APPENDIX G

REPORT ON PVA ANALYSIS FOR GUSG (Miller 2004)

Preliminary Population Viability Assessment for the Gunnison sage-grouse (*Centrocercus minimus*)

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In collaboration with

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Introduction

The Gunnison sage-grouse (*Centrocercus minimus*) is a newly described species that became an immediate candidate for Federal listing under the Endangered Species Act. There are perhaps 2,500-3,500 breeding individuals, about 2,500 in the Gunnison basin and another 1,000 or so spread across seven smaller populations in southwest Colorado and southeast Utah. These populations have been isolated from each other and from the main population for perhaps 50-75 years and do not seem to have unique genotypes. Detailed genetic information now exists and field researchers will have results on increased sample sizes and additional markers near the end of 2004.

The current strategy adopted by the Colorado State Department of Wildlife is to manage to conserve all of the genetic diversity currently in existence and insure that this level of diversity is maintained with a high probability for a 50-year planning horizon. The Department will manage the Gunnison Basin population as the main reservoir of genetic diversity, and the smaller populations as alternative reservoirs that contain subsets of genetic diversity. The goal across the seven smaller populations will be to retain much (hopefully all) of the genetic diversity present in the entire population, but also to ensure that a sufficiently large number of individuals exist to protect against extinction risk and loss of diversity from demographic stochasticity. This will probably require significant habitat restoration in some populations to get them above that threshold number. If they dip below that number, or appear to have lost significant genetic diversity, translocations will be effected to rescue that population.

There is interest by some in the Colorado Department of Natural Resources to establish captive breeding facilities. While a bit controversial, this option will allow for the conduct of research on improving translocation techniques and captive-rearing methodologies. If a captive breeding program is deemed beneficial, then it would be important to obtain advice from a genetic standpoint on the ideal characteristics of such a program.

Population viability analysis (PVA) can be an extremely useful tool for investigating current and future risk of wildlife population decline or extinction. In addition, the need for and consequences of alternative management strategies can be modeled to suggest which practices may be the most effective in managing populations of the Gunnison sage-grouse in its wild habitat. *VORTEX*, a simulation software package written for population viability analysis, was used here as a mechanism to study the interaction of a number of Gunnison sage-grouse life history and population parameters treated stochastically, 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 Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild 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 stepping through the series of events that describe the typical life cycles of sexually reproducing, diploid organisms.

VORTEX is not intended to give absolute answers, since it is projecting stochastically the interactions of the many parameters used as input to the model and because of the random processes involved in nature. Interpretation of the output depends upon our knowledge of the biology of the Gunnison sage-grouse, the environmental conditions affecting the species, and possible future changes in these conditions. For a more detailed explanation of *VORTEX* and its use in population viability analysis, refer to Appendix 1, Lacy (2000) and Miller and Lacy (2003 [cited as Miller and Lacy 2003a in RCP Literature Cited section]).

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

- What is our best estimate of stochastic population dynamics of this species in its current range?
- What are the primary factors that drive population growth dynamics of Gunnison sage-grouse?
- What is the predicted rate of loss of genetic diversity from isolated Gunnison sage-grouse populations, and how does the restrictive lek mating system influence this rate of loss?
- How vulnerable are small, fragmented populations of Gunnison sage-grouse to local extinction in the absence of demographic interaction with other populations?
- What might be the impacts to Gunnison sage-grouse population viability of potential habitat loss?
- How successful might augmentation be as a conservation management strategy for smaller populations of Gunnison sage-grouse?
- How many birds could be removed from a given source population such as the Gunnison Basin for augmentation of smaller populations at risk of extinction without negatively impacting the persistence of the source?

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.

Baseline Input Parameters for Stochastic Population Viability Simulations

Much of the data discussed below are gleaned from the studies on Greater sage-grouse of Hausleitner (2003) in Moffat County, Colorado and Peterson (1980) in North Park, Colorado. Some recruitment data collected by Colorado Division of Wildlife (CDOW) in 2002 are specific to Gunnison sage-grouse. These data were collected during what was assumed to be a rather marked period of drought, so any results obtained from these data are to be interpreted accordingly.

Breeding System: The Gunnison 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 given 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 before becoming

reproductively successful. 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 15 years. In reality, achieving this age is highly unlikely given 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, May – June. Based on data from Greater sage-grouse in Moffat County, Colorado, it is estimated that 92% of adult females beyond the age of one year initiate nests, with 58% of those individuals being successful. Of those that were unsuccessful on their first try, 16% try to renest and they enjoy a 75% success rate. Taken together, this means that, on average, about 58% of adult grouse over the age of one year are successful breeders in a given year. About 79% of yearlings nest, and 46% of those are successful. This means that about 36% of yearling females successfully reproduce in a given year. 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.

Reproduction data on Gunnison sage-grouse collected by Young (1994) indicated as few as 43% of adult female birds were successfully reproducing. This value was also used in the development of an alternative baseline model to investigate its impact on population dynamics.

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 data from Gunnison sage-grouse populations suggests that annual variability in reproductive success among yearling females can be high (SD = 15%) and slightly lower among older birds (SD = 10%).

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 (such data do not yet exist for Gunnison sage-grouse).
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.

At this time, there are no data to support density dependence in reproduction in Gunnison 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 reproducing offspring 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: Age-sex-specific mortality rates are based on Greater sage-grouse studies in Colorado and surrounding states as specific data on Gunnison sage-grouse do not yet exist. Specifically, we needed to estimate chick mortality as mortality from hatching to October, and then adding in overwintering mortality from October to May of the following year. Early chick mortality data are based on the study in Wyoming described in June (1963), while overwintering mortality estimates come from studies conducted in Moffat County, Colorado. Yearling and adult data are derived as averages of Moffat County telemetry and North Park banding studies.

Age Class	% Mortality (SD)	
	Females	Males
0 – 1	72.0 (7.0)	72.0 (7.0)
1 – 2	23.0 (5.0)	48.0 (5.0)
2 - +	41.0 (6.0)	62.0 (6.0)

In addition, we included a catastrophic impact on chick mortality through the action of a simulated severe 3-year drought event. We assumed that such an event would occur, on average, just once in 100 years; however, when it occurred, average mortality would increase linearly from 72% in a "normal" year to 78% in drought year 1, 84% in drought year 2, and finally 90% in drought year 3. This was simulated through the use of a complex function directly within the field for chick mortality. The event is assumed to impact both males and females equally.

Mortality data collected from Gunnison sage-grouse populations in 2002 by CDOW indicated lower levels of yearling and adult survival during the period of data collection. These values are listed in the following table:

Age Class	% Mortality (SD)	
	Females	Males
0 – 1	72.0 (7.0)	72.0 (7.0)
1 – 2	39.0 (5.0)	25.0 (5.0)
2 - +	52.0 (6.0)	69.0 (6.0)

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 Gunnison sage-grouse, the group concluded that this option should not be included in our models.

Initial Population Size: A total of eight discrete populations of Gunnison sage-grouse are thought to exist across Colorado and eastern Utah. These populations are listed below, with their estimated numbers based on spring breeding counts of males on leks and a presumed 2:1 female:male ratio.

Population	Breeding Males	Total
Gunnison Basin	1000	3000
San Miguel Basin	50	150
San Juan County, Utah	35	100
Glade Park / Piñon Mesa	25	100
Crawford	24	75
Cimarron / Cerro / Sims Mesa	6	25
Dove Creek	8	20
Poncha Pass	7	20

Because of the uncertainty in these estimates, and because of a greater interest in the more general results that can be obtained from a systematic analysis of population size and its influence on persistence in the face of random demographic fluctuations in sage grouse populations, we decided to focus instead on a set of population size classes throughout the analysis. The size classes studied were:
$N_0 = 20, 25, 50, 75, 100, 150, 250, 500, 1000, 1500, 3000$

Our initial baseline model was parameterized with an initial population size of 250 birds. This was chosen to represent a mid-sized population that would allow us to investigate the dynamics of population growth in the absence of significant extinction probability.

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. Our approach was to identify the largest spring breeding counts of males and compare them to the current counts. These data are shown below:

Population	Highest Male Count in past 10 years (Year)	2003 Highest Male Count
Cim/Cerro/Sims	12 (2001)	6
Dove Crk	73 (1994)	8
San Juan, UT	57 (2000)	35
San Miguel Basin	91 (1998)	50
Glade Pk	33 (2000)	25
Gunnison Basin	723 (1993)	500
Poncha	9 (2002)	7
Crawford	64 (1991)	24

Population Augmentation: An important issue for management of Gunnison sage-grouse is the feasibility of using larger populations like that in the Gunnison Basin, or perhaps a newly-established *ex situ* population, to augment smaller populations at significant risk of extinction. Specifically, the question revolves around how frequently a population must be augmented in order to minimize the risk of extinction below a given threshold. Therefore, a set of scenarios were developed that included augmentation of existing sage grouse populations with birds from an external source. Populations subject to augmentation began with 100, 200 or 300 individuals and a carrying capacity equal to twice the initial size. Calculation of gene diversity under these conditions assumes that each new bird added to the population is unrelated to all others, thereby infusing the population with two new unique alleles at the locus of analysis. Fecundity and mortality values roughly corresponding to a 0.0% long-term stochastic population growth rate among populations of intermediate size were used in all simulations (see Table 4 below). Augmentation was triggered any time the size of a population was reduced to less than 50% or 25% of the initial number of birds. The current plan calls for 40 birds (67% hens, 33% males) to be added to a given population in the fall, with 40% mortality likely to occur within a few weeks after release. Therefore, the simulations included the "effective" release of 24 birds (16 hens, 8 males) at the end of the *VORTEX* time cycle, roughly corresponding to the end of the calendar year. To assess the impact of smaller numbers of birds used for augmentation, additional models were constructed that included effective releases of 18, 12, or 6 birds (i.e., a total release of 30, 20, or 10), while maintaining the original sex ratio used for the larger augmentation simulations.

