# 7.0 POPULATION VIABILITY ANALYSIS (PVA) AND VORTEX MODELING

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## 7.1 Introduction

These scenarios model the population(s) of scarlet macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve (MBR). Studies support the contention that this subspecies is morphologically and genetically distinct from *A. m. macao* that is present in South America and southern Central America (Wiedenfeld 1994, K. Schmidt and G. Amato, unpublished data). Although the nominate subspecies is listed as Least Concern by IUCN, *A. m. cyanoptera* has been proposed for Endangered status and will likely qualify. *A. m. cyanoptera* is currently known to occur in Mexico, Guatemala, and Belize. The largest and best known breeding population occurs in the Petén of Guatemala, where the Wildlife Conservation Society (WCS) has been working to conserve scarlet macaws since 2001. Most of the data used to set values for model parameters are based on information collected by WCS Guatemala and national partners.

## 7.2 Baseline Scenario Settings:

In addition to the narrative below, a summary table with values for deterministic r, stochastic r, final population size, and probability of extinction for each scenario is included at the end of this document (Appendices 7-1 and 7-2). A spreadsheet documenting parameters for all the runs is included in the report CD as a file name "Ara PVA ver2.xls" and a printout of that Excel file is attached as the second Appendix.

Number of Populations: One population was simulated for 100 years, 500 iterations. For the baseline model, we assume that there is only one population, i.e. that birds in the three range countries can/do traverse the MBR for complete gene flow among disjunct areas. Genetic data to date indicate that birds from Guatemala are not genetically distinct from birds in Mexico and Belize (K. Schmidt and G. Amato, unpublished data). Extinction was defined as no animals of one or both sexes. There was assumed to be no inbreeding depression as genetic studies to date have found a high level of heterozygosity among mitochondrial haplotypes of wild birds ($H_d$ = 0.911; K. Schmidt and G. Amato, unpublished data).

Reproduction: Scarlet macaws are assumed to have a long-term monogamous pair bond with 100% of adult males participating in breeding. Based on input from aviculturists, the sex ratio at birth is assumed to be 50:50 and the age of first reproduction for females and males is six years. Based on published values for captive macaws (Brouwer et al. 2000) and input from field biologists, the maximum breeding age (senescence) was set at 25 years. Based on field data from Guatemala, the average percentage of adult females breeding successfully was 52% with a standard deviation of 16% (based on 79 nests at two sites over four years). These data, however, are based solely on protected nests and are likely an overestimate as many nests in the population are unprotected and subject to poaching. A revised estimate of 30% success was calculated based on the following assumptions: 1) Approximately 77% of nests in Guatemala (34/44) are

protected (with a breeding success of 52%), 2) of the remaining nests in Guatemala, Mexico, and Belize, roughly half are unprotected (subject to poaching), and 3) poaching results in 0% breeding success. Based on field data from Guatemala, of those females producing progeny, 76% produce one chick, 23% produce two chicks, and 1% produce three chicks in an average year (back-calculated from productivity of 104 nests from seven sites over five years). Both field and captive data previously supported the maximum number of successfully fledged progeny as two, but new observations from the field have documented that broods of three, while rare, do occur (WCS Guatemala, unpublished data); as many as four chicks may hatch.

Mortality: Males and females are assumed to have identical mortality schedules with average first year mortality at 35% and environmental variation (EV) of 5%. Birds between 1-2 and 2-3 years are assumed to have a mortality rate of 10% and EV of 3%. Thereafter birds are assumed to have a mortality rate of 5% with an EV of 2%. These data are largely guesstimates, though probably realistic ones. The only available data come from captive scarlet macaws released in Costa Rica and Peru (Brightsmith et al. 2005), where first year survivorship averaged 75% (mortality = 25%, range 8-40%) and post-first year survivorship was 96% (mortality = 4%). Even the author of these published values, who was present at the meeting, thought that they might be a little optimistic for wild birds. Environmental variation in mortality was assumed to be concordant among age-sex classes but independent from EV in reproduction.

Population size, structure, and carrying capacity: Initial population size was set at 354 based on habitat modeling that predicted the remaining extent of nesting habitat based on characteristics of sites currently in use by breeding birds (WCS Guatemala and CEMEC[1], unpublished data). This number only represents the potential number of breeding birds, but the history of poaching in the area and documentation of suitable, unoccupied nesting cavities suggests that a significant non-breeding population is unlikely. This number could also be interpreted to represent the carrying capacity for the breeding population rather than the existing population, but to avoid artificially constraining population growth in the model, carrying capacity was set at 1200 with an EV of 120 (10%). In the baseline model, it is further assumed that carrying capacity does not change in the future, i.e., the Guatemalan National Park Service (CONAP) and partners such as WCS Guatemala are able to hold the line on habitat destruction in the MBR. The population is assumed to not have a stable age structure, given the long history of poaching that has likely suppressed recruitment. The baseline model presents a scenario where individuals are present in all age classes but the distribution is skewed towards older individuals.

Catastrophes: Six diseases were identified as being of sufficient risk to screen birds in the event of any attempt at population augmentation: *Polyomavirus*, psitticine beak and feather disease (PBFD), psitticine *Herpes* 3, PMV 1 (Newcastle's), *Chlamydia*, and *Salmonella*. Because of the prevalence of both poultry and captive psitticines in the region, these diseases have the potential for introduction into wild populations whether or not augmentation is attempted and so can be considered potential catastrophes. However, with the exception of PMV 1 (severity of effects on survival 0.25, i.e. only 25% of birds survive), all diseases have low rates of infection, morbidity, and mortality of adults; two have no effect on survival (*Polyomavirus* and *Herpes* 3, severity = 1.0) and the other three have a minimal effect on survival (severity = 0.9). Effects on reproduction are also most severe for PMV 1 (severity = 0.1). Chicks are disproportionately

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[1] CEMEC is the Center of Monitoring and Evaluation of the Guatemalan National Park Service, CONAP

affected in PBFD (severity of effects on reproduction = 0.75) but reproductive effects in other diseases are minimal (severity = 0.9). For this reason, the baseline model was simplified to only include PMV 1 with a frequency of 1% (one disease event every 100 years).

Harvesting, supplementation, genetic management: The baseline model assumes no harvesting as the effects of poaching are taken in to consideration as reduced nesting success. The baseline also assumes no supplementation. Genetic management is not necessary due to high heterozygosity.

## 7.3 Results of the Baseline Scenario

Deterministic calculations: Deterministic projections show rates of population growth in the absence of any stochastic fluctuations (changes in population associated with random events). As a result, they are a good indication of whether or not rates of reproduction and survival are sufficient to allow populations to persist under the best of conditions, since stochastic events (such as catastrophes) tend to depress population growth. The deterministic rate of exponential growth for the baseline scenario is slightly negative ($r = -0.002$), indicating that the population is unsustainable and will decline gradually over time.

