

# Comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the whooping crane (*Grus americana*)

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## Abstract

Population viability analysis (PVA) is widely used in conservation biology to compare management strategies and predict probabilities of extinction for endangered species. However, it remains unclear whether the available range of generic PVA programs produce similar predictions when applied to common data sets. A comparative analysis was carried out using six commonly applied PVA packages (GAPPS, INMAT, RAMAS Age, RAMAS Metapop, RAMAS Stage and VORTEX), based on the extensive population data available for the endangered whooping crane, *Grus americana*. Significant differences were found between the projections of the PVA packages. In particular, the introduction of stochastic variation in breeding structure led to large differences between some packages. Surprisingly, two versions of VORTEX produced very different predictions due to a subtle difference in the way monogamous breeding was modelled. The pattern of similarities and differences among the projections of the packages differ depending on the species examined. In contrast to the predictions of comprehensive (realistic) models, simplified (standardized) models were found to be relatively congruent, which probably reflects similarities in the fundamental biological processes being modelled by the PVA packages. The implications for conservation are clear; caution must be exercised when interpreting the projections of a model built using any one PVA package since, due to seemingly subtle differences in what biological assumptions and threatening processes are included in the models, the predictions among PVA packages (or versions of the same program) are not necessarily concordant.

## INTRODUCTION

Many of the world's species are threatened with extinction from habitat loss, over-exploitation, introduced species, pollution, demographic, genetic and environmental fluctuations, and natural catastrophes (World Conservation Monitoring Centre, 1992). Population Viability Analysis (PVA) has been developed to assess extinction risk and to compare management options. PVA is a methodology for predicting the future fate of wildlife populations based on demographic, environmental and genetic parameters (Shaffer, 1981; Gilpin & Soulé, 1986; Boyce, 1992; Burgman, Ferson & Akçakaya, 1993; Norton, 1995), most commonly with the use of computer simulation.

The PVA process provides an important framework

for interdisciplinary discussion and synthesis, and is now an influential and widely applied management tool in conservation biology. PVA is used for ranking management strategies according to their relative impacts on the persistence of wildlife populations (Clark, Backhouse & Lacy, 1991; Lindenmayer, Clark *et al.*, 1993). The Conservation Breeding Specialist Group (CBSG) of the World Conservation Union (IUCN) has conducted more than 80 PVAs using VORTEX (Miller, 1995), and many more have been done using other generic PVA packages (Lindenmayer & Possingham, 1994). The results of PVAs can be used to categorize endangerment and support the conclusions reached on the basis of other IUCN criteria (IUCN, 1994).

The use of PVA for quantitative categorization presupposes that the output is reliable and consistent. Its use for comparing management options requires that the relative impacts of different threats are correctly predicted. However, the dichotomy between quantitative

and qualitative (relative) results is not always distinct. As conservation actions entail costs, management decisions are based not just on what will work best, but also on whether the likely benefit of a management action will justify the costs, and if the proposed actions will be enough to achieve recovery. Both these questions require that the PVA predictions be quantitatively reliable. If PVA predictions are inaccurate or differ depending on the PVA package used, inappropriate or sub-optimal programmes for managing endangered species may be implemented.

Since PVA is used to make critical, real-world decisions, it is essential that the predictions of PVA be compared and evaluated (Soulé, 1987, 1989; Soulé & Kohm, 1989; Lacy & Clark, 1990; Lacy, 1995; Mills, Baldwin, *et al.*, 1996; Brook *et al.*, 1997). PVA comparisons should ideally be carried out on a varied range of taxa (i.e. mammals, birds, amphibians, reptiles, fish and insects), to determine whether PVA packages differ in the consistency and sensitivity of their predictions depending on life-history strategy.

The objective of this study was to compare the predictions of six of the most widely used generic PVA packages (GAPPS, INMAT, RAMAS Age, RAMAS Metapop, RAMAS Stage and VORTEX) under controlled conditions, and to evaluate how program selection may influence the conclusions of a PVA. We do not attempt to assess the predictive accuracy of the simulation outcomes, but simply ask if the predictions of different PVA packages are concordant. Detailed and biologically realistic simulations based on the autecological data available on the endangered whooping crane were built, utilizing the full capabilities of each PVA package. An earlier comparative PVA based on a grizzly bear, *Ursus arctos horribilis*, data set (Mills, Baldwin *et al.*, 1996) considered four PVA packages, but could not completely standardize the input across packages due to the bear's relatively complex life history. Underlying deterministic differences then carried over to the stochastic simulations, and became exaggerated over time.

