Population Viability Analysis (PVA) of Crocodile populations (*Crocodylus acutus*) in the Pacific of Costa Rica

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Population Viability Analysis (PVA) of Crocodile populations (*Crocodylus acutus*) in the Pacific of Costa Rica

Summary

The population recovery of the American crocodile (*Crocodylus acutus*) on the Pacific coast of Costa Rica since the 1980s and 1990s has been such, that the subpopulations of the Tempisque River basin and the Tárcoles River basin are considered as two sites with a high density of individuals for the species. The growth of crocodilian subpopulations in these and other sites has resulted in a growing conflict between this species and humans, including fatal attacks. For this reason, an analysis of crocodilian subpopulations on the Pacific coasts is necessary to understand the demographic factors that influence the growth of these subpopulations, to estimate the relative effect of different management strategies and to guide discussions about their feasibility.

To understand the population dynamics is fundamental for the conservation and management of wildlife, since it provides the most direct measures of the situation and trends of the populations. However, the long-term studies necessary to identify the most important factors in the long-term viability of species are scarce and laborious. Population Viability Analysis can help identify the most important factors in the population growth of wildlife species. Models can also be used to assess the effects of alternative management strategies to identify the most effective conservation actions for a population or species and to identify research needs.

To evaluate the viability of the population of the species by virtue of the current estimated demographic situation, a base model of a hypothetical population of crocodiles with different conditions and assumptions was developed using the computer program *Vortex*, with the aid of published literature on the American crocodile and similar species, or based on the expert knowledge of the biology of the species. This model was used to help assess the viability of the population, to estimate the relative effect of management strategies and to guide discussions about their effectiveness.

The deterministic results of the base model show that the demographic parameters of the crocodilian population that was modeled are within the ranges observed in free-living and captive populations of this and other crocodile species. Stochastic results reveal that the population has a positive stochastic growth of 6.0%, which leads to a population size of around 90% of its carrying capacity (5,000 individuals) over a 15-year period.

A sensitivity analysis on population size shows that, in the absence of threats such as illegal hunting or habitat loss, small populations of 100-500 individuals may reach values close to

carrying capacity within a period of less than 100 years. Another sensitivity analysis shows that the percentage of males at birth, mean number of eggs per clutch and reproductive age of females are the most sensitive parameters for population growth. These parameters are related to the number of females within the population and their ability to recruit individuals to it over time. It is recommended to research and monitor these demographic parameters to establish management actions of crocodile populations.

The scenarios assessed with a lower percentage of females breeding per year (80% and 90%) result in a lower population growth rate than the baseline scenario. However, populations increase and at the end of 100 years population values are above 90% of the carrying capacity.

More detailed analyzes reveal that a high bias towards males at birth (90% males) may affect population growth. This is because by reducing the number of females that reach adulthood, the population does not grow at the rate of the baseline model and its final size is smaller.

Additionally, there are three important factors in removing individuals to manage a crocodile population: the sex of these individuals, the percentage of individuals to be extracted, and the frequency of extraction events. Removing adult females from the population has a greater impact on population growth than taking adult males. The impact increases as the percentage of females is increased and the period between extraction events is reduced. To avoid extinction risks it is also important to condition the extraction to the minimum population size that is wanted to manage.

In order for the extraction of adult males to have a declining effect on the population, other demographic elements must be taken into account, such as the maximum number of females with which a male can breed, the effect of density-dependent reproduction on the population, or make the extraction events before the males can breed with the females, avoiding the recruitment of individuals in the population. In scenarios where the number of adult females available to each adult male is limited to 10, an annual removal of 95% or more of them, is required for the final population size to be below 90% of the carrying capacity. It is necessary to extract the totality of adult males each year for the population to fall below the initial population of 2,500 individuals. However, the difficulty of estimating these parameters or logistics to carry out, make them impractical in reality. This group of scenarios re-emphasize characteristics of the species that make it so resilient, such as its polygamous breeding system, the number of eggs per nest and its long-life expectancy. These factors contribute to the fact that a handful of adult males can recruit a high number of individuals when breeding with several females during many years of life, so any management actions aimed at controlling population size should take females into account.

Introduction

The American crocodile (*Crocodylus acutus*) is the most widely distributed species of New World crocodiles. In the Atlantic, it is distributed from the extreme south of Florida, the Caribbean islands, on the coasts of Yucatan in Mexico and in Central America, to the north of Venezuela. In the Pacific, it occurs from northern Sinaloa in Mexico to the limits of coastal mangrove habitats in northern Peru. This species is found up to 1,200 m above sea level (Thorbjarnarson, 1989, IUCN 2012).

This species is mainly observed in coastal habitats such as lagoons, mangroves and other brackish water bodies; there are even individuals who can venture out to sea. However, it can also be found in inland habitats such as rivers and lakes (Savage 2002, IUCN 2012).

Because of the commercial value of its skin and because it was considered a dangerous species for humans, the crocodile was disproportionately hunted between the 1930s and 1970s, which led to a serious decline in the subpopulations of this species (Savage 2002, Thorbjarnarson 2010, IUCN 2012). Thus, the species is classified as Vulnerable (VU) in the IUCN Red List and appears in Appendix I of CITES with the exception of the subpopulations of Cuba appearing in Appendix II (IUCN 2012, CITES 2016). Currently, thanks to the protection of the species and its habitat, the species has recovered in different countries including Costa Rica (Savage 2002, Thorbjarnarson 2010, IUCN 2012).

In the Pacific coast of Costa Rica, the population recovery since the 1980s and 1990s has been such that the subpopulations of the Tempisque River basin and the Tárcoles River basin are considered as two sites with the highest density of crocodiles per square kilometer (Sasa and Chaves 1992, Sánchez et al., 1997, Sánchez 2001, Mauger et al., 2012). The growth of crocodilian subpopulations in these and other sites has resulted in a growing conflict between humans and crocodiles, including fatal attacks (Jiménez 1998, Ross and Larriera 2001, Savage 2002, Arguedas and Hernández 2014 Fendt 2016). A Population and Habitat Viability Assessment (PHVA, see Miller et al., 2008, Lacy et al., 2015) was recommended since the 1990s to analyze possible population management actions and reduce conflict (Ross and Larriera 2001), but has been postponed repeatedly.

At present, the measure that is applied is to sacrifice or put into captivity the dangerous animal after it has attacked one or more persons (Fendt 2016, Jimenez 2016). Therefore, an analysis of crocodilian subpopulations on the Pacific coasts is necessary to understand the demographic factors that influence the growth of crocodiles to estimate the relative effect of different management strategies and to guide discussions about their feasibility.

Understanding population dynamics is fundamental for the conservation and management of wildlife, since it provides the most direct measures of the situation and trends of populations (Block et al. 2001). However, the long-term studies necessary to identify the most important factors in the long-term viability of species are scarce and laborious (Block et al., 2001, Lindenmayer and Likens 2010, Lindenmayer et al. 2012, Clements et al. 2015). The population-based computational modeling assessments known as Population Viability Analysis (PVAs) are a key element of a PHVA (Miller et al. 2008, Lacy et al. 2015) and may help to identify the most important factors in the population growth of wildlife species. Models can also be used to assess the effects of alternative management strategies to identify the most effective conservation actions for a population or species and to identify research needs (Akçakaya and Sjögren-Gulve 2000, Brook and Kikkawa 1998, Ellner et al. 2002, Fessl et al. 2010, Wakamiya and Roy 2009).

The PVA was carried out with Vortex (v10.0.8.0) (Lacy et al. 2015, Lacy and Pollak 2014). The program uses a Monte Carlo simulation to model the effect of deterministic and stochastic factors on wild and captive populations. Deterministic events are constant over time (i.e. harvest, habitat loss, contamination and habitat fragmentation); whereas stochastic events are linked to a probability of occurrence and are classified as demographic (i.e. probabilities of survival, reproduction, sex determination), environmental (fluctuations in demographic rates caused by fluctuations on weather, competition, food supply, diseases), catastrophes (i.e. hurricanes, prolonged droughts, oil spills, epidemic diseases) and genetic (i.e. genetic drift, inbreeding). Initially, the program generates individuals to form the initial population, then each animal moves through different life cycle events such as birth, mate selection, reproduction, mortality and dispersion, which are determined per the probability of occurrence that are entered into the model. Consequently, each simulation run (iteration) of the model gives a different result. By allowing random variables changed within certain limits, the program predicts at the end of the simulation: the extinction risk, the average size of the surviving populations, and genetic diversity retained by the population, among other statistical results. By running the model hundreds of times, it is possible to examine the probable outcome and range of possibilities.

Vortex is not intended to give absolute answers, since it is projecting stochastically the interactions of the many parameters used as input to the model and because of the random processes involved in nature. Interpretation of the output depends upon our knowledge of the biology of the species, the environmental conditions affecting the species, and possible future changes in these conditions. For a more detailed explanation of Vortex and its use in population viability analysis refer to the software manual (Lacy et al. 2015) or visit www.vortex10.org and www.cbsg.org.

Crocodile demographic patterns vary from country to country and from population to population (Thorbjarnarson 1989, G. Chaves pers. com. 2016), making it difficult to project population dynamics in the long term. However, some elements are known quite well and others can be assumed with some certainty. These elements necessarily imply general demographic consequences that with the help of a PVA can present answers to different questions of scientific significance and population management, namely:

At what rate, could the population of crocodiles be growing?