Stochastic calculations: In the real world, rates of reproduction and survival are not uniform from year to year, and particularly in small populations, a bad year or years can put a population in a tailspin. As expected, rates of population growth are lower under a stochastic model ($r = -0.017 \pm 0.162$). Because the baseline model assumes an age structure biased towards older birds, there is a rapid drop in population size during the first seven years which then tapers off to a very gradual decline (Figure 7-1). Because the population growth rate is negative, the population will eventually go extinct, but it will take a very long time (hundreds of years). Within the 100 year time frame, the probability of extinction is 12.4% ($\pm1.5\%SE$). Various assumptions associated with the model are evaluated below.



Figure 7-1
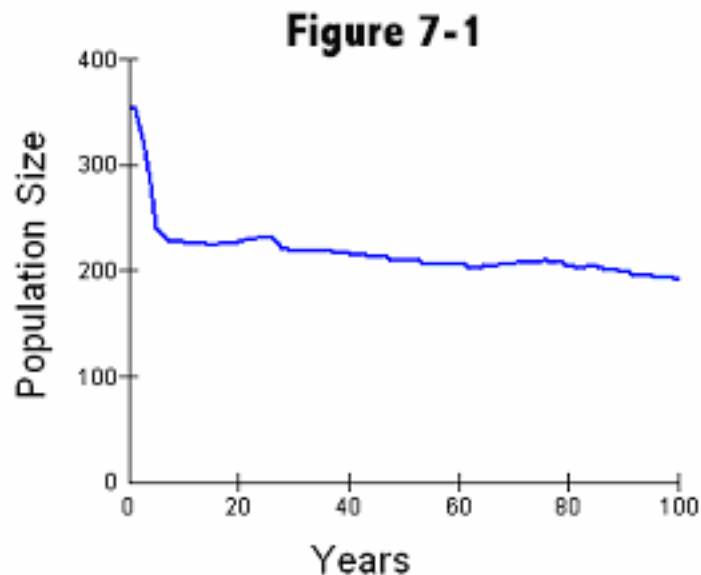
**7.4 Effect of Population Age Distributions**

One of the major uncertainties of the baseline model is the age distribution of the population. While we can be virtually certain that poaching has significantly reduced recruitment into the population and that the population lacks a stable age distribution, there are no data to indicate the true structure of the distribution. The baseline model (weighted towards older age classes) was compared to a stable age distribution (weighted towards younger age classes, representing normal recruitment into the population) and a uniform distribution which assumes equal numbers of individuals in each age class.

The effect of assuming a stable age distribution (normal recruitment) is that the extinction rate is halved ($6.0\%\pm1.1\%SE$) and the population declines less rapidly ($r = - 0.010\pm0.152$). The most significant difference between a stable and unstable age distribution is that the initial rapid drop in population size is lost and as a result the population is maintained at a higher level (Figure 7-2). This means that even if protection efforts effectively "hold the line" on poaching and other non-natural sources of mortality, a significant population decrease could occur in the next decade; whether a decline occurs and the size of the drop will depend on the true age structure of the population. It is likely that the production of offspring from protected nests since 2001 has already begun to restore a stable age distribution.



**Figure 7-2**
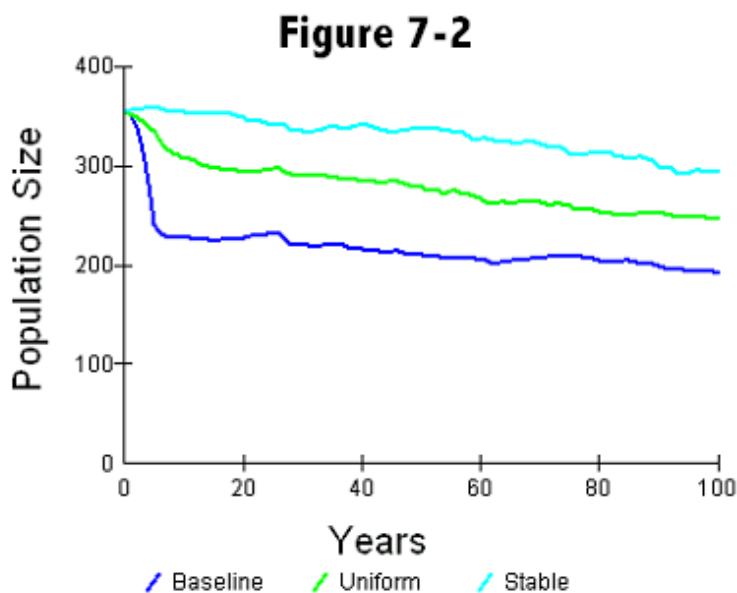
**7.5 Effect of Population Size**

The habitat modeling performed by WCS predicts a nesting population of 354 birds in the tri-national area including the Maya Biosphere Reserve in Guatemala, Montes Azules of Mexico, and the Chiquibul area of Belize. Extrapolating from 29 known nests in Guatemala, we assume a

population of roughly 150 birds in this area. Based on field observations reported by Mark McReynolds, we have assumed a minimum estimate of 100 birds in Belize. The remaining 100 birds are assumed to be in Mexico. It should be noted, however, that modeling only predicts the number of birds that *could* be present based on habitat; there is no guarantee that the model is equally representative of all three countries included or that the habitat is actually full, and thus the population size could be smaller or larger than predicted.

The baseline model was compared to scenarios with initial populations of 554 and 254. A similar age structure, unstable and weighted towards older individuals, was maintained.

Because the characteristics of the population are the same in each scenario, population growth rates and the pattern of decline are similar; the curves are simply offset as a result of different starting points (Figure 7-3). Although population size is a determining factor in population growth rates, the differences between scenarios are small and therefore the effect is minimal. The most significant aspect of changing population size is that since the variability around growth rates does not change, smaller populations are more likely to go extinct when population size fluctuates (Figure 7-4).

Figure 7-3



Figure 7-4
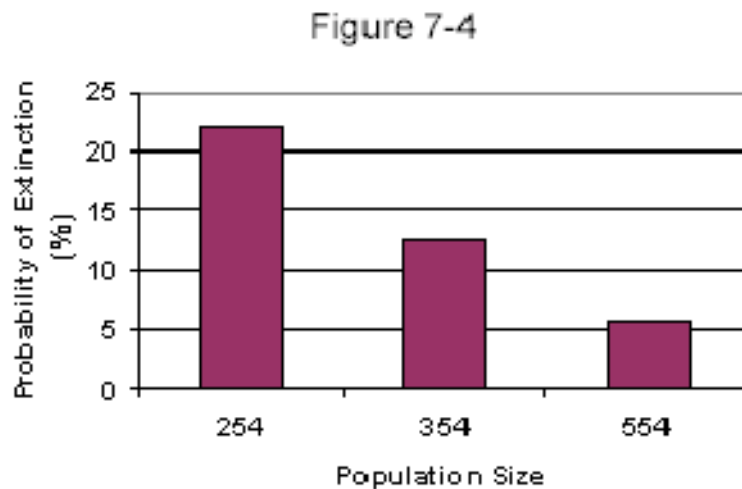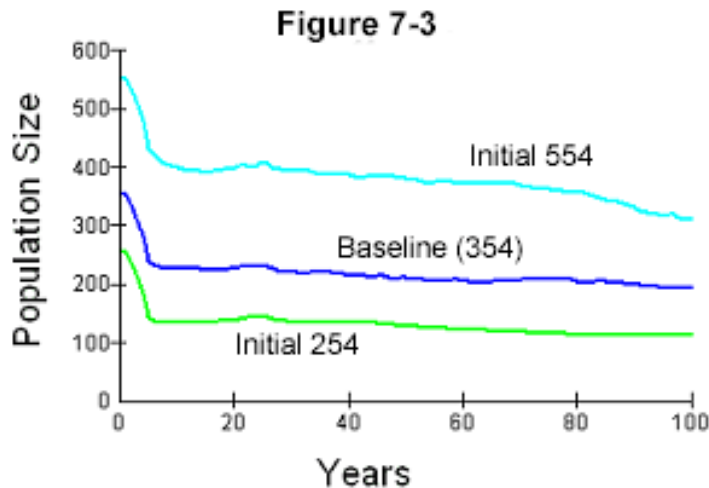
## 7.6 Effect of Population Structure