In addition to the comprehensive models, we also constructed completely standardized models that were directly comparable across packages. Although the standardized models are by necessity artificially simple (in practice few use the packages in such an uncomplicated form), if the various generic PVA packages do indeed model the same fundamental biological and population processes in a similar fashion, the predictions of the standardized models are expected to be congruent.

### The whooping crane

The whooping crane (*Grus americana*) is one of the world's most endangered cranes (U.S. Fish and Wildlife Service, 1994). It is currently restricted to one natural wild population, two experimental introduced wild populations, and approximately 130 captive birds. The one natural wild flock winters in the vicinity of the Aransas National Wildlife Refuge, Texas, and migrates annually to breed at Wood Buffalo National Park in the Northwest

Territories, Canada. The Aransas/Wood Buffalo population has gradually recovered from a severe bottleneck of 14 adult birds (with an estimated 3–6 breeding pairs) in 1941, and currently numbers ~155 (Mirande, Cannon *et al.*, 1997). The whooping crane's precarious situation was recognized by 1939, and the population has since been continuously monitored, providing 57 years of detailed demographic data (Binkley & Miller, 1983; Nedelman, Thompson & Taylor, 1987). Annual counts have been conducted several times during the winter season at Aransas providing fairly accurate counts of the entire population (including juveniles). Surveys have also been conducted annually on the breeding grounds at Wood Buffalo National Park since 1969, to estimate the number of nests, hatchlings and fledglings. Concern over the future fate of the whooping crane has led to captive breeding, genetic studies, and two previous PVAs (using VORTEX only; see Mirande, Lacy & Seal, 1991; Mirande, Cannon *et al.*, 1997).

Whooping cranes are monogamous, annual breeders, although not all adults are able to breed every year. The age of first breeding is unclear, but probably ranges between 4–5 years. Two eggs are usually produced per nest, but since 1967, one egg from several nests has been removed for the purpose of stocking other populations (except in the summers of 1970, 1972 and 1973). However, regression analysis showed no significant change over time in the average population growth rate ( $F = 0.01$ ,  $P = 0.984$ ). Analyses of the census data does not reveal any evidence of density-dependence (Bulmer's test statistic  $R = 17.2$  (non-significant), see Bulmer, 1975). Consequently, there is good reason to believe that the current size of the population is probably well below the environment's carrying capacity. The data analysis and parameterization of the PVA models is summarized in Table 1.

## METHODS

### PVA packages used

Six generic PVA packages (including two versions of VORTEX) were compared. Of these, GAPPS version 3.1 (Harris, Metzgar & Bevin, 1986), and VORTEX versions 5.1 and 8.1 (Lacy & Kreeger, 1992; Lacy, 1993; Lacy, Hughes & Miller, 1995) are individual-based, whilst INMAT version 6 (Mills & Smouse, 1994), RAMAS® Age version 2.0 (Ferson & Akçakaya, 1990), RAMAS® Metapop version 2.0 (Akçakaya, 1996) and RAMAS® Stage version 1.4 (Ferson, 1994) simulate cohorts based on projection matrices (Leslie, 1945; Lefkovich, 1965).

These complex programs all incorporate age (or stage) structure, demographic and environmental stochasticity. Other factors modelled include density dependence (all programs), inbreeding depression (GAPPS, INMAT and VORTEX), systemic pressures such as habitat decline (RAMAS Metapop, RAMAS Stage and VORTEX), catastrophic events (GAPPS, RAMAS Metapop, RAMAS Stage and VORTEX) and metapopulation structure

**Table 1.** A summary of the input parameters used in the PVA packages, as estimated from the historical data available for the Aransas/Wood Buffalo whooping crane population

