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Simulation Modeling to Evaluate the Restoration of an Elk Population to Southern Illinois

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ABSTRACT

As part of a study of the feasibility of re-establishing a free-ranging elk population in southern Illinois, I used simulation modeling to examine population growth relative to variation in carrying capacity, initial release size, calf production, yearling cow recruitment, adult cow survival, maximum growth rate, and the probability of a demographic catastrophe. Sensitivity analysis suggested that the performance of a simulated elk population was relatively robust to variation in all factors except maximum growth rate and probability of demographic catastrophe. These results indicate that the establishment phase of an elk restoration project in Illinois is likely to be successful given the assumptions made about elk demographics. Population control programs and the detrimental effects of endemic disease (a possible source of demographic catastrophe), and loss of genetic variation remain important management considerations.

INTRODUCTION

In the fall of 1995, members of the General Assembly of the State of Illinois directed the Illinois Department of Natural Resources to study the feasibility of reestablishing a wild population of elk (*Cervus elaphus*) in southern Illinois. Re-establishing populations of large free-ranging wild species is expensive and time-consuming. Such populations necessarily start from small initial releases and are therefore vulnerable to extinction from chance catastrophes and demographic stochasticity. Several authors (Lehmkull 1984, Griffith et al. 1989, Leberg 1993) have recommended the use of simulation modeling based on published demographic information as a means of predicting the likely demographic characteristics of an introduced population. Projected population growth can then be used to estimate important management parameters such as population persistence and time required to reach a certain density threshold (ie. a "huntable" population).

Experience in other states suggests that managers must consider the number of elk released in order to assure sufficient survival through the first several breeding cycles (Witmer 1990). Most founding events for large ungulates are characterized by small initial population sizes (Shonewald-Cox 1986). Nonetheless, Griffith et al. (1989) estimated that for large game species, the probability of successfully re-establishing a population becomes asymptotic as the number of released animals approached 20 - 30.

Although it is dangerous to try to infer population estimates from untested habitat models (Edge et al. 1990), analysis of the vegetation and landscape composition in southern Illinois suggests that there is sufficient habitat to sustain a population of re-introduced elk (Van Deelen et al. 1997). This report describes a population modeling exercise that used the habitat characteristics of southern Illinois and published information on the demography of a newly-established elk population to estimate the likely growth characteristics of an elk population re-introduced to southern Illinois. Specific objectives were to (1) estimate potential population growth, and (2) suggest parameters population managers can use as sensitive descriptors of elk population growth.

METHODS

A re-introduced population of elk in southern Illinois was modeled using RAMAS/GIS software (Applied Biomathematics, Setauket, New York). RAMAS/GIS links Geographic Information System (GIS) -based habitat models with matrix population models (Caswell 1989) to produce demographic models that are spatially explicit for a given landscape's habitat quality and configuration (Akcakaya 1994).

Habitat modeling was done with ARC/INFO software using digital cover type maps derived from Thematic Mapper satellite imagery. Modeling assumptions and methods are described elsewhere (Van Deelen et al. 1997). Habitat modeling produced digital raster-based maps (grids) of habitat configuration in southern Illinois. The habitat model used in RAMAS/GIS classified habitat quality for elk based on forage:cover ratios and road densities (road density served as an index of human disturbance, Lyon 1984, Van Deelen et al. 1997). This map was resampled to a 1 km^2 grid cell resolution and each cell received a "habitat" score based on a function that integrated forage:cover ratios and the negative effects of road density (Lyon 1984, Van Deelen et al. 1997). Allowable habitat scores could range between 0 and 1 (1 = optimal). When the model was applied to the southern Illinois landscape, habitat scores ranged between 0 and 0.48.

I constructed a spatially-explicit population model for elk in southern Illinois based on probable estimates for demographic and habitat characteristics reported in the literature. This best estimate model was defined as the reference model. The influence of various parameters on elk population growth was then explored by constructing other models in which the parameter of interest was changed and the subsequent growth characteristics were compared to the reference model. The performance of each model represents 1000 simulations of 50 generations.

