

Climate Change on Crocodilians: Modeling the Effects of Variations in Rainfall on Crocodilians and their Ecosystem

*Karin Ebey**

Los Alamos High School, Los Alamos, NM

ABSTRACT

Climate change is projected to cause significant changes to global precipitation patterns. To explore how crocodilians and their ecosystems are impacted by variations in rainfall, a model was created using a novel adaptation of the Lotka-Volterra equations. The model uses a time step of months and includes a crocodilian population, three plant species, and eight other animal species. Each year, populations are impacted by predator-prey interactions and reproduction. Rainfall only impacts the ecosystem through the plant populations. This model was validated by running it with Louisiana rainfall data from 1970-2018 and comparing the outputs to measured alligator nest count data from that time. The model populations followed similar patterns to the nest count data, showing that the model accurately describes how rainfall affects the ecosystem. Changes in the amount of rainfall cause the populations to increase or decrease in proportion to the change in rainfall. Changes in the timing of rainfall affect the seasonal variation of plant populations, which causes animal populations to increase or decrease depending on whether the plant populations are above or below average when they reproduce. Using the results of this model, a management program was designed with specific recommendations to protect crocodilians and their ecosystems from rainfall variations.

KEYWORDS: Crocodilians, Simulation, Rainfall

INTRODUCTION

Climate change is projected to have many effects on the earth including higher mean global temperatures, increased hurricane severity, and changes in global precipitation patterns (Walsh et al., 2014; USGCRP, 2017; National Aeronautics and Space Administration, 2019). Changes in global precipitation patterns are likely to have a significant impact on ecosystems because water is essential to life (USGCRP, 2014). The timing and amount of precipitation determine the amount of energy available for use in ecosystems through the growth of plants (Zeppel et al., 2014). In the future, precipitation is predicted to be more extreme with some regions receiving increased rainfall while others suffer from drought. Also, the timing of precipitation is projected to shift, for example, precipitation shifting from summer to winter (Walsh et al., 2014).

There are 25 species of crocodilians living in wetlands around the world (Grigg and Kirshner, 2015). Crocodilians are important natural resources because as apex predators, they are

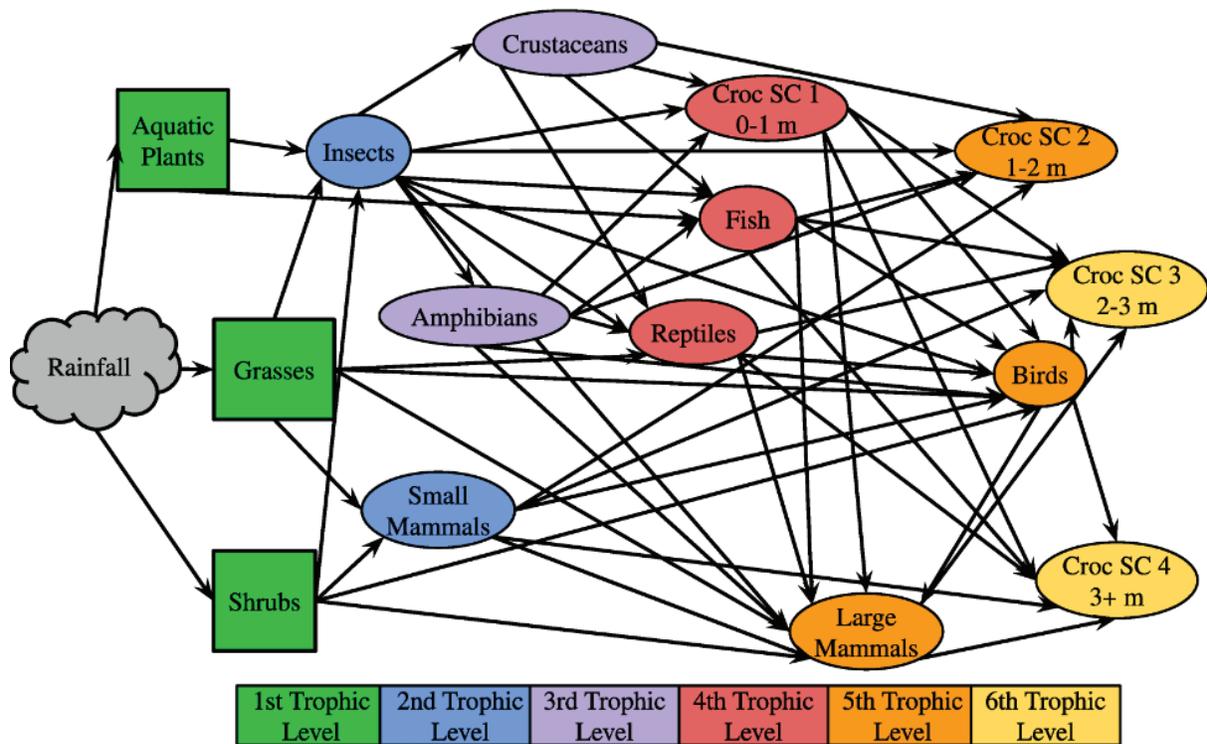


Figure 1. The food web modeled. Arrows show the flow of energy through the ecosystem pointing from prey species to their predator species.

essential for maintaining ecosystem health, and they serve as ecosystem engineers creating extensive burrows and nest mounds which provide other species habitat and access to water (Somaweera et al., 2020). Crocodylians are also important culturally and economically through tourism and the sale of their hides (Grigg and Kirshner, 2015; Somaweera et al., 2020). In the coming years, crocodylians and their ecosystems are likely to be impacted by climate change through changes in their habitat, prey availability, and their temperature dependent sex determination (Stevenson, 2019), although temperature dependent sex determination is unlikely to significantly affect crocodylians because they produce females at both high and low temperatures (Gonzalez et al., 2019). This project focuses on the effects of variations in rainfall on the populations of species in crocodylian's ecosystems. Knowledge of how crocodylians may respond to climate change is essential to prepare management programs to protect them. The purpose of this experiment was to better understand how crocodylians and their ecosystems are impacted by variations in rainfall patterns with the goal of developing a management program to keep their ecosystem stable. In this project, the effects of variations in the magnitude and timing of rainfall on the ecosystem were explored to better understand how changes in rainfall affect all the species through interspecific interactions in the crocodylian's ecosystem.

EXPERIMENTAL METHODS

For this experiment, a computer model of a crocodylian population in a representative general ecosystem in a generic location was created using an adaptation of the Lotka-Volterra equations. A general ecosystem is used to get a basic understanding of the effects of variations

in rainfall on crocodilians as a first step towards creating detailed models of each crocodilian species for accurate and specific management information. A model was used because it allows exploration of how variations in rainfall affect ecosystems in a controlled setting and without any risk to the species. Additionally, a model allows for the projection of the effects of more extreme rainfall patterns than have been observed to date (Gotelli, 2008).

Model

The model was created by writing a code using the Python 3.6.1. language. This model includes a crocodilian population, three plant types, and eight other general animal classes, for example, fish or birds, as shown in Figure 1 and Table 1. The classes included in the model are representative of typical species in aquatic ecosystems inhabited by crocodilians. In this work, these classes are referred to as species because each class is modeled as one population. In the food web in Figure 1, the species are arranged by trophic level, with arrows showing energy flow through the ecosystem (National Geographic, 2019). The food web is simplified using a single population for each representative class and simplified predator-prey interactions, to give a basic understanding of a generic crocodilian ecosystem. The crocodilian population is modeled with four size classes (SC). Crocodilians cannibalize their young, so hatchling crocodilians are a prey source for the adults (Delany et al., 2011). The other animal species are modeled as homogenous populations, which are assumed to not cannibalize themselves. Plants are modeled as biomass in kilograms of plant matter. In Table 1, each species individual mass, reproductive rate, hatch rate, and energy needs are shown. The animal species' energy needs were calculated based on the mass of the animals and whether they are ectothermic or endothermic (Nagy et al., 1999). The model uses discrete time, with time modeled as separate steps, to represent the seasonal impact of different processes on each species, with predator-prey interaction occurring each month, animals reproducing at different times of the year, and seasonal rainfall variations (Gotelli, 2008).

Model Summary

The Lotka-Volterra equations are the standard way to model predator-prey interactions (Gotelli, 2008). For this project, a novel adaptation of the Lotka-Volterra equations was developed based on Gotelli, 2008. Some limitations of the Lotka-Volterra model include that it describes only a two species system, that reproduction occurs each time step, that prey species make up a fixed proportion of the predator's diet, that the system's energy is constant, and that predator populations do not die out immediately without prey (Gotelli, 2008). The model created for this experiment is innovative by modeling a complex ecosystem with many species, having species reproduce only in specific months as they do in the wild, using a dynamic approach to vary predator diets to match prey abundances, including plants to make the system's energy dynamic, and modeling starvation deaths proportional to the amount of prey with predators dying out if there is no prey.

In the model, rainfall only affects the ecosystem through the plant populations. Every month the populations are affected by predator-prey interactions, which cause prey to die from being consumed and predators to die if their energy needs are not met. Plants reproduce every month and animals reproduce only in certain months as shown in Table 2. Once a year the crocodilian population ages with some members of each size class moving up to the next.

The equations used are described in the Appendix.

Species	Mass (grams)	Reproductive Rate (young/female)	Hatch Rate (percent of young that are viable)	Mass Based Energy Needs (grams/year/individual) (calculated based on Nagy et al., 1999)
In: Insects (Snallshire and Swash, 2014)	1	300	5%	23
Sm: Small mammals (Lee, 2013)	340	8	55%	41040
Cr: Crustaceans (Dunover, 2016)	32	350	10%	285
Am: Amphibians (Mitchell, 2019)	45	2000	5%	385
Fs: Fish (Indiana Division of Fish and Wildlife, 2012)	340	6000	0.7%	2990
Re: Reptiles (Wilson, 2019)	230	10	50%	2090
Br: Birds (Cornell Lab, 2017)	680	8	60%	76320
Lm: Large mammals (National Park Service, 2016)	45000	3	83%	737640
Croc: Crocodilians (in four Size Classes [SC]) (Grigg and Kirshner, 2015)	SC1-500 SC2-10000 SC3-30000 SC4-75000	40	30%	SC1-3280 SC2-51840 SC3-138600 SC4-312840

Table 1. The animal species in the model. All are homogeneous populations except for the crocodilians. Abbreviations given in Column 1 are used in Table 2.

Rainfall Effects on Plants

Plants die if the amount of rainfall received varies from their water needs, either higher or lower (Good et al., 2017). Aquatic plants require 3 inches of rain each month; grasses, 4.3 inches; and shrubs, 4 inches (Davis and Fromme, 2016; University of California, 2019). Plants die at a higher rate when there is too little rain than too much (Good et al., 2017). Rainfall also affects plant growth, that is their reproduction defined as the addition of biomass to the population either through physical growth or production of seeds, which occurs every month. The plant growth rate varies by month (Orsenigo et al., 2014) as shown in Table 2. Plant growth is limited by a carrying capacity determined by the amount of rainfall in the previous season. Although other factors affect plant growth, in this simplified model their effects are assumed negligible to focus on the effects of variations in rainfall.

