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POPULATION DYNAMICS AND MANAGEMENT OF THE
OKAVANGO RIVER CROCODILES IN BOTSWANA

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POPULATION DYNAMICS AND MANAGEMENT OF THE OKAVANGO RIVER CROCODILES IN BOTSWANA

By

Goran Ernst Daniel Blomberg

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ABSTRACT

POPULATION DYNAMICS AND MANAGEMENT OF THE OKAVANGO RIVER CROCODILES IN BOTSWANA

By

Goran Ernst Daniel Blomberg

Behavior of the *Crocodylus niloticus* population in the Okavango River and its upper delta was modeled, to guide conservation practice. Background knowledge and data were acquired in Botswana, 1974 through mid-1976. In preliminary simulations the population, when undisturbed, equilibrated at 21,000, in 130-140 years. Four consecutive years of severe floods every 20 years caused noticeable decreases, though the population recovered quickly. Droughts on the same schedule had less severe effects. Simulated hunting of animals 120-190 cm long lowered the population to 1,400-2,000. Following corrections and alterations, data were varied for several parameters, to gauge the model's response. The population curve varied with changes in initial population size, initial age structure, age-specific percentages of nesting females, and age-specific clutch sizes. Sensitivity was also ascertained from changed data for age-specific survival rates, including arbitrarily lowered rates for juveniles; their rates are believed to be reduced by adults' aggression, in nature. Growth rates of crocodiles were expressed in age spans cannibalized, initial ages of cannibalistic behavior, initial age of egg laying, and age spans subjected to hunting (which superseded, up to a point, natural mortality). Response to altered data was considerable for all but the first of these parameters, and for certain combinations. Replacement of the present data with field data thus appears worthwhile (1 exception), and should make the model more reliable. Raising the first value for age-specific survival rates from 42.3 to 100.0 raised the population's equilibrium from 26,500 to 65,900. The latter population size might have allowed a total harvest of 40,000 during 1958-69. Uncertainty regarding original population size makes postponement of proposed hunting, of 1,000-1,400 crocodiles annually, until the population approaches or attains equilibrium phase, seem wise. Ranching (dependent on eggs or young from the wild), and more moderate hunting by local people, appear workable as commercial management schemes, however. If ranches become farms (dependent on captive breeders), the latter scheme may remain an incentive for conserving the wild population, and the model could predict allowable hunting rates.

Dedicated to my mother, Mrs. Karin J. Blomberg, whose knowledge of and interest in biology nurtured my interest therein, from early childhood. Her interest and encouragement proved invaluable when serious studies were undertaken. Her tenacity, in circumstances that would have daunted many, has been, and remains, an inspiration.

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Much of my understanding of the FORTRAN computer language I owe to Mr. J. E. Underwood, formerly at Lansing Community College. His interest and donated time were indispensable. Dr. W. E. Magnusson, Departado de Ecologia, INPA, C.P. 478, Manaus, AM, Brazil, offered invaluable advice on further development of the model. This development, and testing, would have been impossible without frequent advice from consultants at the MSU Computer Center, notably Mr. P. Pirozzo, Mr. M. Riordan, Mr. R. Wiggins, and Mr. C. Severance. Dr. D. McGroarty at Lansing Community College and Dr. M. Taylor, formerly with the Department of Fisheries and Wildlife, are thanked for advice that motivated further scrutiny of the computer program, which in turn revealed the need for an important correction.

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CHAPTER 1

INTRODUCTION

This work reports on a model of the behavior of the Nile crocodile (Crocodylus niloticus) population in the Okavango River and its upper delta, in Botswana, Africa. Its purpose is to provide management implications, by which to conserve the crocodile population on a biologically sound basis.

Sensitivity analyses are performed on the population simulation model for a number of parameters. Much of the original data are based on extrapolations, estimations, or are obtained from the literature. The parameters are (1) initial (1975) population size, (2) initial age structure, (3) age-specific percentages of nesting females in a given year ("PERBRD"), (4) age-specific clutch sizes ("CLUTCH"), (5) age-specific survival rates ("PSURV"), and (6) growth rates of crocodiles. Sensitivity to changed data for these parameters, as reflected in behavior of the population curve, provides a more reliable guide to biologically sound management of the crocodile population.

The biological background for this computer model, and some data supporting it, were gained in Botswana, in a position of Peace Corps Volunteer/Crocodile Biologist, from 1974 through mid-1976. The project began in connection with a concession, bought by Botswana Game Industries (Pty.) Ltd. (hereafter BGI) of Francistown, to hunt 500 crocodiles a year in the Okavango panhandle and upper delta. This concession, intended to last 3 years (Taylor 1973), was abandoned after the second season. Unable to meet their quota then, BGI reported a financial loss, and forfeited further crocodile hunting. At the same time P. Becker (1974, pers. comm.), executive director of BGI, recommended a 10-year ban on commercial hunting.

Crocodiles and their relatives constitute a distinct group of reptiles, worthy of study and protection. They are the only survivors of the Archosaurian stock of the reptile age, over 100,000,000 years ago. They are of exceptional scientific importance, as they can provide indirect information on several aspects of the biology of reptiles long extinct (Cott 1961).

Crocodilians furthermore deserve study because of their potential economic importance. The commercial value of the skins of many species is generally acknowledged (Cott 1954, 1961; Chabreck 1966, 1967a; Graham 1968; Bustard 1970; Downes 1970; Parker and Watson 1970; Yangprapakorn et al. 1971; Puffet 1972, 1973; Pooley 1973a; and Blake 1974), and needs no elaboration. They also have value as a tourist attraction (Cott 1961, Pooley 1973a).

Crocodilians appear to have ecological value. Cott (1961) and Pooley (1962) believed that crocodiles help control predators on fish esteemed by man. Kellogg (1929) expressed the same belief regarding the American alligator (<u>Alligator</u> <u>mississipiensis</u>). Improved angling following the introduction of crocodiles into the Zambezi River above Victoria Falls has been claimed, according to Child (1974). Fittkau (1970) hypothesized a direct relationship between caiman populations and yield of fish in the oligotrophic mouth-lakes of certain tributaries to the Amazon River, in Brazil. In a follow-up he (Fittkau 1973) considered the nutrients excreted by the caimans, assumed primarily of allochthonous origin, to significantly increase the primary productivity in the electrolyte-poor Central Amazonian waters. Pooley (1962, 1969a) reported 2 adult Nile crocodiles to burrow under Ficus sycamorus roots on the Mkuzi River (Zululand, Natal, R.S.A.) during a drought. The pool thus formed in the dry river bed lasted until the rains again filled the river (over 2 months), and was important to small game mammals, birds, amphibians, fish, and insects. Kolipinski and Higer (1966) stated that the holes made by American alligators, in many tree islands, are vital refuges for fish and other wildlife in the dry season, and are therefore essential to the biological survival of the Everglades.

The world-wide decline in numbers of crocodilians is widely documented (Cott 1961; Chabreck 1966, 1967a; Graham 1968; Pooley 1969b, 1969c, 1970, 1971, 1973a; Bustard 1970; Charnock-Wilson 1970; Parker and Watson 1970; Lekagul et al. 1971; Joanen and McNease 1971, 1974; Ogden 1973), and is cause for concern. In light of the present status of crocodilians, studies of general biology, artificial hatching, reproductive behavior, effects on fisheries following drastic crocodile reduction, and population surveys to determine breeding stocks and recruitment rates, have been urged by Cott (1961), Fitter (1970), Parker and Watson (1970), and Pooley (1973a). Blake and Loveridge (1975) stressed the need for assessment of mortality patterns in a natural population, in connection with the 5% replacement rate of 1 m long crocodiles from eggs collected for captive rearing.

The "vulnerable" status (IUCN 1982) of the Nile crocodile calls for management intended to prevent slippage to "endangered" status, or possibly even extinction, in the future. It is far better to practice preventive maintenance of the crocodile population now, than to frantically and probably at great expense try to save it from extinction some decades later. Commercial utilization of the crocodile, on a sustained-yield basis, will motivate conservation of the Nile crocodile; human sentiment alone is not believed sufficient (Blake and Loveridge 1975). Graham (1976, 1977) believed that if the Okavango crocodiles are not harvested commercially, they will be viewed merely as pests, and will therefore be eliminated, passively and actively, by the local people.

CHAPTER 2

REVIEW OF LITERATURE

The scope of this chapter is to summarize modelling of crocodilian populations, and the models' relation to sustained-yield commercial utilization. It is additionally intended to report on commercial utilization, and on potentially useable populations, in relation to conservation of crocodilians.

Bustard (1970) stated that commercial use of wild crocodilians is the best way to conserve them. Crocodilian skins can be the basis for a sustained-yield industry that will make people accept crocodile conservation as sensible, practicable, and profitable. Essentially the same rationale for sustained-yield utilization, of several species, was given by Bustard (1972) Downes (1973, 1975), Blake and Loveridge (1975), Graham (1976, 1977), Whitaker and Whitaker (1979), Bustard and Choudhury (1980), Jenkins (1980, 1982), Whitaker (1980, 1982a), Ross (1984), and Webb (1985). Bustard (1970) and Blake and Loveridge (1975) maintained that public sympathy for crocodilians, as a motivating force in conservation, would be difficult to arouse.

A computer model of any wildlife population is intended to logically and mathematically mimic the dynmamics of the population, and the external forces that act upon it. In the case of commercial utilization, the chief purpose of a model is to optimize sustained cropping (Graham 1976, 1977, Nichols 1976). A computer model is also useful in suggesting management strategies, monitoring progress, and directing research (Graham 1976, 1977). An advantage of trying to model a population is that its biological characteristics that are in greatest need of being researched are highlighted, e.g., improvement of age criteria and age-specific mortality rates. Simultaneously the characteristics of no direct relevance to management become obvious (Graham 1977).

Experimental harvest manipulations are potentially more dangerous to populations of alligators than to those of many other wildlife species, due to high vulnerability to hunting, also to the long time to reach sexual maturity (typically 9 years in Louisiana), and the drastic effects on the populations of certain natural phenomena, e.g., hurricanes, drought, and severe freezes (Nichols 1976; Nichols, Viehman, Chabreck, and Fenderson 1976). Nichols (1976) considered these facts as reason for simulating experimental harvests that in practice could do lasting damage to the population. He further stated that computer models make available immediate predictions of effects on population growth of certain management practices. Lastly, Nichols (1976) mentioned the large number of management options available for alligators, i.e., restocking programs, various combinations of size- and sex-specific harvest rates, and various methods of harvest.

Graham (1976, 1977) reported a model, largely dependent on data on the structure of 2 annual harvests of Nile crocodiles, also on the known size and age structure of nesting females, in the Okavango River. Various population sizes can be tested until 1 containing these observed segments emerges. The model thus circumvents the extreme difficulty, or great expense, or both, of estimating the size of the population in the field. A logic diagram is presented in Graham (1977). Graham (1976, 1977) stated that though simulated population size will initially be rough, it will improve with more accurate measurements of the model's parameters, also that even a rough estimate will enable preliminary cropping to avoid dangerously large or unnecessarily small numbers. The next step is to use the model to simulate population growth over possibly 20 years, at various cropping rates. Finally it would be used to optimize yields from any given situation (Graham 1976, 1977).

The model of Nichols, Viehman, Chabreck, and Fenderson (1976) was constructed to simulate the dynamics of a commercially harvested alligator population inhabiting privately owned coastal marshland of Cameron and Vermillion parishes in Louisiana. Nesting effort, nest flooding, dessication mortality, and predation on eggs and young were all determined as functions of monthly water depth averages. Cannibalism was considered the major density-dependent factor operating on the population, and was determined as a function of population density and water depth. A freeze mortality based on minimum winter temperatures was included, as was a harvest option. Harvest regulations were designed to protect mature females and animals under 1.2 m in length. The model contained the possibly erroneous assumption that hunting mortality of alligator populations is entirely additive to natural mortality. Simulated hunting therefore had maximal detrimental effects on the population.

The management plan for the Okavango crocodiles, which centers on Graham's (1976, 1977) model rests on 2 assumptions: (1) that the crocodiles, if not exploited, become "pests" regardless of legal status, and (2) that planned and monitored exploitation turns the animals to economic advantage and produces information that confers ability to manage the crocodiles for preservation, exploitation, or a combination of both. Prerequisites for a successful management plan are: (1) values for certain population biology parameters that are accessible to monitoring, (2) the offer of a reasonable and predictable return to Botswana's government and to the cropper, and (3) adequate conservation safeguards that can be observed and enforced. Use of a model to compile information gained from research, cropping and monitoring makes possible more rapid accumulation of knowledge and skill in management, and forestalling drastic mistakes (Graham 1977).

The model of Nichols, Viehman, Chabreck, and Fenderson (1976) was used to examine the alligator population's response to various differential harvest rates in which age- and sex-specific proportions of animals were similar to those observed in the 1972 and 1973 hunting seasons in Louisiana. These simulations demonstrated that a base population of 100,000 animals, under existing habitat conditions, should be maintained for a minimum of 20 years when subjected to an annual differential harvest rate of slightly greater than 5%. Simulations were conducted in which animals were taken in proportion to their abundance in the population. Effects of proportional harvests, compared with those of differential harvests, indicated that the former can give increased yields of hides.

In further work on the above model, Nichols, Chabreck, and Conley (1976) examined potential use of restocking programs to reduce or eliminate effects of harvests on population growth, while maintaining harvest yields. Population growth rates and harvest yields were examined for various simulated restocking quotas. The authors proposed, as a result, that harvesters be required to collect eggs, for rearing and release of young after 2 years, in proportion to the number of female alligators killed in the preceding season.

Crocodilians may, in addition to, or in lieu of, hunting, be raised on farms or ranches (the latter sometimes are termed "rearing stations"), for their skins. The term "farm" denotes a self-sufficient establishment in which eggs come from captive breeders (Chabreck 1967b, 1971, 1973; Pooley 1973a; Blake 1974; Blake and Loveridge 1975). Farming does not directly relate to conservation, and receives only brief mention in this work. A ranch is usually defined as an establishment dependent on wild-caught young, or young hatched in captivity from eggs collected in the wild (Pooley 1973a, Blake 1974, Blake and Loveridge 1975).

Magnusson (1984) reported that Papua New Guinea, Zimbabwe, and the U.S.A. are the only countries with extensive farming and ranching operations. The last, though significantly dependent on farmed alligators, produces most of its skins via controlled hunting in Louisiana. The other 2 countries have limited farming, and produce most of their skins by ranching. Magnusson (1984) concluded that (1) in no country are crocodilians produced in commerical quantities by captive propagation (farming), and (2) projects that most effectively help in maintaining wild stock and its habitat involve hunting of adults, or collecting of eggs or hatchlings by local land owners.

The government of Papua New Guinea, after uncontrolled hunting and depletion of estuarine and New Guinea crocodiles (<u>Crocodylus</u>

porosus and C. novaeguinea, respectively), eased the hunting pressure by organizing a network of village rearing pens and commercial ranches (Downes 1971a, 1971b, 1975; Puffet 1972; Montague 1981a). This also gave native people, even if in isolated areas, a chance to earn money, and a vested interest in conserving wild populations (Montague 1981a, Magnusson 1984). Downes (1975) stated that the rearing of wild-caught young is the way to conserve Papua New Guinea's crocodile populations, if it is established and controlled for national benefit. There are legally set maximum and minimum belly widths for the harvested crocodiles, namely 51 cm (20") (total length being about 180 cm) and 18 cm (7") (total length being about 90 cm). The former protects the breeding stock; the latter ensures growth to economic size (Bustard 1970, Lever 1975a, Montague 1981a, Kwapena and Bolton 1982). Downes (1975) and Bustard and Choudhury (1980) stated that the industry in Papua New Guinea could have a major impact on conservation of crocodiles. Puffet (1972) stated that the future of the industry is in the hands of the native people, and that management would be unworkable without their cooperation. He and Montague (1981a) commented on the people's interest in raising crocodiles.

The Department of National Parks and Wildlife Management in Zimbabwe agreed in 1966 to establishment of private rearing stations for young Nile crocodiles. Permission to capture young crocodiles (later prohibited), or collect eggs, was granted on condition that a 10% (but currently 5%) equivalent of young be released to the wild at an age to be determined by the Department (Blake 1974). Blake and Loveridge (1975) stated that wild breeding populations now have substantial value as basis for rearing stations, a fact not to be underestimated as a motive for crocodile conservation. They also considered juveniles of rearing stations a valuable resource for supplementing wild recruitment and restocking suitable habitat. Ferrar (1974) and Nathan (1977) also pointed out the conserving effect of Zimbabwe's 3 ranches. The purpose of the commercial management is to achieve maximum sustained annual harvest (Zimbabwe Department of National Parks and Wildlife Management 1974). Blake and Loveridge (1975) and Loveridge (1980) reported that repeated egg collections, since 1967, have not adversely affected the now large and stable crocodile population in Zimbabwe. Ferrar (1974), Zimbabwe Department of National Parks and Wildlife Management (1974) and Nathan (1977) discussed farming of crocodiles in the future. It now takes place concurrently with ranching at Spencer Creek Crocodile Ranch in Victoria Falls (Blake 1974, Medem 1981). Magnusson (1984) pointed out that if ranches turn into farms, the incentive to maintain wild crocodile populations will be reduced, which would put the Department in a difficult situation. The possibility of sustained hunting of crocodiles has been considered, but would be actively discouraged until the populations could withstand it (Zimbabwe Department of National Parks and Wildlife Management 1974).

