POPULATION VIABILITY ANALYSIS OF THE BLUE-THROATED MACAW

(*Ara glaucogularis*) USING INDIVIDUAL-BASED AND COHORT-BASED

PVA PROGRAMS

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ABSTRACT

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In this study, a demographic model was developed to perform a population viability analysis (PVA) of the Blue-throated Macaw (*Ara glaucogularis*), a critically endangered species endemic to Bolivia. PVA simulations were run using individual-based (VORTEX 9.72) and cohort-based (RAMAS GIS 4.0) programs. A baseline simulation allowed the assessment of the status of the species based on estimates of extinction risk and population declines under current conditions of abundance and habitat availability over the next 50 years. The role of multiple demographic, environmental, and anthropogenic parameters was evaluated to assess changes affecting population declines and extinction risk. The baseline simulation showed that the Blue-throated Macaw has a relatively low probability of extinction during the next fifty years, but the consistent declines in abundance, small population size, and the low population growth rates make this species highly vulnerable to any change or threat. Elasticity analysis of the baseline simulation and sensitivity analysis of changes in different demographic parameters demonstrated that increases in adult mortality had the greatest effect on population growth rate and extinction risk. Simulations of anthropogenic impacts showed that small increases in habitat loss (2%) and population harvesting (3%) had drastic effects on population decline. Comparison of PVA outcomes from VORTEX and RAMAS GIS were consistent with previous studies, showing that individual-based programs like VORTEX tend to be more conservative, predicting not only higher probabilities of extinction but lower population growth rates than the cohort-based program RAMAS GIS. Results from this study emphasize the need for conservation actions

aimed at protecting breeding individuals (decreasing adult mortality), preventing poaching

activities, and promoting the conservation of available habitat (particularly for nesting sites).

Active conservation strategies will be essential for the long-term persistence of this species.

I dedicate this research to my parents Juan and Dalcy,

for all their support, encouragement, and love along every step of my life.

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INTRODUCTION

Recent discussions about biodiversity are frequently based on species extinction due to the detrimental effects of habitat loss, fragmentation, and many other ecological and anthropogenic factors (Hoekstra et al. 2005; Lande 1998; Soulé 1986). As populations become small and isolated, genetic, demographic, and environmental stochasticities increase the probability of extinction, making populations more vulnerable (Gilpin and Soule 1986; Hanski et al. 1996; Hedrick et al. 1996). On the other hand, large populations are more likely to be resilient to stochastic changes given that independent random events among individuals tend to equalize within larger groups (Lande 1998). In an effort to characterize a quantifiable measure of extinction risk, conservation scientists have defined the concept of minimum viable population (MVP). Minimum viable population is an estimate of the minimum number of individuals in a population that has a given probability of surviving for a relatively long period of time (Soulé 1980). The MVP is difficult to be determined in practice (Soulé 1987) and the applicability of the concept for conservation management has been questioned (i.e., Lacy 1992; Ludwig 1999; Reed et al. 2003; Traill et al. 2007). However, the emergence of this concept highlights the need for a quantitative analysis of the risk of population extinction, particularly under the current world wide biodiversity crisis.

One of the main causes of endangerment and extinction are anthropogenic factors such as land development, overexploitation, species introduction, and pollution (Bessinger and Westphal 1998; Hedrick et al. 1996; Lande 1998). These factors may amplify ecological and genetic effects that contribute to the extinction risk of populations. In addition, habitat destruction and fragmentation create new edges among habitats reducing the quality of habitats, decreasing

dispersal and, as a consequence, increasing isolation. Once the populations become small and isolated, random individual variation in vital rates of mortality and reproduction, and random variation in adult sex ratio may cause significant deviations in the growth rates of populations (Lande 1998).

Population Viability Analysis

During the last decades, Population Viability Analysis (PVA) has been one of the most commonly used techniques to determine extinction risks and population declines (Boyce 1992; Coulson et al. 2001). PVA is a process that allows the estimation of extinction probabilities by incorporating identifiable threats to population survival into stochastic models of the extinction process (Brook et al. 2000a; Lacy 1993). This is a useful tool to assess population declines under different scenarios subject to genetic, demographic, and environmental stochasticities (Burgman et al. 1993; Brook et al. 1997). PVA can also be used to predict the future size of a population, estimate the probability of a population going extinct over a given period of time, and assess management or conservation strategies aimed at maximizing the probability of population persistence. In addition, PVA allows the evaluation of different model assumptions on the dynamics of small populations (Burgman 2000; Coulson et al. 2001).

Uncertainties concerning the predictive reliability of PVA have led to questioning the validity of conclusions drawn from some PVA analyses (Brook et al. 1999). However, PVA has proven to be useful not only when there is a large amount of information on the biology of the target species, and the data adequately reflect the distribution of the species vital rates (e.g., Coulson et al. 2001; Reed et al. 2002), but also when the predictions from PVA with limited data are analyzed cautiously clarifying the assumptions, integrating the knowledge from all available

sources, and forcing biologists to be explicit and rigorous in their reasoning (Brook 2000; Burgman and Possingham 2000; Lindenmayer et al. 2000). As many conservation actions and management options are based on PVA results, whether the proposed actions are sufficient to achieve recovery, or whether the results will justify the expenditure, PVA predictions should be quantitatively reliable (Brook et al. 1999; Brook et al. 2000a).

There are several computer programs developed for population viability analysis, which are structured differently and model important aspects of population dynamics in different ways. Among the most commonly applied PVA packages are VORTEX (Vortex: A Stochastic Simulation of the Extinction Process; Lacy et al. 2005) and GAPPS (Generalized Animal Population Projection Process; Harris et al. 1986). These programs are individual-based, tracking the fate of each individual independently by stepping through a series of events that describe the typical life cycle of sexually reproducing diploid organisms (Chapman et al. 2001). Alternatively, ALEX (Analysis of the Likelihood of EXtinction; Possingham et al. 1992), INMAT (INbreeding MATrix; Mills & Smouse 1994), and RAMAS GIS (Risk Assessment and Management Alternatives System; Akcakaya 1998) are cohort-based programs (Brook et al. 2000a) that use projection matrices tracking the fate of the metapopulation as a whole (Leslie 1945; Lefkovitch 1965). Although all PVA packages are suitable for general applications, each was designed with fairly different purposes in mind, and this is reflected in their present structure, capabilities, assumptions, and limitations (Brook et al. 1997; Lindenmayer et al. 1995; Yang et al. 2007).

The selection of the most appropriate program for PVA should be based on a range of criteria including the key questions and objectives of the specific study and the strengths, limitations, and assumptions of the program. Attributes such as life history and available data

for the target species play an important role in determining which program should be used (Lindenmayer et al. 1995). Sometimes, different programs allow the researcher to address different questions, even for the same species. In this research, we selected two of the most widely used programs for PVA analysis: VORTEX, version 9.72 (Lacy et al. 2005) and RAMAS GIS, version 4.0 (Akcakaya and Root 2002). These programs were used to assess the outcome predictions of an endangered species through individual-based versus cohort-based PVA programs.

VORTEX models the effects of demographic rates, environmental variation, catastrophes, and other stochastic events, as well as anthropogenic impacts such as habitat loss and harvesting. This program allows testing the effects of different management options on the viability of wildlife populations using a metapopulation framework, describing the typical life cycle of sexually reproducing, diploid organisms. VORTEX also facilitates the analyses of density-dependent reproduction and changing habitat availability, and most demographic rates can optionally be specified as flexible functions of density, time, population gene diversity, inbreeding, age, and sex. VORTEX projects changes in population size, age, sex structure, and genetic variation, estimating probabilities and time to extinction and recolonization (Lacy 2000; Miller and Lacy 2005).

Alternatively, RAMAS GIS consists of a suite of five programs. The main program is the Metapopulation Model, which combines spatial information of the landscape with ecological parameters of the species to complete a metapopulation model. This program is commonly used to build stage-structured matrices and run simulations to predict the risk of population extinction, time to extinction, expected population abundance, and spatial distribution (Akcakaya and Root 2002).

The Blue-throated Macaw

In neotropical countries, many members of the Psittacidae family are facing population declines and are threatened by extinction due to habitat loss, illegal pet trade, and the use of feathers for indigenous ornamental dresses (Juniper and Parr 1998; Snyder et al. 2000). A clear example of population decline in a wild species is represented by the Blue-throated Macaw (*Ara glaucogularis*), a species endemic to the Beni savannas in Bolivia (Figure 1; Stattersfield et al. 1998). The Blue-throated Macaw is currently considered one of the most threatened bird species of the world (BirdLife International 2000) and is placed in the category Critically Endangered under the criteria C2a(i) of the International Union for the Conservation of Nature Red List (BirdLife International 2004, in IUCN 2006). This species has been protected since 1986 by the national legislation of Bolivia as well as by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to which Bolivia has been a signatory party since 1979.

During the last two years, surveys by the local non-governmental organization Armonía / Loro Parque Fundación documented the presence of nearly 200 Blue-throated Macaws in the wild (Armonía 2007, unpublished data). Even though the minimum population size for the species in 1994 was estimated to be 54 individuals and its size has apparently increased during the last few years, the most optimistic estimation of the population size for this species is around 200 individuals (Yamashita and Machado 1997; Hesse and Duffield 2000). Its seems that the species could be limited by the lack of nesting sites and interspecific competition with the Blue-and-yellow Macaw. Scattered over different areas, the species is distributed into two apparently

disconnected sub-populations to the northwest and the south of Trinidad city, the Capital of the Beni Department, with an estimated 160 and 25 individuals for each population, respectively (Figure 2; Kyle 2005; Mauricio Herrera /Armonía, pers. comm.). It seems that the populations may be isolated from each other due not only to the distance between them (approximately 200 km), but also to the fact that Trinidad, the main city of Beni Department with 276,174 habitants (INE 2001), is located between the populations. In spite of the availability of habitat between these putative populations, no records of the species have been detected in this area, which suggest that Trinidad and surrounding areas may act as a dispersal barrier for the species. Moreover, the area between both populations has been historically inhabited by indigenous people who subsisted by using natural resources in the area including the Blue-throated Macaw (Herrera 2007).

The Blue-throated Macaw inhabits the Llanos de Moxos area (Jordan and Munn 1993), throughout a geographic range of 2508 km² (Hesse and Duffield 2000). The habitat consists of islands of forest associated with *Attalea phalerata* palm trees located in tropical savannas commonly flooded between October and April (Hanagarth 1993). The main feeding of the macaw is the fruit's mesocarp of palm trees such as *Attalea phalerata, Acrocomia aculeata* and *Mauritia fleuxosa* (Bueno 2000). The Blue-throated Macaw nesting sites consist of cavities in the trunks of these palm trees species, as well as cavities in the curupau (*Anadenanthera macrocarpa*) and the guayabochi (*Callycophylum spruceanum*) trees (Gutierrez 1997; Yamashita and Machado 1997; Herrera et al. 2007).

The reproductive characteristics for the Psittacidae family have been described by several authors who stated that most of the species from the genus *Ara* are monogamous (Forshaw 1973; Snyder et al. 2000). According to Boussekey et al. (1997) and Brightsmith (1999), the breeding

season of Blue-throated Macaws in the wild begins during the dry season lasting from August to November. However, Lanning (1982), Hesse (1996), and Duffield and Hesse (1997) asserted that the breeding season for the Blue-throated Macaw in the Beni region initiates with the rainy season between October and November, and lasts for about three months. As the latter authors mentioned, the timing of the breeding coincides with the fruiting season of many tree species guaranteeing optimal feeding conditions for the nestlings.

On average, the Blue-throated Macaw reaches sexual maturity at the age of five years old (Bueno 2000; Voss 2005). The clutch size in captivity varies from 2 to 4 eggs, with 2 and 3 eggs being most common. Eggs are laid at 2 to 3 day intervals, incubation period is 25-26 days, and nestlings fledge after 90 days from hatching (Bueno 2000). Data on sex ratio in the wild does not exist; nevertheless, the sex ratio (males/females) in the Loroparque Fundación, the largest captive population in the world with approximately 150 individuals, is close to 1:1 (Bueno 2000).

The major reason for the decline of the Blue-throated Macaw in the wild is assumed to be related to past and present trafficking of live specimens for the national and international pet market. Before 1982 there appear to be no estimates of population size in the wild. Lanning (1982) reported a population size between 500 and 1000 individuals based on separate reports by two local bird exporters. During the 1980's, up to 1200 Blue-throated Macaws were detected in international markets (Soye and Acheson 2002). Moreover, as with many other species, habitat loss seems to be a determining factor influencing the decline of the Blue-throated Macaw (Hesse and Duffield 2000). Even though the Llanos de Moxos, the main habitat for the species, is mostly distributed throughout private cattle ranches, the deforestation rate in the Beni Department has been estimated around 0.20% during the last few years (Pacheco 2006). This rate

of deforestation may have significant impacts on the Blue-throated Macaw populations, since the species depends heavily on forest patches for nesting, which are limited throughout the savannas.

Research Goals

In this study, we developed a demographic model for the population dynamics of the Blue-throated Macaw to perform a population viability analysis using both VORTEX and RAMAS GIS. The overall goal of this research was to assess the status of the species based on estimates of extinction risk or population declines under current conditions of abundance and habitat availability over the next 50 years. We also evaluated the role of multiple demographic, environmental and anthropogenic parameters affecting population declines. In addition, we compared the outcomes of the two PVA programs to evaluate if predictions were similar given the structure of the programs (individual- versus cohort-based) and the natural history of the species.

Specifically, this research was aimed at answering the following questions:

1. What is the extinction risk of the Blue-throated Macaw under current demographic and environmental conditions during the next 50 years?
2. What are the demographic and environmental parameters that have a major influence on the extinction probabilities of the Blue-throated Macaw?
3. How do anthropogenic factors such as habitat loss and harvesting affect the population decline of the Blue-throated Macaw?

4. How do PVA outcome predictions differ from an individual-based versus a cohort-based PVA program?

Considering that the Blue-throated Macaw is restricted to the Beni savannas and is very vulnerable due to the threats and small size of the remaining populations, the results of this research will help us better understand the demographic dynamics of the species, highlight areas in need of additional information, and finally, suggest management options to ensure the species recovery and long-term persistence.

METHODS

Studied Population and Input Data

The Blue-throated Macaw distribution in the Llanos de Moxos area of the Beni department, Bolivia, is restricted to two putative populations: a northwest and a south population (Figure 1) with 160 and 25 individuals, respectively (Hesse and Duffield 2000; Jordan and Munn 1993; Kyle 2007; Mauricio Herrera/Armonía, unpublished data). Input data used for the PVA is specified in Table 1 and Appendices I and II. The species has a monogamous mating system (Forshaw 1973; Snyder et al. 2000) reaching sexual maturity, on average, at the age of five years old (Bueno 2000; Voss 2005). The clutch size in captivity varies from 2 to 4 eggs, with 2 and 3 being most common. Data on sex ratio in the wild does not exist; nevertheless, the sex ratio (males/females) in the Loroparque Fundación captive population approximates to an ideal sex ratio of 1:1 (Bueno 2000).

The proportion of Blue-throated Macaw reproducing was calculated by Kyle (2005) by dividing the number of pairs reproducing by the total number of individuals observed in the wild, giving a percentage of 36.7%. Currently, there is no data on the mean number of Blue-throated Macaw offspring in the wild, but there are some studies reporting reproductive success in the field for other macaw species. For example, Harper and Guedes (1992) reported 1.64 fledglings per nest for the Hyacinth Macaw (*Anodorhynchus hyacinthinus*), Guedes (1993) reported 0.77 chicks fledged per pair of Green-winged Macaw (*Ara chloroptera*), and Bianchi (1998) reported a reproductive success of 0.698 chicks for the Blue-and-Yellow Macaw (*Ara ararauna*).

In terms of mortality rates Kyle (2007) reported 57% in chicks for the Blue-throated

Macaw. In addition, Vaughan et al. (2005), in a study of the Scarlet Macaw (*Ara macao*),

reported a 5% annual adult decline from a closed population of an average of 160 individuals.