Recent genetic studies indicate that birds from Guatemala are not genetically distinct from birds in Mexico and Belize and therefore, at least historically, there was movement between populations.  It is possible, however, that population declines have recently isolated these populations from one another, and that while still genetically similar, there is no longer communication among them, resulting in two or three smaller populations instead of one large one.  It is also possible that regardless of genetic similarities, birds nesting in different areas may have different reproductive rates.

A series of Two Population and Three Population scenarios were created in which birds from Mexico, Guatemala, and Belize have different levels of annual exchange.  Genetic analyses to date suggest that there is full gene flow among all three countries.  However, it is important to note that there is a time lag between changes in connectivity and detecting changes in genetic structure.  We have therefore modeled various levels of exchange ranging from no exchange (0%) to full exchange (4%).  The Two Population scenarios all assume full genetic exchange (4%) between Guatemala and Mexico; the models differ in the level of symmetrical exchange that they assume between Mexico/Guatemala and Belize (0%, 0.04%, 0.4%, and 4%).  Using the same assumptions described under the baseline model, the percentage of successfully breeding females in Belize would be 26% (half of nests with 52% and half unprotected with 0% success) and the percent breeding success of the combined Mexico/Guatemala population would be 31% (67 nests protected and 44 unprotected).  Because these values imply that there is no source population for scarlet macaws in the MBR, another scenario was run with Belize as a source population with a 39% success rate.  Recent data show that four out of ten monitored nests in Belize were poached (which would give a success rate of 31% if representative of the entire population) but only the most accessible nests were monitored, so success for the overall population could be higher.  The Belize birds were assigned a uniform age distribution, largely as a matter of convenience due to the small population size.  The Three Population scenarios assume each population is isolated from the others to differing degrees.  In one set of scenarios, all populations are assumed to have symmetrical exchange at different levels (0%, 0.04%, 0.4% and 4%).  In three additional scenarios there is moderate (0.4%) symmetrical exchange between Mexico and Guatemala with varying levels of symmetrical exchange with Belize (0%, 0.04%, 0.4%).  In the last scenario there is full exchange between Mexico and Guatemala (4%) and symmetrical exchange between Belize and other populations at a rate of 0.04%.  This last scenario is genetically equivalent to a Two Population scenario but assumes populations are reproductively distinct.  In all Three Population scenarios, Belize and Mexico each have a 26% breeding success rate and Guatemala has a 40% success rate.  See Appendix 7-2 for a list of population structure scenarios.

In the Two Population scenarios the rate of exchange between Mexico/Guatemala and Belize populations had little effect on the populations until rates of full exchange were approached (Fig. 7-5).  At full exchange between populations, the Belize population benefited from exchange while the Mexico/Guatemala population was negatively impacted; both maintained a negative growth trajectory.  When Belize was considered a source population with even a minimal level of growth ($r = 0.005 \pm 0.016$) and a minimal level of exchange with Mexico/Guatemala (0.04%), populations not only increased in Belize but stabilized in Mexico/Guatemala (Fig. 7-6).
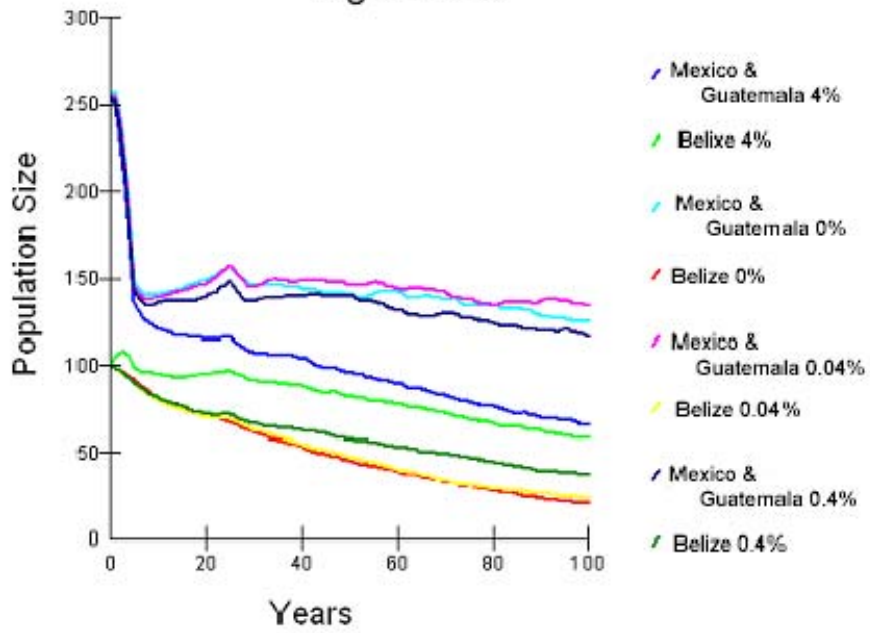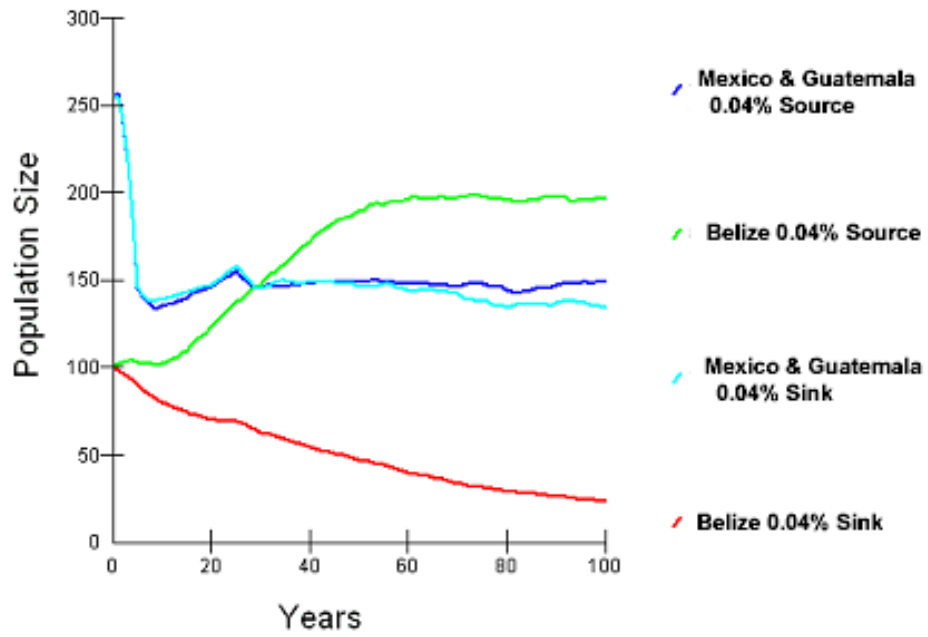
Figure 7-5