Parameter	Value	Comments/estimation technique
$\lambda$	1.0477	Mean ratio (jack-knifed geometric mean of $N_{t+1}/N_t$ ) from time-series
Initial size	18	Measured, distribution unknown so set at stable age distribution
Sex ratio	0.5	Monogamous breeding
Density dependence	$K = 1000$	Ceiling $K$ assumed
Inbreeding	3.14 lethals	see Mirande, Lacy & Seal (1991)
Catastrophes	0.786	Multiplier on survivorship, estimated from 7 outlier years
Survivorship	0.9064	Weighted mean over 57 years (not age-specific)
EV <sup>a</sup> in survivorship	0.0757	SD of mean over 57 years, with expected binomial variation removed
Lifespan (years)	50	Based on survivorship schedule, < 1% of adults would reach 50
Age of first breeding (years)	4	Exact age of first breeding unclear, but likely to be 4 years old
Max. litter size	2	Estimated from summer studies at Wood Buffalo National Park
Percentage breeding (%)	47	Average annual percentage of females successfully producing broods
EV in fecundity	0.0682	SD of mean over 57 years
Correlation of EV (%)	21.5	Pearson's product moment correlation

<sup>a</sup>EV, annual environmental variability

(RAMAS Metapop and VORTEX). Each PVA program was designed with slightly different objectives in mind, and this is reflected in their capabilities and underlying assumptions (see Possingham, Lindenmayer & Norton, 1993; Lindenmayer, Burgman *et al.*, 1995). Nevertheless, they are all intended to be applicable to a wide range of taxa. For example VORTEX has been applied to birds, mammals, fish, amphibians, reptiles and insects. All have been used in the management and conservation of endangered species (e.g. Ginzburg, Ferson & Akçakaya, 1990; Lacy & Clark, 1990; Clark *et al.*, 1991; Dixon *et al.*, 1991; Dobson *et al.*, 1992; Lindenmayer & Lacy, 1995; Akçakaya & Baur, 1996).

### Comprehensive model construction

Detailed models were built using the full capabilities of each of the PVA packages. Where possible, a monogamous breeding structure and the actual correlation coefficient between survivorship and recruitment (21.5%) was used. In GAPPS and VORTEX the actual litter distribution and percentage of females breeding was specified. In GAPPS, RAMAS Metapop, RAMAS Stage and VORTEX it was possible to model catastrophes, defined according to a specified impact (a fractional multiplier on survivorship), and probability of occurrence (based on 7 years between 1939–1996 that showed significantly increased mortality). Inbreeding depression was modelled in GAPPS, INMAT and VORTEX. The Aransas/Wood Buffalo whooping crane flock is derived from at most 6 pairs, and is undoubtedly inbred. However, evidence for the actual impact of inbreeding depression on the whooping crane is scant, so the median mammalian value of 3.14 lethal equivalents, applied to the juvenile survival component of the life cycle (see Ralls, Ballou & Templeton, 1988), was arbitrarily used. No general figure of lethal equivalents is available for birds. Unpublished analyses (R. Frankham, unpublished results) show no significant differences between mammals, birds, insects and plants in the risk of extinction due to inbreeding depression, so this surrogate value is

probably reasonable. Further, since the inbreeding models we used affect only juvenile survivorship, the impact is likely to be conservative.

Both of the individual-based packages (GAPPS and VORTEX) and one of the matrix-based packages (RAMAS Stage) possess the capability to simulate stochastic variation in the sex ratio and availability of mates; factors which may be important to small, monogamously breeding populations. Conventional matrix population models implicitly assume sex ratio is incorporated within the estimate of fecundity (or recruitment: Caswell, 1989), and do not explicitly model stochasticity in mate availability (thereby assuming polygamy). Since GAPPS, RAMAS Stage and VORTEX can model either monogamous or polygamous mating, both options were included in the comparisons.