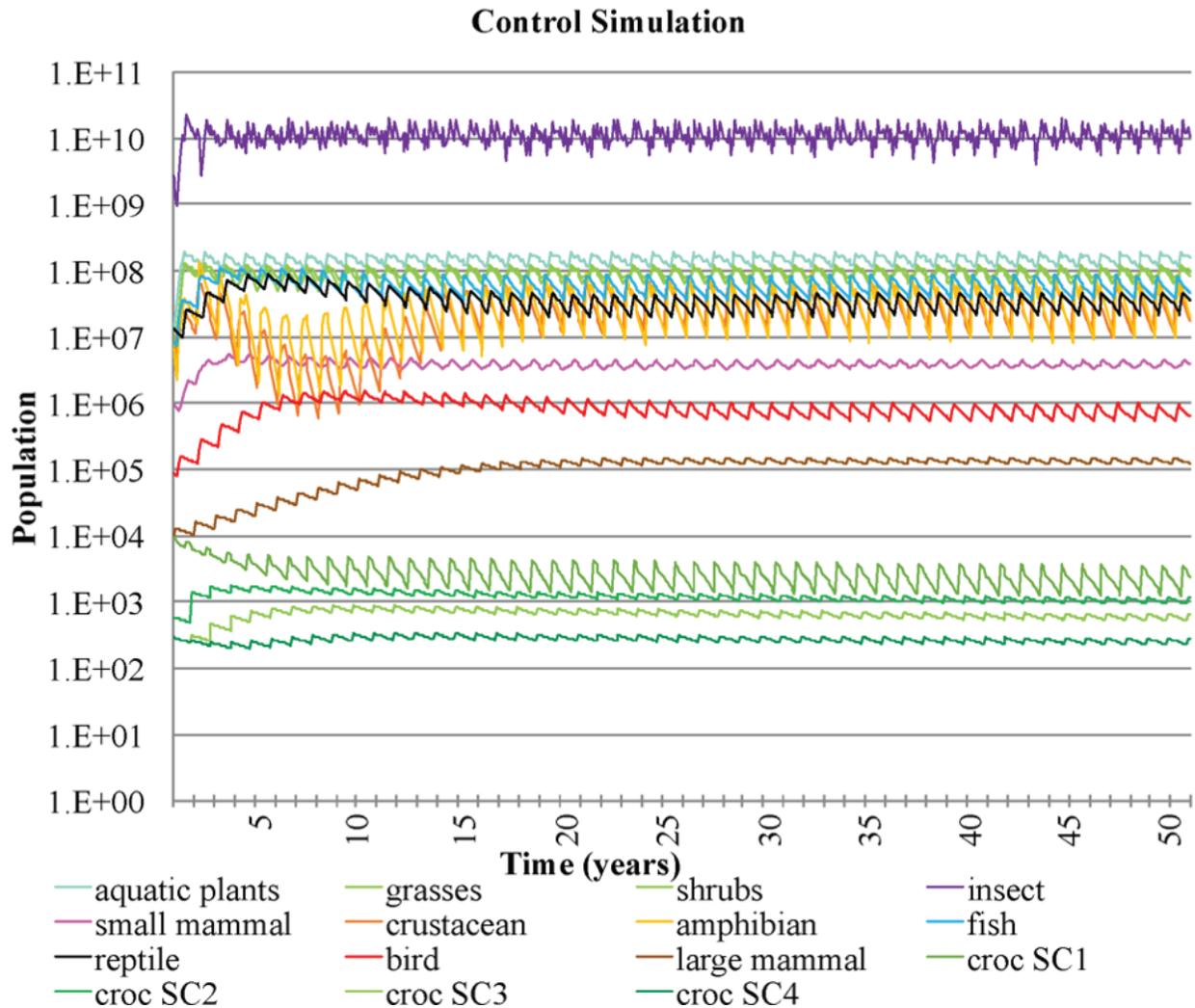


Figure 2. The control simulation, with normal rainfall values as shown in Table 2. Population is plotted as a function of time in years. The populations are plotted using a logarithmic scale to show all the populations in proportion to one another.

Predator Prey Interactions

Each month, predator and prey populations interact with one another as shown in Figure 1, resulting in consumption and starvation deaths. In this simplified model, it is assumed that all individual deaths can be accounted for by either starvation or consumption. From these interactions, prey dies from being consumed and predators die in proportion to the fraction of their energy requirements not met. Crocodylians do not have food preferences and consume species in proportion to their abundance (Grigg and Kirshner, 2015); this trait was assumed for all predators in this model. For predators that consume multiple species of prey, a dynamic approach was taken to divide their energy requirements among their prey species. The proportion of the predator’s diet that a certain prey species fulfills varies from month to month based on their abundance relative to the other prey species.

Season	Winter			Spring			Summer			Fall		
Month	1	2	3	4	5	6	7	8	9	10	11	12
Normal Rainfall (Louisiana averages inches) (National Weather Service and National Oceanic and Atmospheric Administration)	5.23	3.46	3.66	3.33	5.20	6.85	5.63	4.86	5.26	4.90	4.43	4.68
Proportion of Yearly Rain	21.5%			26.75%			27.5%			24.25%		
Species Reproducing (Wilson, 2019; Indiana Division of Fish and Wildlife, 2012; Lee, 2013; Snallshire and Swash, 2014; Grigg and Kirshner, 2015; Dunover, 2016; National Park Service, 2016; Cornell Lab, 2017; Mitchell, 2019)	In	In Lm	In Sm Cr	In Sm Cr Am Fs Br	In Sm Cr Am Fs Br	In Sm Cr Am Fs	In Sm Am Re	In Sm Re Croc	In Sm	In	In	In
Plant Growth Rate (Orsenigo et al., 2014)												

Table 2. A year in the model. The normal rainfall is the monthly averages for Louisiana from 1970-2018 and is used for the control simulation. Animals reproduce in only certain months of the year as they do in the wild. Plants grow every month, but their base growth rate varies from season to season.

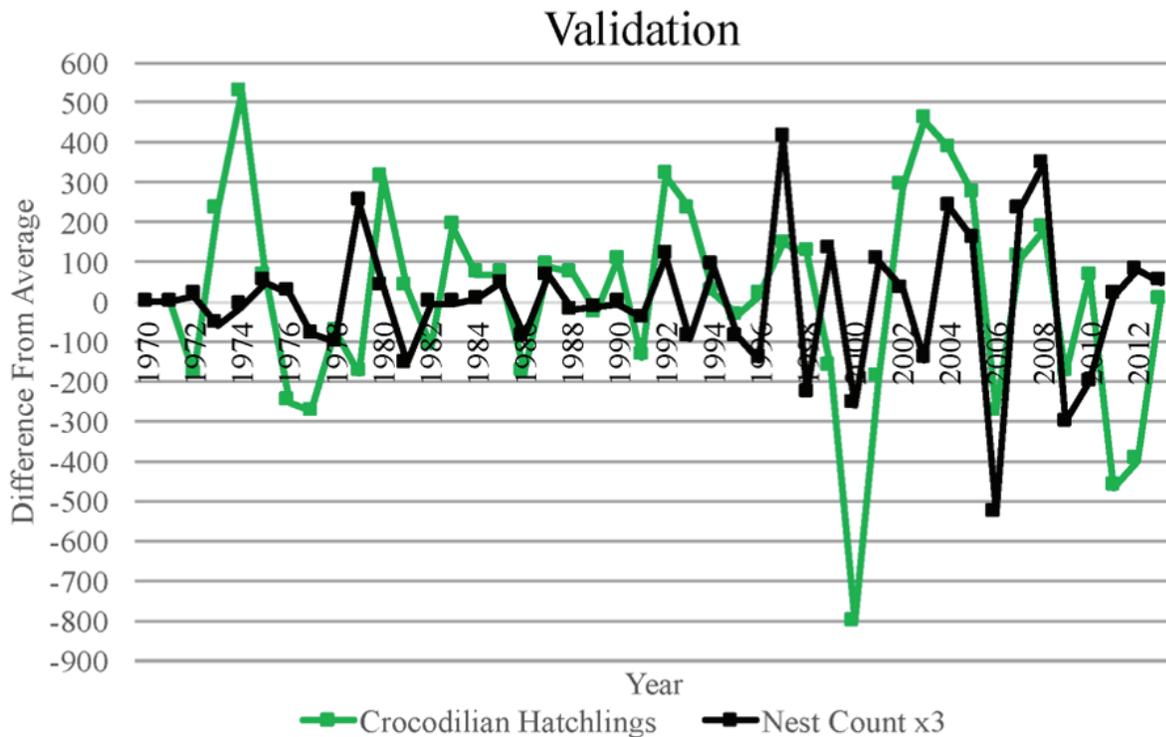


Figure 3. The detrended nest count data and crocodilian hatchling data from the model. The detrended nest count data is tripled to allow for easy comparison to the crocodilian hatchling data in the plot. The trends in the two data sets are compared for similarity, rather than exact magnitudes, as many factors affect the wild populations that are not included in the model. After 1985, the crocodilian hatchling population follows a similar pattern to the nest count data.

Animal Reproduction

Animal reproduction occurs in certain months for each species based on when they reproduce in the wild as shown in Table 2. In this simplified model, animal reproduction is limited by the species prey populations (National Geographic, 2019), and all other factors affecting reproduction like habitat quality are assumed negligible. Reproduction is limited by a carrying capacity, set by the species' prey populations. The number of possible young can exceed the carrying capacity, but the actual number of young never does.

Crocodilian Aging

Once a year the crocodilians age. A small portion of each size class moves up to the next one because individuals spend several years in each size class (Grigg and Kirshner, 2015). Changes in size classes are limited by the amount of prey in the system because growth requires energy.

Control Simulation

To establish a baseline, the simulation was first run with normal rainfall values as shown in Table 2. This control simulation was run for 50 years, as shown in Figure 2, where all the

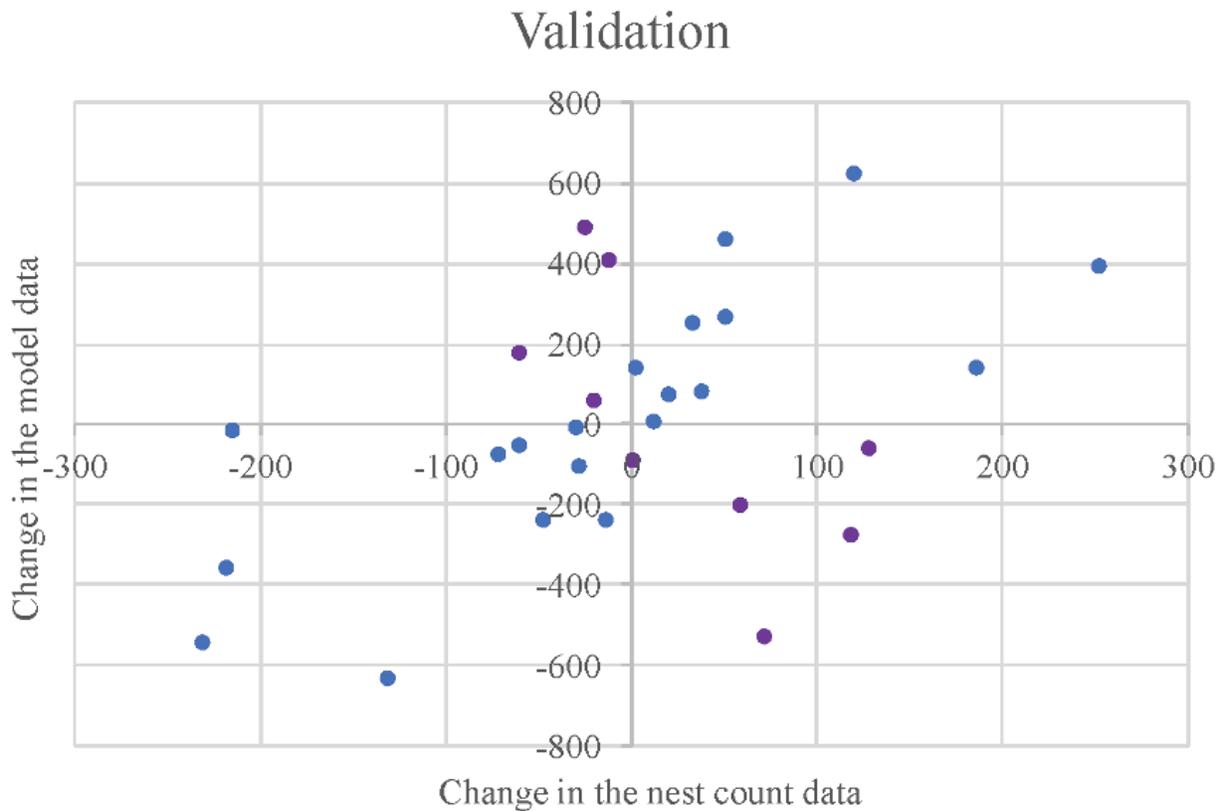


Figure 4. Scatter plot of the year to year change in the nest count data (x-axis) and the change in the model data (y-axis). Points in quadrants I and III are blue and represent years when the nest count and model data followed the same trend, and points in quadrants II and IV are purple and represent years when they did not follow the same trend. 20 of the 29 points are in quadrants I and III.