In the U.S.A., Louisiana's alligator management program resulted from research begun in 1958. Legislation to set up the basic framework for hunting seasons in 3 parishes was enacted in 1970 (Palmisano et al. 1973). Chabreck (1971) recommended establishment of size limits to protect breeders, designing regulations so as to harvest surplus males, also use of a population's size, composition, annual production, and annual mortality as basis for harvest regulations. Palmisano et al. (1973) considered the management program an excellent example of modern, goal-oriented wildlife research, enforcement, and management. The first hunt took place in 1972 in a parish judged to have the largest coast-wide population. Hunting was allowed gradual expansion, to become state-wide in 1981 (Joanen and McNease 1982). Joanen and McNease (1972) and McNease and Joanen (1978) expressed eagerness to initiate wild harvests of alligators, because this motivates land owners to maintain, rather than drain, wetlands, to benefit other wildlife as well. Recovery of depleted alligator populations in the U.S.A., in response to management, is reported by Chabreck (1967a, 1971), Palmisano et al. (1973) Gore (1978), Brazaitis (1984), and Niering (1985).

Abercrombie et al. (1980) believed that Morelet's crocodile (C. moreleti) in Belize, after a 5-10-year cessation of hunting, needed a carefully monitored harvest program. They felt that the population here, unlike those in many other developing countries, still had a capacity for rapid recovery. Abercrombie et al. (1982) felt, however, that production should be on a small scale, to prevent establishment of a large tannery requiring enormous numbers of skins.

The possibility of restoring the American and Cuban crocodiles C. acutus and C. rhombifer, respectively) to levels at which they perform normally in Cuba's ecosystems, has been mentioned. It would be followed by a careful harvest program for the international hide market, and meat for local people (IUCN 1978).

Graham (1968) discussed a possible commercial management plan for the Nile crocodile in Lake Turkana, Kenya. He considered cropping of younger age classes, possibly supplemented by artificial rearing of young.

For Uganda, Cott (1954) mentioned the need to give thought to the breeding stock of the Nile crocodile, if the skin industry were to be saved. He (Cott 1961) also recommended for Uganda and Zambia, effective conservation measures with regard to modern hunting procedures and to the animals' slow growth rate.

Medem (1981) recommended that the Okavango crocodiles be managed by farming or by rearing stations. He stated that the rural people would benefit thereby.

In the face of pressure for land development in Mozambique, Whitaker (1981) recommended ranching projects at 2 locations. Examination of other locations for utilization of the Nile crocodile should follow.

Bustard and Choudhury (1980) and Whitaker (1982a) recommended well-managed commercial utilization of the estuarine crocodile in India, as a conservation measure. The marsh crocodile (_C_. _palustris_) responds rapidly to effective management, making substantial economic returns possible (de Waard 1978, Whitaker 1979). A described scheme allows for establishment of a large number of village pens to be used for raising juveniles. Local people would get increased income and employment opportunities (de Waard 1978). Without incentive, based on governmental guidelines for large-scale rearing, the marsh crocodile will never again be plentiful, according to de Waard (1978). He believed that, with large-scale rearing, the gharial (_Gavialis_ _gangeticus_) in India might respond to effective management, and that substantial economic returns are possible. Whitaker and Daniel (1978) stated that important populations of the estuarine crocodile exist on Little Andaman and Nicobar Islands, and that they could support a forest-based industry to benefit indigenous tribes.

For Nepal Whitaker (1982a) stated that survival of the marsh crocodile and gharial, outside Royal Chitwan National Park, might depend on developing controlled commercial interest among river dwellers and fishermen. Seed stock would come from the rearing scheme of Chitwan.

For Bangla Desh, Whitaker (1982a) stated that development of crocodiles as economic and ecologic resource appears to be the best option. He alluded to the estuarine species, which appears not uncommon in the Sunderbans (Ganges delta).

For the estuarine crocodile in Sri Lanka, Whitaker (1979, 1982a) recommended farming and wild propagation for economic return, outside of national parks. He (Whitaker 1982a) recommended the same for the marsh crocodile. Whitaker and Whitaker (1979) recommended cropping quotas, upper size limits, and publicity to ensure the continued existence of the latter species.

Whitaker (1982a, 1982b) reported interest in Burma, in rearing young estuarine crocodiles. This was on the village level, as in Papua New Guinea.

In Malaysia there is recent history of small rearing stations, so controlled harvest of young crocodiles (presumably meaning estuarine) would be a logical approach (Whitaker 1982a). Some states are interested in conservation and management, and initial surveys have been drafted.

Whitaker (1982a) suggested, for Indonesia, a crocodile management program like Papua New Guinea's network. He reported a similar recommendation, specifically for Irian Jaya (which is not surprising), by an unnamed FAO consultant surveying the crocodile industry.

Controlled exploitation, in the Philippines, will probably be the key to obtaining significant official involvement in crocodile conservation (Whitaker 1982a). The government would be interested in how crocodiles can benefit people, not in conservation of a non-commercial resource (Ross 1984). The Agusan River drainage could be a sanctuary for the estuarine species if local inhabitants and political dissidents were convinced that they could ranch or crop on a sustained-yield basis (Ross 1984).

For the estuarine crocodile in Australia, Bustard (1972) and Jenkins (1980) believed commercial use, after population recovery, would offer an excellent conservation solution. According to Jenkins (1982) and Webb (1985) the subadult segment could be harvested without adverse effect, once the populations reached equilibrium. Webb (1984) stated that strictly controlled commercial use of Johnson's crocodile (C. johnsoni) is now possible, and can play a positive role in its conservation, granted that its hide is less valuable than that of the estuarine species (Jenkins and Forbes 1983). Webb (1984) stated that if crocodilians are of commercial value, their wetland habitat will be an asset, and destruction thereof would be a liability.

For Papua New Guinea's island provinces, i.e., Manus, New

Ireland, East New Britain, West New Britain, and the North Solomons, Whitaker (1980) mentioned status, needs, and commercial possibilities of the estuarine crocodile populations. He stated that proving and sustaining economic value of crocodiles as a resource may be the only way to guarantee survival.

The estuarine crocodile in the Solomon Islands is partly protected (Whitaker 1982a, 1982b). It could become a valuable resource to villagers interested in rearing or capturing young for sale to a commercial farm (presumably meaning "ranch"), according to Whitaker (1982a). He added that tourist viewing of wild crocodiles could provide an additional source of income to local villagers.

CHAPTER 3

MATERIALS AND METHODS

POPULATION MODEL

The model, written in FORTRAN IV, represented a first attempt at describing the behavior of the crocodile population. It projected population growth from 1975, and incorporated simulated hunting as an option. The program "CROC", in updated form, with its function sub-programs and subroutines, is in Appendix A. The reader may wish to refer to it frequently in relation this chapter. Figure 1 shows a condensed flow chart.

The model began by naming and dimensioning a number of variables, and providing numerical values for some, including the number of females in each of 66 age classes ("FPOP(K)"). Then it initialized the population ("TPOP") for year 0 (1975) and the variable for hunting kill of males ("MHKIL") and of females("FHKIL"). Next it calculated the population size, and the number of females by age class.

The initial population estimate (for 1975) was made as follows. It was first assumed that BGI's kill of sexually mature females (1974-75) was not intense enough to get the more remote nesting portion, but only that portion which did not nest and which numbered 11. An unbiased sampling of the sexually mature females would have numbered 33, assuming that 2/3 of the mature females nested that year. Scanty field observations suggest that this is so. Thirty-three sexually mature females would increment the entire female kill, by 22, to 220, of which these 33 females constitute 15.0%. It is then assumed that there were 123 sexually mature females in the population (2/3 of which

Figure 1. Condensed flow chart of the computer model. Because of the assumed sex ratio of 1:1 and emphasis on the female cohort, separate calculation of the size of the male cohort takes place only during hunting (CRHUNT set at .TRUE.), and then because age spans of hunted males and of hunted females differ. TPOP and FPOP (in second comment) represent size of population and of female cohort, respectively. Each iteration of the main do loop represents a year. FLAG is a water level index dependent on a random number, and can have a value of 2, 1, or 0, each of which corresponds to premature flood conditions, drought (hence low water levels), and normal water levels, respectively. In case of flood, function subprogram TABLIE is called to determine a value for F1. If FLAG is 1 or 0, F1 is 0. HATCH represents the number of successfully hatching eggs. F3M1 is the multiplier function, either equal to 1 (normal water levels), or to a value determined by function subprogram TABLIE, on the rate of cannibalism on 0-2-year old crocodiles. M2 is a density index of 0-2-year old crocodiles, and equals 0, 1, or 3. NORPRED is the assumed constant rate of cannibalism.

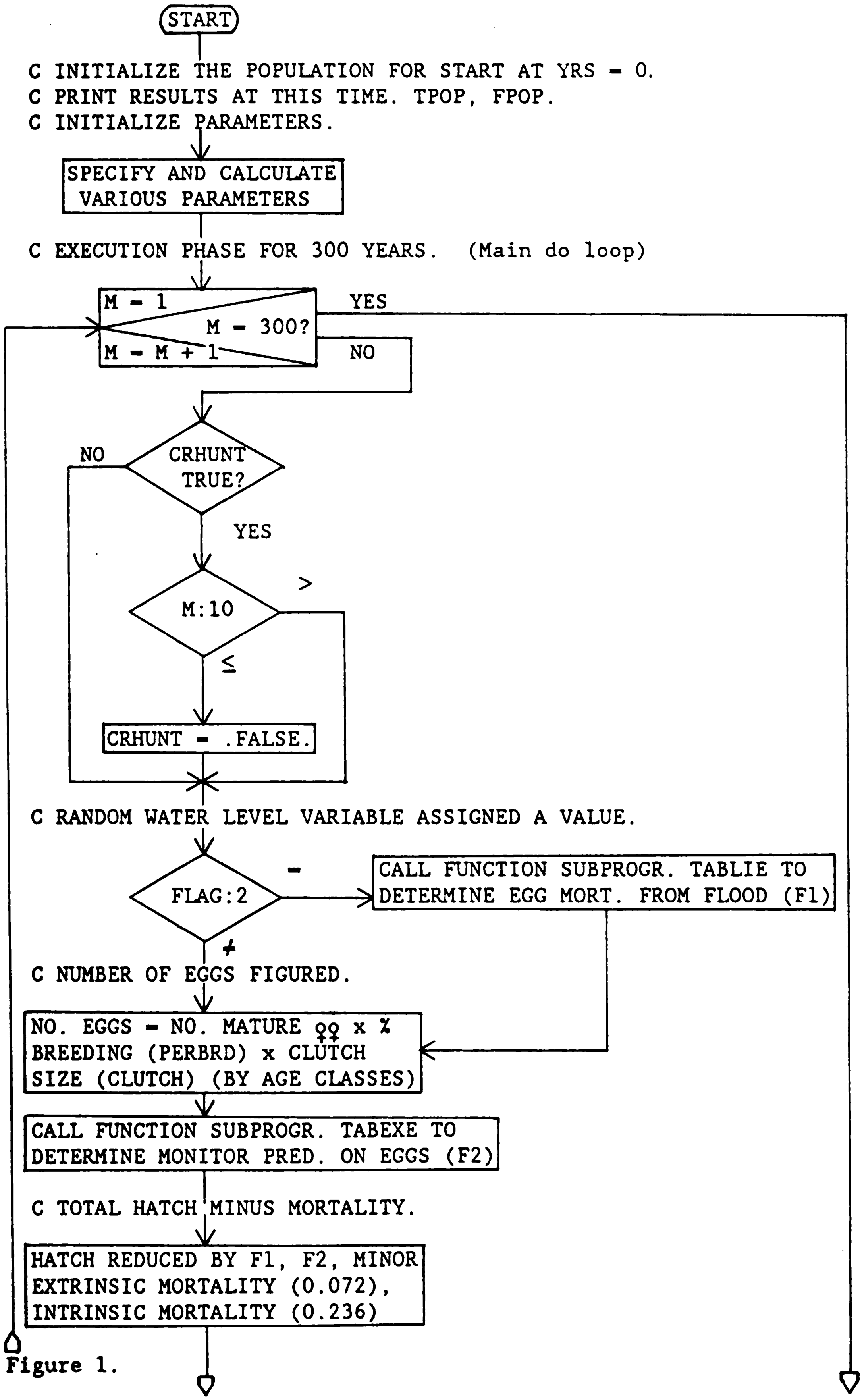

START
C INITIALIZE THE POPULATION FOR START AT YRS = 0.
C PRINT RESULTS AT THIS TIME. TPOP, FPOP.
C INITIALIZE PARAMETERS.
SPECIFY AND CALCULATE VARIOUS PARAMETERS
C EXECUTION PHASE FOR 300 YEARS. (Main do loop)
M = 1
M = 300?
M = M + 1
YES
NO
NO
CRHUNT TRUE?
YES
>
M:10
≤
CRHUNT = .FALSE.
C RANDOM WATER LEVEL VARIABLE ASSIGNED A VALUE.
=
FLAG:2
≠
CALL FUNCTION SUBPROGR. TABLIE TO DETERMINE EGG MORT. FROM FLOOD (F1)
C NUMBER OF EGGS FIGURED.
NO. EGGS = NO. MATURE ♀♀ x % BREEDING (PERBRD) x CLUTCH SIZE (CLUTCH) (BY AGE CLASSES)
CALL FUNCTION SUBPROGR. TABEXE TO DETERMINE MONITOR PRED. ON EGGS (F2)
C TOTAL HATCH MINUS MORTALITY.
HATCH REDUCED BY F1, F2, MINOR EXTRINSIC MORTALITY (0.072), INTRINSIC MORTALITY (0.236)

Figure 1.

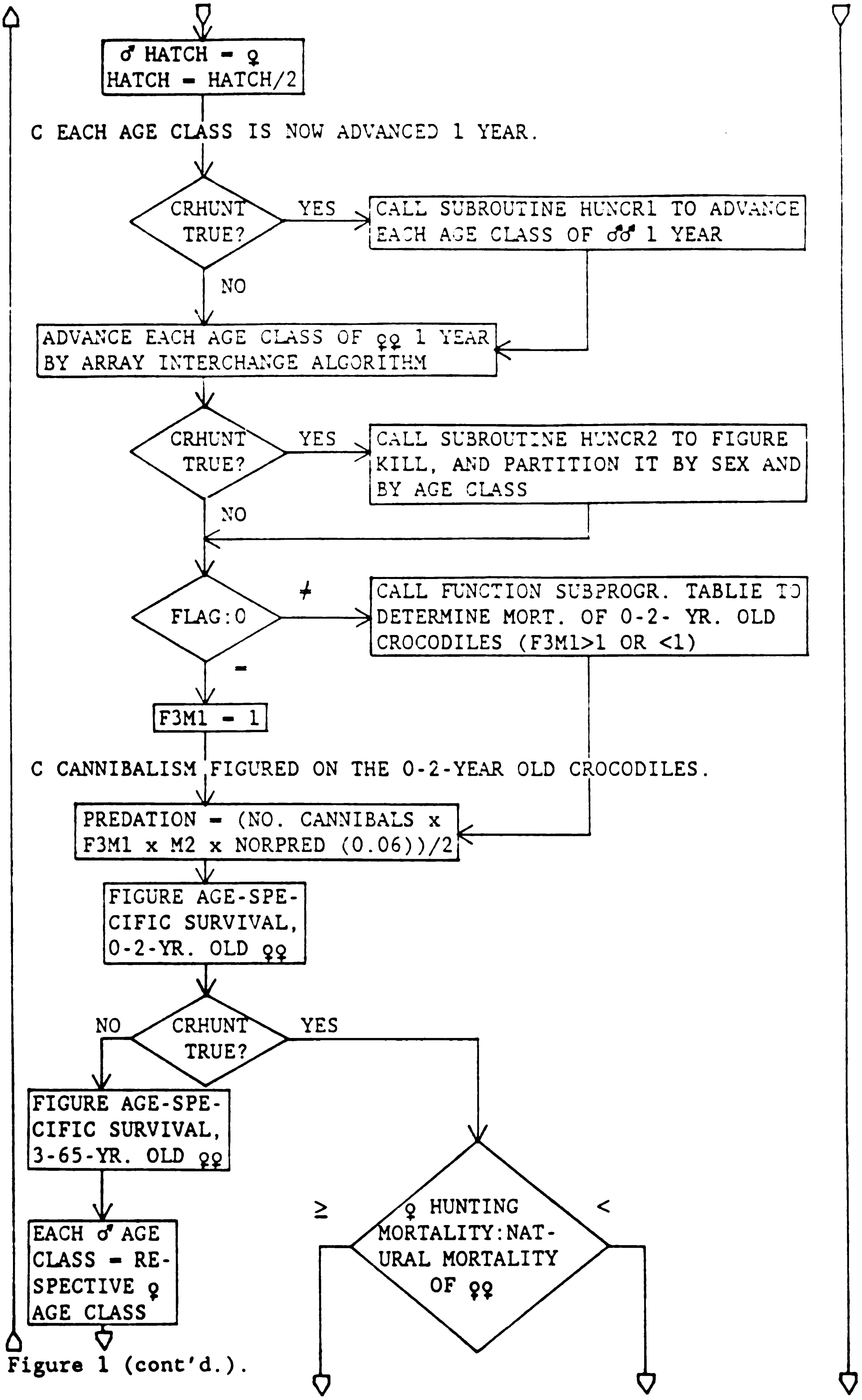
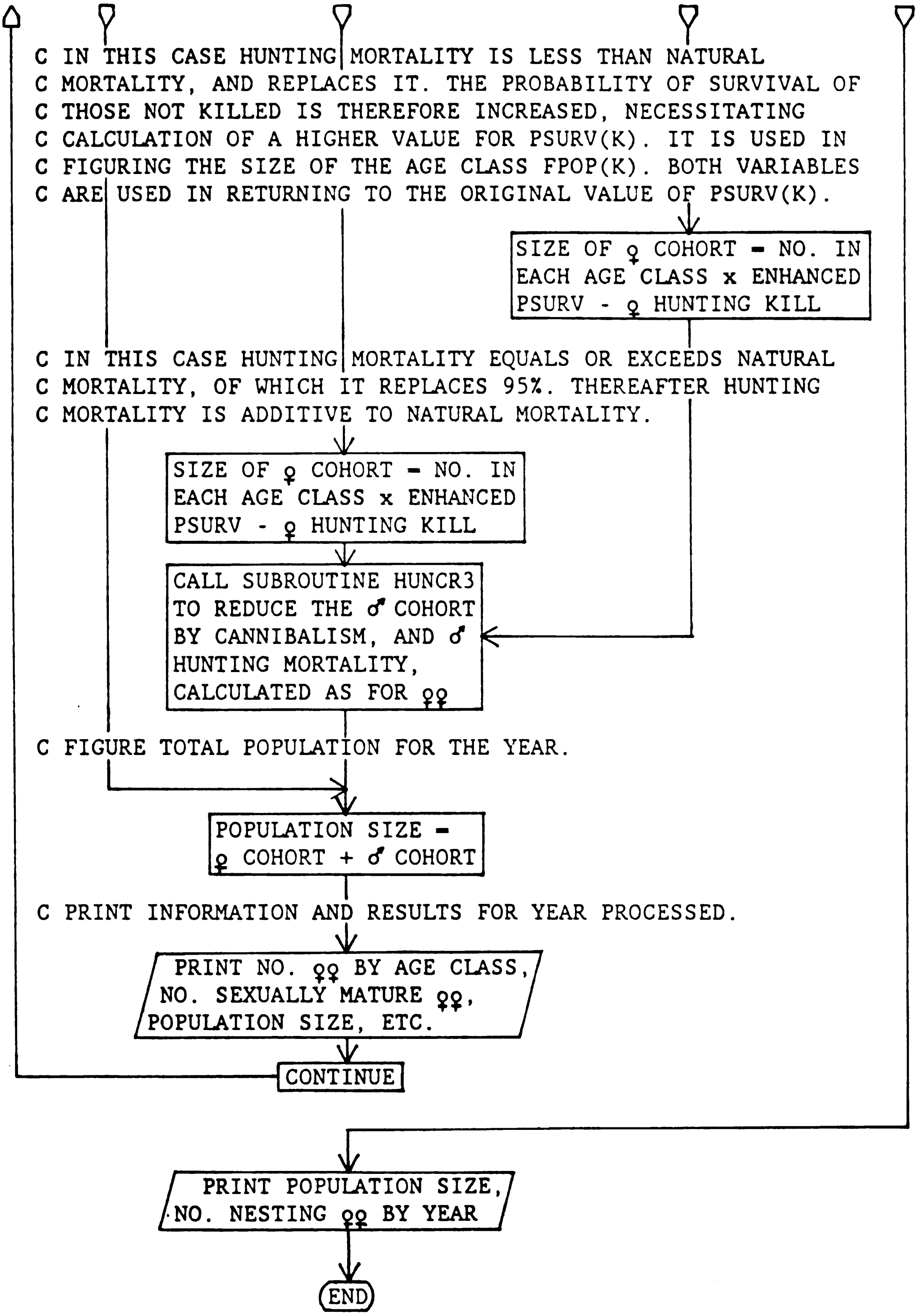


