
Factors Leading to Different Viability Predictions for a Grizzly Bear Data Set

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Abstract: *Population viability analysis programs are being used increasingly in research and management applications, but there has not been a systematic study of the congruence of different program predictions based on a single data set. We performed such an analysis using four population viability analysis computer programs: GAPPS, INMAT, RAMAS/AGE, and VORTEX. The standardized demographic rates used in all programs were generalized from hypothetical increasing and decreasing grizzly bear (*Ursus arctos horribilis*) populations. Idiosyncrasies of input format for each program led to minor differences in intrinsic growth rates that translated into striking differences in estimates of extinction rates and expected population size. In contrast, the addition of demographic stochasticity, environmental stochasticity, and inbreeding costs caused only a small divergence in viability predictions. But, the addition of density dependence caused large deviations between the programs despite our best attempts to use the same density-dependent functions. Population viability programs differ in how density dependence is incorporated, and the necessary functions are difficult to parameterize accurately. Thus, we recommend that unless data clearly suggest a particular density-dependent model, predictions based on population viability analysis should include at least one scenario without density dependence. Further, we describe output metrics that may differ between programs; development of future software could benefit from standardized input and output formats across different programs.*

Factores que Conducen a Diferentes Predicciones de Viabilidad para un Conjunto de Datos del Oso Pardo

Resumen: *Los programas de análisis de viabilidad de poblaciones están siendo usados cada vez mas en investigación y aplicaciones de manejo. Sin embargo, no existe un estudio sistemático de la congruencia de predicciones de diferentes programas basadas en un solo conjunto de datos. Realizamos un análisis usando cuatro programas de computadora para análisis de viabilidad poblacional (GAPPS, INMAT, RAMAS/AGE y VORTEX). Las tasas demográficas estandarizadas usadas en todos los programas fueron generalizadas para poblaciones de osos que incrementan y disminuyen hipotéticamente. La idiosincrasia del formato de entrada para cada programa condujo a diferencias menores en la tasa de crecimiento intrínseco, mismas que se tradujeron como diferencias notables en las estimaciones de tasas de extinción y tamaño poblacional esperado. En contraste, la adición de aleatoriedad demográfica, aleatoriedad ambiental y consanguinidad causaron únicamente pequeñas divergencias en las predicciones de la viabilidad de esta especie. Sin embargo, la adición de dependencia de la densidad ocasionó grandes desviaciones entre los programas a pesar de nuestros mejores esfuerzos por usar las mismas funciones densodependientes. Los programas de viabilidad de poblaciones difieren en como se incorpora la dependencia a la densidad y las funciones necesarias son difíciles de parametrizar con precisión. Es por ello que recomendamos que, a menos que los datos sugieran claramente un modelo particular de dependencia de la densidad, las predicciones de análisis de viabilidad de po-*

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blaciones (PVA) deberán incluir por lo menos un escenario sin dependencia de la densidad. Mas aún, se describen datos de salida que pueden diferir entre programas. El desarrollo de paquetería de computo podría beneficiarse si se estandarizaran los formatos de registro y resultados arrojados por diferentes programas.

Introduction

How consistent are predictions of population persistence using different population viability programs? Less complex tasks in conservation biology, such as estimating effective population size, have been found to depend strongly on the model chosen (Harris & Allendorf 1989; Reed et al. 1993). The same is likely to hold true for population viability analysis (PVA; Gilpin & Soulé 1986), given that current techniques range from simple rules of thumb to intricate computer models that track individuals in age-structured and sometimes multiple populations (Soulé 1987; Boyce 1992; Burgman et al. 1993; Lindenmayer et al. 1993).

A biologist fortunate enough to have data to parameterize a simulation model that is quantitative and demographically explicit has the potential advantage of being able to capture the interacting factors that influence population persistence. In most cases, however, there is neither the time nor expertise to develop a complex, species-specific PVA computer program; the reality is that biologists must choose from more generalized and readily available programs. Although user manuals describe the technical characteristics and idiosyncracies of these programs (Lindenmayer et al. 1995), it is not known how the different program outputs or predictions compare given a single set of demographic data.

We consider the consequences of program choice on predictions of vertebrate population dynamics, focusing only on a subset of PVA programs that are demographically explicit. We do so by performing viability analysis on the same data with different PVA computer programs. The four programs we examined have been marketed commercially and/or described in published papers, and they represent the types of PVA programs currently available and used most often with detailed demographic data. Within each program there are a number of different models related to factors such as density dependence, correlations, and stochasticity. To focus on how consistent the PVA predictions are among the programs, we attempted to use the same conceptual models and assumptions for each.