populations are plotted as a function of time. The populations settle in the first decade and are arranged based on the food chain, where prey have higher populations than their predators. Oscillations each year are due to reproduction.

Validation

A model must be validated with data from the real system (Gotelli, 2008). To validate this model, it was run using Louisiana rainfall data from 1970 to 2018 (National Centers for Environmental Information and National Oceanic and Atmospheric Administration, 2019). This simulation was initialized by running it for nine years with normal rainfall to allow the populations to settle and then with the Louisiana rainfall data. The model results were compared to Louisiana alligator nest count data from 1970 to 2018 (Louisiana Department of Wildlife and Fisheries, 2019). The nest count data approximates the alligator hatchling population, so the crocodilian size class 1 population in the model was used for comparisons. The raw nest count values (not shown) have an upward trend reflecting the alligator's endangered status in the 1970s and the significant conservation efforts since then (Louisiana Department of Wildlife and Fisheries, 2019). Nest count data is affected by the time of year, time of day, and habitat type surveyed (Chabreck, 1966).

Many factors affect wild alligator populations including human interactions, hurricanes, temperature, and habitat quality (Lance et al., 2010; Louisiana Department of Wildlife and Fisheries, 2019; Grigg and Kirshner, 2015). These factors were not accounted for in the model, so the model data cannot be directly compared to the nest count data. To remove the significant increase due to conservation from 1970 to 1990, nest count data was detrended by calculating a five-year running average and subtracting the average from the data, removing the overall increasing trend in the nest count data due to conservation to examine the year to year variation in the populations. This detrending does not remove the effects of other factors on the nest count data. The crocodilian size class 1 population data was also detrended by calculating the average population and subtracting that from the yearly average, so the model data could be compared to the nest count data as shown in Figure 3. The detrended data are centered around zero, as they represent the difference from the average. If the values are greater or less than zero, then the population is above or below average, respectively. The general pattern of the variations in the nest count data was compared to the variations in the crocodilian hatchling (size class 1) population because the nest count data was affected by factors not included in the model.

The crocodilian hatchling population in the simulation generally followed the pattern of the nest count data as shown in Figure 3, but the correlation is not perfect. For the first 15 years of the Louisiana rainfall data, the variations in the model population do not correlate significantly with the variations in nest count, likely because those were the first years of taking nest count data, so the counts may not be as accurate. From 1985 on, the model population variations correlate with the variations in the nest count data. When the nest count data is above or below average, the model population is also above or below average, well demonstrated in 1985–1987 and 2004–2009, where the model hatchling population variations are the same as the nest count variations.

To get a quantitative understanding of the correlation, for both data sets, the year to year difference in the detrended data was calculated and compared as shown in Figure 4, with

each point being the change in the nest count data (x-axis) and the change in the model data (y-axis) for a specific year. In Figure 4, only data from after 1985 was used since there was little correlation between the nest count and model data prior. A positive value means that the population increased compared to the previous year and a negative value means that it decreased. Points in quadrants I and III represent years when the nest count data and the model data both increased or decreased respectively, whereas points in quadrants II and IV represent years when the nest count data and the model population followed a different pattern. The majority of the points, 20 out of 29, fall in quadrants I and III as shown in Figure 4.

Differences are due to uncertainties in both the data and the model. The nest count data is the best population data available for crocodilians, despite its limitations (Chabreck, 1966). The model does not perfectly represent the ecosystem as it does not include many factors that affect the populations. For example, the model is more sensitive to changes in rainfall than the real system. In the validation simulation, the insect population in the model died out

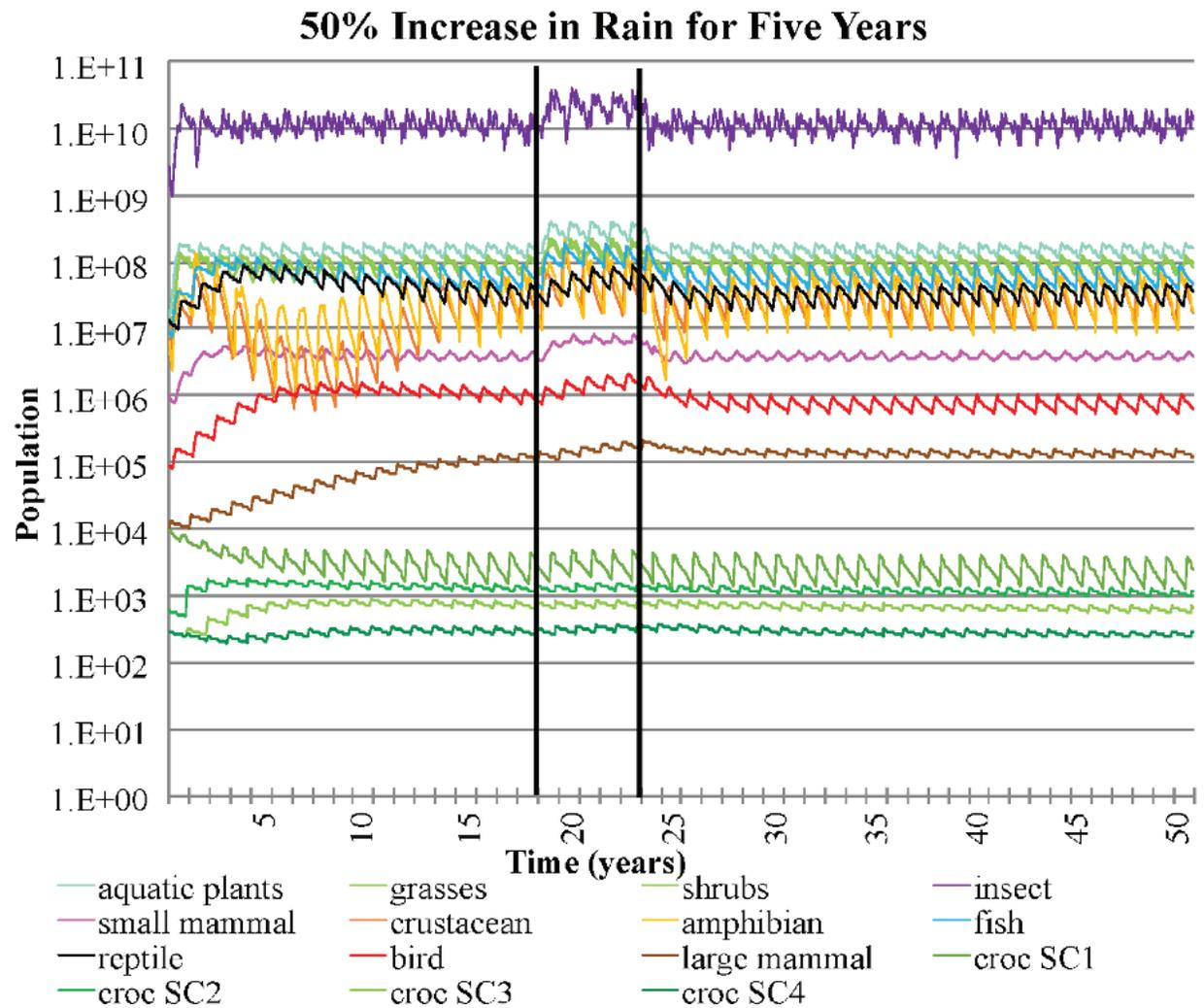


Figure 5. The populations with 19 years of normal rainfall, five years with a 50% increase in rainfall, and normal rainfall for the remainder of the simulation in the same format as Figure 2. In all plots, vertical lines indicate when the rain is changed. The populations increase in response to the rainfall change and return to normal quickly when the rain returns to normal.