Metapopulation Structure

RAMAS/GIS identifies metapopulation structure in two steps (Akcakaya 1994). It first finds habitat patches by aggregating adjacent grid cells whose habitat score is above some threshold value believed to represent the minimum level of habitat quality at which a species will reproduce. It then groups these patches into subpopulations if their centers are within a user-defined distance within which the species is assumed to be panmictic.

Using a similar elk habitat model in Oregon, Wisdom et al. (1986) reported that habitat values in the 0.20 to 0.30 range represented marginal habitat. Therefore I chose 0.25 as the threshold value for identifying habitat patches in southern Illinois. Elk, whether migratory or not, typically move substantial distances (i.e., $\rangle$ 10 km seasonally or during dispersal, Moran 1973). I chose 10 km as the "neighborhood distance" (Akcakaya 1994) used to group patches of suitable habitat into sub-populations.

Demographics of the Reference Model

The demographic characteristics of the modeled elk population were based on 20 years of count data for a colonizing elk population in eastern Washington (Table 1 in Eberhardt et al. 1996). Eberhardt et al. (1996) describe the growth and demographic characteristics of an isolated herd that began with a small number of individuals colonizing unoccupied habitat on a military facility. These elk were largely protected from hunting and had few or no large predators, making their situation similar to that of a re-introduced herd in Illinois.

The demographic model is a stage-based matrix consisting of yearly "transition rates" between 5 stages; calf, yearling cow, adult cow, yearling bull, adult bull (Caswell 1989, Akcakaya 1994; Appendix A). This is a generalization of the more familiar Leslie matrix that allows for modeling both sexes and grouping of older (i.e., adult) year-classes. The basic equation is ...

$$\mathbf{N}_{t+1} = \mathbf{A}\,\mathbf{N}_t$$

where:

$\mathbf{N}_{t+1}$ = the vector of stage-class abundances at time t+1
$\mathbf{A}$ = the matrix of stage transition rates
$\mathbf{N}_t$ = the vector of stage-class abundances at time t.

Parameters for **A** were estimated using regression techniques recommended by Caswell (1989, see Appendix A).

Other characteristics of the reference model included an estimate of demographic stochasticity calculated from the variance in stage-specific survival and fecundity in Eberhardt et al. (1996, Appendix A) and a "scramble-type" density dependence (Akcakaya 1994) characteristic of logistic growth that is constrained as the population approaches carrying capacity (K, Wilson and Bossert 1971). To model this type of density dependence, RAMAS/GIS requires user inputs of K and the maximum allowable growth rate (R_{max}, more commonly known as λ in birth-pulse populations [Caughley 1977]). Eberhardt et al. (1996) estimated that the maximum possible growth rate in free-ranging elk was $\lambda = 1.33$, thus $R_{max} = 1.33$ was used in modeling. K was estimated as a function of the habitat modeling and was one of the parameters that was varied (see below).

Sensitivity of simulated elk growth to select model parameters

Trial 1: Variation in Carrying Capacity (K). K for the reference model was estimated from information on Michigan's elk herd (the nearest successfully re-established elk population for which there is extensive demographic information). A digital map of HSI modified by road density (Van Deelen et al 1997) was spatially re-sampled to 1 km^2 cell size and was imported into RAMAS/GIS. Using a threshold value of 0.25 ("marginal habitat", Van Deelen et al. 1997) to identify suitable elk range, RAMAS calculated ΣHSI = 713 for all cells with HSI > 0.25. RAMAS/GIS then estimated K as a function of ΣHSI and multipliers that relate habitat quality to elk density. Moran (1973) estimated a K of 1.9 elk/km^2 for Michigan's elk range. Assuming that the average HSI for each km^2 in the Michigan range was 0.75 ("highly viable", Wisdom et al. 1986), $1.9 \div 0.75 = 2.53$ provides a multiplier for calculating K from ΣHSI. In the reference model, I assume that the relationship between habitat suitability and elk density in southern Illinois is equivalent to that of Michigan ($K = 713 * 2.53 \approx 1800$). Comparisons include hypothetical situations where the suitability/density relationship is 1/3 (K = 600) and 2/3 (K = 1200) that of Michigan as well as situations were the suitability/density relationship is 4/3 (K = 2400) and 5/3 (K = 3000) that of Michigan.