### Standardized model construction

Since the comprehensive models showed differences in predictions, standardized models were compared to determine whether this was due to the incorporation of different features, or because of differences in the internal workings of the same modules. The standardized model required simplification, incorporating only partial age-structure (an age of first breeding of 4 years old, but fecundity and survivorship constant across age classes), a polygamous mating structure (with 100% of adults breeding), complete correlation between recruitment and survival, and no density dependence, but including demographic and environmental stochasticity. The models were started with the initial population at stable age distribution (as calculated from the life table). Mirande, Cannon *et al.* (1997) showed very little difference between the results of runs in which the estimated actual age-distribution was used (as calculated from annual survival rates) compared with those in which the population was set at a stable age-distribution. Deterministic predictions based on this model showed an overall annual increase of 4.45% for all packages.

## Simulation output

As discussed in Mills, Baldwin *et al.* (1996), key output variables sometimes have different definitions across PVA packages, and are therefore not directly analogous. To ensure a comparable output, analysis software was written in PASCAL that produced a suite of standardized metrics using the unprocessed simulation output. Since we were not concerned with comparing the PVA packages with reality, it was not necessary that performance measures had clear biological interpretations, only that they represented a common measure across packages. These included the risk of extinction, the likelihood of recovering to a specific size (quasi-recovery probability), the geometric mean stochastic growth rate, the mean and median population size at each time interval. To reflect the variability within individual replicate runs, the coefficient of variation (CV) of abundances (SD/mean for each replicate trajectory), the average deviation (mean square (MS) error) from regression, and the SD of the average stochastic growth rate were calculated. The first two measures were based on log-transformed data, to minimize the effects of curvilinearity of the trajectories. It was not possible to access the raw simulation output for RAMAS Age, and so some of the complex metrics could not be calculated for this package.

## Statistical analyses

All simulations were projected for 50 years. To ensure statistical reliability, each simulation was replicated 500 times (see Harris, Maguire & Shaffer, 1987). With 500 iterations the predicted values of extinction or recovery probability are bounded by a 95% confidence interval of approximately 4% (based on the Kolmogorov–Smirnov test statistic  $D$ ; Sokal & Rolf, 1995), and for statistical purposes a sample size of 500 represents a high degree of replication.

Comparisons of the PVAs' output were quantified with statistical analyses, performed using MINITAB version 8.1 (Ryan, Joiner & Ryan, 1994). The distribution of the log of mean final population sizes was found to be approximately normal. Log-transformed final year means were compared with a one-way analysis of variance (ANOVA), and variances with an  $F$ -test. Where the

ANOVA revealed significant differences, individual paired comparisons (t-tests with a Bonferroni correction for the number of comparisons) were used to isolate these differences. Contingency  $\chi^2$  tests were used to compare the overall predicted extinction probability. The number of extinct versus persisting replicates were used for the  $\chi^2$  tests. Bonferroni-corrected Kolmogorov–Smirnov tests (applying the confidence interval for percentages based on the binomial distribution) were used for pairwise comparisons of extinction and recovery probabilities.

## RESULTS

### Comprehensive PVA models

The projections of the full models constructed for each of the PVA packages varied considerably (Table 2). An ANOVA test showed that the predicted mean size after 50 years differed significantly among packages ( $F = 82.5$ , d.f. = 2994,  $P < 0.001$ ). Multiple t-tests (with Bonferroni correction) found the projections of RAMAS Age were significantly higher than all other packages, whilst GAPPS, RAMAS Stage and VORTEX were lower. There was no significant difference between final population size of INMAT and RAMAS Metapop. The median final sizes were lower than the respective means, but nevertheless showed the same trends. The PVA packages differed significantly in the predictions of extinction risk ( $\chi^2 = 42.0$ , d.f. = 5,  $P < 0.001$ ) and the likelihood of population recovery ( $\chi^2 = 185.6$ , d.f. = 5,  $P < 0.001$ ). Since the predicted risk of extinction is small, the recovery probability (likelihood of exceeding a population size of over 100) is the more informative measure in this case. The predicted recovery probability ranges from 25% to 59% (a 34% difference). According to the Kolmogorov–Smirnov test, for a  $P$ -value  $< 0.01$  the differences need be only greater than 6%. The differences between packages are therefore highly significant.