Iterations and Years of Projection: All population projections (scenarios) were simulated 500 times. Each projection extends to 100 years, with demographic information obtained at annual intervals. For our purposes, we are most interested in viewing the results of our simulations at 50 years; in this way we are able to discern the dynamics emerging from a given input dataset while reducing the uncertainty of our projections if extended out to 100 years or more. All simulations were conducted using *VORTEX* version 9.42 (March 2004).

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* Gunnison sage-grouse models. See accompanying text for more information.

Model Input Parameter	Baseline, Greater	Baseline, Gunnison
Breeding System	Polygynous	Polygynous
Age of first reproduction ($\female$ / $\male$)	1 / 2	1 / 2
Maximum age of reproduction	15	15
Annual % adult females reproducing	36 (A = 1); 58.4 (A<1)	43
Density dependent reproduction?	No	No
Maximum clutch size	9	9
Mean clutch size[†]	6.75	6.75
Overall offspring sex ratio	0.5	0.5
Adult males in breeding pool	10%	10%
% annual mortality, $\female$ / $\male$ (SD)		
0 – 1	72.0 / 72.0 (7.0)[‡]	72.0 / 72.0 (7.0)[‡]
1 – 2	23.0 / 48.0 (5.0)	39.0 / 25.0 (5.0)
2 – +	41.0 / 62.0 (6.0)	52.0 / 69.0 (6.0)
Initial population size / carrying capacity		
	20 / 40	20 / 40
	25 / 50	25 / 50
	50 / 100	50 / 100
	75 / 150	75 / 150
	100 / 200	100 / 200
	150 / 300	150 / 300
	250 / 500	**250 / 500**
	500 / 1000	500 / 1000
	1000 / 2000	1000 / 2000
	1500 / 3000	1500 / 3000
	3000 / 6000	3000 / 6000

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

[‡] Chick mortality includes 3-year drought catastrophe that linearly increases mortality to 90%. See text for additional details.

Results of Baseline Simulations

Results reported for each modeling scenario include:

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.

$P(E)_{50}$ – 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.

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

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.

Our two alternative baseline models either rely heavily on more historical Greater sage-grouse data or utilize recent data from Gunnison sage-grouse population collected during drought years. The results of these two models are shown in Table 2 and Figure 1.

Table 2. Gunnison sage-grouse PVA. Demographic output from two alternative baseline simulation models. See text for accompanying information.

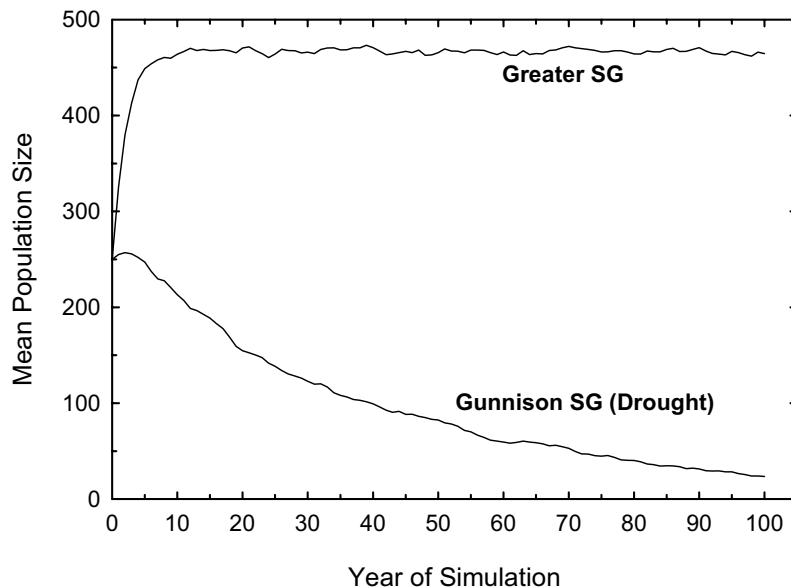| Baseline Model	r_s (SD)	$P(E)_{50}$	N_{50} (SD)	GD_{50}
Greater SG	0.146 (0.229)	0.000	465 (65)	0.795
Gunnison SG (Drought)	-0.051 (0.299)	0.372	82 (122)	0.596

Figure 1. Projections of mean population size for two alternative baseline demographic models of Gunnison sage-grouse population dynamics. See text for accompanying information on model construction and parameterization.

Inspection of the Table and Figure point out the dramatic differences between the two datasets. When our model is based largely on demographic data from Greater sage-grouse, we see a robust population capable of increasing at an average rate of nearly 15% per year. Under these conditions, the simulated population can rapidly reach its habitat-based carrying capacity with no risk of population extinction. It is our assumption that many of these data were collected from large, healthy Greater sage-grouse populations established in optimal environments in the Axial Basin and Moffat County. Such favorable conditions will give rise to the strongly positive growth rates displayed in our model.

On the other hand, when our baseline model includes recent data from Gunnison sage-grouse populations experiencing drought conditions, we see a dramatically different picture: average growth rates drop to a 5% rate of annual decline with a probability of 37% that this population will become extinct within 50 years. Once again, members of the Science Team are mindful of the fact that the Gunnison sage-grouse – specific data were collected during a period of drought – perhaps even one as sever as the event we are simulating here – and therefore population dynamics are expected to become significantly impacted.

It is extremely unlikely that populations of Gunnison sage-grouse are currently experiencing long-term annual population growth rates as high as 15% or as low as -5%. Unfortunately, detailed data do not yet exist on long-term growth patterns of this species inside or outside Gunnison Basin. This baseline model analysis, however, is very instructive in that it provides plausible upper and lower bounds on population growth that are reasonable in the shorter-term, i.e., on the order of 5-10 years or perhaps longer.
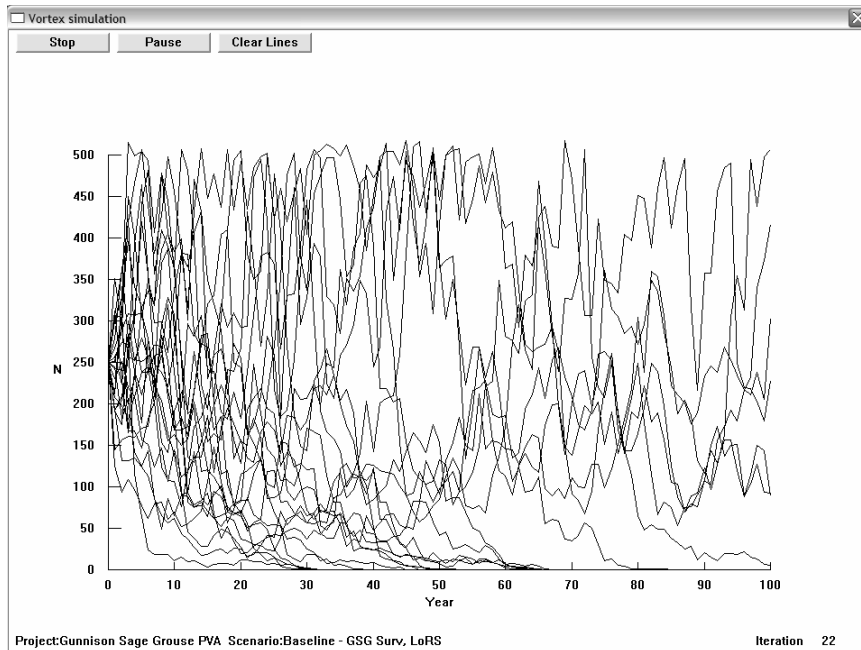

Figure 2. Plot of subset of individual iterations of Gunnison sage-grouse baseline model. Note level of variance in the model as defined by both demographic and environmental sources of stochasticity included in the *VORTEX* model. See text for accompanying details.

A review of Figure 2 also gives us an appreciation for the variability in growth rate – both within and between replicate runs of the model (iterations) – that is a defining characteristic of stochastic simulation models of wildlife demography. While we may observe a longer-term growth rate that is either positive or negative, we see significant fluctuations in population size across years. It is therefore difficult to confidently ascribe a high level of accuracy to a particular modeling scenario when the model results must be compared to a very short timeframe of detailed observation of the

wild population being studied. This is indeed the case with the Gunnison sage-grouse, where longer-term trends in population size have yet to be determined with a reasonable degree of confidence. Because of this wide disparity in growth rates observed in our two baseline models, we opted to develop a larger set of models that differed in their underlying growth rates through manipulation of demographic parameters within *VORTEX*. These model will be discussed in more detail in a later section of this report.

Demographic Sensitivity Analysis

During the development of the baseline input dataset, it quickly became apparent that a number of demographic characteristics of Gunnison 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 biologically plausible 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. Values in bold are those used in the baseline model using Greater sage-grouse data in the absence of Gunnison sage-grouse data. See accompanying text for more information.

Model Parameter	Minimum	Estimate Midpoint	Maximum
Maximum Age	5	10	**15**
% Adult Females Reproducing	26 / 48	**36 / 58**	46 / 68
% Chick Mortality	66.0	**72.0**	78.0
% Adult Female Mortality	31.0	**41.0**	51.0
Drought Frequency (%)	**1.0**	3.0	5.0
% Males in Breeding Pool	**10**	20	33

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 six 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 12 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 this comparison, we have chosen the model relying heavily on data from Greater sage-grouse population.

For the entire suite of sensitivity analysis models, we will consider a generic population of 250 individuals and a carrying capacity of 500 individuals.

The results of the sensitivity analysis are shown in tabular form in Table 4 and graphically in Figure 3.