<u>Trial 2: Variation in initial release size</u>. The initial release size in the reference model was 30 adult elk with a 2:1 (F:M) sex ratio. Since the transport and release of large ungulates is expensive, and successful releases of elk have involved small founding populations, I compared the reference model to models wherein the initial release was 24, 18, 12, and 6 (2:1 [F:M] sex ratio).

<u>Trial 3: Variation in calf production</u>. In the reference model, adult cows produce about 0.65 calves/year. This figure is based on the cow:calf ratios counted by Eberhardt et al. (1996) during the summer, thus it represents an integration of cow fecundity and neonatal survival in both sexes. The influence of calf production on population growth rates and extinction probabilities was explored by comparing the reference model with models in which calf production was decreased by 0.05, 0.10, 0.15, and 0.20.

<u>Trial 4: Variation in recruitment of yearling cows</u>. In the reference model, the transition rate from calves (both sexes) to yearling cows was 0.66. This value is roughly equivalent to recruitment and represents high survival to the yearling stage for female calves relative to that of male calves. I assessed the influence of recruitment rate of yearling cows by comparing the reference model to models in which the transition rate from calves to yearling cows was reduced to 0.61, 0.56, 0.51 and 0.46.

<u>Trail 5: Variation in the survival of adult cows</u>. In the reference model, the survival rate of adult cows was very high (0.90) reflecting the growth of Eberhardt et al.'s (1996) population that was in the early stages of colonization and thus largely free from density dependence. I assessed the influence of adult cow survival by comparing the reference model to models in which the survival of adult cows was reduced to 0.85, 0.80, 0.75, and 0.70.

<u>Trial 6: Variation in R_{max}</u>. R_{max} is one of the parameters that determines the density-dependence of the simulated population as it grows larger (above). In the reference model R_{max} was set at 1.33. To evaluate the influence of R_{max}, the reference model was compared to models in which R_{max} was decreased to 1.28, 1.23, 1.18, and 1.13.

<u>Trial 7: Effect of demographic catastrophes</u>. Catastrophes are rare events that result in significant mortalities in a population (i.e., severe disease outbreaks, region-wide wildfires, unusual weather). For the purposes of simulation modeling, catastrophes were

designated as events that caused a 75% decrease in the yearly transition rates in all stage-classes. This is roughly equivalent to a 75% drop in survival and reproduction. In the reference model, the yearly probability of a catastrophe was 0. To explore the effects of catastrophes on simulated population growth and extinction probabilities, the reference model was compared with models in which the yearly probability of encountering a catastrophe was 0.05, 0.10, 0.15, and 0.20.

Each trial consisted of the reference model and a series of comparison models wherein a parameter was changed. Within each trial, the growth curves of the comparison models were compared to the growth curve of the reference model using the Kolmogov-Smirnov test statistic D. This statistic is a measure of the maximum vertical distance between curves (Akcakaya 1994). Statistical significance is based on the null hypothesis that one curve is equivalent to another.

RESULTS

Metapopulation structure

Given the HSI threshold for reproduction and the neighborhood distance supplied to the program, RAMAS/GIS classified all the suitable habitat in southern Illinois as belonging to one large population with no metapopulation structure. This greatly simplified the population modeling since the interaction among metapopulations does not become a factor. At neighborhood distances 〈 10 km, RAMAS/GIS recognize metapopulation structure consisting of 2 sub-populations - Shawnee National Forest and Heron Pond area. At neighborhood distances 〈 5 km, RAMAS/GIS recognizes three subpopulations (eastern Shawnee National Forest, western Shawnee National Forest, and Heron Pond). The "no metapopulation" situation is probably the most realistic because the estimate of 10 km for neighborhood distance is very conservative since movements of 15 - 20 km are more commonly reported (Georgii and Schroder 1983, Moran 1973) and dispersal in excess of 50 km is known (C.L. Marcum, Univ. of MT, pers. commun.).

