#  OF A MODEA FOR SIMULATNG  

## Dissariaion for the Degree of Ph. D. MOHGAR STME UNUERETH IAMES DAIE NHCHOLS 1978

This is to certify that the
thesis entitled
Development and Application of a Model
For Simulating Alligator Population Dynamics
presented by

James Dale Nichols
has been accepted towards fulfillment
of the requirements for
Ph.D._degree in Fisheries \& Wildlife

Date July 2, 1976



13 (1) R


# ABSTRACT <br> DEVELOPMENT AND APPLICATION OF A MODEL FOR SIMULATING ALLIGATOR POPULATION DYNAMICS 

By
James Dale Nichols

A model was constructed to simulate the dynamics of a commercially harvested alligator (Alligator mississippiensis (Daudin)) population inhabiting the privately owned coastal marshland of Cameron and Vermilion parishes, Louisiana. In the model, nesting effort, nest flooding, desiccation mortality, and predation on alligator eggs and young were all determined as functions of monthly water depth averages. Cannibalism was considered to be the major density dependent factor operating on the population and was determined as a function of total population density and marsh water depth. The model contained a freeze mortality which was based on minimum winter temperatures. In addition, the model included a harvest option which resulted in alligator hunting mortality.

Comparison of simulation results with 1970-1973 nest count results demonstrated reasonably close agreement between simulated and observed data. Simulations of a severe summer drought and an August hurricane produced drastic population declines, although rapid recoveries were made in subsequent years. Environmentally stochastic simulations produced extremely irregular population response curves and resultant age structures. Examination of simulation results
led to the suggestion that alligator life history patterns correspond closely to an hypothesis extended by Murphy (1968).

Theoretical arguments and simulation experiments were used to compare two possible harvest strategies for the modeled population. The differential strategy involved application of unequal harvest rates for different size and age classes, while the alternative proportional strategy resulted in equal harvest rates for all sizes. Comparison of observed differential hunting rates and alligator reproductive values indicated that the differential strategy resulted in higher harvest rates for females of greater reproductive value. Simulation experiments confirmed that proportional hunting was superior to the differential alternative with respect to effect on population growth and harvest yield. Proportional hunting was thus recommended for the studied alligator population.

The use of egg collection and restocking programs in the management of crocodilian populations was discussed. It was argued that the key to the biological and economic feasibility of such programs results from certain behavioral characteristics and mortality patterns of crocodilians. Simulations demonstrated that alligator population growth rates can be greatly increased through the use of restocking programs. A method of crocodilian harvest management was described in which harvesters are required to collect and hatch crocodilian eggs and release young animals in numbers which are directly proportional to the number of
harvested females. Simulations demonstrated that the use of such restocking quotas can produce elevated finite rates of increase. Examination of simulated harvest yields demonstrated that restocking quota management is economically feasible. This form of management was recommended for harvested crocodilian populations currently persisting at low densities.

# DEVELOPMENT AND APPLICATION OF A MODEL FOR SIMULATING ALLIGATOR POPULATION DYNAMICS 

By

James Dale Nichols

## A DISSERTATION

Submitted to<br>Michigan State University<br>in partial fulfillment of the requirements for the degree of<br>DOCTOR OF PHILOSOPHY<br>Department of Fisheries and Wildife

## ACKNOWLEDGMENTS

My principle debt is to my major professor, Dr. Walt Conley, whose contagious enthusiasm and excitement about science served to produce an ideal environment for the development and exchange of ideas. I am grateful to the other members of my doctoral committee, Drs. Eric Goodman, Harold Prince and Max Hensley, for numerous helpful suggestions and for critical reviews of the thesis manuscript. Dr. Goodman also provided considerable assistance in the development and implementation of the model. I wish to thank Drs. George Petrides, Richard Hill, and Martin Balaban, who were helpful in the structuring of my doctoral program.

I am indebted to Dr. Robert Chabreck for providing continued encouragement and for generously sharing his considerable knowledge of alligator ecology. My appreciation is extended to Dr. Chabreck, Ted Joanen, Larry McNease, Dr. William Palmisano, Howard Dupuie and Robert Kleibert for use of unpublished data. Dr. Don Hall, Lynn Viehman, and Bruce Fenderson provided helpful suggestions during the early stages of this work.

I am especially grateful to have been associated with fellow lab members, Dr. Alan Tipton and Jay Hestbeck, whose discussions were a constant source of intellectual stimulation.

I also wish to thank Jackie Church and Judy Boger for technical assistance in manuscript preparation.

Use of Michigan State University computing facilities was made possible through support, in part, from the National Science Foundation.

Finally, I wish to thank my wife, Lois, and my parents for their support and encouragement during the last 3 years.

TABLE OF CONTENTS
Page
LIST OF TABLES ..... vii
LIST OF FIGURES ..... ix
INTRODUCTION ..... 1
DESCRIPTION OF STUDY AREA ..... 7
ALLIGATOR POPULATION ECOLOGY ..... 10
Size-Age Relationship ..... 10
Reproductive Biology ..... 13
Courtship and nesting ..... 13
Age at sexual maturity ..... 14
Nesting effort ..... 15
Nest flooding ..... 19
Levee nesting ..... 19
Nest predation ..... 22
Hatching success ..... 26
Alligator Population Structure and Mortality Relationships ..... 26
Average annual mortality and survival rates ..... 26
Population age structure ..... 29
Specific mortality functions ..... 35
Desiccation ..... 37
Cannibalism ..... 41
Page
Predation ..... 44
Natural mortality ..... 46
Freeze mortality ..... 46
Hunting mortality ..... 48
THE SIMULATION MODEL ..... 51
Description ..... 51
Monthly population changes during April through October ..... 53
Monthly population changes during November through March ..... 55
Yearly population changes ..... 55
Implementation ..... 57
RESULTS AND DISCUSSION ..... 59
Alligator Population Structure ..... 59
Model - Field Data Comparison ..... 61
Water Level Fluctuations ..... 65
Alligator Harvest Strategies ..... 71
Theoretical development ..... 71
Harvest simulation experiments ..... 80
Discussion and recommendations ..... 86
Egg Collection and Restocking Management ..... 88
Crocodilian characteristics and restocking management ..... 89
Restocking simulations ..... 92
Restocking quotas and crocodilian harvest management ..... 94
Page
Theoretical restocking quota calculation ..... 96
Restocking quota simulations ..... 98
Discussion and recommendations ..... 103
LITERATURE CITED ..... 105

## LIST OF TABLES

Table Page
1 Marsh water depths for Cameron parish,Louisiana.
2
Estimated relationship between size and ..... 12age for alligators inhabiting the coastalmarshland of Cameron and Vermilion parishes,Louisiana.
3 Computed percentages of females nesting as ..... 17related to marsh water depths during Mayand June.
4 Selected marsh water depths and corresponding ..... 20nest flooding percentages.5Survival rate estimates for alligators in-30habiting the coastal marshland of Cameronand Vermilion parishes, Louisiana.
The results of night counts and total popu- ..... 31lation computation for alligators onRockefeller Wildife Refuge, 1966.
Size-specific sex ratios used in the con- ..... 33 struction of alligator population structures.
Natural mortality rates for alligators in- ..... 47habiting the coastal marshland of Cameronand Vermilion parishes, Louisiana.
10
Percent composition of the combined 1972 and ..... 49 1973 Louisiana alligator harvest.
Calculated age structure for the alligator ..... 36 population of Cameron and Vermilion parishes, Louisiana, September, 1972.
11 Computer-generated initial age structure for ..... 62an alligator population of 100,000.
12 Theoretical $l_{x}$ and $m_{x}$ values for female ..... 75 alligators inhabiting the coastal marshland of Cameron and Vermilion parishes, Louisiana.
Table Page
13 Two schedules of prices paid to hunters for ..... 79alligator hide.
14 Population $\bar{\lambda}$ values resulting from 30- ..... 82year stochastic simulations with 7\%differential and proportional hunting rates.
15
Mean harvest yields for differential and ..... 85proportional hunting rates producingequivalent $\bar{\lambda}$ values.
16
Results of 32-year alligator simulation runs ..... 101under various management options.

## LIST OF FIGURES

Figure Page
1 Relationship between total length and age ..... 11 in alligators. Years begin September 1 and end August 31.Relationship between the percentage of18mature female alligators nesting and marshwater depth (May-June average).
Relationship between percent nest flooding ..... 21and marsh water depth.
4
Relationship between nest predation and ..... 25marsh water depth.Relationship between both predation and38desiccation mortality and marsh water depthin l-year-old alligators.Relationship between both predation and 39desiccation mortality and marsh water depthin 2-year-old alligators.7 Relationship between desiccation mortality40and marsh water depth in female alligatorsaged 3-2l years and male alligators aged3-6 years.Relationship between cannibalism mortality43and total density in the alligator populationof Cameron and Vermilion parishes, Louisiana.Cannibalism rate multiplier function.45
58Simulated population growth using the
September initial age structure shown inTable 8. Water depths were held constantat 15 cm (. 5 foot) and no winter freezesoccurred.
12 Comparison of simulated nests (dashed line) ..... 64 with observed nest count data, 1970-1973 (solid line). Nest count data source: Palmisano et al. (1973).

| Figure | Page |
| :---: | :---: |
| 13 | Series of 2-year simulations demonstrating population response to varied marsh water depths in single selected months. The varied water depths occurred in selected months during the first year, and depths for all other months were held constant at 15 cm (. 5 foot). |
| 14 | Simulated population response to August hurricane (plot B) and severe summer drought (plot C). A constant water depth simulation (plot A) is provided for comparison. |
| 15 | Simulated population response to constant (plot A) and randomly generated (plots B and C) marsh water depths and winter freezes. |
| 16 | Theoretical absolute reproductive values for the alligator population inhabiting the coastal marshland of Cameron and Vermilion parishes, Louisiana. Values correspond to the assumptions of constant marsh water depth at 15 cm , constant population density of 71,900 animals (1973 density), and no severe winter freezes. |
| 17 | Age-specific female alligator harvest rates for proportional and observed differential harvest strategies. These age-specific rates correspond to an overall harvest rate of $7 \%$ and were calculated using the age structure of Table ll. Differential rates were computed using the size composition of the combined 1972 and 1973 Louisiana alligator harvest (Table 10). |
| 18 | Simulated alligator population response to $7 \%$ differential and proportional harvest rates. Differential and proportional rates were applied to identical initial populations (Table ll) under identical sets of randomly generated environmental conditions. |
| 19 | Simulated alligator population response to $5 \%$ differential and 7\% proportional harvest rates. These rates were applied to identical sets of randomly generated environmental conditions. The mean finite rates of increase for the $5 \%$ differential rate $(\bar{\lambda}=1.0012)$ and the $7 \%$ proportional rate $(\bar{\lambda}=1.0031)$ are approximately equivalent. |

20 Hypothetical alligator $1_{x}$ schedules corresponding to natural conditions (broken line) and egg collection and incubation with two years of artificial rearing (solid line).

21 Simulated population response to egg 93 collection management programs. Plot A corresponds to no management. Plot B corresponds to a management program in which 10,000 eggs were collected annually, and hatchlings were reared for 1 year and released. Plot $C$ corresponds to a management program in which 10,000 eggs were collected annually, and hatchlings were reared for 2 years and released. In each simulation water depths were held constant at 15 cm (. 5 foot) and no winter freezes occurred.

22 Simulated alligator population response to various restocking management options: (A) harvest rate $=0$, egg collection quota $=0$; (B) harvest rate $=12 \%$, egg collection quota = 15; (C) harvest rate $=12 \%$, egg collection quota $=10$; (D) harvest rate $=12 \%$, egg collection quota $=5$; (E) harvest rate $=12 \%$, egg collection quota $=0$.

## INTRODUCTION

The American alligator (Alligator mississippiensis (Daudin)) is native to the southeastern portion of the United States and occurs in Louisiana, Florida, Georgia, South Carolina, Texas, Arkansas, Mississippi, Alabama, and North Carolina. Reports of early settlers and explorers in the southeastern part of the country emphasized the abundance of alligators, and in the early l9th century the reptile was apparently present in tremendous numbers (Chabreck 1967a).

Commercial harvesting of alligators began in the mid19th century (Smith 1893). Peak harvests were realized in the late l800's (McIlhenny 1935). Stevenson (1904) estimated that the alligator populations of Florida and Louisiana were reduced by $80 \%$ between 1880 and 1904. Heavy harvests continued and by 1960 the alligator had been practically eliminated from most of its original range (Chabreck 1967a).

Despite a continuous decline in numbers since 1950, no significant effort was made to protect the alligator until the 1960 's when protective legislation was enacted by all states within the animal's range. In 1966 the alligator was placed on the federal list of rare and endangered
species. In 1970 the United States Congress established the Endangered Species Conservation Act and an amendment to the 1906 Lacey Act which prohibited interstate shipment of illegally taken alligators (Palmisano 1972). The combined effect of this federal action and various state laws was sufficient to largely curtail illegal killing of alligators (Chabreck 197la).

Alligator numbers in the southeastern United States have increased in recent years (Powell 1971; Bara 1971; Schemnitz 1972; Palmisano 1972; Joanen and McNease 1972a, 1972b; Palmisano et al. 1973). These increases resulted in the transfer of the American alligator from the "critically endangered" category to the "recovered" category in 1971 (Bustard 1971).

In 1958, the Louisiana Wildlife and Fisheries Commission initiated an intensive alligator research program, the results of which have been summarized by Chabreck (1971a), Joanen and McNease (1973a) and Palmisano et al. (1973). The Commission also initiated various management procedures including strict harvest control, restocking, and increased law enforcement efforts against poaching. These management efforts resulted in dramatic increases in alligator numbers until, by the late 1960's, high alligator densities existed in the coastal marshes of southeastern Louisiana. In 1970, the Louisiana state legislature established the framework for an open alligator season, and in 1972, 1973, and 1975, experimental harvests were conducted
in the marshland of Cameron and Vermilion parishes. Preliminary results indicate that the 1972 and 1973 harvests had no detrimental effect on the alligator population of these parishes (Palmisano et al. 1973, Joanen et al. 1974). The management of any wild animal population is an extremely complex task. While the wildife biologist often has a number of different management options at his disposal, the selection of an optimal or even a "good" option is difficult. As a result, biologists have begun to use computer simulation models as means of examining management alternatives.

The use of computer simulation models in the planning of management programs is of greater potential importance to alligators than to many other wildife species. This increased importance results, in part, from the high vulnerability of alligators to hunting. Because of this extreme vulnerability, experimental harvest manipulations involving wild populations are potentially more dangerous to alligators than to many other more resilient wildife species. Computer simulation provides a means of conducting harvest experiments without jeopardizing natural populations.

Another reason for the particular importance of computer simulation to alligator management involves the long time period required to reach sexual maturity. Female alligators in Louisiana typically reach sexual maturity at an age of 9 years (Kleibert pers. comm.). Selective harvesting of large, mature alligators can thus result in populations that require long time periods for recovery.

Again, this argues for the use of computer experimentation rather than actual harvest experiments that may have longlasting detrimental effects.