To our surprise, there was a large difference between the predictions of the two versions of VORTEX under monogamous breeding (Table 3). Although the input data was identical, VORTEX v5 projected a much lower final population size, variability and stochastic growth

**Table 2.** Comparison of the predictions of the PVA software packages GAPPS, INMAT, RAMAS Age, RAMAS Metapop, RAMAS Stage and VORTEX (version 8) for the comprehensive models, projected for 50 years

PVA package	Mean (SD) size			Median after 50 years			
	10 years	50 years	$P(\text{Ext} / \text{Rec})$	Final size	Log DR	Log CV	Stochastic $\lambda$ (SD)
GAPPS	19 (7)	78 (80)	0.054 / 0.47	68	55.2	0.198	1.0319 (0.125)
INMAT	19 (8)	95 (79)	0.040 / 0.32	79	48.1	0.182	1.0338 (0.119)
RAMAS Age	23 (7)	129 (72)	0.012 / 0.59	107	N/A	N/A	N/A
RAMAS Meta	20 (8)	95 (68)	0.010 / 0.37	70.5	40.5	0.174	1.0343 (0.126)
RAMAS Stage	19 (7)	69 (68)	0.062 / 0.26	63	61.4	0.184	1.0315 (0.129)
VORTEX	19 (7)	66 (61)	0.076 / 0.25	55	33.4	0.192	1.0294 (0.101)

$P(\text{Ext})$ , represents the probability of extinction;  $P(\text{Rec})$ , is the predicted probability of recovering to a population size greater than 100; Log DR, log deviation (mean square error) from regression; and Log CV, (coefficient of variation of abundances) are measures of within replicate variability. N/A, not applicable.

**Table 3.** A comparison of the predictions produced by two versions of the PVA package VORTEX for the comprehensive model

Version / breeding	Mean (SD) / median final size	Probability of extinction	Stochastic $\lambda$ (SD)
VORTEX v5 (M)	35 (33) / 27	0.094	1.0147 (0.107)
VORTEX v8 (M)	71 (65) / 55	0.046	1.0294 (0.101)
VORTEX v5 (P)	93 (68) / 76	0.032	1.0366 (0.104)
VORTEX v8 (P)	92 (69) / 77	0.034	1.0368 (0.102)

Under monogamous breeding (M) there is a significant difference between the predictions of the two versions. However, there is no difference between versions under a polygamous (P) breeding system.

rate than did VORTEX v8 ( $t = 14.4$ ,  $P < 0.001$ ). The predicted extinction probability was also significantly higher ( $\chi^2 = 8.8$ ,  $P < 0.001$ ). However, under a polygamous breeding structure, there was no detectable differences between versions ( $t = 0.1$ ,  $P = 0.86$ ).

### Standardized comparisons

The results of the standardized model comparisons proved very similar. There were only small differences between the mean predictions of the various PVA packages with a polygamous breeding structure. This was true regardless of whether demographic and environmental stochasticity (Table 4;  $F = 5.6$ , d.f. = 2994,  $P > 0.05$ ), or only demographic stochasticity (Table 5;  $F = 5.3$ , d.f. = 2994,  $P > 0.05$ ) were simulated.

Contingency  $\chi^2$  tests on the differences between predicted extinction probabilities under demographic and environmental stochasticity did not prove significant ( $\chi^2 = 5.6$ , d.f. = 5,  $P > 0.05$ ). Based on the probability of recovering to a population size of 100,  $\chi^2$  tests also

revealed no significant differences among packages ( $\chi^2 = 13.2$ , d.f. = 5,  $P > 0.05$ ). All of the PVA packages in the standard comparison were set up under a polygamous breeding structure. When monogamous breeding was modelled in GAPPS, RAMAS Stage and VORTEX, the simulation projections were significantly depressed compared to the polygamous models, but again congruent within the group (see Fig. 1).

There were, however, important differences between the variance around the mean trajectories. Under demographic stochasticity only, GAPPS and VORTEX (the two individual-based packages) produced a significantly higher variance than did the other packages ( $P < 0.001$ ). Surprisingly, these differences disappeared when environmental stochasticity was introduced to the simulations.

### DISCUSSION

There were significant differences between the projections of the PVA packages when used to their full potential. Surprisingly, the projections of two versions of the most commonly applied PVA program, VORTEX, differed substantially. Conversely, the predictions of all the packages were relatively concordant when the models were fully standardized.