Trial 1: Carrying Capacity. Variation in K had little influence on the probability of functional extinction or the time required to cross the N = 200 threshold (Table 1). I use the time to reach N = 200 as a convenient benchmark with which to compare population growth. Though somewhat arbitrarily chosen, N = 200 elk would indicated a measure of success comparable to that of the elk population in Pennsylvania (Witmer 1990). At K = 2400, and 3000 the growth curves were significantly different from that of the reference model. These patterns are expected given the influence of K on density-dependent population growth. At low N there is little density-dependence regardless of K, thus the parameters that are mostly a function of growth in the early stages (probability of extinction, time to N = 200) do not differ.

Trial 2: Initial Release Size. Variation in the initial number of elk released significantly influenced the growth of model elk populations, affecting time to N = 200 and time to K when the release sizes were 24, 18, 12, and 6 (Table 2). Probability of functional extinction remained low (<0.01) until the number of released elk dropped below 12 suggesting a threshold level of adult elk to be included in the initial release.

Trail 3: Calf Production. Variation in the rate of calf production had slight but significant influence on the growth of model elk populations (Table 3.). Curiously, the population grew faster in the face of declining calf production - a phenomena probably due to a shift in the age and sex structure of the model populations that favors stage classes with high survival (i.e., adult cows), although this may also indicate a weakness in the model. In a practical sense, the magnitude of the differences in growth parameters (i.e., time to N = 200, time to K) relative to the reference model is small and probably not biologically meaningful; statistical significance is due to the large sample sizes in the comparison.

Trial 4: Yearling Cow Recruitment. Variation in the transition rate from the calf stage to the yearling cow stage (recruitment rate of yearling cows) produced small changes in the time to N = 200 and time to K relative to the reference model (Table 4). Differences were again significant when the transition rate was decreased by ≥ 0.10 although the magnitude of the differences was trivial. Functional extinction probabilities were < 0.01. Similar to trial 3, the trend was for faster growth with declining recruitment of yearling cows due to a shift in the age structure that favored adult cows and their relatively higher survival.

Trial 5: Adult Cow survival. Variation in the yearly survival rates of adult cows had little influence on growth of simulated elk populations relative to the reference model (Table 5). The probability of functional extinction remained <0.01 and time to N = 200 was unchanged. The time to K decreased as the survival of adult cows decreased but although significant in 3 of the comparisons, the magnitude of the difference was trivial.

Trail 6: Maximum Growth Rate. Variation in the maximum growth rate significantly influenced the growth of the simulated elk populations relative to the reference. Time to N = 200 and time to K increased with decreasing maximum growth rate and the probability of extinction increased.

Trial 7: Catastrophes. The introduction of demographic catastrophes into the model had a profound effect on the growth of the simulated elk populations (Table 7). Increasing the probability of a catastrophe produced significantly different growth curves and substantially increased the probability of functional extinction. Time to N = 200 and time to K became much longer.

DISCUSSION

Simulations and sensitivity analysis indicated that the growth of a re-introduced elk population is relatively robust to variation in calf production, yearling cow recruitment, and adult cow survival when each of these parameters is varied independently. Variation in maximum growth rate and the potential for demographic catastrophes had greater influence. Variation in carrying capacity was most influential at the upper end of the growth curve where density dependence was greatest. In most of the simulations, early population growth was similar with low probabilities of functional extinction and median values of 7 - 9 years for populations to cross the N = 200 threshold.

In the reference model, R_{max} was based on Eberhardt et al.'s (1996) estimate of the maximum growth rate for elk. Modeling suggested that this estimate influences growth in the early and late stages of density dependence. Managers of a re-introduced elk herd require accurate estimates of R_{max} to project when population growth crosses certain thresholds (i.e., a "huntable" population). R_{max} may be substantially different for an elk population in southern Illinois due to habitat differences (dry shrub-steppe vs. humid deciduous/cropland mix). Managers should track the yearly growth of the elk herd with some reliable index to be able to estimate R_{max} for southern Illinois.