Considerable time lags can also occur between the implementation of beneficial management practices and their eventual effects on population growth rates. For example, simulated alligator management programs employing egg collection and the restocking of young animals produce increases in population growth rates which are not fully realized for $8-10$ years. Computer simulation permits us to avoid the time lag which would accompany the evaluation of such a program in the field and to make immediate predictions about the eventual effects of management practices.

A final reason for the advocation of the use of computer simulation for alligators involves the large number of possible management options which exist for these animals. For example, restocking programs, which have proven to be ineffective for many wildlife species, appear to hold considerable potential for alligators (Chabreck 197la), and can be employed either alone or in conjunction with harvest programs. A high degree of harvest selectivity is also possible for alligators, and various combinations of sizeand sex-specific harvest rates can be achieved. There are notable sex-specific differences in movement patterns and habitat preferences among alligators (Chabreck 1965; Joanen and McNease 1970a, 1972b). In Louisiana, these differences have been employed in the development of regulations that
increase the proportion of males in the harvest (Palmisano et al. 1973). In addition, different alligator harvest methods result in different harvest size distributions (Palmisano et al. 1973). Regulations specifying particular harvest methods can thus be imposed in order to achieve a desired size distribution. In cases of organisms such as alligators for which numerous possible management options exist, computer simulation is especially valuable as a means of examining various combinations of management practices and of developing overall programs which are both biologically and economically desirable.

This paper concerns the development and application of a model for simulating alligator population dynamics. The first objective of the study was to assemble all available information on the natural history and population dynamics of alligators and to use this information to construct a simulation model. The general approach to model construction was to sacrifice statistical rigor, when necessary, in order to obtain a reasonably complete model. The model was intended to represent a preliminary hypothesis about alligator population ecology, and about the interaction between alligator survival and fecundity rates and certain environmental parameters. The second objective of the study was to use the model to project the consequences of this hypothesis and to examine population response to various sets of environmental conditions. The third objective involved using the simulation model to investigate the consequences
of various alligator management strategies. Predictions about management strategies were developed from general principles of population dynamics and were conditionally tested via simulation experiments.

## DESCRIPTION OF STUDY AREA

The model was constructed to simulate the alligator population inhabiting the privately owned marshland of Cameron and Vermilion parishes, Louisiana. This area comprises l,144,600 acres of marsh (Joanen and McNease 1973b) and includes the land on which both the 1972 and 1973 Louisiana alligator harvests were conducted. The 1972 Louisiana alligator harvest was restricted to 278,168 acres of Cameron parish marshland (Joanen et al. 1972, Palmisano et al. 1973), and the 1973 harvest was conducted on 541,361 acres in Cameron and Vermilion parishes (Joanen et al. 1973).

The Louisiana coastal region has been divided into three major physiographic zones: the chenier plain, the subdelta and the active delta (O'Neil 1949). The study area was located in the chenier plain marsh zone of southeastern Louisiana, which contained the largest alligator population of the three zones. The chenier plain marsh zone borders the Gulf of Mexico, extends inland approximately $32 \mathrm{~km}(20$ miles), and consists of coastal marshland interlaced with a network of bayous, canals, and lakes. The surface is relatively flat and elevations average about 30 cm (l foot) above mean sea level; consequently, drainage in the area is slow. The only relief features are spoil deposits along
canals and stranded beach ridges, locally called cheniers.

The Louisiana coastal marshes have been subdivided into four primary vegetative types: fresh, intermediate, brackish and saline (Penfound and Hathaway 1938, Chabreck 1972). The study area included fresh, intermediate and brackish marsh types. Recent descriptions of these types have been provided by Chabreck (1972). The fresh marsh was preferred by nesting female alligators to the other marsh types (Joanen and McNease 1972a).

Water depth in the marsh appeared to be an environmental parameter of extreme importance to alligators, and 9 years of water level data were obtained for April through October from stations within the study area (Table l). Extreme fluctuations in water levels are associated with periods of prolonged drought, with levels declining to as much as 61 cm ( 2 feet) below the marsh surface (Nichols 1959) or hurricanes with water inundating the marsh to a depth of 91 to 274 cm ( 3 to 9 feet). In the construction of various water level functions in the model, 15 cm (.5 foot) was generally considered to be the mean annual marsh water depth value (after Chabreck 1960).
Table 1. Marsh water depths for Cameron parish, Louisiana.

| Year | April | May | June | July | August | September | October |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | - - - - - - - - - - - - - Cm (feet) - - - - - - - - - - - - - |  |  |  |  |  |  |
| 1965 | 12(.4) | 21 (.7) | 18(.6) | O(.0) | 6 ( . 2 ) | 18(.6) | 24(.8) |
| 1966 | 12(.4) | 49 (1.6) | 27 (.9) | 24(.8) | $34(1.1)$ | $55(1.8)$ | 58 (1.9) |
| 1967 | 21 (.7) | 46 (1.5) | 27 (.9) | 15 (.5) | $24(.8)$ | 49 (1.6) | 27 (.9) |
| 1968 | 24 (.8) | 18 (.6) | $12(.4)$ | 21 (.7) | 27 (.9) | 27 (.9) | 21 (.7) |
| 1969 | 18(.6) | 46 (1.5) | 27 (.9) | 3 (.1) | 15 ( . 5) | $24(.8)$ | $18(.6)$ |
| 1970 | $30(1.0)$ | 27 (.9) | 37 (1.2) | 24(.8) | 21 (.7) | 34(1.1) | 40 (1.3) |
| 1971 | 18(.6) | 3 ( .1) | $12(.4)$ | $0(.0)$ | 37 (1.2) | 24(.8) | 43 (1.4) |
| 1972 | $9(.3)$ | 24(.8) | 18(.6) | $9(.3)$ | 21 (.7) | 15(.5) | 40 (1.3) |
| 1973 | 18(.6) | 24(.8) | 27 (.9) | 24(.8) | $37(1.2)$ | 24(.8) | 40 (1.3) |
| Mean | $18(.6)$ | $27 \text { (.9) }$ | $24(.8)$ | $12(.4)$ | $24(.8)$ | $30(1.0)$ | $34(1.1)$ |
| St. Dev. | 5.2(.17) | 13.4(.44) | 8.5(.28) | 8.8(.29) | 8.5(.28) | 11.9(.39) | $11.0(.36)$ |
| a Source: Chabreck and Joanen (1966, 1967); Joanen et al. (1968, 1969, 1970, 1971, 1972,1973, 1974). |  |  |  |  |  |  |  |

## ALLIGATOR POPULATION ECOLOGY

## Size-Age Relationship

Alligator growth rate data have been presented by Reese (1915), Neill (1971), Chabreck (1965), Hines et al. (1968) and McIlhenny (1934). McIlhenny (1934) marked and released 38 alligator hatchlings on Avery Island, Louisiana, and followed their growth for 11 years. I derived curves from McIlhenny's data and projected them beyond the last data points through 21 years (Fig. l). It should be noted that these curves are not actually continuous throughout each year. Alligator growth slows during winter months and increases during spring, summer and fall. These curves were used to establish a general size-age relationship table which applies to alligators in the late summer of the specified years (Table 2). Table 2 was used in all conversions of size-specific to age-specific data. Although McIlhenny's (1934) data are considered adequate for the model, additional research on alligator growth rates is needed.

Food intake and temperature are variables which can affect alligator growth rate (Coulson et al. 1973), but no accurate data regarding these relationships are available for wild populations. McIlhenny's (1934) data were obtained in the coastal marshland of southwestern Louisiana, and I

Figure 1. Relationship between total length and age in alligators. Years begin September 1 and end August 31.


Table 2. Estimated relationship between size and age for alligators inhabiting the coastal marshland of Cameron and Vermilion parishes, Louisiana.a

| Age (years) | $\text { Body length }{ }^{\text {b }}$ |  |
| :---: | :---: | :---: |
|  | Males | Females |
|  | - - - - Met | t) - - - - |
| 1 | . 3- . 6 (1-2) | . 3- . 6 (1-2) |
| 2 | .6-. 9 (2-3) | .6-. 9 (2-3) |
| 3 | . 9-1.2(3-4) | .9-1.2(3-4) |
| 4 | 1.2-1.5 (4-5) | 1.2-1.5(4-5) |
| 5 | 1.5-1.8(5-6) | 1.2-1.5(4-5) |
| 6 | 1.5-1.8(5-6) | 1.5-1.8(5-6) |
| 7 | 1.8-2.1(6-7) | 1.5-1.8(5-6) |
| 8 | 2.1-2.4(7-8) | 1.5-1.8(5-6) |
| 9 | 2.4-2.7(8-9) | 1.8-2.1(6-7) |
| 10 | 2.4-2.7(8-9) | 1.8-2.1(6-7) |
| 11 | 2.7-3.0(9-10) | 1.8-2.1(6-7) |
| 12 | 2.7-3.0 (9-10) | 2.1-2.4(7-8) |
| 13 | 3.0-3.4(10-11) | 2.1-2.4(7-8) |
| 14 | 3.0-3.4(10-11) | 2.1-2.4(7-8) |
| 15 | 3.4-3.7(11-12) | 2.4-2.7(8-9) |
| 16 | 3.4-3.7(11-12) | 2.4-2.7(8-9) |
| 17 | 3.7-4.0(12-13) | 2.4-2.7(8-9) |
| 18 | 3.7-4.0(12-13) | 2.4-2.7(8-9) |
| 19 | 3.7-4.0(12-13) | 2.4-2.7(8-9) |
| 20 | 3.7-4.0(12-13) | 2.4-2.7(8-9) |
| 21 | 3.7-4.0(12-13) | 2.4-2.7(8-9) |

abasically derived from McIlhenny (1934).
${ }^{\mathrm{b}}$ Sizes generally apply to alligators at the beginning (September) of the designated year class.
assumed that the general temperature regime and the types of alligator prey species available were much the same as those existing on the study area. Alligators utilize a wide variety of food sources, and are probably not subjected to food shortages as frequently as other more specialized predators. Alligators exposed to saline conditions consume less food than animals inhabiting fresh water areas (Chabreck 1971). The study area for the simulated population, however, included virtually no saline areas, and this variable was thus ignored.

## Reproductive Biology

## Courtship and nesting

Courtship and breeding occur between May 18 and May 31 in southwestern Louisiana (Joanen and McNease 1970a). Courtship activity during this time is apparently restricted to open water areas including bayous and canals, and marsh lakes and ponds greater than one acre in size (Joanen and McNease, 1970a). After courtship adult females travel to dens in the interior marsh to construct nests and lay eggs. Details of alligator nest construction have been provided by Reese (1907), Kellogg (1929), Arthur (1931), McIlhenny (1934), Bellairs (1969), Joanen (1969) and Neill (1971).

In southwestern Louisiana the peak alligator nesting period varies between June 15 and June 28 (Joanen 1969). Joanen correlated these peak nesting periods with average March, April and May temperatures. However, he found only a

13-day difference between dates of peak nesting activity, and the temperature-nesting period relationship was thus ignored in the model. In the model, nesting was allowed to occur at the end of June in each year.

The mean number of eggs per nest is 38.9 with a range of 2 to 58 (Joanen 1969). This mean was incorporated in the model as a constant. The incubation period for alligator eggs is approximately 63 to 65 days (Chabreck 1967b, Joanen 1969). In the model, hatching thus occurred at the end of August.

Age at sexual maturity
The female alligator reaches maturity at 1.8 meters (6 feet) (see Chabreck 1966, Giles and Childs 1949, Joanen 1969). Females generally begin nesting at age 9 (Kleibert pers. comm.) corresponding to the beginning of the year during which females move to the 1.8 to 2.1 meter ( 6 to 7 feet) size class (Table 2). In the model, I assumed that female alligators become sexually mature at age 9 and continue breeding throughout the remainder of their lives.

All 1.8-4.0 meter (6-13 feet) male alligators examined by Joanen and McNease (1973a) were found to be physiologically capable of reproduction. Because of the usual surplus of males in adult alligator populations (Chabreck 1966) and because of the ability of individual males to breed with more than one female per season (Chabreck 1965), the number of adult males was considered to be unimportant for the computation of nesting females.

## Nesting effort

Chabreck (1966) cited data from Sabine Refuge (southwestern Louisiana) kill survey records indicating that 68.18 of a sample of 69 adult females nested during one year. Also, Joanen and McNease (1973a) indicated that $67 \%$ of the adult female segment of an alligator population is capable of reproducing during any given year.

In 1971, alligator nest counts in southwestern Louisiana indicated that nesting had decreased by $39.5 \%$ from the previous year (Joanen and McNease 1972c). Joanen and McNease felt that the decreased number of nests was due to dry nesting conditions rather than to a decrease in the mature female segment of the population. They further stated that "nesting success may be proportional to the amount of surface water accrued during the spring on until actual egg deposition" (Joanen and McNease 1972c). This 1971 nesting decline has also been attributed to dry nesting conditions in later reports (Joanen and McNease 1973b, Palmisano et al. 1973), and Schemnitz (1972) has cited low water levels as the reason for a 1971 decline in alligator nesting in the Florida Everglades. In addition, Joanen and McNease (1970a, 1972a) have stressed the need of female alligators for open water during courtship.

The nesting effort-water depth relationship appears to be extremely important to population growth and was thus included in the model. The average of the water depths for May and June, the months of alligator breeding and nesting,
was assumed to be the environmental parameter of importance (Chabreck pers. comm.). Changes in nesting effort reported by Joanen and McNease (1972c) for the sub-delta and chenier plain marsh zones were used to compute nesting percentages for 1970 and 1971. A summary of nesting percentages and corresponding May-June marsh water depth averages is presented in Table 3.

I assumed a minimum nesting percentage of $33.5 \%$ (a 50\% decrease from years of normal water depth). This minimum nesting percentage was set to correspond to a marsh water depth of 0 cm . A curve (Fig. 2) representing the nesting percentage-water depth relationship was derived from the various data sources of Table 3. In the model, the percentage of mature females nesting was determined from the curve, and this percentage was then applied to the number of mature females in the population at the end of June for each year.

Variation in breeding percentages in response to variable environmental cues has been observed in numerous organisms (e.g. Conley et al. 1976, Nichols et al. 1976). Such variation can have profound demographic effects and is an important component of an organism's life history strategy. In the case of alligators, one evolutionary interpretation of this variation involves nest site availability. After breeding, mature female alligators travel to den ponds in the interior marsh to begin nest construction. Since these ponds are among the first areas to dry up in times of drought, I hypothesize that decreased nesting percentages

Table 3. Computed percentages of females nesting as related to marsh water depths during May and June.

| Marsh zone | Year | Water depth <br> $[\mathrm{cm}($ feet $)]$ | Percent mature <br> females nesting |
| :--- | ---: | ---: | :--- |
| Chenier Plain | 1970 | $32(1.05)^{\mathrm{a}}$ | 67.0 |
| Sub-Delta | 1970 | $20(.65)^{\mathrm{b}}$ | 67.0 |
| Chenier Plain | 1971 | $8(.25)^{\mathrm{a}}$ | $40.5^{\mathrm{c}}$ |
| Sub-Delta | 1971 | $15(.50)^{\mathrm{b}}$ | $63.0^{\mathrm{c}}$ |

$a_{\text {From Joanen et al. (1971). }}$
${ }^{b}$ In the absence of sub-delta water depth measurements, these data were derived from a rainfall-marsh water depth plot.
${ }^{\text {C Computed }}$ from percent changes in nesting success reported by Joanen and McNease (1972c).