What are the main demographic factors driving the growth of crocodile populations?

What are the expected demographic impacts of a management strategy that involves the extraction of individuals from the population?

Glossary

Results reported for each modeling scenario include the following parameters:

Det-r: Deterministic population growth or decline in the absence of demographic fluctuations due to stochastic factors; reflecting a constant population growth without any source of variation in model parameters. For example, a growth rate of 0.05 or -0.05 equals a population growing or decreasing by 5% each year, respectively.

Stoch-r: The mean rate of stochastic population growth or decline demonstrated by the simulated populations, averaged across years and iterations, for all those simulated populations that are not extinct. It includes all sources of demographic and environmental variation input in the model. Usually, it is different from det-r because such fluctuations affect the viability of the population.

P(survive): The probability of population survival, determined by the proportion of iterations within a given scenario that do not become extinct in the simulation. For example, if the simulation shows a probability of extinction of 0.60, this means a probability of survive of 0.40.

N-all: Mean population size of a given scenario at the end of the simulation (averaging both survival and extinct iterations).

N-all/K: Ratio of final population size to carrying capacity. The proportion of the mean population size of a given scenario at the end of the simulation (averaging both survival and extinct iterations) with respect to its carrying capacity (K). Used when comparing scenarios with populations of different sizes. It becomes more important as the risk of extinction of a population decreases.

Baseline model

These are general explanations of how the values of the different parameters for the baseline model were estimated (Table 1).

Model assumptions and precautions

The input values of the model were derived from published literature and knowledge of the authors on the biology of the species and modeling of populations. Much of the information required by Vortex is scarce and most of the data used or estimated were from a few scientific papers including other crocodilian species. However, these species are sufficiently similar in size, therefore, it was assumed that their demographic structure is similar. The baseline model describes a population without current anthropogenic threats, so population growth does not have any artificial limitation. The baseline model was subsequently used as a basis for sensitivity analysis and evaluation of management actions.

General model parameters

Number of iterations: 1,000.

Number of years of the simulation: 100.

Extinction definition: Only individuals of one sex remain.

Population-based modeling: Yes.

The simulation is run as a population-based model rather than as an individual-based model. In a population-based simulation, all genetic options and modeling (e.g. inbreeding depression) are disabled as is individual variation (demographic stochasticity); environmental variation (EV) is still considered in the models. Recommended for large populations (see below), population-based models run much faster than do individual-based ones, with no detectable change in results.

Population parameters

Number of populations: One.

Initial population size (N_0): 2,500 individuals.

Carrying capacity (K): 5,000 individuals.

Vortex requires a quantitative carrying capacity to limit maximum population size. This value defines an upper limit for the size of the population, which Vortex randomly imposes additional mortality over all age and sex classes to return the size of the population to the value of K. For this assessment, the value was set at 50% above the value of N0. Also, it was assumed that K was not affected by environmental variation because this is already included in other parameter's values within the model.

Concordance between environmental variation in reproduction and survival: 0.5. Environmental variation (EV) is the annual variation in reproduction and survival due to random variation in environmental conditions. These factors can affect reproduction and survival independently or simultaneously. If this value is set to 0.0, then EV in reproduction will be independent from EV in mortality. If this value is set to 1.0, then EV in reproduction and EV in survival will be completely synchronized. As a result, good years for reproduction are also good for survival. If this correlation is set to an intermediate value, then EV in reproduction will be partly correlated with EV in survival.

Reproductive parameters

Mating system: Long-term polygamy. During the breeding season, males keep female harems, (Thorbjarnason 1989). The mating system was set as polygynous, which allows males to mate with more than one female. Therefore, under conditions of unequal sex ratio in which there are fewer males than females, 'extra' females will have the opportunity to breed rather than remain unpaired for the year. Once the harems are formed, the individuals who form them will remain together through the years of simulation until the male or one of the females dies and is replaced by another individual.

Age of first clutch: 10 years in females and 15 years in males. In *Vortex*, this parameter represents the average age of the first reproduction, not the age of sexual maturity or the earliest reproductive age observed. Different elements were considered to estimate this value in the model. Field data suggest that females reach sexual maturity when they are 2.5-2.8 m in length (Thorbjarnarson 1989, J. Bolaños com. pers. 2016), while males reach maturity at 2.8 m (Thorbjarnarson 1989). Savage (2002) estimates that individuals of both sexes reach sexual maturity between seven and nine years of age. In Thorbjarnarson (1989) it is estimated that, based on the growth rate of individuals, the minimum age of reproduction in females is about 10 years. On the other hand, Soberón et al. (2000) estimate that both sexes of the Cuban crocodile (*C. rhombifer*) start breeding at 10 years of age. However, data from *C. moreletii* indicate that males reach maturity at a larger size than females (Casas-Andreu et al., 2011). A further complication is that individuals may be physiologically mature, but excluded from reproduction because of social factors, which occurs in both sexes, especially in males (Thorbjarnarson 1989, Sánchez 2001, J. Bolaños and G. Chaves. pers. comm 2016).

Percentage of females breeding: 100% (EV = 10%). Thorbjarnarson (1989) found that the annual breeding effort of *C. acutus* females varied between populations with a ranging between 64% -72%, a value that could reach up to 90% in other populations (J. Bolaños pers. comm. 2016). However, there are reports of displaced non-dominant females by the dominant ones, breeding with non-dominant males (J. Bolaños pers. comm. 2016), which could increase this value even more. For this evaluation, however, it was estimated that in an average year, all females could be part of a harem and reproduce with the corresponding male. As to environmental variation (EV) from year to year, it was estimated that this parameter has little effect on the species.

Density-dependent reproduction: No. *Vortex* models this parameter with an equation that specifies the proportion of females that reproduce as a function of the total population size. Normally, the proportion of breeding females would decrease as the population size becomes larger. In addition, it is possible to model an Allee effect: a decrease in the proportion of breeding females at low densities, due, for example, to difficulty in finding reproductive partners. In the case of crocodile populations in Costa Rica, it was assumed that reproduction is independent of population density.

Percentage of adult males in the reproductive pool: 20%. In many species, there are adult males that cannot mate despite being physiologically capable due to the social behavior of the species. This can be modeled in *Vortex*, specifying a percentage of adult males that can be considered "available" to breed each year. During the breeding season, adult males of larger size are dominant and only accept the approach of one or several females and remove the other males from their territory by aggressive means; keeping them from accessing the females (Sánchez 2001, G. Chaves and M. Sasa pers. comm. 2016). As previously mentioned, non-dominant males and females can breed (J. Bolaños, pers. 2016), though the percentage of males with access to females is expected to be low.

Number of clutches per year: 1. The female digs a hole in the sand or earth and makes a nest that covers it with earth and vegetation. The female takes care of this nest for a period between 75 - 90 days until the sound of the newborn stimulates it to open the nest with the paws and the snout (Savage 2002).

Sex ratio at birth: 50%. The sex ratio among crocodilian offspring may vary from year to year, depending on nesting sites and local climatic conditions (Lance et al. 2000). It was assumed that if data were taken from all nests in the long-term it would be 1:1. However, there are studies that show variability in this parameter (Lance et al. 2000). In the American alligator (*Alligator mississippiensis*), Lance et al. (2000) found a bias toward males in the juvenile cohort, while in *C. acutus*, Murray et al. (2015) also found a bias toward males in the neonatal cohort of 3.5: 1 between 2012-2014. This parameter was modeled with different values in other scenarios.

Maximum number of eggs per clutch: 40. There is a large variability in the size of the clutch, ranging from 22 to 105 eggs (Thorbjarnarson 1989). However, extremely large clutch sizes may be the result of more than one female ovopositing at the same site at the same time (Thorbjarnarson 1989, J. Bolaños pers. obs.). In this baseline model 40 eggs were entered as maximum value (J. Bolaños pers. obs.).

Average number of eggs per clutch: 27 ± 10. For *C. acutus* there are values between 20 and 30 eggs per nest. For other species such as *C. rhombifer* and *C. moreletti* there are data ranging from 25 eggs to 29 (Soberón et al., 2000, Sánchez 2001, Platt et al. -Andreu et al., 2011). For this baseline model, an intermediate value of this data was entered.

Survival Parameters

Mortality values: These values are age and sex specific and are shown in Table 1. In *Vortex*, once reproductive age is reached, the annual probability of mortality remains constant throughout the life of the individual and is introduced only once.

There are few qualitative studies on cohort mortality according to age and sex in crocodiles. Mortality from eggs to the first year of age is very high in this species, surpassing even 90% (Gaby et al., 1985, Thorbjarnarson 1989, Sánchez 2001). The different factors that influence mortality during this first year are: fertility, egg and neonatal predation, droughts and floods (Gaby et al. 1985, Thorbjarnarson 1989, Sánchez 2001). In the present analysis, it was estimated that these four factors together make mortality during the first year of life to be 95% ± 3%. During the first years of life, mortality remains high, but as individuals grow, the number of predators is rapidly reduced (Thorbjarnarson 1989, Savage 2002) and thus the mortality decreases and may reach very low values. For the rest of the age classes we used data from Soberón et al. (2000) for *C. rhombifer*. In Soberón et al. (2000), the mortality value of each cohort is equal for both sexes, which makes the total sexual ratio of the population to be 1:1. In other studies, populations may be skewed towards males (Lance et al. 2000, Murray et al. 2015) or toward females (Mauger et al. 2012), but there may also be no differences in the proportion of sexes on the total number of individuals of the population (Cedeño-Vásquez et al., 2006, Platt et al., 2011).