Demographic Model

To perform the PVA we defined a model with three age-classes based on age specific

mortality and fecundity data obtained from different sources (Armonía / LoroParque Fundación,

unpublished data; Kyle 2005, 2007). In cases where there was a lack of information, we used

available data from other species with similar life histories such as the Blue-and-yellow Macaw

(*Ara ararauna*), the Scarlet Macaw (*Ara macao*), and the Hyacinth Macaw (*Anodorhynchus*

hyacinthinus) from the Pssitacidae family, or we used assumptions that were tested later. Most

of the data used in the model was based on previous field studies and few were based on data

from captivity. Age classes included (1) 0-2, from hatching to 2 years, with relatively high

mortality rates of 60% for year 1 and 30% for year 2; (2) 2-5 years, representing juveniles with

15% mortality rate; and (3) 5-40 years, representing adults with a mortality rate of 5% (Figure 3).

Model Assumptions. - Given that the first record of the species in the wild was in 1992 (Jordan

and Munn 1993) and only few studies and data are available for the Blue-throated Macaw,

several assumptions have been made to built the demographic model. The model assumed two

independent populations without dispersal due to the lack of information about this parameter in

the field and a 1:1 sex ratio; this was based on the current distribution of the species (Figure 2)

and the observed sex ratio for the largest captive population of the Blue-throated Macaw at

LoroParque Fundación (Bueno 2000). Based on historical data on the population size of the

species during the 1980's (Hesse and Duffield 2000), we assumed that the carrying capacity was ceiling density dependence with 500 individuals (400 for the Northwest population and 100 for the South population). Since there are no data on environmental variation, we set up 10% of variation in fecundity and mortality rates and in carrying capacity. This value seems to be appropriate given the seasonal variation in rainfall patterns from year to year. In captivity there are reports of individuals from different macaw species living around 60 years (Brouwer et al. 2000); therefore, we used 40 years as the maximum breeding age in the wild. Although there are studies in other species focusing on reproductive success of individuals, there are no data for the Blue-throated Macaw. We used 1.4% hatching success to account for the higher mortality rates seen in hatching individuals (Kyle 2007). Given that we only have data on mortality rates for chicks (60% for 0-1 year old individuals; Kyle 2007) and adults (5%; Vaughan et al. 2005), we used values of 30% mortality for 1-2 year old chicks, and 15% of mortality for juveniles (2-5 years old). In all simulations we model both demographic and environmental stochasticity. Finally, we assumed that there were no catastrophes affecting the populations.

PVA Simulations

PVA simulations were performed using VORTEX, version 9.72 (Lacy et al. 2005), and RAMAS GIS, version 4.0 (Akcakaya and Root 2002). VORTEX uses mortality rates and calculates fertility based on the number of females and males in the breeding pool and the mean number of progeny per year. On the other hand, RAMAS GIS uses survival rates, and we calculated the fecundity by multiplying hatching success by the proportion of individuals that breed. Furthermore, the environmental variation in fecundity is also calculated in different ways

by each program. Whereas RAMAS GIS models variability as the standard deviation of the

fecundity parameters, VORTEX models variability in the percentage of breeding; this means that

the environmental variation in reproduction is modeled entering a standard deviation for the

percent females producing offspring. Since VORTEX and RAMAS GIS are structured in

different ways, we tried to organize and arrange the data in the simplest way to standardize the

baseline simulation as well as a series of alternative scenarios changing the demographic

parameters (see input data for both programs in Appendices I and II). We also run the

simulations in RAMAS GIS using both a sex structure including all individuals (i.e., males and

females) and a sex structure using only females (i.e., using half of the values for each parameter:

half of the initial population size value and half of the fecundity value assuming that the sex ratio

was 1:1). This was done with the purpose of determining if the sex structure could have any

effect on the outcome predictions obtained by VORTEX and RAMAS GIS.

Furthermore, given the differences in the structure and capabilities of the programs, an

elasticity analysis of the baseline was performed with RAMAS GIS, whereas anthropogenic

impacts such as habitat loss and harvesting were modeled only using VORTEX. The elasticity

analysis allowed us to assess which age-class of the model had the greatest contribution or

impact to the eigenvalue (λ) compared with the other age-classes in the baseline. Sensitivity

tests were performed to measure the impact of specific parameters on population decline. In all

simulations, we used the baseline as a template changing the value of the specific parameter of

interest (e.g., mortality, fecundity, and environmental variation) for each alternative simulation.

Based on the apparent distribution of the populations, PVA models were run as two independent

populations with no migration and as part of a metapopulation. Most simulations were run over

a 50-year period, using 5000 replications to estimate decline and extinction probabilities, median time to extinction, and estimates of population growth rates.

The following simulation scenarios were performed:

Baseline Simulation. - This simulation was based on current demographic data estimated for the species. The data was gathered from different sources and field studies (Table 1). When there was a lack of information in any of the parameters, this was completed with information obtained from other species from the same family or using assumptions that were later tested. Complete input files for VORTEX and RAMAS GIS are provided in Appendices I and II. For the programs outcome comparison we ran the baseline simulation for 25, 50, and 100 years, and each of them with 1000, 5000, and 10000 replications. Different time periods were run to evaluate how much the year to year variation could affect predictions on extinction probabilities. Different numbers of iterations were used to assess effects on measures of variation of parameter estimates, including standard errors and confidence intervals.

Demographic Simulations. - Models of extinction consider both deterministic and stochastic factors (Lacy 1994; Soule 1986). Deterministic factors can lead species from long-term average population growth to population decline through different threats affecting essential demographic parameters such as mortality and fecundity rates. Once the population becomes small and isolated, its dynamics and fate can become dominated by a number of random or stochastic processes (Gilpin and Soule 1986; Shaffer 1981). Therefore, a series of simulations were based on changes on multiple values of mortality rates and fecundity for each age-class of the model. To assess the effect of changes in age specific mortality on the risk of population decline, we performed simulations in which mortality rates were increased 10% in each specified age-class (i.e., from 60 to 66% and 30 to 33% in chicks, 15 to 16.5% in juveniles, and 5 to 5.5% in adults).

In addition, we performed simulations with an increase of 10% as an absolute value for each mortality rate (i.e., from 60 to 70% and 30 to 40% in chicks, 15 to 25% in juveniles, and 5 to 15% in adults). Similarly, we decreased by 10% fecundity rates, initial abundance, and carrying capacity to evaluate how much changes in these parameters affected population growth rates and declines. To assess potential changes in environmental variation, we performed simulations with both 10 and 20% of environmental variation in mortality and fecundity rates, and in carrying capacity.

Anthropogenic Simulations. - Very little is known about the history of the Llanos de Moxos area. Some authors such as Beck (1984) and Erickson (1995) reported habitat use by native people who inhabited the area before the introduction of cattle around 300 years ago. However, the impact of indigenous people on the landscape and its vegetation cover is not known. With the setting of the cattle farming in the Llanos de Moxos, annual systematic burning of the savannas ("chaqueo") to improve grazing conditions for cattle has became a wide-spread practice (LoroParque Fundación/Armonía 2003). Agriculture is not perceived as a major threat to the Llanos de Moxos due to the dispersed and limited extension of areas devoted to cultivars. Floods during the rainy season, which increased as a result of a decrease in vegetation cover and deforestation, also limit agricultural practices. Even though agriculture was not considered an attractive alternative to the Llanos de Moxos area, the conversion from savannas to rice fields and many other types of cultivars has increased since 2001, particularly in the Trinidad and Magdalena regions (Herrera 2007). The deforestation caused by disorganized colonization, the annual pampas burning for agricultural use, and the overexploitation of natural resources are increasing rates of habitat loss in the Llanos de Moxos area (Langstroth 2001). A current estimate of the deforestation rate for the Department of Beni is 0.20 % annually (Pacheco 2006).

To assess the effects of habitat loss, we performed simulations by decreasing carrying capacity (K) over time, including 0.5, 1, 2, and 5% decrease in carrying capacity each year.

In addition, harvesting has been and still is considered one of the most serious threats to many parrot species, which are particularly vulnerable to over-exploitation (Collar and Juniper 1992). However, the effects of poaching have been poorly demonstrated. Wright et al. (2001) suggested that the average nest poaching rate in neotropical parrots is 30%, while Gonzales (2003) documented harvesting quotas of 61.1% for the Orange-winged Parrot (*Amazona amazonica*) and 25.9% for the Blue-and-yellow Macaw (*Ara ararauna*) in the northeastern Peruvian Amazon areas with major harvesting pressure. One of the major reasons for the decline of the Blue-throated Macaw is assumed to be illegal trade of wild individuals. Consequently, we simulated the harvesting of individuals from one and two years old over a consecutive period of 10 years to assess the poaching effects over population declines. Probabilities of extinction were assessed under different harvesting quotas including 1, 2, 3, and 5% during 50 and 100 years, respectively.

Data Analyses

We modeled the baseline simulation as well as the alternative simulation scenarios assuming that conditions for each simulation were going to persist during the 50-year period. Kolmogorov-Smirnov statistic D tests (K-S test), with a Bonferroni correction on the probability threshold for the number of comparisons (Sokal and Rohlf 1995), were used for pairwise comparison of extinction probabilities or risk of decline between each of the individual simulations with the baseline as well as among each other.

In addition, to assess potential differences on simulation outcomes, we compared three specific results including differences in the probability of extinction or risk of decline, median time to extinction, and population growth rate (Lambda) between VORTEX and two sets of simulations with RAMAS GIS using a sex structure including all individuals (i.e., males and females) as well as females only. Although the programs are structured differently, the input data was standardized as much as possible to perform a qualitative comparison of results.

RESULTS

PVA Simulations

Overall results for each of the simulations in VORTEX and the two sets of simulations from RAMAS GIS are reported for the metapopulation. Common parameter outputs reported in both programs included probability of extinction (PE), population growth rates (λ), and in cases where the populations went extinct in at least 50% of the iterations, we reported the median time to extinction (mT). Results for each individual population were also obtained for the VORTEX simulations (reported in Appendix III). In addition, K-S tests were used to compare simulations with the baseline as well as with each other to assess which simulation had higher impact over the probabilities of population extinction.

Baseline Simulation.- To assess the current status of the species we run a baseline simulation with VORTEX as well as with RAMAS GIS using a sex structure including all individuals and only females. In the baseline, VORTEX reported a probability of extinction of 0.005 over the next 50 years with a growth rate (λ) of 0.988 (Table 2). RAMAS GIS using all individuals reported a probability of extinction of 0.001 and a growth rate (λ) of 1.031. Contrary to the results obtained with RAMAS GIS using all individuals, RAMAS GIS based on females only revealed a higher probability of extinction (PE=0.238) and a lower growth rate (λ=0.977), the latter similar to that obtained with VORTEX.

Considering each population separately, the south population had a higher probability of extinction than the population in the northwest. This was most likely because the former had a lower number of individuals. The elasticity analysis performed with RAMAS GIS showed that,

compared with other age-classes, the changes in survival of 5-40 years old (adults age-class) had

the greatest effect on the dominant eigenvalue (λ) of the model (see Appendix IV).

Running the simulations with different number of replications in both programs showed

no significant differences in the estimated parameters (Appendix V). In all cases, K-S tests for

the VORTEX simulations showed P values which were not significant between simulations

performed with different time periods. On the other hand, RAMAS GIS reported a significant

difference when the simulations were run with 5,000 iterations. Differences in measures of

variation such as standard error in VORTEX and confidence intervals in RAMAS GIS decreased

when the number of iterations increased (see Appendix VI). As expected, simulations run for

different periods of time did not altered predictions on population growth rates, but it did have an

effect on the predictions of the probability of extinction. When the simulations were run for a

period of 50 years, the extinction probability predictions were more similar between VORTEX

and RAMAS GIS using all individuals.

Demographic Simulations. - We present a summary of each simulation highlighting the

parameters that had greater effects on the population declines and that were significantly

different from the baseline simulation. When we increased each mortality rate by 10%,

VORTEX simulations showed that mortality of chicks had a greater effect on the population

decline than mortality of juveniles and adults, with a growth rate of 0.978 and a probability of

extinction of 0.011, which was significantly different from the baseline (K-S test D=0.3800,

P=0.001). Simulations with increased juvenile and adult mortality rates, revealed probabilities of

extinction and population growth rate estimates that were not significantly different from the

baseline (Table 2). These results were consistent with the ones obtained with RAMAS GIS

using a sex structure with all individuals (λ=1.0200; PE=0.0026; K-S test D=0.181, P=0.0000) as

well as using a sex structure of only females (λ=0.9729; PE=0.3032; K-S test D=0.066, P=0.0000). Furthermore, when we increased each mortality rate with an absolute value of 10%, the risk of decline for the three age-classes was significantly different when compared with the baseline in both programs (Table 3), though a comparison between each simulation showed that adult mortality had the greatest effect (VORTEX: λ=0.914; PE=0.884; mT=38; K-S test D=0.8400, P=0.000; RAMAS GIS all individuals: λ=0.9640; PE=0.1948; mT=0; K-S test D=0.916, P=0.000, and RAMAS GIS females only: λ=0.8932; PE=0.9410; mT=28; K-S test D=0.693, P=0.000). This result suggests that adults represent the most influential age-class in the model, and any change in this class may have drastic effects on population decline. This is consistent with the elasticity analysis of the baseline, which confirmed that adults represented the class contributing most to the eigenvalue of the model (Appendix IV).

Decreases of 10% in the carrying capacity and the initial abundance had no significant effects on the populations decline in VORTEX, while in the two set of RAMAS GIS simulations, the decrease of 10% in the initial abundance did have a significant difference compared with the baseline (Tables 2 and 3). Changes in fecundity (i.e., 10% decrease) had an even higher effect on the decline (VORTEX: λ=0.977; PE=0.014; K-S test D=0.4000, P=0.000; RAMAS GIS all individuals: λ=1.0254; PE=0.0010; K-S test D=0.117, P=0.000; and RAMAS GIS females only: λ=0.9751; PE=0.2688; K-S test D=0.059, P=0.000).

Finally, increasing standard deviation due to environmental variation on carrying capacity, fecundity and mortality rates by 10-20% did not produce results significantly different from the baseline in VORTEX (Tables 2 and 3). Changes in environmental variation in mortality rates, however, had a much higher impact on the likelihood of extinction (PE=0.127) than changes in environmental variation associated with fecundity. When using RAMAS GIS

using all individuals, a 20% standard deviation due to environmental variation on mortality rates significantly increased the probability of extinction. In contrast, RAMAS GIS simulations using only females showed that EV applied to fecundity resulted in a significant increase in the probability of extinction compared with the baseline simulation.

Anthropogenic Simulations. - Results from simulations with different percentages of habitat loss showed an expected trend, since increases in habitat loss increased the probabilities of extinction. Simulations with 0.5% of habitat loss had no apparent effect on the populations. However, reducing the habitat by 1% each year decreased by 15% the final size of the populations. This difference was not statistically significant from the baseline simulation (Table 4). A 2% of habitat loss each year had a significant impact on the population decline as might be expected, reducing the population size by 20% during the first 30 years, and by 57% after 40 years. A 5% habitat loss had an even greater effect on population extinction, decreasing by 90% the number of individuals during the first 20 years of the simulation. Changes in habitat loss affected more drastically the northwest population probably since it had a higher number of individuals than the south population (Figure 4).

Harvesting different percentages of individuals during the first 10 years over a 50-year period resulted in no changes on the population growth rates, but it did increase the probabilities of extinction. Simulation comparison with the K-S test showed that starting at 3% of harvesting the results of the simulations are significantly different from results of the baseline. Expanding simulations over a 100-year period also resulted in no changes in population growth rates, but increases in the probabilities of extinction. On the other hand, results from the K-S test comparison showed that simulation outcomes were statistically significant compared with the baseline only after 5% of harvesting (Table 5).

Harvesting in the northwest population seemed to have a higher impact on population declines than harvesting the south population. This was most likely due to the fact that we modeled harvesting using a constant percentage for both populations, which resulted in more individuals being removed from the northwest population (Figure 5).

Simulation Comparisons. – In order to evaluate which were the most significant parameters affecting the probabilities of extinction, we performed K-S test between simulations. The results showed that increasing by 10% adult mortality had the greatest effect on the population decline compared with the other simulations. This was supported by the lowest growth rate (λ) and the highest probability of extinction observed in this simulation (Table 6). The rest of the simulations were not statistically different between each other, though 2% of habitat loss had the second greatest impact on the risk of decline in the species (Figure 6). Figures for each group of simulations run in VORTEX as well as in RAMAS GIS are provided in Appendix VII.