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

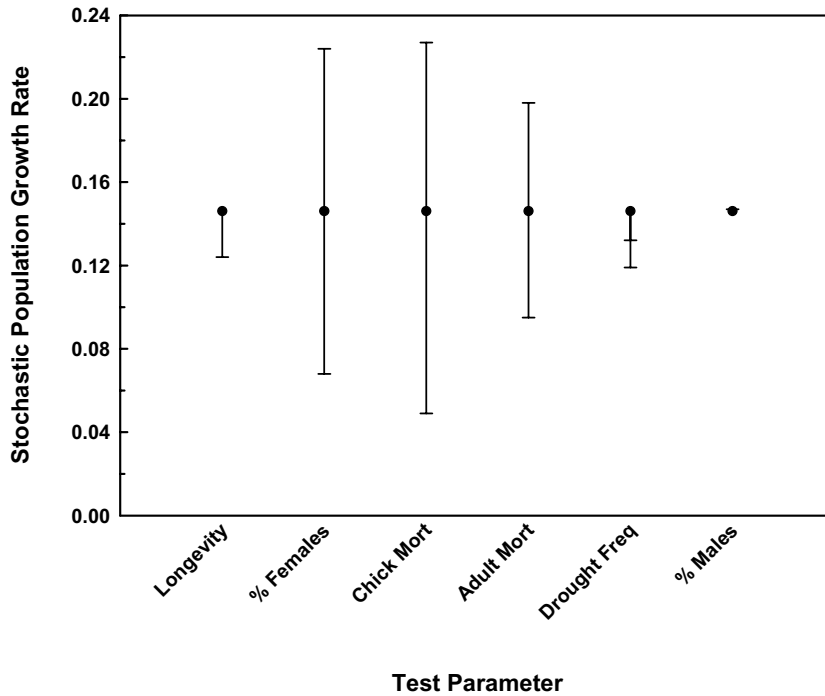| Model conditions	r_s (SD)
Baseline	0.146 (0.229)
Maximum age	
5	0.124 (0.226)
10	0.146 (0.226)
Adult Females Reproducing (%)	
26 / 48	0.068 (0.233)
46 / 68	0.224 (0.223)
Chick Mortality (%)	
66	0.227 (0.215)
78	0.049 (0.248)
Adult Mortality (%)	
31	0.198 (0.220)
51	0.095 (0.230)
Drought Frequency (%)	
3	0.132 (0.238)
5	0.119 (0.250)
Males in Breeding Pool (%)	
20	0.147 (0.227)
33	0.146 (0.226)

Figure 3. Demographic sensitivity analysis of a simulated Gunnison sage-grouse population. Stochastic population growth rate for a set of models in which the specific parameter is varied across a range of biologically plausible values. The baseline model growth rate of 0.146 is given by the central data point for each parameter. The general model of sage grouse population dynamics is most sensitive to uncertainty in those parameters giving the widest range in simulated population growth rates. See text for additional details.

It is clear from the analysis that our model of Gunnison sage-grouse population dynamics is most sensitive to uncertainty in adult female reproductive success (defined here as the percentage of adult females that successfully raise a clutch of eggs to hatching) and to mortality of chicks. Uncertainty in adult female mortality also leads to significant model response, but not to the level of that seen among the youngest age class. As might be expected, the longevity of sage grouse does not significantly alter the results of the analysis until this maximum age is reduced from 15 years of age down to 5 years. This is easily explained by a more detailed inspection of the results of these models, which indicates that a precious few birds actually survive beyond 10 years of age given the mortality schedule used in our baseline model. Similarly, in a purely demographic analysis we may predict that the percentage of adult males that are available for breeding is not a driving force in the growth dynamics of this model. The results presented here bear this out.

However, given the complex relationship that often exists between population genetic structure and demographic performance, we may wish to investigate in more detail the potential impact of uncertainty in lek mating structure among adult males on the retention of population genetic diversity. Figure 4 shows the rate of loss of genetic diversity over time for three different scenarios corresponding to a relatively low, medium and high degree of polygyny in simulated Gunnison sage-grouse populations.
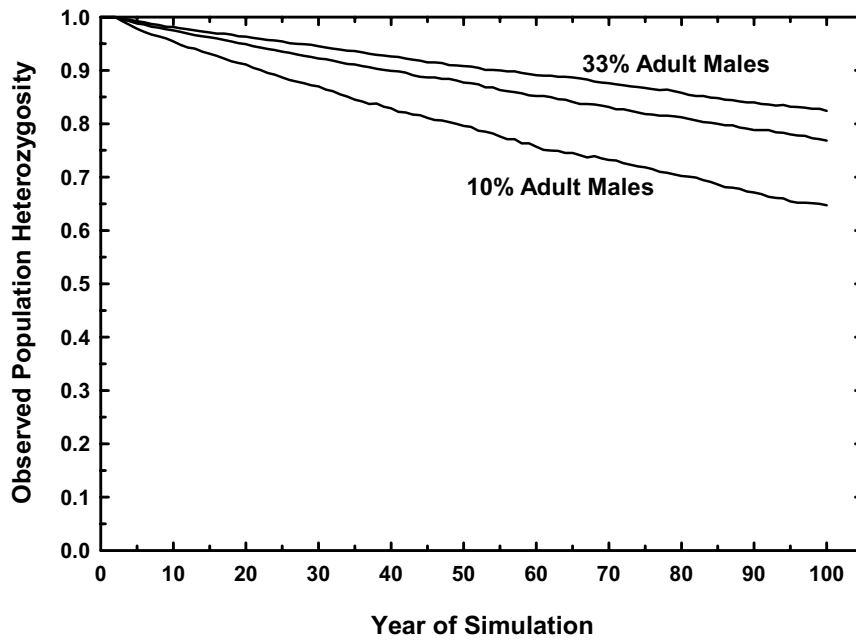
Figure 4. Projected rate of loss of genetic diversity (observed heterozygosity) in simulated populations of Gunnison sage-grouse under different expectations of degree of polygyny. Degree of polygyny is defined here as the percentage of adult males available for breeding. In this type of analysis, each individual at time 0 is assumed to be heterozygous and the plot tracks the relative rate of loss of this original diversity. See text for additional details.

Once the generalized sensitivity analysis was successfully completed, we set out to develop a set of models with the goal of identifying minimum levels of survival necessary to prevent Gunnison sage-grouse population decline. This was done in order to provide a better understanding of species population dynamics, to define a broad set of minimal conditions necessary to increase the chances of population persistence, and to gain additional insight into the magnitude of any detrimental impact of proposed major mortality factors. It is important to note that this particular analysis does not include certain stochastic elements of population dynamics, most notably the addition of the catastrophic drought event. This was intentional, as we were focused in this task on developing estimates of annual mortality that were consistent with populations that were remaining stable in size or perhaps slightly increasing. This can provide a simple benchmark to which wild population management and associated field monitoring efforts can be directed.

A total of 60 individual models were constructed that provided all possible combinations of two levels of reproductive success, five levels of chick mortality, and six levels of adult mortality. This was done in order to more effectively address the relationship between reproductive success and age-specific mortality required for population growth.

Figure 5. Gunnison sage-grouse population mortality analysis. Plots give average population growth rate (*r*) as a function of annual mortality rate of adults with individual lines corresponding to different levels of chick mortality. Two panels correspond to variable levels of adult female reproductive success (see text for additional details on the determination of success).
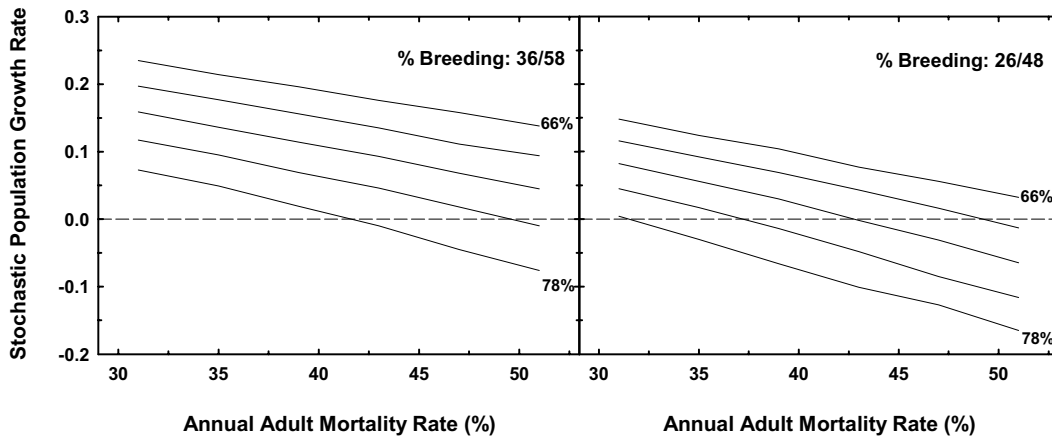
The results of this analysis are shown in Figure 5. It is clear that a number of combinations of chick and non-chick mortality can result in a population that is not expected to decline over time (i.e., *r* > 0.0). Inspection of these graphs lead to the following conclusions:

- As the mortality of adults increases from 31% to 51%, the maximum level of chick mortality consistent with a positive growth rate decreases. In other words, greater adult mortality results in less flexibility in allowable levels of chick mortality.
- Higher levels of reproductive success allow for higher levels of acceptable mortality. Under the conditions of lower reproductive success (right panel), many scenarios yield a negative growth rate – even under relatively favorable conditions for survival.
- A given percentage change in chick mortality results in a proportionally larger change in mean population growth rate compared to a change in adult mortality of the same magnitude. In other words, the results of our simulation models are more sensitive to chick mortality.

While it is very instructive to investigate the sensitivity of our model to uncertainty in demographic input, it is also important to recognize that detecting mortality rates to the level of precision discussed here is rather impractical at best. For example, statistical power analyses conducted on typical types of field demographic and survey data (e.g., Forcada 2000) suggest that either large sample sizes (say, in the hundreds of individuals) or long periods of observation (10 – 15 years) are necessary to detect changes in population numbers in the short term with reasonable levels of precision. Similarly, very large and detailed field studies would be required to successfully differentiate between, for example, a chick mortality rate of 75% and 78%. Consequently, the analysis presented here is typically to be used at more of a "strategic" level; when faced with the need for population management in the face of measurement uncertainty and limited institutional resources, research and/or management prioritization can be accomplished through a comparative study of sensitivity analysis data. Having said this, it is also important to note that those parameters to which a demographic model is most sensitive may **not** be the same parameters that are most directly affected by human activities and are therefore putting the population at risk. Successful conservation requires careful additional study to identify the specific risks the populations face and to develop appropriate remedial actions.