Figure 7-6

In the Three Population scenarios, the population trajectories for the metapopulation were generally positive because of the presence of a source population (Guatemala). As with the Two Population scenarios, exchange rates had little effect on the overall population except at the level of full exchange (Fig. 7-7). With full exchange, birds were siphoned from the source population into the two sink populations with the effect that Belize and Mexico populations were stabilized at the cost of a declining population in Guatemala (Fig. 7-8). The most significant aspect to a structured population, therefore, was not the division of birds into smaller populations, but the potential impact of source/sink dynamics between areas of differing reproductive potential. Although there is reason to believe that the genetic structure of the MBR follows a one-population model, because of regional differences in reproductive success, one, two, and three population scenarios (all assuming full exchange between Mexico and Guatemala) produced slightly different results even at the level of the metapopulation (Fig. 7-9).
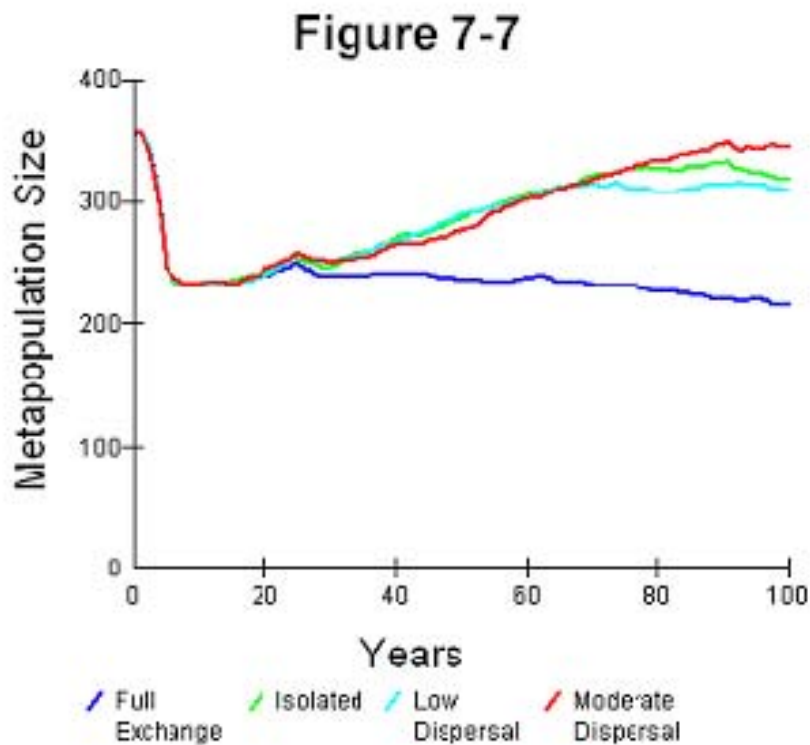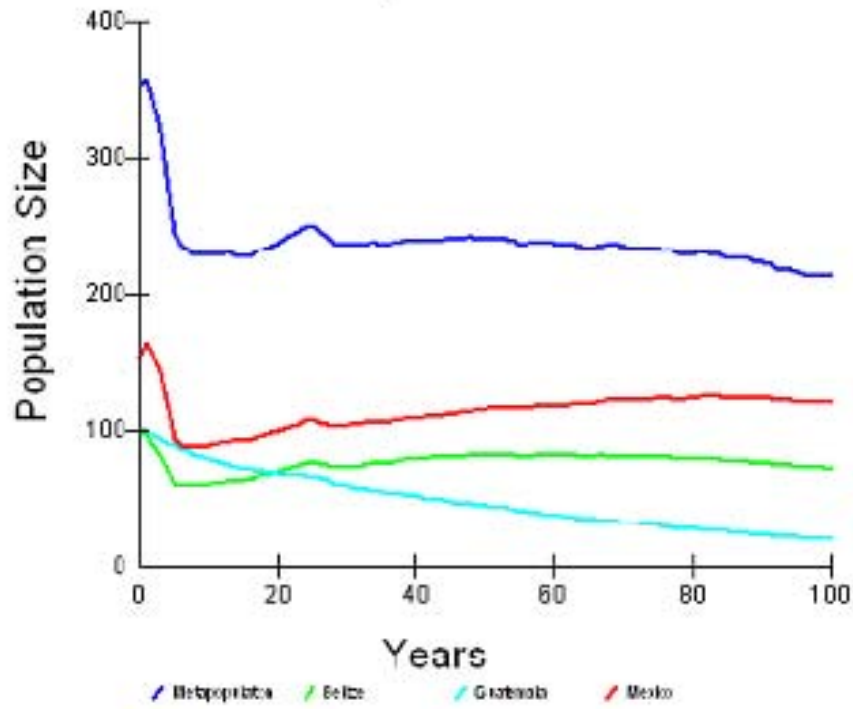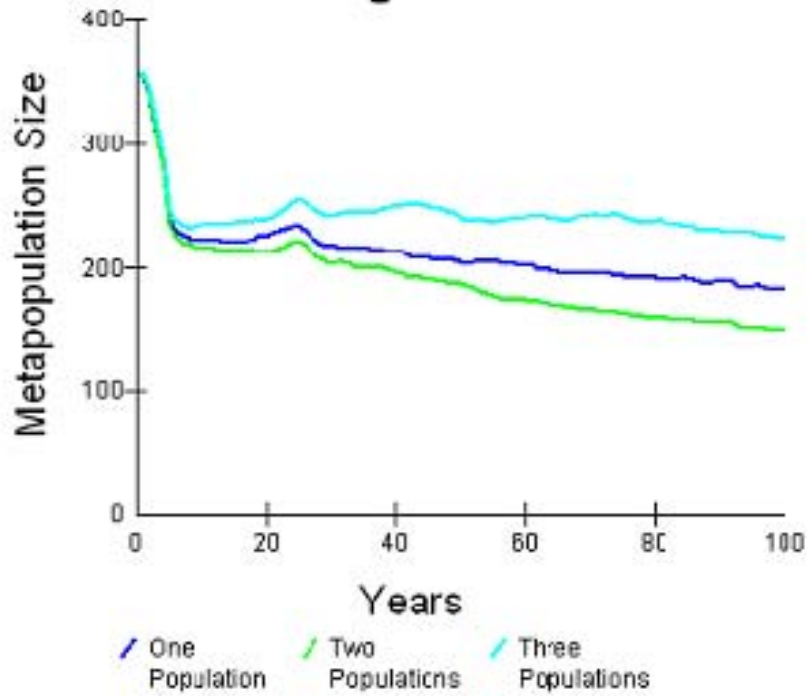


Figure 7-7

## Figure 7-8



## Figure 7-9

## 7.7 Effect of Catastrophes (Disease)

Disease is the primary candidate for a catastrophic decline in this species and region. Annual variation in food as a result of El Niño/La Niña events is expected to be captured in natural environmental variation, poaching is captured under changes in the percentage of adult females nesting successfully, and fires (also related to El Niño/La Niña events) infrequently impact significant numbers of nest trees and generally burn low with minimal impact on food plants (McNab pers. comm.).