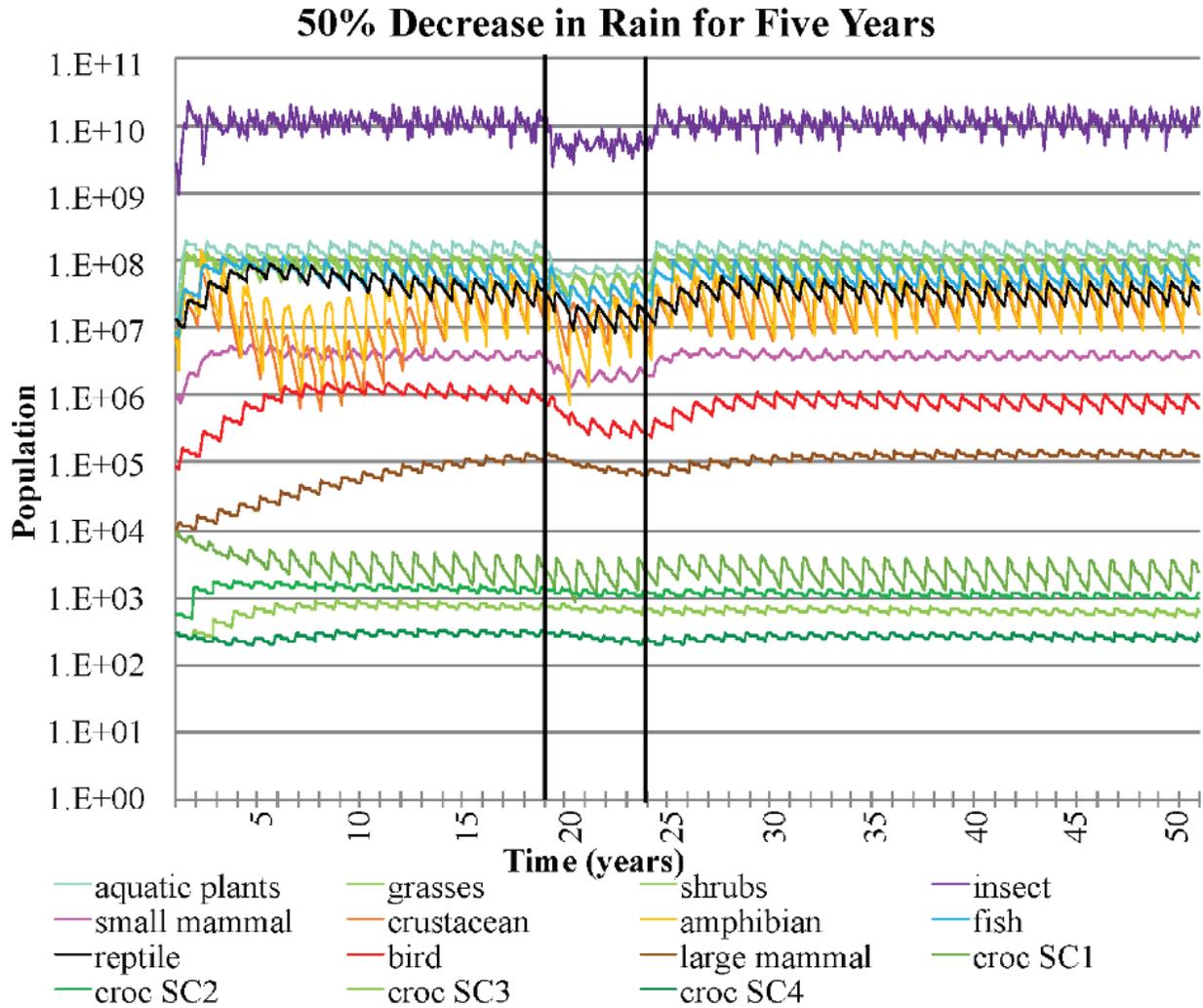


Figure 6. The populations with 19 years of normal rainfall, five years with a 50% decrease in rainfall, and normal rainfall for the remainder of the simulation in the same format as Figure 2. The populations drop in response to the rainfall change and return to normal quickly when the rain returns to normal.

in 2016. This occurred because there was an unusually large amount of rainfall after several months with little, causing the insect's predator populations to increase, while the insect population was low. Given the limitations with the nest count data and the limitations with the model, the correlation observed in response to specific rainfall conditions shows that the model describes how crocodilian populations respond to changes in rainfall. This model thus can be used to explore and predict how crocodilians and their ecosystems may respond to new rainfall patterns.

Variations in Rainfall

Once the model was validated it was then run with variations in rainfall. Over 50 simulations were run. First, the simulation was run with variations in the amount of rainfall, with normal rainfall for 19 years, then increased or decreased rainfall for 5, 10, 15 years, and finally normal rainfall for the rest of the simulation. Many magnitudes were tested ranging from a

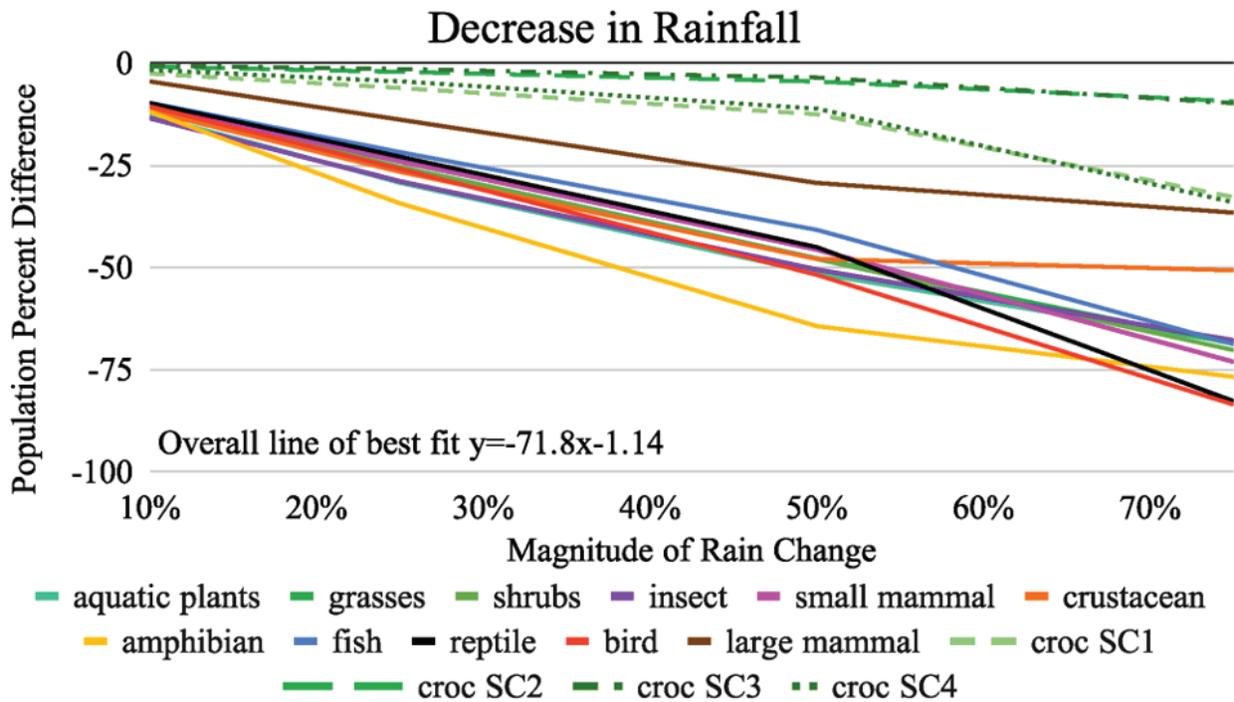


Figure 7. The percent difference in the populations as a function of the magnitude of the rain change when the amount of rainfall is decreased. Overall a linear trend is followed. The colors for the species are the same as in Figure 2.

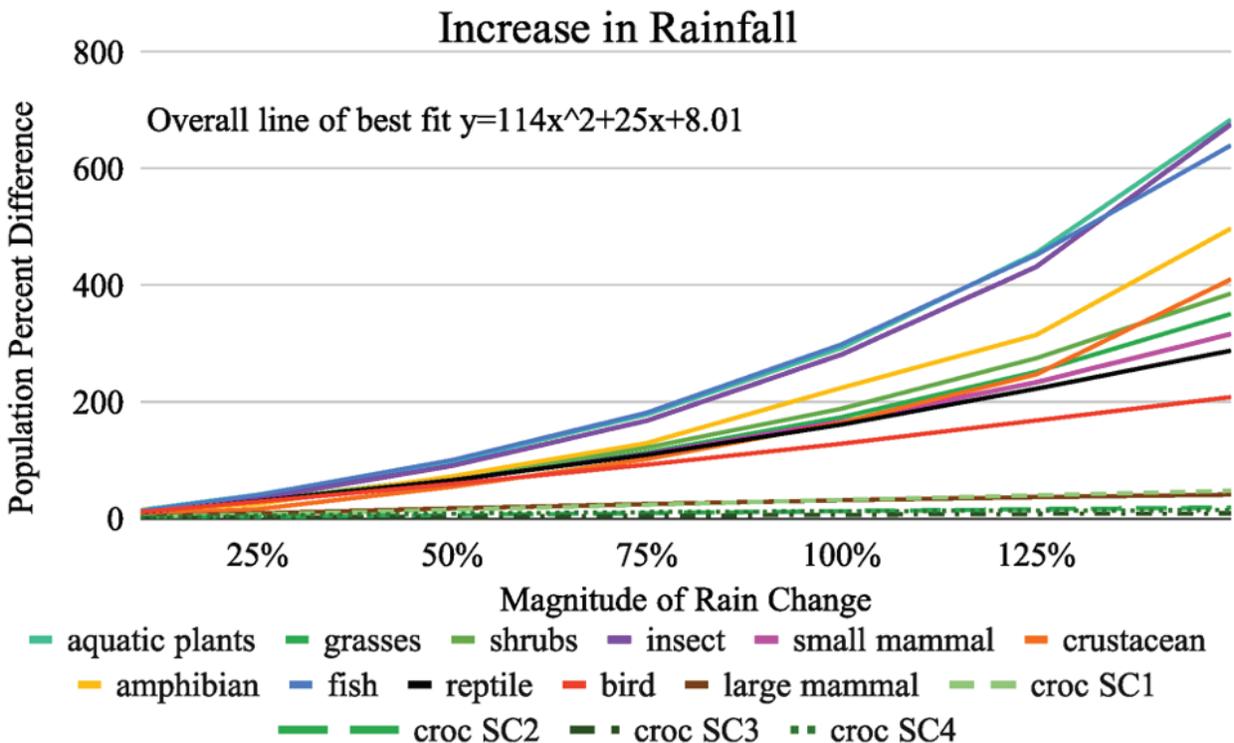


Figure 8. The percent difference in the populations as a function of the magnitude of the rain change when the amount of rainfall is increased. Overall there is a quadratic trend. For the crocodilians and large mammals, the trend is linear. The format is the same as in Figure 7.

100% decrease to a 150% increase in rainfall. Then, the simulation was run with variations in the timing of rainfall, with normal rainfall for 19 years, then a change in the timing of rainfall for 15 years, and finally normal rainfall for the rest of the simulation. With a change in rainfall timing, the system receives the same amount of rain each year, but with different amounts coming in each season. Many timing changes were tested including the same amount of rain each season (25% of the yearly rainfall each season, 25-25-25-25) and having a peak or a drop in the amount of rainfall each year (Peak: 40% of the rain in one season and 20% in each of the other three seasons, 40-20-20-20; Drop: 10% of the rain in one season and 30% in three seasons, 10-30-30-30). Finally, the simulation was run with a change in both the amount and timing of rainfall, with normal rainfall for 19 years, then a change in the amount and timing of rainfall for 15 years, and finally normal rainfall for the rest of the simulation.