Maximum age of reproduction: 70 years. It is known that crocodiles can live many years, but there are no quantitative data on this in wildlife. In this analysis, we estimated a maximum age of 70 years without reproductive senescence effects (i.e. all adult individuals are considered capable of reproducing until the age of their death).

Additional Model Options

Catastrophic events: 2. Catastrophes are natural or artificial events that occur infrequently but drastically and affect reproduction or survival. Any environmental changes that have a relatively large effect on survival or fecundity of individuals in a population are modeled in *Vortex* by assigning an annual probability of occurrence and a pair of severity factors that describes their impact on mortality (across all age and sex classes) and on the proportion of females that successfully breed in a given year. As mentioned above, both droughts and floods affect the survival of eggs (Thorbjarnarson 1989, Soberón et al. 2000). The eggs and juveniles of the American alligator (*A. mississippiensis*) are also sensitive to both environmental factors and although it is difficult to determine how often they produce catastrophic mortality events, the data suggest that they are not uncommon (Abercrombie 1989). There is evidence that El Niño and La Niña can dramatically increase the mortality of crocodilian eggs and hatchlings (G. Chaves and M. Sasa com. Pers. 2016) and both phenomena alternate with each other and each separately occurs every 5-10 years. Therefore, a catastrophe with a frequency of 20% (every 5 years) was created with a reproductive severity factor of 50% (equivalent to an extra mortality of 50% in nest survival). Additionally, Reed et al. (2003), when examining populations of 88 vertebrate populations, found that the risk of a severe population reduction (≥ 50%) for a catastrophe is 14% for generation time (T). In the case of the baseline model, the species has a T of 23.55 years, so the frequency would be around 0.60% per year (60% in 100 years). This value was incorporated along with a survival severity factor of 50% for all cohorts.

Harvest and Supplementation: Not included in the baseline model.

Table 1: *Vortex* values used for the baseline model of the crocodile. See text for more details.

Parameter	Value		
Populations	**1**		
Concordance between environmental variation, reproduction and survival	**0.5**		
Breeding system	**Long-term polygamy**		
Age of first reproduction (♀/♂)	**10/15**		
Density dependent reproduction	**No**		
Annual % adult females breeding (EV)	**100% (10)**		
% adult males in the breeding pool	**20%**		
Maximum number of clutches per year	**1**		
Maximum number of eggs per clutch	**40**		
Maximum age of reproduction	**70**		
Maximum lifespan	**70**		
Mean clutch size (SD)	**27 (10)**		
Sex ratio at birth	**50% (1:1)**		
% Annual mortality (EV)	**Age**	**Females**	**Males**
	0-1	**95 (3)**	**95 (3)**
	1-2	**33 (10)**	**33 (10)**
	2-3	**24 (8)**	**24 (8)**
	3+	**5 (3)**	**5 (3)**
Catastrophes	**Name**	**Annual frequency**	**Effect**
	La Niña-El Niño	**20%**	**Reprod: 50%**
	Generic	**0.60%**	**Mort: 50%**
Initial population size (N_0)	**2,500 individuals**		
Carrying capacity (K)	**5,000 individuals**		

Results of the baseline model

Deterministic results

The demographic values (reproduction, mortality and catastrophes) included in the baseline model can be used to calculate the deterministic characteristics of the population of the model. These values are used to compare them with values observed in other demographic studies of the species and to be able to validate the species and population being modelled.

Generation time (T), which is the average age of reproduction is 23.55 years when averaging both sexes. Value very close to the 23 years for *C. acutus* estimated in O'Grady et al. (2008).

The deterministic population growth rate, describes a population with a positive growth rate (det-r = 0.063). In the absence of stochastic events, the population grows at around 6% per year. This value is close to the growth range for *C. rhombifer* PVA (7% - 10%), which has a higher average in eggs per nest and lower mortality for the cohort of 0 -1 years, among others (Soberón et al. 2000).

The sex ratio of adult individuals is 1:1.88 (males:females). This value is highly variable among populations (Thorbjarnarson 1989), can be very skewed towards females (Sánchez 2001) or towards males (Murray et al., 2015), and may even have no differences between both sexes (Platt et al. 2011). The value of the baseline model is similar to the average values reported for several studies in Florida (1: 2) (Thorbjarnarson 1989).

On the age and sex distribution of the baseline model, the percentage of adults is less than 5%, which differs greatly from results from other studies where the percentage of adults may be between 25.0% and 36.5% (Gaby et al. 1985, Sasa and Chaves 1992, Platt and Thorbjarnarson 2000). However, in studies involving neonates, the percentage of adults is considerably reduced, reaching between 3.0% and 22.3% of the population (Thorbjarnarson 1989, Sánchez et al., 1996, Sánchez 2001, Mauger et al., 2012). It is therefore not surprising that in the baseline model that takes into account the egg stage, adults account for less than 5% of the population.

Stochastic results

When including environmental variation, the baseline model results show a population with a stoch-r = 0.059. And a P (survive) of 1,000. The population grows until reaching and stabilizing in a value of about 4,500 individuals in a period of 15 years; about 90% of the carrying capacity (Fig. 1). This value is among the estimated values to explain the recovery of the Tárcoles River subpopulation after the hunting pressure disappeared (Chaves pers. comm. 2016).

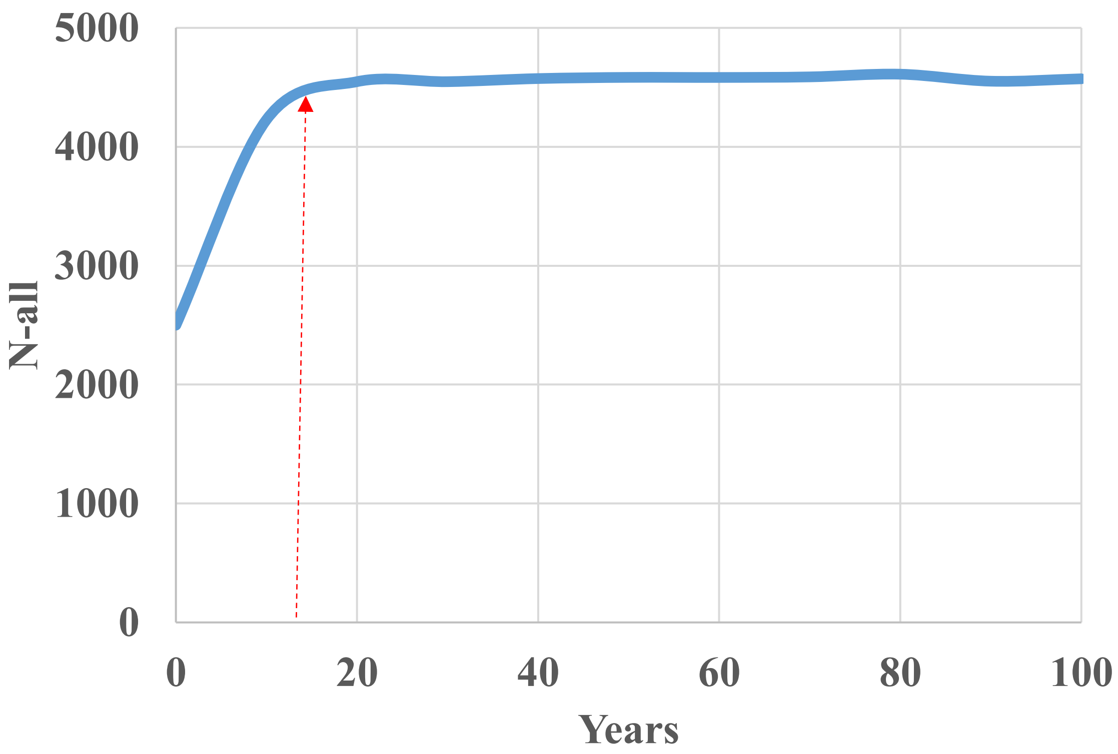


Figure 1: Results of the baseline model for a crocodile population, which shows the average population size over a period of 100 years. See text for more details.

Sensitivity analysis

What are the most important demographic factors affecting population growth?

General sensitivity analyzes were performed on the main demographic rates of the baseline model to determine the parameters that most affect the viability of the population. These analyzes indicate the parameters that could be important in population management and to identify future research in areas of high uncertainty.

Scenario parameters: initial population size

Since the population size of crocodiles varies between different basins of the country, a sensitivity analysis was performed for the initial population size to evaluate how important is the uncertainty of this parameter. In addition to the initial population size of the baseline model of 2,500 individuals, three other scenarios with initial sizes of 250, 500 and 1,000 individuals were all performed with the same carrying capacity set in the baseline model (K = 5,000).

Table 2: *Vortex* output values of crocodile populations with different initial population sizes (N(0)), at the end of 100 years. See text for more details.