Figure 2. Relationship between the percentage of mature female alligators nesting and marsh water depth (May-June average).

constitute a response to decreased nest site availability.

## Nest flooding

Alligator nests are vulnerable to flooding during times of high water. Flooding loss was reported to be a major source of egg mortality in the Florida Everglades (Hines et al. 1968) and can also cause considerable damage in the Louisiana coastal marshland during certain years (Ensminger and Nichols 1957, Chabreck 1965).

Egg incubation generally occurs during the last week of June and during the entire months of July and August. In the model, the percentage of nests lost to flooding was determined as a function of the highest monthly water depth average of the months June, July, and August. A variety of sources was utilized in the construction of the nest flooding-water depth relationship (Table 4). The maximum flooding percentage listed in Table 4 is 93.3, corresponding to all nests constructed in the marsh itself. Joanen (1969) reported that $6.7 \%$ of the nests he observed were constructed on levees, above normal flood levels. I assumed that even these levee nests would be lost at water depths of 122 cm ( 4 feet) and greater, levels representative of flood conditions associated with hurricanes. The derived nest flooding-water depth relationship is shown in Fig. 3.

## Levee nesting

Levee nests apparently have different probabilities of being flooded and destroyed by predators than do marsh nests.

Table 4. Selected marsh water depths and corresponding nest flooding percentages.

| Maximum water depth of <br> June, July and August | Percent <br> nests lost |
| :---: | :---: |
| cm (ft.) |  |
| 24 (..8) | $0.0^{\mathrm{a}}$ |
| 34 (1.1) | $8.0^{\mathrm{b}}$ |
| $37(1.2)$ | $46.7^{\mathrm{C}}$ |
| $46(1.5)$ | $93.3^{\mathrm{a}}$ |

${ }^{\text {a }}$ Computed from egg cavity measurements of alligator nests (Joanen 1969).
$\mathrm{b}_{\text {Computed }}$ from nest flooding data of Joanen (1969). ${ }^{\text {C Computed }}$ from nest flooding data of Flemming (1974).


It has been suggested that adult females tend to use margins of ridges as nesting sites when marsh water levels are abnormally high (Giles and Childs 1949, Ensminger and Nichols 1957). However, Chabreck (1965) did not observe a relationship between nest location and water depth. Nesting alligators are very territorial and tend to nest in the same vicinity each year (Joanen 1969, Joanen and McNease 1970a). Joanen's (1969) $6.7 \%$ figure for levee nests was thus assumed to remain constant.

## Nest predation

Nest predation can be an important source of egg mortality. Joanen (1969) followed 266 nests during a 4-year period and reported that $16.5 \%$ of these nests were destroyed by raccoons, Procyon lotor. Joanen (1969) found that $50 \%$ of the levee nests which he followed were destroyed by raccoons. Palmisano (pers. comm.) observed that 18-20\% of all marsh nests are generally destroyed by rac-c-ons, while approximately $50 \%$ of levee nests are destroyed.

The raccoon is by far the most important alligator nest predator, and it was the only predator considered in the model. Nest predation by raccoons occurs just after the eggs begin to crack along the longitudinal axis, usually after seven weeks of incubation. After locating a nest, raccoons generally return every few days for three or four visits until all eggs have been eater (Joanen 1969). A
raccoon which located a nest after 49 days of incubation and periodically returned to the nest every few days, would probably finish with the nest at approximately the time of hatching. Therefore, it is unlikely that a raccoon would ever prey upon more than one nest per year, and certainly never more than two. Because of this temporal limitation of nest availability, I hypothesized that the predation rate would not increase as a function of alligator nest density.

Raccoon density must certainly affect the rate of nest predation. Raccoon density in the Louisiana coastal marsh varies from approximately one raccoon per 5 acres to one per 10 acres (Palmisano, pers. comm.). Unfortunately, raccoon density data were not available for years in which raccoon predation rates on alligator nests were known and thus this relationship could not be incorporated into the model.

Flemming (1974) felt that nest predation is possibly related to marsh water depth, with higher predation rates occurring in dry years. He believed that raccoon predation on nests is linked to food availability, and that more food is available to raccoons during wet years. Unpublished data on annual 1965-1968 predation rates were made available by Joanen (pers. comm.), and these rates were compared with August marsh water depths. Percent predation was plotted against August marsh water depth and three points were taken directly from Joanen's (pers. comm.) data. The lowest observed nest predation rate was $1.7 \%$, which was reported in 1965 when the August marsh water depth averaged
$6 \mathrm{~cm}(.2$ foot). This predation rate seemed extremely low (Chabreck pers. comm.), and the $1.7 \%$ value was arbitrarily doubled to obtain a minimum predation rate of $3.5 \%$. Flemming (1974) observed no nest predation on 20 nests which he followed in 1973. The August marsh water depth during that year was $37 \mathrm{~cm}(1.2$ feet). Therefore, the minimum predation rate of $3.5 \%$ was also set to correspond to this water depth.

These data were plotted and a general nest predationwater depth relationship was derived (Fig. 4). The portion of the curve lying above $24 \mathrm{~cm}(.8$ foot) follows the pattern predicted by Flemming (1974), with predation rate increasing as water level decreases. Below 24 cm (. 8 foot), however, the relationship is contrary to what was expected.

If low predation rates do actually occur at low water levels, then such a relationship could be explained in several possible ways. The majority of alligator nests are built in the marsh interior, and perhaps during times of severe drought raccoons are less likely to leave large, permanent water sources and venture into the dry marsh in search of food. In times of drought, numerous raccoon prey species would probably be concentrated in any available bodies of water. Such a situation would eliminate the raccoon's need to venture into the interior marsh. Finally, most alligator nests are constructed near the female's hole or den, and females tend to remain near the den site during periods of drought (Chabreck 1965). In a telemetric study

1SO7
S1SヨN 1NヨつYヨd
of nesting females, Joanen and McNease (1970a) also noted that female movement was restricted during the period of the year exhibiting the lowest water levels. By remaining in the proximity of the den and nest site during times of drought, females are probably better able to defend the nest against raccoons.

The relationship graphed in Fig. 4 was used in the model, despite some doubts regarding the nature of the function. The inability to incorporate raccoon density into the model was unfortunate, and it is essential that the raccoon density-nest predation relationship be studied in the future.

## Hatching success

Total hatching success and predation and flooding loss values from Joanen (1969) were used to compute a hatching success of 76.8\%. This value was incorporated in the model as a constant and was applied to all eggs surviving predation and flooding.

Alligator Population Structure and Mortality Relationships

Average annual mortality and survival rates
Before investigating alligator population structure and specific mortality functions, it was necessary to obtain average annual mortality rates for the different age classes in the alligator population. Alligator population dynamics have never been adequately studied, however, and no reliable mortality rate estimate could be found in the literature.

Chabreck (1966), presented night count results which indicated the size structure of the Rockefeller Refuge alligator population at the time of his study. This size structure could theoretically be used to construct a time-specific life table, and mortality rates could be obtained in this manner. Time-specific life tables, however, require the assumptions that the environment does not change from year to year and that the population is at equilibrium (Krebs 1972), and neither of these assumptions could be met for the Rockefeller Refuge alligator population.

Harvest data were available for the 1972 and 1973 experimental seasons, and these data were manipulated to obtain one annual mortality estimate for 7-year-old males. This specific age and sex class was used because both 7 and 8-year-old males occupy single size classes, and mortality estimates for these animals are thus not confused by the existence of more than one age class per size category. The calculations invoked the assumption that 7-year-old males in 1972 and 8-year-old males in 1973 were harvested in proportion to their relative abundance in the sample population each year.

Two methods were used for taking alligators during the experimental harvest seasons, "fishing" with baited hook and line, and shooting. The fishing method was selective for larger animals (Palmisano et al. 1973), and the mortality estimate was calculated based on the total samples of fished animals in both seasons. The percent (25.30) mature
male alligators caught by hook and line in the 1973, 2.1-2.4 meter (7-8 feet) size class, was subtracted from the percent (32.11) mature male alligators caught by hook and line in the 1972, 1.8-2.1 meter (6-7 feet) size class. This difference of $6.81 \%$ was divided by $32.11 \%$ (again representing the 1.8-2.1 meter males in the 1972 sample) and a mortality rate of $21.2 \%$ was obtained.

After age 2, alligators are relatively free of predation. Therefore, I assumed that mortality rates are the same for the alligator age classes 3-21, and the $21.2 \%$ annual mortality rate was considered to apply to all of these classes. After reaching maturity, female alligators move into the marsh interior, and their mortality rates probably decrease at this time (Chabreck 1965). Adult males, however, travel extensively (Joanen and McNease 1972b) and are subjected to a variety of hazards. Therefore $I$ assumed that adult males have twice the annual mortality rate of adult females (after Chabreck pers. comm.).

The $21.2 \%$ annual mortality rate was separated into seven equal monthly survival rates (corresponding to the number of months during which alligators are active) and a . 967 monthly survival rate was thus calculated. The .967 rate was applied to males and females aged 3 through 8 years. Assuming an adult sex ratio of $60.1 \%$ males (Chabreck 1966), differential annual survival rates became .750 per year for males and .875 per year for females. The male mortality rate is therefore twice as high as the female rate.

Annual survival rates reduce to .960 per month for males and . 981 per month for females, and were applied to animals 9 through 21 years old.

Based on field observations of alligator populations, Chabreck (pers. comm.) estimated an averaqe $65 \%$ mortality rate for l-year-old animals and a $40 \%$ mortality rate for 2-year-olds. Both sexes are equally vulnerable at these ages, thus average monthly survival rates were .861 for one-year-olds and .930 for two-year-olds. Average annual and monthly survival rates are summarized in Table 5. As previously mentioned, all annual survival rates were divided into seven monthly rates. I assumed that all alligator mortality sources other than freezes occurred during the months, April through October. Alligators are semidormant during the five months, November through March, and few mortality sources probably operate during this period.

## Population age structure

A general knowledge of the age structure of the alligator population was necessary before various mortality functions could be calculated. Chabreck (1966) presented results of night count surveys indicating size structure of the Rockefeller Refuge alligator population (Table 6). Chabreck believed his night count sample was representative and combined these results with nest count data to estimate the total alligator population of Rockefeller Refuge.

Chabreck's (1966) night count data indicated the size structure of the alligator population at approximately the

Table 5. Survival rate estimates for alligators inhabiting the coastal marshland of Cameron and Vermilion parishes, Louisiana.a

| Age | Annual survival rate |  | Monthly survival rate |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Male | Female | Male | Female |
| 1 | . 350 | . 350 | . 861 | . 861 |
| 2 | . 600 | . 600 | . 930 | . 930 |
| 3 | . 788 | . 788 | . 967 | . 967 |
| 4 | . 788 | . 788 | . 967 | . 967 |
| 5 | . 788 | . 788 | . 967 | . 967 |
| 6 | . 788 | . 788 | . 967 | . 967 |
| 7 | . 788 | . 788 | . 967 | . 967 |
| 8 | . 788 | . 788 | . 967 | . 967 |
| 9 | . 750 | . 975 | . 960 | . 981 |
| 10 | . 750 | . 875 | . 960 | . 981 |
| 11 | . 750 | . 875 | . 960 | . 981 |
| 12 | . 750 | . 875 | . 960 | . 981 |
| 13 | . 750 | . 875 | . 960 | . 981 |
| 14 | . 750 | . 875 | . 960 | . 981 |
| 15 | . 750 | . 875 | . 960 | . 981 |
| 16 | . 750 | . 875 | . 960 | . 981 |
| 17 | . 750 | . 875 | . 960 | . 981 |
| 18 | . 750 | . 875 | . 960 | . 981 |
| 19 | . 750 | . 875 | . 960 | . 981 |
| 20 | . 750 | . 875 | . 960 | . 981 |
| 21 | . 750 | . 875 | . 960 | . 981 |

[^0]Table 6. The results of night counts and total population computation for alligators on Rockefeller Wildlife Refuge, 1966.a

| Total length <br> size classes <br> [meters (feet)] | Number <br> seen | Percentage <br> composition | Total number <br> on refuge |
| :--- | :---: | :---: | :---: |
| $.3-.6(1-2)$ | 45 | 25.3 | 1339 |
| $.6-.9(2-3)$ | 33 | 18.5 | 979 |
| $.9-1.2(3-4)$ | 30 | 16.8 | 888 |
| $1.2-1.5(4-5)$ | 24 | 13.5 | 714 |
| $1.5-1.8(5-6)$ | 18 | 10.1 | 534 |
| $1.8-2.1(6-7)$ | 13 | 7.3 | 386 |
| $2.1-2.4(7-8)$ | 8 | 4.5 | 238 |
| $2.4-2.7(8-9)$ | 4 | 2.3 | 122 |
| $2.7-3.0(9-10)$ | 2 | 1.1 | 58 |
| $3.0+$ | $(10+)$ | 1 | 100.0 |
| Total |  |  |  |

[^1]end of May and the beginning of June, 1966. However, my calculations required a knowledge of September age structure, and because of the differential mortality rates operating on the population, the September size structure is expected to differ from the June size structure. It was therefore necessary to back calculate from June, 1966 to September, 1965. This was accomplished by dividing the number of animals comprising each size class, by the monthly size-specific survival rate taken to the fourth power (there are four months involved). These calculations yielded a new size structure characteristic of the beginning of September.

The September population size structure was then separated using size-specific sex ratios (Table 7). These ratios were obtained from 1816 alligators captured alive in Louisiana during the period 1959-1966. It is virtually impossible to accurately determine the sex of alligators less than . 6 meters ( 2 feet) in length, and the average adult value of $60.1 \%$ males (Chabreck 1966) was thus used for these small animals. The $60.1 \%$ male value was also used for size classes in which an insufficient number of animals was examined.

The assumption of a sex ratio deviating from $50 \%$ male at hatching implies either differential energy expenditure by parents or differential pre-hatching survival rates (see Fisher 1958, Kolman 1960, Pianka 1974). While there is no direct evidence supporting the action of either of these

Table 7. Size-specific sex ratios used in the construction of alligator population structures.a

| Total body length |  | Males | Females |
| :---: | :---: | :---: | :---: |
| --Meters | (feet)-- | ------- | ----- |
| . 3-. 6 | (1-2) | $60.1{ }^{\text {b }}$ | 39.9 |
| .6-. 9 | (2-3) | 64.6 | 35.4 |
| . 9-1.2 | (3-4) | 62.8 | 37.2 |
| 1.2-1.5 | (4-5) | 53.5 | 46.5 |
| 1.5-1.8 | (5-6) | 52.4 | 47.6 |
| 1.8-2.1 | (6-7) | 64.1 | 35.9 |
| 2.1-2.4 | (7-8) | $60.1{ }^{\text {c }}$ | 39.9 |
| 2.4-2.7 | (8-9) | $60.1{ }^{\text {c }}$ | 39.9 |
| 2.7-3.0 | (9-10) | $60.1^{\text {c }}$ | 39.9 |
| 3.0-3.4 | (10-11) | 100.0 | 0.0 |
| 3.4-3.7 | (11-12) | 100.0 | 0.0 |
| 3.7+ | (12+) | 100.0 | 0.0 |

a Unless otherwise indicated, sex ratio data were obtained from 1816 alligators captured alive in Louisiana from April, 1959, to December, 1966 (Chabreck unpubl. data).
$b_{\text {Average adult sex ratio (Chabreck 1966) was used because }}$ of inability to sex young alligators.