VORTEX and RAMAS GIS PVA Outcome Comparisons

In this section we present the results obtained from the outcome comparisons from the simulations run with VORTEX and the two set of simulations run with RAMAS GIS (i.e., using all individuals and females only). Considering that each of the programs gives different types of results, we report the parameter estimates common to both programs such as population growth rate, median time to extinction, and probability of extinction.

Population Growth Rates.- When we run the simulations in RAMAS GIS with a sex structure using all individuals (i.e., males and females), the population growth rates were consistently higher than those predicted by VORTEX. However, when RAMAS GIS simulations were run

using females only, growth rate estimates were closer to those calculated by VORTEX (Figure 7). Moreover, the two set of simulations with RAMAS GIS and the set of simulations with VORTEX showed the same pattern of growth rates except for the fecundity simulation, where changes in this parameter and its relative impact on population growth rate varied depending on the program and the specific simulation performed.

Probability of Extinction.- In contrast to the growth rate, predictions about the probabilities of extinction estimated with VORTEX were more similar to those estimated with RAMAS GIS using all individuals (Table 7). The set of simulations from RAMAS GIS using only females predicted higher probabilities of extinction than the other two, as it could be expected given that we used half of the individuals in this model. Both sets of RAMAS GIS showed a similar pattern in the relative impact of simulations on the probabilities of extinction, as it could be expected (Figure 8).

Median Time to Extinction.- VORTEX as well as RAMAS GIS report median times to extinction for each simulation as long as at least 50% of the iterations of each simulation goes extinct. In this study, none of the populations went extinct in most simulations except when adult mortality was increased by an absolute value of 10% (i.e., an increase in mortality from 5 to 15%), where the simulation revealed consistent results with VORTEX and RAMAS GIS using only females. Therefore, median time to extinction did not provide a good measure for the comparison of the PVA outcomes (Table 2).

DISCUSSION

PVA Simulations

The Blue-throated Macaw is a critically endangered species endemic to Bolivia with very low number of individuals in its populations. As many other species from the same family, its main threats include habitat loss and the illegal trade of individuals for the national and international markets. Since the species was discovered in the wild at the beginning of the 1990's, limited data exist about important vital rates of its populations. Results of the baseline simulation suggested that the species has a relatively low probability of extinction over the next 50 years under current conditions. Nevertheless, estimates of the populations growth rate based on current conditions did not reach the rate of replacement to maintain the populations over a longer period of time, making the species vulnerable to any change or threat. Considering each population separately, the south population reveled a higher probability of extinction than the northwest, most likely because the former had a considerably low number of individuals.

Sensitivity analysis to test changes in different demographic parameters and assumptions revealed that changes in adult mortality had the greatest effect over the probabilities of extinction and population growth rate. This result was consistent with the elasticity analysis of the baseline, where changes in survival of 5-40 years old class were the most influential class in the dominant eigenvaule (λ) of the model. Saether and Bakke (2000) analyzed published data of 49 species of birds to determine how population growth rate (λ) was influenced by variation in different demographic traits such as fecundity and mortality rates. This study showed that interspecific differences in the contribution of two demographic traits (I.e., fecundity and adult survival) to the population growth rate were strongly associated to the life history trails of the

species. The contribution of adult survival was highest among long-lived species that matured late and laid few eggs, which are demographic characteristics found in the Blue-throated Macaw. This is consistent with other studies not only in birds but also in other taxa (e.g., Barnes 2007; Brooks et al. 1991; Gerber and Heppell 2004; Heppell et al. 2000; Wielgus et al. 2001), which suggest that protection of adult breeding individuals is crucial for the species.

Simulated changes in environmental variation did not show significant differences in the estimated parameters compared with the baseline, though they seemed to consistently increase the probabilities of extinction due to changes in mortality rates more than changes in fecundity. This result was also obtained by Galimberti et al. (2001) in a study on the viability of the southern elephant seal populations (*Mirounga leonina*). The PVA showed that environmental variation, especially in adult mortality, had a much greater impact on the likelihood of this species extinction than did variability in fecundity (Galimberti et al. 2001).

As with many other species, habitat loss was also an important limiting factor for the Blue-throated Macaw. A 2% of habitat loss per year reduced by half the population abundance in the first 40 years of the simulation. As it could be expected, a 5% of habitat loss had an even greater effect, reducing by 90% the population size during the first 20 years of the simulation.

Another threat for the species assessed in this study was the harvesting of individuals. We tested different harvesting quotas during a consecutive 10 year-period in simulations run for 50 years as well as 100 years. The results showed that when running the simulations for 50 years, even a 3% rate of harvesting had a significant effect on the populations. The same simulations run during 100 years showed that the species could tolerate and recover from a 3% of harvesting.

VORTEX and RAMAS GIS PVA Outcome Comparisons

Most PVA programs are structured in different ways, in most cases reflecting what the architects of the programs consider to be the most important factors influencing the viability of populations (Brook et al. 2000b; Lindenmayer et al. 1995). This means that it is not always possible to input exactly the same information, and as a result, this could lead to differences in the projected results, both in terms of projected population growth and predicted extinction probabilities (Brook et al. 1997; Brook et al. 2000a). Several studies of PVA comparisons have been published in the last several years, not only across different species and taxa, but also across multiple PVA packages and versions (Brook et al. 1997; Brook et al. 1999; Brook et al 2000a; Brook et al. 2000b; Lindenmayer et al. 1995; Mills et al. 1996). In most of these studies, when the programs were used in their full capabilities, the outcomes were quite different. However, when standardized simplified models were used, outcome predictions were concordant and similar between multiple packages. For example, Brook et al. (2000b) compared five PVA packages with different species and found that individual-based packages predicted a consistently higher risk of extinction than their matrix-based counterparts. This result was consistent with a study on the Lord Howe Island Woodhen (*Tricholimnas sylvestris*), which suggested that individual-based programs consider the effect of demographic stochasticity on sex ratio, while matrix-based programs either ignored differences between the sexes or, alternatively, modeled only females (Brook et al. 1997). This could be a problem when modeling monogamous species like the Blue-throated Macaw, where the number of breeding females depends critically on the number of available males. For example, in these species, a stochastic shortage of males could generate a corresponding reduction in the number of females able to

breed. Potential differences between individual- and matrix-based programs could be eliminated by considering only the limiting sex in the matrix-based programs (Brook et al. 1997).

Results from PVA simulations of the Blue-throated Macaw were consistent with those obtained by Brook et al. (1997; 2000b). The predictions from the individual-based program VORTEX not only estimated higher probabilities of extinction than the cohort-based RAMAS GIS, but also revealed lower population growth rates. When the simulations were run in RAMAS GIS considering only females, the population growth rates were similar with those obtained using VORTEX, but contrary to other studies, the probabilities of extinction were even higher than those obtained with VORTEX and RAMAS GIS including all individuals. This was probably due to the fact that the set of simulations run with RAMAS GIS using a sex structure of only females was using half of the values in each parameter (e.g., fecundity and initial abundance).

CONCLUSION

The primary aim of this research was to evaluate the risk of extinction of the Blue-throated Macaw under current demographic and environmental conditions as well as under a series of alternative scenarios (i.e., habitat loss and poaching) that the species could face in the near future. It is important to emphasize that the PVA does not give absolute answers regarding to the probability of extinction of the species, not only because of the assumptions and lack of knowledge about important demographic parameters used in the models, but also because of the inherent stochasticity associated with the extinction process in small populations and the possible changes in environmental conditions. The predictions of the simulations may, however, be considered to be projections about what could most likely happen to the species under the specific conditions modeled.

Even though the baseline simulation revealed a low probability of extinction over the next 50 years, the small population size as well as low population growth rates makes this species very vulnerable to any threat or change. Moreover, all simulations resulted in a consistent decrease of the initial abundance, further increasing the detrimental effects of stochastic processes operating in small populations. Our simulations clearly demonstrated that increases in adult mortality had the greatest effect on population decline. Different effects of anthropogenic impacts, such as habitat destruction and harvesting, also had significant effects on the probabilities of extinction. In this study, even small increases in habitat loss (2%) or populations harvesting (3%) had drastic effects on extinction risk over a short period of time.

Comparison of the PVA outcomes using VORTEX and RAMAS GIS showed concordant results regarding the relative effect of each simulation on the probability of extinction and

population growth. Although VORTEX estimated higher probabilities of extinction, in most cases the predictions were not significantly different from those estimated with RAMAS GIS. In contrast, population growth rate predictions were consistently different between both programs. VORTEX, once again, provided more conservative results, with lower population growth rates than RAMAS GIS. On the other hand, RAMAS GIS simulations run using a sex structure including only females resulted in very similar population growth rate estimates compared to those obtained with VORTEX. However, when RAMAS GIS was run using only females, the probabilities of extinction were higher than those estimated with either VORTEX or RAMAS GIS using all individuals (i.e., males and females).

Implications for Conservation

The discovery of the Blue-throated Macaw in the wild during the 1980's highlights the necessity for developing conservation strategies aimed at protecting the biodiversity of the Beni savannas in northeastern Bolivia. As with many other critically endangered species, small populations at the verge of extinction are subjected to stochastic processes that tend to further decrease population size, increasing the probability of extinction. Results from the baseline simulations showed that the Blue-throated Macaw has a relatively low probability of extinction over the next 50 years. This result is not unexpected, given that the Blue-throated Macaw is a long-lived species and that simulations were run for a relatively short period of time. It is worth noting, however, that after the 50-years period considered for the simulations, population sizes decreased considerably to approximately half of the initial abundance.

Based on the simulation results, it is fundamental to protect adults given that even a small increase in the mortality rate of this group could have a significant impact over the risk of species extinction. In addition, as with many other species, habitat loss can be an important limiting factor leading to the species extinction, as it was shown through the simulations. As indicated above, the Blue-throated Macaw habitat consists of savannas with small isolated patches of forest associated with palm trees, which the species uses as nesting sites. It is therefore essential to target these regions as areas of conservation concern, since they represent breeding and nesting grounds for the species. In addition, PVA simulations also showed that poaching may have an important impact on the species. Thus, enforcing laws against poaching and illegal trade of individuals would have direct beneficial effects for the conservation and potential recovery of the species.

This dissertation provides an initial step in assessing and quantifying, through a population viability analysis, potential threats affecting Blue-throated Macaw populations in the wild. Further studies would be necessary to estimate important demographic and environmental parameters to better understand the natural history and population dynamics of the species and, thus, propose more efficient conservation strategies for the long-term survival of the Blue-throated Macaw.

FIGURES

Figure 1. Pictures of the Blue-throated Macaw. A) Blue-throated Macaw in the wild (© Mark Sttaford-Parrots International). B) Llanos de Moxos area in the Beni Department - Bolivia, the habitat of the species (© Armonía). C) Blue-throated Macaw chicks in a natural nest (© Hernan Vargas-Armonía).
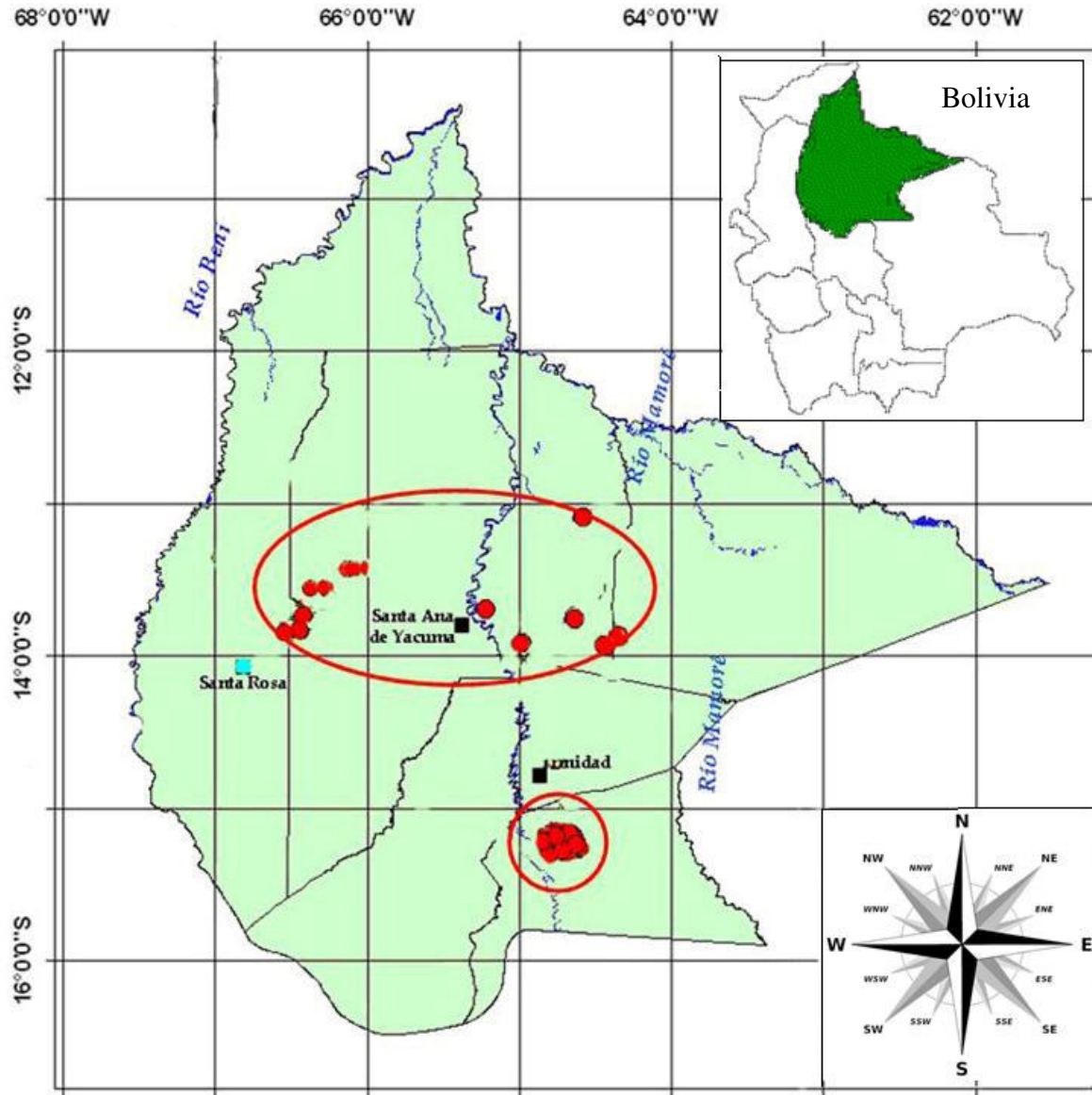
Figure 2. Map of the distribution range of the Blue-throated Macaw in Bolivia. The inlet map shows the location of the Beni Department in the northeast of Bolivia (shadow area). Red dots represent locations where the presence of the species has been confirmed by Armonía/LoroParque Fundación (unpublished data). Circles define two putative populations of the species remaining in the wild.
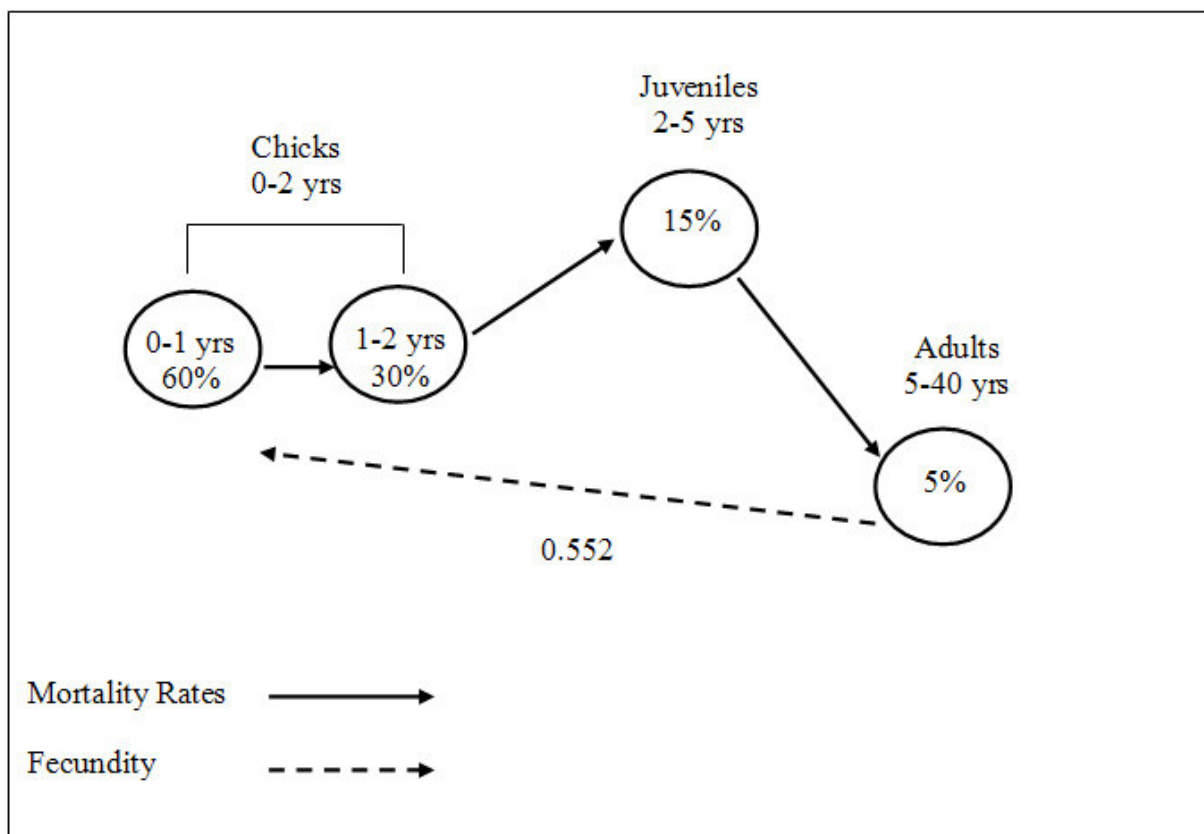
Figure 3. Demographic model used for PVA simulations. Fecundity and annual mortality rates are specified for each class (chicks, juveniles, and adults).