N(0)	stoch-r	P(survive)	N-all	N-all/K
250	0.0597	1.000	4613	0.923
500	0.0598	1.000	4573	0.915
1,000	0.0594	1.000	4573	0.915
2,500 (Baseline)	0.0594	1.000	4572	0.914

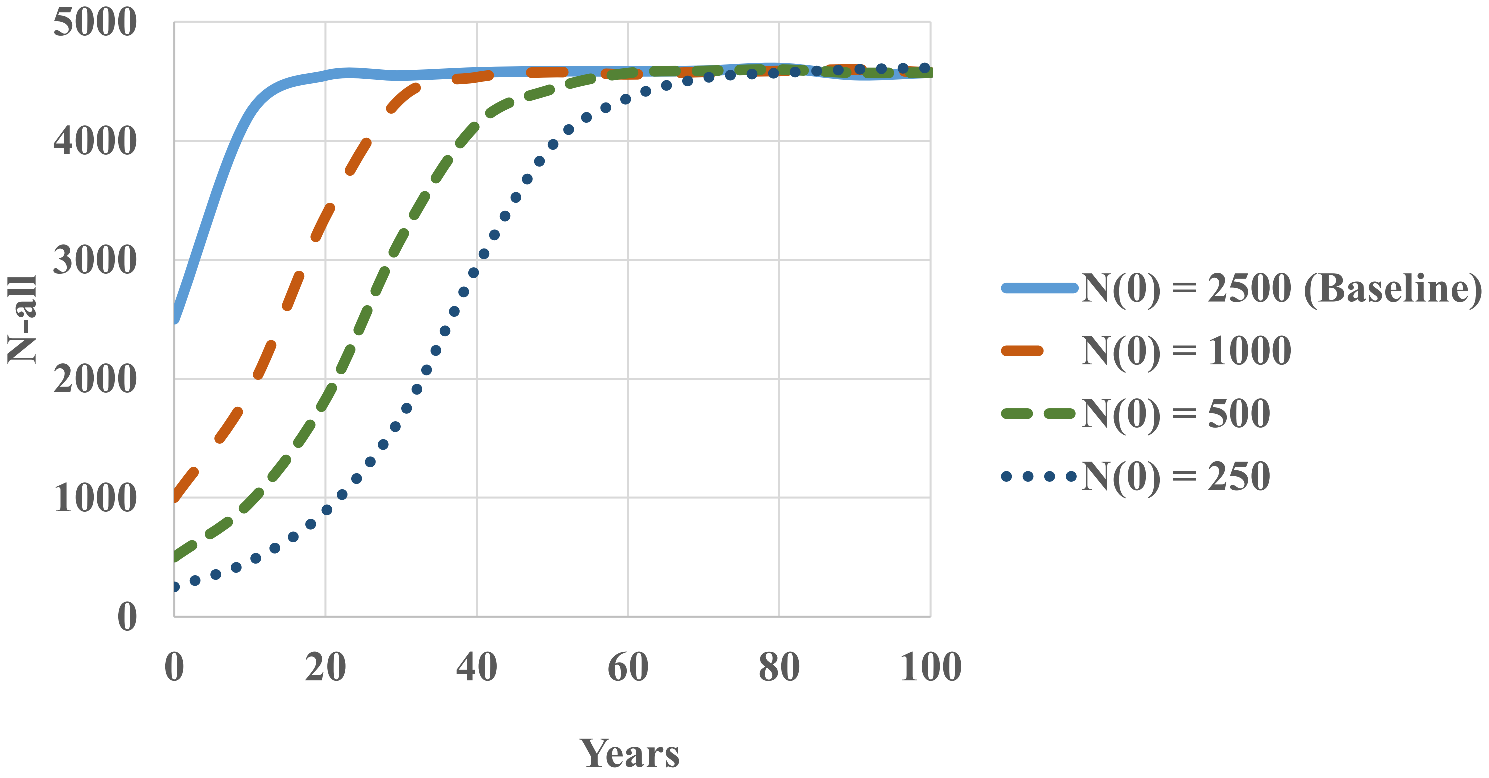


Figure 2: Final population size of the crocodile population, in scenarios with different initial population sizes (N(0)), in a period of 100 years. See text for more details.

Scenario parameters: percentage of females breeding annually

The baseline model considers that 100% of females breeds each year, if it is considered that non-dominant individuals can breed. However, other studies and observations consider that this value may be lower (Thorbjarnarson 1989, J. Bolaños comm. pers. 2016), thus scenarios were made varying this value to 90% and 80%.

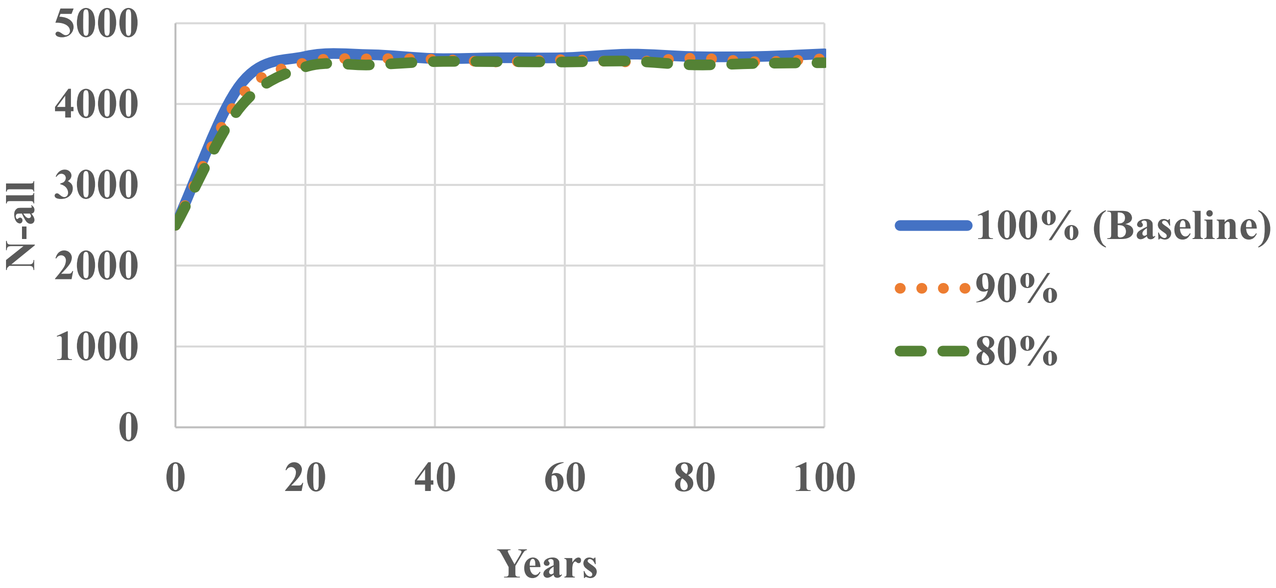
Results

The population of crocodiles remains robust if the percentage of breeding females decreases. Although the growth rate is affected and decreases to a value of around 5%, the population increases until it reaches values close to the carrying capacity, as the base scenario (Table 3, Fig 3).

Table 3: *Vortex* output values at the end of 100 years of crocodile populations with different percentage values of females reproduced annually. See text for more details.

Percentage of females breeding	stoch-r	P(survive)	N-all	N-all/K
100% (Baseline)	0.0594	1.000	4572	0.914
90%	0.0555	1.000	4562	0.912
80%	0.0497	1.000	4512	0.902

Figure 3: Final population size of crocodile population over a period of 100 years, with different percentage values of females reproduced annually (the baseline scenario is included as a comparison). See text for more details.}



Scenario parameters: demographic values

The following parameters were tested with an increase and decrease in the value of the baseline model in ± 10% or ± 1 year, where the range of the tested values was biologically plausible for the species:

- Juvenile mortality in females (1-2 years cohort)
- Juvenile mortality in males (1-2 years cohort)
- Mortality in adult females (10+ years old)
- Mortality in adult males (15+ years old)
- Percentage of males at birth

- Percentage of adult males in breeding pool
- Average clutch size
- Maximum age of reproduction of females (rounded to the nearest whole number)
- Maximum age of reproduction of males (rounded to the nearest whole number)
- Frequency of El Niño - La Niña

Results

Figure 4 shows the resulting stochastic growth rates for each parameter according to the values assesses. The parameters that show the greatest sensitivity in their impact on the stochastic growth rate of the population according to the range of modeled values are: percentage of males at birth, average number of eggs per clutch and reproductive age of the females. The results also show parameters with lower sensitivity: mortality in juvenile females and mortality in adult females. All parameters that showed sensitivity are related to the number of females in the population or their ability to recruit individuals to it over time. Regarding the parameters related to the number of males in the population, as long as there are enough of these to breed with a high percentage of adult females, their role in the recruitment of individuals within the population is fulfilled. The most sensitive parameters are those that need greater attention in research and monitoring projects, so as not to overestimate or underestimate the long-term viability of the population and the effect of possible management strategies.