Risk Analysis I: Population Size, Stochastic Growth Rate, Extinction and Maintenance of Genetic Diversity

With our demographic sensitivity analysis complete, our next task was to investigate the relationship between the size of a Gunnison sage-grouse population, its intrinsic stochastic growth rate, and its vulnerability to extinction. Because of our inherent uncertainty in our understanding of current trends in Gunnison sage-grouse population sizes in Colorado, we elected to develop our risk analysis under a quite of scenarios that differed in their underlying growth rates. We did this so that we could provide insight into the future potential dynamics of dispersed Gunnison sage-grouse populations that may be assumed to be growing or declining at rates within the scope of this analysis. We are thereby developing a sort of "template" upon which the future of a given population may be evaluated under presumed conditions of growth and size.

We began by iteratively working on the demographic rates required to produce a population with the desired long-term stochastic growth rate. The results of this process are given in Table 5.

Table 5. Gunnison sage-grouse PVA. Demographic parameters required to achieve the desired growth rate for subsequent population size risk analysis. ♀ : ♂ is the female:male ratio among adults, while ♀ : ♂* includes yearling males (considered here as subadults). Initial population size in all simulations was 250 individuals.

| | Demographic Parameter Estimate | | | | | |
| | | Mortality | | | | |
Desired Growth Rate	**% ♀♀**	**Chick**	**Adult**	r_s	**♀ : ♂**	**♀ : ♂***
0.15	58.4	72.0	41.0	0.145	3.60	1.42
0.10	58.4	74.0	45.0	0.094	3.21	1.35
0.08	58.4	75.0	45.0	0.079	3.36	1.41
0.06	58.4	75.5	46.0	0.062	3.31	1.41
0.04	58.4	76.5	46.5	0.042	3.17	1.41
0.02	55.4	76.5	48.0	0.024	3.16	1.39
0.00	51.9	77.0	48.0	-0.005	3.15	1.42
-0.02	48.0	76.5	48.0	-0.018	3.28	1.45
-0.04	45.0	76.5	48.0	-0.039	3.24	1.48

With this underlying dataset in hand, we then ran simulations for each initial population size mentioned in the Input Parameters section across each growth rate scenario. This yielded a total of 99 different models [9 growth rates X 11 population sizes] to be tested for their sensitivity to extinction at 25 and 50 years.

Our goal in this analysis is to identify, for a given scenario of population growth or decline, the minimum population size necessary to minimize the risk of extinction below a defined threshold. Unfortunately for us biologists, the identification of this extinction threshold is based more on political and social factors than on anything else. The agreement upon a threshold must be done within a more participatory framework that includes a diversity of perspectives among those involved in the management and utilization of the taxon under study.

Figure 6 and Table 6 present the aggregate results of this analysis.
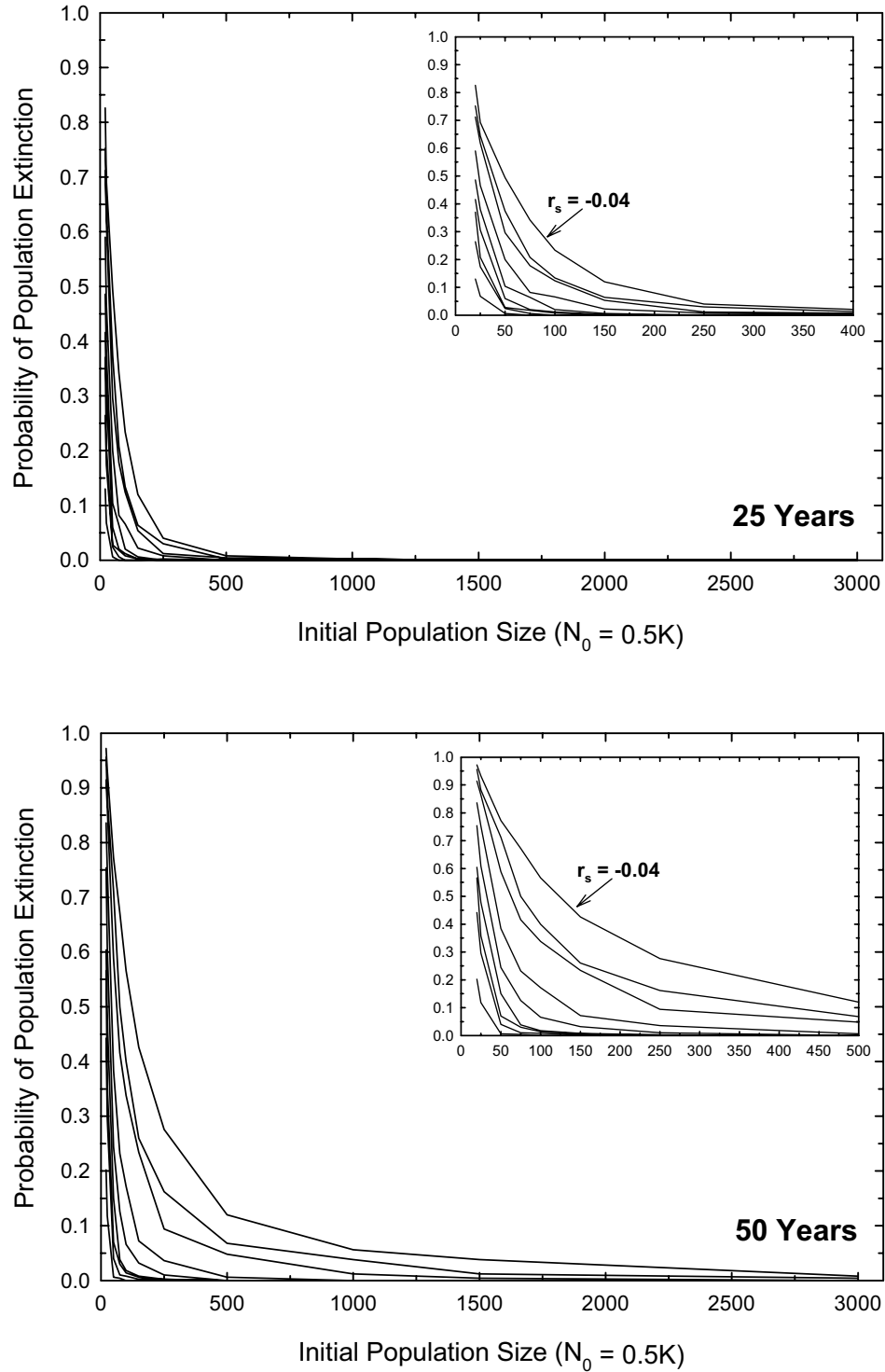
Figure 6. Gunnison sage-grouse population risk analysis. Plots show risk of extinction after 25 years (top panel) and 50 years (bottom panel) for simulated populations with specific long-term expected annual stochastic growth rates ranging from -0.04 (towards the top-right portion of each primary panel) to 0.15 (towards the bottom-left portion of each primary panel). For a given initial population size, higher growth rates lead to lower risks of extinction. Smaller inset panels magnify the results for smaller initial population sizes. See text for additional information on model construction and interpretation.

Table 6. Gunnison sage-grouse PVA. Results of population size risk analysis models under conditions of different underlying stochastic growth rates. See page 8 (RCP pg. F-11) for definitions of column headings.

r_s (Exp)	N_0	r_s (Obs) (SD)	P(E) $_{50}$	N_{50} (SD)	GD$_{50}$
0.150	20	0.125 (0.306)	0.202	27 (16)	0.259
	25	0.134 (0.284)	0.118	39 (17)	0.323
	50	0.143 (0.250)	0.006	92 (16)	0.432
	75	0.148 (0.235)	0.004	138 (23)	0.497
	100	0.148 (0.232)	0.000	187 (27)	0.577
	150	0.148 (0.226)	0.000	281 (37)	0.683
	250	0.147 (0.225)	0.000	472 (59)	0.800
	500	0.148 (0.226)	0.000	935 (128)	0.890
	1000	0.149 (0.228)	0.000	1871 (239)	0.921
	1500	0.149 (0.226)	0.000	2747 (358)	0.948
	3000	0.149 (0.223)	0.000	5618 (714)	0.957
0.100	20	0.067 (0.326)	0.442	17 (17)	0.243
	25	0.075 (0.306)	0.296	28 (21)	0.320
	50	0.091 (0.260)	0.040	80 (26)	0.419
	75	0.093 (0.247)	0.010	128 (32)	0.494
	100	0.096 (0.238)	0.008	171 (41)	0.576
	150	0.095 (0.234)	0.002	262 (57)	0.674
	250	0.093 (0.232)	0.002	436 (98)	0.782
	500	0.095 (0.232)	0.000	882 (182)	0.879
	1000	0.096 (0.233)	0.000	1750 (380)	0.919
	1500	0.097 (0.232)	0.000	2620 (568)	0.937
	3000	0.098 (0.232)	0.000	5185 (1083)	0.944
0.080	20	0.044 (0.337)	0.566	13 (17)	0.269
	25	0.057 (0.313)	0.358	24 (21)	0.310
	50	0.070 (0.269)	0.070	75 (31)	0.422
	75	0.075 (0.256)	0.030	118 (41)	0.491
	100	0.078 (0.247)	0.014	163 (48)	0.556
	150	0.078 (0.242)	0.006	242 (70)	0.653
	250	0.077 (0.237)	0.000	419 (106)	0.767
	500	0.077 (0.238)	0.000	845 (214)	0.874
	1000	0.075 (0.239)	0.000	1659 (431)	0.915
	1500	0.077 (0.237)	0.000	2474 (658)	0.931
	3000	0.078 (0.237)	0.000	5136 (1367)	0.940
0.060	20	0.033 (0.342)	0.604	11 (16)	0.269
	25	0.035 (0.323)	0.478	19 (21)	0.290
	50	0.054 (0.278)	0.150	65 (37)	0.401
	75	0.060 (0.261)	0.038	113 (42)	0.486
	100	0.061 (0.254)	0.018	150 (56)	0.542
	150	0.064 (0.246)	0.008	239 (76)	0.641
	250	0.064 (0.241)	0.002	404 (116)	0.751
	500	0.064 (0.240)	0.000	799 (244)	0.865
	1000	0.063 (0.242)	0.000	1594 (482)	0.908
	1500	0.063 (0.241)	0.000	2354 (730)	0.919
	3000	0.063 (0.240)	0.000	4612 (1487)	0.929
0.040	20	0.004 (0.350)	0.754	7 (13)	0.322
	25	0.017 (0.338)	0.608	13 (19)	0.292
	50	0.030 (0.292)	0.244	51 (38)	0.403
	75	0.036 (0.273)	0.126	90 (53)	0.478
	100	0.041 (0.263)	0.066	133 (65)	0.531
	150	0.042 (0.252)	0.032	202 (90)	0.623
	250	0.042 (0.249)	0.010	347 (148)	0.726
	500	0.043 (0.245)	0.000	712 (275)	0.839