These simulations suggest that, given the assumption of demographic characteristics similar to that of Eberhardt et al.'s (1996) elk population, the establishment phase of a re-introduced population of elk in southern Illinois should be biologically successful. Later growth and optimal size for a sustainable population are more difficult to predict. Habitat modeling and assumptions about habitat quality suggest that the absolute biological carrying capacity of the southern-most 11 counties in Illinois might be quite high (i.e., K = 1800). McCoquodale (1991) hypothesized that elk in mesic habitat would require less space than elk in relatively arid habitat due to higher quality forage. Thus, I may have underestimated K by applying habitat quality/elk density relationships from western states. Multiple use of the proposed elk range (Shonewald-Cox 1986) and the potential for conflict with agriculture and other land uses (Van Deelen et al. 1997) indicates that landowner tolerance and, hence, management goals will be substantially lower than biological K. The experience of other eastern states (Witmer 1990) suggests that a population of elk in southern Illinois will not be tolerated at populations that are higher than 500 - 1000 individuals. Since the projected biological K is higher than 500 - 1000, managers should prepare to control the elk herd as population growth approaches re-introduction goals. Since density-dependent population growth is a function of biological K rather than management goals, elk in southern Illinois will very likely need to be maintained at a population level well below K, requiring that a long-term population control program (i.e., culling or hunting) be in place.

Release of fewer than 12 individual adults (8 females, 4 male) resulted in an unacceptably high probability of functional extinction. Multiple releases and the sex and age composition of released individuals can affect the success of a translocation. Griffith et al. (1989) noted that the typical translocation consisted of 6 releases over 3 years. They report that in the case of large native game animals the probability of success becomes asymptotic above 20-40 animals/release. Reed et al (1986) cautioned that management goals should be well above minimum estimates since the margin of error is unknown.

In the context of selecting founding populations for re-introductions, Leberg (1993) noted that when the number of founders is low, the loss of genetic heterozygosity is high, but founding populations with fewer than 10 individuals can retain most (>95%) of the heterozygosity in the source population if numbers are increased rapidly (Lehmkuhl 1984). Fortunately, this is true of elk populations in favorable habitat (Gogan and Barrett 1987, McCorquodale et al. 1988). The optimal strategy is to release as many unrelated, reproductive-age animals as possible; select source populations from similar habitats to favor adaptive genotypes; and avoid captive stock as source populations because of uncertain genetic backgrounds and high probability of relatedness (Leberg 1990).

For long-term maintenance of genetic heterozygosity, populations of less than 500 should be considered short-term and in danger of extinction. They should be augmented occasionally with other individuals to provide new genetic material (Lehmkull 1984). Schonewald-Cox (1986) calculated that an elk population needed 90 breeders (15 male, 75 female) to prevent inbreeding, and 900 breeders (150 male, 750 female) to prevent genetic drift. If one includes calves and non-breeders the former population would contain 150-200 elk, the latter 1500-2000. A elk population of 1500-2000 would require approximately 400 mi^2 of dedicated elk range and would be unlikely in southern Illinois as discussed above. Other eastern states manage elk populations that are substantially smaller (≈150 in Pennsylvania, ≈800 in Michigan, Witmer 1990). A long-term management plan for elk in southern Illinois may need to consider periodic introductions of new genetic material.

Analysis suggests that catastrophic events may profoundly affect the growth of a population of elk in southern Illinois. Weather conditions in southern Illinois are relatively benign and unlikely to cause catastrophic mortality, although natural die-offs may be possible (Young 1994). Potential catastrophes in the form of disease (Gogan and Barrett 1987) may exist as well. Vulnerability to demographic catastrophes in the simulations suggests that managers may need to take a closer look at the potential for disease in southern Illinois. Several diseases in white-tailed deer in southern Illinois have the potential to limit the growth of a re-introduced elk herd. Kistner et al. (1982) believed that endemic infections of meningeal worm in white-tailed deer doomed elk re-introductions in the eastern states to failure. Although elk in Michigan and Pennsylvania seem to tolerate brainworm fairly well, the Wisconsin re-introduction plan recommended that deer in the proposed elk range be sampled for parasites and disease. This sampling would determine the diseases to which elk might be exposed, and document the preexistence of disease that might be blamed on the elk (Parker 1991). In an experimental study, Samuel et al. (1992) found that the meningeal worm is capable of completing its life cycle in elk. Fewer larvae were shed in elk feces relative to white-tailed deer and elk were judged to be “less suitable” hosts. Endemic infection of meningeal worms in local deer need not preclude elk translocation although it may reduce elk productivity. Release sites should be areas with low levels of infection.