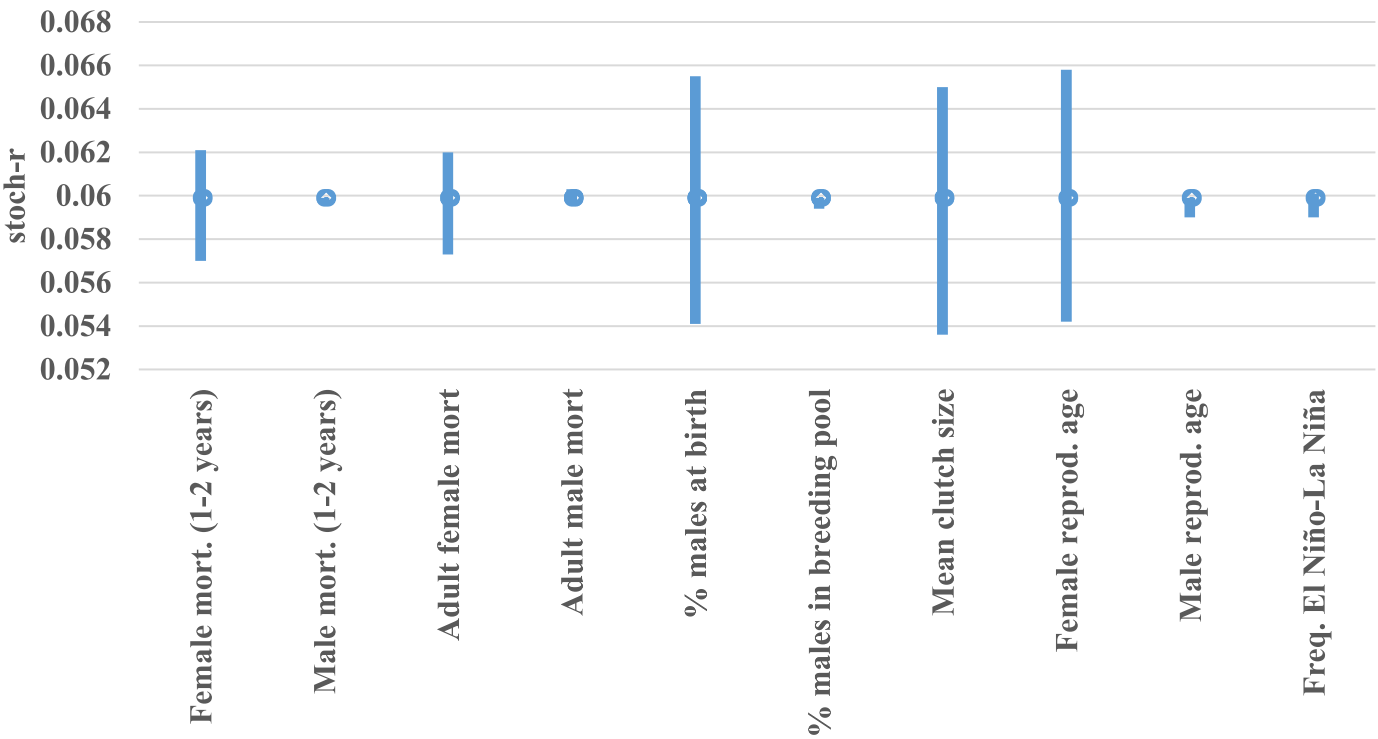


Figure 4: Sensitivity testing of primary parameters for impacts on stochastic growth rate (stoch-r), by changing ±10% the baseline values. The baseline model growth rate is given by the central data point in the figure. Population is most sensitive to uncertainty in those parameters giving the widest range in population growth rates. See text for more details.

What if…?

A recent study in the Tempisque River between 2012-2014 found that the population in this area had a skewed sex ratio to males from the neonate stage (3.5: 1) to the adult stage (1.5:1) (Murray et al. 2015). The sex ratio at birth was a parameter that showed sensitivity in the growth rate, thus a set of scenarios was analyzed to see the long-term effect of a skewed sex ratio on males at birth, on the viability of the population.

Scenario parameters

In this group of scenarios different percentages of males at birth were modeled: 60% (1.5:1), 70% (2.3:1), 80% (4:1). The rest of the input parameters were maintained with the same values as those of the baseline model.

Results

A skewed sex ratio to males at birth has effects on the population growth rate. Table 4 shows that the growth rate decreases by about 1.0% compared to the baseline model when the percentage of males at birth is 60% and if males represent 80% of births, the growth is reduced a 4.5%. With more males in the population the number of females decreases. If this reduction is small the population takes more years to reach values similar to the baseline model in terms of number of individuals, but if the number of females begins to decline too much the population does not grow at the rhythm of the baseline model and its final size is smaller (Table 4, Fig. 5). In the scenarios, the proportion of adult males to adult females is less than the proportion at birth, as a result of the age at which each sex reaches adulthood in the model (10 years in females vs. 15 years in males), but as found by Murray et al (2015) may in fact be lower because the dispersal of juvenile and sub-adult males outside the population to avoid competition with adult males; with the possible effect of increasing the crocodile-human conflict if the individuals that are dispersed settle down near human populations.

Table 4: *Vortex* output values at the end of 100 years, in scenarios with a sex ratio at birth skewed towards males. See text for more details.

Scenario	stoch-r	P(survive)	N-all	N-all/K	Adult males:Adult females
50% males (1:1, Baseline)	0.060	1.000	4622	0.924	0.566:1
60% males (1.5:1)	0.048	1.000	4531	0.906	0.895:1
70% males (2.3:1)	0.033	1.000	4449	0.890	1.497:1
80% males (4.0:1)	0.015	1.000	4014	0.803	2.803:1
85% males (5.66:1)	0.002	1.000	2885	0.577	4.200:1
90% males (9.0:1)	-0.013	0.997	945	0.189	7.135:1

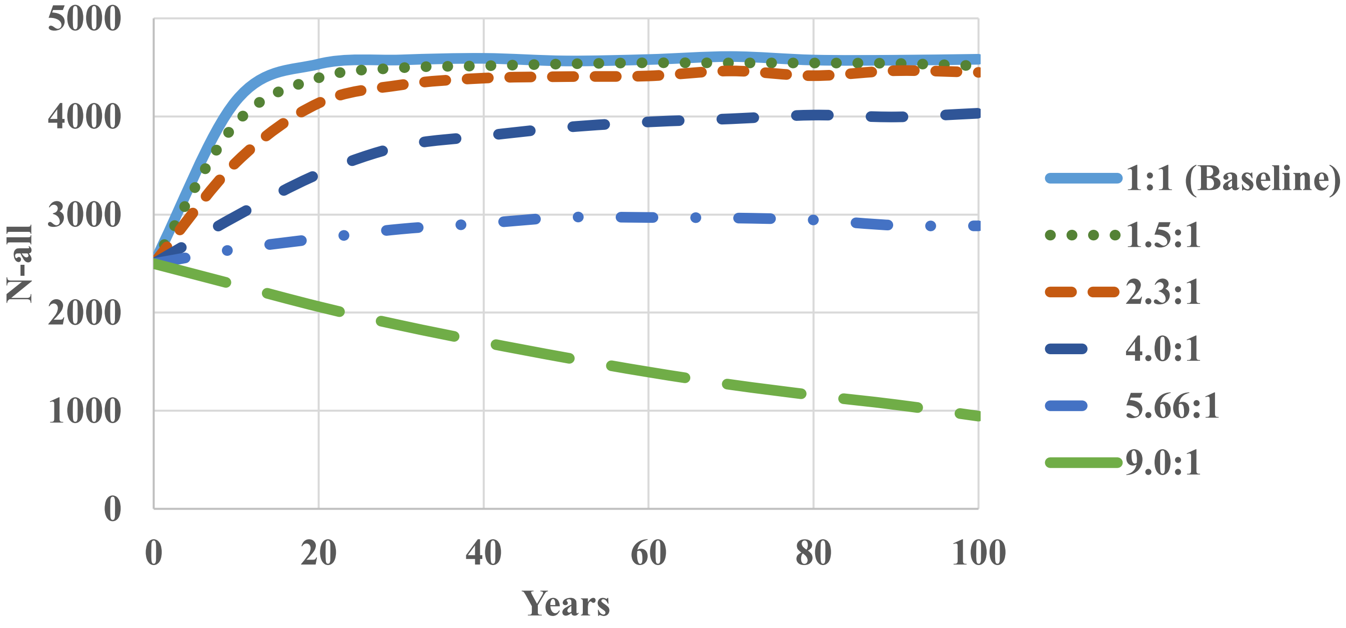


Figure 5: Final population size of crocodiles in a period of 100 years, in scenarios with a sex ratio at birth skewed towards males (the baseline is included as a means of comparison). See text for more details.

Extraction 1

At present, problematic males associated with attacks on humans are removed from the population to avoid further conflict. To assess the effect of removing individuals on sexual ratio and population growth, several scenarios were made where different percentages of adult individuals are removed at different extraction intensities. This scenario was originally designed to investigate the potential effect of extracting individuals on the viability of the population. However, it could also be applied to the dispersion of individuals outside the population to avoid competition of resources.

Scenario parameters

In all the scenarios 10%, 30% and 50% of adult individuals were extracted, and to avoid a possible extinction of the population in all the scenarios the extraction was conditioned to a population greater than 1,000 individuals. Three sets of scenarios were run to test different extraction options.

Group 1: To compare the effect of removing males vs. females, adult individuals of each sex were harvested separated every five years from the simulation, starting in Year 1.

Group 2: To evaluate the effect of the intensity of extraction of individuals, the same scenarios were run but individuals were extracted each year from the simulation instead of every five years.

Group 3: To reduce the population bias caused by an exclusive extraction to either sex in the previous scenarios, an equal percentage of adult males and females were extracted.