r_s (Exp)	N_0	r_s (Obs) (SD)	P(E) $_{50}$	N_{50} (SD)	GD$_{50}$
	1000	0.043 (0.244)	0.000	1415 (539)	0.902
	1500	0.043 (0.242)	0.000	2072 (876)	0.915
	3000	0.042 (0.243)	0.000	4143 (1779)	0.922
0.020	20	-0.018 (0.361)	0.836	5 (12)	0.252
	25	-0.012 (0.347)	0.752	8 (16)	0.257
	50	0.003 (0.303)	0.384	37 (37)	0.377
	75	0.010 (0.285)	0.232	72 (56)	0.436
	100	0.015 (0.275)	0.172	98 (73)	0.489
	150	0.020 (0.262)	0.072	169 (103)	0.596
	250	0.024 (0.253)	0.036	304 (160)	0.712
	500	0.028 (0.252)	0.006	634 (314)	0.821
	1000	0.032 (0.251)	0.000	1283 (617)	0.888
	1500	0.030 (0.250)	0.000	1738 (950)	0.900
	3000	0.031 (0.250)	0.000	3467 (1854)	0.908
0.000	20	-0.047 (0.369)	0.914	2 (8)	0.274
	25	-0.046 (0.356)	0.864	4 (11)	0.311
	50	-0.029 (0.318)	0.588	21 (32)	0.368
	75	-0.022 (0.302)	0.416	39 (47)	0.434
	100	-0.019 (0.294)	0.338	61 (68)	0.489
	150	-0.013 (0.282)	0.234	108 (102)	0.559
	250	-0.004 (0.269)	0.094	198 (163)	0.664
	500	0.002 (0.261)	0.048	440 (322)	0.785
	1000	0.004 (0.259)	0.012	913 (648)	0.855
	1500	0.008 (0.257)	0.004	1383 (895)	0.891
	3000	0.007 (0.256)	0.000	2795 (1921)	0.899
-0.020	20	-0.061 (0.375)	0.956	1 (6)	0.154
	25	-0.056 (0.360)	0.882	3 (10)	0.265
	50	-0.045 (0.321)	0.712	14 (27)	0.375
	75	-0.034 (0.306)	0.500	31 (44)	0.399
	100	-0.027 (0.294)	0.400	52 (63)	0.457
	150	-0.024 (0.287)	0.260	82 (92)	0.517
	250	-0.021 (0.276)	0.162	149 (149)	0.616
	500	-0.011 (0.265)	0.068	341 (304)	0.749
	1000	-0.013 (0.262)	0.038	652 (588)	0.830
	1500	-0.007 (0.259)	0.012	1082 (919)	0.872
	3000	-0.007 (0.258)	0.048	1975 (1746)	0.884
-0.040	20	-0.089 (0.384)	0.972	0.5 (4)	0.185
	25	-0.070 (0.361)	0.932	2 (7)	0.250
	50	-0.062 (0.331)	0.772	10 (22)	0.351
	75	-0.057 (0.315)	0.672	18 (37)	0.396
	100	-0.050 (0.307)	0.566	29 (47)	0.429
	150	-0.045 (0.297)	0.426	53 (76)	0.504
	250	-0.038 (0.286)	0.276	100 (131)	0.593
	500	-0.032 (0.276)	0.120	235 (275)	0.709
	1000	-0.029 (0.268)	0.056	489 (527)	0.802
	1500	-0.026 (0.265)	0.038	747 (798)	0.841
	3000	-0.026 (0.260)	0.008	1399 (1517)	0.883

Inspection of these results lead to the following conclusions:

- Very small Gunnison sage-grouse populations are at a high risk of extinction, even when the population is expected to increase in size over the long-term ($r_s > 0.0$). For example, when the assumed long-term growth rate is 8% in a population of just 20 individuals and the carrying capacity is no more than 40 birds, the risk of extinction of this population is 37% after just 25 years, and this risk increases to nearly 57% after 50 years. These results dramatically illustrate the impact of stochastic demographic fluctuations on the viability of very small populations – a characteristic that is lost in simpler matrix-based deterministic calculations of population growth.
- The stochastic nature of population growth as simulated here results in populations often experiencing a slight decrease in population size over the duration of the simulation, even under conditions of expected positive population growth. Periodic catastrophic droughts can play a significant role in this phenomenon.
- Under assumed conditions of positive population growth (r_s just above 0.0), and if we choose an extinction threshold of 5% over 50 years, Gunnison sage-grouse populations can only be considered "secure" under this definition if they can maintain a maximum number of 500 birds (yearlings and adults). More vigorous population growth potential can, of course, reduce this required number of animals.
- If we continue to accept this definition of extinction threshold, even under the most optimistic conditions – evaluation of risk at 25 years and vigorous long-term population growth – all known Gunnison sage-grouse populations with less than 30 – 40 individuals are not viable. Over a 50-year time horizon, and even under minimal conditions of long-term population growth, populations of more than 500 individuals appear to be at low risk of extinction.

Based on this analysis, an attempt was made to fit an equation to the extinction risk data at 0.0% stochastic growth rate so that an estimate of extinction risk could be obtained for any desired population size. A slightly modified dose-response curve, used primarily in the biomedical community, was used as it seemed an appropriate descriptor of the relationship between population size and extinction risk. The modified form of the equation is

$$P(E) = \frac{1}{1 + e^{[B - C(\ln(N))]}}$$

where B is the location parameter, C is the steepness parameter, and N is the initial population size included in the appropriate model. Results of the nonlinear regression analysis of the 25-year and 50-year extinction risk data are presented in Table 7.

Table 7. Gunnison sage-grouse PVA. Parameter estimates for nonlinear regression analysis of extinction risk as a function of population size under conditions of approximately 0.0% stochastic population growth. See text for functional form of regression equation and additional information.

Extinction Risk Timeframe	B	C
25 Years	-6.442	-1.853

50 Years	-7.109	-1.697

The fit of this equation to the observed data is shown in Figure 7. The fit for both datasets is excellent, with mean corrected R-square for 25 and 50 years determined to be 0.999 and 0.996, respectively.

Figure 7. Observed population extinction risk probabilities (circles and inverted triangles) and predicted risk values based on nonlinear regression analysis (solid and dashed curves) for simulated Gunnison Sage Grouse populations at 25 and 50 years, respectively, under conditions of approximately 0.0% population growth. See text for function form of regression equation and additional information.
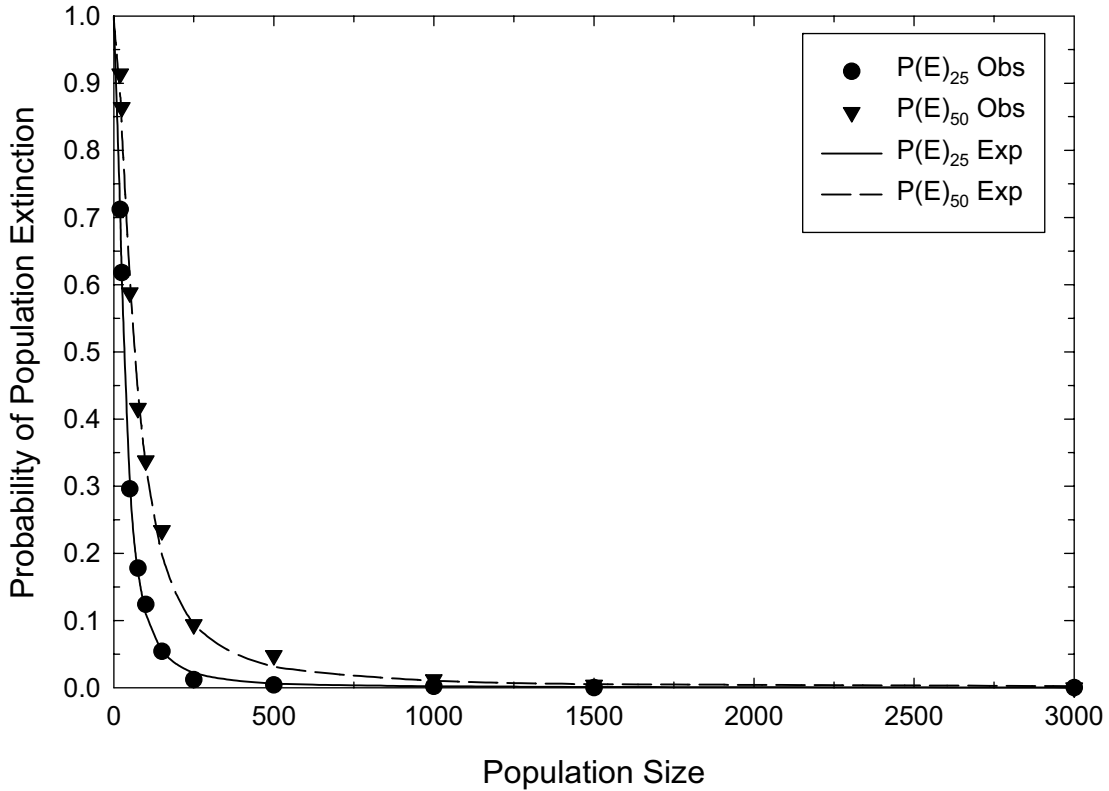
Another issue of concern with respect to Gunnison sage-grouse population conservation is the maintenance of genetic diversity within the Gunnison Basin population, particularly in light of the species' lek mating system and the small proportion of adult males that successfully breed each season. To address this issue, a series of models were run with initial population sizes of 2000, 2500 and 3000 with carrying capacity set at twice the initial size. In addition, the degree of male polygyny (defined here as the percentage of adult males available for breeding) was set at the minimum value of 10%, a medium value of 20%, and the maximum estimate of 33%.