South Population

Northwest Population
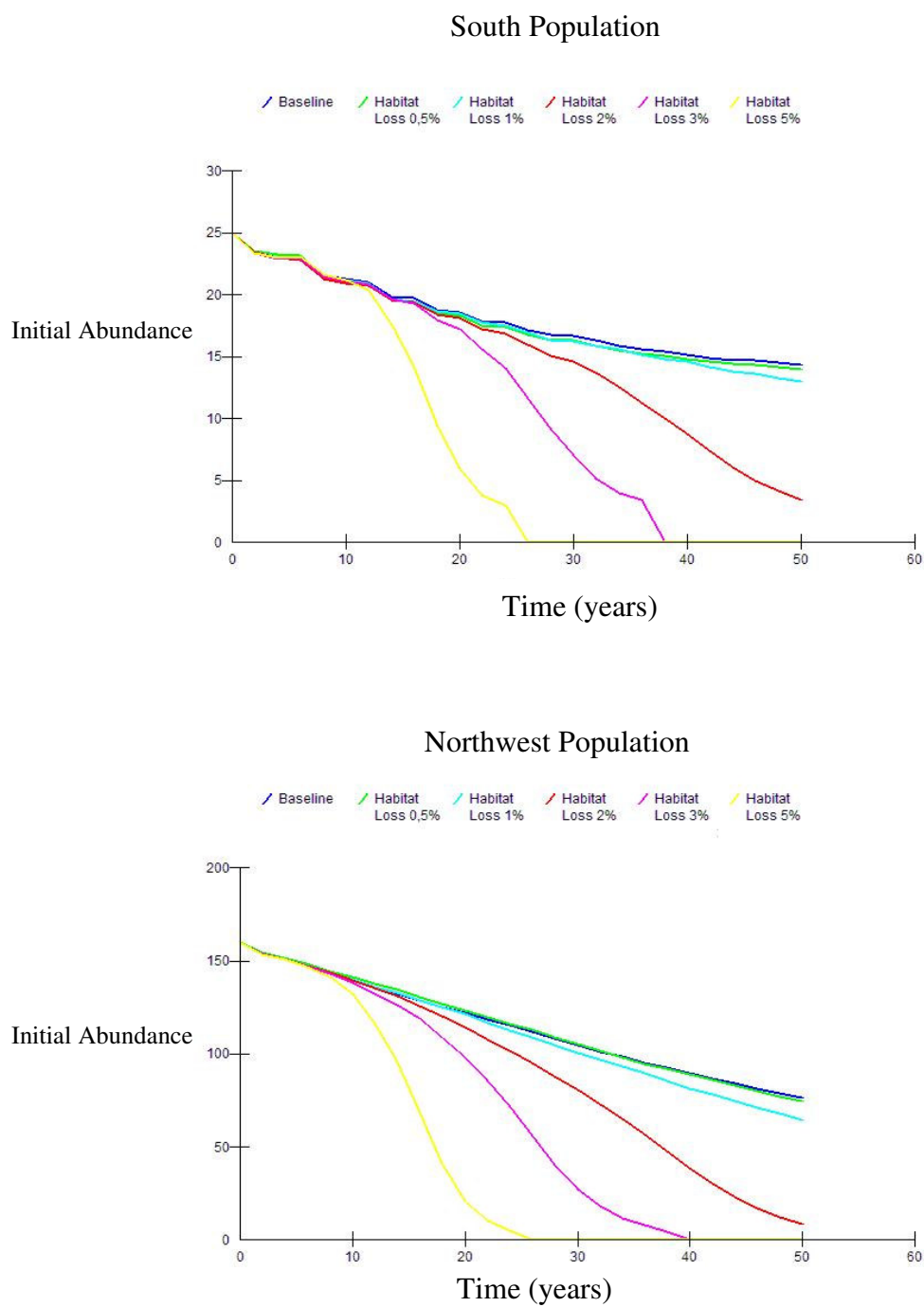
Figure 4. Habitat loss simulations. Lines of different colors represent the mean final abundance of the populations in simulations with different percentages of habitat loss.

South Population

Time (years)

Northwest Population

Time (years)
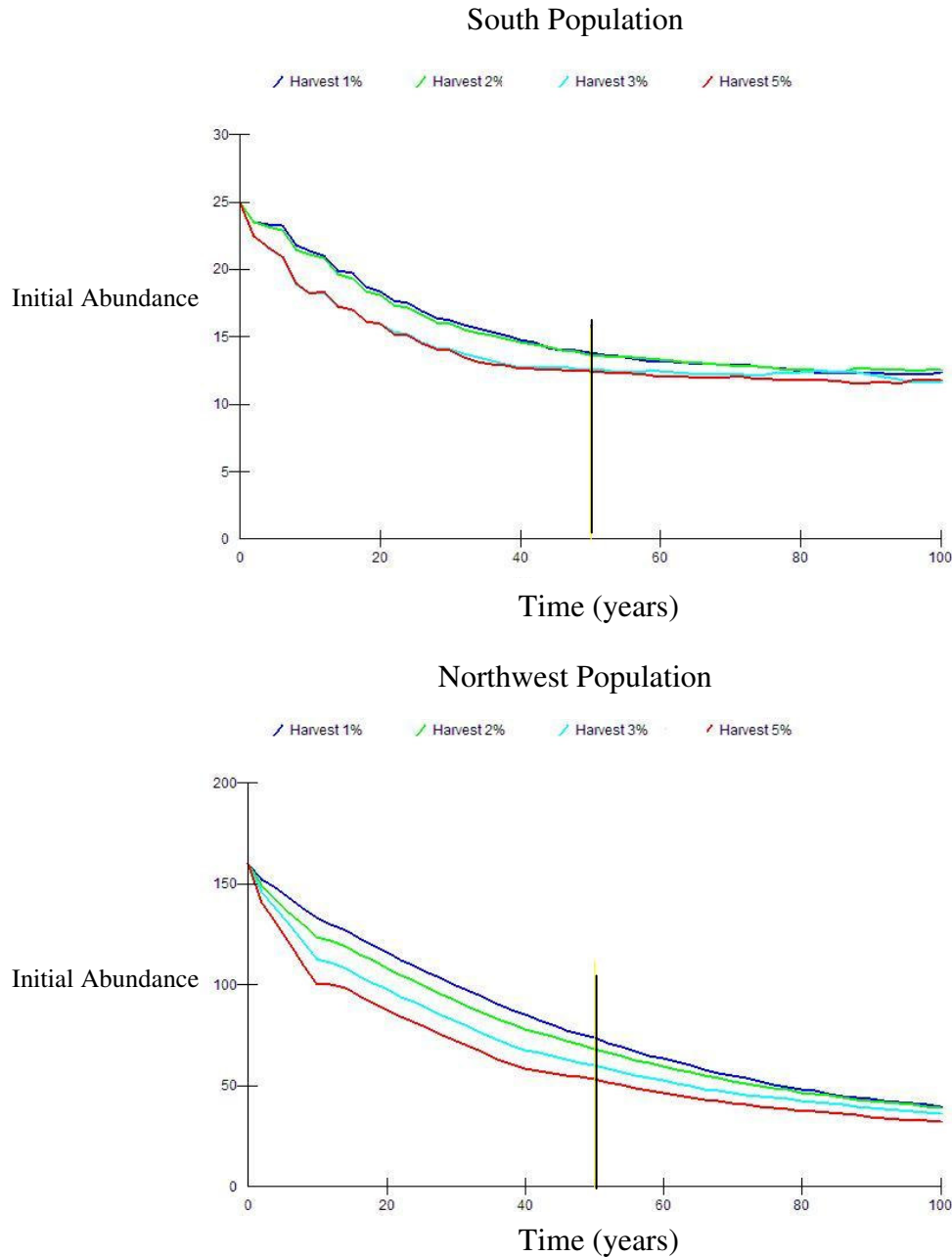
Figure 5. Harvesting simulations. Lines of different colors represent the mean final abundance of the populations in simulations with different percentages of harvesting. The black line represents the division between the 50 and 100-year period, showing that in simulations run over a 50-year period a 3% of harvesting had a significant effect compared with the baseline, but when the simulations were run over a 100-year period, the 3% of harvesting became not significant compared with the baseline.
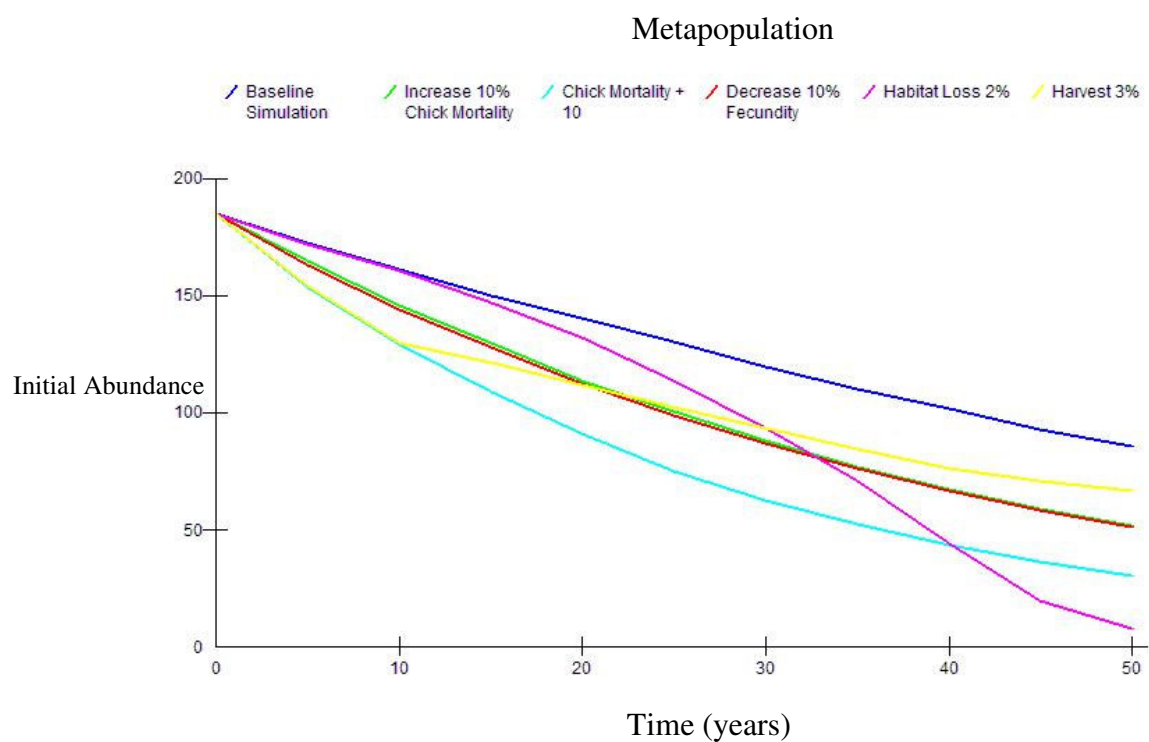
Metapopulation