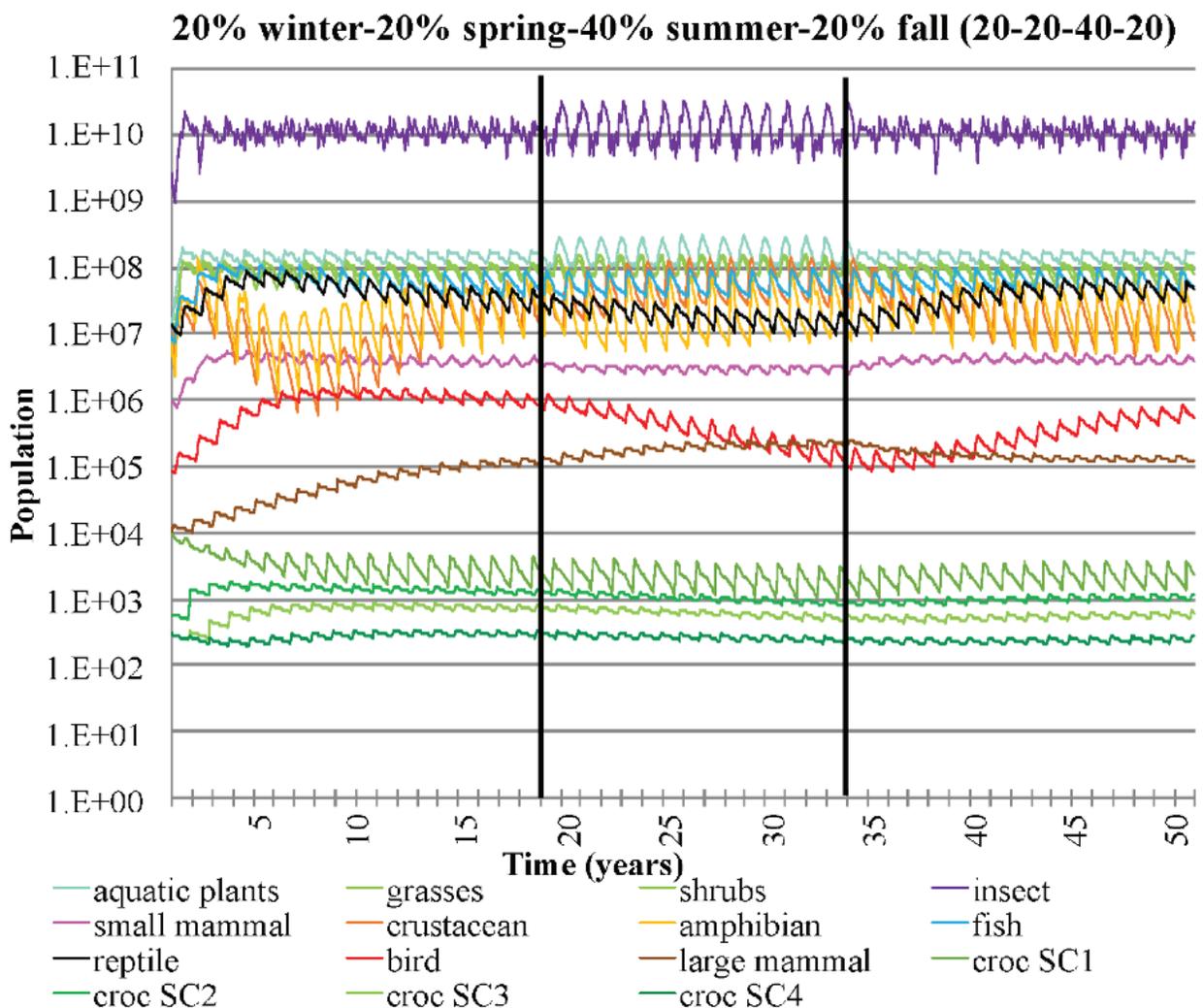


Figure 9. The populations with normal rain for 19 years, 40% of rainfall coming in summer and 20% in the other seasons for 15 years, and normal rainfall for the rest of the simulation in the same format as Figure 2. The populations had only slight changes as rainfall peaks in summer with normal rainfall patterns.

RESULTS AND DISCUSSION

Variations in the Amount of Rainfall

Simulations were run with variations in the amount of rainfall with 19 years of normal rainfall, 5 years with a change in the amount of rainfall between years 19 and 24, and normal rainfall for the remainder of the simulation as shown in Figure 5 with a 50% increase in rainfall and Figure 6 with a 50% decrease in rainfall. Figures 5 and 6 show the populations plotted as a function of time in years. In Figure 5, all the populations increase when the rainfall is increased, and in Figure 6, all the populations decrease when the rainfall is decreased. When the rainfall returns to normal, the populations increase or decrease back to their original levels.

The amount of rainfall determines the amount of energy in the ecosystem through the plant populations, so with increased rainfall there is more energy and with decreased rain-

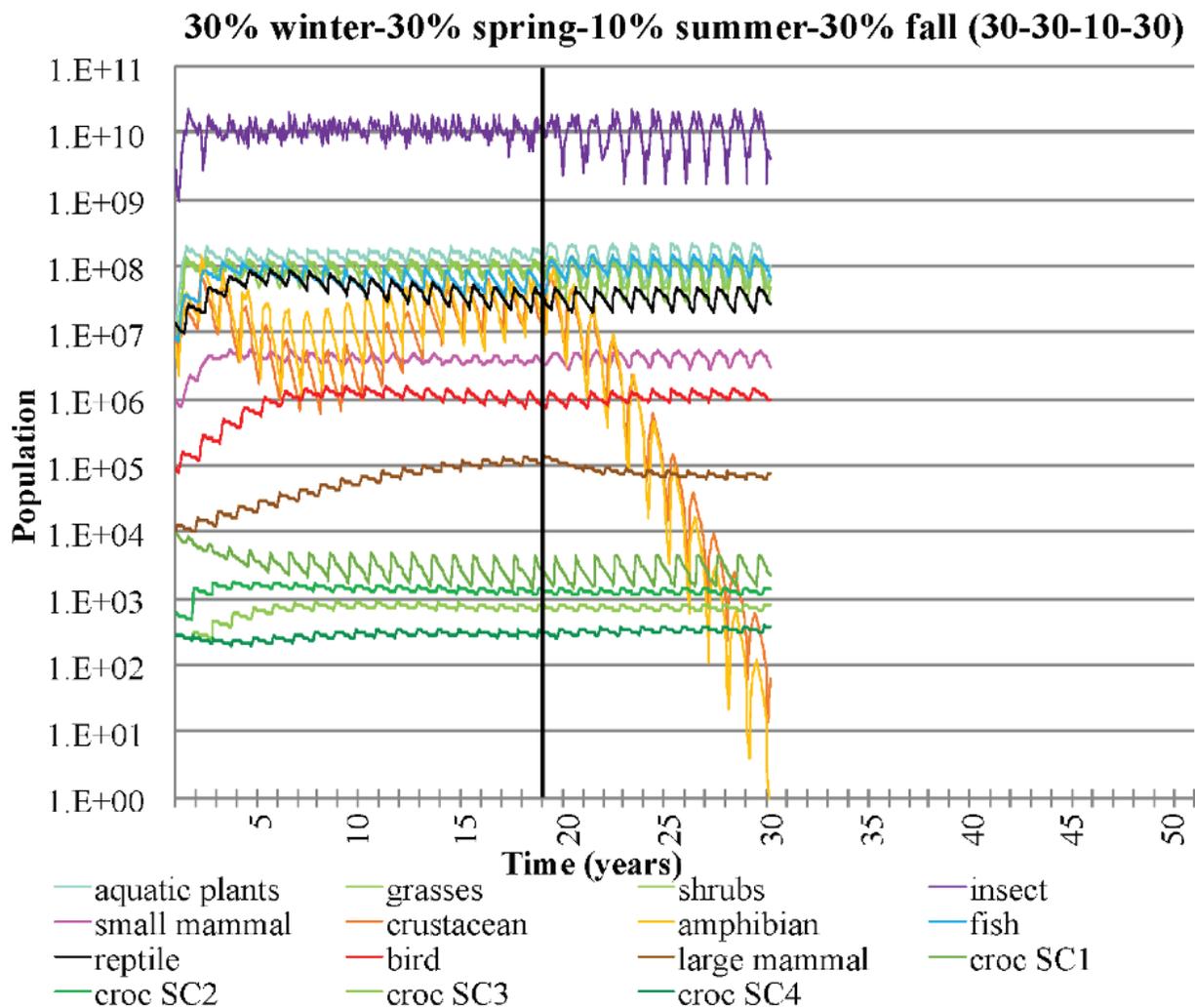


Figure 10. The populations with normal rain for 19 years, 10% of rainfall coming in summer and 30% in the other seasons for 15 years in the same format as Figure 2. The plant and insect populations were high for most of the year with a large quick drop. The amphibians and crustaceans died out, ending the simulation run, as the insect population was low when they reproduced.

fall less, and the populations vary directly with the amount of energy in the system. After the rainfall amount is changed, populations of species at the bottom of the food chain, like insects and amphibians, quickly plateau at their new base population level, which is higher or lower than normal depending on the rain change. Populations of species at the top of the food chain, like large mammals, do not plateau, rather they continue to increase or decrease until the rainfall returns to normal. This occurs because these populations take longer to be impacted by the rainfall as they are not directly dependent on the plant populations. There is a time lag between when prey species and their predators are affected by the change in rainfall. The duration of the rainfall change affects only how much populations at the top of the food chain are impacted because these populations continue to increase or decrease over the entire period of the rain change, while species lower down the food chain plateau and remain at the same level. Once the amount of rainfall returns to normal, the populations also return to normal. If the rainfall was decreased, the populations simply increase back to their original levels. If the rainfall was increased, the populations decrease back to their original level, but some populations, like the crustaceans and amphibians, drop further than their baseline before returning to normal. This occurs because their population exceeds a level that can be sustained by their prey populations, which have just decreased back to normal, causing them to miss out on reproduction.

The magnitude of the increase or decrease in rainfall determines the magnitude of change in the populations as shown in Figures 7 and 8. Figures 7 and 8 show the percent difference in the populations from normal rainfall as a function of the change in the amount of rainfall. With decreased rainfall, the magnitude of the change in the populations increases linearly with the magnitude of the rainfall change as shown in Figure 7, but with increased rainfall, it increases quadratically as shown in Figure 8. That is, an increased magnitude of change in the amount of rainfall has more effect on the populations when the rain is increased than decreased. This occurs because the plant carrying capacity is modeled as an exponential function, so there is a greater difference in the plant carrying capacity with increased rainfall than with decreased rainfall at the same magnitude compared to normal. Species at the top of the food chain, like crocodilians, are less impacted by variations in the amount of rainfall than species lower down the food chain, like amphibians and plants. When the amount of rainfall is increased, species at the top of the food chain show a linear relationship between the magnitude of the rain change and change in the populations as shown in Figure 8. Changes in the amount of rainfall can have significant effects on the ecosystem leading populations to die out with large changes in rainfall. Populations died out when there was a greater than 80% decrease in rainfall or a greater than 125% increase in rainfall when the rainfall returns to normal.

Variations in the Timing of Rainfall

Changes to the timing of rainfall affect the relative magnitudes of the populations and the seasonal variations in the plant populations: the plant populations increase in seasons when the carrying capacity is high and decrease when low. Some animal populations increase while others decrease, based on the seasonal variations of the plant population and when the species reproduce. Figure 9 shows the populations with a change in the timing of rainfall between years 19 and 34 where 40% of the rainfall comes in summer and 20% of the rainfall comes in each of the other seasons (20-20-40-20, last row of Table 3). With the rainfall peaking

in summer, the bird population decreases while the large mammal population increases, as the birds reproduce in spring and the large mammals reproduce in winter, which is closer to the peak in rainfall, and the other populations are relatively unchanged. Figure 10 shows the populations with a change in the timing of rainfall between years 19 and 34 where 10% of the rainfall comes in summer and 30% of the rainfall comes in each of the other seasons (30-30-10-30, second row of Table 3). With the rainfall being lowest in summer, the amphibian and crustacean populations drop significantly, while the other populations are less affected, with the large mammal population decreasing slightly, and the reptile population increasing slightly. In Figure 10, the amphibian and crustacean populations die out because their reproduction is reduced by drop in rainfall, coupled with all the species that reproduce in late spring and summer having normal reproductive rates. The effects of changes to the timing of