Figure 1 (cont'd.).



C IN THIS CASE HUNTING MORTALITY IS LESS THAN NATURAL
C MORTALITY, AND REPLACES IT. THE PROBABILITY OF SURVIVAL OF
C THOSE NOT KILLED IS THEREFORE INCREASED, NECESSITATING
C CALCULATION OF A HIGHER VALUE FOR PSURV(K). IT IS USED IN
C FIGURING THE SIZE OF THE AGE CLASS FPOP(K). BOTH VARIABLES
C ARE USED IN RETURNING TO THE ORIGINAL VALUE OF PSURV(K).

C IN THIS CASE HUNTING MORTALITY EQUALS OR EXCEEDS NATURAL
C MORTALITY, OF WHICH IT REPLACES 95%. THEREAFTER HUNTING
C MORTALITY IS ADDITIVE TO NATURAL MORTALITY.

C FIGURE TOTAL POPULATION FOR THE YEAR.

C PRINT INFORMATION AND RESULTS FOR YEAR PROCESSED.

Figure 1 (cont'd.).

were the 82 known nesters) in 1975, and that these 123 females likewise constituted 15.0% of the then huntable females (at least 120 cm long). The huntable females in the population would therefore number 820. The huntable cohort, as determined by repeated night counts, constituted 17.0% of the entire population. By use of this percentage the entire female cohort in the study area should equal 4,820, and because of the approximately 1:1 sex ratio obtained from the 1974-75 kill on the Okavango River, and the 1973 kill (Taylor 1973), also kills in Uganda and Zambia (Cott 1961), and kills from Lake Turkana, Kenya (Graham 1968), the entire population was estimated at 9,640. This estimate was arbitrarily raised to 9,730, an inconsequential 0.9%, to get the numbers of nonhuntable crocodiles (under 120 cm long) to better fit the structure of the rest of the population, as determined by length-frequency data in the kill.

Next (under comment "INITIALIZE PARAMETERS") a number of variables for the main program (CROC) were initialized. This included "THUNT" (total number hunted) at 0, "MINHUNT" (minimum permissible number of crocodiles of allowable length for hunting) at 300, and "EFFIC" (the assumed efficiency of the hunter in the field) at 0.3, when hunting was simulated. Huntable crocodiles in this program were 120-190 cm long, based on current hide prices and the paucity of adults (Graham 1977), also due to the need to protect breeders (Bustard 1970), and corresponded with 2- to 4-year-old males and 3- to 6-year-old females. In additon, parameters for the 2 function subprograms "TABLIE" and "TABEXE" (Llewellyn 1966) were initialized. The first of these calculated values for egg loss due to premature floods, and for a multiplier function on cannibalism during drought, while the second calculated a predation rate on eggs by the Nile monitor (Varanus niloticus). Thereafter the program recalculated the values for the variables "PSURV" (percent survival to the next age class), "PERBRD" (percent nesting females by age class in a given year), and "CLUTCH" (cube root of clutch size for each age class).

Variable PSURV (Figure 2) represented the probability of survival from age 0 to age 65. The maximum age span approximates that hypothesized by Graham (1968). For the first 4 age classes, the increasing portion of the curve was based on derived population structure and thereafter is hypothetical. Ages were assigned to lengths based on the growth curve for 1 free-living probable female in Zimbabwe (reported in Cott 1961 and Graham 1968). Calculations showed that PSURV gives an individual crocodile a 2% probability of survival to age 20. As the chance of survival to reproductive age is believed to be 1-5% (Blake and Loveridge 1975), PSURV seems realistic.

Variable PERBRD (Figure 3) was used to determine the percentage of nesting females for each age class. The earliest a female could mature sexually is age 10 (Cott 1961). Yangprapakorn et al. (1971) reported that C. porosus, which grows approximately as large as C. niloticus, matures sexually in 10-15 years. It is assumed that roughly the same age span holds for the Okavango River, and therefore that all or nearly all females are mature by age 15, even if the percent nesting in any given year is still relatively low. By age 37 (length = 290 cm, based on the free-living specimen in Zimbabwe) 2/3 of the females will nest in any 1 year (see Figure 18 in Cott 1961).

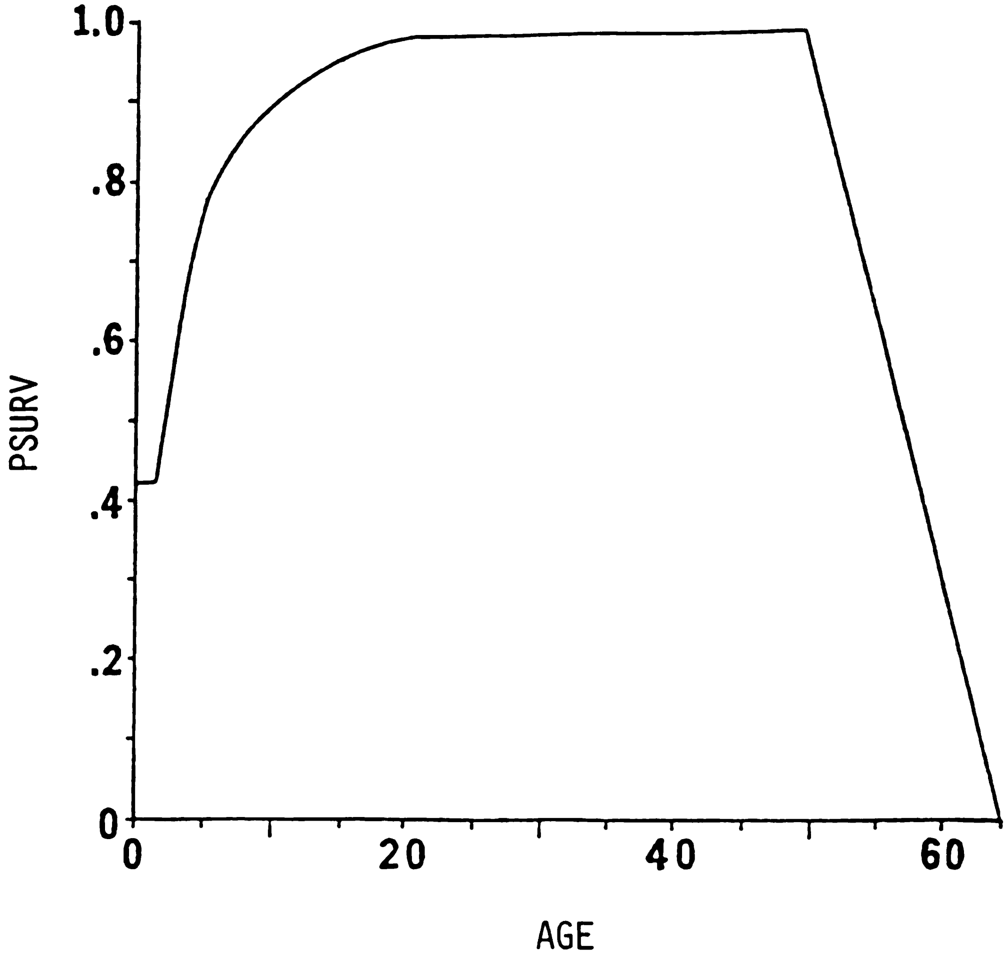


Figure 2. Curve of survival rates for Okavango crocodiles (PSURV), based on the assigned age structure of the 1974-75 kill and hypothetical points.

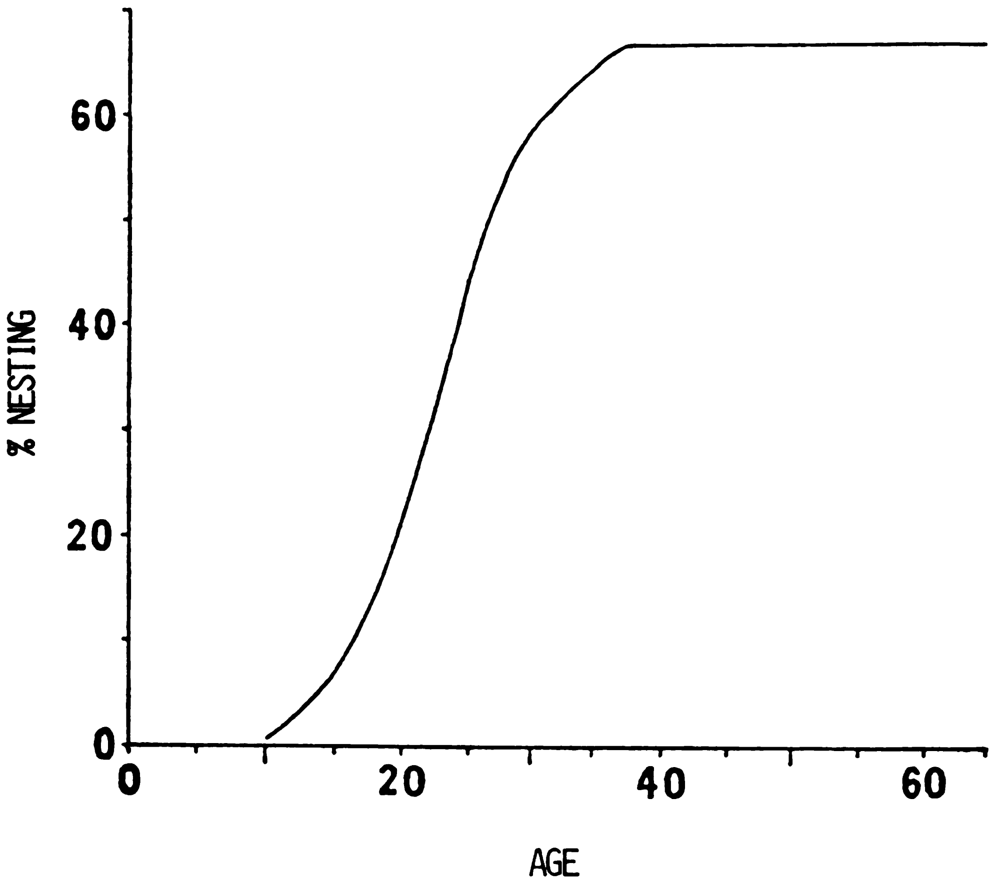


Figure 3. Percent of female cohort nesting as a function of age (PERBRD).

Variable CLUTCH (Figure 4) was the cube root of clutch size (Graham 1968) in relation to the age of the crocodile. The cube of CLUTCH is used to calculate the clutch size in the model. This variable was also adapted from Cott (1961).

Recalculation of the 3 variables above was followed by calculation of values for "WLEV(I)". This was 1 of several dummy arguments used in getting a randomly obtained value for the water level.

At this point (comment "EXECUTION PHASE FOR 300 YEARS.") began the program's main do loop. It was set at 300 iterations, each representing 1 year's events affecting the crocodile population. If hunting were simulated, the size of the huntable male and female cohorts were initialized at 0, prior to being assigned specific values.

Weather, because of its effect on water levels, was considered an important influence on survival of eggs and young. Therefore a random value, ranging from 1 to 10, for "KK", the subscript of WLEV (above) was generated (under comment "RANDOM WEATHER VARIABLE ASSIGNED A VALUE"). The variable corresponded to the type and severity of the water levels (see Figure 5). Only 1 of the 3 possible types of water levels, i.e., premature flood, drought, or normal, could exist in a given year, and these types were represented by values of 2, 1, and 0, respectively, for "FLAG", a water level index on which certain decisions in the program were based. The distribution of KK was based on the probability of a drought equal to 0.4, and probabilities of flood and normal levels equal to 0.3 each. In case of flood, function subprogram TABLIE, which calculated consequent egg mortality ("F1"), was called.

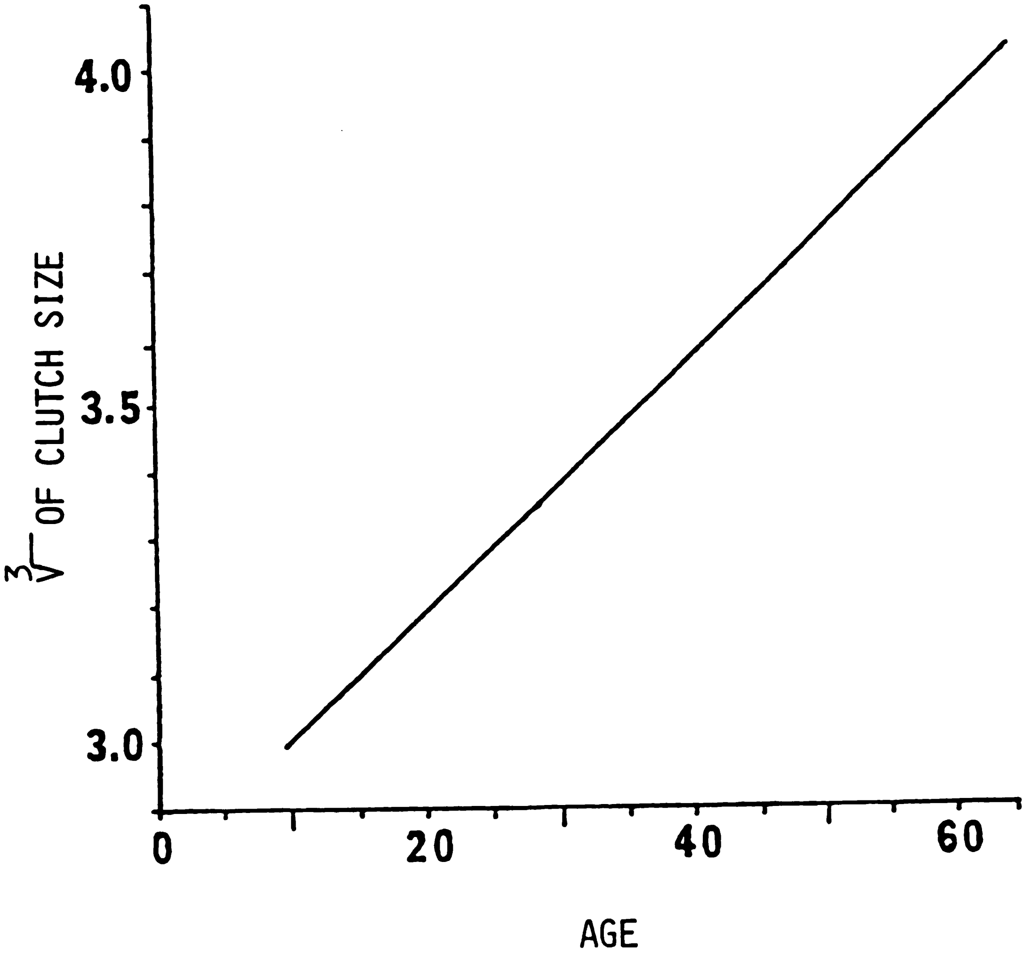


Figure 4. Relation of cube root of clutch size to age of female (CLUTCH).

