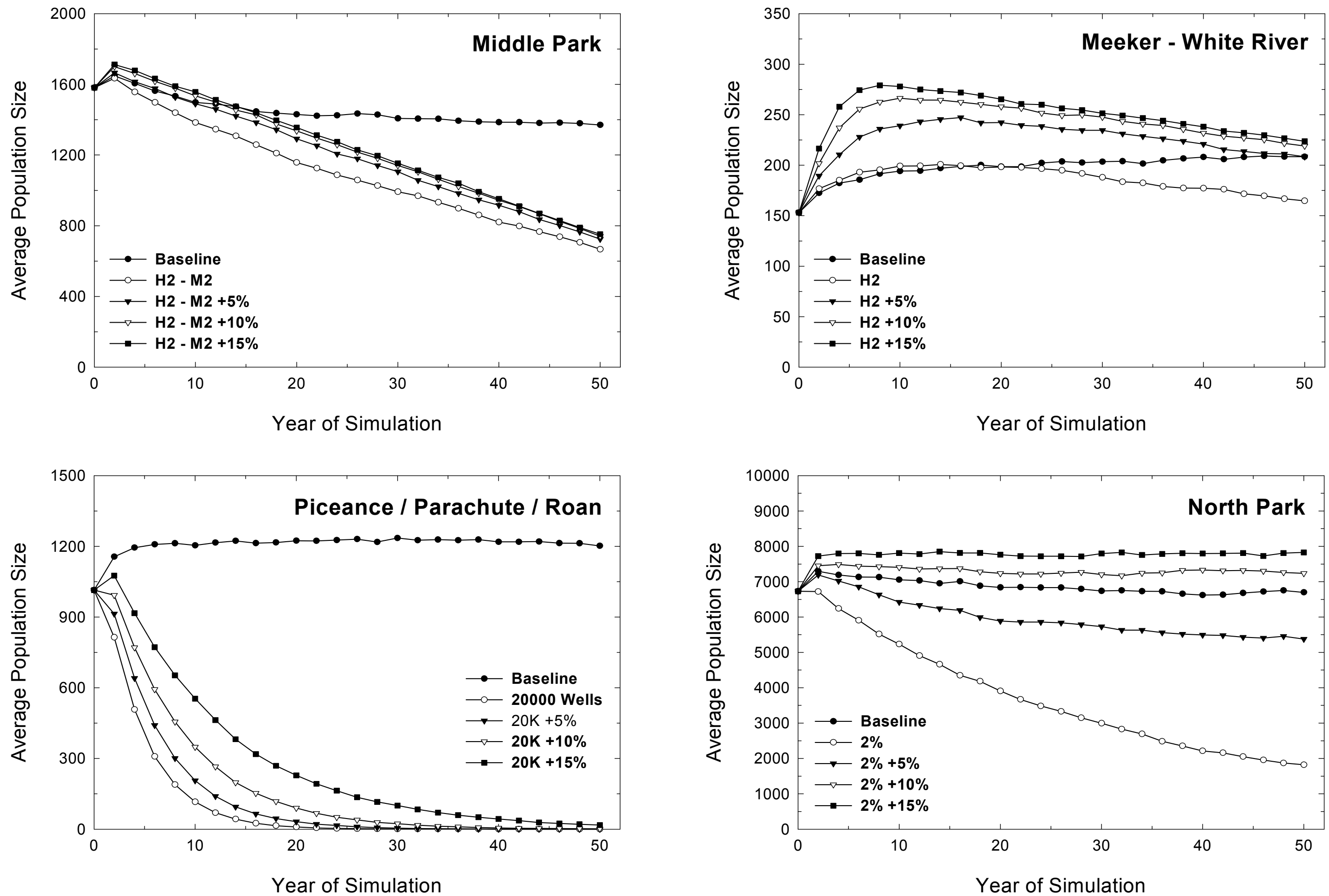


Figure 15. Average projected size of simulated greater sage-grouse populations in the presence of region-specific human activities and with varying levels of reproductive mitigation. “H2” and “M2” refer to high levels of habitat loss through housing and surface mining activities, respectively, in Middle Park and Meeker / White River. “20000 Wells” refers to a given level of oil and natural gas activity in the Piceance / Parachute / Roan region, and “2%” in North Park refers to specific level of harvest mortality through hunting. Reproductive mitigation is simulated through a 5%, 10% or 15% increase in the number of yearling and adult females that breed in a given year. See accompanying text for additional information on model construction and results

Reproductive Success Mitigation
Revised O&G; Regions considered:

In addition to investigating well-field mitigation and reclamation, another set of models was developed for both Piceance / Parachute / Roan and Northwestern Colorado that included increasing reproductive success as a complementary tool for greater sage-grouse management. As in earlier models, female breeding success was increased in selected models by 5%, 10%, or 15% in accordance with an assumed level of intensity of any of a number of alternative management activities such as improvements in habitat quality / availability, population augmentation, and predator mitigation.

Reproductive Mitigation: Results for Revised Oil and Natural Gas Development Model

Piceance / Parachute / Roan

Progressive Well Field Development and Mitigation - The combined effects of well-field mitigation / reclamation and additional reproductive mitigation activities are shown in Table 13 and Figure 16. If full demographic recovery is possible with aggressive well-field mitigation, significant increases in growth rate can be achieved with as little as a 5% increase in greater sage-grouse reproductive success through additional mitigation (Figure 16A). If well-field mitigation is less aggressive, larger increases in reproductive success through additional mitigation are required to offset the impacts of well-field disturbance. At the other end of the well-field mitigation spectrum, where only partial demographic recovery is possible, high levels of increased reproductive success are required to offset well-field disturbance (Figure 16C, D).