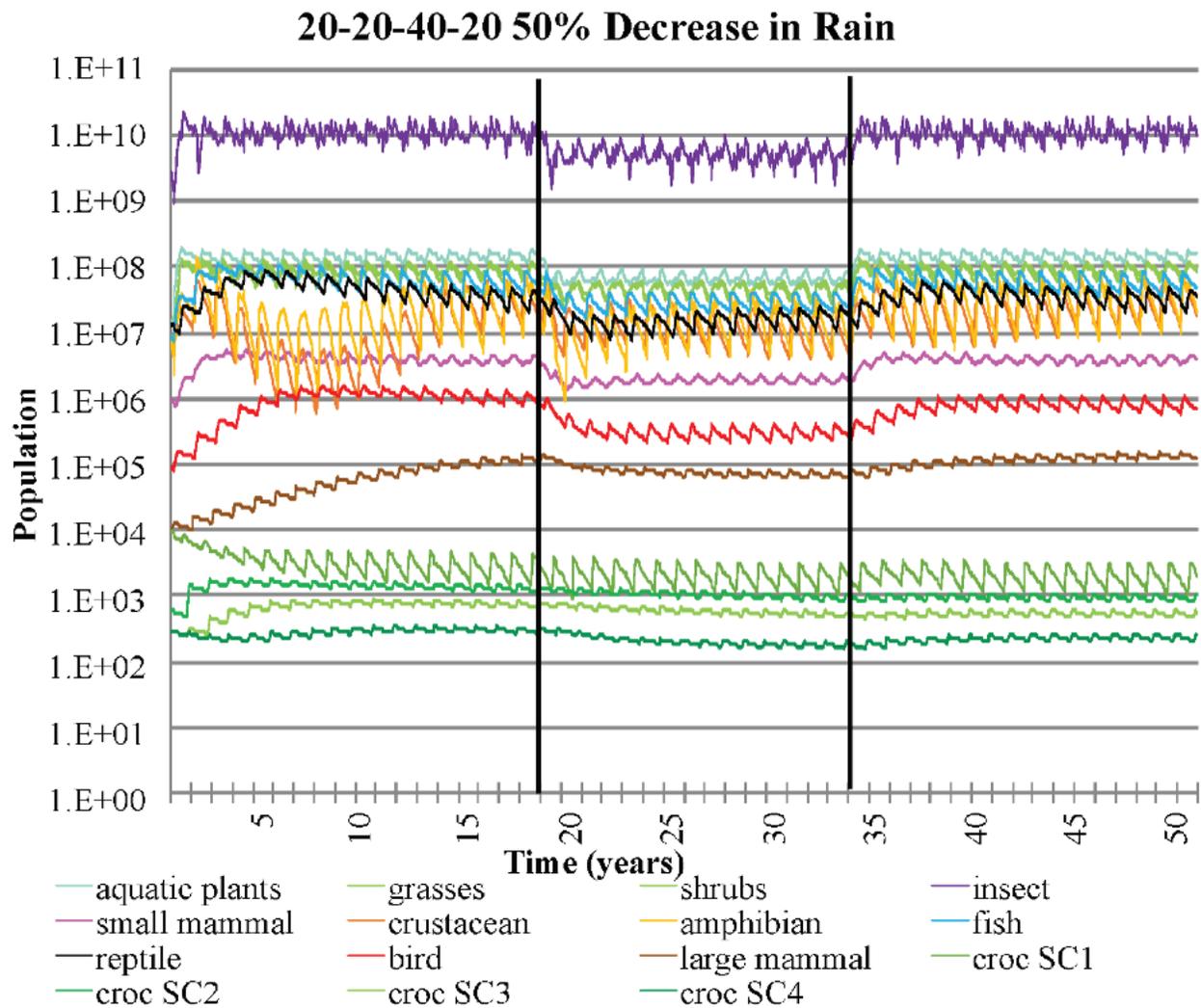


Figure 11. The populations with normal rain for 19 years, a 50% decrease in rainfall with 40% of rainfall coming in summer and 20% in the other three seasons for 15 years, and normal rainfall for the rest of the simulation in the same format as Figure 2. All the populations decrease with slight variations in their relative magnitude and then return to normal quickly once the rain is back to normal.

rainfall range from mild, as in Figure 9, with populations behaving rather normally, to severe, with populations dying out as in Figure 10. Populations die out when prey and predator populations get out of balance, due to a large difference in plant populations between seasons.

In Table 3, several simulations with changes to the timing of rainfall are summarized, where the first column tells the percent of the yearly rainfall that comes in winter, spring, summer, and fall, the second column describes the key rainfall pattern for the simulation, and the third column tells when and how the plant carrying capacity is affected. The plant carrying capacity is determined by the previous season's rainfall so there is a one-season time lag in the response to rainfall. For example, if there is little rain in winter, the plant carrying capacity will be low in the spring as shown in Table 3.

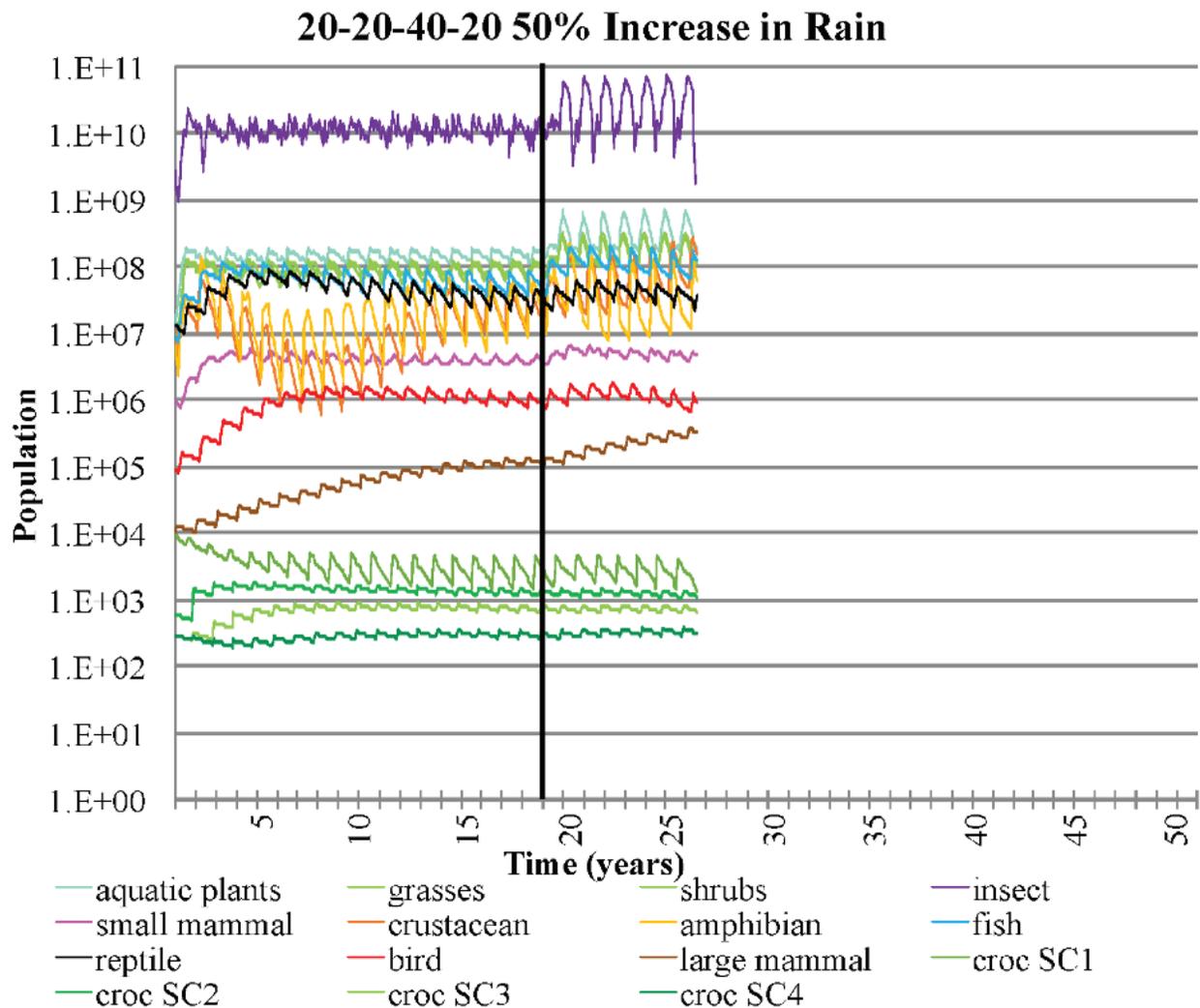


Figure 12. The populations with normal rain for 19 years, a 50% increase in rainfall with 40% of rainfall coming in summer and 20% in the other three seasons for 15 years in the same format as Figure 2, the insect population dies out.

Simulation	Rainfall	Plant Carrying Capacity	Population	Season Species Reproduces			
				Winter	Spring	Summer	Fall
10-30-30-30	Drops in Winter	Drops in Spring	Increases	Large mammals	Fish		
			Decreases		Birds, Amphibians, Crustaceans	Small mammals, Reptiles, Crocodilians	
30-30-10-30	Drops in Summer	Drops in Fall	Increases		Fish, Birds	Small mammals, Reptiles, Crocodilians	
			Decreases	Large mammals	Amphibians, Crustaceans		
40-20-20-20	Peaks in Winter	Peaks in Spring	Increases		Fish, Birds	Small mammals, Reptiles, Crocodilians	
			Decreases	Large mammals	Amphibians, Crustaceans		
20-20-40-20	Peaks in Summer	Peaks in Fall	Increases	Large mammals	Crustaceans		
			Decreases		Fish, Birds, Amphibians	Small mammals, Reptiles, Crocodilians	

Table 3. Simulations with a timing change. In general, animal populations increase when the plant population is elevated when they reproduce and decrease when the plant population is low when they reproduce. There are exceptions: for example, the amphibian population always decreases.

The plant populations increase overall when their carrying capacity is high during spring or summer when their base growth rate is higher, and decrease when their carrying capacity is high in fall or winter as their base growth rate is lower. Insects are the first animals impacted by variations in the timing of rainfall because they reproduce each month, and their population follows the plant population pattern. The other animal species are impacted later and these populations follow their normal seasonal patterns because they reproduce only at certain times of the year. These animal populations increase or decrease depending on whether the plant population is above or below average when they reproduce as shown in Table 3, where species are placed in the last four columns based on when they reproduce. These columns are divided into two rows, with species whose populations increase in the upper row and species whose populations decrease in the lower row.