The demographic rates we used approximated those of wild grizzly bears (*Ursus arctos horribilis*). Bears have overlapping generations and vital rates that change with age. Using these data therefore forces the programs to deal with several complexities typical of many long-lived, terrestrial vertebrates. Also, demographic data are more extensive for grizzly bears than for many species,

allowing us to base our comparison on a relatively comprehensive, real-world data set. We emphasize that we are investigating the process of PVA and are not performing a PVA for any particular species or population.

By standardizing program inputs and comparing outputs, we explored two issues critical to viability analysis. First, we showed the extent that predictions of population persistence can be affected merely by program choice, at least for this life history. Second, and perhaps more important, we used the comparison to highlight specific input decisions that lead to the greatest disparity in predictions. We hope to alert modelers to elements requiring the greatest attention in development of computer programs. Illuminating these variables should also help focus field research on factors critical to viability analysis, thereby helping to bridge the gap between models and field data (Doak & Mills 1994).

Assumptions and Data

Four primary factors are usually considered in population viability analyses (Shaffer 1987). We stress that these factors are inextricably intertwined in the wild and are separated here for heuristic purposes only. One advantage of computer-based approaches is that they are more amenable to incorporating feedback loops that cause the extinction vortices described by Gilpin and Soulé (1986).

The first and most important of the four factors is the deterministic events that caused the population to decline to small numbers (Caughley 1994). The other three factors are typically treated as stochastic phenomena: demographic, environmental, and genetic (e.g., inbreeding depression). Our input of extinction factors, as well as additional demographic characteristics, was based on consistent assumptions across PVA programs for deterministic factors, demographic and environmental stochasticity, inbreeding depression, density dependence, and simulation conditions.

Deterministic Factors

For maximum generality in our comparison, we considered both increasing and decreasing populations (Table 1), using data derived from generalized grizzly bear demography. These growth rates are within the range of actual values from field studies on grizzlies in the Yel-

lowstone ecosystem (Knight & Eberhardt 1985; Knight et al. 1988; Eberhardt et al. 1994; Pease & Mattson unpublished data), with the negative growth rate consistent with effects of perturbations in habitat quality (Doak 1995) or behavior (Mattson et al. 1992). Demographic rates were compiled assuming post-birth pulse sampling (Caswell 1989). The Appendix details how these vital rates were incorporated into each program.

Demographic and Environmental Stochasticity

For three of the four programs, demographic stochasticity was incorporated using Monte Carlo sampling of individual birth and death events. One program, RAMAS/AGE, sampled the birth and death events of cohorts rather than of individuals.

Although a wide range of environmental variation, or

stochasticity, could plausibly be used in each of the PVA programs, we let demographic values vary such that standard deviations were equal to approximately one-third of the mean (i.e., the coefficient of variation for survivorship and fecundity values was 0.3). Although there is some biological rationale for this particular value (Mattson 1987; also Mills & Smouse 1994), we prioritized consistency across programs over attempts to accurately reflect the environmental relationships of any particular population.

Some of the programs incorporated "catastrophes" as variation in vital rates apart from environmental stochasticity while others did not. Those that included this extreme variation did so in divergent ways that defied a standardized approach. Consequently, we did not impose any additional variation due to catastrophes.

The importance of correlated environmental variation across birth and death rates and across age classes has only recently been emphasized for viability analysis (Doak et al. 1994; Ferson & Burgman 1995). Unfortunately, the actual correlation structure for a population is seldom known. The programs we used differed in their capability and approach to incorporating correlation among vital rates. We simplified the task of comparing programs by making variation in vital rates perfectly and positively correlated in the three programs that allowed control of the correlation. The fourth (INMAT) has a pre-set correlation structure in which environmental variation affects survival and fecundity in the same direction but not necessarily with the same magnitude (Mills & Smouse 1994). The natural history context of setting correlation equal to one is a scenario in which all vital rates are identically affected by, for example, climatic events or variation in food supply.

Inbreeding Depression and Starting Population Conditions

Because one of the programs (VORTEX) incorporates inbreeding costs only on juvenile survival, we imposed costs only on the first age class. Although a range of costs are possible for juvenile survival — as well as for other survival and litter-size rates (Mills & Smouse 1994) — we used a lethal equivalent of 1.57 per haploid genome, the median value for juvenile survival in 40 mammal species (Ralls et al. 1988). Because no inbreeding costs were imposed on other vital rates, our inbreeding costs were probably conservative with respect to the range possible in the wild.

For simplicity we assumed that sex ratios were equal in all simulations and that demographic rates were a composite of male and female rates. Each simulation began with 250 individuals (125 males and 125 females) distributed across age classes in a stable age distribution, or as close as possible within the constraints of the PVA programs.