Modeling disease effects involves significant uncertainties in both potential frequency of occurrence and in the severity of effects on survival and reproduction. The baseline model assumes an overall frequency of one catastrophic event every 100 years that results in a 90% decline in reproduction and a 75% reduction in survival for one year resulting from an outbreak of Newcastle's Disease (PMV 1), which has high rates of infection, morbidity, and mortality. This is compared to a scenario where *Chlamydia*, which has a similar origin and therefore a similar likelihood of occurrence; but low rates of infection, morbidity, and mortality, causes the outbreak. An "all disease" scenario was also run with all six diseases having the same cumulative frequency of occurrence (1%) and severity but with each disease having a lower individual likelihood of occurrence (e.g. PMV 1 and *Chlamydia* each at 0.25%).

Because the baseline model has only a slightly negative growth trajectory, reducing either the severity of disease or the frequency of disease was sufficient to cause the population to increase, with a reduction in severity having a more pronounced impact (Fig. 7-10). In addition to increasing the population growth rate, the variability around population growth rates was dramatically lower ($r_{chalmydia} = -0.001 \pm 0.062$, $r_{all\ diseases} = -0.005 + 0.100$). Lower variability is significant because it reduces the probability of extinction, especially at low population sizes; in this case extinction probabilities were reduced to zero or near zero ($P[E]_{chlamydia} = 0\%$, $P[E]_{all\ diseases} = 1.4\%$).



Figure 7-10
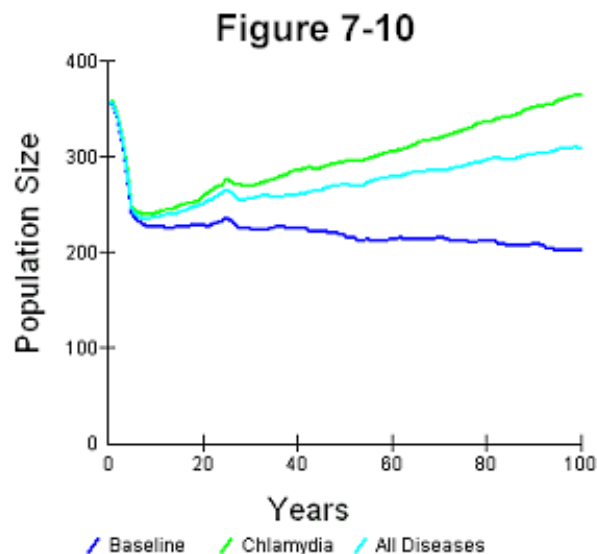
One important aspect of disease not captured here is the potential for long term effects. Four of the six diseases (PBFD, psittacine herpes 3, *Chlamydia*, *Salmonella*) considered important to monitor can permanently affect reproduction and may continue to be transferred to other members of the population. Thus, while these diseases may have little short term impact on the population if introduced, the long term affects on population sustainability are uncertain. The issue of disease will be revisited again in the supplementation scenarios.

## 7.8 Effects of Life History Traits: Age at First Breeding and Maximum Age of Reproduction

Uncertainties in life history traits can be important because they influence deterministic growth rates and the inherent ability of a population to increase. Two traits for which we do not have definitive information are the age at which females first breed (AFB) and their maximum age of reproduction, which together determine the reproductive lifespan and the lifetime contribution to population growth.

The baseline model was compared to scenarios in which the AFB was increased or decreased by one year and to scenarios in which the maximum age of reproduction was increased or decreased by five years.

As would be expected, shortening the reproductive lifespan, either by increasing AFB or decreasing the maximum age at reproduction, reduced the deterministic growth rate of the population ($r_{AFB7} = -0.008$, $r_{MaxRepro20} = -0.016$ vs. $r = -0.002$ for Baseline), while increasing the reproductive lifespan was sufficient to create a slightly positive growth trajectory ($r_{AFB5} = 0.004$, $r_{MaxRepro30} = 0.005$). A similar pattern was seen with stochastic growth rates, though these rates were naturally lower (Fig. 7-11).



Figure 7-11
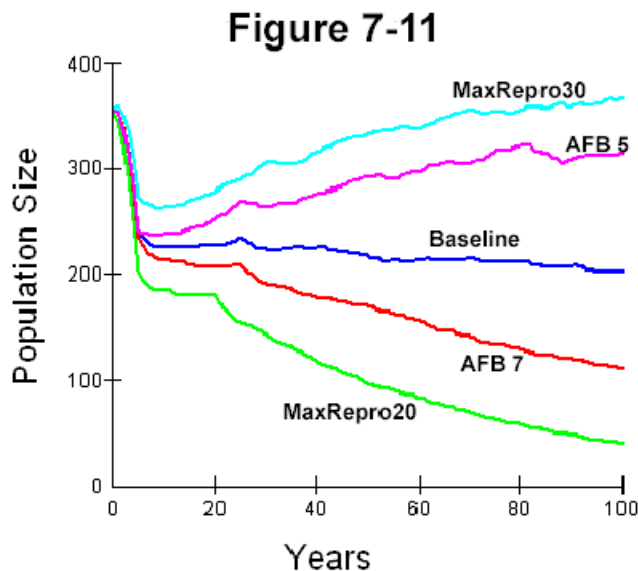
## 7.9 Effects of Reproductive Success (Poaching and Natural Mortality)

The average nesting success in a four year period at WCS sites was 52% and ranged between 30% and 75%. Since WCS has been highly effective at eliminating poaching in these areas, we assume that remaining losses reflect rates of natural mortality in the population. Current management activities attempt to reduce natural sources of mortality and thus elevate the average success rate. Any human incursions into the area that might result in poaching would likewise depress the success rate.

We compared the rate of nesting success of protected nests (52%) to a potential 25% increase (as a result of current and proposed management activities) and a 25%, 50%, and 75% decrease (to see the potential impact of various levels of poaching).

Success rates characteristic of protected nests and higher values produced robust levels of population growth ($r_{52} = 0.029 \pm 0.157$, $r_{65} = 0.047 \pm 0.160$) but values only slightly below 40% (including the 30% used in the Baseline scenario) caused the population to decline (i.e., produced values of $r < 0$; Fig.7-12). Relatively low levels of poaching, therefore, would be expected to result in a population decrease.