CAverage adult sex ratio (Chabreck 1966) was used because of insufficient data (small sample sizes).
mechanisms in alligators, available data do suggest the existence of an excess of males of hatching. For example, the sex ratio of a sample of 305 alligators in the . $6-.9$ meter (2-3 feet) size class was $64.6 \%$ male (Table 7). If the sex ratio at hatching was $50 \%$ male, then the preponderance of males in the succeeding age class would imply differential sex-specific survival rates during the first year of life. However, immature males and females exhibit similar movement and activity patterns (Chabreck 1965), and the operation of differential survival rates is thus not likely. Additional support for the existence of a high proportion of male hatchlings is provided by the low relative survival rates of adult males (Table 5), which necessitate a preponderance of male hatchlings for maintenance of observed adult sex ratios (Table 7). It should finally be noted that data are available on hatchling sex ratio, although sample size is extremely small. Nichols and Chabreck (unpubl. data) dissected 16 alligators which had been artificially hatched and reared for 10 months. This group of animals was comprised of 13 males and 3 females. If the actual sex ratio at hatching was $50 \%$ male, then the probability of randomly obtaining such a sample would be less than . 011.

Finally, it was necessary to determine the number of animals in each age class, within a given size and sex class. This was accomplished by assuming a stable age distribution within each size class and by establishing the following equality:

1) $\quad N=\sum_{i=0}^{z} \quad(p)^{i} n$
and then solving for $n$ :

$$
\text { 2) } \quad n=N / \sum_{i=0}^{z}(p)^{i}
$$

where $z-1$ is the number of age classes in the given size class, $p$ is the annual survival rate, $N$ represents the total number of animals in the size class, and $n$ equals the number of animals in the youngest age class within the size class. The numbers of animals in subsequent age classes were then obtained by multiplying the number of animals in the youngest age class by the appropriate power of the survival rate.

A sample age structure derived from these calculations is shown in Table 8. This particular age structure was obtained starting with the June, 1973, population estimate of 71,897 animals (Palmisano et al. 1973). The derived age structure contains 96,918 alligators and represents the September, 1972, population.

Specific mortality functions
After obtaining general estimates of population age structure and average mortality rates, it was possible to examine specific mortality relationships. Drought can increase mortality from desiccation, predation, and cannibalism in alligators (Hines et al. 1968, Spotila et al. 1972, Truslow et al. 1967). A severe drought can be characterized by a marsh water level of $-61 \mathrm{~cm}(-2.0$ feet) for a period

## Table 8. Calculated age structure for the alligator population of Cameron and Vermilion parishes, Louisiana, September, 1972.

| Age | Males | Females |
| :---: | ---: | ---: |
|  |  |  |
| 1 | 19876 | 13196 |
| 2 | 11487 | 6295 |
| 3 | 8680 | 5141 |
| 4 | 5942 | 2888 |
| 5 | 2435 | 2276 |
| 6 | 1919 | 1642 |
| 7 | 3315 | 1294 |
| 8 | 2043 | 1019 |
| 9 | 609 | 1059 |
| 10 | 479 | 834 |
| 11 | 528 | 657 |
| 12 | 415 | 652 |
| 13 | 174 | 514 |
| 14 | 137 | 406 |
| 15 | 93 | 209 |
| 16 | 74 | 166 |
| 17 | 11 | 130 |
| 18 | 8 | 103 |
| 19 | 7 | 81 |
| 20 | 6 | 64 |
| 21 | 4 | 50 |
|  |  |  |

of 2 months, and such a drought can increase normal mortality by an estimated 20\% (Chabreck pers. comm.). An estimated $60 \%$ of such a drought loss would be suffered by one-year-old animals, $30 \%$ by two-year-olds, and the remaining $10 \%$ by females and other immature males (Chabreck pers. comm.). Adult males inhabit large bodies of permanent water and would be relatively unaffected by drought. Using these estimates and a September age structure (Table 8), monthly drought mortality rates were calculated for the specified age classes. These drought mortality rates indicated the percentages by which normal mortality rates are increased during periods of drought.

Desiccation. Alligators have high rates of evaporative water loss and are threatened by desiccation during times of drought (Spotila et al. 1972). It was estimated that $50 \%$ of the total drought mortality results from desiccation, while the remaining 50\% results from predation and cannibalism (Chabreck pers. comm.). Monthly drought rates were thus divided by two to obtain desiccation mortality rates for a month of -61 cm ( -2.0 feet) marsh water level. Because of the probable relationship of alligator size to mobility and desiccation vulnerability, the estimated minimum water levels at which no desiccation mortality occurs, differ among the three affected age classes. The hypothesized desiccation mortality-water depth relationships have been plotted in Figs. 5, 6 and 7.

## MONTHLY MORTALITY (PERCENT)


Figure 6. Relationship between both predation and desiccation mortality and


## Figure 7. Relationship between desiccation mortality and marsh water depth in female alligators aged 3-21 years and male alligators aged 3-6 years.



Cannibalism. Instances of alligator cannibalism have been reported by Kellogg (1929), Giles and Childs (1949), Valentine et al. (1972), and Truslow et al. (1967). This mortality source is probably the major density dependent factor operating on Louisiana alligator populations. During years of normal water level cannibalism results in an estimated $2 \%$ annual mortality at present pre-saturation population densities, and in a 6\% annual mortality rate at carrying capacity densities (Chabreck pers. comm.).

Carrying capacity estimates for the coastal marshland of Cameron and Vermilion parishes are one alligator per five acres of fresh marsh, one alligator per eight acres of intermediate marsh, and one alligator per 20 acres of brackish marsh (Chabreck pers. comm.). These represent population densities on wildlife refuges in the study area where long histories of rigidly protected alligator populations exist. The total acreage of each marsh type in the study area was divided by the appropriate carrying capacity (acres-peralligator) figure. Then, the carrying capacity populations for each marsh type were summed, and a total carrying capacity figure of 147,590 alligators was obtained for the 1,144,600 acre study area.

Assuming that $60 \%$ of all cannibalism mortality is suffered by one-year-olds, $30 \%$ by two-year-olds, and $10 \%$ by three-year-olds (Chabreck pers. comm.), monthly cannibalism mortality rates were calculated for present population densities and carrying capacity densities at average water
depths. Present population density was assumed to be about 71,900 (Palmisano et al. 1973), and carrying capacity density was again assumed to be 147,590 animals. The densitycannibalism relationship was then plotted (Fig. 8). I assumed that cannibalism would not decrease to 0 , and a minimum cannibalism rate was thus arbitrarily set at . 001 .

Alligators become concentrated as water levels decline and, during years of severe drought, 5 and $15 \%$ cannibalism mortality rates were estimated for present density and carrying capacity density populations, respectively (Chabreck pers. comm.). A monthly cannibalism increase for months of severe drought was calculated using annual average water and severe drought cannibalism rate estimates, and a September age structure.

Age-specific cannibalism rate increases for months of severe drought were calculated for the three affected age classes using a September age structure and the previously calculated cannibalism rates for average water depth and present density. These age-specific rate calculations invoked the assumption that severe drought cannibalism increases are proportional for the three affected age classes. In this manner, it was calculated that normal monthly cannibalism rates are increased by a factor of 4.65 during months of severe drought. A cannibalism rate multiplier was then plotted by setting 4.65 to correspond to a water level of $-61 \mathrm{~cm}(-2.0$ feet), and setting the value 1 to correspond with the average water depth of 15 cm (.5 foot)
Figure 8. Relationship between cannibalism mortality and total density in the
alligator population of Cameron and Vermilion parishes, Louisiana.

(Fig. 9). A minimum value for this multiplier was arbitrarily assumed to be . 25 , because the cannibalism rate probably does not decrease to 0 .

In the model, monthly cannibalism mortality rate was determined as a function of density. This rate was then multiplied by the cannibalism rate multiplier, which was determined as a function of monthly water level. The resulting product constituted the increase in mortality due to cannibalism.

Predation. Alligator young are preyed upon by a wide variety of predators (Neill 1971). Because of this variety it was impossible to incorporate predator densities into the model. Predation rates are probably also a function of alligator density, but again this relationship was not included in the model because of insufficient data. I estimated that during years of average water depths, one-yearold alligators would suffer approximately a $60 \%$ loss to predators and two-year-old animals would lose $15 \%$ annually due to predation, following Chabreck (pers. comm.). These annual age-specific predation rates were converted to monthly rates in the manner previously described.

During times of drought, alligator young and predators are concentrated in remaining water bodies, and alligators suffer high predation rates (Hines et al. 1968). I previously estimated that $50 \%$ of the total alligator mortality suffered during a severe drought (water level at -61 cm

for 2 months) could be attributed to predation and cannibalism. The drought cannibalism rates were determined for each affected age class as previously described, and the drought predation rates were obtained by subtracting the cannibalism rates from the total predation plus cannibalism rates. The predation rate-water depth relationships have been plotted in Figs. 5 and 6. I assumed that predation would never decrease to 0 , and minimum monthly predation mortality rates of .05 and .01 were thus set for one and two-year-old alligators, respectively.

Natural mortality. In the model, natural mortality is simply an age and sex-specific constant which includes all mortality sources in addition to those already separated from the average mortality values. "Natural" mortality includes such mortality sources as animals being shot as pests, poaching, accidental kills, and animals dying from physiological mortality sources unrelated to drought. These mortality rates were obtained by subtracting age and sex-specific cannibalism and predation mortality rates (for months of average water depth) from average total mortality rates. These age and sex-specific rates were then incorporated into the model as constants (Table 9).

Freeze mortality. Chabreck (1965) reported finding dead alligators ranging from .6 to 3.0 meters ( 2 to 10 feet) in length which had suffocated under ice during a severe freeze in January, 1962. Climatological records indicate

Table 9. Natural mortality rates for alligators inhabiting the coastal marshland of Cameron and Vermilion parishes, Louisiana.a

|  | Natural |  |
| :---: | :---: | :---: |
| Age class | Males | Females |
| 1 | .011 | .011 |
| 2 | .044 | .044 |
| 3 | .031 | .031 |
| 4 | .033 | .033 |
| 5 | .033 | .033 |
| 6 | .033 | .033 |
| 7 | .033 | .033 |
| 8 | .033 | .033 |
| 9 | .043 | .020 |
| 10 | .043 | .020 |
| 11 | .043 | .020 |
| 12 | .043 | .020 |
| 13 | .043 | .020 |
| 14 | .043 | .020 |
| 15 | .043 | .020 |
| 16 | .043 | .020 |
| 17 | .043 | .020 |
| 18 | .043 | .020 |
| 19 | .043 | .020 |
| 20 | .043 |  |
| 21 | .043 |  |

[^2]that in January, 1962, the maximum temperature for Lake Charles, Louisiana, was below $0^{\circ} \mathrm{C}$. for a period of between 2 and 3 days. It was assumed in the model that any drop in maximum temperature below $0^{\circ} \mathrm{C}$. for a period of 2 days or more would cause alligator freeze mortality. Such a freeze was set to produce a $5 \%$ loss from the total population and was considered to be neither age nor sex-specific (Chabreck pers. comm.).

Hunting mortality. A major objective of this study was to investigate the effects of hunting mortality on alligator populations, and I included an optional harvest rate which could be applied to the population in September of each year. The optional harvest rate was used in either of two types of calculations of relative age- and sex-specific harvest rates. The first set of calculations produced harvest rates which were similar to those observed in the 1972 and 1973 Louisiana seasons. These calculations involved the use of size and sex-specific harvest percentages which were obtained by summing all wild animals taken in the two Louisiana seasons (from Joanen et al. 1972, Palmisano et al. 1973, Joanen et al. 1973, McNease pers. comm.) and determining the percent composition of this total for each size and sex class (Table 10). The actual computation of these harvest rates in the model is described under the heading "The Simulation Model".

Table 10. Percent composition of the combined 1972 and 1973 Louisiana alligator harvest.a

| Total body length | Males | Females |
| :--- | ---: | ---: |
| --Meters (feet)-- |  |  |
|  |  |  |
| $1.2-1.5(4-5)$ | 13.93 |  |
| $1.5-1.8(5-6)$ | 14.34 | 6.77 |
| $1.8-2.1(6-7)$ | 12.99 | 10.37 |
| $2.1-2.4(7-8)$ | 9.14 | 7.03 |
| $2.4-2.7(8-9)$ | 6.36 | 1.93 |
| $2.7-3.0(9-10)$ | 4.64 |  |
| $3.0-3.4(10-11)$ | 2.49 |  |
| $3.4-3.7(11-12)$ | .53 |  |
| $3.7+$ |  |  |

${ }^{\text {a Data }}$ used to calculate these percentages were taken from Tables 3 and 5 of Palmisano et al. (1973), Table 1 of Joanen et al. (1973) and a table provided by McNease (pers. comm.). Data on total size composition of harvests were corrected to eliminate farm alligators from the computations.

Harvest regulations for the 1972 and 1973 seasons were designed to protect mature female alligators. A lower size limit of 1.2 meters ( 4 feet) total body length was also established to protect young animals. Regulations governing these two seasons are discussed by Joanen and McNease (1972d) and Palmisano et al. (1973). Since the Louisiana hunters apparently selected for large animals (Palmisano et al. 1973), the observed harvest rates will subsequently be referred to as "differential" rates (i.e. differential with respect to size and age).

The second method for calculating harvest rates in the model produced rates which are termed "proportional". The proportional option produced equal harvest rates for all sizes within a given sex (the 70:30 observed male to female harvest ratio was maintained). Proportional rates assume that animals are harvested in proportion to their relative abundance in the population.

In the model, it was assumed that alligator populations do not adjust to hunting mortality with compensatory reductions in natural mortality. This assumption was made because of a lack of contrary evidence and because of the observed vulnerability of alligators to hunting. It may very well be false. Because of the nature of this assumption, simulated hunting produced maximum detrimental effects on the population.

## Description

A mechanistic mathematical model was constructed to simulate the behavior of the population over time. The modeled system was defined as the alligator population existing in the study area, and was divided into components according to sex and age. The state variables of the model were defined as the elements of the population matrix, AGEINIT $i, j$, with $i=1,21$ representing the age classes and $j=1,2$ corresponding to males and females, respectively. The structure of the model incorporated the use of state equations for each component describing its behavior in terms of stimulus and state variables. Initial values for the state variables were chosen for experimental simulations from a set of initial age structures. Response variables for each population component were chosen to be the number of deaths (mortality), the number of nesting females (reproduction), and the number of animals leaving the component (growth). The only endogenous stimulus feature was the number of animals entering each population component through birth or growth. Stimulus variables exogenous to the system were average monthly water levels, temperature, and a harvest rate equal to the percentage of animals taken by hunters.