Results

Group 1: The extraction of individuals of one sex or another changes the sexual proportion of the population. Thus, the removal of males could decrease a possible conflict between males by the access of females and vice versa if only females are extracted (Table 5). However, no matter the percentage of males extracted - within the range of evaluated values - populations have a growth rate similar or equal to the base model, so the final population size is also similar (Table 5, Fig. 6a). A reproductive system of long-termed polygamy leads to an excess of adult males that cannot find mates to breed. An extraction of adult males opens the option for other males to take the role of breeders, thus maintaining a population similar to that of the baseline model. The default order of *Vortex* events may also have a significant effect on the results. By default, the extraction event occurs after the breeding event, so that adult males are removed after new individuals have entered the population. On the other hand, the results show that extracting females cause a decline in the population and reaches to a value close to zero in the scenario where 50% of the females are extracted (stoch-r: 0.004), which in turn causes a final population size of less than 60% of the carrying capacity (Table 5, Fig. 6b). If adult females are removed, there are no replacements for them within the population, resulting in smaller harems and affecting the recruiting capacity of individuals within the population, and in turn population size is smaller than that of the baseline model.

Group 2: With an increasing frequency on the extraction of males, the population needs a few more years to reach population values similar to those of the baseline model, but there is no major affectation (Table 5, Fig. 6c). This suggests that the surplus of adult males that can become breeders remain high enough to compensate for losses by extraction. A greater frequency in the extraction of females further decreases the size of the population. By reducing the time periods between each extraction event, the population has less resilience and in the case of scenarios where 30% -50% of adult females are removed, the population begins to decrease (stoch-r around - 0.010). What prevents extinction is the condition of not extracting individuals when the population is less than 1,000 animals (Table 5, Fig. 6d).

In real populations, a high extraction of males could cause a lot of damage. If very few males are breeding, the population may have high levels of inbreeding within a few generations and be affected by inbreeding depression. However, crocodiles have such a long generation time that it is not expected a high level of inbreeding within the first 100 years. Also, presumably there is a limit on the number of females with which each male can mate. It may be a high limit, but a male is not expected to be able to breed with an unlimited number of females during the breeding season. Even if there is no physiological limit on the number of females to which each male can mate, if the number of males within the population decreases a lot, they will probably be at a density so low that many females will not be able to find a male to breed.

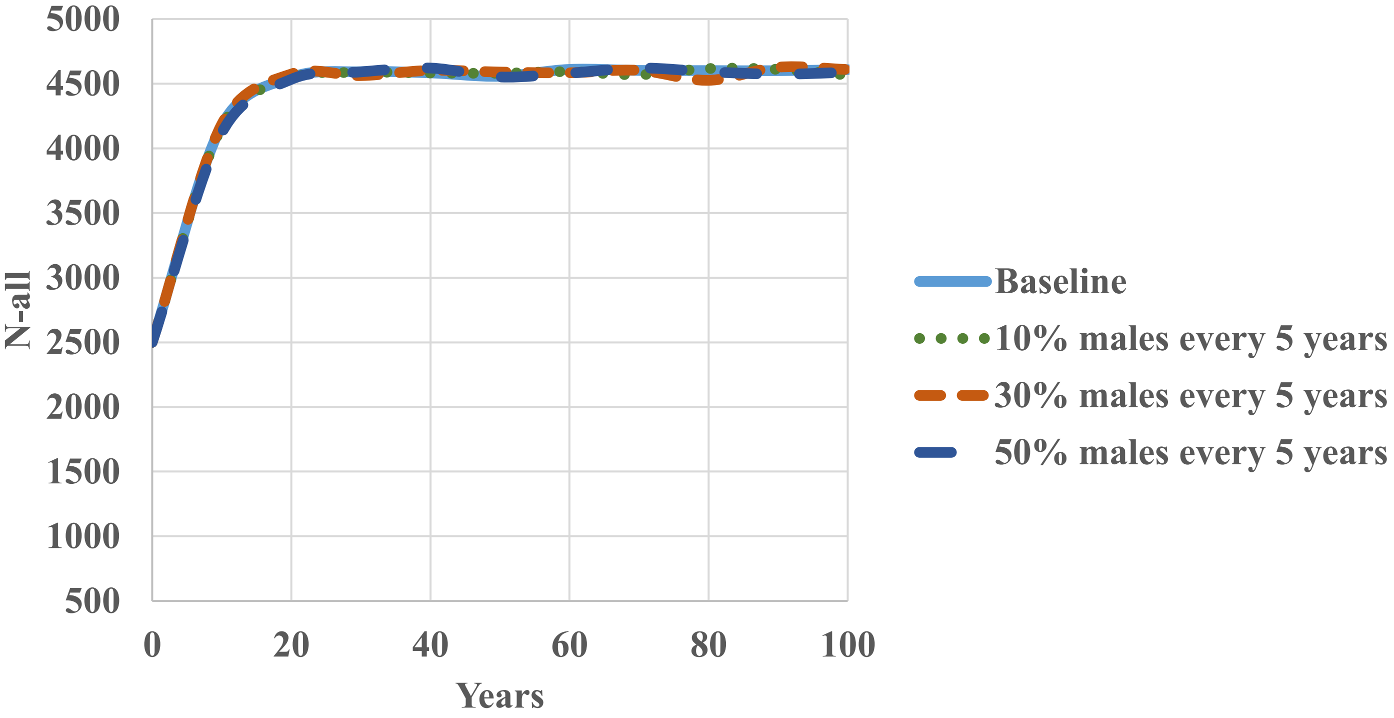
In the scenarios, there is a strange effect, but it could well happen in real life, in which the extraction of males can lead to an increase in the population growth rate. This can happen because the removal of males allows a high number of females in the population near carrying capacity. Since the number of females controls the rate of population growth (if the remaining males can mate with all females), a higher proportion of females leads to a higher growth rate.

Group 3: When extracting an equal percentage of adult males and females each year, the bias towards either sex in this stage decreases reaching values that approach sexual parity (Table 5). Extracting individuals of both sexes causes the population to decrease faster and its size is slightly smaller than previous scenarios where only females were extracted (Table 5, Fig. 6d,e).

Table 5: Vortex output values at the end of 100 years, in scenarios with different percentages of extraction of adult individuals. See text for more details.

Scenario	stoch-r	P(survive)	N-all	N-all/K	Adult males : Adult females
Baseline	0.060	1.000	4609	0.922	0.560 : 1
10% males every 5 years	0.059	1.000	4567	0.913	0.492 : 1
30% males every 5 years	0.060	1.000	4609	0.922	0.384 : 1
50% males every 5 years	0.060	1.000	4588	0.918	0.317 : 1
10% females every 5 years	0.049	1.000	4483	0.897	0.688: 1
30% females every 5 years	0.028	1.000	4358	0.872	1.080 : 1
50% females every 5 years	0.004	1.000	2907	0.581	1.881 : 1
10% males every year	0.059	1.000	4574	0.915	0.279 : 1
30% males every year	0.059	1.000	4540	0.908	0.112 : 1
50% males every year	0.059	1.000	4559	0.912	0.056 : 1
10% females every year	0.014	1.000	3721	0.744	1.861 : 1
30% females every year	-0.010	1.000	964	0.193	2.940 : 1
50% females every year	-0.011	1.000	890	0.178	2.921 : 1
10% both sexes every year	0.013	1.000	3647	0.729	0.701 : 1
30% both sexes every year	-0.001	1.000	942	0.188	0.774 : 1
50% both sexes every year	-0.011	1.000	867	0.173	0.802 : 1