Table 1. Demographic vital rates used in simulations of grizzly bear populations.^a

Age class (years)	Survival rate	Breeding females (%) ^b	Breeding females (%) by litter size (either sex) ^c		
			1	2	3
0	0.87/0.74	0/0			
1	0.87/0.74	0/0			
2	0.87/0.74	0/0			
3	0.87/0.74	0/0			
4	0.86/0.76	23/32	40/25	40/40	20/35
5	0.86/0.76	23/32	40/25	40/40	20/35
6	0.86/0.76	23/32	40/25	40/40	20/35
7	0.86/0.76	23/32	40/25	40/40	20/35
8	0.87/0.85	29/37	5/20	40/40	55/40
9	0.87/0.85	29/37	5/20	40/40	55/40
10	0.87/0.85	29/37	5/20	40/40	55/40
11	0.87/0.85	29/37	5/20	40/40	55/40
12	0.87/0.85	29/37	5/20	40/40	55/40
13	0.87/0.85	29/37	5/20	40/40	55/40
14	0.94/0.75	36/27	60/25	40/40	0/35
15	0.94/0.75	36/27	60/25	40/40	0/35
16	0.94/0.75	36/27	60/25	40/40	0/35
17	0.94/0.75	36/27	60/25	40/40	0/35
18	0.94/0.75	36/27	60/25	40/40	0/35
19	0.94/0.75	36/27	60/25	40/40	0/35
20	0.94/0.75	36/27	60/25	40/40	0/35
21	0.94/0.75	36/27	60/25	40/40	0/35
22	0.94/0.75	36/27	60/25	40/40	0/35
23	0.94/0.75	36/27	60/25	40/40	0/35
24	0.94/0.75	36/27	60/25	40/40	0/35
25	0.94/0.75	36/27	60/25	40/40	0/35
26	0.94/0.75	36/27	60/25	40/40	0/35
27	0.50/0.40	36/27	60/25	40/40	0/35
28	0.25/0.20	36/27	60/25	40/40	0/35
29	0/0	0/0	60/25	40/40	0/35

^aThe first value represents a positively growing population and the second a negatively growing population. The Appendix details how these values were incorporated into each PVA program.

^bAccounts for annual survival of females (Caswell 1989).

^cA weighted mean of these values for each cohort gives the average litter size per female that breeds.

Population Ceiling/Density Dependence

There are two fundamentally different ways to model density dependence, or carrying capacity, in the PVA programs considered. One approach is to modify vital rates as a function of population size. A variety of functions are available, but they all share the common feature of decreasing certain vital rates as the population size grows toward carrying capacity (K). Some functions allow population size to exceed K (Ginzburg et al. 1990), although on average population growth becomes negative above K .

The second approach involves a population ceiling for a carrying capacity. Whenever the population passes K there is proportional truncation across age classes that brings the population back to K in the next time step. Because K is an upper boundary, the mean or equilibrium population size will be less than K to an extent dependent on the population growth rate and its variation (R. Akçakaya, personal communication). In this case vital rates do not depend on density, so a population with long-term growth rate (λ) below 1.0 will decline geometrically (on average) toward zero.

The differences in these two approaches made it impossible to impose density dependence in the same way across programs; that is, the same density-dependent model could not be used in all of the programs. To be as consistent as possible but still meet the various input requirements of the programs, we chose density-dependence models that would impose a ceiling function, or the closest facsimile to a ceiling that was available. The ceiling function was chosen because density depen-

dence in two of the programs is ultimately determined by a ceiling in a way that cannot be modified.

We assumed that the population ceiling, or carrying capacity, for our bear populations was 250, the same as the starting population size. The reproductive rates we input (Table 1) were assumed to correspond to bears at densities less than carrying capacity. Accordingly, for those programs that modify vital rates with density, mean reproductive rates could be up to twice as large at very small population sizes (within biological limits) and as low as 0 near K . We note that Allee effects, or disproportionately low vital rates at very low population sizes (Dennis 1989), further complicate density dependence. Therefore, we ignored Allee effects in our comparisons.

Simulation Conditions

For both the growing and declining bear populations we compared the programs at four different levels, discussed here in order of increasing complexity. First, we considered the case of no environmental stochasticity, no density dependence, and no inbreeding effects — that is, growth or decline with only demographic stochasticity. The second scenario included both demographic and environmental variation without inbreeding costs or density dependence. Third, we added inbreeding costs, without density dependence, to the stochastic (demographic and environmental) model. Fourth, we removed inbreeding costs and ran stochastic simulations with density dependence.