Figure 6. PVA simulations with greatest effects on the metapopulation risk of decline. Lines of different colors represent the mean final abundance of the metapopulation of different simulations.
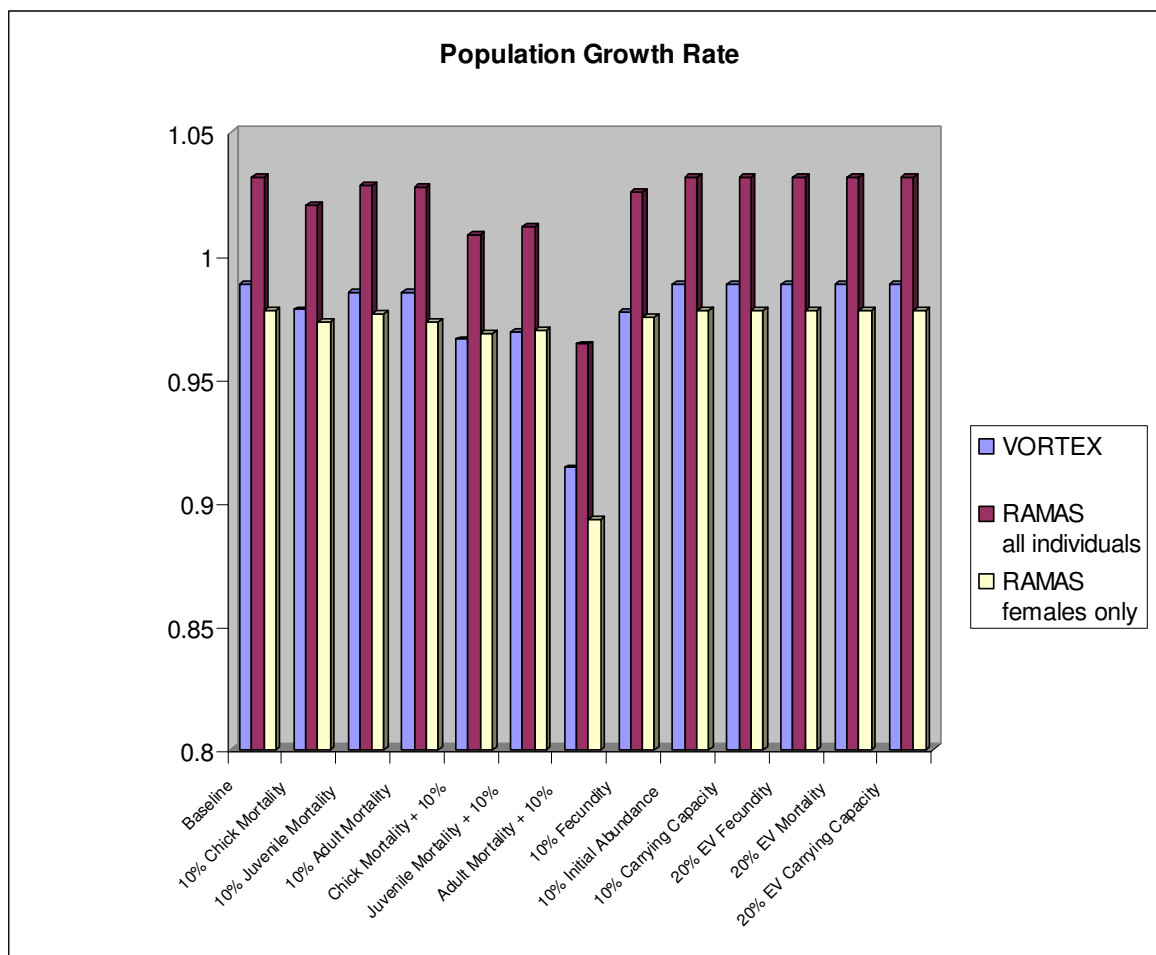
Figure 7. Comparison of the estimates of population growth rate obtained from all the PVA simulations using VORTEX and RAMAS GIS. PVA simulations with RAMAS GIS include simulations run with all individuals as well as females only.
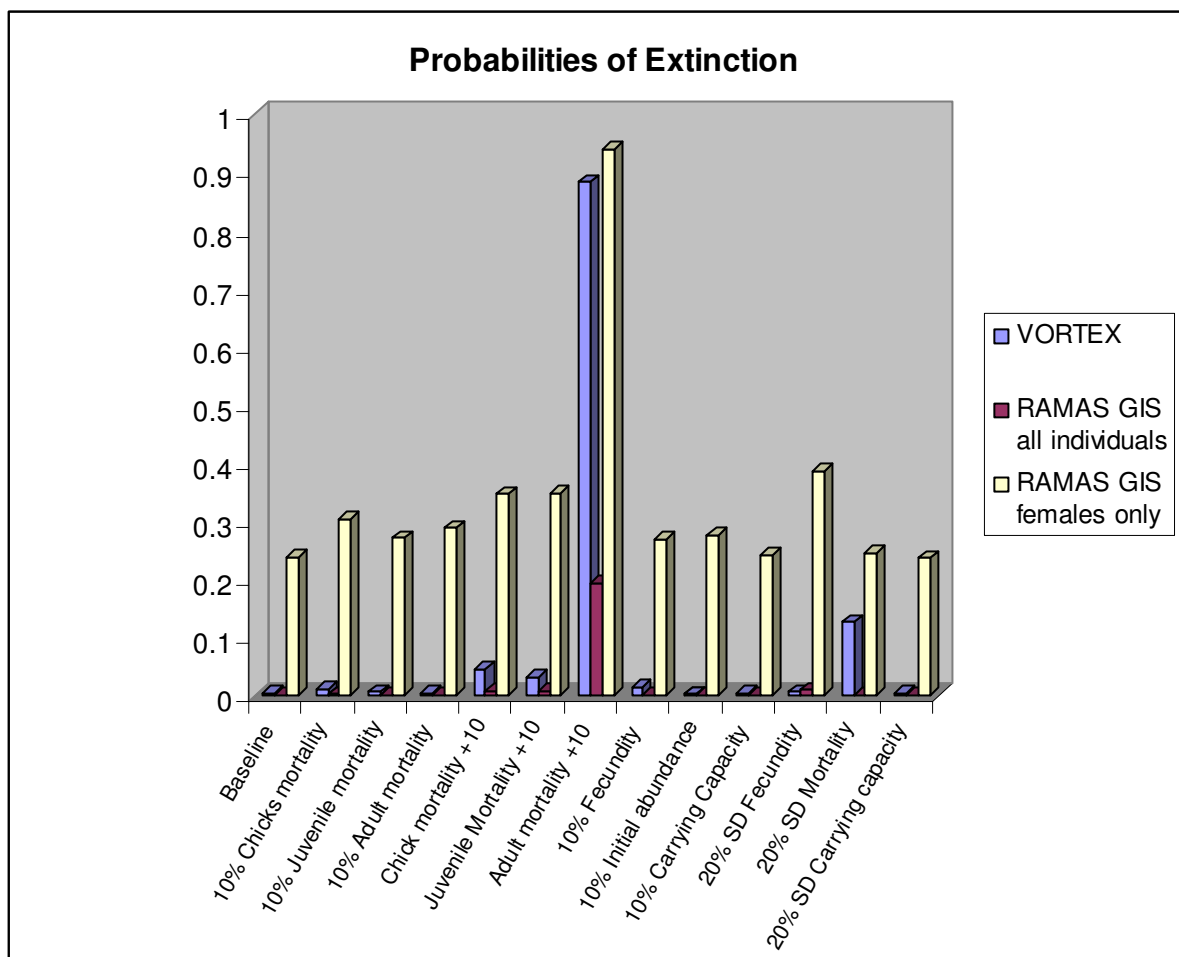
Figure 8. Comparison of extinction probabilities obtained from all PVA simulations using VORTEX and RAMAS GIS. PVA simulations with RAMAS GIS include simulations run with all individuals as well as females only.

TABLES

Table 1. Input data used for the population viability analysis of the Blue-throated Macaw.
Values and annual average rates were obtained from previous studies on the Blue-throated
Macaw or related species within the Psittacidae family.

Parameter	Value	Source
Number of Populations	2	Armonía 2007
Number of iterations	5,000	This study
Number of years	50	This study
Initial abundance	160 NW – 25 S	Armonía 2007; Kyle 2007
Reproductive system	Monogamous	Forshaw 1973; Snyder et al. 2000
Breeding age	5 years	Bueno 2000; Voss 2005.
Maximum breeding age	40 years	This study
Sex ratio	50:50	Bueno 2000
Maximum number of progeny	3	Bueno 2000
% Adults breeding	40	Kyle 2005
Mean number of offspring	1.4	This study
Chicks mortality	0-1=60%; 0-2= 30%	Kyle 2007; This study
Juveniles mortality	15%	This study
Adults mortality	5%	Vaughan et al. 2005
Environmental Variation	10%	This study

Note: Most values used in the model were based on field studies from the Blue-throated Macaw or other
species from the same family with similar natural history. Sex ratio, minimum breeding age and
maximum number of offspring were based on information from a captive population. Values reported in
this study represent assumptions used in the model (see METHODS).

Table 2. Results of the demographic simulations with VORTEX and RAMAS GIS. Population growth rate (λ), probability of extinction (PE), and median time to extinction (mT) are reported for each of the simulations.

Simulations	VORTEX			RAMAS GIS all individuals			RAMAS GIS females only		
	λ	PE	mT	λ	PE	mT	Λ	PE	mT
Baseline	0.988	0.005	0	1.031	0.001	0	0.977	0.238	0
10% Chick Mort.	0.978	**0.011**	0	1.020	**0.002**	0	0.973	**0.303**	0
10% Juvenile Mort.	0.985	0.006	0	1.028	**0.000**	0	0.976	0.271	0
10% Adult Mort.	0.985	0.005	0	1.028	**0.000**	0	0.973	**0.288**	0
Chick Mort. + 10%	0.966	**0.047**	0	1.008	**0.008**	0	0.968	**0.347**	0
Juvenile Mort. + 10%	0.969	**0.031**	0	1.012	**0.008**	0	0.969	**0.349**	0
Adult Mort. + 10%	0.914	**0.884**	38	0.964	**0.195**	0	0.893	**0.941**	28
10% Fecundity	0.977	**0.014**	0	1.025	**0.001**	0	0.975	**0.268**	0
10% I. Abundance	0.988	0.003	0	1.031	0.000	0	0.977	**0.277**	0
10% C. Capacity	0.988	0.005	0	1.031	0.000	0	0.977	0.241	0
20% EV Fecundity	0.988	0.006	0	1.031	**0.009**	0	0.977	**0.387**	0
20% EV Mortality	0.988	**0.127**	0	1.031	**0.001**	0	0.977	0.246	0
20% EV C. Capacity	0.988	0.005	0	1.031	0.000	0	0.977	0.236	0

Mort: Mortality; I. Abundance: Initial Abundance; C. Capacity: Carrying Capacity; EV: Environmental Variation.

Table 3. Kolmogorov-Smirnov test results of the risk of decline between the baseline and each of the PVA simulations reported in this study. Bold values highlight the simulations that were statistically significant.

	VORTEX	RAMAS GIS all individuals	RAMAS GIS females only
10% Chick Mort.	**D=0.380; P=0.001**	**D=0.181; P=0.000**	**D=0.066; P=0.000**
10% Juvenile Mort.	D=0.140; P=0.678	**D=0.038; P=0.002**	D=0.031; P=0.018
10% Adult Mort.	D=0.200; P=0.241	**D=0.040; P=0.001**	**D=0.071; P=0.000**
Chick Mort. +10%	**D=0.580; P=0.000**	**D=0.397; P=0.000**	**D=0.128; P=0.000**
Juvenile Mort. +10%	**D=0.560; P=0.000**	**D=0.338; P=0.000**	**D=0.126; P=0.000**
Adult Mort. +10%	**D=0.840; P=0.000**	**D=0.916; P=0.000**	**D=0.693; P=0.000**
10% Fecundity	**D=0.400; P=0.000**	**D=0.117; P=0.000**	**D=0.059; P=0.000**
10% I. Abundance	D=0.180; P=0.358	D=0.030; P=0.025	**D=0.036; P=0.003**
10% C. Capacity	D=0.040; P=1.000	D=0.022; P=0.194	D=0.015; P=0.661
20% EV Fecundity	D=0.400; P=1.000	**D=0.404; P=0.000**	**D=0.146; P=0.000**
20% EV Mortality	D=0.200; P=0.241	**D=0.047; P=0.000**	D=0.018; P=0.421
20% EV C. Capacity	D=0.100; P=0.954	D=0.014; P=0.677	D=0.017; P=0.465

Table 4. Habitat loss simulation. Population growth rate (λ), probabilities of extinction (PE),

and the median time to extinction (mT) are reported. Bold values show the K-S test results of

the risk of decline from the simulations that were statistically significant compared with the

baseline.

Habitat Loss	λ	PE	mT	K-S test
Baseline	0.988	0.005	0	
0.5%	0.988	0.005	0	D=0.040; P=1.000
1%	0.988	0.003	0	D=0.140; P=0.678
2%	0.988	0.875	47	**D=0.380; P=0.001**
5%	0.988	1.000	21	**D=0.700; P=0.000**

Table 5. Harvesting simulations over 50-year and 100-year periods. Population growth rate (λ), probabilities of extinction (PE), and the median time to extinction (mT) are reported. Bold values show the K-S test results of the risk of decline from the simulations that were statistically significant compared with the baseline.

Simulations	50 years			100 years		
	λ	PE	K-S test	λ	PE	K-S Test
Baseline	0.988	0.005				
1%	0.988	0.003	D=0.0800; P=0.996	0.988	0.187	D=0.0400; P=1.000
2%	0.988	0.007	D=0.2000; P=0.241	0.988	0.210	D=0.0800; P=0.894
3%	0.988	0.010	**D=0.3200; P=0.009**	0.988	0.246	D=0.1700; P=0.099
5%	0.988	0.013	**D=0.4400; P=0.000**	0.988	0.293	**D=0.2500; P=0.003**

Table 6. Kolmogorov-Smirnov test of the risk of decline for the significant PVA simulations. Simulations include: 10% increase in chicks mortality (10% C.M.), increase in adult mortality by an absolute value of 10 (A.M+10), 10% decrease in fecundity (10% F.), 2% increase in habitat loss (H.L. 2%), and 3% increase in harvesting (H. 3%). Bold values show significant simulations (P=0.009).

Simulations	10% C. M.	A. M. +10	10% F.	H. L. 2%
10% C. M.				
A. M. + 10	**D=0.740; P=0.000**			
10% F.	D=0.020; P=1.000	**D=0.740; P=0.000**		
H. L. 2%	D=0.240; P=0.095	**D=0.530; P=0.000**	D=0.240; P=0.095	
H. 3%	D=0.200; P=0.241	**D=0.800; P=0.000**	D=0.200; P=0.241	D=0.300; P=0.017

Table 7. Comparison of extinction probabilities obtained from all PVA simulations using VORTEX and RAMAS GIS.

Simulations	VORTEX	RAMAS GIS All individuals	RAMAS GIS Females only
Baseline	0.005	0.001	0.238
10% Chicks mortality	0.011	0.003	0.303
10% Juvenile mortality	0.006	0.001	0.271
10% Adult mortality	0.005	0.000	0.288
Chick mortality +10	0.047	0.008	0.347
Juvenile Mortality +10	0.031	0.008	0.349
Adult mortality +10	0.884	0.195	0.941
10% Fecundity	0.014	0.001	0.269
10% Initial abundance	0.003	0.000	0.277
10% Carrying Capacity	0.005	0.000	0.241
20% SD Fecundity	0.006	0.009	0.387
20% SD Mortality	0.127	0.001	0.246
20% SD Carrying capacity	0.005	0.000	0.236

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APPENDICES

APPENDIX I

VORTEX input file used for the baseline simulation

EV and SD represent environmental variation and standard deviations, respectively.

Baseline Simulation: 2 population(s) simulated for 50 years, 5000 iterations

  Extinction is defined as no animals of one or both sexes.   No inbreeding depression

  EV in reproduction and mortality will be concordant.

Reproductive System:

       Long term monogamy

       First age of reproduction for females and males: 5

       Maximum breeding age (senescence): 40

       Sex ratio at birth (percent males): 50

Reproductive Rates:

       % of adult males in the breeding pool = 40

       % adult females breeding = 40;   EV: 10%

       mean offspring per year = 1,4;   SD: 0.8

Mortality Rates:

       0-1: 60%;   SD: 10%

       1-2: 30%;   SD: 10%

       2-5: 15%;   SD: 10%

       5-40: 5%;   SD: 10%

Initial Abundance:

       Northwest: 160

       South: 25

Carrying Capacity (Ceiling density dependence):

       Northwest: 400;   EV: 40

       South: 25;   EV: 10

APPENDIX II

RAMAS GIS input file used for the baseline simulation

Input data used for the baseline simulation included a sex structure with all individuals (males and females) as well as with only females.

* **General Information:**

  Title: **Baseline Blue-throated Macaw all individuals mixed**

  Replications: 5000;   Duration: 50 years;   One time step: 1 year

* **Density dependence**

  - Density dependence affects: All vital rates

  - Density dependence (and K) is based on the abundance of: All stages

  - Density dependence type is: Pop-specific.

* **Sex Structure:**

  - Model includes: all individuals (mixed)

  - Sex ratio: 50

* **Stages Matrix:**

  - Fecundity

        Hatching success x Proportion that breed

              1.4   x   0.40   =   0.552

	0-1	1-2	2-3	3-4	4-5	5-40
0-1	0.0	0.0	0.0	0.0	0.0	0.552
1-2	0.4	0.0	0.0	0.0	0.0	0.0
2-3	0.0	0.7	0.0	0.0	0.0	0.0
3-4	0.0	0.0	0.85	0.0	0.0	0.0
4-5	0.0	0.0	0.0	0.85	0.0	0.0
5-40	0.0	0.0	0.0	0.0	0.85	0.95

- **Survival:**

  0-1: 40%; 1-2: 70%

  2-3: 85%; 3-4: 85%

  4-5: 85%; 5-40: 95%

- **SD**:10% Fecundity; 10% Mortality; 10% K;

* **Initial Abundance:** Northwest:160; South:25

***Carrying Capacity - Density Dependence:**

  Northwest: 400; South: 100

RAMAS GIS 4.0 -- Input Data Females Only

* **General Information:**

   Title: **Baseline Blue-throated Macaw Females only**

   Replications: 5000;   Duration: 50 years;   One time step: 1 year

* **Density dependence**

      - Density dependence affects: All vital rates

      - Density dependence (and K) is based on the abundance of: All stages

      - Density dependence type is: Pop-specific.

* **Sex Structure:**

      - Model includes: Females only

      - Sex ratio: 50

* **Stages Matrix:**

   - Fecundity

Sex Ratio	x	Hatching success	x	Proportion that breed		
0.5	x	1.4	x	0.40	=	0.28

	0-1	1-2	2-3	3-4	4-5	5-40
0-1	0.0	0.0	0.0	0.0	0.0	0.28
1-2	0.4	0.0	0.0	0.0	0.0	0.0
2-3	0.0	0.7	0.0	0.0	0.0	0.0
3-4	0.0	0.0	0.85	0.0	0.0	0.0
4-5	0.0	0.0	0.0	0.85	0.0	0.0
5-40	0.0	0.0	0.0	0.0	0.85	0.95

- **Survival:**

    0-1: 40%; 1-2: 70%

    2-3: 85%; 3-4: 85%

    4-5: 85%; 5-40: 95%

- **SD**:10% Fecundity; 10% Mortality; 10% K;

* **Initial Abundance:** Northwest: 80; South: 13

***Carrying Capacity - Density Dependence:**

    Northwest: 400; South: 100

APPENDIX III

VORTEX simulations results reported for each individual population

Results include population growth rate (λ), and probabilities of extinction (PE) and median time to extinction (mT) for the Northwest and South populations of the Blue-throated Macaw.