a


N-all
5000
4500
4000
3500
3000
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2000
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0
20
40
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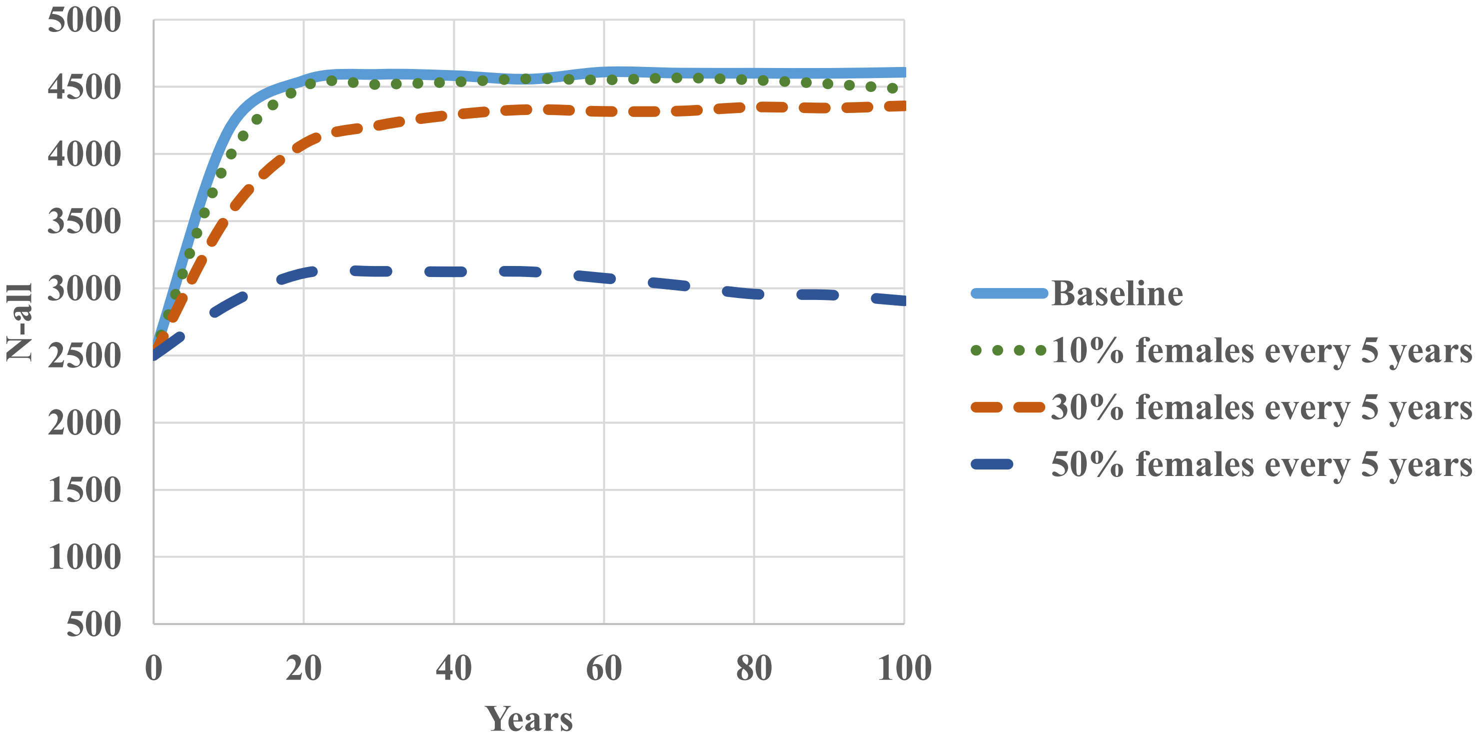
Years
Baseline
10% males every 5 years
30% males every 5 years
50% males every 5 years

b


N-all
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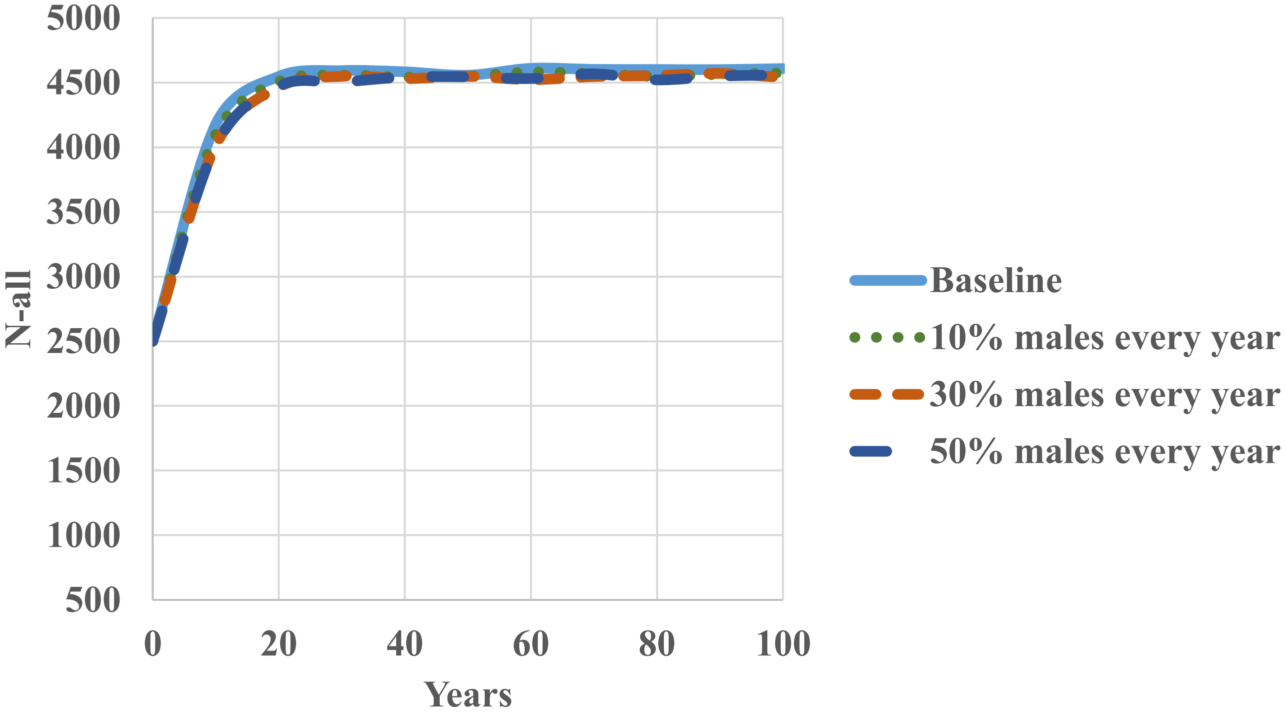
10% females every 5 years
30% females every 5 years
50% females every 5 years

c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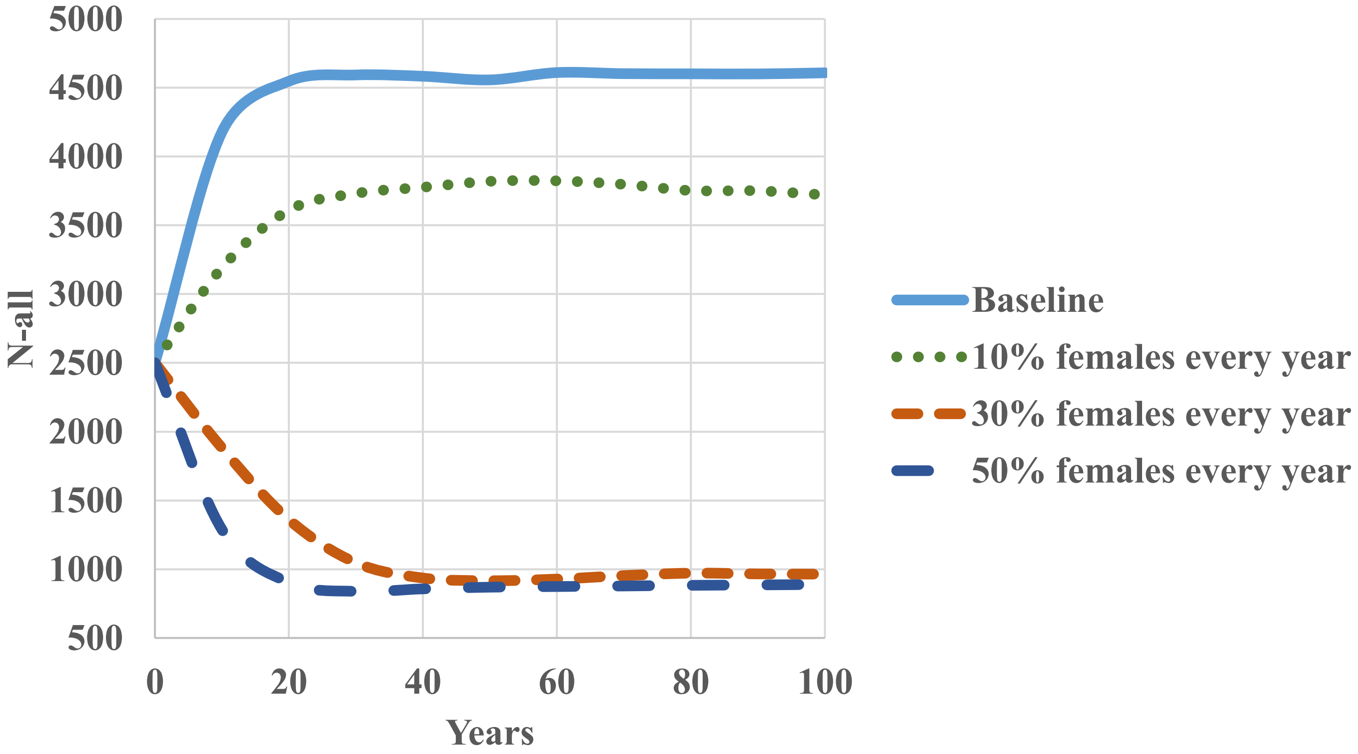
Baseline
10% males every year
30% males every year
50% males every year