Figure 16 shows very explicitly the interactions among the various mitigation activities. When well-field development is extended (*D* increases), the size of the population decreases further and remains at a lower level for a longer period of time. These two processes act to greatly increase the risk of population extinction in the absence of additional mitigation. The additional mitigation activities greatly diminish these risks. Once again, the impact of only partial demographic recovery is clearly demonstrated, as well as the need for aggressive reproductive mitigation in the face of incomplete well-field mitigation.

Table 13. Greater sage-grouse PVA: output from combined analysis of *Progressive Well Field Development and Mitigation* and reproductive mitigation activities in Piceance / Parachute / Roan region. See Figure 8 and text for additional model information.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Full Recovery ($R_1 = R_0$)				
D Low; T_2 Low				
+0% Reprod. success	-0.033 (0.195)	0.058	374 (385)	0.6956
+5%	0.018 (0.170)	0.000	1242 (398)	0.8674
+10%	0.059 (0.167)	0.000	1484 (146)	0.9222
+15%	0.096 (0.165)	0.000	1526 (77)	0.9422
D High; T_2 High				
+0% Reprod. success	-0.107 (0.256)	0.542	59 (137)	0.4951
+5%	-0.030 (0.211)	0.106	480 (484)	0.6582
+10%	0.020 (0.186)	0.006	1238 (444)	0.8168
+15%	0.065 (0.176)	0.000	1514 (108)	0.9087
Partial Recovery ($R_1 = 0.5R_0$)				
D Low; T_2 Low				
+0% Reprod. success	-0.139 (0.248)	0.838	4 (11)	0.4023
+5%	-0.078 (0.205)	0.270	47 (67)	0.6240
+10%	-0.026 (0.167)	0.018	358 (351)	0.8061
+15%	0.019 (0.158)	0.000	1091 (433)	0.9118
D High; T_2 High				
+0% Reprod. success	-0.172 (0.263)	0.948	1 (4)	0.3835
+5%	-0.113 (0.239)	0.590	13 (28)	0.4872
+10%	-0.050 (0.195)	0.122	154 (208)	0.6602
+15%	0.001 (0.165)	0.004	769 (483)	0.8502