We chose a projection span of 48 years (4–5 bear generations). All stochastic simulations were based on 500 rep-

Table 2. Key program attributes that were central to investigation of factors causing divergence in population viability analysis program predictions.*

Attribute	GAPPS version 1.3	INMAT version 6A	RAMAS/AGE version 2.0	VORTEX version 6.1
Data format	Individual —	— Matrix	— Matrix	Individual —
Inbreeding function	Yes	Yes	No	Yes
Density dependence options	Logistic Michaelis-Menton — — — —	— — — — Ceiling	Logistic — Beverton-Holt Ricker Observed —	— — — — Observed Ceiling
Output	Mean N for all/ persisting replicates Median N Extinction (%) Quasiextinction (%)	Mean N for all/ persisting replicates Median N Extinction (%) Quasiextinction (%)	Mean N for all replicates Median N Extinction (%) Quasiextinction (%)	Mean N for persisting replicates — Extinction (%) —

*More recent versions of the software may have different attributes (for example, RAMAS/METAPOP explicitly incorporates ceiling-type density dependence in addition to those listed).

licates. As measures of central tendency for population size, we considered the mean and, when possible, the median.

Population decline to low levels was judged relative to two thresholds: (1) absolute extinction and (2) a management threshold (or "quasiextinction threshold"; Ginzburg et al. 1990; Akçakaya 1992) of 100. Management thresholds are potentially important in PVA modeling because they represent population sizes at which substantive management changes are often made, such as classification of a population as endangered or intense control of limiting factors (Dennis et al. 1991; Scott et al. 1995). In addition, such thresholds can correspond to sizes at which other factors, such as Allee effects, may become important (Akçakaya 1994).

The PVA Simulation Programs

We examined two programs that are based on individuals and two that are based on cohorts in stage- or age-based matrix projections (Table 2, Appendix).

GAPPS II (Version 1.3)

GAPPS (Downer 1993, adapted from Harris et al., 1986) is an individual-based program that has been used previously in large-mammal simulations (Harris & Allendorf 1989; Dixon et al. 1991). We incorporated density dependence into GAPPS by changing the percentage of breeding females as a decreasing linear function of population size relative to K . This model performed similar to a ceiling function for the growing population, whereas for the declining population it increased "breed rate" at population sizes less than the ceiling. Inbreeding coefficients are calculated by GAPPS for each member of the population, and costs were applied only to newborns (0–12 months).

INMAT (Version 6a)

INMAT is a matrix-based program developed to look at short-term inbreeding effects in stochastic environments (Mills & Smouse 1994). Although the published version contains no density-dependent functions, a population ceiling was subsequently added. When population size exceeds the specified ceiling it is truncated across age classes; thus, the next time step begins with a population size equal to the ceiling. To account for potential synergistic effects of inbreeding, INMAT uses a curvilinear relationship between the inbreeding coefficient and fitness (Mills & Smouse 1994).

RAMAS/AGE (Version 2.0)

RAMAS/AGE is a commercially available, commonly used program that uses matrix projections (Ferson &

Akçakaya 1990; Akçakaya 1992). Density dependence in this version of RAMAS/AGE operates solely on reproduction (but see Akçakaya 1994 for descriptions of RAMAS/METAPOP). Available functions include logistic, Ricker, and Beverton-Holt models, as well as user-specified options.

These functions can be parameterized in different ways to elicit varied behaviors of density dependence. We parameterized the Ricker and Beverton-Holt functions to mimic a population ceiling like those modeled under INMAT and VORTEX, in keeping with our goal to model density dependence in a manner as similar as possible across programs. We did this by assigning parameter values to Beverton-Holt that caused fecundity in our growing population to decrease to a level at which reproduction and mortality balanced at 250 bears. This resulted in population equilibrium at 250, similar to the ceiling function.

If parameterized in a similar manner for declining populations, however, the Beverton-Holt function creates an effect in which populations rebound from low sizes. This is different from a ceiling function, which has no density-dependent effect on declining populations below K . Consequently, we assigned parameter values to the Ricker function that caused it to behave in a density-independent manner for our declining population. But this parameterization causes increasing populations to exceed K , contrary to a ceiling. Thus, our efforts to mimic a ceiling function resulted in four density-dependent behaviors: two that were close facsimiles and two that were different. We included all four behaviors in our density-dependent simulations using RAMAS/AGE because all are parameterizations that other users would likely make when attempting to emulate a ceiling. No explicit inbreeding functions are available in RAMAS/AGE.

VORTEX (Version 6.1)

VORTEX is an individual-based program that has been used widely for PVA analysis (Lacy 1993; Lacy & Clark 1993). Although VORTEX allows input of a density dependence function that affects the percentage of adult females that breed, ultimate control of population size is via a ceiling model that truncates populations at K (Lacy et al. 1994). Therefore, we did not impose density dependence on reproduction. Instead we allowed the density-dependent runs to be affected solely by ceiling truncation.