d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50% females every year

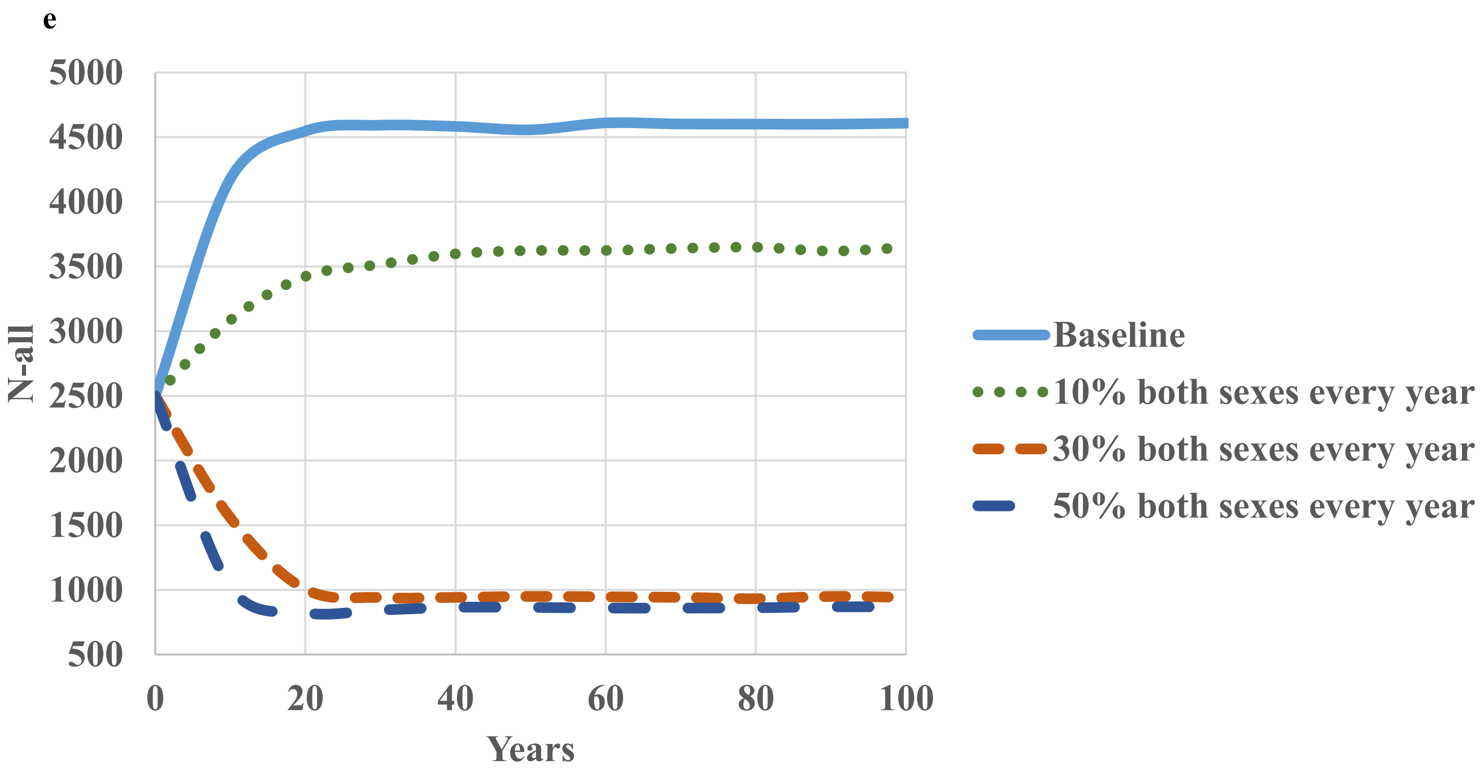


Figure 6: Final population size of crocodiles, in scenarios with different percentages of extraction of adult individuals (the baseline is included as a means of comparison): a. males every five years, b. females every five years, c. males every year, d. females every year, d. both sexes each year. See text for more details.

Extraction 2

The robustness of the population to the extraction of adult males in the previous scenarios raises the question of what percentage of extraction of these is necessary for the population to decline? Although it is more out of curiosity than to establish a recommendation for extraction.

Scenario Parameters

From a strict demographic point of view, in Vortex, breeding adult males will breed with all the adult females available. Therefore, the algorithm does not consider the spatial arrangement of individuals and the environmental and natural history difficulties that a small number of males can mate with all available females. Because of this factor, in this group of scenarios the number of females in a harem was limited to a maximum of 10 per breeding male (although it could well be a larger number). In the harvest section, 90%, 95% 97%, 98%, 99% and 100% of adult males were removed each year, as were the previous scenarios. In addition, like the previous scenarios, the extraction was conditional on the population being greater than 1,000 individuals to avoid a possible extinction of the population in all scenarios.

Results

To make the population decline by harvesting adult males would entail a great effort. Extraction of 95% or more is required for the final population size to be below 90% of the carrying capacity, and it is necessary to remove all adult males every year for the population to fall below of the initial population of 2,500 individuals (Table 6, Fig. 7), in this scenario, the population declines to a degree that the difference between the number of adult males and adult females decreases when compared to other scenarios of the same group (Table 6).

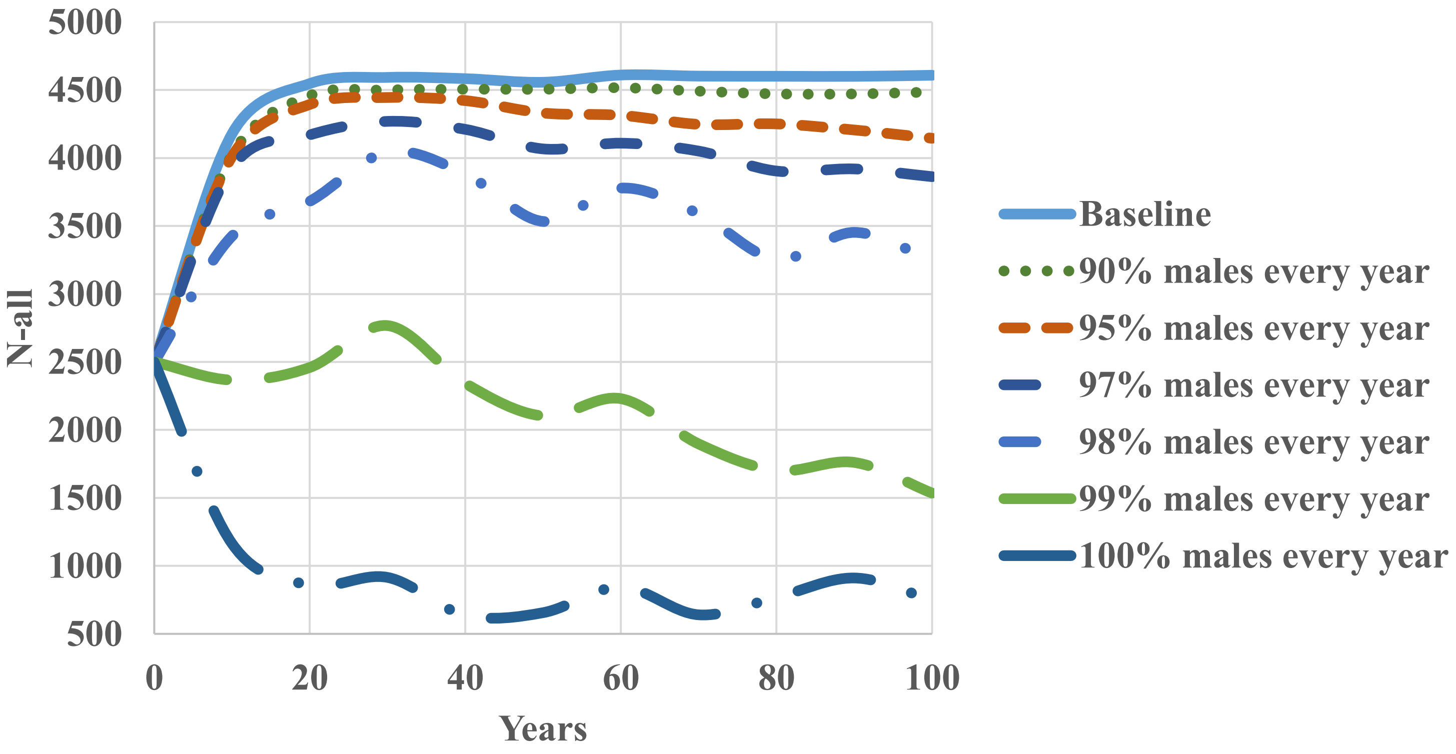
Other factors that may destabilize a population when extracting adult males are the effect of density-dependent reproduction (specifically Allee effects in cases of highly skewed sex ratios) and do the extraction events before the males can breed with the females, avoiding recruitment of individuals into the population. In the first case, if the number of males is very low, it will probably have a density so low that many females will not be able to find a male to mate with. However, it could be very difficult to know the form of that density-dependent relationship. In the second case, logistic complications would be too difficult to apply in real life.

This group of scenarios re-emphasize characteristics of the species that make it so resilient, such as its polygamous breeding system, the number of eggs per nest and its long-life expectancy. These factors contribute to the fact that a handful of adult males can recruit a high number of individuals when breeding with several females during many years of life, so any management actions aimed at controlling population size should take females into account to do it.

Table 6: *Vortex* output values at the end of 100 years, in scenarios with percentages of extraction of adult males greater than 90%. See text for more details.

Scenario	stoch-r	P(survive)	N-all	N-all/K	Adult males : Adult females
Baseline	0.059	1.000	4609	0.922	0.560 : 1
90% males every year	0.056	1.000	4485	0.897	0.064:1
95% males every year	0.047	1.000	4145	0.829	0.062:1
97% males every year	0.037	1.000	3862	0.772	0.056:1
85% males every year	0.023	1.000	3250	0.650	0.063:1
99% males every year	-0.002	1.000	1535	0.307	0.061:1
100% males every year	-0.012	0.995	749	0.150	0.100:1

Figure 7: Final population size of the crocodile population in scenarios with annual percentage extraction of adult males above 90% (the baseline is included as a means of comparison). See text for more details.



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