The model was primarily deterministic but was modified in some experimental simulations to include stochastic functions for environmental factors. Stochastic variables were monthly water levels and temperature. Values for water levels (in feet) were randomly generated from normal distributions defined by the mean and standard deviation for each month (from Table l). Temperature was considered only through the use of a factor representing a freeze during winter, with probability of occurrence equal to .l (once every 10 years).

In order to observe the dynamics of the population over a time period of several years, the month of September was treated as the beginning of a new year ( $t=1$ in the equations below). September was chosen because of the assumption that all eggs were hatched at the end of August, with hatchlings then entering the population in September. The months November through March were treated as one time block designated as winter. All rates affecting the stimulus variables were applied during the months April through October unless otherwise designated.

State equations used to describe component behavior were:
3) $\operatorname{AGEINIT}_{i, j, t+1}=\operatorname{AGEINIT}_{i, j, t} \mathrm{X}$ SURNATM X hURSURV; for $\quad i=1,2, . . .21 ; \quad j=1,2 ; \quad t=0,1,2$ and $\quad t=7,8,$. . 11
4) $\operatorname{AGEINIT}_{i, j, t}=\operatorname{AGEINIT}_{i-1, j, t}$; for $i=2,3, \ldots 21$;

$$
j=1,2 ; \quad t=12
$$

5) $\operatorname{AGEINIT}_{i, j, t}=$ HACHTOT X .601 ; for $i=1$;

$$
j=1 ; \quad t=12
$$

6) $\operatorname{AGEINIT}_{i, j, t}=$ HACHTOT X.399; for $i=1$;

$$
j=2 ; \quad t=12
$$

where AGEINIT was the state variable used to represent the number of animals in each component $(i, j)$. After application of equations 4-6 in month $t=12$, the year variable (NYR) was incremented by 1 and $t$ was set equal to 0 .

Monthly population changes during April through October
State variables were updated monthly by state equation (3). SURNATM was a total survival rate including survival from all mortality factors with the exception of harvesting. During the months April - October this rate was determined by:
7) SURNATM = 1-(APRED+CANNAB+DESS+NATURAL)
where APRED was the predation factor for the young, CANNAB was the cannibalism mortality factor, DESS was the desiccation mortality factor, and NATURAL was the natural mortality factor.

APRED and DESS were computed as functions of average monthly water levels. CANNAB was considered to be the only density dependent factor in the model. Therefore, a
function (CANN) of the total population density was computed and then multiplied by a factor (CANNMUL) which was determined as a function of the average monthly water level. Cannibalism and predation rates were determined by linear equations corresponding to the functions of Figs. 5-9. DESS values were derived from Figs. 5-7 and were included in the model in tabular form. In early simulations, values of the independent desiccation function variable, WATER, were rounded and assumed only specified values. In a later version of the simulation program, a linear interpolation subroutine was utilized. In addition to these rates, NATURAL was applied to all age classes. The natural mortality constants are presented in Table 9 and were calculated as previously described.

HUNSURV was a survival rate obtained from harvest mortality rates and was applied to age classes (4-21) during the month of September only. Either differential or proportional harvest rates were applied depending on the value assigned to the control variable IDIFF. Briefly, differential rates were computed by first determining the total number of animals to be harvested (based on the overall hunting rate control variable, HUNRATE), and then distributing the harvest among the various sex and age classes according to the harvest composition of Table 10. Computation of proportional rates also began with the use of HUNRATE in the calculation of the total number of animals to be harvested. Sex-specific harvest rates were then computed based on the

70:30 male to female ratio, and equal harvest rates were assigned for all sizes within each sex.

Monthly population changes during November through March At the beginning of winter, $t$ was automatically incremented by 4 to give the value $t=7$, which represented the end of March, and the state variables were then updated. It was assumed that the only rate affecting the population components during this time period was a freeze mortality, and equation 7 was thus not applicable in winter months. If the freeze factor was applied, SURNATM was set equal to . 95 for each component. If no freeze occurred, there was no change in the population.

## Yearly population changes

State equation 4 was used to update the state variables for age classes 2-21 at the end of each year. The number of animals leaving one component became the number of animals entering the next component. The last age class was simply "dropped" under the assumption that no animals survived past age 21.

State equations 5 and 6 were used to compute the number of male and female hatchlings, respectively. HACHTOT represented the total number of eggs hatched and was defined by the following expression:
8) $\quad$ HACHTOT $=$ EGGS $X(1-N E S T F L D) X(1-P R E D) X .768$

Rates utilized in this expression were applied at the end of

August. EGGS represented the total number of eggs laid, NESTFLD was the egg mortality rate attributable to nest flooding, and PRED was the raccoon nest predation rate. A survival constant of .768 was applied to all eggs as a hatching success rate. EGGS was computed by summing the eggs produced by each adult female age class (classes 9-21), and was dependent upon the population component size (AGEINIT) and nesting effort (NESTEFF). NESTEFF represented the percentage of females nesting and was determined as a function of the average water depth for May and June (see Fig. 2). This rate was applied to the adult female segment of the population at the end of June in order to obtain the total number of nesting females in each population component (REPRATE). REPRATE was then multiplied by the mean number of eggs laid per female, 38.9 , to obtain the total number of eggs produced by the population component. The percentage of eggs lost to nest flooding (NESTFLD) was determined as a function of the maximum of June, July, and August water depths (Fig. 3). The raccoon predation rate (PRED) was determined as a function of August marsh water depth (Fig. 4). In early simulations, the independent variable (WATER) of the nesting effort and nest flooding functions assumed only specified values. In a later version of the computer program, a linear interpolation subroutine was used in the calculation of nesting effort, while the nest flooding function was expressed in the form of linear equations. Raccoon predation rate was determined using linear equations.

The number of male hatchlings was assumed to be $60.1 \%$ of the total, and the number of females was assumed to be 39.9\%. These constants were multiplied by HACHTOT to give the number of males and females entering the first age class. The new age structure resulting at the end of the simulated year became the new initial age structure for the start of the next year.

## Implementation

The simulation model was written in FØRTRAN IV and simulations conducted on the CDC 6500 computer system at Michigan State University. General block diagrams for the computations involved state equations 3, 5 and 6 are presented in Fig. 10.

Figure 10. Block diagram of model state equations.


## RESULTS AND DISCUSSION

## Alligator Population Structure

Preliminary simulations of population growth were conducted using a September initial age structure (Table 8) calculated from Chabreck's (1966) observed May-June size structure. Results of one such 20-year simulation with constant $15 \mathrm{~cm}(.5$ foot) water depths are shown in Fig. 11. Irregularities in this population growth curve (Fig. 11) resulted from inadequacies in the initial age structure. The high population growth rate for year 1 can be directly attributed to the introduction of a "normal" complement of hatchlings at the end of that year. The other major irregularity in the population growth curve occurred during year 9, the year during which hatchling females from the initial age structure reached sexual maturity. Simulation results thus suggested an inadequate representation of animals in the first age class of the initial age structure. Analysis of Chabreck's (1966) field data provided additional support for the contention that hatchlings were underestimated in the derived September age structure. Calculations assuming (1) average egg mortality rates and hatching success (from Joanen 1969), (2) equivalent hatchling mortality rates from September to May and from June to September, and (3) a
Figure 11. Simulated population growth using the September initial age structure

stationary age distribution (this had probably not been achieved), yielded an unrealistically low number of one-year-old survivors for September, 1966.

Because of this apparent underrepresentation of hatchlings, the use of the Table 8 age structure in experimental simulations would have caused problems in interpreting population response curves. For example, it would have been difficult to separate effects of the irregular age structure from effects of experimental manipulations (such as variations in hunting pressure or environmental parameters) in such response curves. Therefore, the initial proportions of animals in each age and sex class for all subsequent computer runs were based on the population structure generated by the 20-year simulation of Fig. 11. An example of this computer-generated age structure for an initial population of 100,000 is shown in Table 11.

## Model - Field Data Comparison

Nest counts conducted during 1970-1973 provided an opportunity to compare simulation results with observed field data. This comparison was not intended to constitute model "validation". Validation procedures can involve attempts to reproduce past system behavior, providing that components of this past behavior were not used in the construction of the model. Data from 1970 and 1971 were included in the percent nesting function, and data from 1973 were used in the construction of the nest flooding and nest predation

Table 11. Computer-generated initial age structure for an alligator population of 100,000 .

| Age | Males | Females |
| :--- | ---: | ---: |
|  |  |  |
| 1 | 30551 | 20283 |
| 2 | 8962 | 5950 |
| 3 | 4733 | 3142 |
| 4 | 3587 | 2382 |
| 5 | 2777 | 1844 |
| 6 | 2140 | 1421 |
| 7 | 1660 | 1102 |
| 8 | 1289 | 856 |
| 9 | 996 | 661 |
| 10 | 710 | 557 |
| 11 | 504 | 467 |
| 12 | 353 | 386 |
| 13 | 273 | 353 |
| 14 | 201 | 306 |
| 15 | 138 | 248 |
| 16 | 100 | 214 |
| 17 | 73 | 183 |
| 18 | 53 | 158 |
| 19 | 39 | 136 |
| 20 | 29 | 118 |
| 21 | 12 | 53 |
|  | 59180 | 40820 |

functions. Nevertheless the 1970-1973 nest count surveys provided the only available density estimates, and comparisons with model output were thus considered appropriate.

A computer-generated initial age structure was constructed such that the number of nests produced the first year (using observed 1969-1970 marsh water depths) closely approximated the 1970 aerial nest count (error $=.08 \%$ ). The simulation was then run for three additional years with observed 1970-1973 water depth inputs (Table l), and the numbers of nests generated were compared with field observations for 1971, 1972, and 1973, as reported in Joanen and McNease (1970b, 1972c, l973b) and Palmisano et al. (1973) (Fig. 12). The errors between simulated and observed data for these 3 years were $3.13,9.92$, and 22.70 percent, respectively.

Recently, an additional summary of nest count survey data appeared in Joanen et al. (1974). In this report, population estimates based on nest count surveys are presented for an area including a small portion of Calcasieu parish as well as all of Cameron and Vermilion parishes. The numbers of nests counted in 1970 and 1971 are slightly larger than the previously published Cameron and Vermilion counts, probably indicating the slightly larger survey area. However, the numbers of nests reported for 1972 and 1973 (2903 nests in 1972; 2662 nests in 1973) are much lower than indicated in previous reports. This discrepancy occurred in the two years for which my simulation "error" was greatest. The 1972 and 1973 errors between simulation results and these

Figure 12. Comparison of simulated nests (dashed line) with observed nest count data, 1970-1973 (solid line). Nest count data source: Palmisano et al. (1973).

new data (Joanen et al. 1974) were 6.13 and 4.40 percent, respectively, indicating a closer correspondence between model output and actual nest counts.

## Water Level Fluctuations

Environmental variability is an important component of most hypotheses pertaining to the evolution of life history strategies (e.g.Cohen 1966, 1967, 1968; Conley et al. 1976; Gadgil and Bossert 1970; Giesel 1974; Hairston et al. 1970; Hirshfield and Tinkle 1975; MacArthur and Wilson 1967; Murphy 1968; Nichols et al. 1976; Pianka 1970, 1972; Schaffer 1974; Wilbur et al. 1975; Williams 1966). In this system, marsh water level is quite variable and is the most important environmental parameter affecting the modeled alligator population. Therefore, several sets of simulations were designed specifically to examine the potential effects of water level variability on alligator population dynamics.

Initially, a series of 2 -year simulations was conducted using varied water depths for specified months (Fig. 13). In each of these simulations, water depth in a selected month during the first year was set at either 0 or 30 cm (l foot), with water depths for other first year months and all second year months held constant at $15 \mathrm{~cm}(.5$ foot). The difference between the two September runs can be attributed to higher predation, cannibalism and desiccation rates in the low water run. Zero water level in June resulted in a substantial population decrease as a consequence of low nesting
Figure 13. Series of 2 -year simulations demonstrating population response
varied water depths occurred in selected months during the first
year, and depths for all other months were held constant at 15 cm
(. 5 foot).

percentages, although a recovery was made in the following year. Thirty cm (1 foot) water depths in July and August resulted in population declines attributable to nest flooding. Zero water level in August caused a large population increase as a consequence of lowered nest predation and a resultant high number of September hatchlings. Normal predation and increased cannibalism the following year reduced the population, however, primarily by removing large numbers of first-year animals.

Population response to hurricane (100\% nest flooding) and severe drought (increased cannibalism, predation and desiccation) are shown in Fig. 14. The hurricane was simulated with 122 cm (4 feet) water depths in August, and the severe drought was represented by $-61 \mathrm{~cm}(-2$ feet) water levels in both June and July. In these 5-year deterministic simulations, the severe weather conditions occurred in year 1 , and all water depths were held at $15 \mathrm{~cm}(.5$ foot) for the remainder of each run. The rapid population recoveries from both drought and hurricane were of particular interest. The effects of weather were further investigated with stochastic simulations. In these runs, monthly water depths were generated from a normal distribution about the mean level for each month (from Table l). The stochastic modifications also included the 0.1 probability of a winter freeze each year. Results of two stochastic and one deterministic [monthly water depths set at $15 \mathrm{~cm}(.5$ foot), no winter freezes] simulation are shown in Fig. 15.

Figure 14. Simulated population response to August hurricane (plot B) and severe summer drought (plot C). A constant water depth simulation (plot A) is provided for comparison.

Figure 15. Simulated population response to constant (plot A) and randomly


Population response to variable environmental conditions can be quantified through the computation of mean finite rates of increase (Giesel 1974a, 1974b). The finite rate of increase, $\lambda_{t}$, is defined as:
9)

$$
\lambda_{t}=N_{t} / N_{t-1}
$$

where $t$ is time (in this case expressed in years), and $N$ is total population size. The geometric mean of a sequence of realized finite rates of increase is given by:
10)

$$
\bar{\lambda}={\underset{t=1}{n} \lambda_{t}^{l / n}}_{t}^{n}
$$

where n is the total number of years over which the mean is calculated. The $\bar{\lambda}$ values produced by the simulations in Fig. 15 were 1.0352 for plot A, 1.0374 for plot B, and 1.0238 for plot C.

As indicated by the plots of Fig. 15, simulated population size in a stochastic environment is highly variable. Annual realized finite rate of increase, $\lambda_{t}$, provides one measure of population growth or decline. From a randomly selected 20 -year stochastic simulation, $\lambda_{t}$ values for the total population ranged from . 5648 to 1.2291. However, the range of $\lambda_{t}$ values for the adult female segment of the population was .9749 to l.1046. Similar patterns were observed in all stochastic simulations, with total population size exhibiting high variability and mature female numbers maintaining fairly constant growth rates. The relative lack of variability in the breeding female segment of the
population can be attributed to the buffering effect produced by the large number of breeding age classes and to the relatively low adult female mortality rates, which are not greatly affected by environmental extremes. This examination of simulated population response provides insight to general alligator life history patterns, which correspond closely to an hypothesis extended by Murphy (1968). Murphy (1968) predicted that natural selection for long life, late sexual maturity, and repeated reproductions should occur in environments in which survival of pre-reproductives is highly variable. Alligator life history patterns conform to this prediction.