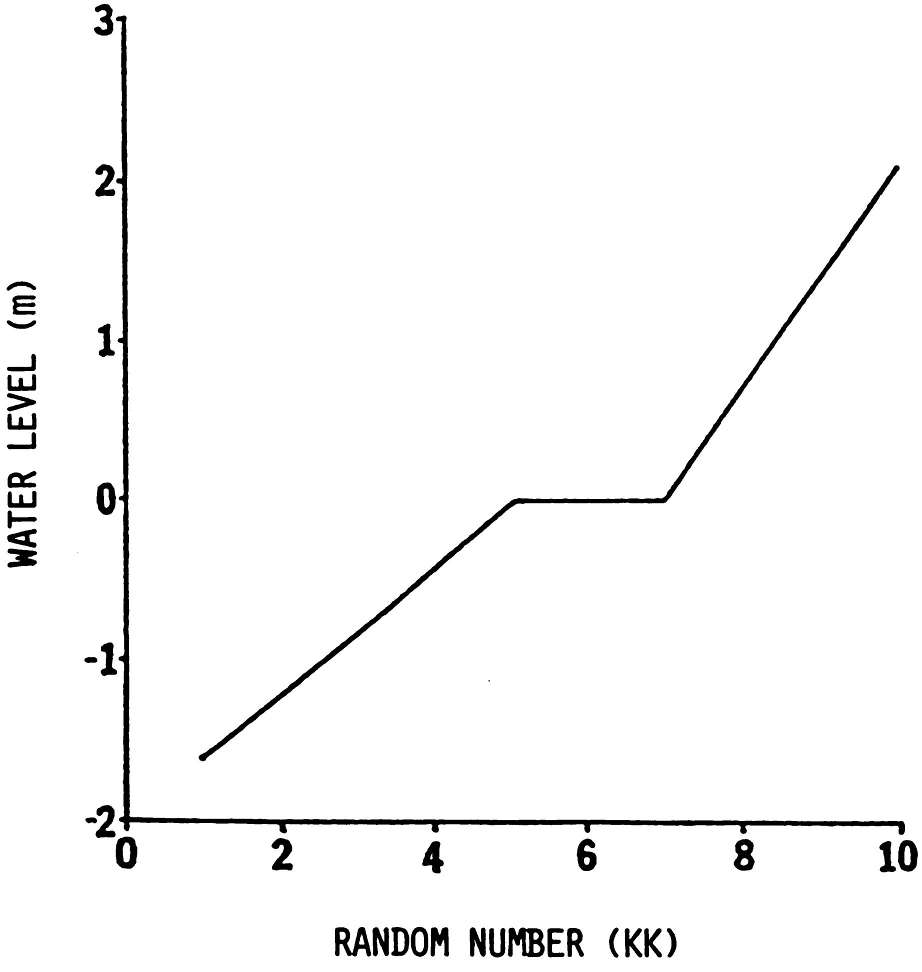


Figure 5. Water levels generated by random numbers. The normal water level is designated by 0.

Function F1 (Figure 6) estimated the percentage of egg mortality due to prematurely high water levels. Its shape is justified by the fact that 68% of the nests will be between 0.8 and 1.8 m above water in normal seasons (mean ± standard deviation = 1.3 ± 0.5), as determined by 40 measurements in the field. If the value of the subscript were smaller, representing drought (FLAG = 1), or water levels were normal (FLAG = 0), the number of eggs ("TEGGS," under comment "NUMBER OF EGGS FIGURED.") was calculated at F1 = 0, for each age class of females. The calculation involved variables PERBRD and CLUTCH above. The average clutch size ("ACLUTCH") was then obtained by dividing TEGGS by the number of nesting females. ACLUTCH was used in calculating the number of nests "NNEST", based on the value of F1 (0 or positive). NNEST was 1 of the arguments used in obtaining the decimating factor on eggs, "F2" (Figure 7) due to Nile monitor predation. Function F2 estimated the percent of egg loss caused by monitor predation. The shape of the function is based solely on 2 data points: apparent lack of predation with 40 nests in 1974 and predation on 23% of 82 nests in 1975 (Blomberg 1977). The difference in nest numbers for the 2 seasons was real. Additional justification for the general shape of the function was the density-dependent nature of predation in general (Emmel 1973). The predation rate for 1975 may have been somewhat lower if visits to nests could have been very brief or not undertaken. The reason is that females tend to leave the nests unguarded if human visits last about 30 min (Graham et al. 1976). The maximum predation rate was set at 28%, which seems reasonable, considering that 20% of nests were robbed at Ndumu, Zululand, R. S. A.,

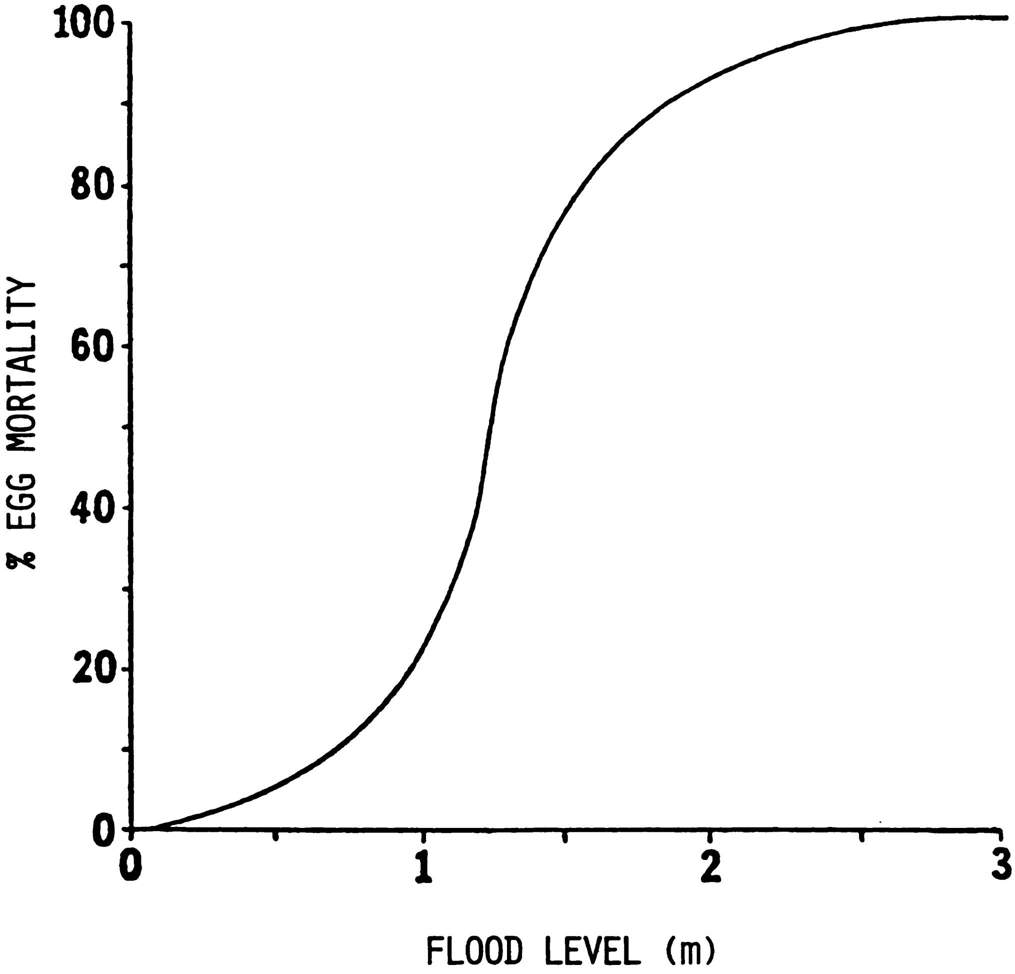


Figure 6. Relation of percent egg loss (Fl) to flood level.

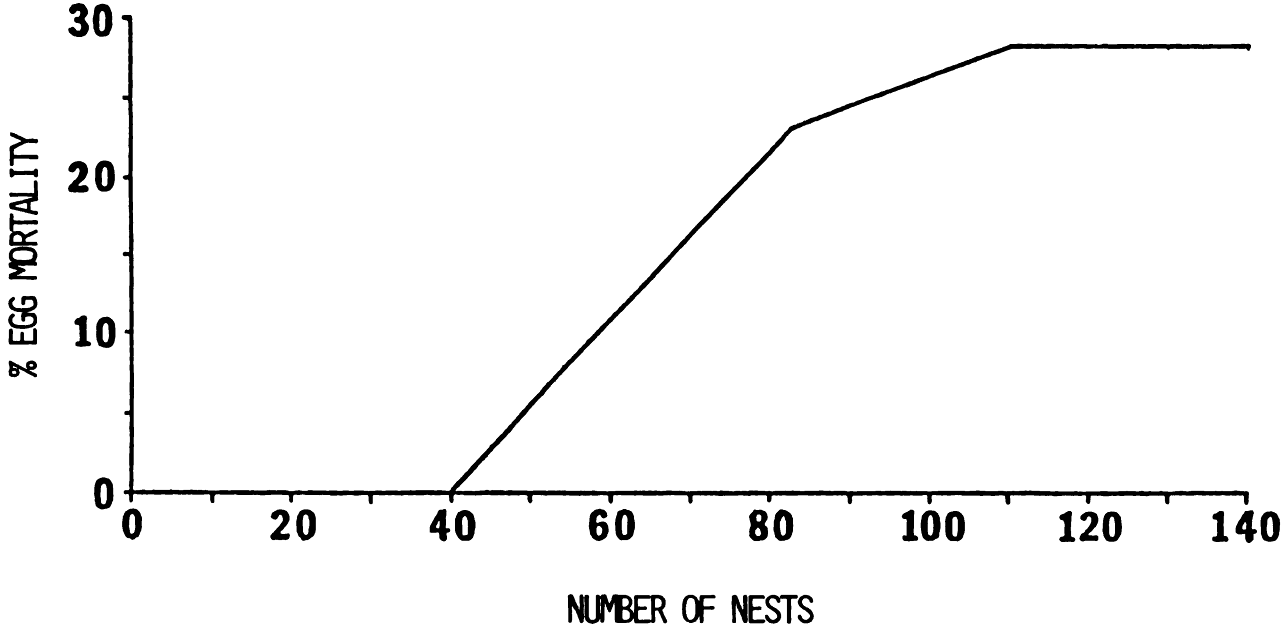


Figure 7. Relation of percent egg loss by monitor predation (F2) to number of nests available.

where density was low (Pooley 1969b), and 33.8% (Pooley 1969b) and 49.4% (Pooley 1973b) at Lake St. Lucia (Zululand) where nest density is high. Nest density was low along the Okavango River.

F2 was calculated by calling function subprogram TABEXE. Thus the program let premature flooding, if it occurred, take its toll prior to predation by monitor lizards. This seems realistic, as F1 is an independent variable inversely proportional to F2.

Next (under comment "TOTAL HATCH MINUS MORTALITY.") the number of hatching eggs, "HATCH," was obtained by subtracting from TEGGS the proportions due to F1 and F2. Also subtracted were proportions due to intrinsic mortality, due mostly to infertility, also to embryonic death ("IEM" = 0.236, Blomberg (1977)), and due to a minor extrinsic mortality factor which summed up effects of occasional heavy rain, abandonment of nest and death of the female ("MEEG" = 0.072, Blomberg (1977)). These were all observed in the field. The simulated hatch was divided by 2, to produce equal numbers of female and male hatchlings ("FHATCH" and "MHATCH", respectively). When hunting was simulated, MHATCH was used in calculating the size of the male cohort as age classes of hunted males differed somewhat from those of hunted females due to greater growth rates in males (Graham 1968, 1976, 1977).

After that (under comment "EACH AGE CLASS IS NOW ADVANCED ONE YEAR.") each age class, beginning with the previous year's hatchlings, was advanced 1 year, to add the present year's hatchlings into the population. This was done only with age classes of females (FPOP(K)) when hunting was not simulated. At this point, if hunting were opted for, the program added up and printed the number of 4- to 7-year old females, and the number of 3- to 5-year old males. The total hunted cohort was obtained by adding the huntable males and females. Hunting was simulated on males and females separately, after which the total hunt was figured and printed.

Cannibalism on the young crocodiles (Cott 1961, Pooley 1969b) was assumed significant in the first 3 years of life. Graham (1968) implied that nearly all young around North and Central Islands in Lake Turkana, Kenya, might be cannibalized, due to virtual lack of shelter. While field data on rates of cannibalism and knowledge of its impact on the crocodile population on the Okavango River were lacking, it was believed that at low water levels the young crocodiles would be forced into the main channels. There large numbers would fall prey to older individuals. During floods it was believed that the cannibalism rate will markedly decrease due to formation of extensive sheltered areas. An entirely hypothetical approach was used, namely "F3M1" (Figure 8). It was a simplified adaptation from Nichols, Viehman, Chabreck, and Fenderson (1976), which computed from a given water level a corresponding multiplier effect on the assumed normal cannibalism rate of 6%. These authors' value of 4.65 was used in severe drought, in diagramming F3M1, though for a water level of -1.3 m. Therefore the slope of F3M1 is only half that of their multiplier function. A multiplier function of some type seemed justified in view of the density-dependent nature of predation (Emmel 1973). If the water level index (FLAG) were not 0, i.e., drought or premature flood occurred, the value of the multiplier that affected cannibalism, F3M1, exceeded or fell below 1, respectively. The actual value of F3M1 was obtained by again calling function subprogram TABLIE.

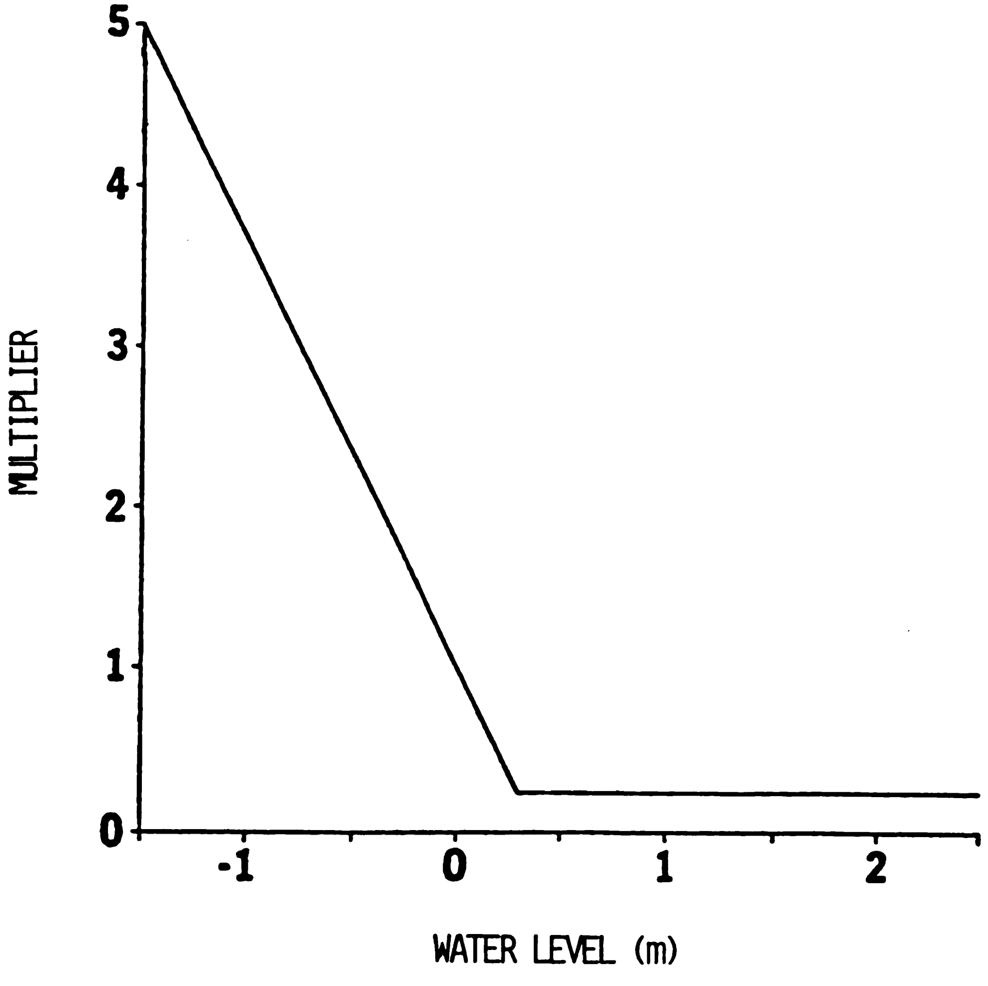


Figure 8. Multiplier function for the cannibalism rate on young crocodiles, in relation to water level (F3M1). The normal water level is designated by 0, where the multiplier equals 1.

If FLAG equalled 0, however, F3M1 equalled 1, and TABLIE was bypassed. The 0- to 2-year old crocodiles were subjected to cannibalism by 19- to 65-year old males and 37- to 65-year old females (under comment "CANNIBALISM FIGURED ON THE 0-2-YEAR OLD CROCODILES"). The age difference was due to the males' greater growth rate, yielding an average length of 1.12 times the length of the females in any given age class (see Graham (1968) for probable age classes). In this model, 19-year old males and 37-year old females had attained a length of 290 cm. This was chosen as a minimum length of cannibals, because Cott (1961) recorded only 2 of 17 cannibals as under 300 cm long.

The total kill of young crocodiles, "TOTKIL", was obtained by use of the size of the cannibalistic cohort ("PREDPOP"), F3M1, a variable "M2" equal to 0 (if the 0-2-year old crocodiles numbered under 500) or 1 (if they numbered at least 500) or 3 (if the number of nesting females reached 1,360, which was thought at first to saturate the nesting areas), and the assumed constant cannibalism rate ("NORPRED") of 0.06. The result was divided by 2, as the program was primarily tracking females. Sixty percent of the value of TOTKIL was assigned to the 0-year old females, 30% to the 1-year old females, and 10% to the 2-year old females in figuring the cannibalism on the 0-2-year old cohort. When hunting was simulated the number of cannibalized males were set equal to that of cannibalized females, and the same rates of TOTKIL were applied separately, to the respective age classes of males. Figuring the size of the cannibalized cohort involved multiplying the original size of each age class by its respective PSURV, subtracting the portion resulting from the appropriate value of TOTKIL, and subtracting the hunting kill (always 0 in cannibalized age classes). The cohort size of females not cannibalized was calculated in the same way, by age class, but without any percentage of TOTKIL. Next the population size for the year was figured by adding the female and male cohorts.