	λ	Northwest		South	
		PE	mT	PE	mT
Baseline	0.988	0.011	0	0.355	0
10% Chick Mortality	0.978	0.029	0	0.496	0
10% Juvenile Mortality	0.985	0.015	0	0.394	0
10% Adult Mortality	0.985	0.015	0	0.407	0
Chick Mortality + 10	0.966	0.079	0	0.651	42
Juvenile Mortality + 10	0.969	0.057	0	0.616	44
Adult Mortality + 10	0.914	0.890	37	0.996	19
10% Fecundity	0.977	0.034	0	0.496	0
10% Initial Abundance	0.988	0.012	0	0.407	0
10% Carrying Capacity	0.988	0.012	0	0.363	0
20% EV Fecundity	0.988	0.015	0	0.378	0
20% EV Mortality	0.988	0.225	0	0.599	42
20% EV Carrying Capacity	0.988	0.014	0	0.342	0
Habitat Loss 0.5%	0.988	0.013	0	0.353	0
Habitat Loss 1%	0.988	0.011	0	0.364	0
Habitat Loss 2%	0.988	0.899	47	0.973	44
Habitat Loss 5%	0.988	1	20	1	20
Harvest 1%	0.988	0.012	0	0.354	0
Harvest 2%	0.988	0.020	0	0.355	0
Harvest 3%	0.988	0.027	0	0.426	0
Harvest 5%	0.988	0.032	0	0.415	0
Harvest 1% 100 years	0.988	0.234	0	0.806	62
Harvest 2% 100 years	0.988	0.264	0	0.805	62
Harvest 3% 100 years	0.988	0.298	0	0.831	57
Harvest 5% 100 years	0.988	0.346	0	0.848	55

Appendix IV

RAMAS GIS elasticity analysis

EIGENANALYSIS obtained from the baseline simulation. Numbers in bold show the population growth rate and the age-class that contribute the most to this value.

Baseline Blue-throated Macaw; 2 populations: 5000 replications; Duration = 50

==

Stage matrix (default):

	1	2	3	4	5	6
1:	0.0000	0.0000	0.0000	0.0000	0.0000	0.1430
2:	0.4000	0.0000	0.0000	0.0000	0.0000	0.0000
3:	0.0000	0.7000	0.0000	0.0000	0.0000	0.0000
4:	0.0000	0.0000	0.8500	0.0000	0.0000	0.0000
5:	0.0000	0.0000	0.0000	0.8500	0.0000	0.0000
6:	0.0000	0.0000	0.0000	0.0000	0.8500	0.9500

Growth rate (lambda) = *0.9775* (approximate)

Stage	Init. distr.	Stable distr.	Reprod. Value	Avg. residence
1	0.077	0.111	1.000	1.00
2	0.077	0.045	2.444	1.00
3	0.000	0.033	3.413	1.00
4	0.000	0.028	3.925	1.00
5	0.000	0.025	4.514	1.00
6	0.846	0.758	5.191	20.00

Elasticities: (approximate)

	1	2	3	4	5	6
1:	0.0000	0.0000	0.0000	0.0000	0.0000	0.0247
2:	0.0247	0.0000	0.0000	0.0000	0.0000	0.0000
3:	0.0000	0.0247	0.0000	0.0000	0.0000	0.0000
4:	0.0000	0.0000	0.0247	0.0000	0.0000	0.0000
5:	0.0000	0.0000	0.0000	0.0247	0.0000	0.0000
6:	0.0000	0.0000	0.0000	0.0000	0.0247	*0.8518*

Sensitivities: (approximate)

	1	2	3	4	5	6
1:	0.0247	0.0101	0.0072	0.0063	0.0055	0.1688
2:	0.0603	0.0247	0.0177	0.0154	0.0134	0.4126
3:	0.0843	0.0345	0.0247	0.0215	0.0187	0.5762
4:	0.0969	0.0397	0.0284	0.0247	0.0215	0.6627
5:	0.1115	0.0456	0.0327	0.0284	0.0247	0.7621
6:	0.1282	0.0525	0.0376	0.0327	0.0284	0.8765

APPENDIX V

Comparison of baseline simulations using VORTEX and RAMAS GIS programs

The table shows the baseline simulation run with different number of iterations for a period of 25, 50, and 100 years. Population growth rate (λ), probability of extinction (PE), and the K-S test comparison between different numbers of iterations are shown.

	Years	Iterations	λ	PE	5000	10000
VORTEX	25	1000	0.988	0.000	D=0.040; P=1.000	D=0.040; P=1.000
		5000	0.988	0.000		D=0.040; P=1.000
		10000	0.988	0.000		
	50	1000	0.988	0.006	D=0.040; P=1.000	D=0.060; P=1.000
		5000	0.988	0.004		D=0.040; P=1.000
		10000	0.988	0.003		
	100	1000	0.988	0.200	D=0.060; P=0.992	D=0.070; P=0.961
		5000	0.988	0.176		D=0.020; P=1.000
		10000	0.988	0.178		
RAMAS GIS females only	25	1000	0.977	0.016	D=0.032; P=0.368	D=0.032; P=0.299
		5000	0.977	0.020		D=0.018; P=0.224
		10000	0.977	0.019		
	50	1000	0.977	0.222	D=0.038; P=0.189	D=0.023; P=0.741
		5000	0.977	0.294		D=0.036; P=0.000
		10000	0.977	0.245		
	100	1000	0.977	0.720	D=0.043; P=0.097	D=0.037; P=0.175
		5000	0.977	0.700		D=0.010; P=0.899
		10000	0.977	0.709		

	Years	Iterations	λ	PE	5000	10000
RAMAS GIS all individuals	25	1000	1.0.31	0.001	D=0.047; P=0.048	D=0.047; P=0.036
		5000	1.0.31	0.000		D=0.012; P=0.742
		10000	1.0.31	0.000		
	50	1000	1.0.31	0.001	D=0.038; P=0.189	D=0.023; P=0.742
		5000	1.0.31	0.000		D=0.036; P=0.000
		10000	1.0.31	0.000		
	100	1000	1.0.31	0.002	D=0.043; P=0.097	D=0.037; P=0.175
		5000	1.0.31	0.002		D=0.010; P=0.899
		10000	1.0.31	0.002		

APPENDIX VI

Comparison of baseline simulations using VORTEX and RAMAS GIS programs

Standard errors (SE; VORTEX) and 95% confidence intervals (CI; RAMAS GIS) estimated for the probability of Extinction (PE) are shown for the simulations run with different number of iterations for a period of 25, 50, and 100 years.

Years	Iterations	VORTEX PE	SE	RAMAS GIS females only PE	95% CI	RAMAS GIS all individuals PE	95% CI
25	1000	0.000	0.000	0.016	0.000-0.044	0.001	0.000-0.029
	5000	0.000	0.000	0.020	0.008-0.033	0.000	0.000-0.013
	10000	0.000	0.000	0.019	0.010-0.028	0.000	0.000-0.009
50	1000	0.006	0.002	0.222	0.194-0.250	0.001	0.000-0.029
	5000	0.004	0.001	0.295	0.241-0.266	0.000	0.000-0.013
	10000	0.003	0.001	0.245	0.236-0.254	0.000	0.000-0.009
100	1000	0.200	0.013	0.720	0.692-0.748	0.002	0.000-0.030
	5000	0.176	0.005	0.701	0.688-0.713	0.002	0.000-0.015
	10000	0.178	0.004	0.709	0.701-0.718	0.002	0.000-0.011

APPENDIX VII

Additional figures of each group of simulations run with VORTEX

VORTEX figures show the metapopulation mean final abundance. Lines of different colors
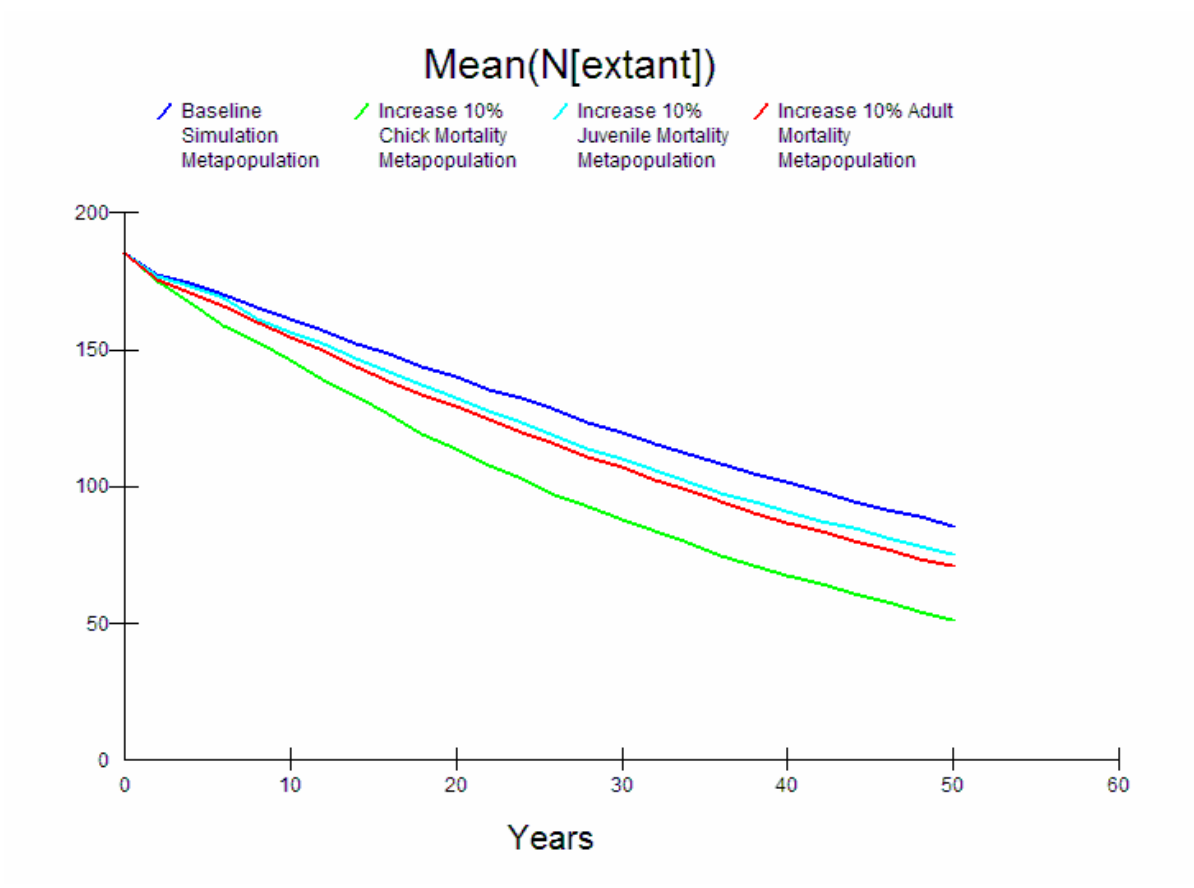
represent each of the simulations.