Figure 7-12
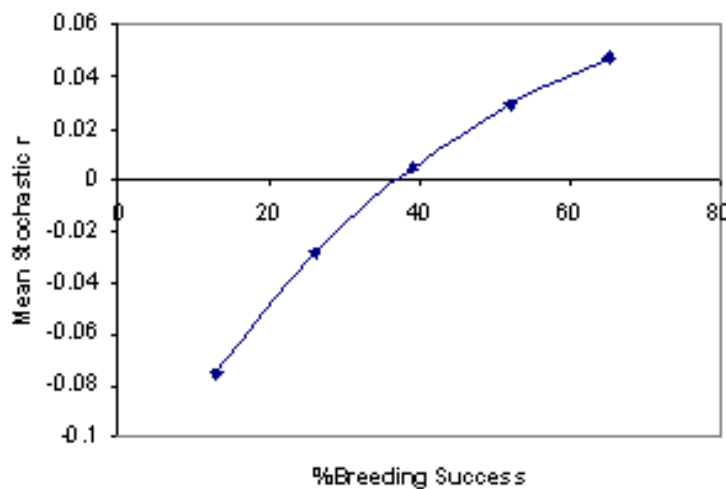
## 7.10 Effects of Supplementation (Population Augmentation)

There are two ways of augmenting the macaw population. One way is to increase the number of chicks fledged from a nest, since pairs are routinely producing clutches larger than they successfully fledge. The second is to add individuals to the population by releases from captive stock.

The baseline scenario (no supplementation) was compared to scenarios that supplemented six, 12, and 18 individuals a year for a 10-year period beginning in the first year of the simulation.

Individuals added were two years of age as discussion of reintroduction procedures suggested individuals would be held from one to three years prior to release. The numbers of individuals supplemented could represent increased numbers of fledglings as a result of *in situ* management (e.g., chick food supplementation), release of captive-produced individuals, or a combination of both strategies. Chick food supplementation is modeled as an addition of birds to the population rather than an increase in the average number of chicks fledged because food supplementation would be feasible for only a few nests, and not the population as a whole.

The addition of young birds to the population had a minimal effect on the overall stochastic growth rate of the population ($r_{baseline}$ = -0.017±0.162, $r_6$ = -0.013±0.158, $r_{12}$ = -0.010±0.154, $r_{18}$ = -0.009±0.156). Supplementation did, however, reduce the initial decline associated with loss of older birds and gave a brief boost to population growth post-supplementation (Fig. 7-13). The net result was that although populations in all supplementation scenarios declined in the long term, supplemented populations achieved a higher population size in the short term. Supplementation decreased the probability of extinction by as much as two-thirds ($P[E]_{baseline}$ = 12.4%, $P[E]_6$ = 8.6%, $P[E]_{12}$ = 6.0%, $P[E]_{18}$ = 4.6%) Supplementation had a much smaller effect on rates of population growth compared to changes in the percent breeding success (Fig.7-14; diamonds represent the baseline scenario).



Figure 7-13
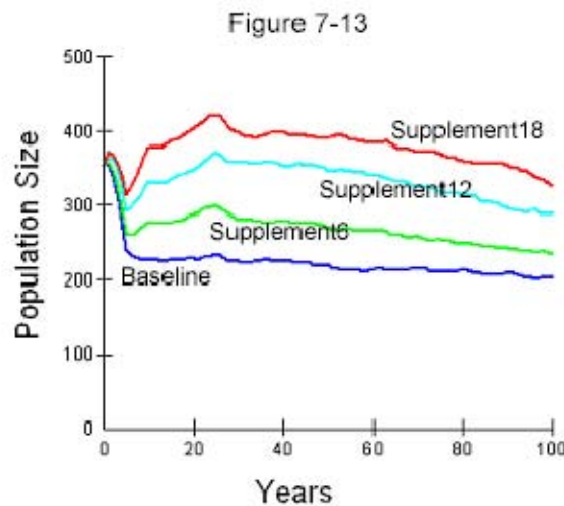
An additional supplementation scenario was run to evaluate the possibility of increasing the risk of disease introduction as a result of releasing captive individuals. In this scenario (Supplementation 18 Disease), the risk of disease introduction was doubled. The result was that the extinction rate was almost doubled above baseline (22.8±1.9%) and the stochastic rate of population growth was reduced to below the non-supplementation level (r = -0.024±0.212).

## 7.11 Effects of Changing Carrying Capacity (Habitat Quality)

Data compiled by WCS shows that deforestation rates in the Petén of Guatemala have fluctuated between 0.05% and 2% between 1967 and 2001. Since 2001, deforestation rates have increased

by an order of magnitude, averaging about 0.5% with a peak of almost 0.9% in 2006. During the same time period, deforestation rates did *not* increase in communities where WCS was working[2] McNab, unpublished data).

We modeled a scenario called "Loss of K" that assumes a cessation of effective protection efforts by CONAP, WCS Guatemala, and our partners, and a corresponding decrease in carrying capacity at an annual rate of 0.5%. This corresponds to a decrease in carrying capacity of about 100 birds for every 20 years of deforestation, assuming rates do not rise above 0.5%. Although population growth rates and populations trends are initially unaffected (because other population parameters are unchanged and because the population is not increasing), the ultimate effect would be a decrease in total size of any recovered population. If the carrying capacity for breeding birds is as low as the habitat modeling suggests (354, compared to the 1200 we have set in the baseline model), current habitat could theoretically be eliminated within the 100 year time frame.

Figure 7-14
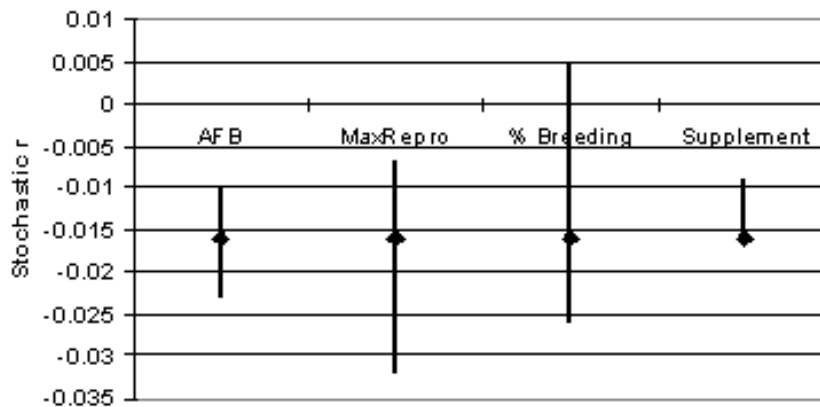


## 7.12 Summary

1) Overall, the deterministic rates of population growth for *A. m. cyanoptera* were slightly negative, indicating an inherent tendency for the population to decrease even in the absence of stochastic (random) events. The reason for this is that rates of poaching are included within the estimates of breeding success and breeding success is the primary force driving population growth rates. In the baseline model and other scenarios based on this model, breeding success rate is modeled at 30%, which is just under the 32% needed for a stable population. These scenarios suggest that a) even moderate levels of poaching could result in

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[2] In 2008, following the scarlet macaw workshop held in Petén, an 120 acre patch of forest was indeed cleared near the Peñon de Buena Vista nesting site. Although this event did not affect the sites of known active nests, the deforestation was close (i.e. some 2 km away), and it did portend to threaten the nesting site in the future. Fortunately, CONAP and their partners including WCS Guatemala successfully addressed the situation by negotiating the exit of the illegal squatters. Subsequently, America Rodriguez of WCS played a key role in organizing a declaration by the community of Paso Caballos stating their opposition to any continued threats to the area, as well as their support for CONAP's protection efforts. In conclusion, despite the brief setback, known areas containing nests have continued intact in WCS focal areas.

a population decrease, b) prior to 2001 the population in Guatemala/Mexico was probably experiencing a significant rate of decline, and c) the work initiated by CONAP with the support of WCS Guatemala and local partners with regard to nest protection has probably been essential in halting that decline.