Variations in the Amount and Timing of Rainfall

The ecosystem response to changes in both the amount and timing of rainfall is a hybrid of the individual responses as shown in Figures 11 and 12 with the timing of rainfall changed so 40% of the rainfall comes in summer and 20% of the rainfall comes in the other seasons with a 50% decrease (Figure 11) and a 50% increase (Figure 12) in rainfall amount during years 19

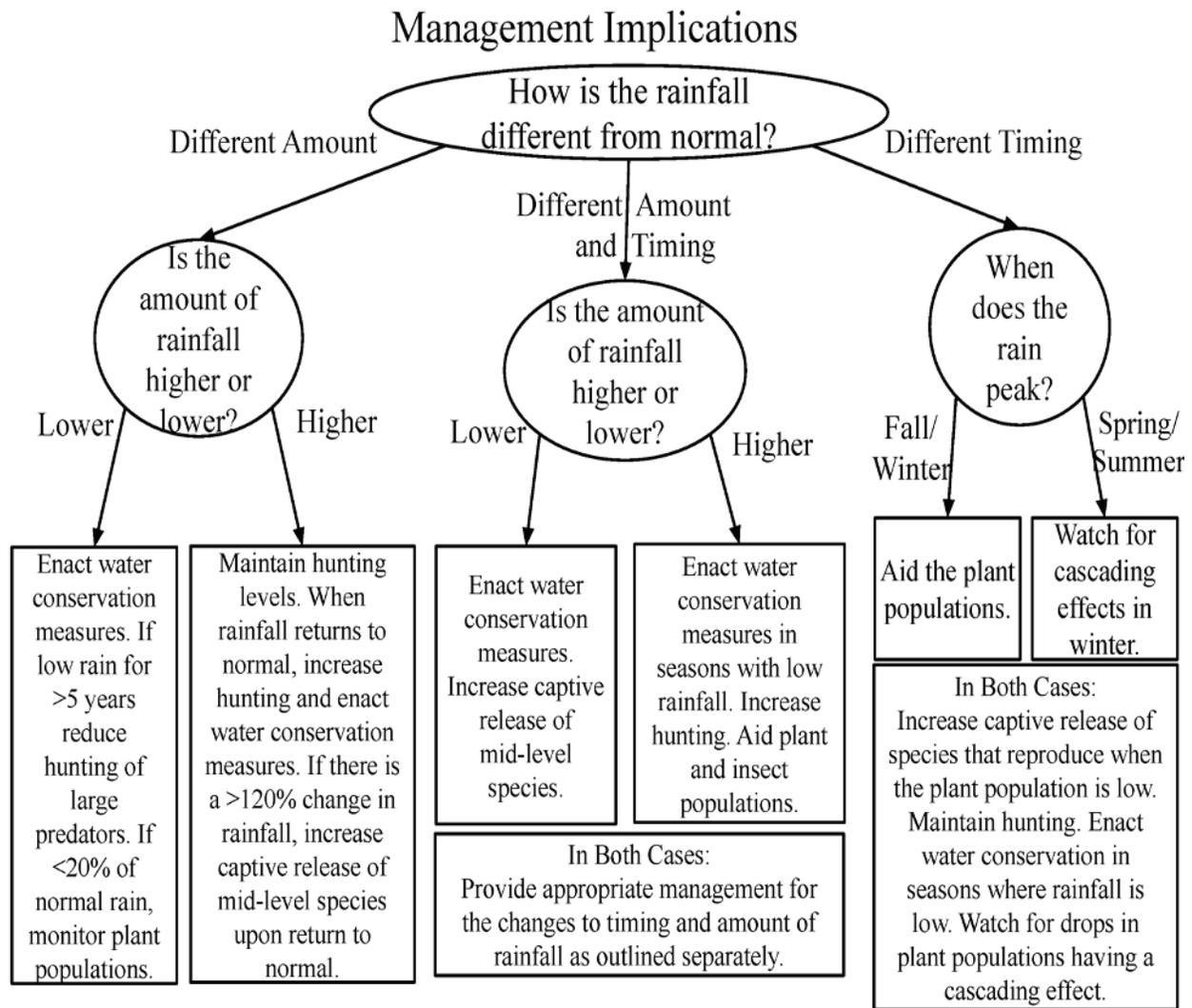


Figure 13. Management program for how humans can help protect crocodilians and their ecosystems from variations in rainfall.

to 29. In Figure 11, the populations decrease because the rainfall is decreased, but the effects of change in the timing of rainfall is reduced as the populations decrease a similar amount. This occurs because having decreased rainfall overall reduces the effects of changes in the timing of rainfall because the seasonal variation in the plant carrying capacity is reduced as shown by the small oscillations in the plant populations in Figure 11. In Figure 12, the populations increase because the rainfall increased, but the populations increase at different rates than without a change in the timing of rainfall. The insect population dies out because of the significant increase in all the populations. Increased rainfall overall amplifies the effects of changes in the timing of rainfall because the seasonal variation in the plant carrying capacity is increased as shown by the large oscillations in the plant populations in Figure 12. The timing of rainfall determines the seasonal variations in the plant populations and the relative magnitudes of the populations, while the amount of rainfall determines the magnitude of seasonal oscillations and the base population levels. Overall, changes in the timing of rainfall have a greater effect on the populations because the relative magnitudes of the populations

are changed, while with changes in the amount of rainfall, these are maintained. Compared to a normal amount of rainfall and this timing change, as shown in Figure 9, the populations have smaller oscillations with decreased rainfall as shown in Figure 11 and larger oscillations with increased rainfall as shown in Figure 12. Populations die out with increased rainfall and timing changes because the ecosystem is unstable due to the large seasonal variation in the plant populations.

CONCLUSIONS

Summary

The results of this simplified model show that variations in rainfall can have significant effects on crocodilians and their ecosystem. Changes in the amount of rainfall cause the populations to increase or decrease in direct relation to the rain change as shown in Figures 5, 6, 7, and 8. Changes in the timing of rainfall cause the populations to increase or decrease depending on whether the plant population is above or below average when a species reproduces, delayed one season from the rainfall pattern as shown in Figures 9 and 10 and Table 3. Changes in both the timing and amount of rainfall yield a hybrid response of those with changes in the amount and timing of rainfall separately as shown in Figures 11 and 12.

Plants are first impacted by rainfall changes because rainfall determines their carrying capacity. Next impacted are animals at the bottom of the food chain, like small mammals and amphibians because they rely directly on plants for food as shown in Figures 5, 6, 9, 10, 11, and 12. It takes time for species at the top of the food chain, like crocodilians, to be impacted because they consume many species of prey and with the predator's diet shifting based on the abundance of the prey populations, all prey populations must be quite different for these species' populations to change. This time lag is very important in the ecosystem response as it determines when species are impacted by changes in rainfall. A similar time lag between prey and predator populations has been observed in hare and lynx populations, where the lynx population follows its prey population, the hare, with a slight delay (Krebs et al., 2001). This model produces this common pattern in prey and predator populations, corroborating the results. The ecosystem is very sensitive to sudden large changes in rainfall because of this time lag. Species lower down the food chain, which are more directly impacted by the rain change, are affected before species higher up the food chain. This leads to an imbalance between predator and prey populations, which can be devastating especially when the amount of rainfall decreases.

Applications

Models, like this one, have the unique potential to explore many future climate scenarios that would otherwise be impossible with field studies. More models need to be developed and validated to prepare for climate change effects on ecosystems.

Extreme and chaotic variations in rainfall are probable in the near future (Walsh et al., 2014). Crocodilians and their ecosystems are apt to be adversely affected by climate change and its effects on rainfall patterns. Chaotic rainfall patterns will likely cause their ecosystems to become unstable because the ecosystem is sensitive to sudden changes in rainfall. Extreme

periods of drought would be harmful to crocodylians because as large predators they are greatly affected by extended periods of low rainfall.

The effects of climate change have the potential to be disastrous for crocodylians and their ecosystems. It is important to slow or prevent climate change before ecosystems are destroyed and biodiversity is lost. Additionally, it is important to prepare for the coming disruption that ecosystems face from climate change by developing and testing management programs to protect ecosystems from becoming unstable due to abnormal rainfall patterns. Proper management response will become increasingly important as rainfall patterns are projected to become more extreme and chaotic.

From the results of this experiment, management recommendations were developed (Figure 13) indicating how human interactions can help the ecosystem respond to variations in rainfall. In general, it is important to monitor rainfall patterns and keep track of how they compare to a region's norms. The management plan gives recommendations based on how the rainfall pattern varies from normal, using management actions such as hunting, water conservation, and captive release of farm raised individuals to aid the populations. For example, if the timing of rainfall is changed so that rainfall peaks in winter, the recommendations are to aid the plant populations with reduced grazing and logging to keep their populations from decreasing overall, increase farm release of birds, amphibians, crustaceans, fish, small mammals, reptiles, and crocodylians, species that reproduce when the plant populations are low, maintain hunting levels so predator populations do not get out of proportion with prey populations, and conserve water in spring and summer to reduce the seasonal variation in the plant populations. The practices outlined in these management recommendations have the potential to help keep the crocodylian ecosystem stable face of changing rainfall patterns. More research, though, is needed to create species specific management recommendations and to determine the efficacy of the recommendations presented here. Modeling techniques can help prepare management programs for future threats and may prove quite valuable in protecting crocodylians and all creatures from climate change because a management program can already in place allowing efforts to aid the populations to begin immediately after unusual rainfall patterns are observed.

Future Directions

The results of a model must be interpreted with regards to the assumptions of the model (Gotelli, 2008). This model represents a generalized crocodylian ecosystem including broad classes of prey with the goal of understanding generally how crocodylians are affected by variations in rainfall. Models for specific crocodylian species and ecosystems should be developed to more accurately represent a system and get more detailed management insights. A major assumption of this model is that rainfall only affects the ecosystem through the plant populations. In reality, rainfall also affects the quality and quantity of freshwater habitats and crocodylian nesting success (Eversole et al., 2013; Grigg and Kirshner, 2015). The effects of rainfall on aquatic habitat should be accounted for in the model. For example, if water levels were decreased, aquatic species would have a lower carrying capacity. This model also assumes that species do not adapt in response to changes in rainfall. In the future, this model should also include species adaptations; for example, plant species becoming more drought resis-

tant or animal species changing their timing of reproduction. These additions to the model would allow for a better understanding of all the effects of variations in rainfall and should be accounted for when designing management programs. Field studies and theoretical techniques should be combined to design and validate models. Data from the field such as how rainfall affects species, what factors most significantly affect species reproduction rates, and the ratio of populations between trophic levels, can improve the accuracy of models and highlight important variables to include. Additionally, accurate population data from all species in the ecosystem should be collected over many years and be used to further validate the model. Conservation is a pressing issue that should be addressed using all tools available by combining field work and modeling.

AUTHOR INFORMATION

Corresponding Author

*Karin Ebey, 47gharials@gmail.com

ACKNOWLEDGMENT

I thank Rosalyn Rael for mentoring me and assisting me with editing. I thank my mother for assisting me with editing. I thank my teacher Ms. Meyer for being my sponsor.

REFERENCES

- Chabreck, R. Methods of Determining the Size and Composition of Alligator Populations in Louisiana. *Proc. Southeastern Game and Fish Comm. Conf.* **1966**, 20:105-112, https://www.rwrefuge.com/uploads/4/9/4/2/49423019/chabreck_1966-_size_and_composition_of_alligator_populations.pdf.
- Cornell University. All About Birds: Great Blue Heron. 2017, www.allaboutbirds.org/guide/Great_Blue_Heron/overview#.
- Davis, S. and Fromme, D. Scheduling Irrigation for Agronomic Crops Using Estimation Methods. LSU Ag Center, 2016, <https://www.lsuagcenter.com/profiles/aiverson/articles/page1475509152276>.
- Delany, M.; Woodward, A.; Kiltie, R.; Moore, C. Mortality of Alligators Attributed to Cannibalism. *Herpetologica*. **2011**, 67(2), p. 174-185.
- Dunover, L. Kentucky Critter Files: Kentucky Crayfish. University of Kentucky Entomology, 2016, www.uky.edu/Ag/CritterFiles/casefile/relatives/crayfish/crayfish.htm.
- Eversole, C.; Henke, S.; Powell, R.; Janik, L. Effect of Drought on Clutch Size and Hatchling Production of American Alligators in Texas. *Herpetological Conservation and Biology*. **2013**, 8(3): 756-763.
- Gonzalez, E.; Martinez-Lopez, M.; Morales-Garduza, M.; Garcia-Morales, R.; Charruau, P.; Gallardo-Cruz, J. The sex-determination pattern in crocodylians: A systematic review of three decades of research. *Journal of Animal Ecology*. **2019**.