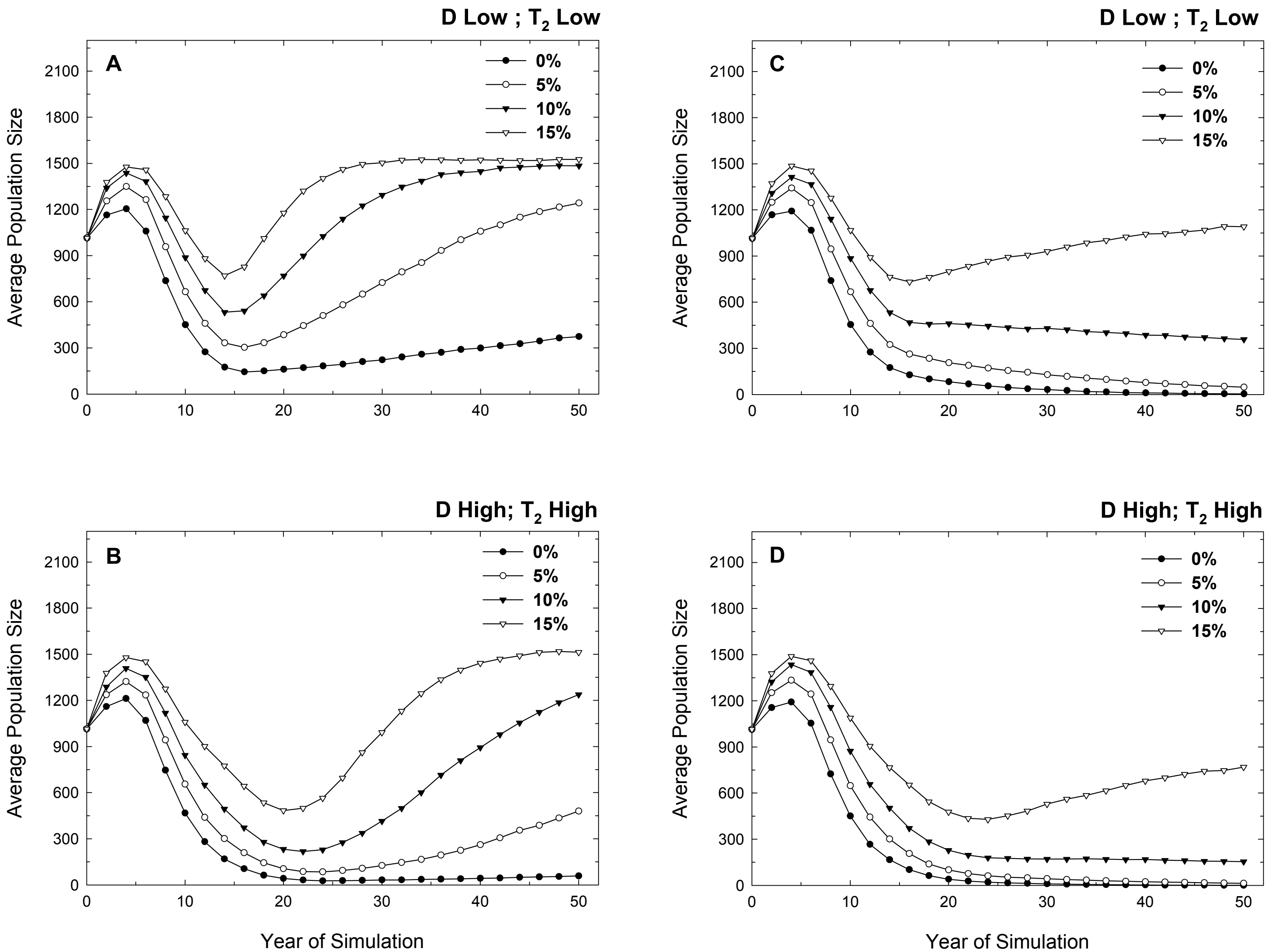


Figure 16. Average projected size of simulated greater sage-grouse populations in the Piceance / Parachute / Roan region in the presence of *Progressive Well Field Development and Mitigation* and additional levels of reproductive mitigation. Reproductive mitigation is simulated through a 5%, 10% or 15% increase in the number of yearling and adult females that breed in a given year. Left-side panels A and B include full demographic recovery following well-field development, while right-side panels C and D include only partial recovery. See Figure 8 and text for accompanying information on model construction and parameterization.

Alternate Disturbance Levels – If we assume the base impacts to be set at the reduced level (50% of initial analysis, which was based on Holloran 2005), the benefits of well-field mitigation are enhanced by reproductive mitigation (Table 14; Figure 17, right panel; compare with trajectories in Figure10). If full demographic recovery is possible through well-field mitigation and reclamation, just a 5% increase in reproductive success through mitigation activities can dramatically increase the growth rate to as high as 0.042, in contrast to a negative growth rate in the absence of reproductive mitigation (Figure 17). Even if demographic recovery is only partial, low levels of reproductive mitigation are sufficient to offset the impacts of well-field development. As expected, this enhancement through mitigation is much more effective when the underlying base impact of oil and natural gas development is assumed to be lower than that estimated initially by Holloran (2005).

Table 14. Greater sage-grouse PVA: output from combined analysis of *Progressive Well Field Development and Mitigation* and additional reproductive mitigation in Piceance / Parachute / Roan region, along with *Alternate Disturbance Levels* of oil and natural gas development. See Figure 9 and text for additional information on model construction

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Full Recovery ($R_1 = R_0$)				
D Low; T_2 Low				
+0% Reprod. success	-0.001 (0.151)	0.000	918 (479)	0.8808
+5%	0.042 (0.147)	0.000	1413 (210)	0.9383
+10%	0.081 (0.048)	0.000	1500 (116)	0.9488
+15%	0.119 (0.148)	0.000	1519 (91)	0.9504
D High; T_2 High				
+0% Reprod. success	-0.020 (0.163)	0.006	517 (426)	0.7918
+5%	0.024 (0.153)	0.000	1302 (341)	0.9108
+10%	0.065 (0.150)	0.000	1486 (142)	0.9446
+15%	0.104 (0.150)	0.000	1524 (90)	0.9490
Partial Recovery ($R_1 = 0.5R_0$)				
D Low; T_2 Low				
+0% Reprod. success	-0.049 (0.167)	0.042	162 (188)	0.7525
+5%	-0.001 (0.147)	0.000	806 (462)	0.8994
+10%	0.043 (0.145)	0.000	1333 (274)	0.9451
+15%	0.081 (0.145)	0.000	1467 (160)	0.9501
D High; T_2 High				
+0% Reprod. success	-0.058 (0.175)	0.080	102 (124)	0.6999
+5%	-0.011 (0.153)	0.002	613 (433)	0.8680
+10%	0.033 (0.147)	0.000	1292 (323)	0.9357
+15%	0.073 (0.146)	0.000	1467 (152)	0.9487