10% Increase of Mortality Rates
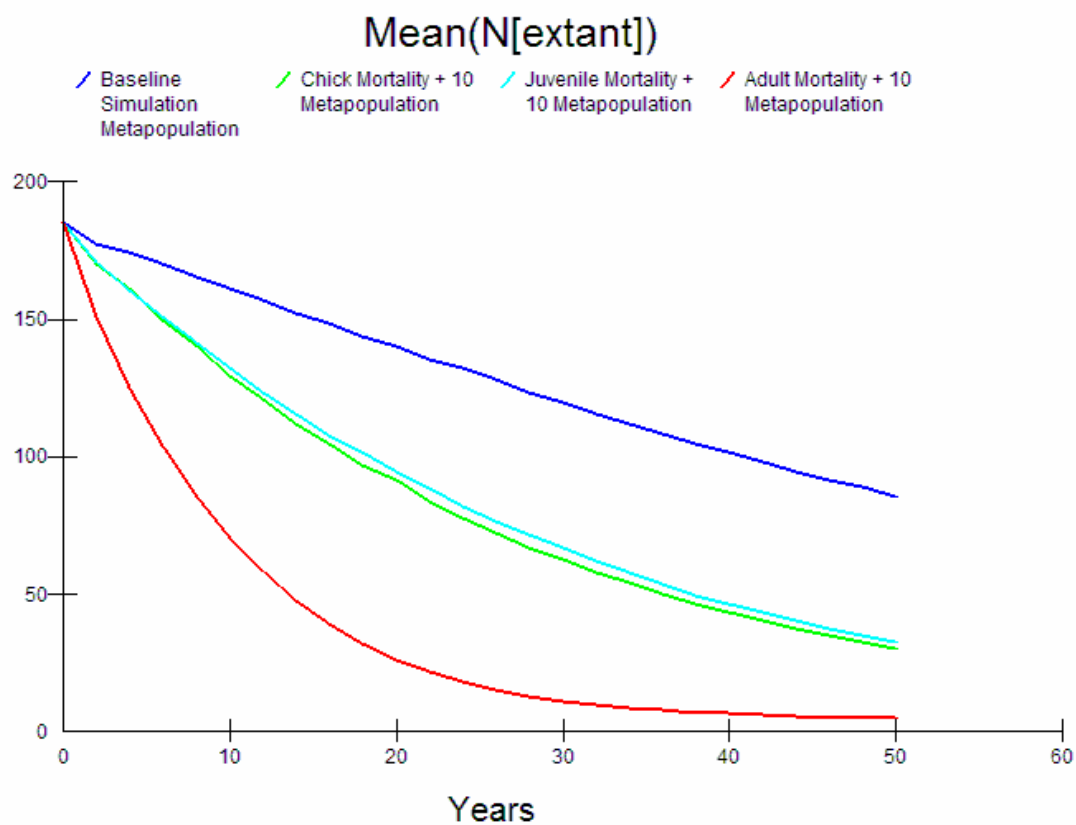
Increase Mortality Rates by an absolute Value of 10%
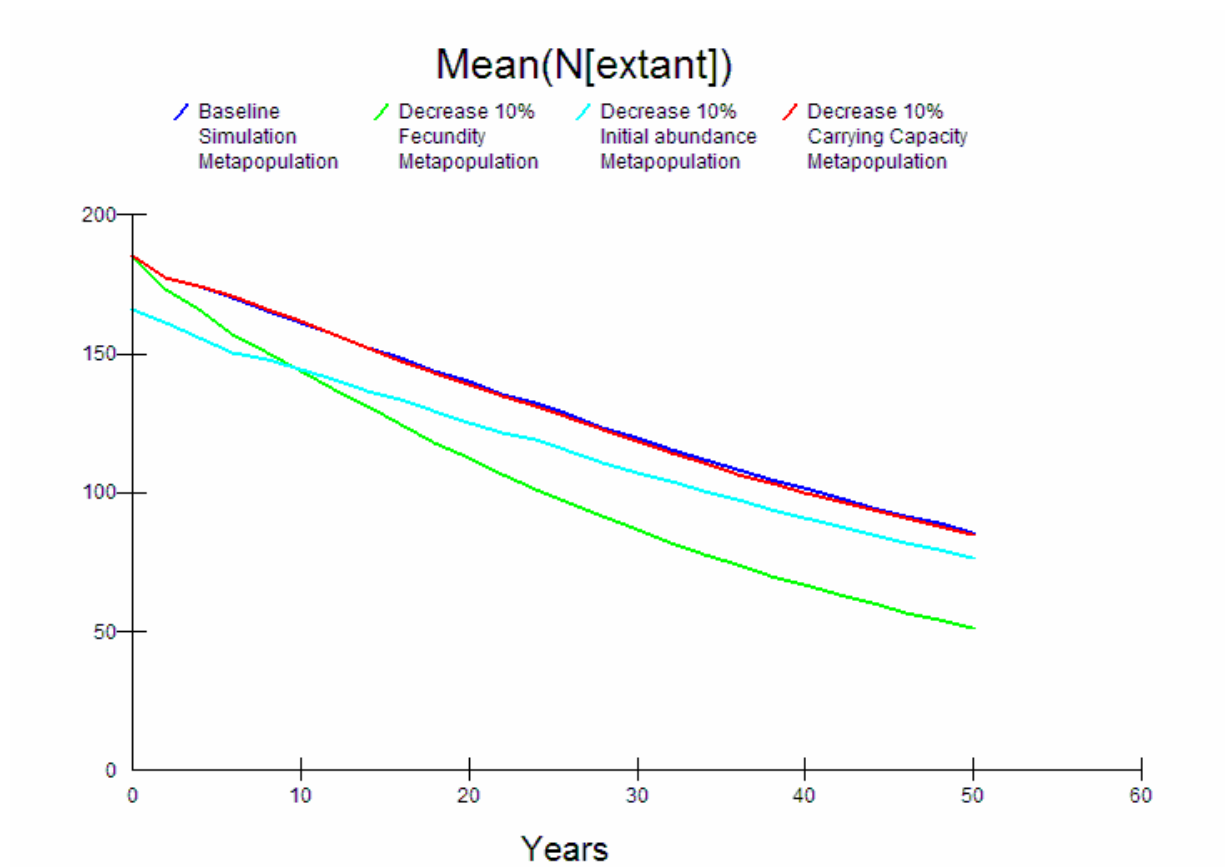
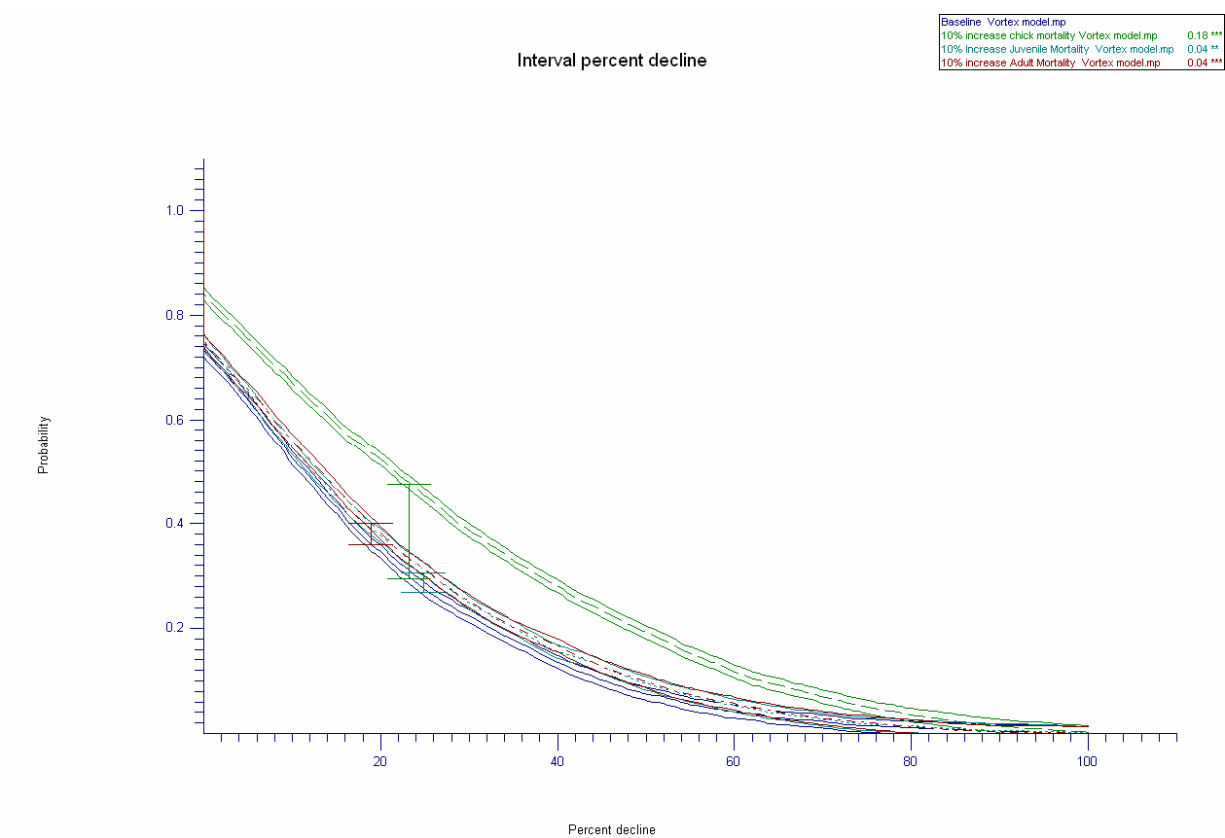10% Decrease in Fecundity, Initial abundance and Carrying Capacity
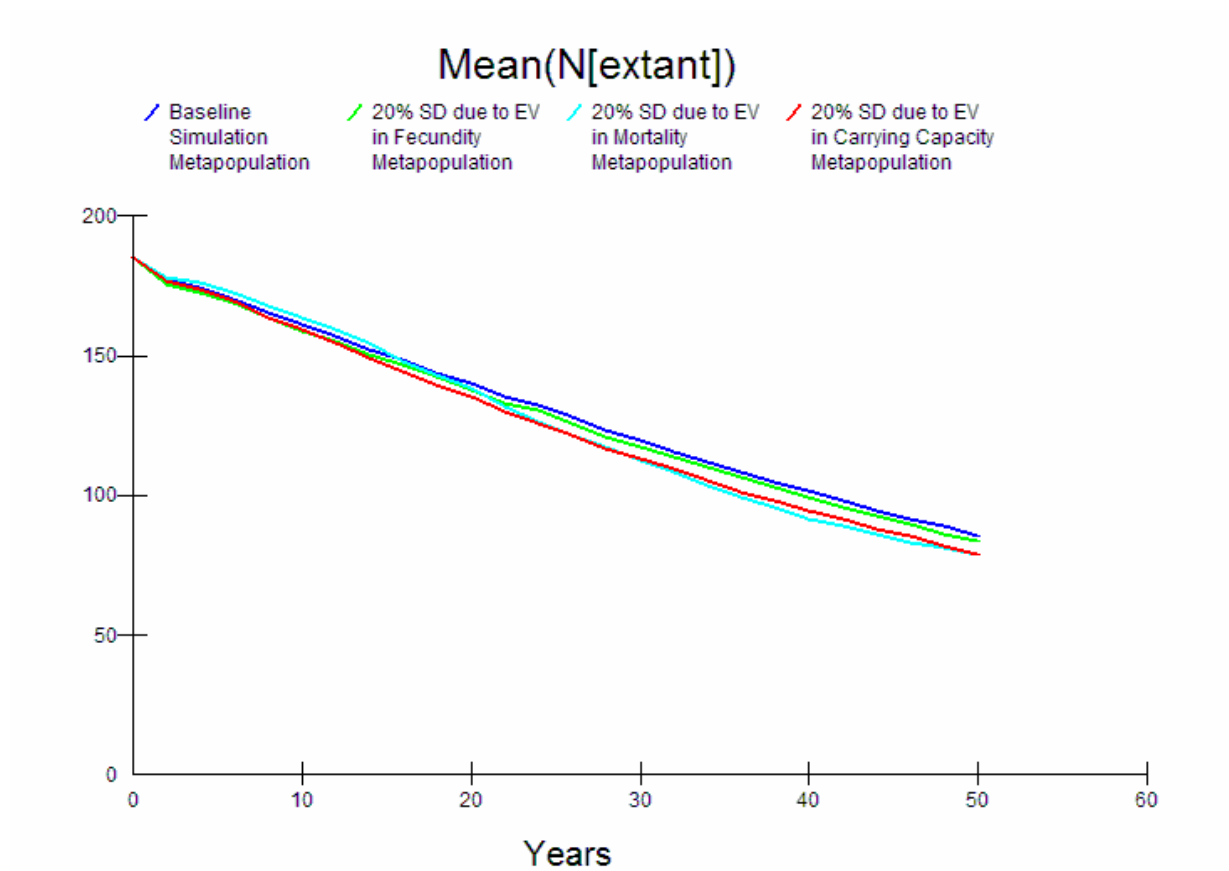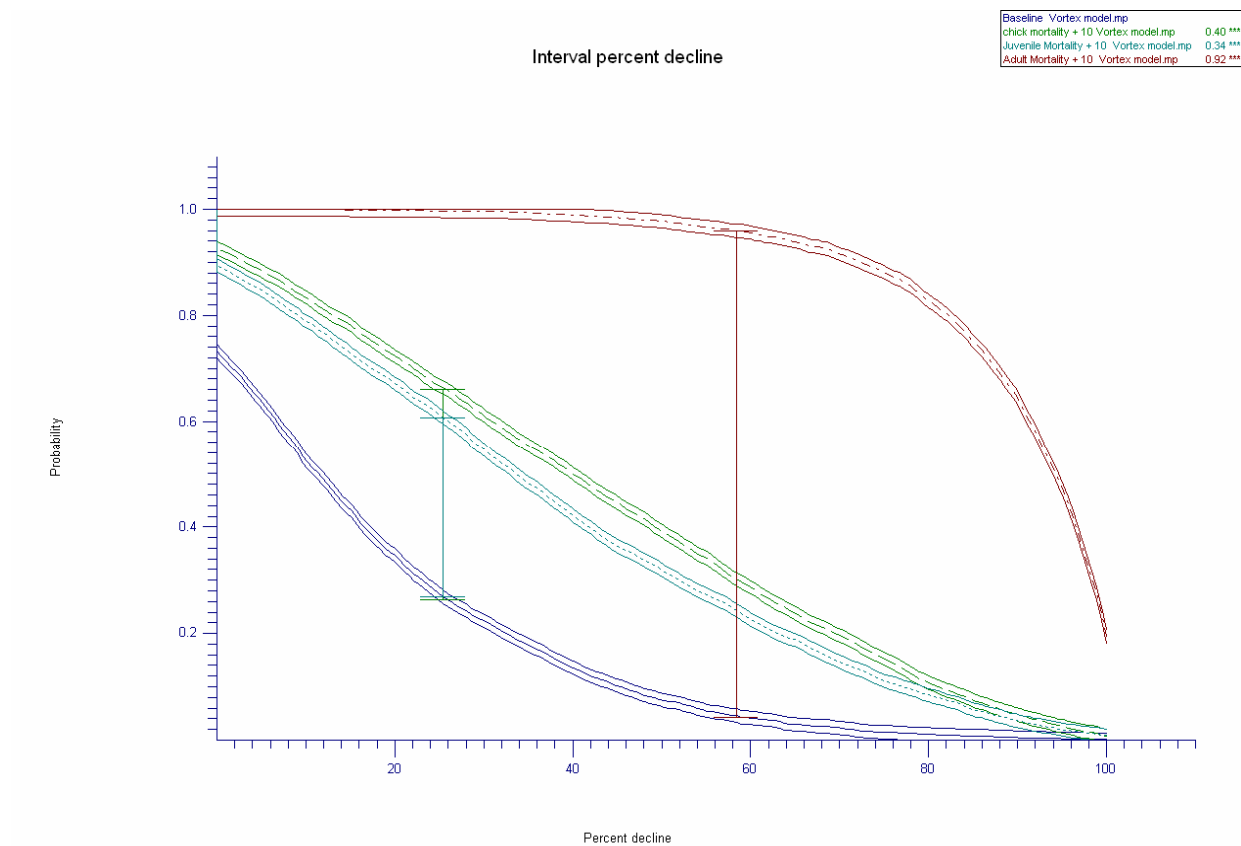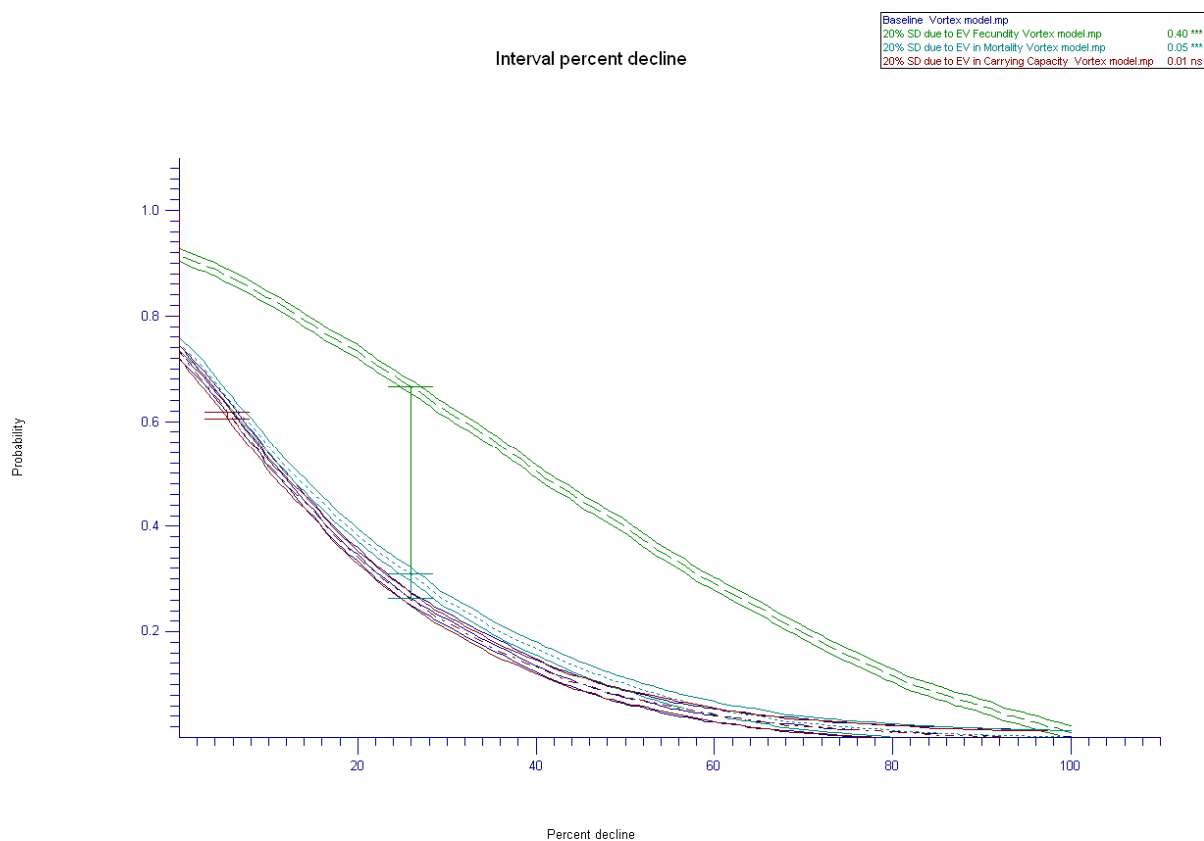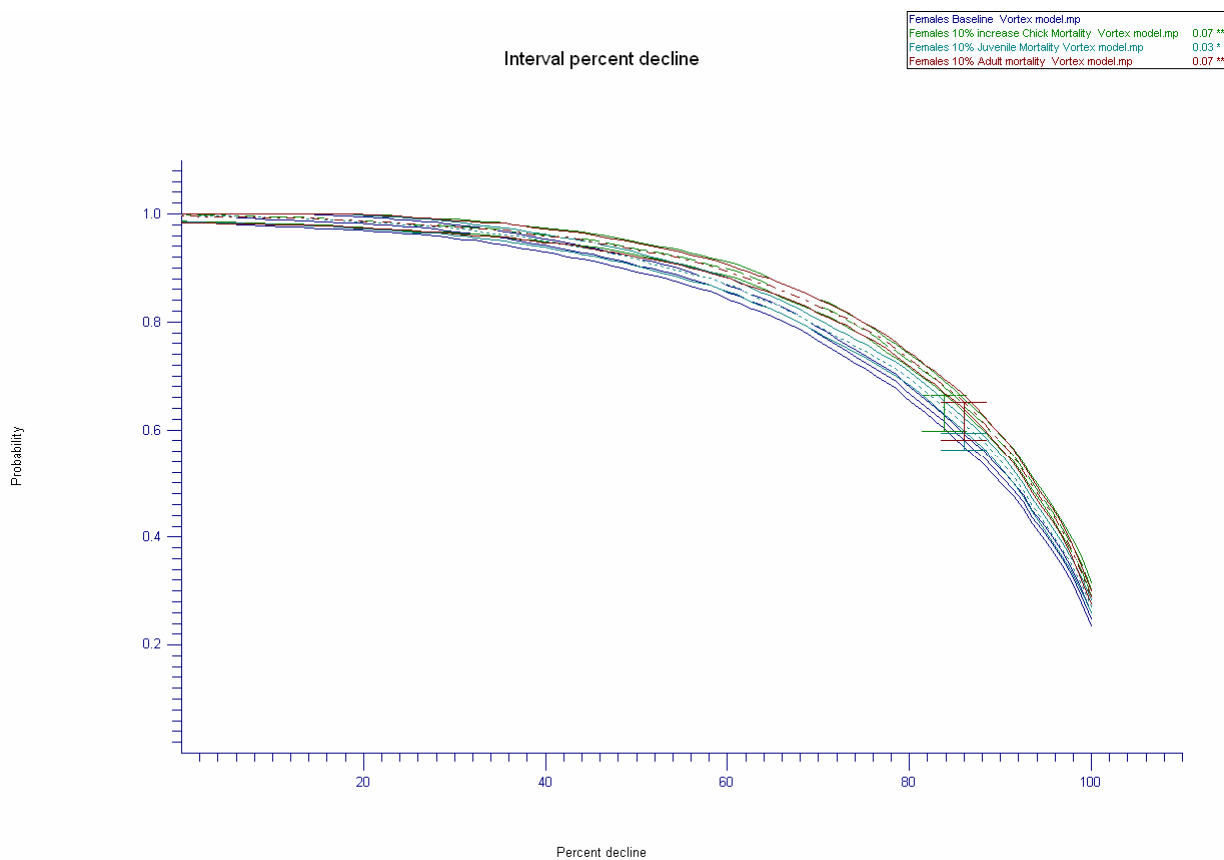
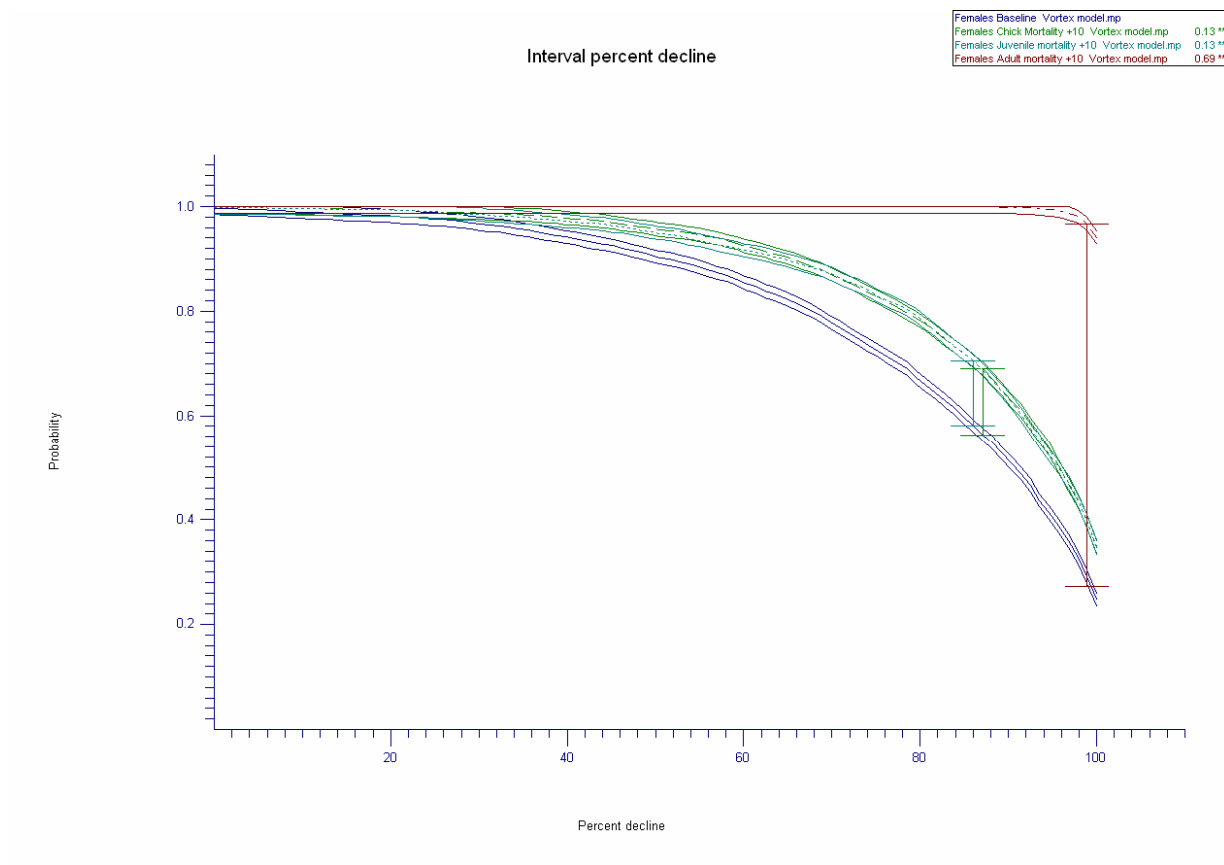20% of Standard Deviation due to Environmental Variation