The results of these models are shown in Table 8. Examination of the table reveals that, while the stochastic population growth rate is just above 0.0, the simulated populations decline very slightly from their initial values through the action of stochastic fluctuations in demographic parameters and occasional catastrophic reductions in population size through drought. Nevertheless, these populations remain at approximately 90% - 95% of their original values. Under these conditions, final gene diversity estimates range from 90% to 94%, with the largest value associated with the largest

population size and highest degree of polygyny. However, even under these most "optimistic" conditions, the amount of genetic diversity retained within the simulated populations does not exceed 95% over the 50 years of the simulation. This threshold of gene diversity retention is crossed in just 27 years under the most strict conditions of population size and degree of polygyny, while this same threshold is crossed in 43 years when population size is large and the degree of polygyny is high.

Table 8. Gunnison sage-grouse PVA. Stochastic growth rate, final population size after 50 years, and final gene diversity (population heterozygosity) for simulated populations of different initial size and degree of polygyny. See page 8 (RCP pg. F-11) for column heading definitions. T_{95} is the timeframe within which 95% of the original population gene diversity can be retained. See text for additional details.

Population Size	% Polygyny	r_s	N_{50}	GD_{50}	T_{95}
2000	10	0.008	1909	0.8967	27
	20	0.007	1860	0.9237	33
	33	0.008	1926	0.9325	35
2500	10	0.006	2261	0.8997	28
	20	0.009	2370	0.9326	39
	33	0.007	2348	0.9372	41
3000	10	0.009	2767	0.9164	31
	20	0.010	2952	0.9301	38
	33	0.006	2738	0.9400	43

Risk Analysis II: Population Augmentation

The results for the set of population augmentation scenarios are presented in Table 9.

Inspection of these results leads to the following conclusions:

- As seen in previous analyses, the relatively larger population sizes reflect the intended growth dynamics (i.e., approaching 0.0% stochastic population growth rate) while the smaller populations, given the same demographic characteristics, display greater instability which leads to negative growth rates and higher risk of population decline or extinction.
- Under the conditions simulated here, vigilant augmentation of as few as 6 "effective" birds (corresponding to a total augmentation of 10 birds) into a small population showing basic underlying demographic stability can be very effective in rescuing it from extinction.
- Under a more conservative criterion for augmentation – i.e., a trigger corresponding to 50% of the initial population size – the number of augmentation events required to successfully reduce extinction risk does not exceed 10 times over a 50-year timeframe. Additionally, the number of events decreases as the number of birds making up the release is increased.
- Larger populations actually require a slightly *greater* number of augmentation events over the time-frame of the simulations. This may seem counter-intuitive at first glance, but may be explained rather readily by considering general Gunnison sage-grouse population dynamics and the means by which augmentation is implemented in these simulations. Based on the demographic data used as input to these models, rapid and significant declines in population size occur rather infrequently. When they do, however, the smaller populations will be bolstered in size more effectively by a given augmentation event because these additional birds will represent a larger proportion of the total recipient population. This event will therefore be more effective at pushing the recipient population above (and sometimes far

above) the augmentation trigger. In contrast, larger populations may require an additional 1-2 years of augmentation to push the total population above the threshold.

- Even under less conservative conditions for augmentation, these methods can be effective in reducing extinction risk. Moreover, since the population is allowed to decline to a smaller level before augmentation is triggered, a smaller number of events is required to achieve the same end. As expected, however, final population sizes and retained levels of gene diversity are reduced under this scenario.

Table 9. Gunnison sage-grouse PVA. Population augmentation scenarios under variable initial population sizes (N_0) and "effective" numbers of birds in the release (total number of released birds is 40% higher, with mortality assumed to occur within a few weeks of release). N^* is the population size trigger for the initiation of augmentation. F_{Aug} is the average number of augmentation events that occurred during the 50-year timeframe of the simulations. See page 8 (RCP pg. F-11) for additional column heading definitions, and see text for additional details of model input.

N_0	N_{Aug}	N^*	r_s (SD)	$P(E)_{50}$	N_{50} (SD)	GD_{50}	F_{Aug}
100	0		-0.019 (0.289)	0.334	93 (63)	0.421	
200	0		-0.004 (0.269)	0.132	183 (127)	0.563	
300	0		0.000 (0.261)	0.060	268 (191)	0.656	
100	24	$0.5N_0$	0.020 (0.243)	0.000	124 (49)	0.675	2.7
200	24	$0.5N_0$	0.020 (0.236)	0.000	241 (99)	0.768	3.1
300	24	$0.5N_0$	0.019 (0.239)	0.000	359 (154)	0.820	4.0
100	18	$0.5N_0$	0.018 (0.241)	0.000	119 (50)	0.690	3.4
200	18	$0.5N_0$	0.018 (0.238)	0.000	245 (105)	0.762	3.8
300	18	$0.5N_0$	0.019 (0.242)	0.000	364 (159)	0.819	4.9
100	12	$0.5N_0$	0.017 (0.243)	0.000	116 (52)	0.666	4.4
200	12	$0.5N_0$	0.016 (0.243)	0.000	225 (106)	0.749	5.2
300	12	$0.5N_0$	0.017 (0.246)	0.000	341 (160)	0.809	5.6
100	6	$0.5N_0$	0.015 (0.252)	0.000	108 (54)	0.657	6.7
200	6	$0.5N_0$	0.012 (0.246)	0.000	213 (110)	0.735	8.1
300	6	$0.5N_0$	0.013 (0.246)	0.000	313 (169)	0.794	8.6
100	24	$0.25N_0$	0.010 (0.263)	0.000	99 (55)	0.594	1.2
200	24	$0.25N_0$	0.012 (0.246)	0.000	206 (109)	0.693	1.1
300	24	$0.25N_0$	0.010 (0.243)	0.000	294 (171)	0.766	1.6
100	18	$0.25N_0$	0.011 (0.261)	0.000	100 (57)	0.600	1.5
200	18	$0.25N_0$	0.009 (0.245)	0.000	197 (117)	0.681	1.6
300	18	$0.25N_0$	0.011 (0.242)	0.000	300 (176)	0.749	1.6
100	12	$0.25N_0$	0.010 (0.260)	0.000	96 (57)	0.601	1.8
200	12	$0.25N_0$	0.009 (0.249)	0.000	187 (117)	0.688	2.2
300	12	$0.25N_0$	0.010 (0.247)	0.000	288 (173)	0.753	2.3
100	6	$0.25N_0$	0.006 (0.263)	0.000	89 (57)	0.591	3.0
200	6	$0.25N_0$	0.009 (0.252)	0.000	184 (116)	0.685	2.9
300	6	$0.25N_0$	0.007 (0.251)	0.000	279 (184)	0.740	3.7

All in all, these simulations indicate that augmentation of smaller populations, under the conditions studied here, would be an effective means of minimizing their risk of extinction. While the total average number of observed augmentation events may be lower than original expectations, it is important to remember that a given population may require more or less of this kind of intensive management than what is described by the average population behavior. Consecutive years of augmentation may be necessary when a recipient population falls far below an identified threshold,

thereby requiring an additional expenditure of resources above and beyond that which may be required by a single event or intermittent events. Additional considerations – which lie outside the bounds of biological analysis – must be considered in order to devise the most reasonable population management strategy.

Future Directions for Additional Analysis

Impacts of habitat loss
An important factor to consider when evaluating the future of Gunnison sage-grouse population persistence is the prospect of loss of habitat within the Gunnison Basin and surrounding area. Private land may be removed from use by sage grouse, leading to reduced habitat availability. There is considerable uncertainty as to the precise mode of impact of this reduced habitat. On a relatively simpler level, one may consider the loss of habitat to be reflected in a corresponding reduction in carrying capacity, K. Alternatively, a more complex perspective may involve the reduction of demographic rates as a function of habitat availability and suitability. While the former option presents its own set of complications when considering the construction of additional PVA models, the latter option is considerably more complex. The functional form of a relationship between, for example, reproductive output and habitat suitability is unknown for Gunnison sage-grouse and, for that matter, the vast majority of threatened fauna worldwide. Because of these uncertainties, we have deferred engaging in this analysis until a later date when the details of this relationship can be discussed much more thoroughly.

Impacts of disease
West Nile virus (WNV) is clearly a disease of great concern to sage 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 Gunnison sage-grouse modeling efforts could be devoted to a deeper evaluation of WNV and its possible affects.

Refinement of demographic description of male reproductive success
Considerable uncertainty still surrounds our estimates of the proportion of adult males that successfully breed on a given lek. Moreover, we are not able to precisely determine the statistical description of male breeding success among a group occupying a given lek: Does each breeding male contribute the same number of offspring to the next generation, or is this distribution highly skewed towards a much smaller number of relatively highly successful males? More accurate estimates of the rate of loss of genetic diversity within a population of Gunnison sage-grouse will require a more detailed treatment of this issue.