The comparative study of Mills, Baldwin *et al.* (1996) on the grizzly bear also found large disparities among packages. However, the rank order of projections found by Mills, Baldwin *et al.* (1996) differed from those found in this study. Mills, Baldwin *et al.* (1996) found GAPPS produced the lowest projections, followed by INMAT, RAMAS Age and VORTEX (highest). In this study however it was VORTEX that produced the lowest

**Table 4.** Comparisons of the standardized comparisons with both demographic and environmental stochasticity for the PVA software packages GAPPS, INMAT, RAMAS Age, RAMAS Metapop, RAMAS Stage and VORTEX, projected for 50 years

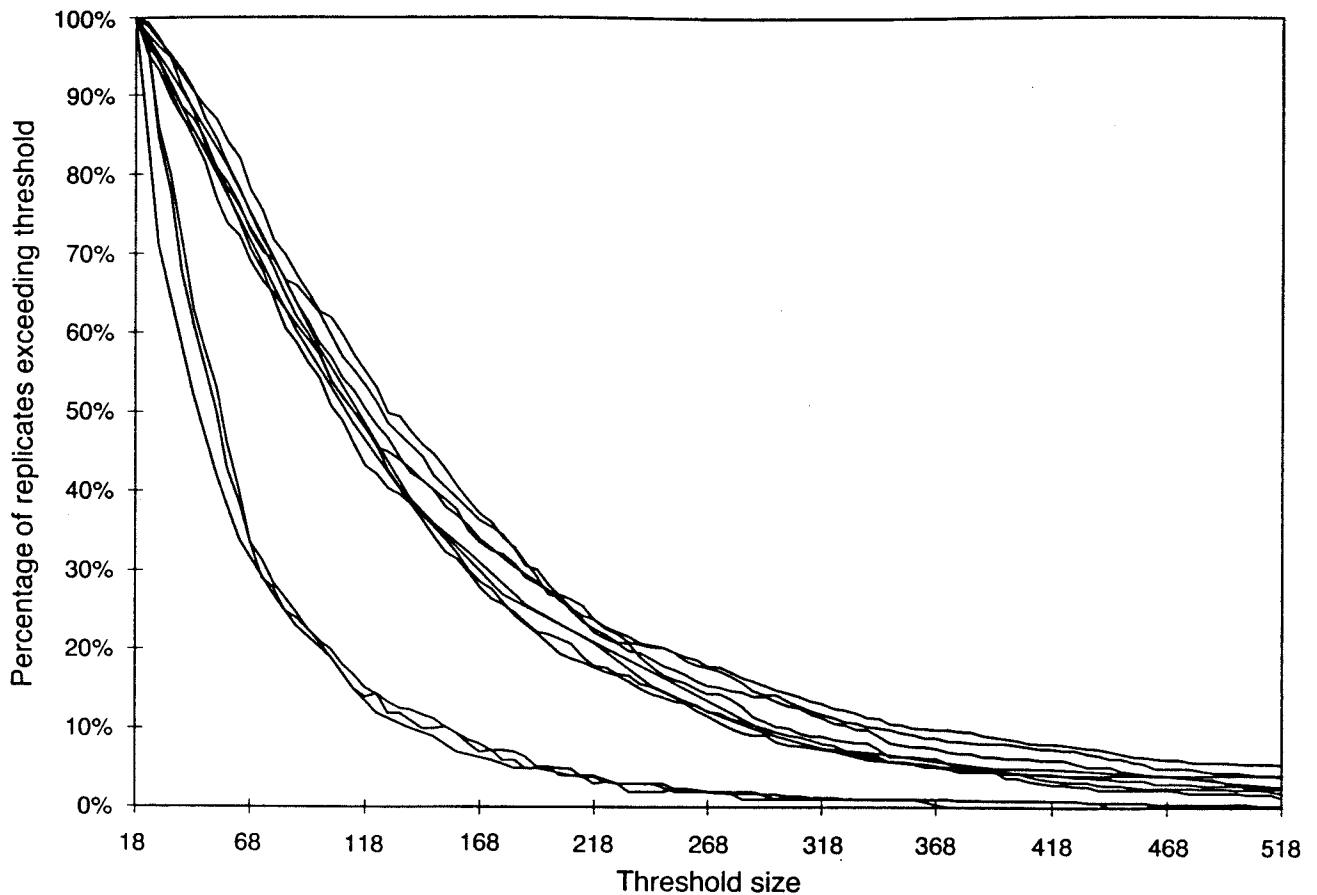
PVA package	Mean (SD) size			Final size	Median after 50 years		
	10 years	50 years	P(Ext / Rec)		Log DR	Log CV	Stochastic $\lambda$ (SD)
GAPPS	27 (9)	151 (125)	0.022 / 0.62	124	18.7	0.173	1.0429 (0.108)
INMAT	29 (13)	138 (142)	0.030 / 0.56	101	38.2	0.182	1.0494 (0.146)
RAMAS Age	28 (12)	137 (138)	0.034 / 0.58	97	N/A	N/A	N/A
RAMAS Meta	29 (12)	142 (132)	0.018 / 0.55	104	32.6	0.179	1.0449 (0.141)
RAMAS Stage	29 (10)	134 (122)	0.032 / 0.58	95	46.3	0.201	1.0423 (0.144)
VORTEX	28 (10)	156 (140)	0.040 / 0.60	125	23.2	0.188	1.0435 (0.114)