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Table 1. Sensitivity of growth parameters to variation in K (carrying capacity) in a simulated elk population.

Treatment	Probability of functional extinction[a]	Time to N=200 (years)	Time to K (years)	K-S comparison to Reference Model[b]
Reference Model (K=1800)	<0.01	7.1	18.7	--
K = 600	<0.01	7.4	14.5	$P > 0.05$
K=1200	<0.01	7.2	17.2	$P > 0.05$
K=2400	<0.01	7.1	19.7	$P < 0.05$
K=3000	<0.01	7.1	20.1	$P < 0.05$

[a] Functional extinction defined as N ≤10 during a simulation

[b] Kolmogrov-Smirnov test, H_0: No difference in extinction risks

Table 2. Sensitivity of growth parameters to variation in initial release size in a simulated elk population.

Treatment	Probability of functional extinction[a]	Time to N=200 (years)	Time to K (years, K=1800)	K-S comparison to Reference Model[b]
Reference Model (30 released)	<0.01	7.1	18.7	--
24 released	<0.01	7.9	14.5	$P < 0.001$
18 released	<0.01	9.1	17.2	$P < 0.001$
12 released	<0.01	10.8	19.7	$P < 0.001$
6 released	0.79	13.7	20.1	$P < 0.001$

[a] Functional extinction defined as N ≤10 during a simulation

[b] Kolmogrov-Smirnov test, H_0: No difference in extinction risks

Table 3. Sensitivity of growth parameters to variation calf production in a simulated elk population.

Treatment	Probability of functional extinction[a]	Time to N=200 (years)	Time to K (years, K=1800)	K-S comparison to Reference Model[b]
Reference Model (F1[c] = 0.65)	<0.01	7.1	18.7	--
F1 = 0.60	<0.01	7.1	18.6	$P < 0.05$
F1 = 0.55	<0.01	6.8	18.5	$P < 0.001$
F1 = 0.50	<0.01	6.5	18.3	$P < 0.001$
F1 = 0.45	<0.01	6.3	18.2	$P < 0.001$

[a] Functional extinction defined as N ≤10 during a simulation

[b] Kolmogrov-Smirnov test, H_0: No difference in extinction risks

[c] F1 = rate at which adult cows produce calves each year in simulation model

Table 4. Sensitivity of growth parameters to variation in yearling cow recruitment in a simulated elk population.

Treatment	Probability of functional extinction[a]	Time to N=200 (years)	Time to K (years, K=1800)	K-S comparison to Reference Model[b]
Reference Model (P1[c] = 0.66)	<0.01	7.1	18.7	--
P1 = 0.61	<0.01	7.0	18.6	$P > 0.05$
P1 = 0.56	<0.01	6.8	18.5	$P < 0.001$
P1 = 0.51	<0.01	6.8	18.3	$P < 0.001$
P1 = 0.46	<0.01	6.6	18.2	$P < 0.001$

[a] Functional extinction defined as N ≤10 during a simulation

[b] Kolmogrov-Smirnov test, H_0: No difference in extinction risks

[c] P1 = the yearly transition rate from calves (both sexes) to yearling cows

Table 5. Sensitivity of growth parameters to variation in adult cow survival in a simulated elk population.