During simulated hunting (under comment "FIGURE TOTAL POPULATION FOR THE YEAR."), the size of the 0- to 2-year old male cohort, and of the non-cannibalized cohort, were figured in the same way as their respective female counterparts. Then the population size for the year was obtained by adding all the male and female age classes.

Toward the end of the main do loop (under comment "PRINT INFORMATION AND RESULTS FOR YEAR PROCESSED.") much of the information that was acquired for the year was printed. In case of simulated hunting, the annual harvest was printed. Then, the following information was printed if needed: number of females in each age class; number of nesting females; total number of crocodiles; values for KK, FLAG, F1, F2, F3M1, M2, and WLEV; and values for the total number of eggs, hatch of females, total number of 0- to 2-year old crocodiles, number of cannibalistic crocodiles, and the kill of 0- to 2-year old crocodiles. At this point 1 iteration of the main do loop was complete. When the 300 iterations were completed, the population size ("ATPOP") and the number of nesting females ("ANNFEM") were listed for each year. Then the program terminated.

TABLIE, the function subprogram sometimes called for determining the value for F1 (the percent egg mortality owing to premature flooding) and the value for F3M1 (the multiplier affecting cannibalism on 0- to 2-year old crocodiles) operated by interpolation from an array (dummy argument) of numerical values. Two such arrays were entered in the beginning of the main program as "VAL1" (used in obtaining F1) and "VAL3" (used in obtaining F3M1). Given a numerical value for "VAL", the dummy variable in TABLIE corresponding to VAL1 and VAL3 in program CROC, TABLIE interpolated to find a corresponding value for F1 and F3M1.

An essential feature of TABLIE was that it did not extrapolate beyond the range of the values given to VAL. The rationale was that there must be limits to VAL, as neither flooding of eggs nor cannibalism on 0- to 2-year old animals can exceed 100%. Furthermore, in the latter case, a fixed ratio of rate of cannibalism to rate of production of adults was assumed.

TABEXE, the function subprogram called in determining a value for F2 (percent egg mortality due to predation by monitors) also operated by interpolation from an array (dummy argument) of numerical values. This array was entered in the beginning of the main program as "VAL2." Given a numerical value for VAL, the dummy variable in TABEXE corresponding to VAL2 in program CROC, TABEXE interpolated to find a corresponding value for F2.

Unlike TABLIE, TABEXE extrapolated beyond the range of values given to VAL when necessary, before interpolating. The rationale was the assumption that the Nile monitor population can expand without bound relative to the number of crocodile nests or eggs. They must find other sustenance during the many months that few or no crocodiles nest.

A working model was produced, and the population size, resulting from no environmental disturbance, was graphed. Also, the effects of 2 sources of disturbance on the population were studied. The first was consecutive years of extreme water levels, and the second was different intensities of hunting.

To simulate consecutive years of extreme water levels, 4 consecutive years of droughts every 50 years were induced, for the duration of the program. Inter-drought intervals of 20 years were also simulated. Finally, the population was subjected to premature floods on the same schedules. Population sizes resulting from the latter 2 simulations were also graphed.

Several simulations, to test harvesting strategies consisting of minimum numbers of 300 and 500 at 3 different efficiencies, 0.3, 0.4, and 0.5 were made. Resultant population sizes were graphed with that resulting from no environmental disturbance. Simulated hunting took males and females according to their relative proportions in the 120-190 cm length range, as it is impossible to sex these animals without cloacal inspection (Graham 1976, 1977). The hunting kill was at this time additive to natural mortality.

ALTERATIONS

A number of alterations were made following the above simulations, but prior to testing of the simulation for sensitivity to altered data for specified parameters. It was felt that these alterations produced a more realistically operating model.

The statements effecting simulated hunting, originally on 7 sets of cards, inserted correctly in the deck, were consolidated into 3 subroutines, "HUNCR1", "HUNCR2", and "HUNCR3". The first printed out the year number and advanced each age class of males 1 year. The second printed the size of the huntable cohorts of both sexes, added these numbers, and multiplied the sum by EFFIC. The product was "HUNT", the actual numbers killed, which was also printed. HUNT was partitioned into numbers of each sex, and lastly numbers in each age class of males and females. This subroutine omitted hunting if the size of the huntable cohort did not exceed a specified minimum number (300), "NONHUNT" (which replaced MINHUNT, mentioned earlier, on the cards), and omitted hunting of either sex if its huntable cohort size did not exceed 0. The last subroutine, HUNCR3, set the number of cannibalized males equal to that of cannibalized females, by age class. Then it subtracted the number cannibalized and the number killed by hunting from respective age classes of the male cohort. The subroutines were accessed by the logical parameter "CRHUNT".

In the process above, 2 variables were eliminated from subroutine HUNCR2, i.e., "FFLAGG" (proved unnecessary), and THUNT (redundant of HUNT), printed at the end. The 2 remaining statements in this last set, "IF(M.LE.10) GO TO ..." and "IF (M/50*50.NE.M) GO TO ...", were incorporated in program CROC a few lines below comment "PRINT INFORMATION AND RESULTS FOR YEAR PROCESSED." to be accessed during simulated hunting (CRHUNT = .TRUE.). The model was run at this point with and without simulated hunting (CRHUNT = .FALSE.), and the resulting population sizes and numbers of nesting females were identical, respectively, to those of prior simulations.

Another logical parameter, "INPRINT", was inserted into the program, under comment "INITIALIZE PARAMETERS.". Its purpose was simply to include (set at "TRUE"), or exclude (set at "FALSE"), all statements beginning with 205, and ending with 305, which governed the printing of number of females in each age class, number of nesting females, etc., mentioned earlier, which often constituted a cumbersome amount of information. The population size remained identical in both test runs, and to population sizes in previous simulations without hunting.

Next, 3 statements making possible the postponement of hunting for 10 years (or any number of years desired) were added directly below the first statement in the main do loop. First "CRHUNT = .TRUE." was moved there followed by "IF(CRHUNT) 103,104" and "103 IF (M.LE.10) CRHUNT = .FALSE.". The reason was the 10-year ban on hunting crocodiles, proposed by BGI (P. Becker 1974, pers. comm.), which began in January 1975. Again test runs with and without simulated hunting were made, and the resultant population size and number of nesting females were identical to those from previous runs without hunting, and reasonable if different from those of previous runs with simulated hunting.

Next, hunting mortality was made to supersede natural mortality, up to a point. This alteration is based on Errington's (1945) threshold of security hypothesis, as elaborated upon by Romesburg (1981) and other authors. In case hunting mortality (FHKIL(K) in program CROC,"MHUNKL(K)" in subroutine HUNCR3) were less than natural mortality ("FPOP(K) * 'NATMORT(K)'" in program CROC, "'MCOHORT(K)' * 'NATUMOR(K)'" in subroutine HUNCR3), hunting mortality was made entirely supersessive of natural mortality. A simple, mathematically correct treatment would be to set FHKIL(K) and MHUNKL(K) equal to 0, as if no hunting had taken place. However, this would make the model logically self-contradictory at these points, so a set of 3 replacement statements were written, to more realistically model what happens. The first of these replacement statements calculated an increased value for PSURV(K) and its counterpart "CHANSRV(K)", in subroutine HUNCR3, as survivors of the hunting efforts, in each hunted age class, would have a higher probability of survival to the next age class if hunting mortality were supersessive. The second replacement statement used the resultant enhanced survival rates in calculating a higher value for the sizes of the hunted age classes, FPOP(K) and MCOHORT(K). From these the number cannibalized (if any), and the harvest, were subtracted. The last replacement statement used the new values for PSURV(K) and FPOP(K), and CHANSRV(K) and MCOHORT(K), to restore the original values of PSURV(K) and CHANSRV(K) respectively. This would prevent cumulative error in the values for these variables. The replacement statements were preceded by descriptive comments, placed below statement 112 in program CROC and below statement 123 in subroutine HUNCR3.

In case hunting mortality equaled or exceeded natural mortality, it was made to supersede 95% of the natural mortality. Beyond that, hunting mortality was additive. This was done by calculating enhanced values for PSURV(K) and CHANSRV(K), though in a different way from that above, in program CROC and subroutine HUNCR3, respectively. Next, values for FPOP(K) and MCOHORT(K) were calculated, based on enhanced values for PSURV(K) and CHANSRV(K), respectively, from which numbers cannibalized (if any), and numbers harvested, are subtracted. Thereafter the original values of PSURV(K) and CHANSRV(K) are reinstated. These replacement statements were preceded by descriptive comments, placed below the previously described sets of 3 replacement statements.

A short test run without hunting (CRHUNT = .FALSE.), with 50 iterations ("'IRNLGTH' = 50"), was then done, which gave values for population size and number of nesting females identical to those of any previous run with no hunting. Then CRHUNT was set at .TRUE., and IRNLGTH at 300, for a full test run. The population size and number of nesting females became greater with supersessive hunting mortality, in the long run.

The value of PERBRD for age class 17 (16-year old crocodiles) was originally and erroneously 1; it was changed to 9 in keeping with the trend of the data set. No change in the values for the population size and number of nesting females resulted.

Experimentally, the first numerical value of PSURV (i.e., "PSURV(1)") was raised from 42.3 to 100.0 in the beginning of the program. The resulting population curve was used to show the main method of presenting results, and to make comparison with a curve resulting from lowering survival rates of juveniles (Figures 12 and 18, respectively). The value of PSURV(1) is the probability of survival to the hatchling stage (0-year old crocodiles). Because all known mortality factors involved here were applied prior to the hatch, keeping a value of less than 100.0 for PSURV(1) is not realistic; it implies influence of mortality factors that do not exist. In other words, the hatch must equal the number of 0-year old crocodiles in the population. (It is the value for PSURV(2) that gives the probability of survival to age 1, and so forth.) Time did not permit experimentation with the value of 100.0 for any other simulations. When hunting was not simulated, the number of males in the population remained at initialized values. This error was corrected by inserting do loop 114, which set the number of males in each age class equal to their female counterparts, toward the end of each simulated year.

The entire program is presented in Appendix A. Lists of variables in program CROC, in function subprograms TABLIE and TABEXE, and in subroutines HUNCR1, HUNCR2, and HUNCR3 are in Appendix B (Tables 11-16).

SENSITIVITY TESTING

The present numerical values for some parameters in the program are general estimates, which should be replaced with data obtained in the field. The parameters are initial population size, initial age structure, age-specific percentages of females nesting in a given year (PERBRD), age-specific clutch sizes (CLUTCH), age-specific survival rates (PSURV) beyond age class 6, and growth rates of crocodiles, (which do not appear directly in the model, but are expressed in age spans cannibalized, initial ages of cannibalistic behavior, initial age of egg laying, and age spans hunted). Acquisition of field data requires that the model proves sensitive to altered hypothetical data, for each of the mentioned arrays. Time, money, and energy should not be allocated for obtaining field data to which the model is unresponsive. With demonstrated sensitivity, the entry of field data would make the model a more realistic, and a more reliable guide regarding management of the Okavango crocodile population.

The population size resulting from each sensitivity test was graphed against time in years. This was done via library program "EZGRAPH", at the Computer Center, Michigan State University.

Initial Population Size

The initial (1975) population size, entered as 9,730 in the model may well be an overestimate. Therefore it was felt necessary to use a lower estimate, of 7,858 and test for sensitivity of the model. This estimate was based on a somewhat larger estimate of the proportion of sexually mature females in the 1974-75 hunting kill (0.184), made in an attempt to lower the population size sufficiently to obtain a number of hatchlings closer to the estimate from the field, of 2,730 (Blomberg 1977). Also an estimate higher than 9,730 by the same percentage (19.2), i.e., 11,598, was used. These population estimates were halved to get 3,929 and 5,799, respectively, as totals for the numerical values of variable FPOP (the female portion of the population). The age structure of the population remained unchanged. In calculating and adding the number of individuals in each age class, the total for FPOP for the lower population estimate actually became 3,920, a deviation of -0.2% from 3,929. In the same way the total for FPOP for the higher population estimate actually became 5,807, a deviation of +0.1% from 5,799. The resultant output of population size was graphed with that resulting from the originally used FPOP, which totaled 4,865 (half of 9,730).

Initial Age Structure

Another parameter to which sensitivity to altered data was investigated was the initial population's age structure. During this testing the size of the initial population was held constant.

Alterations of the poulation's age structure were effected on the data for variable FPOP. Alterations were: (1) an age structure in which the number of individuals in different age classes was somewhat intermediate between the the original one and a perfectly even structure. In the original structure roughly 98% of all individuals were in the 14 youngest age classes (ages 0-13), while in the present one this percentage was spread out into the 28 youngest age classes (ages 0-27). The total number of individuals was 4,857, a deviation of -0.2% from the original 4,865 for FPOP. (2) An even structure; each age class contained virtually the same number of individuals (i.e., 47 of the age classes each contained 74 individuals, and were evenly interspersed among the remaining 19, each of which contained 73 individuals; the total number of individuals was, as originally, 4,865); and (3) an inverted structure in which the 28 youngest age classes contained either 0 or 5 individuals (in 15 of these age classes) and the remaining 38 age classes held individuals, amounting to 98.5% of the total, at progressively greater numbers with age (the total number was 4,868, a deviation of +0.06% from the original 4,865).

A number of inverted age structures had been tried prior to the one used. Some such stuctures resulted in seemingly negligible response in the curve for population size, and several (one being the exact reversal of the original structure) resulted in error messages ("indefinite operand") on the computer terminal, indicating that there were too few reproducing individuals to maintain the population. Another less radically top-heavy structure (the exact reverse of that having about 98% of individuals in the first 28 age classes) produced such a low population curve that the cursor failed to complete graphing on the terminal screen. All the input data for this sensitivity test are listed in Table 1.

Age-specific Percentages of Females Nesting in a Given Year

The percentage of females nesting in each age class (PERBRD) should, if the program is realistic, affect the simulated reproductive rate. It was believed that females begin laying eggs at age 10, on the Okavango River, and this was the initial age in the model.

Four sensitivity analyses of the model to changed values of PERBRD were tested for by entering (1) the original values in the program, but increasing from 66.8% to 80.0% beginning at age 37; (2) the original values, but with a decrease from 66.8% to 0.0%, beginning in age class 51 (as there may be a decrease of ovulation in the oldest females (Graham et al. 1976)); (3) values higher by 15% than the original ones; and values lower by 15% than the original ones.

Age-specific Clutch Sizes

The next procedure was to test the model's sensitivity to changes in age-specific clutch size. The data for variable CLUTCH is given in the program as the cube root of clutch size. The cubed numerical values were increased, and decreased by 15%, to form 2 new data sets. Thereafter the cube roots were obtained for the values of

Table 1. Various initial age structures entered into the model, with initial population size held constant. Numerical values are numbers of females, i.e., data for variable FPOP.

	FPOP			
Age class	Original structure	Other normal structure[a]	Even structure	Inverted structure
0	2,465	1,972	74	5
1	1,043	1,015	73	0
2	525	575	74	0
3	280	349	74	5
4	216	266	74	0
5	56	133	74	0
6	34	101	73	0
7	26	69	74	5
8	12	71	73	0
9	12	49	74	5
10	15	24	74	0
11	4	13	74	5
12	4	12	74	0
13	15	15	73	5
14	7	16	74	0
15	4	10	73	5
16	7	11	74	5
17	4	7	74	5
18	4	8	74	0
19	4	11	74	5
20	4	10	73	0

Table 1 (cont'd.).

	FPOP			
Age class	Original structure	Other normal structure [a]	Even structure	Inverted structure
21	4	4	74	5
22	4	4	73	0
23	4	4	74	5
24	4	4	74	0
25	4	4	74	5
26	4	4	74	5
27	4	4	73	5
28	4	4	74	6
29	4	4	73	7
30	4	4	74	6
31	4	4	74	6
32	4	4	74	7
33	4	4	74	6
34	0	0	73	6
35	4	4	74	7
36	4	4	73	6
37	4	4	74	12
38	4	4	74	17
39	4	4	74	36
40	4	4	74	41
41	0	0	73	45
42	4	4	74	37

Table 1 (cont'd.).

	FPOP			
Age class	Original structure	Other normal structure[a]	Even structure	Inverted structure
43	0	0	73	37
44	4	4	74	49
45	0	0	74	39
46	4	4	74	46
47	0	0	74	53
48	4	4	73	55
49	4	4	74	54
50	4	4	73	75
51	0	0	74	53
52	4	4	74	68
53	0	0	74	75
54	4	4	74	113
55	0	0	73	89
56	4	4	74	135
57	0	0	73	156
58	4	4	74	212
59	0	0	74	200
60	0	0	74	254
61	0	0	74	296
62	4	4	73	396
63	0	0	74	478
64	0	0	73	688

Table 1 (cont'd.).

	FPOP			
Age class	Original structure	Other normal structure [a]	Even structure	Inverted structure
65	4	4	74	927
Totals:	4,865	4,857	4,865	4,868

[a] In this structure approximately 98% of the individuals are stretched into the first 28 age classes (ages 0-27), in contrast to being only in the first 14 age classes (ages 0-13) in the original structure.

these data sets, and entered into the model. The population sizes for different clutch sizes were graphed with those resulting from the original clutch sizes.