Two methods are available in VORTEX for decrementing juvenile survival under inbreeding. We chose the "heterosis" option because it most closely matches how inbreeding costs are implemented in INMAT and GAPPS. Our short projection interval of less than five generation intervals is compatible with the heterosis option, which does not purge deleterious alleles (Mills & Smouse 1994).

Comparison of Program Predictions

The differences in input format among PVA programs (see Appendix) prevented us from beginning simulations with identical intrinsic growth rates in each program. RAMAS and INMAT provide a deterministic (i.e., before stochasticity is added) annual growth rate (λ) derived from the dominant eigenvalue of the Leslie Matrix. For these programs λ was 1.03 and 0.96, respectively, in the increasing and decreasing populations. VORTEX supplies a deterministic λ based on Euler's equation from life table analysis: 1.04 and 0.94, respectively. GAPPS does not provide a deterministic, analytical calculation of growth rate; based on population size change under only demographic stochasticity (below), however, λ in GAPPS was 1.02 and 0.93 for the increasing and decreasing populations, respectively.

We found that these programs defined key output values differently under stochastic conditions (Table 2). For example, "mean population size" is the mean across all replicates in RAMAS, but only over persisting replicates in VORTEX (the other two programs allow both forms of output). The means we report below refer to the mean over all 500 replicates (VORTEX output was converted). Users should be aware that "mean population sizes" reported by different programs may be incongruent.

Similar warnings apply to the fundamental concept of "probability of extinction." Across the programs the number of animals constituting an extinction ranges from 0 to 1 to only animals of one sex, with two programs (GAPPS, RAMAS) allowing the user to choose the extinction threshold (we report probability of one animal or less). These differences again point toward the need to be explicit when describing simulation output.

When demographic stochasticity alone was added to

the projections, the predicted population size and persistence were mostly similar across programs (Table 3), with differences primarily due to our inability to parameterize the four programs with identical intrinsic growth rates. For example, the average N for the increasing population was lowest for GAPPS and highest for VORTEX (Table 3), in keeping with corresponding differences in deterministic lambdas (λ). In the decreasing population, extinction probability was higher in GAPPS and VORTEX, both of which had lower intrinsic growth rates than the other two programs. When we adjusted adult (post-breeding) mortality in GAPPS and VORTEX to make the deterministic lambdas equal 1.03 and 0.96 (similar to RAMAS/AGE and INMAT), respectively, for the increasing and decreasing populations, the output under demographic stochasticity fell within the range of the matrix-based programs for all output measures.

In the rest of the comparisons we used the vital rates unadjusted for different lambdas and asked how much program outputs are affected by other factors. Thus, the disparities due to deterministic lambdas are "carried through" to reflect our goal of asking what happens when PVA analyses of the same data set are conducted using different programs. The effect of adding different factors can be discerned by comparing simulations that are successively more complicated.

Similarity in program outputs was not greatly affected by the addition of environmental stochasticity (Table 4, compared to Table 3). In all cases, environmental variation increased extinction probability.

When inbreeding costs were added to the stochastic increasing population (Table 5, compared to Table 4), the growing population size apparently minimized the increment in the inbreeding coefficient, so extinction probability changed little in any of the program outputs. In con-

Table 3. Descriptors of grizzly bear population growth and persistence with no environmental variation (e.g., only demographic stochasticity) and no inbreeding costs or density dependence.

Population ^b	Computer program ^a			
	GAPPS	INMAT	RAMAS	VORTEX
Increasing				
Average N (SE) at year 48	766.4 (6.5)	924.1 (5.6)	948.6 (5.5)	1683.6 (14.3)
Median N at year 48	753.0	919.0	934.5 ^c	N/A
Proportion extinct ^d	0	0	0	0
Proportion < threshold ^e	0	0	0	N/A
Decreasing				
Average N (SE) at year 48	7.1 (0.3)	33.6 (0.7)	33.0 (0.6)	13.6 (0.3)
Median N at year 48	6.0	31.5	30.0	N/A
Proportion extinct ^d	0.30	0.006	0.0	0.15
Proportion < threshold ^e	1.0	1.0	1.0	N/A

^aMuch of the difference between programs arises from different deterministic growth rates.

^bStarting population size was 250 animals with equal sex ratio and 48-year projection interval.

^cAlthough RAMAS/AGE does not explicitly provide median output, approximation is possible by interpolating between threshold values that surround the threshold probability of 0.5.

^dOut of 500 replicates.

^eManagement or "quasiextinction" threshold is 100 animals.

Table 4. Descriptors of grizzly bear population growth and persistence with demographic and environmental stochasticity, but no inbreeding costs and no density dependence.