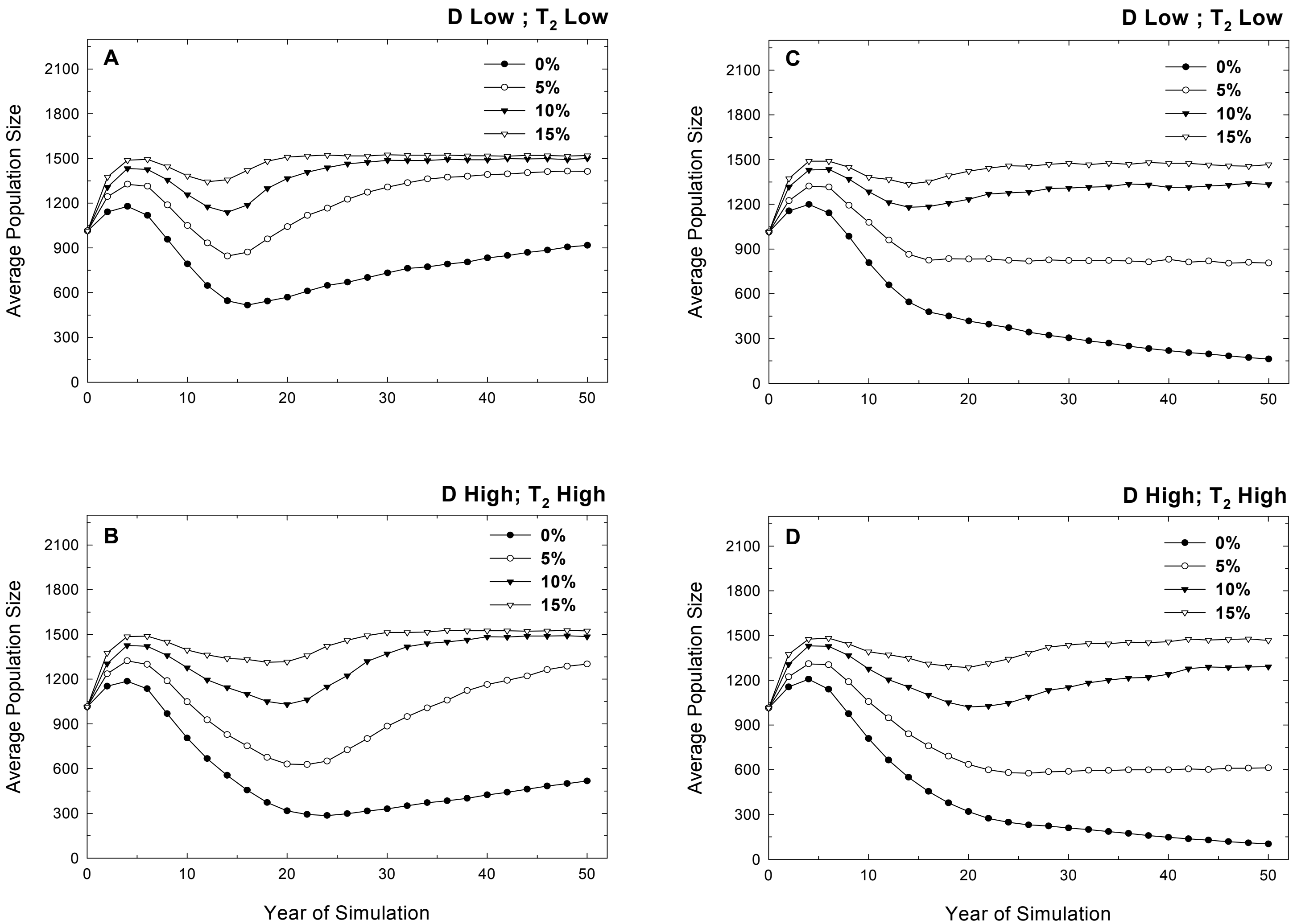


Figure 17. Average projected size of simulated greater sage-grouse populations in the Piceance / Parachute Roan region in the presence of *Progressive Well Field Development and Mitigation* and additional reproductive mitigation, along with *Alternate Disturbance Levels* of oil and natural gas development. Reproductive mitigation is simulated through a 5%, 10% or 15% increase in the number of yearling and adult females that breed in a given year. Left-side panels A and B include full demographic recovery following well-field development, while right-side panels C and D include only partial recovery. See Figure 9 and text for accompanying information on model construction and parameterization.

Northwestern Colorado

An increase in greater sage-grouse reproductive success through mitigation activities may be an option to offset the consequences of demographic disturbances brought on by oil and natural gas development in the region. The predicted consequences of this activity are presented in Table 15 and Figure 18. As in the case of the Piceance / Parachute / Roan analyses, even modest increases in reproductive success through mitigation activities can lead to significant increases in metapopulation growth rate and final population size, even if the base impact of oil and natural gas development as defined by Holloran (2005) is in place (top panel, Figure 18). A small set of additional models was constructed that were meant to investigate the efficacy of an increase in greater sage-grouse reproductive success over a restricted geographic area – namely, only those Zones where the bulk of regional oil and natural gas development activity is predicted to occur (Zones 2, 3A, 3B, and 3C). In general, a 10% increase in reproductive success across the restricted area is as effective in increasing population size as a 5% increase in reproductive success applied to the entire region. The relative merits of each of these tactics would be necessary in order to more logically determine the most beneficial course of action in planning a reproductive mitigation plan, should one be deemed valuable.

Table 15. Greater sage-grouse PVA: output from combined analysis of *Progressive Well Field "Development and Mitigation* and additional reproductive mitigation in the Northwestern Colorado region, under *Alternate Disturbance Levels* of oil and natural gas development. Population size and extinction probability are given for the entire metapopulation. "Restricted" reproductive mitigation refers to increases in reproductive success in greater sage-grouse through mitigation activities in only those Zones that see comparatively high levels of oil and natural gas development activity (specifically, Zones 2, 3A, 3B, and 3C), as opposed to the same levels of increased success realized in all Zones comprising the Northwestern Colorado region. See text for additional information on model construction.

Scenario	r_s (SD)	PE_{50}	N_{50} (SD)	GD_{50}
Base Holloran impact				
No well development	0.030 (0.081)	0.000	15824 (1824)	0.9956
10,000 wells	0.016 (0.083)	0.000	10809 (2526)	0.9951
+5% reprod. success	0.056 (0.084)	0.000	14631 (1694)	0.9956
+10%	0.096 (0.085)	0.000	16285 (1096)	0.9956
+5% restricted reprod. success	0.035 (0.085)	0.000	13112 (2213)	0.9955
+10%	0.055 (0.085)	0.000	14630 (1922)	0.9956
Reduced Holloran impact				
No well development	0.030 (0.081)	0.000	15824 (1824)	0.9956
10,000 wells	0.022 (0.082)	0.000	13484 (2384)	0.9954
+5% reprod. success	0.064 (0.082)	0.000	16217 (1300)	0.9958
+10%	0.103 (0.083)	0.000	17136 (827)	0.9959
+5% restricted reprod. success	0.042 (0.083)	0.000	15278 (1813)	0.9957
+10%	0.062 (0.083)	0.000	16179 (1329)	0.9957