Treatment	Probability of functional extinction[a]	Time to N=200 (years)	Time to K (years, K=1800)	K-S comparison to Reference Model[b]
Reference Model (P3[c] = 0.90)	<0.01	7.1	18.7	--
P1 = 0.85	<0.01	7.1	18.6	$P > 0.05$
P1 = 0.80	<0.01	7.1	18.5	$P < 0.001$
P1 = 0.75	<0.01	7.1	18.3	$P < 0.001$
P1 = 0.70	<0.01	7.2	18.2	$P < 0.001$

[a] Functional extinction defined as N ≤10 during a simulation

[b] Kolmogrov-Smirnov test, H_0: No difference in extinction risks

[c] P3 = the yearly survival rate of adult cows

Table 6. Sensitivity of growth parameters to variation in maximum growth rate in a simulated elk population.

Treatment	Probability of functional extinction[a]	Time to N=200 (years)	Time to K (years, K=1800)	K-S comparison to Reference Model[b]
Reference Model ($\lambda = 1.33$)	<0.01	7.1	18.7	--
$\lambda = 1.28$	<0.01	9.2	27.4	$P < 0.001$
$\lambda = 1.23$	0.03	10.9	34.7	$P < 0.001$
$\lambda = 1.18$	0.04	14.7	46.4	$P < 0.001$
$\lambda = 1.13$	0.10	21.1	68.5	$P < 0.001$

[a] Functional extinction defined as N ≤10 during a simulation

[b] Kolmogrov-Smirnov test, H_0: No difference in extinction risks

[c] λ = the maximum yearly rate of increase in a birth pulse population (N_t / N_{t-1})

Table 7. Sensitivity of growth parameters to variation in the probability of demographic catastrophes in a simulated elk population.

Treatment	Probability of functional extinction[a]	Time to N=200 (years)	Time to K (years, K=1800)	K-S comparison to Reference Model[b]
Reference Model (p[Cat.][c] = 0)	<0.01	7.1	18.7	--
p[Cat.] = 0.05	0.17	7.5	25.3	$P < 0.001$
p[Cat.] = 0.10	0.59	11.0	42.7	$P < 0.001$
p[Cat.] = 0.15	0.94	18.0	170	$P < 0.001$
p[Cat.] = 0.20	0.99	N/A	N/A	$P < 0.001$

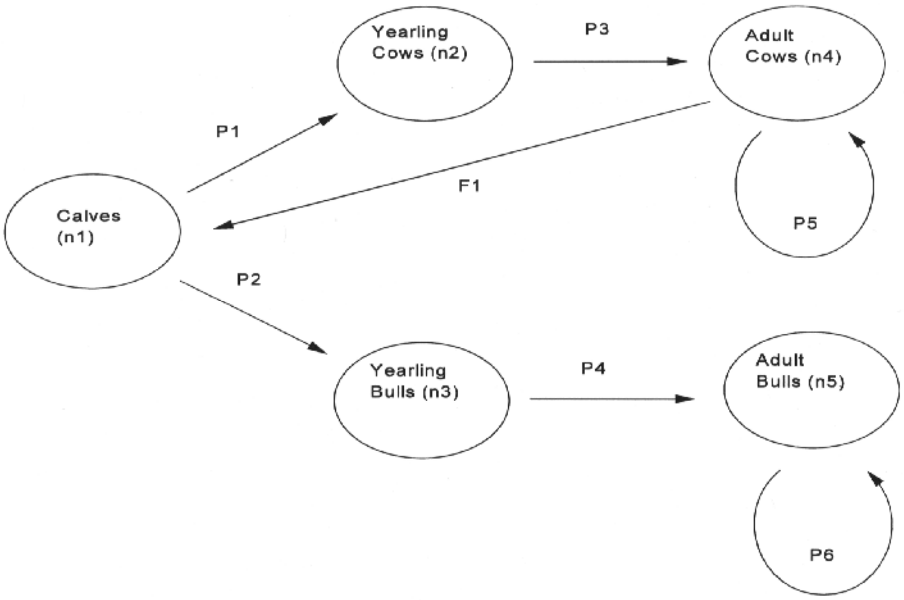
[a] Functional extinction defined as $N \leq 10$ during a simulation

[b] Kolmogrov-Smirnov test, H_0: No difference in extinction risks

[c] p[Cat.] = yearly probability of a catastrophe. Catastrophes are defined as a one-time yearly event that reduces all transition rates (survival and reproduction) by 75% (i.e., disease).