2) The stochastic rates of population growth were naturally lower than deterministic rates (by 87% for the baseline scenario) and the extinction probability was 12.4% for baseline. As with deterministic rates, stochastic rates were dependent on the percentage of successfully breeding females. In a stochastic model, however, the percentage of successfully breeding females needs to be about 37% in order for the population to grow. It should be noted that these target values are averages and the scenarios assume that there will be significant variation around them from year to year.

3) Because the age structure of this population is likely skewed towards older birds as a result of poor recruitment in the past, it is expected that the population may remain at its current level and could even decrease over the next ten years. This is a demographic artifact resulting from previous poaching and would occur regardless of current nest protection efforts. Any decrease in nest protection efforts would exacerbate this trend. The extent of any decrease will depend on the true age structure of the population, but chicks fledged from protected nests over the last seven years should help to mitigate this effect.

4) Although there are uncertainties with regard to the size, distribution, and connectivity of subpopulations, a metapopulation structure in and of itself does not appear to significantly impact population growth. When subpopulations differ in the percentage of successfully breeding females, however, the resulting source/sink dynamic could significantly negatively impact the Guatemala birds and (to a much lesser extent) affect the overall population. This means that if birds in Mexico are under significant pressure, it could delay or even prevent a recovery in the Guatemala and possibly eventually deplete the Guatemala population. It also suggests that the WCS strategy of "holding the line" at the western side edge of the intact forest block in the eastern Maya Biosphere of Petén may be important for maintaining the population as a whole.

5) Although genetic data support using a one-population model, because populations likely have some level of connectivity yet differ in source/sink status, a three-population model will be more accurate and transparent for predicting population trends in different countries.

6) Because of the likelihood of source/sink dynamics and the primacy of breeding success rates as a driving force in population growth rates, improved knowledge of macaw status in all three countries is of the highest importance for accurately predicting population trends. Expansion of nest protection efforts within and beyond Guatemala would have a positive impact on all populations.

7) Generally speaking, disease risks are small because the probable frequency of occurrence is low. If population augmentation raises the risk of disease introduction, however, it would negate any benefits associated with population augmentation and could even depress population growth below baseline levels. Disease severity appears to have a greater impact on populations than frequency of occurrence; it should be noted that severity is a function of which disease is introduced and therefore, unlike the frequency of occurrence, cannot be managed. Of greater concern may be the introduction of a disease that permanently impacts reproduction and remains in the population. Different software (Outbreak) would be required to model these effects.

8) While changing the life history characters (such as age at first breeding or the maximum age of reproduction) can affect population trajectories and therefore model predictions, these are largely determined by evolutionary processes and are not particularly instructive from a management standpoint. However, refining our estimates of these parameters will allow more effective modeling in the future.

9) Of all the variables manipulated in the scenarios (age at first breeding, maximum age of reproduction, age structure, population size, population structure, disease risk and severity, percentage of successfully breeding females, population augmentation, and trends in carrying capacity) the variable that most significantly and consistently impacted population growth was the percentage of successfully breeding females. This variable corresponds to ongoing management activities of nest protection against poaching, colonization by Africanized bees, and predation by forest falcons (*Micrastur ruficollis*). Results suggest that these *in situ* management actions should have the greatest conservation impact and further, that at least some level of *in situ* management is necessary for the population to recover. Additional data on natural causes of nest failures will help evaluate the relative importance of mitigating natural versus anthropogenic causes of nest failure.

10) Population augmentation has the potential to minimize a short term population decrease associated with an unstable age distribution and to raise the baseline population size. Several important caveats bear mentioning: 1) the benefits of population augmentation could be negated and/or population status could worsen if proper biosecurity is not observed during reintroduction; 2) the benefits of population augmentation are contingent upon current assumptions of an unstable age structure and a population growth rate near zero; if the population is performing significantly better or significantly worse, population augmentation at the level that is suggested as feasible would have little impact; 3) population augmentation is strictly a short term solution and does not address the cause of decline nor ultimately prevent population decline.

11) It is important to note that the value of population viability analysis does not lie in the absolute values that come out the scenarios; models are only as good as the data and assumptions they are based on and uncertainties can significantly change model results. This is particularly true in this analysis, where the variable with the greatest weight (breeding success) has been set at a level just below what is needed for a stable population. As a result, small changes in a number of different parameters can dramatically change population trajectories in a way that would not happen if the population was growing or declining more rapidly. Population viability analysis is most valuable for understanding which parameters give the greatest leverage (in this case breeding success) and which management activities have the greatest impact on those parameters (in this case, poaching). This allows managers to focus their efforts on those activities with the greatest conservation impact.

## LITERATURE CITED

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**Appendix 7-1: Scenario Growth Rates, Extinction Rates and Final Population Sizes**