Age-specific Survival Rates

Major Portions of Curve of Survival Rates.--Survival rates (PSURV) for the various age classes were calculated for several simulated years, from printout showing the population's age structure from the program. The percentages were plotted, and curves were fitted to the points. Percentages based on fewer than 30 individuals in an age class were discarded. Some value sets had enough age classes indicating a 0% chance of survival to make any reasonable curve unobtainable. For the first tests with altered data for PSURV, only the rates through age 20 were changed. Figure 9 shows the curves that were obtained and found workable, and Table 2 gives values from these curves and the individual's probability of survival to a given age.

The survival rates for simulated year 50, somewhat higher than those of the original PSURV (listed in program CROC), and with an individual probability of survival to age 20 of 4.5% (Table 2) were entered. Blake and Loveridge (1975) believed an individual's chance of survival to reproductive age to be from 1% to 5%. Values intermediate between those for simulated years 70 and 80 were calculated and graphed, and entered into the model. The probability of an individual's chance of survival to age 20 was 0.5%.

Later, asymptotic values for PSURV (age classes 21-50, see Figure 9) were changed from 99.0% to 95.0% and 90.0% and entered,

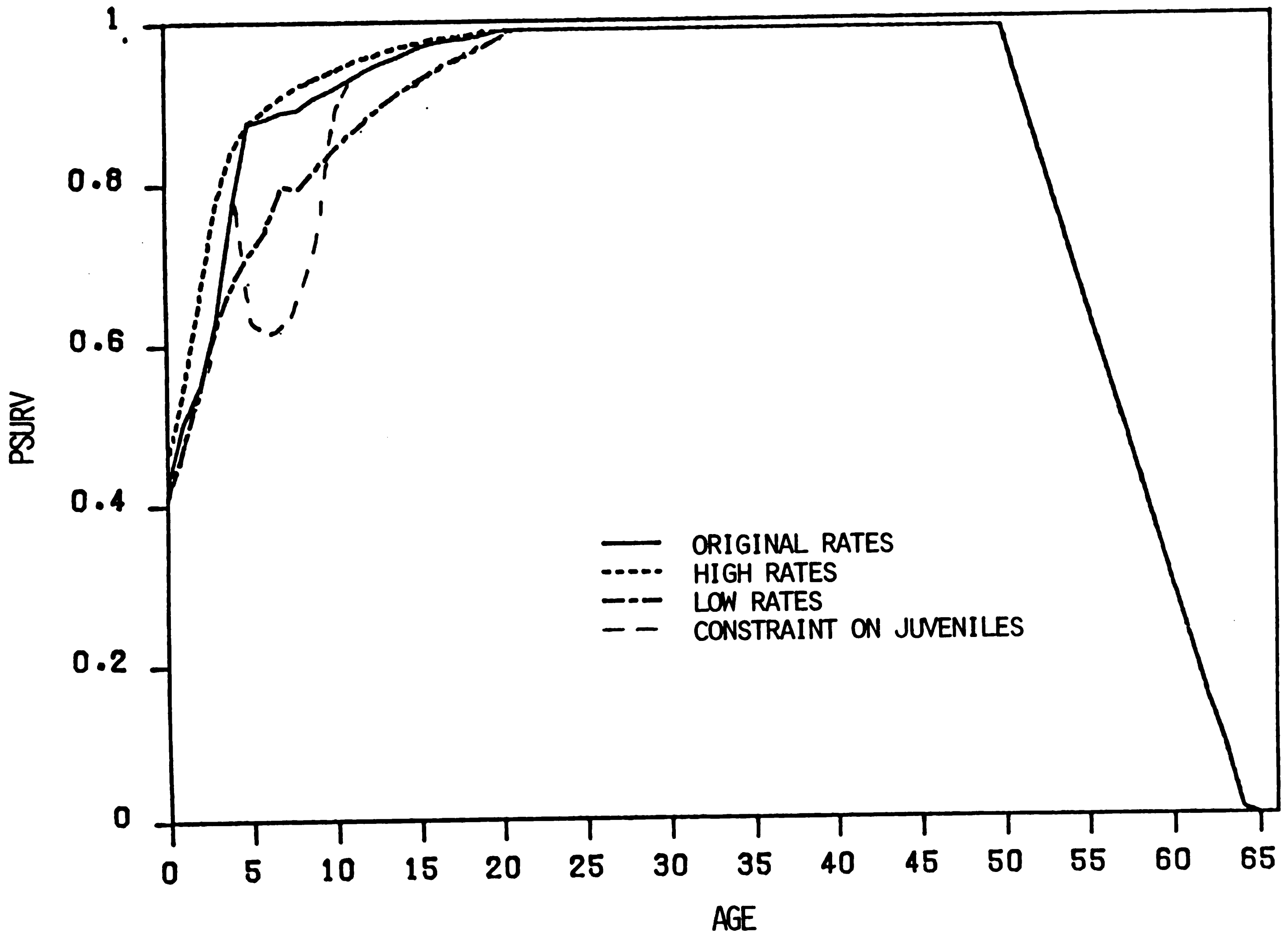


Figure 9. Curves representing various survival rates entered into the model.

Table 2. Smoothed values, original and from selected simulated years, for probability of survival to given age class (PSURV). Individuals' probabilities are given in parentheses.

Age class	Original [a]	Simulated year 50	Simulated year 70-80 [b]
0	0.423 (0.423)	0.450 (0.450)	0.405 (0.405)
1	0.504 (0.213)	0.546 (0.246)	0.476 (0.193)
2	0.550 (0.117)	0.655 (0.161)	0.548 (0.106)
3	0.631 (0.074)	0.771 (0.124)	0.621 (0.066)
4	0.773 (0.057)	0.841 (0.104)	0.676 (0.044)
5	0.876 (0.050)	0.875 (0.091)	0.712 (0.032)
6	0.880 (0.044)	0.892 (0.081)	0.743 (0.023)
7	0.888 (0.039)	0.908 (0.074)	0.769 (0.018)
8	0.892 (0.035)	0.920 (0.068)	0.794 (0.014)
9	0.907 (0.032)	0.931 (0.063)	0.818 (0.012)
10	0.916 (0.029)	0.940 (0.060)	0.840 (0.010)
11	0.928 (0.027)	0.949 (0.057)	0.860 (0.008)
12	0.941 (0.025)	0.956 (0.054)	0.878 (0.007)
13	0.950 (0.024)	0.962 (0.052)	0.896 (0.007)
14	0.957 (0.023)	0.969 (0.050)	0.911 (0.006)
15	0.967 (0.022)	0.973 (0.050)	0.926 (0.006)
16	0.973 (0.022)	0.978 (0.048)	0.939 (0.005)
17	0.976 (0.021)	0.981 (0.047)	0.950 (0.005)
18	0.978 (0.021)	0.983 (0.046)	0.959 (0.005)
19	0.983 (0.020)	0.987 (0.045)	0.970 (0.005)

Table 2 (cont'd.).

Age class	Original [a]	Simulated year 50	 70-80 [b]
20	0.987 (0.020)	0.989 (0.045)	0.978 (0.005)

[a] Based on hunting kill of 1974-75 and hypothetical data.

[b] Values fall midway between those for simulated years 70 and 80.

while insofar as possible the original values for age classes 0-20 were retained. Asymptotic values of 93.0% and 92.0% were also used, and curves for population size were graphed.

Constraint on Juvenile Survival.--It was felt that testing for sensitivity should include a survival bottleneck for juveniles. This constraint was hypothesized by W. E. Magnusson (1984, pers. comm.) and is based partly on his work with smooth-fronted caiman (*Paleosuchus trigonatus*) near Manaus, Brazil. Also, Messel et al. (1984), with whom Magnusson has worked, reported in detail on the disappearance of a major fraction of the subadult cohort of the estuarine crocodile population in northern Australia. The idea is that when young crocodilians reach "medium length" (normally about 1.5 m in *C. niloticus*) they visually resemble adults enough to pose a sexual threat, or a territorial threat, or both, to which the adults would respond by attempting to kill them, or at least drive them away from suitable habitat (Messel et al. 1982). Increased mortality could be expected even in the latter situation.

In this model crocodiles reached roughly 1.5 m by age 4, and so the probabilities of survival to ages 5 through 10 were set below the original values. Specifically, the values for PSURV(6) through PSURV(11) were lowered from 87.6, 88.0, 88.8, 89.2, 90.7, and 91.6 to 62.9, 60.3, 61.7, 66.9, 73.4, and 89.1 (Figure 9), respectively. (PSURV(1) was set at 100.0 in this test.) It was assumed that this mortality would taper off as the initial reproductive age was approached. It should be noted that an individual's probability of survival to age 21 was 1.4%, which seems within reason, in light of the percentages of Blake and Loveridge

(1975) regarding survival to reproductive age. Additional manipulation of PSURV values for younger age classes seemed pointless, as no field data exist.

Growth Rates of Crocodiles

Growth rates did not appear directly in the program. However, changed growth rates would affect the following parameters: (1) age spans at which young are cannibalized, (2) ages at which males and females become cannibalistic (assumed from Cott (1961) to begin at a length of 290 cm), (3) initial age of egg laying, and (4) age spans at which crocodiles are hunted. Growth rates appear to differ markedly among some populations. Graham (1968) found relatively low growth rates for crocodiles in Lake Turkana, Kenya.

Table 3 gives the ages as assumed in this study, ages as suggested by Graham (1976) for the Okavango crocodiles, and ages from growth curves for Lake Turkana crocodiles (Graham 1968), for the affected parameters. It was decided to vary data for each of the 4 parameters separately, to more exactly ascertain sensitivity, or lack thereof, in the model.

Age Spans Cannibalized.--The variable TOTKIL (number of cannibalized female crocodiles, under comment "CANNIBALISM FIGURED ON THE 0-2-YEAR OLD CROCODILES.") was kept constant, but partitioned differently among age classes, due to differing numbers of age classes, as listed in Table 3. To simulate cannibalism on young, in accord with Graham's (1976) suggested growth rates for the Okavango crocodiles, do loop 10 was changed to 4 iterations, and TOTKIL was partitioned for age classes 0-3 in the following respective

Table 3. Ages of crocodiles for parameters affected by different growth rates.

	Ages		
Parameter	Original	Graham's (1976) suggestion	Graham's (1968) growth curve
Subject to cannibalism (under 120 cm)	0-2	0-3	0-10
Onset of cannibalistic behavior (290 cm)			
Males	19	11	35
Females	37	18	46
Onset of egg laying	10 [a]	13 [b]	18 [c]
Subject to hunting (120-190 cm)			
Males	2-4	4-7	11-19
Females	3-6	5-9	11-20

[a] Total length = 223 cm.

[b] Assumed by Graham (1976).

[c] Total length = 180 cm in Lake Turkana, Kenya.

proportions: 0.6, 0.2, 0.1, and 0.1. The same procedure was followed to simulate cannibalism on young in accord with Graham's (1968) growth rates for Lake Turkana. This time, however, TOTKIL was partitioned for age classes 0-10 in the following respective proportions: 0.5, 0.15, 0.10, 0.075, 0.055, 0.040, 0.030, 0.020, 0.015, 0.010, 0.005.

Initial Ages of Cannibalistic Behavior.--Next the initial ages of cannibalistic behavior were varied in accord with the growth rates proposed by Graham (1976) for Okavango crocodiles and growth rates reported by Graham (1968) for crocodiles in Lake Turkana, Kenya (Table 3). The effect was earlier onset of cannibalism and therefore, a greater number of cannibals than with the original ages of onset. For the growth rates of Graham (1968), the effect was later initial ages of cannibalistic behavior, hence fewer cannibals, than with the original ages of onset.

Initial Age of Egg Laying.--To test for sensitivity to changes in age at which females begin to lay eggs, values for PERBRD, and for CLUTCH, were left unchanged. They were, however, set to begin always in synchrony, at age 10, age 13, and age 18, in accord with Table 3. For these situations, the number of iterations in do loop 5 (under comment "NUMBER OF EGGS FIGURED."), hence the number of egg laying age classes, remained the same, i.e., 48. The method is clarified by Table 4.

Age spans cannibalized, initial ages of cannibalistic behavior and initial age of egg laying were, in addition, changed simultaneously to further test the model's response. For this combination, the standard of comparison was population size resulting from the value sets for PERBRD and CLUTCH when initial age of egg laying was

Table 4. Values for PERBRD and CLUTCH in response to varied initial age of egg laying, due to differing growth rates.

	Initial age					
	10 [a]		13 [b]		18 [c]	
Age class	PERBRD	CLUTCH	PERBRD	CLUTCH	PERBRD	CLUTCH
0	0	0	0	0	0	0
.	.	.	.	.	.	.
.	.	.	.	.	.	.
.	.	.	.	.	.	.
9	0	0	0	0	0	0
10	0.42	2.993	0	0	0	0
11	0.98	3.0123	0	0	0	0
12	1.7	3.0216	0	0	0	0
13	3.4	3.0409	0.42	2.993	0	0
14	5.4	3.0602	0.98	3.0123	0	0
15	7	3.0795	1.7	3.0126	0	0
16	9	3.098	3.4	3.0409	0	0
17	10.2	3.1181	5.4	3.0602	0	0
18	13.2	3.1374	7	3.0795	0.42	2.993
19	16.3	3.1567	9	3.098	0.98	3.0123
20	21.1	3.1760	10.2	3.1181	1.7	3.0216
21	24.3	3.1953	13.2	3.1374	3.4	3.0409
22	28.7	3.2146	16.3	3.1567	5.4	3.0602
23	32.6	3.2339	21.1	3.1760	7	3.0795
24	40.6	3.2532	24.3	3.1953	9	3.098
25	44.4	3.2725	28.7	3.2146	10.2	3.1181
26	47.9	3.2918	32.6	3.2339	13.2	3.1374

Table 4 (cont'd.).

Age class	Initial age					
	10 [a]		13 [b]		18 [c]	
	PERBRD	CLUTCH	PERBRD	CLUTCH	PERBRD	CLUTCH
27	51.5	3.3111	40.6	3.2532	16.3	3.1567
28	54.4	3.3204	44.4	3.2725	21.1	3.1760
29	56.8	3.3397	47.9	3.2918	24.3	3.1953
30	58.5	3.3590	51.5	3.3111	28.7	3.2146
31	59.7	3.3783	54.4	3.3204	32.6	3.2339
32	60.9	3.3976	56.8	3.3397	40.6	3.2532
33	62.1	3.4169	58.5	3.3590	44.4	3.2725
34	63.3	3.4362	59.7	3.3783	47.9	3.2918
35	64.4	3.4555	60.9	3.3976	51.5	3.3111
36	65.6	3.4748	62.1	3.4169	54.4	3.3204
37	66.8	3.4941	63.3	3.4362	56.8	3.3397
38	66.8	3.5134	64.4	3.4555	58.5	3.3590
39	66.8	3.5327	65.6	3.4748	59.7	3.3783
40	66.8	3.5520	66.8	3.4941	60.9	3.3976
41	66.8	3.5713	66.8	3.5134	62.1	3.4169
42	66.8	3.5906	66.8	3.5327	63.3	3.4362
43	66.8	3.6099	66.8	3.5520	64.4	3.4555
44	66.8	3.6292	66.8	3.5713	65.6	3.4748
45	66.8	3.6485	66.8	3.5906	66.8	3.4941
46	66.8	3.6678	66.8	3.6099	66.8	3.5134
47	66.8	3.6771	66.8	3.6292	66.8	3.5327

Table 4 (cont'd.).

Age class	Initial age 10 [a] PERBRD	CLUTCH	13 [b] PERBRD	CLUTCH	18 [c] PERBRD	CLUTCH
48	66.8	3.6964	66.8	3.6485	66.8	3.5520
49	66.8	3.7157	66.8	3.6678	66.8	3.5713
50	66.8	3.7350	66.8	3.6771	66.8	3.5906
51	66.8	3.7543	66.8	3.6964	66.8	3.6099
52	66.8	3.7736	66.8	3.7157	66.8	3.6292
53	66.8	3.7929	66.8	3.7350	66.8	3.6485
54	66.8	3.8122	66.8	3.7543	66.8	3.6678
55	66.8	3.8315	66.8	3.7736	66.8	3.6771
56	66.8	3.8508	66.8	3.7929	66.8	3.6964
57	66.8	3.8701	66.8	3.8122	66.8	3.7157
58	0	0	66.8	3.8315	66.8	3.7350
59	0	0	66.8	3.8508	66.8	3.7543
60	0	0	66.8	3.8701	66.8	3.7736
61	0	0	0	0	66.8	3.7929
62	0	0	0	0	66.8	3.8122
63	0	0	0	0	66.8	3.8315
64	0	0	0	0	66.8	3.8508
65	0	0	0	0	66.8	3.8701

[a] Originally used age; total length = 223 cm.

[b] Assumed by Graham (1976).

[c] Total length = 180 cm in Lake Turkana, Kenya (Graham 1968).

10 (see Table 4). These value sets were exactly as the originally used ones, except that the last 8 values were 0. This population size was used to keep the number of egg laying age classes constant at 48, for valid comparison, as when initial age of egg laying alone was varied. Simultaneous changes in the program were identical to those that had previously been made separately, for age spans cannibalized, initial ages of cannibalistic behavior and initial age of egg laying. The changes were first made in accord with the growth rates of Graham (1976), and then in accord with those of Graham (1968). The population sizes for the 2 growth rates were graphed with that from the original growth rates with 48 egg laying age classes.

Age Spans Being Hunted.--The age spans based on growth rates suggested by Graham (1976) were incorporated into the model. These age spans were 4-7 (age classes 5-8) for males, and 5-9 (age classes 6-10) for females (see Table 3).

In subroutine HUNCR2 the number of hunted age classes of females ("FHUNKL"), contained in 2 identical statements, were increased from 4 to 5 (age spans being changed according to Table 3). The first of these statements sets all hunted female age classes at 0 if the size of the entire huntable cohort ("THPOP") did not exceed NONHUNT (set at 300). The second sets all age classes of females killed at 0 if the size if the huntable female cohort ("HFPOP") does not exceed 0. Similarly the 2 identical statements dealing with number of hunted age classes of males were increased from 3 to 4 (age spans being changed according to Table 3). The first of these statements set all hunted male age classes at 0 if the size of THPOP did not exceed NONHUNT (set at 300). The second set all age classes of males killed at 0 if the size of the huntable male cohort ("HMPOP") did not exceed 0. Lastly, it follows that the iterations in the do loop dealing with huntable male age classes, and huntable female age classes, were increased from 3 to 4, and from 4 to 5, respectively. The changes corresponding to those for females in program CROC were made for males in subroutine HUNCR3.