APPENDIX VIII

Additional figures of each group of simulations run with RAMAS GIS using all individuals

RAMAS GIS figures with a sex structure of all individuals show the metapopulation interval

percent of decline. Lines of different colors represent each of the simulations.

10% Increase of Mortality Rates

Increase Mortality Rates by an absolute Value of 10%
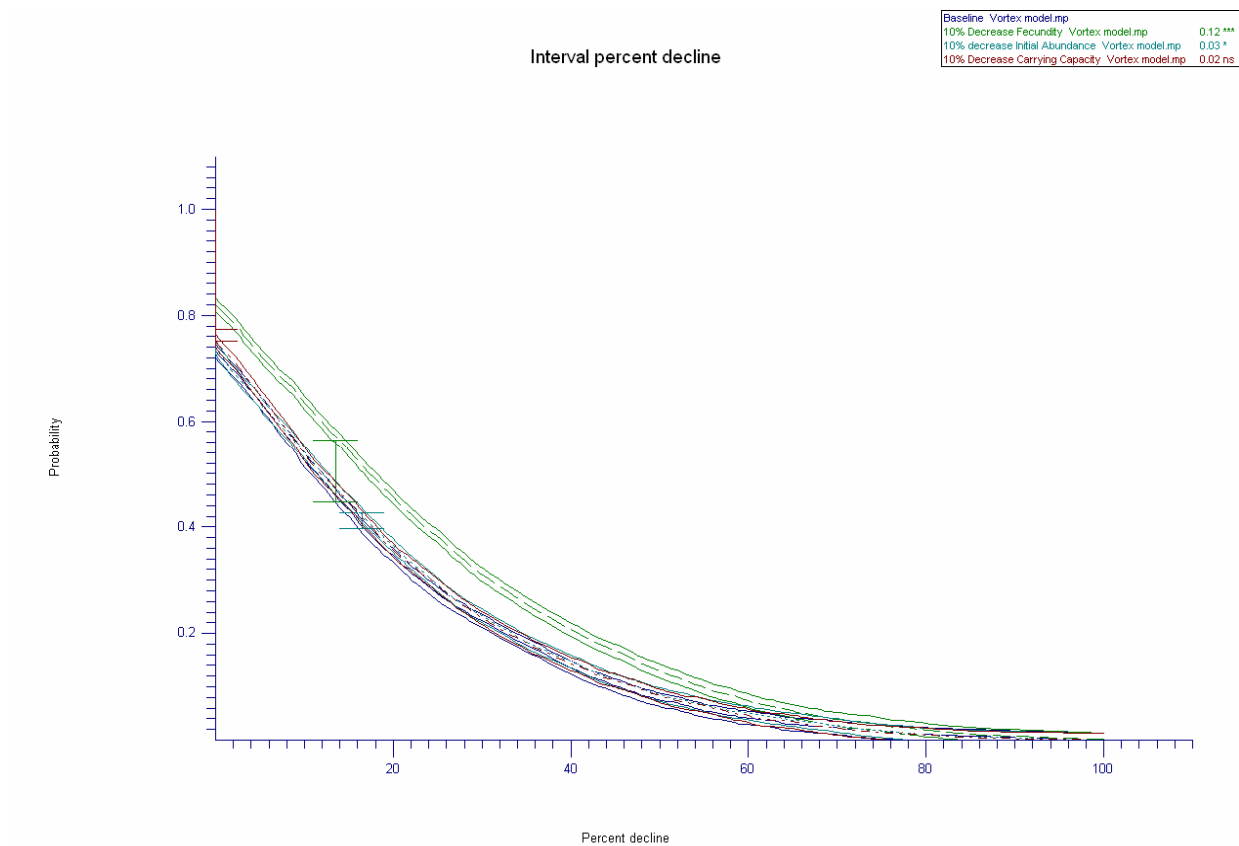
10% Decrease in Fecundity, Initial abundance and Carrying Capacity

20% of Standard Deviation due to Environmental Variation

APPENDIX IX

Additional figures of each group of simulations with RAMAS GIS using only females
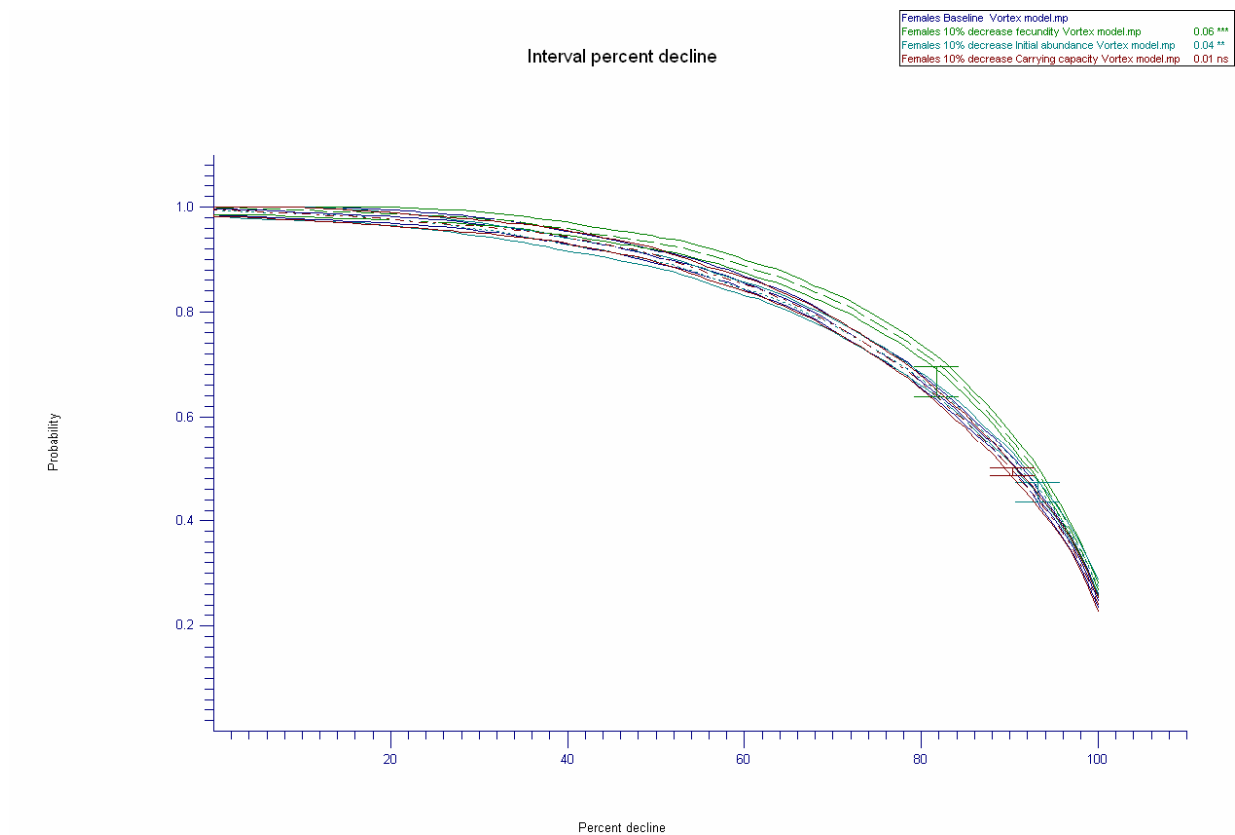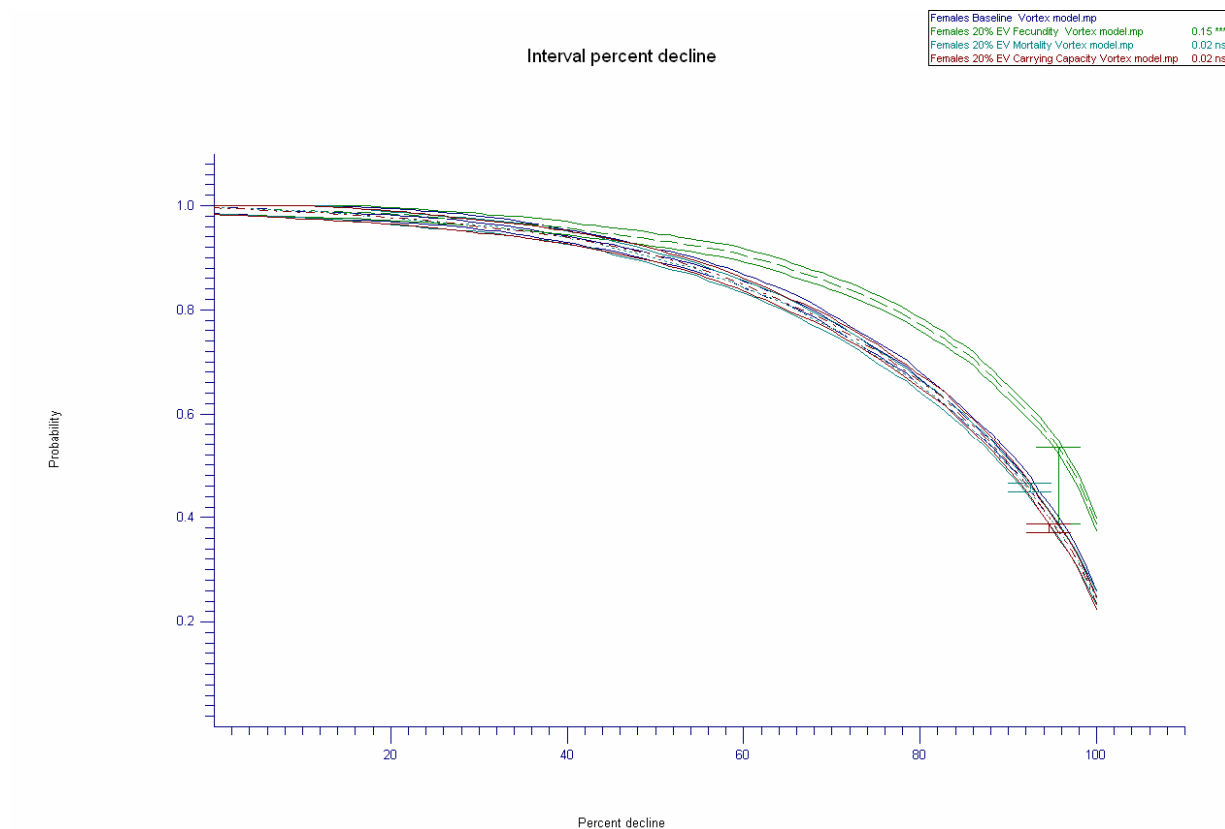
RAMAS GIS figures with a sex structure of only females show the metapopulation interval
percent of decline. Lines of different colors represent each of the simulations.

10% Increase of Mortality Rates

Increase Mortality Rates by an absolute Value of 10%

Interval percent decline

10% Decrease in Fecundity, Initial abundance and Carrying Capacity

20% of Standard Deviation due to Environmental Variation