Population ^b	Computer program ^a			
	GAPPS ^c	INMAT	RAMAS	VORTEX
Increasing				
Average <i>N</i> (SE) at year 48	N/A	907.7 (72.1)	845.9 (54.1)	1832.9 (44.0)
Median <i>N</i> at year 48	N/A	357.5	163.5	N/A
Proportion extinct ^d	N/A	0.008	0.02	0
Proportion < threshold ^e	N/A	0.40	0.35	N/A
Decreasing				
Average <i>N</i> (SE) at year 48	4.8 (0.3)	32.0 (2.3)	34.9 (2.6)	13.7 (0.4)
Median <i>N</i> at year 48	3.0	15.0	7.5	N/A
Proportion extinct ^d	0.74	0.13	0.31	0.26
Proportion < threshold ^e	1.00	0.95	0.96	N/A

^a Much of the difference between programs arises from different deterministic growth rates.

^b Starting population size was 250 animals with equal sex ratio and 48-year projection interval.

^c There are currently memory problems with GAPPS that cause it to crash at the population sizes we considered.

^d Out of 500 replicates.

^e Management or "quasiextinction" threshold is 100 animals.

trast, both extinction probabilities and final population sizes were affected when inbreeding was added to the declining population. INMAT showed the greatest effect, probably because ages 0–2 were included in the "juvenile survival" element of the Leslie matrix (see Appendix). GAPPS and VORTEX, which used 1-year age classes in these projections, showed varying but lesser effects.

The addition of density dependence to the stochastic simulations caused strong divergence among program predictions (Table 6, compared to Table 4), particularly in the declining population. For the declining population, density dependence caused a substantial increase in extinctions in VORTEX, had no effect in INMAT, decreased extinctions in GAPPS, and either increased or decreased extinctions in RAMAS/AGE, depending on the

function used. In addition, mean population sizes differed by nearly an order of magnitude across programs.

Implications for Research and Management

Our analysis demonstrates the difficulty in producing equivalent intrinsic growth rates using the same input data in different PVA programs. Although lambdas differed by only 3%, the slight discrepancies in deterministic growth rates led to disparate population sizes and extinction probabilities throughout the stochastic simulations. If this holds across other taxa, it should be taken as a strong warning that different programs can produce very different output.

Table 5. Descriptors of grizzly bear population growth and persistence with stochasticity and inbreeding costs but no density dependence.

Population ^b	Computer program ^a			
	GAPPS	INMAT	RAMAS ^c	VORTEX ^d
Increasing				
Average <i>N</i> (SE) at year 48	N/A	677.8 (78.4)	N/A	1364.6 (18.7)
Median <i>N</i> at year 48	N/A	253.0	N/A	N/A
Proportion extinct ^e	N/A	0.04	N/A	0
Proportion < threshold ^f	N/A	0.42	N/A	N/A
Decreasing				
Average <i>N</i> (SE) at year 48	7.2 (0.4)	4.1 (0.6)	N/A	10.9 (0.4)
Median <i>N</i> at year 48	5.0	0.0	N/A	N/A
Proportion extinct ^e	0.47	0.73	N/A	0.35
Proportion < threshold ^f	1.0	1.0	N/A	N/A

^a Much of the difference between programs arises from different deterministic growth rates.

^b Starting population size was 250 animals with equal sex ratio and 48-year projection interval.

^c RAMAS does not explicitly incorporate inbreeding costs.

^d Due to large RAM memory requirements with the "heterosis" option we were forced to impose a ceiling of 2000 for these runs; extinction probabilities are unaffected, but average *N* will be biased low.

^e Out of 500 replicates.

^f Management or "quasiextinction" threshold is 100 animals.

Table 6. Descriptors of grizzly bear population growth and persistence with stochasticity and density dependence (ceiling or K equals 250) but no inbreeding costs.

	Computer program				
	GAPPS	INMAT	RAMAS		VORTEX
			Beverton-Holt	Ricker	
<i>Population^a</i>					
Increasing					
Average N (SE)	253.9 (2.6)	133.1 (3.9)	154.8 (3.3)	600.2 (30.1)	226.6 (1.1)
Median N	252.0	133.0	140.0	283.8	N/A
Proportion extinct ^b	0.0	0.008	0.01	0.022	0
Proportion < threshold ^c	0.0	0.67	0.58	0.37	N/A
Decreasing					
Average N (SE)	6.7 (0.3)	24.1 (1.5)	48.6 (2.0)	23.0 (1.5)	6.0 (0.3)
Median N at year 48	6.0	11.0	40.0	5.9	N/A
Proportion extinct ^b	0.37	0.14	0.068	0.36	0.54
Proportion < threshold ^c	1.0	0.98	0.99	0.98	N/A

^aStarting population size was 250 animals with equal sex ratio and 48-year projection interval.