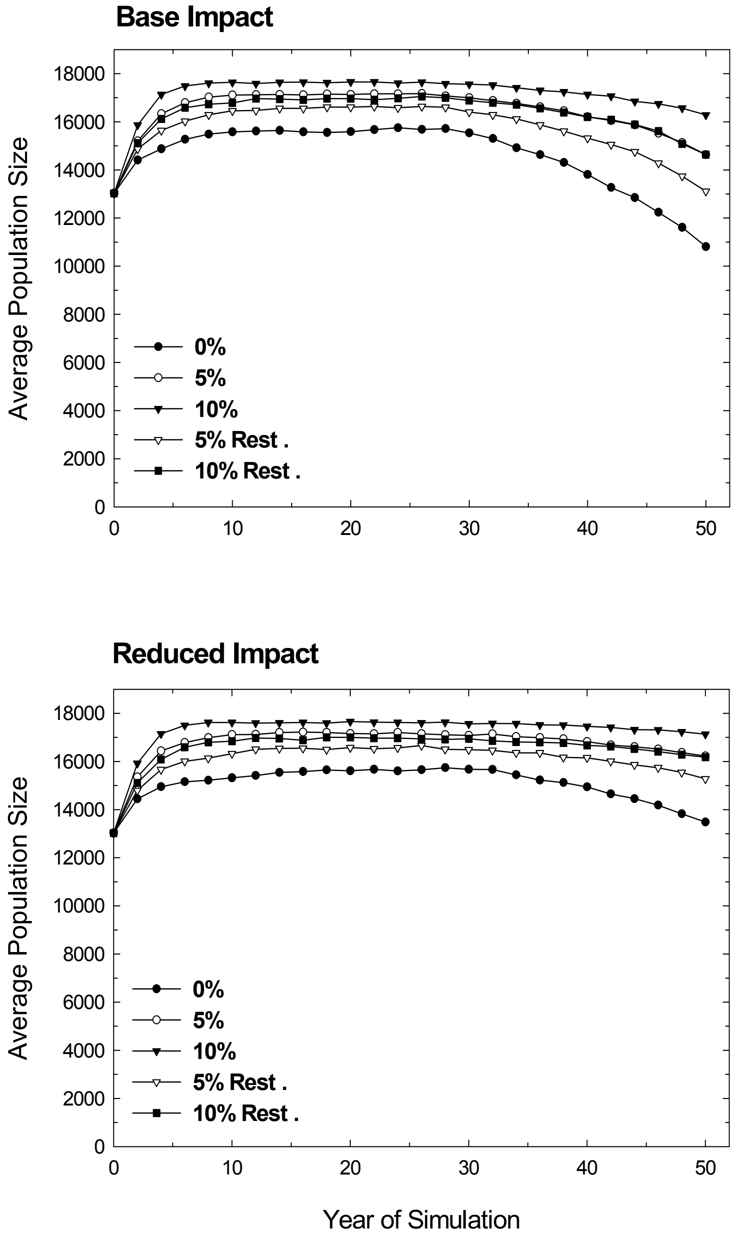


Figure 18. Average projected size of simulated greater sage-grouse populations in the Northwestern Colorado region, under reproductive mitigation *Alternate Disturbance Levels* of oil and natural gas development. "Rest." mitigation refers to increases in reproductive success through mitigation activities in only those Zones that see comparatively high levels of oil and natural gas development activity (specifically, Zones 2, 3A, 3B, and 3C), as opposed to the same levels of increased success realized in all Zones comprising the Northwestern Colorado region. See text for additional information on model construction.

Future Directions for Additional Analysis

Density dependence in demographic rates

The inclusion of density dependence in survival and/or reproduction in greater sage-grouse could possibly alter some of the qualitative results of the PVA models discussed in this document, in particular the analysis of housing development and surface mining activities where habitat loss is considerable and greater sage-grouse populations soon occupy saturated sagebrush habitats. While there is scant evidence to suggest that strong density dependence is operating to modulate demographic rates in greater sage-grouse, the controversy remains vigorous. Additional modeling, including some form of density dependent demographics, could be initiated to demonstrate its effects and stimulate more thoughtful discussion on its mode of operation and intensity.

Revised oil and natural gas scenarios

Because of the issues in model parameterization discussed herein, we feel that the oil and natural gas development models presented in this document may overestimate the long-term impact of this activity on nearby greater sage-grouse populations. Efforts are currently underway to thoroughly assess these models for their realism and to modify them accordingly so that we can come up with a more rigorous analysis of the impact of this activity on the landscape.

Impacts of disease

West Nile virus (WNV) is clearly a disease of great concern to grouse biologists in North America, but the data needed to rigorously evaluate its potential impact is lacking. *VORTEX* can, by itself, simulate fairly complex disease dynamics and their impacts on wildlife population demography. However, we have chosen to delete this option from our current analyses. The Conservation Breeding Specialist Group has also developed *OUTBREAK*, a much more sophisticated simulation model of wildlife disease epidemiology, that can be of tremendous value in studying disease processes in threatened wildlife populations. Future greater sage-grouse modeling efforts could be devoted to a deeper evaluation of WNV and its possible affects.

Conclusions

We may conclude our analysis of greater sage-grouse population viability by returning to the original set of questions that provided the foundation for our study.