## Alligator Harvest Strategies

Another major objective of this study was to evaluate alligator management strategies through the use of computer simulation. This evaluation included consideration of the two described alligator harvest alternatives. The differential strategy was employed in the 1972 and 1973 Louisiana alligator harvests and involved the application of unequal harvest rates for different size and age classes. The proportional strategy is believed to be a feasible harvest alternative and involves application of equal harvest rates for all size classes within a given sex.

Theoretical development
An appropriate way to begin the evaluation of agespecific harvest strategies is with consideration of Fisher's
(1958) reproductive value approximated by:
11)

$$
v_{x} / v_{o}=\lambda^{x} / l_{x} \sum_{\mathrm{y}=\mathrm{x}}^{\infty} \quad \lambda^{-\mathrm{y}} 1_{y^{m}} \mathrm{y}
$$

where $x$ denotes age, $\lambda$ is the finite rate of increase of the population, and $l_{x}$ and $m_{x}$ are age-specific survival and birth rates, respectively. The reproductive value, $\mathbf{v}_{\mathrm{x}}$, represents the expected contribution of a female of age $x$ to future generations, expressed relative to the contribution of a female of age 0 (where $v_{0}=1$ ). Reproductive value can also be thought of as the diminution of future population increase caused by the removal of a female of age $x$. The importance of reproductive value to harvest strategies can be most readily appreciated from this definition.

Since reproductive value for individuals of a particular age class expresses relative importance of these individuals to future population growth, proper management should attempt to remove individuals of low reproductive value and leave individuals of high value. Utilization of such a strategy serves to minimize detrimental effects of harvesting on population growth. If all ages are of equal value to the harvester, selection of individuals with low reproductive values results in optimal yields being obtained from a population for a given rate of increase, $\lambda$. However, in such species as alligators in which individuals of different age classes are of different economic value, the optimal strategy consists of removing individuals of ages for which the ratio, value to harvester/reproductive value, is maximum
(MacArthur 1960). This brief discussion of reproductive value and optimal harvest strategy is analogous, and in some cases equivalent, to discussions of prudent predation in the theoretical ecological literature (eg. Slobodkin 1961, 1968, 1974; MacArthur 1960).

Instead of using Fisher's relative reproductive value, I have chosen to use absolute reproductive value (Ricklefs 1973) defined by:
12) $\quad v_{x}=1 / l_{x} \underset{y=x}{\sum} 1_{y^{m}}{ }_{y}$

This value is similar to Fisher's reproductive value, but is not expressed relative to the equivalent value for an individual of age 0 and is thus not weighted for population growth. Absolute reproductive value for a female of age $x$ is equivalent to the expected number of offspring that will be produced by the female throughout the remainder of its life. This value has been chosen over Fisher's relative reproductive value because it can be used to illustrate the same concepts with respect to harvest strategies and because it is more easily interpreted and computed.

Absolute reproductive values were computed for the modeled alligator population. Absolute reproductive value calculations assume constant $l_{x}$ and $m_{x}$ schedules, and this assumption is certainly false for the modeled population. Therefore, absolute reproductive values were computed assuming constant marsh water depths of 15 cm (.5 foot), constant population density equal to that of 1973 (71,900
animals), and no severe winter freezes. Estimated survival and fecundity rates corresponding to these assumptions were combined to produce theoretical $l_{x}$ and $m_{x}$ values (Table 12). These data were then utilized to calculate absolute reproductive values (Fig. 16). The $m_{x}$ values and absolute reproductive values are expressed in the currency of newlyhatched alligators rather than eggs. Therefore, under the stated survival and fecundity assumptions, the expected number of future hatchling offspring for female alligators entering age classes 1 and 9 are 5.2 and 39.5 respectively. It is the general shape of Fig. 16 , rather than the actual reproductive values themselves, which should be emphasized. It is important to note that reproductive value steadily increases from age 1 to age 9, the age of first reproduction, and then steadily declines.

Given the reproductive values in Fig. 16 , relative effects of differential and proportional hunting rates can be predicted. Age-specific differential female harvest rates based on the observed 1972 and 1973 harvest composition (Table l0) were calculated for an overall harvest rate of 7\% (Fig. 17). Equivalent proportional female harvest rates, calculated for the same overall harvest rate of $7 \%$, are also presented in Fig. 17. As previously noted, the proportional rates were calculated using the same approximate harvest sex ratio ( $30 \%$ females) as in the observed differential rates.

Table 12. Theoretical $l_{x}$ and $m_{x}$ values for female alligators inhabiting the coastal marshland of Cameron and Vermilion parishes, Louisiana.a

| Age class (x) | $\mathbf{l}_{\mathbf{x}}^{b}$ | $\mathrm{~m}_{\mathbf{x}}^{\mathrm{c}}$ |
| :---: | :---: | :---: |
| 1 | .350 |  |
| 2 | .210 | 0 |
| 3 | .165 | 0 |
| 4 | .130 | 0 |
| 5 | .103 | 0 |
| 6 | .081 | 0 |
| 7 | .064 | 0 |
| 8 | .050 | 0 |
| 9 | .046 | 6.01 |
| 10 | .040 | 6.01 |
| 11 | .035 | 6.01 |
| 12 | .031 | 6.01 |
| 13 | .027 | 6.01 |
| 14 | .023 | 6.01 |
| 15 | .021 | 6.01 |
| 16 | .018 | 6.01 |
| 17 | .016 | 6.01 |
| 18 | .014 | 6.01 |
| 19 | .012 | 6.01 |
| 20 | .011 | 6.01 |
| 21 | .009 | 6.01 |

a These theoretical values were calculated assuming constant marsh water depths at 15 cm , constant population density equal to that of 1973 (71,900 alligators), and no severe winter freezes.
$\mathrm{b}_{\text {The }} \mathrm{l}_{\mathrm{x}}$ values were calculated using survival rates from Table 5 .
$C_{\text {The }} m_{x}$ values were calculated using clutch size and hatching success data of Joanen (1969) combined with sex ratio, percent breeding, and egg predation rate information previously synthesized.
Figure 16. Theoretical absolute reproductive values for the alligator population
inhabiting the coastal marshland of Cameron and Vermilion parishes,
Louisiana. Values correspond to the assumptions of constant marsh
water depth at 15 cm , constant population density of 71,900 animals
(1973 density), and no severe winter freezes.

Age-specific female alligator harvest rates for proportional and
observed differential harvest strategies. These age-specific rates
correspond to an overall harvest rate of 78 and were calculated using
the age structure of Table ll. Differential rates were computed using
the size composition of the combined 1972 and 1973 Louisiana alligator
harvest (Table l0). harvest (Table 10).
Figure 17.

$$
\text { A } 12
$$

əןDy łSəへ」DH $9!f!\partial \partial d s-\partial 6 \forall$

A comparison of Figs. 16 and 17 leads to the prediction that the proportional harvest rates should be much less detrimental to population growth than the observed differential harvest rates. The differential rates are lower for age classes of low reproductive value and higher for age classes of high reproductive value than the equivalent proportional rates.

This concentration of hunting effort on size classes of high reproductive value constitutes poor management strategy. If alligators of all age classes were of equal value to harvesters, then the optimal strategy would be to remove only very young and very old animals (i.e. only animals of low reproductive value), assuming that harvest methods permitting such selection were practical. However, the economic value of an individual alligator is an increasing function of total body length (Table 13). Therefore, optimal harvest strategy involves concentration of hunting effort on age classes for which the ratio (value to harvester/reproductive value) is maximized (MacArthur 1960). However, as previousIy stated, the calculation of relative reproductive value requires constant $l_{x}$ and $m_{x}$ schedules, and this assumption is unrealistic for the modeled population. Therefore, the analytic approach to the yield problem was discarded in favor of stochastic simulations in which survival, fecundity, age distribution, and population growth rate were allowed to vary in response to environmental conditions.

Table l3. Two schedules of prices paid to hunters for alligator hide.

| Total body length | Price per linear foot |  |
| :---: | :---: | :---: |
|  | Schedule $1^{\text {a }}$ | Schedule $2^{\text {b }}$ |
| --Meters (feet)-- | ---------- | --------- |
| 1.2-1.5 (4-5) | 14.00 | 7.50 |
| 1.5-1.8 (5-6) | 14.00 | 12.00 |
| 1.8-2.1 (6-7) | 14.00 | 12.00 |
| 2.1-2.4 (7-8) | 15.00 | 12.00 |
| 2.4-2.7 (8-9) | 15.00 | 12.00 |
| 2.7-3.0 (9-10) | 16.00 | 12.00 |
| 3.0-3.4 (10-11) | 16.00 | 12.00 |
| 3.4-3.7 (11-12) | 16.00 | 12.00 |
| $3.7+\quad(12+)$ | 16.00 | 12.00 |

$a_{\text {Price schedule }} 1$ corresponds to prices paid for alligators taken during the 1973 harvest season (Mirandona Brothers, pers. comm.).
$b_{\text {Price }}$ schedule 2 corresponds to predicted future hide prices (Mirandona Brothers, pers. comm.).

Harvest simulation experiments
Simulation experiments were conducted in order to test the predictions regarding population growth under the two harvest strategies, and to examine expected harvest yields using differential and proportional hunting rates. In order to compare population response to these two harvest strategies, five 30-year simulations were conducted for each strategy using a 7\% overall harvest rate. Simulations within a given pair (differential vs. proportional) were conducted using identical sets of randomly generated water depths and winter temperatures. Thus, the effects of differential and proportional hunting were compared for five sets of fluctuating environmental conditions similar to those actually observed in coastal Louisiana. Total population density and adult female density for one pair of simulations are plotted in Fig. 18. Mean finite rates of increase for these simulations provide a measure of population response to the two harvest strategies (Table l4). The overall $\bar{\lambda}$ values were . 9879 for the differentially harvested populations and 1.0042 for proportional harvesting. This difference between the $\bar{\lambda}$ values is quite important, as reflected by plots of total population density exhibiting these rates of increase (e.g. Fig. 18). I conclude that proportional hunting rates allow higher $\bar{\lambda}$ values than equivalent differential rates similar to those observed for the two Louisiana seasons. This conclusion supports the prediction that differential harvesting, in which hunting effort is
Figure 18.


Table 14. Population $\bar{\lambda}$ values resulting from 30 -year stochastic simulations with $7 \%$ differential and proportional hunting rates.a
concentrated on age classes of high reproductive value, is more detrimental to population growth than proportional harvesting.

I utilized experimental simulations to compare yields for differential and proportional harvest rates producing equivalent $\bar{\lambda}$ values. These comparisons involved five pairs of 30 -year simulations, with each pair using a common set of randomly generated environmental conditions. Each pair of simulations consisted of one population subjected to a 5\% differential harvest rate and an identical population subjected to the proportional harvest rate (expressed to the nearest 1\%) which produced an equivalent $\bar{\lambda}$. Total population density and adult female density are plotted for a representative pair of simulations (Fig. 19). In four of the five pairs of simulations, a $7 \%$ proportional harvest rate produced $\bar{\lambda}$ values which were equivalent to those of the differentially hunted populations, while an $8 \%$ proportional rate was equivalent to the $5 \%$ differential rate in the remaining pair. Mean yields, expressed in linear feet of hide and in dollars under two possible hide price schedules (see Table 13), are shown in Table 15. Proportional harvesting resulted in an average annual yield increase of either $\$ 11,000$ or $\$ 21,000$ (depending on the price schedule used) over the equivalent differential procedure. I conclude that, for a given population growth rate, proportional hunting produces greater harvest yields than the observed differential harvest rates.
Simulated alligator population response to $5 \%$ differential and 7\%
identical

ident | 0 릍 |
| :---: |
| 0 |
| 0 |
| -1 |
| 0 |
| 0 |
| 0 |
| 0 |
| 0 |
| 0 |
| 0 |
| 3 |

irate $(\bar{\lambda}=1$ condition
tes
respons
proportional harvest rates.
sets of randomly generated e
finite rates of increase for the $5 \%$ differential rate ( $\bar{\lambda}=1.0012$ )
and the $7 \%$ proportional rate $(\bar{\lambda}=1.0031)$ are approximately
equivalent.
Figure 19.

producing
hunting rates
proportional
pue
 equivalent $\lambda$ values.a

Table 15.
Mean annual yield ${ }^{b}$

| Harvest regime | $\bar{\lambda}$ | Linear feet of hide |  | Price schedule $1^{\text {c }}$ |  | Price schedule 2 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | - - - | - - Dol | ars- - - | - - - |
| Proportional (7 and 8\%) ${ }^{\text {d }}$ | 1.0033 | 11,098 | (545.70) | 159,890 | (7753.85) | 120,962 | (5687.31) |
| Differential | 1.0023 | 9,390 | (365.41) | 138,576 | (5400.33) | 110,158 | (4294.46) |
| Yield difference (proportional-differential) |  | 1,708 | (320.98) | 21,314 | (4463.67) | 10,804 | (3161.35) |

${ }^{\text {a }}$ Initial population structure for all 30 -year simulations is shown in Table ll.
${ }^{\circ}$ Standard deviations were calculated for the mean yields of all 30-year simulations and are shown in parentheses. These values express variation between the different stochastic simulations.
${ }^{\text {CPrice schedules }}$ are shown in Table 13.
Proportional harvest rates were selected which produced $\bar{\lambda}$ values most closely approximating
the $\bar{\lambda}$ value for the $5 \%$ differentially harvested populations.

## Discussion and recommendations

I have demonstrated in the simulations that proportional harvest rates are less detrimental to population growth than equivalent differential harvest rates similar to those observed in the 1972 and 1973 seasons. Experimental simulations of differential and proportional harvest rates, equivalent with regard to effect on alligator population growth, indicated that higher annual yields of hide and resultant income can be produced by proportional hunting. The observed differential harvest procedure resulted in the expenditure of a higher portion of the hunting effort on young, sexually mature females; i.e., the individuals expected to produce the largest number of future offspring and thus to make the largest contribution to future population growth. The proportional harvest strategy resulted in the expenditure of equal hunting effort on all harvestable size classes and thus produced equal harvest rates for females of all ages.

It is important to note that the foregoing demonstration involved only a comparison between two possible harvest strategies and that a true optimal strategy was not derived. Simulation experiments could be used to predict yields resulting from the selective removal of all possible combinations of alligator sizes, and a theoretically optimal harvest strategy could thus be obtained. However, it is possible that only two basic alligator harvest strategies can be feasibly employed in the southwestern Louisiana marshland. In both 1972 and 1973, Louisiana hunters selected large animals
(Palmisano et al. 1973, Joanen et al. 1974). This selection, which produced the size distribution shown in Table 10, was implemented by the intentional placement of baited hooks (used to "fish" for alligators) high above the water surface (Palmisano et al. 1973, Joanen et al. 1974). I suggest that a proportional harvest strategy could be imposed by introducing regulations to lower the heights of baited hooks above the water surface, thus giving animals of all sizes an equal opportunity to strike.