^bOut of 500 replicates.

^cManagement or "quasiextinction" threshold is 100 animals.

After adjusting for these differences, however, the three stochastic factors affecting extinction — demographic, environmental, and genetic — caused little divergence in predictions of population size and persistence among the four PVA programs. In contrast, density dependence caused substantial differences in predictions among programs. Put simply, fundamental differences in the programming of density-dependent damping functions produced disparity in the predictions, despite our best efforts to impose analogous conditions. Furthermore, our use of two different functions in RAMAS shows that, within a program, the choice of how density dependence is imposed can radically affect PVA predictions.

The observation that density dependence causes different effects in different programs is particularly interesting because the most-cited guidance regarding the effect of density dependence on PVA predictions comes from a study that used just one particular program and a particular density dependence function (Ginzburg et al. 1990). Our analysis shows that the results of Ginzburg et al. (1990) cannot be generalized to all PVA analyses because some will use different density dependence functions.

The sensitivity of PVA predictions to the choice of PVA programs under density dependence is further complicated because most programs require the user to choose not only a density dependence function, but also the parameters describing the function, such as its shape and slope (Burgman et al. 1993). There is no doubt that habitat quality and availability — and therefore carrying capacity — are crucial to the persistence of fragmented populations. But our comparison highlights the troubling outcome of projecting ignorance about specific functions of density dependence and carrying capacity, and it illustrates the critical need to address these issues in field studies (Murray 1994; for review and for promis-

ing methods see Dennis & Taper 1994; Stacey & Taper 1992).

In view of the divergence between PVA programs when density dependence is added, we recommend two strategies. First, PVA predictions should include density dependence when data indicate an appropriate density-dependent model. A model of this nature would be especially important if a species had a restricted habitat and if population growth was known to be limited above a certain threshold. The second strategy is to include a scenario without density dependence (see also Burgman et al. 1993:164). Although this can lead to unrealistically high numbers, especially when populations are intrinsically increasing and time periods are long, the estimates of animal numbers and extinction metrics will be less dependent simply on the particular programs used. Furthermore, in many conservation contexts the population of concern is not increasing, so population growth to unrealistically large numbers is less of a consideration.

Finally, we underscore the often-stated maxim that several PVA programs should be used, as well as a range of parameter estimates within each. Better data from field studies will allow more-reliable estimates of extinction metrics by PVA programs, but fundamental differences in how density dependence is currently modeled within different programs will still lead to different predictions, even with better knowledge from the field. It should be emphasized that we found divergences in program output with the luxury of a relatively complete and simple data set. As one increases guesswork, or adds complicating factors such as multiple populations or sex-specific vital rates, the repeatability of predictions will decrease. Thus, PVA predictions with different results should be taken as "bracketing" a real-world expectation, as opposed to implying a precise prediction of the future.

Obviously, our attempts to make the different PVA programs comparable constrained some of the most prominent features of each program. Thus, none was allowed to perform as would be possible if the constraints of our comparison were removed.

In addition to looking at factors causing disparity between PVA predictions, our exercise casts light on the use of different metrics to assay persistence. For example, the programs that calculated both mean and median population sizes indicated large discrepancies between these measures of central tendency. As noted elsewhere (Dennis et al. 1991; Boyce 1992), extreme values arising in skewed distributions caused the differences to be greatest for the increasing population growing without limit. To avoid basing management evaluations or predictions on measures heavily weighted by a few extreme values, evaluation of the median is important. Other metrics, such as the mode, may also be useful.

We also noted disparate values yielded by the commonly used probability of extinction and the alternate probability of passing a management threshold. Three of the four PVA programs provide the probability of reaching a management threshold, set at 100 in our case. In nearly every case there was more than 50% difference between the probability of extinction and the probability of declining to the management threshold of 100. In practice, this means that extinction probability may lead us to conclude that a population will fare well, when in fact there is a considerable probability that it will decline to a number deemed alarming for reasons such as policy implications or biological concerns. Clearly, management thresholds are useful in modeling population persistence.

Conclusion

Under some conditions, the results of a PVA can depend strongly on which simulation program is used, supporting admonitions to carefully consider the appropriateness of different programs for the life history and questions of interest (Lindenmayer et al. 1995). More important, for this grizzly bear life history we have identified density dependence as the most prominent factor affecting divergence among programs; the impact of these factors may differ for other species. The differences we observed between PVA programs are likely conservative because we strove for continuity in assumptions across programs and did not include factors such as Allee effects, catastrophes, multiple populations, or sex-specific vital rates.