- *Can we build a series of simulation models with sufficient detail and precision that can accurately describe the dynamics of greater sage-grouse populations distributed across Colorado?*

  Our retrospective demographic analysis indicates that we are indeed capable of building such models. It is extremely important to remember, however, that reliance on the absolute outcome predicted by any one modeling scenario must always be interpreted with extreme caution due to the inherent uncertainty in model input parameterization. A comparative analysis between models, in which a single factor (or at most two factors) is studied while all other input parameters are held constant, provides a much more robust environment in which alternative management scenarios can be evaluated for their effectiveness in increasing the viability of the target species.

- *What are the primary demographic factors that drive growth of greater sage-grouse populations in Colorado?*

  Our demographic sensitivity analysis indicates that models of greater sage-grouse population dynamics are most sensitive to variability in female juvenile (chick) survival, the proportion of females that successfully reproduce per year, and clutch size per successful female.

- *How vulnerable are small, fragmented populations of greater sage-grouse in Colorado to extinction under current management conditions? How small must a population become to increase its risk of extinction to an unacceptable level?*

  A formal analysis of this question is not yet part of this larger modeling effort; consequently, this question has yet to be fully determined. The analyses presented here, however, provide some preliminary insight into this issue. For example, the rather small Meeker / White River population has an intrinsically higher risk of population decline and extinction even under conditions of equivalent underlying demographic rates used as model input. The higher levels of instability we see are directly tied to the smaller size of this population and the resulting higher levels of annual random variation in survival and reproductive rates. Overall, the relatively low levels of environmental variability included in these PVA models leads to a comparatively higher level of population stability and, by extension, a lower probability of population extinction.

- *What are the predicted impacts of current and potential future levels of housing development on selected greater sage-grouse populations in Colorado?*

  This activity, manifest largely through reductions in available sagebrush habitat, appears to have comparatively minor impact on the long-term demographic viability of greater sage-grouse populations in Colorado as long as underlying population demographic rates remain robust. However, the reduced population sizes that result from the gradual erosion of available habitat cannot be ignored and, in combination with other anthropogenic factors, could lead to longer-term increases in risk of population decline.

- *What are the predicted impacts of current and potential future levels of mining and other surface activities on selected greater sage-grouse populations in Colorado?*

  This activity, manifest largely through reductions in available sagebrush habitat, appears to have comparatively minor impact on the long-term demographic viability of greater sage-grouse populations in Colorado as long as underlying population demographic rates remain robust. However, the reduced population sizes that result from the gradual erosion of available habitat cannot be ignored and, in combination with other anthropogenic factors, could lead to longer-term increases in risk of population decline.

- *What are the predicted impacts of current and potential future levels of hunting on selected greater sage-grouse populations in Colorado?*

  Through field-based evaluations of population status, current levels of greater sage-grouse harvest in North Park appear sustainable. However, our analyses presented here provide evidence to suggest that even relatively low levels of additional harvest mortality – if sustained for long periods of time (i.e., one to two decades) can lead to marked increases in the risk of significant population decline. A more complete understanding of the demographic consequences of harvest, such as the degree of compensation that acts in a harvested greater sage-grouse population, is recommended before specific adjustments to harvest quotas are made.

- *What are the predicted impacts of current and potential future levels of petroleum and* *natural gas development on selected greater sage-grouse populations in Colorado?*

Oil and natural gas development, manifest through direct impacts on demographic performance of individual birds, may have major and severe consequences for greater sage-grouse populations in Colorado. This conclusion is based on models that use data from research studies on greater sage-grouse in nearby habitats. Consequently, it is important to thoroughly and critically review this available literature and to determine the applicability of these biological studies to Colorado's greater sage-grouse populations.

- *Can reproductive mitigation improve the viability of greater sage-grouse populations in Colorado in the face of other anthropogenic processes?*

  Improving reproductive success through alternative mitigation activities could possibly lead to significant increases in greater sage-grouse demographic performance. However, these benefits can only be realized under certain conditions, particularly where specific human activities appear to directly affect population demographic rates to a relatively small degree. In other cases, the observed benefits do not appear to offset the declines in performance brought about by human activities on the landscape.

As before, we conclude our revised analysis by returning to those original questions that guided the development of the scenarios described herein.

- *How would the demographic behavior of our simulated populations of greater sage-grouse respond if we modify the model to more accurately reflect the progression of impacts, reclamation, and mitigation at and/or near individual well pad sites, throughout the oil and natural gas development process?*

  Our analysis of projected oil and natural gas development activity in the Piceance / Parachute / Roan region suggests that well-field mitigation can potentially be effective in reducing the demographic disturbance to greater sage-grouse populations occupying nearby sagebrush habitats. These mitigation measures must be conducted aggressively, however, in order for disturbance to be minimized. Most importantly, mortality and reproductive rates must rebound to as close to their original rates as practical as the field shifts to a production phase and reclamation of the surrounding habitats is undertaken. Secondarily, the duration of maximum well-field related disturbance must be minimized.

  The degree to which additional mitigation measures – such as increased reproductive success through various mitigation activities – must be undertaken is closely related to the intensity of well-field mitigation. Under conditions of aggressive well-field mitigation, lower levels of reproductive mitigation may be required to further increase the long-term viability of nearby sage-grouse populations.

- *To what extent will the demographic behavior of our simulated populations of greater sage-grouse change if we assume a less severe direct impact of oil and natural gas development, even in the absence of mitigation?*

  Our analyses indicate that even if the impacts on greater sage-grouse demography are reduced in magnitude by 50%, the extent of demographic disturbance of oil and natural gas development is sufficient to cause significant population decline soon after development begins. However, this lower overall demographic impact means that given levels of both well-field mitigation and increases in reproductive success through mitigation can have much greater benefit to the long-term viability of impacted grouse populations. Consequently, a more thorough understanding of the detailed demographic impacts of oil and natural gas development in Colorado is critical to the formulation of a specific well-field mitigation strategy.