Impacts of population genetic structure
The recent work of Sara Oyler-McCance on elucidating the genetic structure within and between Gunnison sage-grouse populations would be a valuable addition to the parameterization of genetic aspects of our evolving Vortex models. In the future, we could perhaps evaluate the impacts of reduced heterozygosity in existing isolated populations, or include a much more realistic treatment of inbreeding depression and its impacts on persistence of small isolates.

Conclusions

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

- *What is our best estimate of stochastic population dynamics of this species in its current range?*
  This is difficult to estimate. Recent demographic data suggest Gunnison sage-grouse populations are in decline. This is likely the result of a recent and ongoing drought event that depresses reproductive performance to a level that drives a population into short-term decline. This does not necessarily mean, however, that the population will remain in that state of decline when the environmental stressor is released.

- *What are the primary factors that drive population growth dynamics of Gunnison sage-grouse?*
  Based on our analysis, measure of adult female reproductive success, such as the percentage of adult females that successfully hatch chicks from a nest, and the resulting mortality of those chicks, are the primary determinants of population growth dynamics in this species. It is important to remember that such factors may not be under direct threat from anthropogenic stressors and, therefore, may not specifically require active management in a particular situation.

- *What is the predicted rate of loss of genetic diversity from isolated Gunnison sage-grouse populations, and how does the restrictive lek mating system influence this rate of loss?*
  Most Gunnison sage-grouse populations are so small that the rate of loss of genetic variation is comparatively rapid. The lek mating system characteristic of this species increases the rate of loss of variation through a dramatic reduction in the effective population size. Even under relatively optimistic conditions of population size and degree of polygyny, populations will likely retain less than 95% of their original heterozygosity over a 50-year time span.

- *How vulnerable are small, fragmented populations of Gunnison sage-grouse to local extinction in the absence of demographic interaction with other populations?*
  Because of stochastic fluctuations in demographic rates and the impact of infrequent but severe droughts, Gunnison sage-grouse populations totaling less than 50 individuals are at a serious risk of population extinction within the next 50 years (assuming some degree of consistency in environmental influences on sage grouse demography during that time). Active and intense management would likely be required to maintain these populations for any extended period of time.

- *What might be the impacts to Gunnison sage-grouse population viability of potential habitat loss in the Gunnison Basin?*
  While the precise mechanisms are as yet unknown, there is no doubt that loss of quality habitat for Gunnison sage-grouse would lead to increased extinction risk unless remedial measures are undertaken. More accurate analysis of this process will require additional efforts devoted to model construction and parameterization.

- *How successful might augmentation be as a conservation management strategy for smaller populations of Gunnison sage-grouse?*
  Augmentation can be a very effective means of dramatically minimizing the risk of population extinction. However, its success depends on careful monitoring of the recipient population both

prior to an augmentation, to verify the need for such a process, and after the event has been implemented in order to determine its short-term success in boosting population numbers.

- *How many birds could be removed from a given source population such as the Gunnison Basin for augmentation of smaller populations at risk of extinction without negatively impacting the persistence of the source?*

  It is unclear at present how the removal of birds from a larger source population in Gunnison Basin for augmentation of smaller populations elsewhere would impact the viability of the source. It is probable that eggs would be removed instead of adult birds. At the present time preliminary analyses indicate that, given this suggested method of removal and the ability of the species to re-nest following "failure" of a clutch, negative impacts to the population would be minimal. However, additional discussions on the precise nature of the removal / augmentation methodologies are required before accurate evaluation of alternative strategies can be undertaken.

Acknowledgements

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Appendix 1
Simulation Modeling and Population Viability Analysis

A model is any simplified representation of a real system. We use models in all aspects of our lives, in order to: (1) extract the important trends from complex processes, (2) permit comparison among systems, (3) facilitate analysis of causes of processes acting on the system, and (4) make predictions about the future. A complete description of a natural system, if it were possible, would often decrease our understanding relative to that provided by a good model, because there is "noise" in the system that is extraneous to the processes we wish to understand. For example, the typical representation of the growth of a wildlife population by an annual percent growth rate is a simplified mathematical model of the much more complex changes in population size. Representing population growth as an annual percent change assumes constant exponential growth, ignoring the irregular fluctuations as individuals are born or immigrate, and die or emigrate. For many purposes, such a simplified model of population growth is very useful, because it captures the essential information we might need regarding the average change in population size, and it allows us to make predictions about the future size of the population. A detailed description of the exact changes in numbers of individuals, while a true description of the population, would often be of much less value because the essential pattern would be obscured, and it would be difficult or impossible to make predictions about the future population size.

In considerations of the vulnerability of a population to extinction, as is so often required for conservation planning and management, the simple model of population growth as a constant annual rate of change is inadequate for our needs. The fluctuations in population size that are omitted from the standard ecological models of population change can cause population extinction, and therefore are often the primary focus of concern. In order to understand and predict the vulnerability of a wildlife population to extinction, we need to use a model which incorporates the processes which cause fluctuations in the population, as well as those which control the long-term trends in population size (Shaffer 1981). Many processes can cause fluctuations in population size: variation in the environment (such as weather, food supplies, and predation), genetic changes in the population (such as genetic drift, inbreeding, and response to natural selection), catastrophic effects (such as disease epidemics, floods, and droughts), decimation of the population or its habitats by humans, the chance results of the probabilistic events in the lives of individuals (sex determination, location of mates, breeding success, survival), and interactions among these factors (Gilpin and Soulé 1986).

Models of population dynamics which incorporate causes of fluctuations in population size in order to predict probabilities of extinction, and to help identify the processes which contribute to a population's vulnerability, are used in "Population Viability Analysis" (PVA) (Lacy 1993/4). For the purpose of predicting vulnerability to extinction, any and all population processes that impact population dynamics can be important. Much analysis of conservation issues is conducted by largely intuitive assessments by biologists with experience with the system. Assessments by experts can be quite valuable, and are often contrasted with "models" used to evaluate population vulnerability to extinction. Such a contrast is not valid, however, as *any* synthesis of facts and understanding of processes constitutes a model, even if it is a mental model within the mind of the expert and perhaps only vaguely specified to others (or even to the expert himself or herself).

A number of properties of the problem of assessing vulnerability of a population to extinction make it difficult to rely on mental or intuitive models. Numerous processes impact population dynamics, and many of the factors interact in complex ways. For example, increased fragmentation of habitat can make it more difficult to locate mates, can lead to greater mortality as individuals disperse greater distances across unsuitable habitat, and can lead to increased inbreeding which in turn can further

reduce ability to attract mates and to survive. In addition, many of the processes impacting population dynamics are intrinsically probabilistic, with a random component. Sex determination, disease, predation, mate acquisition -- indeed, almost all events in the life of an individual -- are stochastic events, occurring with certain probabilities rather than with absolute certainty at any given time. The consequences of factors influencing population dynamics are often delayed for years or even generations. With a long-lived species, a population might persist for 20 to 40 years beyond the emergence of factors that ultimately cause extinction. Humans can synthesize mentally only a few factors at a time, most people have difficulty assessing probabilities intuitively, and it is difficult to consider delayed effects. Moreover, the data needed for models of population dynamics are often very uncertain. Optimal decision-making when data are uncertain is difficult, as it involves correct assessment of probabilities that the true values fall within certain ranges, adding yet another probabilistic or chance component to the evaluation of the situation.

The difficulty of incorporating multiple, interacting, probabilistic processes into a model that can utilize uncertain data has prevented (to date) development of analytical models (mathematical equations developed from theory) which encompass more than a small subset of the processes known to affect wildlife population dynamics. It is possible that the mental models of some biologists are sufficiently complex to predict accurately population vulnerabilities to extinction under a range of conditions, but it is not possible to assess objectively the precision of such intuitive assessments, and it is difficult to transfer that knowledge to others who need also to evaluate the situation. Computer simulation models have increasingly been used to assist in PVA. Although rarely as elegant as models framed in analytical equations, computer simulation models can be well suited for the complex task of evaluating risks of extinction. Simulation models can include as many factors that influence population dynamics as the modeler and the user of the model want to assess. Interactions between processes can 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. In theory, simulation programs can be used to build models of population dynamics that include all the knowledge of the system which is available to experts. In practice, the models will be simpler, because some factors are judged unlikely to be important, and because the persons who developed the model did not have access to the full array of expert knowledge.

Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon, facilitate testing of the effects of unknown or uncertain data, and expedite the comparison of the likely results of various possible management options.

PVA models also have weaknesses and limitations. A model of the population dynamics does not define the goals for conservation planning. 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. Because the models incorporate many factors, the number of possibilities to test can seem endless, and it can be difficult to determine which of the factors that were analyzed are most important to the population dynamics. 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 probably underestimate the threats facing the population. Finally, the 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.

The *VORTEX* Population Viability Analysis Model

For the analyses presented here, the *VORTEX* computer software (Lacy 1993a) for population viability analysis was used. *VORTEX* models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. *VORTEX*

VORTEX Simulation Model Timeline

Events listed above the timeline increase N, while
events listed below the timeline decrease N.
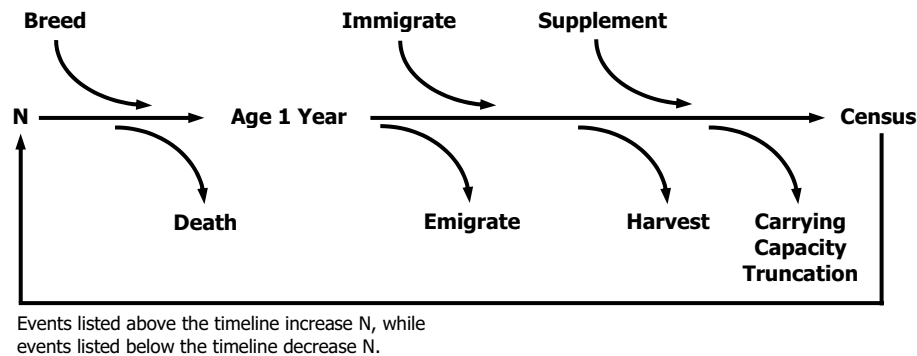
also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations.

Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. The carrying capacity can be specified to change linearly over time, to model losses or gains in the amount or quality of habitat. Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size.

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. During the simulation, *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or "expected heterozygosity") relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

 VORTEX is an *individual-based* model. That is, *VORTEX* creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *VORTEX* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. (See figure below.) Events occur according to the specified age and sex-specific probabilities. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because *VORTEX* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

Further information on *VORTEX* is available in Lacy (2000) and Miller and Lacy (2003 [cited as Miller and Lacy 2003a in RCP Literature Cited section]).

Dealing with Uncertainty

It is important to recognize that uncertainty regarding the biological parameters of a population and its consequent fate occurs at several levels and for independent reasons. Uncertainty can occur because the parameters have never been measured on the population. Uncertainty can occur because limited field data have yielded estimates with potentially large sampling error. Uncertainty can occur because independent studies have generated discordant estimates. Uncertainty can occur because environmental conditions or population status have been changing over time, and field surveys were conducted during periods which may not be representative of long-term averages. Uncertainty can occur because the environment will change in the future, so that measurements made in the past may not accurately predict future conditions.

Sensitivity testing is necessary to determine the extent to which uncertainty in input parameters results in uncertainty regarding the future fate of the pronghorn population. If alternative plausible parameter values result in divergent predictions for the population, then it is important to try to resolve the uncertainty with better data. Sensitivity of population dynamics to certain parameters also indicates that those parameters describe factors that could be critical determinants of population viability. Such factors are therefore good candidates for efficient management actions designed to ensure the persistence of the population.

The above kinds of uncertainty should be distinguished from several more sources of uncertainty about the future of the population. Even if long-term average demographic rates are known with precision, variation over time caused by fluctuating environmental conditions will cause uncertainty in the fate of the population at any given time in the future. Such environmental variation should be incorporated into the model used to assess population dynamics, and will generate a range of possible outcomes (perhaps represented as a mean and standard deviation) from the model. In addition, most biological processes are inherently stochastic, having a random component. The stochastic or probabilistic nature of survival, sex determination, transmission of genes, acquisition of mates, reproduction, and other processes preclude exact determination of the future state of a population. Such demographic stochasticity should also be incorporated into a population model, because such variability both increases our uncertainty about the future and can also change the expected or mean outcome relative to that which would result if there were no such variation. Finally, there is "uncertainty" which represents the alternative actions or interventions which might be pursued as a management strategy. The likely effectiveness of such management options can be explored by testing alternative scenarios in the model of population dynamics, in much the same way that sensitivity testing is used to explore the effects of uncertain biological parameters.

Demographic Stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination, and death with a pseudo-random number generator. For each life event, if the random value sampled from a specified distribution falls above the user--specified probability, the event is deemed to have occurred, thereby simulating a binomial process. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), based on the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value, according to:

$$N = \frac{p(1-p)}{s^2}$$

N binomial trials are then simulated by sampling from the uniform 0-1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

Environmental Variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modeled as binomial distributions. Environmental variation in carrying capacity is modeled as a normal distribution. Environmental variation in demographic rates can be correlated among populations.

Catastrophes

Catastrophes are modeled in *VORTEX* as random events that occur with specified probabilities. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors 50% for the year. Such a catastrophe would be modeled as a random event with 0.02 probability of occurrence each year, and severity factors of 0.75 for survival and 0.50 for reproduction. Catastrophes can be local (impacting populations independently), or regional (affecting sets of populations simultaneously).

Genetic Processes

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical neutral (non-selected) genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. Each offspring created during the simulation is randomly assigned one of the alleles from each parent. *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or "expected heterozygosity") relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

Inbreeding depression is modeled as a loss of viability of inbred animals during their first year. The severity of inbreeding depression is commonly measured by the number of "lethal equivalents" in a population (Morton et al. 1956). The number of lethal equivalents per diploid genome estimates the average number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due entirely to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual, it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles which equate in effect with one lethal allele per individual.

VORTEX partitions the total effect of inbreeding (the total lethal equivalents) into an effect due to recessive lethal alleles and an effect due to loci at which there is heterozygote advantage (superior fitness of heterozygotes relative to all homozygote genotypes). To model the effects of lethal alleles, each founder starts with a unique recessive lethal allele (and a dominant non-lethal allele) at up to five modeled loci. By virtue of the deaths of individuals that are homozygous for lethal alleles, such alleles can be removed slowly by natural selection during the generations of a simulation. This diminishes the probability that inbred individuals in subsequent generations will be homozygous for a lethal allele.

Heterozygote advantage is modeled by specifying that juvenile survival is related to inbreeding

$$\ln(S) = A - BF$$

according to the logarithmic model:
in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is the portion of the lethal equivalents per haploid genome that is due to heterozygote advantage rather than to recessive lethal alleles. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at loci in which the heterozygote has higher fitness than both homozygotes, because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under heterozygote advantage, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.
Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects apparently varies considerably among species (Falconer 1981; Ralls et al. 1988; Lacy et al. 1992) and even among populations of the same species (Lacy et al. 1996). Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterozygote advantage), PVAs must make assumptions about the effects of inbreeding on the population being studied. If genetic effects are ignored, the PVA will overestimate the viability of small populations. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3.14 lethal equivalents per diploid) reported in the survey by Ralls et al. (1988). In other cases, there might be reason to make

more optimistic assumptions (perhaps the lower quartile, 0.90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5.62 lethal equivalents). In the few species in which inbreeding depression has been studied carefully, about half of the effects of inbreeding are due recessive lethal alleles and about half of the effects are due to heterozygote advantage or other genetic mechanisms that are not diminished by natural selection during generations of inbreeding, although the proportion of the total inbreeding effect can vary substantially among populations (Lacy and Ballou 1998).

A full explanation of the genetic mechanisms of inbreeding depression is beyond the scope of this manual, and interested readers are encouraged to refer to the references cited above.

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

Deterministic Processes

VORTEX can incorporate several deterministic processes, in addition to mean age-specific birth and death rates. Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation. The carrying capacity can be specified to change over time, to model losses or gains in the amount or quality of habitat.

Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size. The default functional relationship between breeding and density allows entry of Allee effects (reduction in breeding at low density) and/or reduced breeding at high densities.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodeled) population. The numbers of additions and removals are specified according to the age and sex of animals.

Migration Among Populations

VORTEX can model up to 50 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. Migration among populations can be restricted to one sex and/or a limited age cohort. Emigration from a population can be restricted to occur only when the number of animals in the population exceeds a specified proportion of the carrying capacity. Dispersal mortality can be specified as a probability of death for any migrating animal, which is in addition to age-sex specific mortality. Because of between-population migration and managed supplementation, populations can be recolonized. *VORTEX* tracks the dynamics of local extinctions and recolonizations through the simulation.

Output

VORTEX outputs: **(1)** probability of extinction at specified intervals (e.g., every 10 years during a 100 year simulation), **(2)** median time to extinction, if the population went extinct in at least 50% of the simulations, **(3)** mean time to extinction of those simulated populations that became extinct, and **(4)** mean size of, and genetic variation within, extant populations.

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction is reported by *VORTEX* as:

$$SE(p) = \sqrt{\frac{p(1-p)}{n}}$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Sequence of Program Flow

(1) The seed for the random number generator is initialized with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for an output file name, duration of the simulation, number of iterations, the size below which a population is considered extinct, and a large number of population parameters.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

$$K_{max} = (K + 3s)(1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change during a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it has been adjusted downward because of limiting memory often will not hamper the analyses.

(5) The deterministic growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also calculated. Life-table calculations assume constant birth and death rates, no limitation by carrying capacity, no limitation of mates, no loss of fitness due to inbreeding depression, and that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7 through 26 below.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age-sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical neutral genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. *VORTEX* therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant neutral alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by

$$H_e = 1 - \sum \left(p_i^2 \right)$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity through random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by *VORTEX* is the mean inbreeding coefficient of the population.

(9) For each of the 10 alleles at five non-neutral loci that are used to model inbreeding depression, each founder is assigned a unique lethal allele with probability equal to 0.1 x the mean number of lethal alleles per individual.

(10) Years are iterated via steps 11 through 25 below.

(11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) for the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for changes over time.

Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of adult males specified to be breeding. Breeding males are selected independently each year; there is no long-term tenure of breeding males and no long-term pair bonds.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. If the user specifies that the breeding system is monogamous, then each male can only be paired with a single female each year. Males are paired only with those females which have already been selected for breeding that year. Thus, males will not be the limiting sex unless there are insufficient males to pair with the successfully breeding females.

If the breeding system is polygynous, then a male may be selected as the mate for several females. The degree of polygyny is determined by the proportion of males in the pool of potential breeders each year.

The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified birth sex ratio. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) The genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal A, and another existing animal, B, is

$$f_{AB} = 0.5(f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_A = 0.5(1 + F)$. (See Ballou 1983 for a detailed description of this method for calculating inbreeding coefficients.)

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If a newborn individual is homozygous for a lethal allele, it is killed. Otherwise, the survival probability for individuals in their first year is multiplied by

$$e^{-b(1-\Pr[Lethals])F}$$

in which b is the number of lethal equivalents per haploid genome, and $\Pr[Lethals]$ is the proportion of this inbreeding effect due to lethal alleles.

(18) The age of each animal is incremented by 1.

(19) If more than one population is being modeled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, *VORTEX* continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age-class are created. Each immigrant is assumed to be genetically unrelated to all other individuals in the population, and it carries the number of lethal alleles that was specified for the starting population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to ($N - K$)/N, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate are calculated across iterations and output.

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