Obviously, declining populations have lower chances of persistence, and the causes of these declines should be foremost in the attention of researchers and managers (Caughley 1994). Population viability analysis programs contribute most by their ability to make intuition

explicit — that is, to incorporate a number of the factors that influence population growth, thereby suggesting potential consequences of a range of management options. To this end program developers would benefit by including input and output options — ranging from correlation in vital rates to specific definitions of extinction — that are directly comparable across programs. Concurrently, we need more-specific information from the field about the interactions among density dependence, inbreeding, and vital rates in wild populations. Merging these contributions of theory and data will increase our confidence in both predictions and management decisions.

We do not believe that divergence in program outcomes is a damning indictment of PVA modeling, but rather a reminder that these programs carry the same strengths and dangers of other applications of theory to conservation (Doak & Mills 1994). We should take care that our grip on any one program as a mirror of reality is not too tight. By using more than one PVA approach to a particular management question, we can consider a range of factors to uncover qualitative conclusions without implying we have captured a precise snapshot of the future.

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Appendix

How Demographic Rates Were Used in PVA Programs

For the matrix-based programs (RAMAS and INMAT), matrix size limitations forced us to collapse data into 10 age classes of 3 years each; 3 years was a logical span because the birth interval of Yellowstone grizzly bears is approximately 3 years (Knight & Eberhardt 1985; Knight et al. 1988). Survival rates for a 3-year age class (the subdiagonal of the matrix) were simply the products of the annual rates. The top row of the matrix is comprised of fertility values that, in the case of post-birth pulse sampling, take into account litter size, nonbreeders in the cohort, and survival of females to breed (Caswell 1989; Burgman et al. 1993). Given that the population is comprised of equal numbers of males and females, the percentage of the population breeding is one-half the percentage of females that breed in a given year (a value that already accounts for survival of females to breed; Table 1). This value is then multiplied by the mean litter size to give the fertility rate for a year, and summing these for a 3-year cohort provides the elements in the top row of the Leslie matrix. These fertility values can be interpreted as the average number of either-sex offspring produced per individual, or the average number of females produced per female in the population. To model such conditions RAMAS/AGE requires an input sex ratio of 1.0.

The dominant eigenvalue of the matrix gives growth rate over the 3-year interval represented by each matrix element, and the third root of that value gives the annual growth rate.

Unlike the other programs, VORTEX prompts only for a single survival and reproductive rate for all animals after initial breeding age. These cannot simply be calculated as means of the age-specific values in the life table because younger adults contribute more to population growth than do older age classes; that is, lambda is most sensitive to survival of young adults. Therefore, the single survival and reproductive rates for adult bears (ages 4-29) in VORTEX were calculated by

weighting the annual rate for each age class (Table 1) by the proportional sensitivity (Crouse et al. 1987; Caswell 1989) calculated for the annual rate. In this fashion we estimated that annual survival for post-reproductive-age adults would be 0.88 and 0.79 in the increasing and decreasing populations, respectively. In VORTEX the percentage of females breeding does not take into account survival (as in Table 1), so values from Table 1 were divided by cohort survival rates. The weighted mean using relative sensitivity values for percent females breeding is thus 32% and 42% for increasing and decreasing populations respectively. Litter size for females that breed is 2.0/2.1, so in the format required for VORTEX these reproductive values give the fraction of all females with a litter size of 0 = 68/58, 1 = 9/12, 2 = 14/16, 3 = 9/14. Population growth in VORTEX is quite sensitive to the precise value used for adult survival in a long-lived species such as bears.

GAPPS allows the direct input of annual survival rates, by age class, into each simulation. For reproduction, GAPPS requires input of a litter size distribution and probabilities that a female will breed, given that she is available to breed. The observation of percent females that breed (Table 1) is the intersection of the event of being available to breed and the event of breeding. The conditional probability required

by GAPPS was calculated by dividing the observed breeding rate (Table 1) by the probability of being available to breed. Breeding availability is a function of weaning rates and survival of subadults; the combination produces an average birth interval. The probability of being available to breed was calculated by assuming an average birth interval of 2.5 years. With a birth interval of 2.5 years, each year $(1/2.5) = 0.4$ of all females are available to breed. Thus, the conditional probabilities were calculated by dividing each of the breed rates in Table 1 by 0.4. Environmental stochasticity in GAPPS was simulated by selecting breed and mortality probabilities from normal distributions with a standard deviation of one-third of the mean. For some age classes mean probabilities approached 1.0, resulting in truncated normal distributions and realized breed and mortality rates that were biased low. Density dependence was incorporated into GAPPS as follows: the percentage of breeding females (Table 1) was assumed to have been observed when the population was at $(1/4)K$. Thus, the linear function consisted of the line between the points (0.25, observed rate) and (1,0). The lower value of the breeding rate was set so that the population remained roughly at $K = 250$ for the growing population when density dependence was imposed.