- Good, S.; Morre, G.; Miralles, D. A Mesic Maximum in Biological Water Use Demarcates Biome Sensitivity to Aridity Shifts. *Nature Ecology and Evolution*. **2017**. Vol 1:1883-1888.
- Gotelli, N. *A Primer of Ecology*; Sinauer Associates: Sunderland, MA, 2008.
- Grigg, G. and Kirshner, D. *Biology and Evolution of Crocodylians*; Cornell University Press: Ithaca, NY, 2015.
- Indiana Division of Fish and Wildlife. Animal Information Series: Crappies (Pomoxis). 2012, www.in.gov/dnr/fishwild/files/fw-crappies.pdf.
- Krebs, C.; Boonstra, R.; Boutin, S.; Sinclair, A.R.E. What Drives the 10-year Cycle of Snowshoe Hares? The ten-year cycle of snowshoe hares—one of the most striking features of the boreal forest—is a product of the interaction between predation and food supplies, as large-scale experiments in the yukon have demonstrated. *BioScience*. **2001**, 51(1): 25-35, [https://doi.org/10.1641/0006-3568\(2001\)051\[0025:WDTYCO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0025:WDTYCO]2.0.CO;2).
- Lance, V.; Elsey, R.; Butterstein, G.; Troclair, P.; Merchant, M. The Effects of Hurricane Rita and Subsequent Drought on Alligators in Southwest Louisiana. *Journal of Experimental Zoology*. **2010**, 313A:106-113.
- Lee, E. Eastern Cottontail Rabbit. Pennsylvania State University, 2013, www.psu.edu/dept/nkbiology/naturetrail/speciespages/cottontail.htm.
- Louisiana Department of Wildlife and Fisheries. Louisiana's Alligator Management Program 2018-2019 Annual Report. 2019, www.wlf.louisiana.gov/assets/Resources/Publications/Alligator/2018-2019_Alligator_Annual_Report.pdf.
- Mitchell, J. Barking Treefrog. *Amphibia Web*, University of California, 2019, amphibiaweb.org/species/808.
- Nagy, K.; Girard I.; Brown, T. Energetics of Free Ranging Mammals, Reptiles, and Birds. *Annual Review of Nutrition*. **1999**.
- National Aeronautics and Space Administration. Climate Change. *Precipitation Measurement Missions*, 2019, pmm.nasa.gov/science/climate-change.
- National Centers for Environmental Information and National Oceanic and Atmospheric Administration. Climate Data Online. 2019, www.ncdc.noaa.gov/cdo-web/datasets#G-SOM.
- National Geographic. Food Web. *Resource Library Encyclopedia Entry*, 2019 www.national-geographic.org/encyclopedia/food-web/.
- National Park Service. Black Bears. 2016, www.nps.gov/subjects/bears/black-bears.htm.
- National Weather Service and National Oceanic and Atmospheric Administration. Climate Information: Lake Charles, Louisiana. www.weather.gov/lch/KLCH.
- Orsenigo, S.; et al. Some like it hot and some like it cold, but not too much: plant responses to climate extremes. *Plant Ecology*. **2014**, 215(7).

- Snallshire, D. and Swash, A. Life Cycle and Biology. British Dragonfly Society, 2014 british-dragonflies.org.uk/content/life-cycle-and-biology/.
- Somaweera, R.; et al., The Ecological Importance of Crocodylians: Towards Evidence Based Justification for their Conservation. *Biological Reviews*. **2020**.
- Stevenson, Colin. *Crocodiles of the World*; New Holland Publishers: London, U.K., 2019.
- University of California. Landscape Water Conservation and Irrigation Management. University of California Center for Landscape and Urban Horticulture. Department of Agriculture and Natural Resources, 2019, ucanr.edu/sites/UrbanHort/Water_Use_of_Turfgrass_and_Landscape_Plant_Materials.
- USGCRP. Groffman, P. M., P. Kareiva, S. Carter, N. B. Grimm, J. Lawler, M. Mack, V. Matzek, and H. Tallis. *Ch. 8: Ecosystems, Biodiversity, and Ecosystem Services. Climate Change Impacts in the United States: The Third National Climate Assessment*. J. M. Melillo, Terese (T.C.) Richmond, and G. W. Yohe, Eds., U.S. Global Change Research Program, 200-201, **2014**.
- USGCRP. *Climate Science Special Report: Fourth National Climate Assessment, Volume I*. Chapter 1, "Our Globally Changing Climate". Wuebbles, D.J., D.W. Fahey, K.A. Hibbard, D.J. Dokken, B.C. Stewart, and T.K. Maycock (eds.). U.S. Global Change Research Program, **2017**, doi: 10.7930/J0J964J6. <https://science2017.globalchange.gov>.
- Walsh, J.; Wuebbles, D.; et al. *Our Changing Climate*. "Precipitation Change." *National Climate Assessment*, **2014**, nca2014.globalchange.gov/report/our-changing-climate/precipitation-change.
- Wilson, J. D. Glossy Crayfish Snake. Savannah River Ecology Laboratory, University of Georgia, 2019, srelherp.uga.edu/snakes/regrig.htm.
- Zeppel, M.; Wilks, J.; Lewis, J. Impacts of extreme precipitation and Seasonal changes in precipitation on plants. *Biogeosciences*. **2014**, 11:3083-3093, doi.org/10.5194/bg-11-3083-2014.

APPENDIX-MODEL EQUATIONS

For the model created in this experiment, a novel adaptation of the Lotka-Volterra model, the base predator-prey interaction model, was used. Each month the populations are impacted by rainfall, predator-prey interaction, and reproduction. Energy enters the ecosystem only through plant growth which is dependent rainfall. Rainfall only affects the ecosystem through the plant populations. The equations used in the model are described here with the variables used defined in Table A-1.

Variable	Definition	Variable	Definition
P (Name)	Population of Name Plants-pl; Prey-vt; Predators-me	CO	Conversion Coefficient
D	Plant Death Rate	DF	Percent of Predator's Diet Prey Species Fulfills
RN	Rain Needed by Plant Species	M	Mass of Individual
RR	Rain Received	Q	Reproductive Rate
G	Plant Growth Rate	X	Percent of Population Reproducing
RA	Rainfall Average	CC	Prey Determined Carrying Capacity
CU	Consumption Rate	H	Hatch Rate
F	Feeding Limit	A	Aging Rate

Table A-1. Variables used in the model equations in order of use.

Rainfall Effects on Plants

Plants die if the rainfall varies from their water needs, whether there is too little or too much rain as shown in Equation 1 (Good et al., 2017). Plants die at a higher rate when there is too little rain than when there is too much rain. The amount of plant deaths is directly proportional to the difference between the amount of rain received and the amount of rain needed.

$$P(pl) = P(pl) - \left(D * P(pl) * \left(\frac{|RN-RR|}{RN} \right) \right) \quad (1)$$

Rainfall also affects plant growth, their reproduction, which occurs every month. Plant growth is modeled using the logistic growth equation, where exponential growth is limited by a carrying capacity (Gotelli, 2008). Plant growth is governed by a growth rate and a carrying capacity, both depend on the amount of rainfall as shown in Equation 2. The base growth rate varies seasonally as shown in Table 2 (Orsenigo et. al, 2014), but is also dependent on the current month's rainfall. There is a set minimum growth rate when there is no rainfall, but with rainfall the growth rate increases steadily until the rainfall is about 1.5 times the plants' water needs, where it levels off (Good et al., 2017). This was modeled using a variation of the exponential function, e^x . The carrying capacity (the last term in Equation 2) limits the actual

amount of plant growth based on the previous season's rainfall. The carrying capacity has a set minimum of $10^{7.6}$ kilograms of plant matter when there is no rainfall. A rainfall average is calculated in each of the four seasons and is compared to the water needs of the plant species. This value is used to determine the next season's carrying capacity.

$$P(pl) = P(pl) + P(pl) * G * \left(1 - \left(e^{-2 * \left(0.05 + \frac{RR}{RN}\right)}\right)\right) * \left(1 - \frac{P(pl)}{10^{7.6 + 0.4 * \frac{RA}{RN}}}\right) \quad (2)$$

Predator Prey Interactions

Each month, predator and prey populations interact with one another as shown in Figure 1, resulting in consumption and starvation deaths. In consumption, prey die from being consumed by predators as shown in Equation 3. In starvation, the predators die in proportion to the fraction of their energy requirements that are not met as shown in Equation 4, where all predators automatically die to represent the scenario if no prey is consumed with individuals added back to the population, do not die, for every unit of prey consumed. These processes are described with three parameters: consumption rate, conversion rate, and feeding limit; each interaction has a unique set of parameters (Gotelli, 2008). The consumption rate limits the amount of prey consumed based on the time required for the predator to capture the prey. The conversion coefficient defines the amount of prey that must be consumed by individual predators so they do not die of starvation. The feeding limit defines the maximum amount of prey the predators consume based on their energy needs.

$$P(vt) = P(vt) - \Sigma \left(\frac{P(vt) * P(me) * CU}{1 + P(vt) * CU * F} \right) \quad (3)$$

$$P(me) = P(me) - P(me) + \Sigma \left(\frac{CO * P(vt) * P(me) * CU}{1 + P(vt) * CU * F} \right) \quad (4)$$

The feeding limits were calculated each month by determining the amount of prey the predators need to consume based on their energy requirements as shown in Table 1. Many of the predators consume multiple species of prey, so their energy requirements are split among their prey species using a dynamic approach, assuming that predators do not have food preferences. The proportion of a predator's energy requirements that a certain prey species fulfills varies each month based on their relative abundance to the other prey species. The relative abundance of prey species is determined by comparing the total mass of a specific prey species to the total mass of all prey species for that predator as shown in Equation 5. The feeding limit for the specific predator and prey interaction is determined by multiplying the proportion of the energy requirements that the prey species fulfills with the total feeding limit.

$$DF = \frac{P(vt) * M}{\Sigma P(vt) * M} \quad (5)$$

Animal Reproduction

Animal reproduction occurs in certain months for each species as shown in Table 2. Animal reproduction is modeled using the logistic growth equation, where exponential growth is limited by the resources in the system as shown in Equation 6 (Gotelli, 2008). In Equation 6, the population is multiplied by one half because only the females reproduce. For species that reproduce over several months, like amphibians, the population used is from the first month of their reproductive season because hatchlings are not reproductively mature. The reproductive rate, shown in Table 1, is the number of young per adult female, without limitations on population growth. The population growth is then limited by a carrying capacity based on the prey populations as shown in Equation 7, where the prey populations are multiplied by the conversion rate to determine how many predators can be sustained, the proportion of the predator's diet that prey species fulfills, and 0.2 because reproduction requires more energy than survival. The hatch rate, shown in Table 1, determines how many of the young are successfully added to the population depending on a species parental care habits.

$$P = P + Q * P * 0.5 * X * \left(1 - \frac{P}{CC}\right) * H \quad (6)$$

$$CC = \Sigma(CO * P(vt) * DF * 0.2) \quad (7)$$

Crocodilian Aging

Once a year the crocodilians age where small portion of each size class moves up to the next one. Aging is limited by the amount of prey in the system, and because growth requires more energy than what is needed to survive, aging is limited further than reproduction as shown in Equation 8.

$$P(aged) = P * A * \left(1 - \left(\frac{P}{0.01*CC}\right)\right) \quad (8)$$