Alligators harvested by shooting during 1972 and 1973 seasons were generally in the smaller size classes (Palmisano et al. 1973, Joanen et al. 1974) and were probably taken in porportion to their abundance in the population. Therefore, it is probable that no additional regulations would be required to insure the proportional harvest of alligators by shooting.

If necessary, additional regulations could be imposed to implement proportional hunting. Alligator harvest rates in the 1972 and 1973 seasons were controlled by issuing a designated number of tags to hunters, who were required to tag each alligator taken. Proportional harvest could be insured by issuing tags on a basis of size classes as well as total numbers of animals. In order to make the proportional harvest more attractive to hunters, the issuance of bonus tags for a predetermined number of alligators with low reproductive values should be considered.

In addition to the observed differential and the proposed proportional harvest strategies, it is possible that any combination of sizes could be selected using the livetrapping techniques of Chabreck (1963). However, these methods are less efficient than the shooting and fishing methods normally employed, and I do not consider them economically viable alternatives. Thus, for practical reasons, the observed differential and the proposed proportional harvest strategies are believed to be the most reasonable alligator harvest options for southwestern Louisiana. Until other alternatives are introduced, a proportional strategy is recommended.

## Egg Collection and Restocking Management

In this section, the potential use of egg collection and restocking programs is examined as a means of managing populations of alligators and crocodilians in general. Historically, restocking programs have been regarded as ineffective tools in the continued management of wildife populations (Allen 1974). Despite this history of limited success, however, restocking holds considerable potential for crocodilian management. Recently, successful hatching and rearing programs have been reported for numerous crocodilians including the American alligator, (Chabreck 1967b, 1973; Joanen and McNease 1971), the Nile crocodile, Crocodylus niloticus, (Pooley 1966, 1969b, 1971; Atwell 1973; Blake 1974), and several other species (Yangprapakorn et al. 1971,

Downes 1973, Honegger 1973). The restocking of areas with artificially hatched and reared young has also been generally successful (Chabreck 1971a; Pooley 1971, 1973a).

Crocodilian characteristics and restocking management
The feasibility of egg collection and restocking programs results directly from certain specific characteristics of crocodilian populations. One such characteristic is the behavior and viability of artificially reared animals. Unlike individuals of many wildlife species, artificially reared crocodilians respond as wild animals when released into natural populations (Chabreck 197la). This qualitative similarity between wild and artificially reared animals is essential to the success of any restocking program.

In addition, crocodilians exhibit little maternal care relative to many other commercially important wildlife species, and artificial rearing and restocking programs are thus relatively inexpensive and simple to operate. Although crocodilians do show some forms of maternal care (Cott 1971; Kushlan 1973), such behavior is primarily directed at protection of the nest and at release of hatchlings from the nest. Crocodilians do not actively incubate eggs or feed hatchlings; forms of parental care which require expensive techniques in restocking programs.

Survival patterns of crocodilian populations form the basis for the applicability of restocking management. In the wild, crocodilian survivorship curves typically approximate the Type III theoretical curve of Deevey (1947).

Crocodilian eggs and young generally suffer very high mortality rates, while adult animals exhibit high survival rates (Cott 1961; Pooley 1962, 1966, 1969a; Cott and Pooley 1972; Guggisberg 1972). Artificial hatching and rearing programs can greatly reduce mortality rates of crocodilian eggs and young, and animals can be reintroduced to natural populations at a size and age of low vulnerability. For example, Chabreck (pers. comm.) has obtained a $75 \%$ hatching rate for collected and artificially incubated alligator eggs. First and second year annual mortality rates for artificiallyreared young were estimated to be $10 \%$ and $5 \%$, respectively, (Chabreck pers. comm.).

As an illustration of the effect of egg collection and restocking programs on survival patterns, hypothetical female survivorship curves have been plotted for the modeled alligator population (Fig. 20). These two $1_{x}$ schedules correspond to: 1) natural conditions and; 2) artificial incubation with 2 years of rearing young. The $l_{x}$ values were calculated assuming constant marsh water depths at 15 cm (. 5 foot), constant population density equal to that of 1973, and no severe winter freezes. These $l_{x}$ values were calculated for freshly-laid eggs and thus represent the probability that a new egg will produce an alligator which enters age class $x$. The $l_{1}$ values include both egg mortality and mortality of hatchlings during their first year of life. A comparison of the two survivorship curves in Fig. 20 illustrates the great increase in survival which can be achieved
Figure 20.

through the use of artificial incubation, rearing, and restocking methods. The finite rate of increase of a population ( $\lambda$ ) is determined by the $l_{x} m_{x}$ schedule. Assuming a common $m_{x}$ function, restocking management thus serves to increase the population $\lambda$, by increasing $l_{x}$ values. Because of the unrealistic assumptions of constant and favorable environmental conditions, $I$ do not wish to emphasize the $1_{x}$ values themselves, but the magnitude of the difference between the two $l_{x}$ schedules is worthy of note.

## Restocking simulations

Simulations were conducted to examine the potential effect of egg collection and restocking management on alligator population growth. In these simulations, 10,000 eggs were collected in early July, each year and the young alligators released after either 1 or 2 years of rearing. A $75 \%$ hatching rate was assumed for the artificially incubated eggs (Chabreck pers. comm.), and first and second year mortality rates for reared young were assumed to be $10 \%$ and $5 \%$, respectively.

The simulated restocking program proved to be a highly successful management strategy as indicated by the deter-. ministic simulations of Fig. 2l. The one and two year rearing programs resulted in $\bar{\lambda}$ values of 1.0449 and 1.0521 , respectively, while the $\bar{\lambda}$ for the unmanaged population was 1.0352. The managed populations began to diverge rapidly from the unmanaged population during year 9, the year in which the first group of artificially raised females reached
Figure 21. Simulated population response to egg collection
management programs. Plot A corresponds to
no management. Plot B corresponds to a manage-
ment program in which 10,000 eggs were col-
lected annually, and hatchlings were reared
for 1 year and released. Plot corresponds
to a management program in which 10,000 eggs
were collected annually, and hatchlings were
reared for 2 years and released. In each
simulation water depths were held constant
at 15 cm (.5 foot) and no winter freezes
occurred.

sexual maturity.
An egg collection program with one year of rearing young was also simulated using the same set of randomly generated water levels and winter freezes used for the unmanaged population shown in Fig. 15, plot C. Under this particular set of environmental conditions, the managed population exhibited a $\bar{\lambda}$ of 1.0358, while the $\bar{\lambda}$ of the unmanaged population was 1.0238. This difference between managed and unmanaged populations was somewhat larger than the difference indicated by the deterministic simulations. Thus, it appears that the beneficial effects of an egg collection management program are increased during periods of water level fluctuations. This tentative conclusion was expected, since egg collection management results in the protection of eggs and first year animals, which suffer the greatest increases in mortality during times of drought.

Restocking quotas and crocodilian harvest management
In many underdeveloped countries crocodilians are overhunted and persist at relatively low densities, with harvest yields being achieved at the expense of population growth. In such low density situations, increased harvest rates result in temporary increases in yield and in decreased population growth. Here, I examine the potential use of restocking programs as a means of reducing or eliminating the detrimental effect of harvesting on population growth, while still maintaining harvest yields.

The usual approach to wildife harvest management is to obtain some sort of population density or growth rate estimate prior to each harvest season. Decisions are then made regarding the number of animals which can be removed from the population, and appropriate harvest regulations and quotas are established.

Here, I propose a method of harvest management that can be used to supplement the restocking program described above. Basically, the method involves the requirement that harvesters collect eggs and rear and release young animals in numbers which are directly proportional to the number of female crocodilians harvested during the previous season. Specifically, I suggest that eggs be collected during the first nesting period following each harvest, and that young animals be reared and reintroduced to the population two years subsequent to that time. As a practical consideration, it is suggested that the actual egg incubation and rearing and release of young be conducted by the appropriate management agency and that the quota for harvesters take the form of financial compensation for this service. The number of eggs to be collected for each harvested female is specified by the management agency and is dependent upon the desired rate of increase for the harvested population. If annual harvest yields exceed annual restocking costs, then the proposed system will succeed in accomplishing its objectives of promoting population growth while maintaining harvest yields.

Theoretical restocking quota calculation. As an idealized illustration, consider calculation of restocking quotas necessary to maintain population growth rates similar to those of unharvested populations. For each year subsequent to a female's removal it is possible to calculate the number of young which she would have produced had she lived. However, this requires keeping extensive records, since young would have to be released each year throughout the original expected lifespan of every harvested female. It is more practical to assign single egg collection quotas immediately subsequent to each season, and I thus demonstrate the calculation of quotas for this management system.

Earlier, Fisher's reproductive value, $v_{x}$, was defined and discussed. Total reproductive value, $V_{t}$, for the segment of the population harvested at time $t$ is:

$$
v_{t}=\sum_{x=0}^{\infty} n_{x, t} v_{x}
$$

$n_{x, t}$ denoting the number of females harvested in each age class $x$, at time $t . ~ V_{t}$ is equivalent to the number of individual females of age 0 (new eggs) which should be added to the population to compensate for the loss of the harvested animals and to restore to the population the total reproductive value it exhibited immediately prior to the harvest. If it is assumed (see MacArthur 1960) that populations with different age distributions which do not differ in total reproductive value also do not differ in instantaneous rate of increase $(r)$, then the addition of $V_{t}$ new
female eggs to the population will result in maintenance of preharvest rates of increase.

The goal of this restocking program is to increase the survival rates of eggs and young animals and then to reintroduce animals which have passed the period of highest mortality. For most crocodilians, a large reduction in natural mortality can be achieved with a rearing period of 2 years. Therefore, if $Y_{t+2}$ denotes the number of 2-yearold females to be introduced to the population in year $t+2$ then:

$$
Y_{t+2}=v_{t} l_{2}
$$

where $V_{t}$ is the total reproductive value of the female segment of the population harvested in year $t$, and $l_{2}$ is the probability that a new egg will survive to enter age class 2 under natural conditions.

Given $Y_{t+2}$, we must finally calculate the number of eggs to be collected in year $t$, in order to obtain $Y_{t+2}$ 2-year-old females in year t+2. This is accomplished by:

$$
E_{t} P_{2}^{\prime}=Y_{t+2}+E_{t} P_{2}
$$

where $E_{t}$ denotes the necessary egg collection quota for year $t, p$ represents the sex ratio for eggs (expressed as proportion of females), and $l_{2}^{\prime}$ is the 2 -year-old survival rate under artificial incubation and rearing conditions. $\mathrm{E}_{\mathrm{t}} \mathrm{Pl}_{2}$ compensates for the number of collected eggs which would have survived to age 2 in the absence of egg collection.

The final calculation of egg collection quotas is achieved by rearranging equation 15:
16)

$$
E_{t}=Y_{t+2} / P\left(1_{2}^{\prime}-1_{2}\right)
$$

This expression stresses the importance of the difference between artificial and natural survival rates $\left(l_{2}^{\prime}-l_{2}\right)$. The magnitude of this difference has previously been cited as one of the primary reasons for the feasibility of crocodilian restocking management.

The above calculations unrealistically assume constant $l_{x}$ and $m_{x}$ schedules. The described restocking calculations also require assignment of exact ages to harvested individuals. This is difficult for large, mature crocodilians. It would be advantageous to assume a relatively constant proportion of females of different age classes in the harvest, and then to use one specific egg collection quota for all females, regardless of age. In order to relax restrictive assumptions, to test the applicability of a single quota management system, and to examine the relationship between harvest yields and restocking costs, various restocking quotas have been investigated via computer simulation of the Louisiana alligator population.

Restocking quota simulations. In the restocking management simulations, harvests occurred in September of each year. Egg collection occurred at the end of June and the first of July, immediately after egg laying. Simulations were conducted with different restocking quotas, expressed as number
of eggs to be collected per female harvested in the previous season. In the simulations it was assumed that a maximum of $50 \%$ of the nests produced by the population could be located in a given year. In practice this percentage will be a species- and population-specific variable depending on nesting habits of the species (e.g. whether the species is a "mound-nester" or a "hole-nester") and the nature of the habitat occupied by the population. In the Louisiana coastal marshland, a very high percentage of alligator nests can be located each year (Chabreck 1966). However, the hole nests of Nile crocodiles inhabiting swampland would be more difficult to locate.

During years of low breeding percentages, it is possible for the total egg collection quota to exceed the maximum number of eggs which can be located. In the simulations, the negative quota balance was carried over to the next year, and the normal harvest rate was reduced by a factor of . 5 for that year and all subsequent years until the negative quota balance was eliminated. Negative balances were observed in only 3 of the 480 total years represented by the simulations.

In the proposed management scheme, eggs are incubated and young animals are reared for 2 years under artificial conditions and then reintroduced to the wild population. In the simulations, the number of animals introduced to the population as 2-year-olds thus depended on the number of eggs collected 2 years previous and on the 2 year survival
rates ( $l_{2}^{\prime}$ ) for artificially reared animals (Fig. 20). Actual $l_{2}^{\prime}$ values were allowed to vary randomly (using a uniform distribution) between $\pm 5 \%$ of the expected value. All experimental simulations were conducted for a period of 32 years. Harvesting occurred during years 1-30 of each simulation, and restocking occurred during years 2-32.

Simulations were designed to evaluate the potential utility of restocking quotas as a means of reducing the detrimental effect of harvesting on alligator populations, while still maintaining harvest yields. In these simulations, harvest rates remained constant at $12 \%$ except during years of negative egg collection quota balances. The stochastic modification was employed to obtain five sequences of randomly generated marsh water depths and winter temperatures. A Monte Carlo approach was used, and five simulations corresponding to these different sets of abiotic factors were run for each management option.

A summary of simulation results is presented in Table
16. Population responses to different management options for one specific set of environmental conditions are plotted in Fig. 22. In the absence of restocking, the $12 \%$ harvest rate produced declines in the simulated population and resulted in an overall $\bar{\lambda}$ value of .9870 . The simulated collection of five eggs per harvested female and the introduction of the artificially reared 2 -year-old survivors from these eggs was sufficient to produce an overall $\bar{\lambda}$ value slightly greater than one. A collection quota of 15
Table 16. Results of 32 -year alligator simulation runs under various management options.


Figure 22. Simulated alligator population response to various restocking management options: (A) harvest rate $=0$, egg collection quota $=0$; (B) harvest rate $=12 \%$, egg collection quota = 15; (C) harvest rate $=12 \%$, egg collection quota $=10$; (D) harvest rate $=12 \%$, egg collection quota $=5$; (E) harvest rate $=12 \%$, egg collection quota $=0$.

eggs per harvested female resulted in an overall $\bar{\lambda}$ value which was slightly greater than that of populations not subjected to annual harvests (Table 16).

Mean annual yields of hide and costs of restocking programs are also presented in Table 16. In all cases the net yields of the restocking simulations (mean annual yieldmean annual restocking costs) exceeded the mean annual yields from the no-restocking simulations. Thus, the restocking programs not only produced greater population growth rates than the no-restocking simulations, but also resulted in greater net monetary yields. It must be noted, however, that restocking costs and hide prices are variable and that the observed yield differences are subject to variation also.