N/A, not applicable. For other abbreviations see Table 2.

**Table 5.** Comparisons of the standardized comparisons with only demographic stochasticity for the PVA software packages GAPPS, INMAT, RAMAS Age, RAMAS Metapop, RAMAS Stage and VORTEX, projected for 50 years

PVA package	Mean (SD) size			Final size	Median after 50 years		
	10 years	50 years	P(Ext / Rec)		Log DR	Log CV	Stochastic $\lambda$ (SD)
GAPPS	29 (8)	161 (95)	0.008 / 0.74	146	8.8	0.142	1.0441 (0.070)
INMAT	29 (8)	145 (73)	0 / 0.78	137.5	8.3	0.148	1.0430 (0.083)
RAMAS Age	29 (9)	167 (77)	0 / 0.80	149	N/A	N/A	N/A
RAMAS Meta	29 (8)	164 (71)	0 / 0.79	151	6.4	0.178	1.0461 (0.080)
RAMAS Stage	29 (8)	161 (71)	0 / 0.78	153	10.8	0.154	1.0449 (0.082)
VORTEX	27 (8)	154 (90)	0.012 / 0.72	151	9.9	0.157	1.0423 (0.074)

N/A, not applicable. For other abbreviations see Table 2.



**Fig. 1.** The quasi-recovery probability (likelihood of the population recovering to a defined threshold size) over 50 years, as predicted by the PVA packages GAPPS, INMAT, RAMAS Age, RAMAS Metapop, RAMAS Stage and VORTEX (version 8), under standardized models of whooping crane population dynamics. The upper group of curves reflect models that assume a polygamous breeding system. The lower group of curves represent GAPPS, RAMAS Stage and VORTEX when set-up to simulate demographic stochasticity in mate availability under a monogamous breeding system. The 95% confidence intervals for these curves is 4%, based on the Kolmogorov–Smirnov test statistic.

projections, and GAPPS the highest. Clearly the patterns of similarities and differences among the predictions of the various PVA packages differ depending on the species and type of life history examined. Apparently minor differences in the way the biology of a species is modelled can lead to large differences in the population projections. In an earlier PVA on the Lord Howe Island woodhen (Brook *et al.*, 1997), the two VORTEX versions did not produce different predictions, since the woodhen has a different breeding biology. Detecting such differences between packages and versions and determining their consistency requires comparative studies on species with a range of different biologies.

The dissimilarities found between the comprehensive PVA models could stem from either the inclusion of different features, or different projections for the same feature. The primary reason seems to be due to differences among PVA packages in the factors they can simulate. Some PVA packages ignore threats included in other packages. For example, GAPPS, INMAT and VORTEX include inbreeding depression, whilst the RAMAS packages do not. Further, those programs that were able to simulate the stochastic variation associated with monogamous breeding (possible in GAPPS, RAMAS Stage and

VORTEX) produced much lower projections than those in which polygamy is assumed (due to the relatively small initial population size, this extra source of variability greatly depressed the stochastic population growth rate). In addition to structural differences between PVA packages, it is likely that different users will create different PVA models due to their own understanding, biases and preferences, even when supplied with the same data and PVA package. Finally, there are several alternative, but equally valid ways of implementing more complex aspects of a species biology (such as catastrophes and inbreeding depression), which may also introduce differences between the projections.