| Scenario | Det r | Stoch r | SD (stoch r) | Final N | SD (Final N) | P (extinction) |
|---|---|---|---|---|---|---|
| Baseline | -0.002 | -0.016 | 0.16 | 204 | 242 | 0.122 |
| Uniform | -0.002 | -0.13 | 0.162 | 248 | 283 | 0.108 |
| Stable | -0.002 | -0.01 | 0.152 | 293 | 304 | 0.06 |
| Initial Population 554 | -0.002 | -0.14 | 0.16 | 310 | 321 | 0.056 |
| Initial Population 254 | -0.002 | -0.02 | 0.167 | 113 | 145 | 0.22 |
| Two Pops 0%: M&G | 0 | -0.016 | 0.162 | 20 | 32 | 0.16 |
| Two Pops 0%: Belize | -0.013 | -0.027 | 0.161 | 297 | 125 | 0.464 |
| Two Pops 0%: Meta | | -0.019 | 0.157 | 167 | 201 | 0.148 |
| Two Pops 0.04%: M&G | 0 | -0.018 | 0.168 | 129 | 166 | 0.174 |
| Two Pops 0.04%: Belize | -0.013 | -0.026 | 0.169 | 20 | 32 | 0.424 |
| Two Pops 0.04%: Meta | | -0.02 | 0.162 | 150 | 188 | 0.152 |
| Two Pops 0.4%: M&G | 0 | -0.02 | 0.162 | 105 | 135 | 0.186 |
| Two Pops 0.4%: Belize | -0.013 | -0.019 | 0.164 | 36 | 49 | 0.306 |
| Two Pops 0.4%: Meta | | -0.021 | 0.161 | 141 | 178 | 0.168 |
| Two Pops 4%: M&G | 0 | -0.023 | 0.167 | 72 | 87 | 0.21 |
| Two Pops 4%: Belize | -0.013 | -0.014 | 0.169 | 62 | 75 | 0.232 |
| Two Pops 4%: Meta | | -0.021 | 0.156 | 133 | 161 | 0.182 |
| Two Pops Source: M&G | 0 | -0.016 | 0.164 | 138 | 164 | 0.144 |
| Two Pops Source: Belize | 0.017 | 0.006 | 0.157 | 198 | 145 | 0.086 |
| Two Pops Source: Meta | | -0.005 | 0.157 | 336 | 287 | 0.072 |
| Three Pops 0%: Mexico | -0.013 | -0.033 | 0.168 | 11 | 20 | 0.552 |
| Three Pops 0%: Belize | -0.013 | -0.027 | 0.161 | 19 | 32 | 0.434 |
| Three Pops 0%: Guat | 0.19 | 0.004 | 0.163 | 297 | 223 | 0.086 |
| Three Pops 0%: Meta | | -0.005 | 0.158 | 327 | 252 | 0.086 |
| Three Pops 0.04%: Mexico | -0.013 | -0.027 | 0.166 | 17 | 26 | 0.394 |
| Three Pops 0.04%: Belize | -0.013 | -0.024 | 0.165 | 24 | 36 | 0.37 |
| Three Pops 0.04%: Guat | 0.019 | 0.003 | 0.164 | 287 | 221 | 0.092 |
| Three Pops 0.04%: Meta | | -0.006 | 0.157 | 328 | 261 | 0.09 |
| Three Pops 0.4%: Mexico | -0.013 | -0.015 | 0.168 | 52 | 55 | 0.22 |
| Three Pops 0.4%: Belize | -0.013 | -0.015 | 0.163 | 54 | 61 | 0.198 |
| Three Pops 0.4%: Guat | 0.019 | -0.002 | 0.163 | 240 | 212 | 0.116 |
| Three Pops 0.4%: Meta | | -0.008 | 0.154 | 346 | 317 | 0.108 |
| Three Pops 4%: Mexico | -0.013 | -0.014 | 0.182 | 56 | 61 | 0.202 |
| Three Pops 4%: Belize | -0.013 | -0.014 | 0.181 | 58 | 67 | 0.218 |
| Three Pops 4%: Guat | 0.019 | -0.017 | 0.179 | 74 | 87 | 0.21 |
| Three Pops 4%: Meta | | -0.017 | 0.159 | 189 | 213 | 0.168 |
| Three Pops 0%: Mexico Asym | -0.013 | -0.014 | 0.171 | 51 | 53 | 0.208 |
| Three Pops 0%: Belize Asym | -0.013 | -0.027 | 0.165 | 21 | 37 | 0.44 |
| Three Pops 0%: Guat Asym | 0.019 | 0.001 | 0.162 | 258 | 214 | 0.09 |
| Three Pops 0%: Meta Asym | | -0.007 | 0.155 | 330 | 285 | 0.086 |
| Three Pops 0.04%: Mexico Asym | -0.013 | -0.014 | 0.166 | 52 | 54 | 0.19 |
| Three Pops 0.04%: Belize Asym | -0.013 | -0.023 | 0.159 | 25 | 34 | 0.354 |
| Three Pops 0.04%: Guat Asym | 0.019 | 0.001 | 0.16 | 262 | 216 | 0.072 |
| Three Pops 0.04%: Meta Asym | | -0.006 | 0.152 | 339 | 289 | 0.068 |
| Three Pops 0.4%: Mexico Asym | -0.013 | -0.016 | 0.176 | 45 | 51 | 0.234 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Three Pops 0.4%: Belize Asym | -0.013 | -0.016 | 0.168 | 49 | 59 | 0.248 |
| Three Pops 0.4%: Guat Asym | 0.019 | -0.004 | 0.169 | 223 | 211 | 0.118 |
| Three Pops 0.4%: Meta Asym | | -0.01 | 0.161 | 318 | 311 | 0.108 |
| Three Pops 4%: Mexico Asym | -0.013 | -0.008 | 0.176 | 75 | 74 | 0.176 |
| Three Pops 4%: Belize Asym | -0.013 | -0.025 | 0.166 | 21 | 34 | 0.426 |
| Three Pops 4%: Guat Asym | 0.019 | -0.012 | 0.175 | 128 | 142 | 0.16 |
| Three Pops 4%: Meta Asym | | -0.014 | 0.161 | 224 | 237 | 0.136 |
| Chlamydia | 0.005 | -0.001 | 0.062 | 366 | 210 | 0 |
| All Diseases | 0.003 | -0.005 | 0.1 | 309 | 225 | 0.014 |
| AFB 5 | 0.005 | -0.1 | 0.16 | 315 | 334 | 0.09 |
| AFB 7 | -0.008 | -0.022 | 0.159 | 111 | 140 | 0.18 |
| Max Repro 20 | -0.016 | -0.32 | 0.162 | 39 | 54 | 0.288 |
| Max Repro 30 | 0.005 | -0.007 | 0.155 | 382 | 370 | 0.046 |
| Breeding Success 65% | 0.058 | 0.047 | 0.159 | 991 | 306 | 0 |
| Breeding Success 39% | 0.017 | 0.005 | 0.157 | 627 | 417 | 0.022 |
| Breeding Success 26% | -0.013 | -0.026 | 0.159 | 65 | 83 | 0.19 |
| Breeding Success 13% | -0.06 | -0.074 | 0.17 | 0.3 | 1.4 | 0.95 |
| Supplement 6 | -0.002 | -0.013 | 0.16 | 237 | 269 | 0.08 |
| Supplement 12 | -0.002 | -0.011 | 0.157 | 279 | 294 | 0.058 |
| Supplement 18 | -0.002 | -0.008 | 0.156 | 329 | 324 | 0.064 |
| Supplement 18 Disease | -0.01 | -0.24 | 0.212 | 146 | 249 | 0.228 |

**Appendix 7-2: Summary of Scenarios with Different Population Structures**

Single Population (Mexico/Guatemala/Belize)

Full Exchange (4%), 30% average success all regions

Two Populations (Mexico/Guatemala and Belize)

| Exchange (M/G and B) | Success (M/G) | Success (B) |
|---|---|---|
| 0% | 31% | 26% |
| 0.04% | 31% | 26% |
| 0.04% | 31% | 39% |
| 0.4% | 31% | 26% |
| 4% | 31% | 26% |

Three Populations (Mexico and Guatemala and Belize)

| Exch (M/G) | Exch (G/B) | Exch (B/M) | Success (M) | Success (G) | Success (B) |
|---|---|---|---|---|---|
| 0% | 0% | 0% | 26% | 40% | 26% |
| 0.04% | 0.04% | 0.04% | 26% | 40% | 26% |
| 0.4% | 0.4% | 0.4% | 26% | 40% | 26% |
| 4% | 4% | 4% | 26% | 40% | 26% |
| 0.4% | 0% | 0% | 26% | 40% | 26% |
| 0.4% | 0.04% | 0.04% | 26% | 40% | 26% |
| 0.4% | 0.4% | 0.4% | 26% | 40% | 26% |
| 4% | 0.04% | 0.04% | 26% | 40% | 26% |