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Appendix I:
Population Viability Analysis and Simulation Modeling

Phil Miller
Conservation Breeding Specialist Group (IUCN / SSC)

Introduction

Thousands of species and populations of animals and plants around the world are threatened with extinction within the coming decades. For the vast majority of these groups of organisms, this threat is the direct result of human activity. The particular types of activity, and the ways in which they impact wildlife populations, are often complex in both cause and consequence; as a result, the techniques we must use to analyze their effects often seem to be complex as well. But scientists in the field of conservation biology have developed extremely useful tools for this purpose that have dramatically improved our ability to conserve the planet's biodiversity.

Conservation biologists involved in recovery planning for a given threatened species usually try to develop a detailed understanding of the processes that put the species at risk, and will then identify the most effective methods to reduce that risk through active management of the species itself and/or the habitat in which it lives. In order to design such a program, we must engage in some sort of predictive process: we must gather information on the detailed characteristics of proposed alternative management strategies and somehow predict how the threatened species will respond in the future. A strategy that is predicted to reduce the risk by the greatest amount – and typically does so with the least amount of financial and/or sociological burden – is chosen as a central feature of the recovery plan.

But how does one predict the future? Is it realistically possible to perform such a feat in our fast-paced world of incredibly rapid and often unpredictable technological, cultural, and biological growth? How are such predictions best used in wildlife conservation? The answers to these questions emerge from an understanding of what has been called "the flagship industry" of conservation biology: Population Viability Analysis, or PVA. And most methods for conducting PVA are merely extensions of tools we all use in our everyday lives.

The Basics of PVA

To appreciate the science and application of PVA to wildlife conservation, we first must learn a little bit about population biology. Biologists will usually describe the performance of a population by describing its demography, or simply the numerical depiction of the rates of birth and death in a group of animals or plants from one year to the next. Simply speaking, if the birth rate exceeds the death rate, a population is expected to increase in size over time. If the reverse is true, our population will decline. The overall rate of population growth is therefore a rather good descriptor of its relative security: positive population growth suggests some level of demographic health, while negative growth indicates that some external process is interfering with the normal population function and pushing it into an unstable state.

This relatively simple picture is, however, made a lot more complicated by an inescapable fact: wildlife population demographic rates fluctuate unpredictably over time. So if we observe that 50% of our total population of adult females produces offspring in a given year, it is almost certain that more or less than 50% of our adult females will reproduce in the following year. And the same can be said for most all other demographic rates: survival of offspring and adults, the numbers of offspring born, and the offspring sex ratio will almost always change from one year to the next in a way that usually defies precise prediction. These variable rates then conspire to make a population's growth rate also change unpredictably from year to year. When wildlife populations are very large – if we consider seemingly endless herds of wildebeest on the savannahs of Africa, for example – this random annual fluctuation in population growth is of little to no consequence for the future health and stability of the population. However, theoretical and practical study of population biology has taught us that populations that are already small in size, often defined in terms of tens to a few hundred individuals, are affected by these fluctuations to a much greater extent – and the long-term impact of these fluctuations is always negative. Therefore, a wildlife population that has been reduced in numbers will become even smaller through this fundamental principle of wildlife biology. Furthermore, our understanding of this process provides an important backdrop to considerations of the impact of human activities that may, on the surface, appear relatively benign to larger and more stable wildlife populations. This self-reinforcing feedback loop, first coined the "extinction vortex" in the mid-1980's, is the cornerstone principle underlying our understanding of the dynamics of wildlife population extinction.

Once wildlife biologists have gone out into the field and collected data on a population's demography and used these data to calculate its current rate of growth (and how this rate may change over time), we now have at our disposal an extremely valuable source of information that can be used to predict the *future* rates of population growth or decline under conditions that may not be so favorable to the wildlife population of interest. For example, consider a population of primates living in a section of largely undisturbed Amazon rain forest that is now opened up to development by logging interests. If this development is to go ahead as planned, what will be the impact of this activity on the animals themselves, and the trees on which they depend for food and shelter? And what kinds of alternative development strategies might reduce the risk of primate population decline and extinction? To try to answer this question, we need two additional sets of information: 1) a comprehensive description of the proposed forest development plan (how will it occur, where will it be most intense, for what period of time, etc.) and 2) a detailed understanding of how the proposed activity will impact the primate population's demography (which animals will be most affected, how strongly will they be affected, will animals die outright more frequently or simply fail to reproduce as often, etc.). With this information in hand, we have a vital component in place to begin our PVA.

Next, we need a predictive tool – a sort of crystal ball, if you will, that helps us look into the future. After intensive study over nearly three decades, conservation biologists have settled on the use of computer simulation models as their preferred PVA tool. In general, models are simply any simplified representation of a real system. We use models in all aspects of our lives; for example, road maps are in fact relatively simple (and hopefully very accurate!) 2-dimensional representations of complex 3-dimensional landscapes we use almost every day to get us where we need to go. In addition to making predictions about the future, models are very helpful for us to: (1) extract important trends from complex processes, (2) allow comparisons among different types of systems, and (3) facilitate analysis of processes acting on a system.