A large disparity was found between the predictions of two versions of VORTEX. However, this is not due to an error in the software, but is explained by the way monogamous pairing is modelled. If breeding males are temporarily in short supply (due to a stochastic variation in the sex ratio), version 5 (and previous versions) may pair males with females that subsequently fail to produce a litter. This can result in occasional shortages of males as mates for potentially breeding females. In version 6 and above, breeding males are only assigned to mating partners (females) that do produce progeny

(GAPPS and RAMAS Stage also essentially work in this manner). Hence, males are rarely the limiting sex. In reality, it is likely that some females that fail to produce a clutch are paired to a faithful mate, while others do not breed because they have no mate, so neither model can be considered unrealistic.

In contrast to the differences among packages found with full implementation, the projections of the simplified standardized models were found to be very similar. Moderate deviations did emerge between some of the packages in the predicted variance and extinction probabilities, but not between mean trajectories, stochastic growth rates, or quasi-recovery probability. For us to fully standardize the input models across packages for the whooping crane, it was necessary to include only partial age-structure (an age of first breeding of 4 years old, but constant fecundity and survivorship across all age classes), complete correlation in vital rates, no catastrophes, no inbreeding depression, no density dependence, a polygamous breeding structure, and no stochasticity in mate availability or sex ratio. However, when PVA is applied in conservation assessments, it is usually desirable to produce conservative estimates of risk (Akçakaya, Burgman & Ginzburg, 1997), which means that the full range of possible threats faced by the population should be incorporated within the model. The apparent caveat is that when more complex (and therefore potentially more realistic) PVA models are constructed, their predictions are likely to be strongly influenced by which PVA package is selected, and what factors are included in the model.

This paper has not attempted to address the important question of whether PVA packages produce accurate predictions, and despite the urgent need for such investigations there remains little progress in this area (Brook *et al.*, 1997). Retrospective evaluations based on long-term historical data represent one potentially useful strategy for determining the reliability of PVA, but the overall assessment of PVA predictions will require a meta-analysis that synthesizes the results of many such studies (see Arnquist & Wooster, 1995). Using the results of these evaluations, an adaptive feedback loop can be established with the software development, which should lead to improvements in the PVA process. Detailed historical data has commonly been used in this way to compare and improve complex climate (McCracken, 1995; Wrigley, 1995), economic (Ramanathan, 1995) and ecological models (Swartzman & Kaluzny, 1987).

## CONCLUSIONS

What are the implications for conservation? Different PVA packages cannot be relied upon to produce concordant predictions, since program (or version) choice can significantly influence the results of a PVA. Assessments of endangerment derived from different PVA software packages are therefore likely to differ. This may also lead to the recommendation of conflicting management options, or at least different cost-benefit

analyses for recovery strategies. Until information on the relative predictive capabilities of different PVA packages is available, it is advisable that more than one simulation package be used when conducting a PVA, to help decide if any important differences arise solely due to model choice.

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**APPENDIX****Availability of PVA packages**

- GAPPS is available from the Montana Co-operative Wildlife Research Unit, University of Montana, Missoula, MT, 59812, USA.
- INMAT can be obtained upon request to the author L. S. Mills. E-mail: [smills@selway.umt.edu](mailto:smills@selway.umt.edu).
- RAMAS<sup>®</sup> is a trademark of Applied Biomathematics. For further information on updates and availability, see the RAMAS internet website at <http://www.ramas.com>.
- VORTEX is regularly updated. A detailed description of the availability, application, and pseudocode can be found at the VORTEX website <http://www2.net-com.com/~rlacy/vortex.html>.
- The complete input files for each of the PVA packages are available on the internet at <http://www.bio.mq.edu.au/bbrook/pvainput.html>.