In the same way the age spans of vulnerability to hunting, based on growth rates in Lake Turkana, Kenya (Graham 1968), were incorporated in program CROC, and in subroutines HUNCR2 and HUNCR3. These age spans were 11-19 (age classes 12-20) for males and 11-20 (age classes 12-21) for females (see Table 3). The population size was graphed for age spans vulnerable to hunting in the original model, age spans based on Graham (1976), and age spans based on Graham (1968). Differences due to variation in age spans vulnerable to hunting were graphed for population size.

With simulated hunting it became necessary to make the number of age classes of males cannibalized ("MKANN") in subroutine HUNCR3 the same as the number of age classes of females cannibalized ("KIL") in program CROC. There were thus 4 age classes with the suggested growth rates of Graham (1976), and 11 with the growth rates of Graham (1968).

Additional parameters thought to be affected by postponing and lenghtening the age spans vulnerable to hunting were the number of huntable males, number of huntable females, and the harvest. Mean values for these parameters were tabulated according to the different age spans. The values were based on a sample of 59 years, the first being year 11, followed by year 15 and every 5th year thereafter. For each set of age spans the number of years during which no hunting took place was also listed from all 290 years of simulated hunting.

The last test of the model's sensitivity consisted of simultaneous changes in the program, identical to those earlier made separately for age spans cannibalized, initial ages of cannibalistic behavior, initial age of egg laying, and age spans being hunted. For this combination the standards of comparison were population size, mean huntable male cohort, mean huntable female cohort, and hunting kill, resulting again from the values for PERBRD and CLUTCH for initial age of laying being 10 (Table 4), and from inclusion of hunting. The population sizes for the 2 growth rates were graphed with those resulting from the original growth rates exactly as in the previous combination, but with the inclusion of the original age classes being hunted (i.e., males of ages 2-4, females of ages 3-6).

Again, mean values for the number of huntable males, number of huntable females, and the harvest, were tabulated according to growth rates. As before, these values were based on a sample of 59 years, the first being year 11, followed by year 15 and every 5th year thereafter. For each growth rate the number of years during which no hunting took place was listed, from all 290 years of simulated hunting.

CHAPTER 4

RESULTS

PRELIMINARY SIMULATIONS

Normal Conditions

The population grew from 9,730 to a consistent oscillation around roughly 21,000 individuals in 130-140 years, prior to alterations and sensitivity testing, under undisturbed (normal) conditions (upper curve, Figure 10). Yearly changes exceeding 4,000 crocodiles were not uncommon.

The upper curve in Figure 10 resulted after reduction of the maximum rate of predation on eggs to 28%. At first a rate of 56%, approximating that in Kabalega Falls National Park, Uganda (Cott 1968), was tested, which severely lowered the population. From this pattern it was concluded that mortality of young, which normally seems to exceed 80% in the first 3 years of life (Blake and Loveridge 1975), dictates that a hatching rate over 50% is necessary for perpetuation of the crocodile population. This conclusion agrees with the hatching rate of 54.6% on the Okavango River (Blomberg 1977).

Extreme Water Levels

No significant effects on the population size appeared from 4 consecutive years of droughts every 50 years, nor every 20 years, (Figure 11). The 4 years of consecutive floods every 20 years resulted in destruction of all eggs laid. The population size, with complete elimination of 4 consecutive year classes, often dropped noticeably every 20 years, but recovered quickly. The nesting female

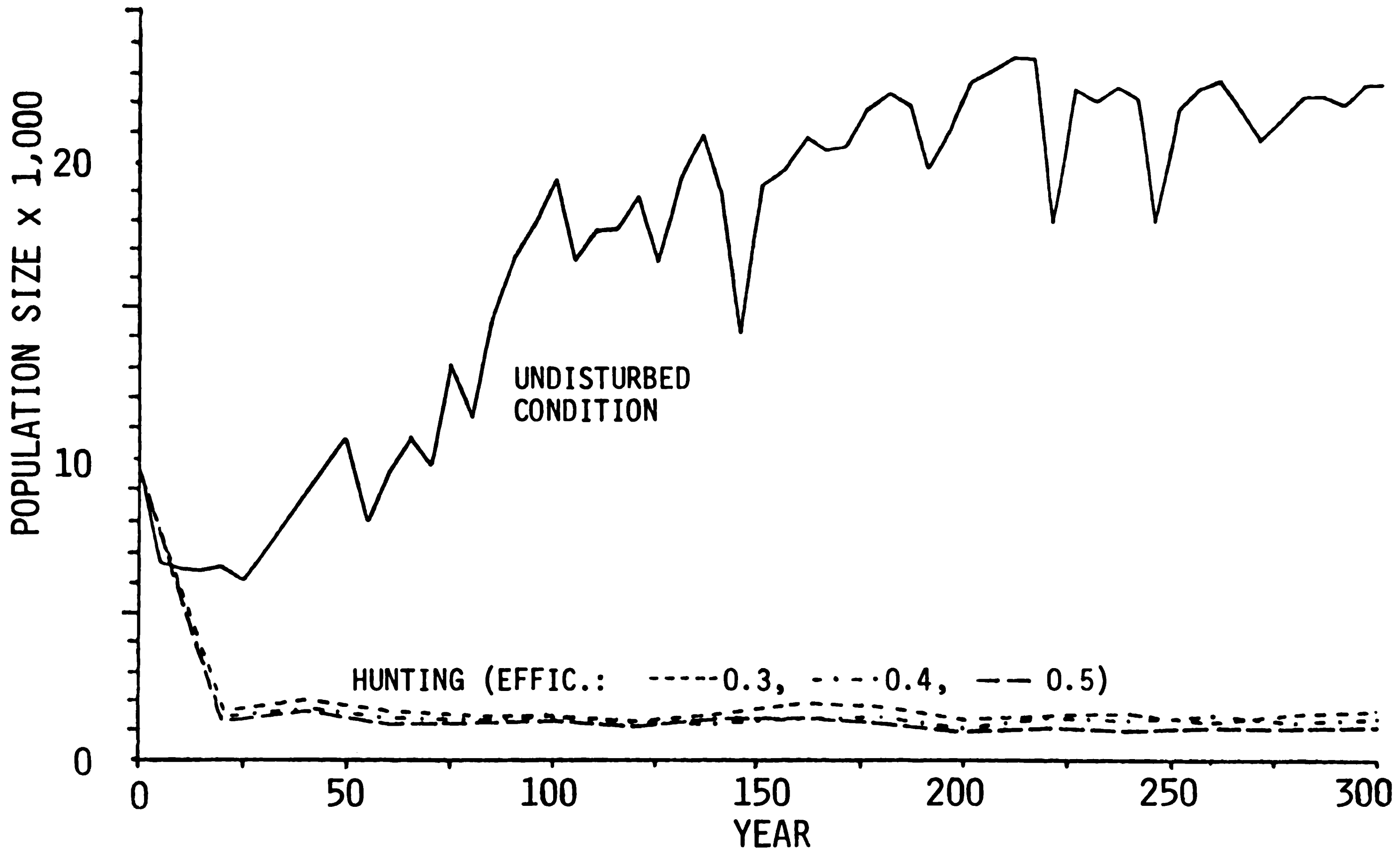


Figure 10. Trend of population size without unusual environmental disturbance, and response to various levels of hunting efficiency at a minimum of 300 harvestable crocodiles.

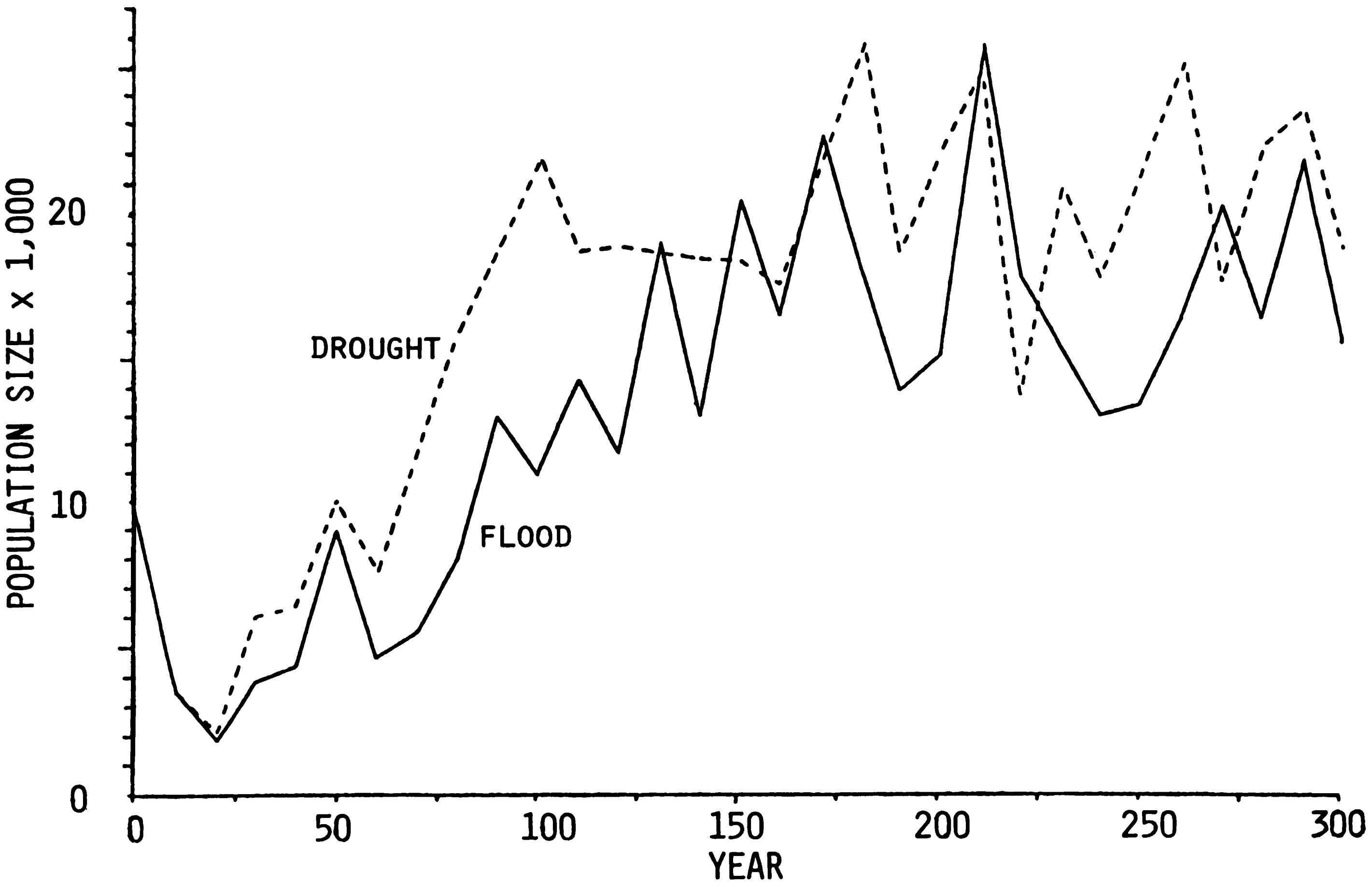


Figure 11. Response of population size to 4 consecutive years of droughts and floods every 20 years.

cohort appeared unaffected by the drought and flood conditions.

The water level simulations showed that the population size was more responsive to floods than to droughts. Premature floods caused extensive destruction of the eggs, but had little other effect. Droughts, however, should mainly affect juveniles by inducing intensified cannibalism and other predation. Although predation may be significant, the number of juvenile crocodiles lost during drought was small compared to the number of eggs lost during severe floods. Thus, the model indicates that factors affecting eggs effect greater changes in the population.

Hunting

At a minimum of 300 harvestable crocodiles (120-190 cm long), the population size reacted similarly at all 3 hunting efficiencies (Figure 10). Smaller oscillations occurred with increasing efficiency, but all 3 tended toward a level of 1,400 animals. At a minimum of 500 harvestable crocodiles the population fluctuated around 2,000. The best yearly hunt was realized at an efficiency of 0.3, at the 300 minimum, which also gave the fewest years without hunting (Table 5).

SENSITIVITY TESTING

The model's reliability and accuracy as a management guide should increase with entry of field data for a number of parameters. Prerequisite to the entry of field data, however, is to ascertain that the model is sufficiently responsive to altered hypothetical data, for the parameters, to justify the time and expense of the field work.

The response of the model to changed hypothetical data was tested

Table 5. Harvests of crocodiles under tested hunting schemes.

Minimum number of huntable crocodiles [a]	Efficiency	Total harvest (300 yr.)	Mean annual harvest	Number of years of no hunting
500	0.30	24,700	82	164
500	0.40	23,700	79	192
500	0.50	23,200	77	223
300	0.30	26,000	87	85
300	0.40	24,500	82	137
300	0.50	23,800	79	180

[a] Total length = 120-190 cm.

following the alterations described in the previous chapter. The results of the testing follow.

Two groups of parameters can be recognized, according to whether they indirectly or directly affect the number of young produced, and the number surviving to the first reproductive age and beyond. The first group changed the time of attainment of equilibrium phase, but had negligible effect on the mean value of that phase, of the population curve. Parameters in this group were initial population size, initial age structure, age-specific percentages of females nesting in a given year (PERBRD), and initial age of egg laying (an expression of individual crocodiles' growth rates). The second group noticeably changed the time of attainment of equilibrium phase (1 exception) and the mean value of the equilibrium phase. In some cases, however, the survival rates were so low that the population curve dropped and remained below initial population size. This group included age-specific clutch sizes (CLUTCH, which in effect mimics survival rates), age-specific survival rates (PSURV), initial ages of cannibalistic behavior (time of attainment virtually unaffected) and age spans hunted (the last 2 being expressions of individual crocodiles' growth rates).

Figure 12 exemplifies the primary way of analyzing the model's output. This curve results from no changes in the data (other than the alterations described in the preceding chapter, including PSURV(1) set at 100.0), and no simulated hunting. The mean height of the equilibrium phase (65,900) and the year of attainment (78) are indicated on the axes. With PSURV(1) set at 42.3, as in most simulations, the equilibrium values averaged 26,500, and the year of attainment was 96.

Table 6 summarizes effects of varied data for the mentioned

Figure 12. Main method of presentation of output from the model. With unchanged data for all parameters (except that PSURV(1) = 100.0) and no simulation of hunting, the equilibrium phase averages 66,000 individuals; it is reached in 78 years.

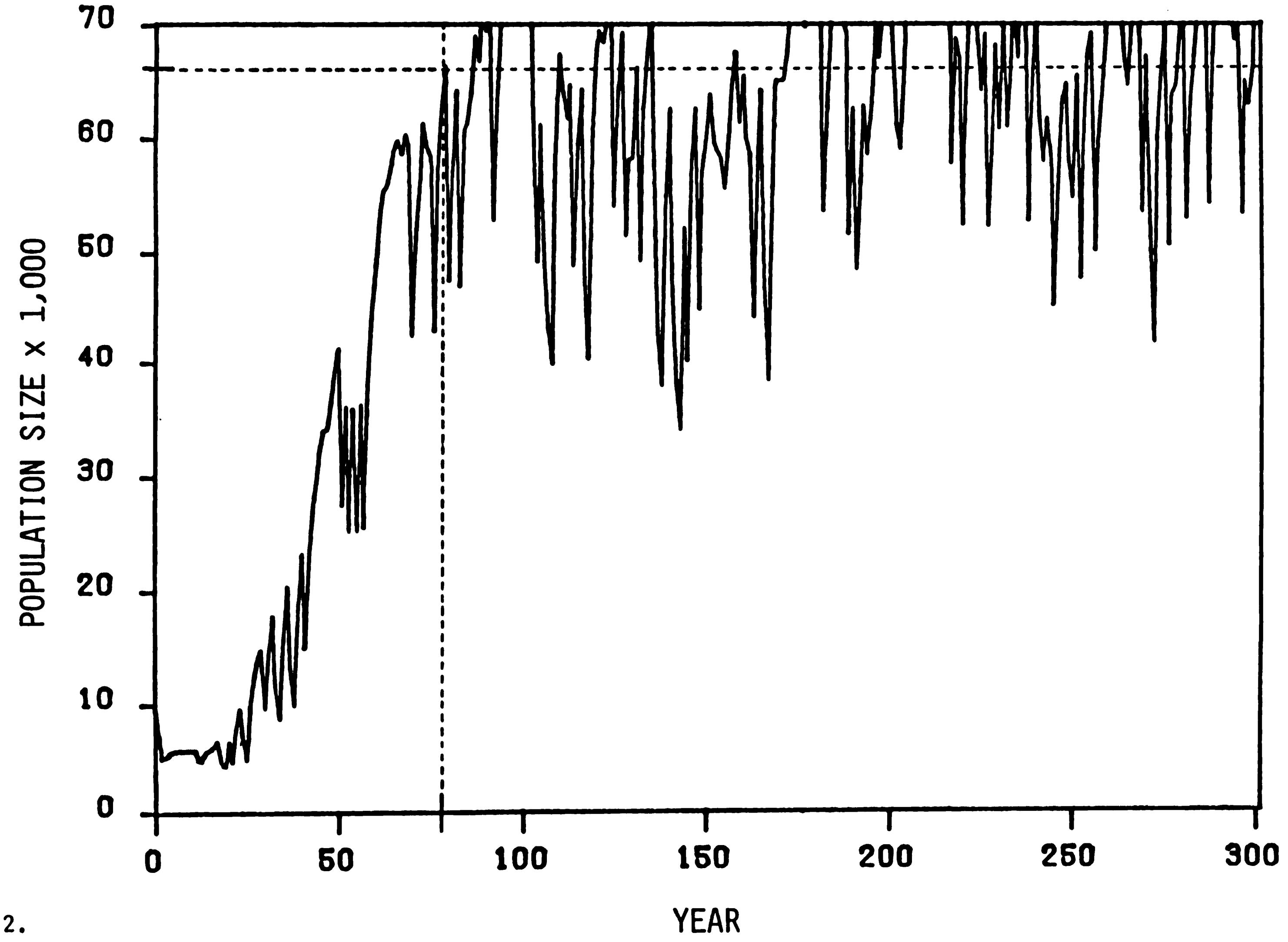

70
60
50
40
30
20
10
0
POPULATION SIZE x 1,000
0
50
100
150
200
250
300
YEAR

Figure 12.