Discussion and recommendations. The simulated use of restocking quotas in conjunction with traditional harvest management was successful in elevating mean finite rates of increase for the harvested alligator populations. In addition, the simulated restocking system produced increased harvest yields, which exceeded restocking costs in all cases. Restocking thus appeared to be successful in both maintaining harvest yields and reducing the detrimental effect of harvesting on alligator population growth.

With the exception of the American alligator in certain areas of coastal Louisiana, I know of no harvested crocodilian population which currently exists at high densities. In fact, many populations of commercially valuable crocodilians
are overhunted (Bustard 1971; Pooley 1973b). For such populations it would be highly desirable to enact restocking programs designed to elevate rates of increase. Because of the maintenance of harvest yields under restocking management, such programs should be acceptable to harvesters. It is thus suggested that the use of restocking quotas may be a politically feasible method of promoting population growth in overhunted crocodilian populations.

```
LITERATURE CITED
```


## LITERATURE CITED

Allen, D. L. 1974. Our wildife legacy. Funk and Wagnalls Co., New York. 422p.

Arthur, S. 1931. The fur animals of Louisiana. Louisiana Dept. of Conservation, New Orleans. 444 p .

Attwell, R.I.G. 1973. Crocodile status report for Rhodesia. Proc. Second Working Meeting of Crocodile Specialists, IUCN Supplementary Paper 41:41-43.

Bara, M.O. 1971. Alligator research project. Annual progress report for period August 1970-December 1971. South Carolina Wildl. and Marine Resources Dept., Columbia. 24p. (mimeo.)

Bellairs, A. 1969. The life of reptiles. Vol. 2. Weidenfeld and Nicholson, London. p.283-590.

Blake, D.K. 1974. The rearing of crocodiles for commercial and conservation purposes in Rhodesia. Rhodesia Science News 8:315-324.

Bustard, H.R. 1971. Summary of the meeting. Proc. Working Meeting of Crocodile Specialists, IUCN Supplementary Paper 32:15-28.

Chabreck, R.H. 1960. Coastal marsh impoundments for ducks in Louisiana. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 14:24-29.

Chabreck, R.H. 1963. Methods of capturing, marking and sexing alligators. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 17:47-50.

Chabreck, R.H. 1965. The movement of alligators in Louisiana. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 19:102-110.

Chabreck, R.H. 1966. Methods of determining the size and composition of alligator populations in Louisiana. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 20:105-112.

Chabreck, R.H. 1967a. The American alligator--past, present and future. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 21:554-558.

Chabreck, R.H. 1967b. Alligator farming hints. Louisiana Wild Life and Fisheries Commission, New Orleans. 2lp. (mimeo.)

Chabreck, R.H. 197la. Management of the American alligator. Proc. First Working Meeting of Crocodile Specialists, Vol. I, IUCN Supplementary Paper 32:137-144.

Chabreck, R.H. 197lb. The foods and feeding habits of alligators from fresh and saline environments in Louisiana. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 25:117-124.

Chabreck, R.H. 1972. Vegetation, water and soil characteristics of the Louisiana coastal region. Louisiana Agricultural Experiment Station Bull. 664. 72p.

Chabreck, R.H. 1973. Current trends in alligator farming in the southeastern United States. Proc. Second Working Meeting of Crocodile Specialists, IUCN Supplementary Paper 41:63-65.

Chabreck, R.H., and T. Joanen. 1966. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. 9p. (mimeo.)

Chabreck, R.H., and T. Joanen. 1967. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. 10p. (mimeo.)

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. J. Theoret. Biol. 12:119-129.

Cohen, D. 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. J. Theoret. Biol. 16:1-14.

Cohen, D. 1968. A general model of optimal reproduction in a randomly varying environment. J. Ecol. 56:219-228.

Conley, W., J.D. Nichols, and A.R. Tipton. 1976. Reproductive strategies in desert rodents. in Roland $H$. Wauer and David H. Riskind, eds. Transactions-symposium on the biological resources of the Chihuahuan Desert region, U.S. and Mexico. National Park Service, Washington, D.C. (in press).

Cott, H.B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (Crocodylus niloticus) in Uganda and Northern Rhodesia. Trans. Zool. Soc. London 29:211-358.

Cott, H.B. 1971. Parental care in the Crocodilia, with special reference to Crocodylus niloticus. Proc. First Working meeting of Crocodile Specialists, Vol. I, IUCN Supplementary Paper 32:166-180.

Cott, H.B., and A.C. Pooley. 1972. The status of crocodiles in Africa. Proc. First Working Meeting of Crocodile Specialists, Vol. II, IUCN Supplementary Paper 33:l-98.

Coulson, T.D., R.A. Coulson, and T. Hernandez. 1973. Some observations on the growth of captive alligators. Zoologica 58:47-52.

Deevey, E.S., Jr. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.

Downes, M.C. 1973. The literature of crocodile husbandry. Proc. Second Working Meeting of Crocodile Specialists, IUCN Supplementary Paper 41:93-115.

Ensminger, A.B., and L.G. Nichols. 1957. Hurricane damage to Rockefeller Refuge. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 11:52-56.

Fisher, R.A. 1958. The genetical theory of natural selection (2nd ed.). Dover, New York. 291p.

Flemming, D.M. 1974. Movement patterns of the coastal marsh rascoon in Louisiana and notes on its life history. Unpubl. Master's thesis, Louisiana State Univ., Baton Rouge. 90p.

Gadgil, M., and W.H. Bossert. 1970. Life historical consequences of natural selection. Amer. Natur. 104:1-24.

Giesel, J.T. 1974a. Fitness and plymorphism for net fecundity distribution in iteroparous populations. Amer. Natur. 108:321-331.

Giesel, J.T. 1974b. The biology and adaptability of natural populations. The C.V. Mosby Co., St. Louis. 177p.

Giles, L.W., and V.L. Childs. 1949. Alligator management on the Sabine National Wildlife Refuge. J. Wildl. Manage. 13:16-28.

Guggisberg, C.A.W. 1972. Crocodiles: their natural history, folklore and conservation. Stackpole Books, Harrisburg, Pennsylvania. 195p.

Hairston, N.G., D.W. Tinkle, and H.M. Wilbur. 1970. Natural selection and the parameters of population growth. J. Wildl. Manage. 34:681-690.

Hines, T.C., J.J. Fogarty, and L.C. Chappell. 1968. Alligator research in Florida: a progress report. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 22:166-180.

Hirshfield, M.F., and D.W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. Proc. Nat. Acad. Sci. 72:2227-2231.

Honegger, R.E. 1973. Stocks and captive breeding, 1969-1972. Proc. Second Working Meeting of Crocodile Specialists, IUCN Supplementary Paper 41:59-62.

Joanen, T. 1969. Nesting ecology of alligators in Louisiana. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 23:141-151.

Joanen, T., and L. McNease. 1970a. A telemetric study of nesting female alligators on Rockefeller Refuge, Louisiana. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 24:175-193.

Joanen, T., and L. McNease. 1970b. 1970 coastal alligator census. Louisiana Wild Life and Fisheries Commission, New Orleans. 7p. (mimeo.)

Joanen, T., and L. McNease. 1971. Propagation of the American alligator in captivity. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 25:106-116.

Joanen, T., and L. McNease. 1972a. Population distribution of alligators with special reference to the Louisiana coastal marsh zones. Presented at a Symposium of the American Alligator Council, Lake Charles, Louisiana. 12p. (mimeo.)

Joanen, T., and L. McNease. 1972b. A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 26:252-275.

Joanen, T., and L. McNease. 1972c. 1971 coastal alligator census. Louisiana Wild Life and Fisheries Commission, New Orleans. 10p. (mimeo.)

Joanen, T., and L. McNease. 1972d. Population estimates and recommendations for experimental harvest program on alligators for Cameron parish, Louisiana. Louisiana Wild Life and Fisheries Commission, New Orleans. 6p. (mimeo.)

Joanen, T., and L. McNease. 1973a. Developments in alligator research in Louisiana since 1968. Presented at a Symposium of the American Alligator Council, Winter Park, Florida. 20p. (mimeo.)

Joanen, T., and L. McNease. 1973b. Population estimates and recommendations for experimental harvest program on alligators for Cameron and Vermilion parishes, Louisiana. 8p. (mimeo.)

Joanen, T., L. McNease, and H. Dupuie. 1968. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. llp. (mimeo.)

Joanen, T., L. McNease, and H. Dupuie. 1969. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. l3p. (mimeo.)

Joanen, T., L. McNease, and H. Dupuie. 1970. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. 12p. (mimeo.)

Joanen, T., L. McNease, and H. Dupuie. 1971. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. 12p. (mimeo.)

Joanen, T., L. McNease, and H. Dupuie. 1972. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. 12p. (mimeo.)

Joanen, T., L. McNease, and H. Dupuie. 1973. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. 12p. (mimeo.)

Joanen, T., L. McNease, and H. Dupuie. 1974. Vegetation survey of Rockefeller Refuge impoundments. Annual progress report. Louisiana Wild Life and Fisheries Commission, New Orleans. 12p. (mimeo.)

Joanen, T., L. McNease, and A.W. Palmisano. 1972. Preliminary results of the experimental alligator harvest program - 1972. Louisiana Wild Life and Fisheries Commission, New Orleans. 3p. (mimeo.)

Joanen, T., L. McNease, and G. Linscombe. 1973. Preliminary results of the experimental alligator harvest program - 1973. Louisiana Wild Life and Fisheries Commission, New Orleans. 4p. (mimeo.)

Joanen, T., L. McNease, and G. Linscombe. 1974. An analysis of Louisiana's 1973 experimental alligator harvest program. Louisiana Wild Life and Fisheries Commission, New Orleans. 20p. (mimeo.)

Kolman, W.A. 1960. The mechanism of natural selection for the sex ratio. Amer. Natur. 94:371-377.

Krebs, C.J. 1972. Ecology: the experimental analysis of distribution and abundance. Harper and Row, Publishers, New York. 694p.

Kushlan, J.A. 1973. Observations on maternal behavior in the American alligator, Alligator mississippiensis. Herpetologica 29:256-257.

MacArthur, R.H. 1960. On the relation between reproductive value and optimal predation. Proc. Nat. Acad. Sci. 46:143-145.

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey. 203p.

McIlhenny, E.A. 1934. Notes on incubation and growth of alligators. Copeia. 1934:80-88.

McIlhenny, E.A. 1935. The alligator's history. The Christopher Publishing House, Boston. ll7p.

Murphy, G.I. 1968. Patterns in life history and the environment. Amer. Natur. 102:391-404.

Neill, W.T. 1971. The last of the ruling reptiles: alligators, crocodiles, and their kin. Columbia University Press, New York. 486p.

Nichols, J.D., W. Conley, B. Batt, and A.R. Tipton. 1976. Temporally dynamic reproductive strategies and the concept of $r$ and $K$ selection. Amer. Natur. (in press).

Nichols, L.G. 1959. Geology of Rockefeller Wildife Refuge and Game Reserve. Louisiana Wild Life and Fisheries Commission, New Orleans. 28p.

O'Neil, T. 1949. The muskrat in the Louisiana coastal marshes. Louisiana Dept. Wild Life and Fisheries, New Orleans. 152p.

Palmisano, A.W. 1972. The alligator: a wildife resource in Louisiana. Louisiana Conservationist 24(7):4-11.

Palmisano, A.W., T. Joanen, and L. McNease. 1973. An analysis of Louisiana's 1972 experimental alligator harvest program. Proc. Southeastern Assoc. Game and Fish Commissioners Conf. 27:184-206.

Penfound, W.T., and E.S. Hathaway. 1938. Plant communities in the marshland of southeastern Louisiana. Ecol. Monogr. 8:1-56.

Pianka, E.R. 1970. On $r$ and $K$ selection. Amer. Natur. 100: 592-597.

Pianka, E.R. 1972. $r$ and $K$ selection or $b$ and $d$ selection. Amer. Natur. 106:581-588.

Pianka, E.R. 1974. Evolutionary ecology. Harper and Row, Publishers, New York. 356p.

Pooley, A.C. 1962. The Nile crocodile, Crocodylus miloticus. Lammergeyer 2:1-55.

Pooley, A.C. 1966. Crocodiles and crocodile farming. African Wild Life 20:211-216.

Pooley, A.C. 1969a. Preliminary studies on the breeding of the Nile crocodile, Crocodylus niloticus, in Zululand. Lammergeyer 3:22-44.

Pooley, A.C. 1969b. Some observations on the rearing of crocodiles. The Lammergeyer 3:45-57.

Pooley, A.C. 1971. Crocodile rearing and restocking. Proc. First Working Meeting of Crocodile Specialists, Vol. I, IUCN Supplementary Paper 32:104-130.

Pooley, A.C. 1973a. Notes on the ecology of the Lake St. Lucia crocodile population. Proc. Second Working Meeting of Crocodile Specialists, IUCN Supplementary Paper 41:81-90.

Pooley, A.C. 1973b. Conservation and management of crocodiles in Africa. J. South Afr. Wildl. Manage. Assn. 3:101-103.

Powell, J.H., Jr. 1971. The status of crocodilians in the United States, Mexico, Central America, and the West Indies. Proc. Working Meeting of Crocodile Specialists, IUCN Supplementary Paper 32:72-82.

Reese, A.M. 1907. The breeding habits of the Florida alligator. Smithsonian Misc. Collections 3:381-387.

Reese, A.M. 1915. The alligator and its allies. G.P. Putnam's Sons, New York. 358p.

Ricklefs, R.E. 1973. Ecology. Chiron Press, Newton, Massachusetts. 861p.

Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. Amer. Natur. 108:783-790.

Schemnitz, S.D. 1972. Distribution and abundance of alligator, bear, deer, and panther in the Everglades region of Florida. Florida Game and Fresh Water Fish Commission, Fort Lauderdale. 26p. (mimeo.)

Smith, H.M. 1893. Notes on the alligator industry. Bull. U.S. Fish Commission (1891) 11:343-345.

Spotila, J.R., O.H. Soule, and D.M. Gates. 1972. The biophysical ecology of the alligator: heat energy budgets and climate spaces. Ecology 53:1094-1102.

Stevenson, C.H. 1904. Utilization of the skin of aquatic animals. U.S. Commission Fish and Fisheries Dept. 1901:281.

Truslow, F.K., F.G. Vosburg, and O. Imboden. 1967. Threatened glories of Everglades National Park. National Geographic 132:508-552.

Valentine, J.M., J.R. Walther, K.M. McCartney, and L.M. Ivy. 1972. Alligator diets on the Sabine National Wildife Refuge, Louisiana. J. Wildl. Manage. 36:809-815.

Wilbur, H.M., D.W. Tinkle, and J.P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Amer. Natur. 108:805-817.

Williams, G.C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey. 307p.

Yangprapakorn, U., J.A. McNeely, and E.W. Cronin. 1971. Captive breeding of crocodiles in Thailand. Proc. First Working Meeting of Crocodile Specialists, Vol. I, IUCN Supplementary Paper 32:98-103.



[^0]:    ${ }^{\mathbf{a}}$ See text for discussion.

[^1]:    ${ }^{\text {a Source: }}$ Table 2 of Chabreck (1966).

[^2]:    ${ }^{\text {a }}$ See text for explanation.