Appendix A: Schematic of Stage class relationships and transition rates

F1 and P(n) are yearly transition rates between the various stage-classes (n1 - n5). Arrows indicate dependence, i.e., the number of adult bulls in year t depends on the number of adult bulls in time t - 1 and the number of yearling bulls in time t-1.



Population projections use the equation

$$\mathbf{N}_{t+1} = \mathbf{A}\ \mathbf{N}_t$$

where:

$\mathbf{N}_{t+1}$ = the vector of stage-class abundances at time t+1
$\mathbf{A}$ = the matrix of stage transition rates
$\mathbf{N}_t$ = the vector of stage-class abundances at time t.

or alternately:

$$\mathbf{N}_{t+1} = \begin{vmatrix} \mathbf{n}1_{t+1} \\ \mathbf{n}2_{t+1} \\ \mathbf{n}3_{t+1} \\ \mathbf{n}4_{t+1} \\ \mathbf{n}5_{t+1} \end{vmatrix}, \quad \mathbf{A} = \begin{vmatrix} 0 & 0 & 0 & \mathbf{F}1 & 0 \\ \mathbf{P}1 & 0 & 0 & 0 & 0 \\ \mathbf{P}2 & 0 & 0 & 0 & 0 \\ \mathbf{O} & \mathbf{P}3 & 0 & \mathbf{P}5 & 0 \\ 0 & 0 & \mathbf{P}4 & 0 & \mathbf{P}6 \end{vmatrix}, \text{ and } \quad \mathbf{N}_t = \begin{vmatrix} n1_{t+0} \\ n2_{t+0} \\ n3_{t+0} \\ n4_{t+0} \\ n5_{t+0} \end{vmatrix}$$

Where:

ni_j = number of individuals in stage I at time j
F1 = the rate at which adult cows produce calves
P1 = the yearly transition rate from calves (both sexes) to yearling cows
P2 = the yearly transition rate from calves (both sexes) to yearling bulls
P3 = the yearly survival rate of yearling cows
P4 = the yearly survival rate of yearling bulls
P5 = the yearly survival rate of adult cows
P6 = the yearly survival rate of adult bulls

Initial transition rates (= survival rates) were calculated from count data in Eberhardt et al. (1996)'s table 1. Calculations suggested that yearly survival of yearling and adult cows was 1.0. Since this rate was unrealistic over a 50 year simulation, 0.95 was used for yearlings and 0.90 for adults in the model. Initial stage abundances were set at 20 adult cows and 10 adult bulls for a total of 30 released elk. Size of the initial release is based on the release sizes commonly reported for large ungulates (Griffith et al. 1989, Witmer 1990). Initial values for **N** , and the reference values for **A** were...

$$\mathbf{N}_{t=0} = \begin{vmatrix} 0 \\ 0 \\ 0 \\ 20 \\ 10 \end{vmatrix}$$

and

$$\mathbf{A} = \begin{vmatrix} 0 & 0 & 0 & 0.65 & 0 \\ 0.66 & 0 & 0 & 0 & 0 \\ 0.34 & 0 & 0 & 0 & 0 \\ 0 & 0.95 & 0 & 0.90 & 0 \\ 0 & 0 & 0.94 & 0 & 0.56 \end{vmatrix}$$

Demographic stochasticity was simulated by a matrix of transition rate standard deviations (**S**) corresponding to **A**. Values were estimated from the variance surrounding Eberhardt et al.'s (1996) survival and fecundity rate estimations.

$$\mathbf{S} = \begin{vmatrix} 0 & 0 & 0 & 0.16 & 0 \\ 0.17 & 0 & 0 & 0 & 0 \\ 0.17 & 0 & 0 & 0 & 0 \\ 0 & 0.11 & 0 & 0.11 & 0 \\ 0 & 0 & 0.17 & 0 & 0.17 \end{vmatrix}$$