Recent advances in computer technology have allowed us to create very complex models of the demographic processes that define wildlife population growth. But at their core, these models attempt to replicate simple biological functions shared by most all wildlife species: individuals are born, some grow to adulthood, most of those that survive mate with individuals of the opposite sex and then give birth to one or more offspring, and they die from any of a wide variety of causes. Each species may have its own special set of circumstances – sea turtles may live to be 150 years old and lay 600 eggs in a single event, while a chimpanzee may give birth to just a single offspring every 4-5 years until the age of 45 – but the fundamental biology is the same. These essential elements of a species' biology can be incorporated into a computer program, and when combined with the basic rules for living and the general characteristics of the population's surrounding habitat, a model is created that can project the demographic behavior of our real observed population for a specified period of time into the future. What's more, these models can explicitly incorporate random fluctuations in rates of birth and death discussed earlier. As a result, the models can be much more realistic in their treatment of the forces that influence population dynamics, and in particular how human activities can interact with these intrinsic forces to put otherwise relatively stable wildlife populations at risk.

Many different software packages exist for the purposes of conducting a PVA. Perhaps the most widely-used of these packages is *VORTEX*, developed by the IUCN Conservation Breeding Specialist Group (CBSG) for use in both applied and educational environments. *VORTEX* has been used by CBSG and other conservation biologists for more than 15 years and has proved to be a very useful tool for helping make more informed decisions in the field of wildlife population management.

Strengths and Limitations of the PVA Approach

When considering the applicability of PVA to a specific issue, it is vitally important to understand those tasks to which PVA is well-suited as well as to understand what the technique is not well-designed to deliver. With this enhanced understanding will also come a more informed public that is better prepared to critically evaluate the results of a PVA and how they are applied to the practical conservation measures proposed for a given species or population.

The dynamics of population extinction are often quite complicated, with numerous processes impact the dynamics in complex and interacting ways. Moreover, we have already come to appreciate the ways in which demographic rates fluctuate unpredictably in wildlife populations, and the data needed to provide estimates of these rates and their annual variability are themselves often uncertain, i.e., subject to observational bias or simple lack of detailed study over relatively longer periods of time. As a result, the elegant mental models or the detailed mathematical equations of even the most gifted conservation biologist are inadequate for capturing the detailed nuances of interacting factors that determine the fate of a wildlife population threatened by human activity. In contrast, simulation models can include as many factors that influence population dynamics as the modeler and the end-user of the model wish to assess. Detailed interactions between processes can also be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes.

PVA models have also been shown to stimulate meaningful discussion among field biologists in the subjects of species biology, methods of data collection and analysis, and the assumptions that underlie the analysis of these data in preparation for their use in model construction. By making the models and their underlying data, algorithms and assumptions explicit to all who learn from them, these discussions become a critical component in the social process of achieving a shared understanding of a threatened species' current status and the biological justification for identifying a particular management strategy as the most effective for species conservation. This additional benefit is most easily recognized when PVA is used in an interactive workshop-type setting, such as the Population and Habitat Viability Assessment (PHVA) workshop designed and implemented by CBSG.

Perhaps the greatest strength of the PVA approach to conservation decision-making is related to what many of its detractors see as its greatest weakness. Because of the inherent uncertainty now known to exist in the long-term demography of wildlife populations (particularly those that are small in size), and because of the difficulties in obtaining precise estimates of demographic rates through extended periods of time collecting data in the field, accurate predictions of the future performance of a threatened wildlife population are effectively impossible to make. Even the most respected PVA practitioner must honestly admit that an accurate prediction of the number of mountain gorillas that will roam the forests on the slopes of the eastern Africa's Virunga Volcanoes in the year 2075, or the number of polar bears that will swim the warming waters above the Arctic Circle when our great-grandchildren grow old, is beyond their reach. But this type of difficulty, recognized across diverse fields of study from climatology to gambling, is nothing new: in fact, the Nobel Prize-winning physicist Niels Bohr once said "Prediction is very difficult, especially when it's about the future." Instead of lamenting this inevitable quirk of the physical world as a fatal flaw in the practice of PVA, we must embrace it and instead use our very cloudy crystal ball for another purpose: to make **relative**, rather than **absolute**, predictions of wildlife population viability in the face of human pressure.

The process of generating relative predictions using the PVA approach is often referred to as sensitivity analysis. In this manner, we can make much more robust predictions about the relative response of a simulated wildlife population to alternate perturbations to its demography. For example, a PVA practitioner may not be able to make accurate predictions about how many individuals of a given species may persist in 50 years in the presence of intense human hunting pressure, but that practitioner can speak with considerably greater confidence about the relative merits of a male-biased hunting strategy compared to the much more severe demographic impact typically imposed by a hunting strategy that prefers females. This type of comparative approach was used very effectively in a PVA for highly threatened populations of tree kangaroos (*Dendrolagus* sp.) living in Papua New Guinea, where adult females are hunted preferentially over their male counterparts. Comparative models showing the strong impacts of such a hunting strategy were part of an important process of conservation planning that led, within a few short weeks after a participatory workshop including a number of local hunters (Bonnaccorso et al., 1998), to the signing of a long-term hunting moratorium for the most critically endangered species in the country, the tenkile or Scott's tree kangaroo (*Dendrolagus scottae*).

PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models often underestimate the threats facing the population, or the total risk these threats collectively impose on the population of interest. To address this limitation, conservation biologists must try to engage a diverse body of experts with knowledge spanning many different fields in an attempt to broaden our understanding of the consequences of interaction between humans and wildlife.

Additionally, models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed (see Lacy and Miller (2002), Nyhus et al. (2002) and Westley and Miller (2003) for more details).

Finally, it is also important to understand that a PVA model by itself does not define the goals of conservation planning of a given species. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used.

Further Reading

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