Table 6. Summary of response of population curve to changed data in selected parameters.

		Timing of equilibrium		Level of equilibrium	
Parameter	Treatment	Year	Measure of sensitivity	Population size	Measure of sensitivity
Initial population size	7,858	110	0.76	26,400	0.02
	9,730 [a]	96	--	26,500	--
	11,598	90	0.33	26,600	0.02
Initial age structure	Wide pyramid [a]	96	--	26,500	--
	Narrow pyramid	87	--	26,700	--
	Even	9	--	26,000	--
	Inverted pyramid	88	--	26,700	--
Age-specific percentages of nesting females (PERBRD)	Maximum: 56.8	122	1.81	26,200	0.08
	Maximum: 66.8 [a]	96	--	26,500	--
	Maximum: 76.8	85	0.76	27,000	0.13
Age-specific clutch size (CLUTCH)	Range: 23-55 [b]	120	1.67	22,100	1.11
	Range: 27-65 [a]	96	--	26,500	--
	Range: 31-75 [b]	89	0.49	31,100	1.16
Age-specific survival rates (PSURV)					
- First 21 age classes	Lower [c]	--	--	1,000	14.4
	Unchanged [a]	96	--	26,500	--
	Higher [c]	64	8.15	36,600	9.32
- Asymptotic [d] (age classes 22-51)	95%	--	--	2,600	22.3
	93%	--	--	1,800	15.4

Table 6 (cont'd.).

		Timing of equilibrium		Level of equilibrium	
Parameter	Treatment	Year	Measure of sensitivity	Population size	Measure of sensitivity
- Age classes 5-10	Unchanged [a] [e] mean: 89.3	78	--	65,900	--
	Lowered [e] mean: 69.1	--	--	6,600	3.97
Growth rates of crocodiles					
- Initial ages of cannibalistic behavior	M 11, F 18 [f]	100	0.09	22,500	0.32
	M 19, F 37 [a]	96	--	26,500	--
	M 35, F 46 [f]	96	0.00	30,800	0.30
- Initial age of egg laying	18	236	1.82	25,600	0.04
	13	123	0.94	25,500	0.13
	10 [a]	96	--	26,500	--
- Combined cannibalism and initial age of egg laying	0-10; M 35, F 46; 18	237	--	27,300	--
	0-3; M 11, F 18; 13	158	--	23,400	--
	0-2; M 19, F 37; 10 [a]	96	--	26,500	--
- Age spans hunted	M 2-4, F 3-6 [a]	--	--	1,800	--
	M 4-7, F 5-9	--	--	2,700	--
	M 11-19, F 11-20	--	--	2,700	--
- Combined cannibalism, initial age of egg laying, and age spans hunted	0-2; M 19, F 37; 10; M 2-4, F 3-6 [a]	--	--	1,800	--
	0-3; M 11, F 18; 13; M 4-7, F 5-9	--	--	2,600	--

Table 6 (cont'd.).

		Timing of equilibrium		Level of equilibrium	
Parameter	Treatment	Year	Measure of sensitivity	Population size	Measure of sensitivity
	0-10; M 35, F 46; 18; M 11-19, F 11-20	--	--	2,400	--

[a] Values in original simulation.

[b] Values changed by 15% from the original ones.

[c] Means of deviations, from original values, for lower and higher rates, were 6.7% and 4.1%, respectively.

[d] The original value was 99%.

[e] PSURV(1) was raised from 42.3 to 100.0.

[f] Unweighted means of males' and females' deviations, from original values, for higher (Graham 1976) and lower growth rates (Graham 1968), were 46.8% and 54.2%, respectively.

parameters. The decimal fractions by which year of attainment of equilibrium phase, and the mean value of the equilibrium phase, differ due to altered data, from their counterparts resulting from original data, were calculated whenever feasible. Likewise, the decimal fractions by which altered input data for each parameter differ from the original data were calculated, whenever quantification was possible. For all sensitivity tests in which both fractions were obtainable, the former fraction was divided by the latter to obtain a measure of sensitivity (Johnson and Sargeant 1977).

A feature common to all population curves, except that resulting from an even age structure (i.e., 73 or 74 individuals in each age class, Figure 14), is a dip that begins immediately and lasts 24-123 years. Its depth, 1,800-3,800, is well below initial population size. Its main cause may be the low number of sexually mature individuals in the population's age structure for year 0. Fourteen (25%) of the 56 age classes of sexually mature females contained no individuals, and only 2 of the 42 remaining age classes held more than 9 individuals. Also relevant to the initial dips may be that in most simulations only 7% of the females survive to age 10, and only a fraction of these lay eggs. This percentage of survival is close to the hypothesized span of 1-5% (Blake and Loveridge 1975). When the largest (reproductive) animals are harvested first, followed by progressively smaller individuals, as has happened on the Okavango River and in other areas of Africa (Cott 1961, Graham 1976, Loveridge 1980), an initial dip might well occur before reproduction can begin to surpass natural mortality. Possibly such a dip occurred in the Okavango crocodile population shortly before or after 1969, when the late B. Wilmot abandoned his destructive 12-year hunting concession (Taylor 1973, Graham 1976, Loveridge 1980). Graham (1976) stated that the cohort of breeding females has steadily increased during 1974-76. Therefore any such dip admittedly coincides poorly with those in the diagrams that follow.

The initially low number of reproductive individuals also appears to be a factor in the very delayed equilibrium phase; at 78-237 years it exceeds the turnover time of roughly 60 years. (Within a given species, the percentage by which attainment of equilibrium exceeds, or falls short of, the turnover time might be a useful indicator of the relative size of the breeding cohort.) Exceptions are in Figures 14 and 17a, and they seem to rule out any unexplained artefact of the computer program. The rather gradual increase relative to age, in percentage of nesting females, is another factor delaying attainment of equilibrium phase. This can be inferred from Figure 2, and the factor is well established in Cott (1961:255), where percentage of nesting females increases directly with size, and therefore, presumably with age.

In every diagram that follows, the solid curve results from unchanged data for each parameter. The solid curve is in any case the standard of comparison for each test of the model's sensitivity. Numerical data for all curves are in Appendix C (Tables 17-46). Values for consecutive years are found by reading down a column.

Initial Population Size

A population estimate of 7,858 for year 0 in the model, which is possibly more accurate than the originally used value (9,730), was used to ascertain response of the simulation. Likewise an estimate higher by the same percentage (19.2), 11,598, was used. Age structure of the population remained the same with each estimate of size. The higher estimate of population size resulted in earlier attainment of equilibrium phase, by 6% (from year 96 to year 90), and the measure of sensitivity is 0.33. The lower estimate of population size delayed this attainment by 15% (year 110), effecting a measure of sensitivity of 0.76. Regardless of estimate, the equilibrium phases of the curves appear virtually identical (Figure 13). Numerical values for population size at the original, the lower, and higher estimates of initial size, are in Tables 17, 18, and 19, respectively.

Initial Age Structure

Equilibrium phases of resultant population curves seem virtually identical, but noticeable differences in initial growth resulted from change in the population's age structure at year 0, with size held constant (Figure 14). In the unchanged age structure, which forms a wide pyramid, roughly 98% of all crocodiles were in the 14 youngest age classes (ages 0-13). A narrower pyramid, resulting from redistribution of this percentage into the 28 youngest age classes (ages 0-27) resulted in an earlier attainment by 9% (year 87) of equilibrium. The curve resulting from the even age structure resulted in earlier attainment of the equilibrium phase by 91% (year 9), attributable to a larger proportion of females of reproductive age. The inverted age structure (97% of crocodiles concentrated in the 28 oldest age classes) caused the population curve to reach equilibrium phase earlier by 8% (year 88). It is believed that the model would respond markedly to increased concentration of individuals in the very oldest

Figure 13. Response of population size to varied estimates of its initial size. The age structure at year 0 is held constant.

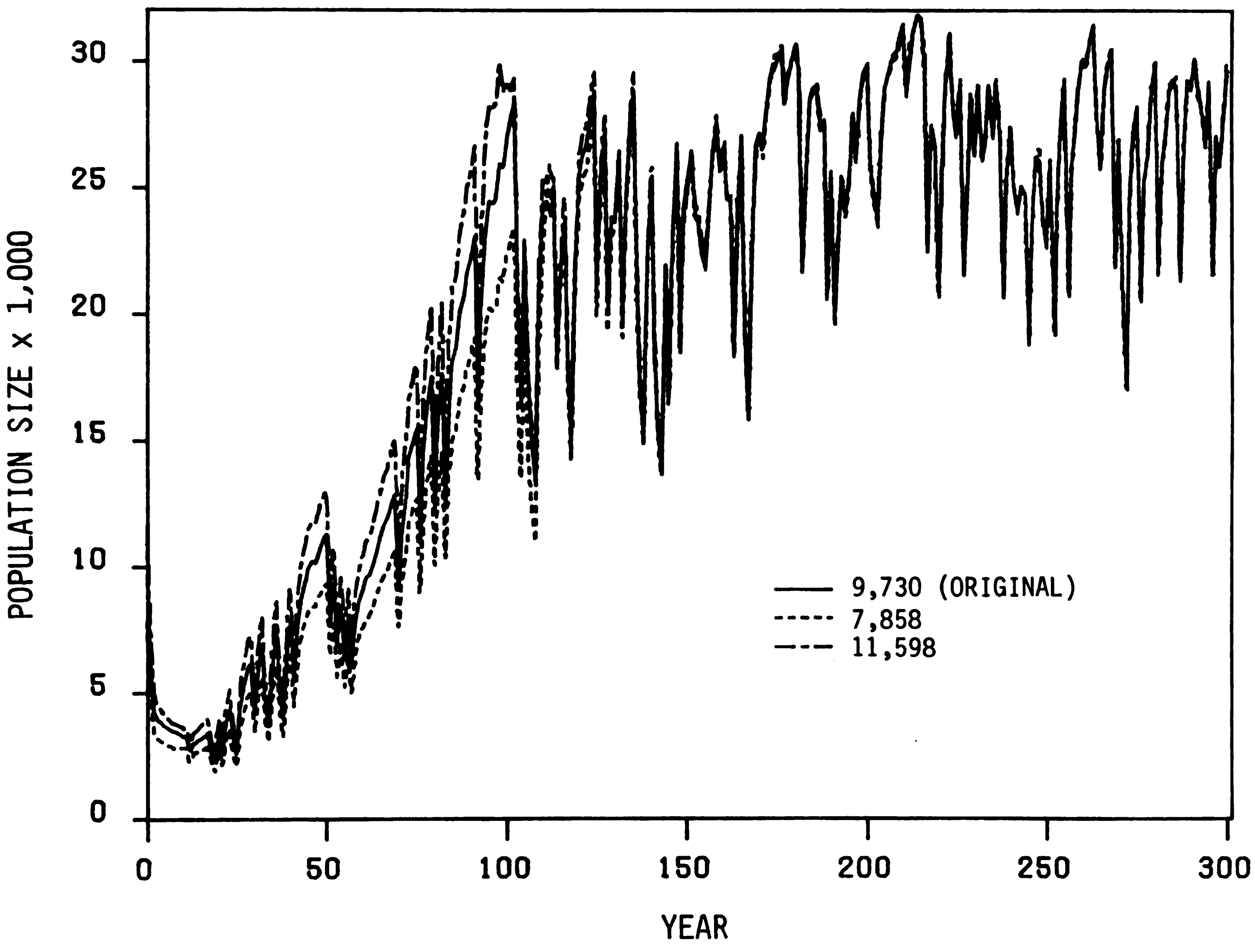

POPULATION SIZE x 1,000
0
5
10
15
20
25
30
YEAR
0
50
100
150
200
250
300
9,730 (ORIGINAL)
7,858
11,598

Figure 13.

Figure 14. Response of population size to varied initial age structure. The size at year 0 is held constant.

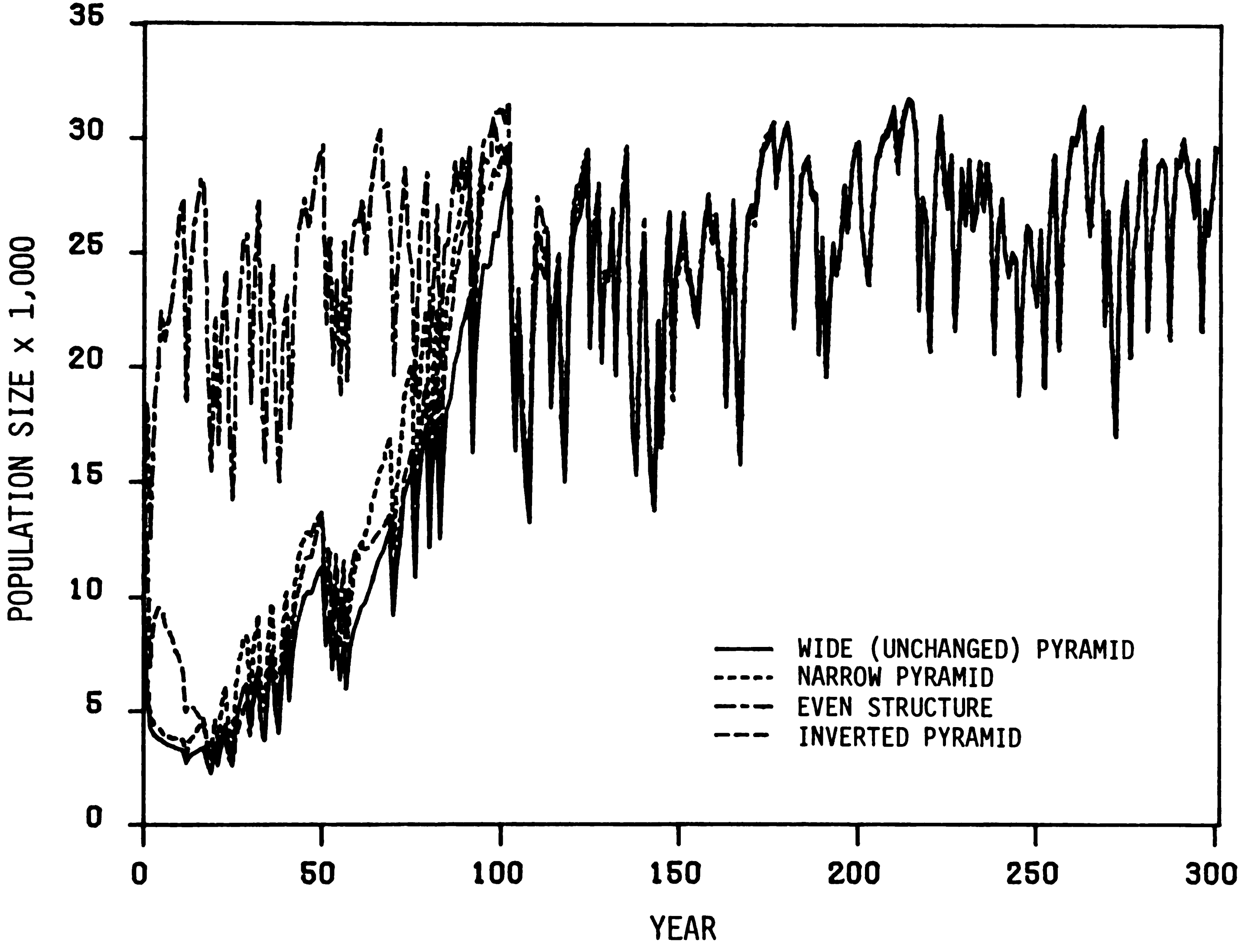

35
30
25
20
15
10
5
0
POPULATION SIZE x 1,000
0
50
100
150
200
250
300
YEAR
WIDE (UNCHANGED) PYRAMID
NARROW PYRAMID
EVEN STRUCTURE
INVERTED PYRAMID

Figure 14.

age classes, as the computer prematurely terminated several runs, due to prompt depletion of most reproductive females. It is believed, however, that a more intermediate inverted structure would instead simply delay, markedly, attainment of equilibrium. Numerical data on population size, resulting from age structures describable as a narrow pyramid, an even structure, and an inverted pyramid, are in Tables 20, 21, and 22, respectively.

Age-specific Percentages of Females Nesting in a Given Year

Because possibly only 2/3 of the sexually mature females appear to nest in any given year on the Okavango River, percentages of females in the model that did nest were assigned to each age class, beginning with 0.42 for those 10 years old, and gradually increasing to a maximum of 66.8 for those at least 37 years old, in construction of the model. These figures are adapted from the S-curve in Cott (1961:255), which relates percent nesting to length. For testing the model's sensitivity, the original set of data (PERBRD) was treated as follows: (1) an increase from 66.8% to 80% beginning at age 37, (2) a decrease from 66.8% to 0.0%, beginning in age class 51, (3) an increase of, and (4) a decrease of, 15%. The last 2 data sets thus had maxima of 76.8 and 56.8, respectively.

The first 2 data sets resulted in little change in the population curve. The last 2 data sets effected population curves with very similar values in the equilibrium phase, but with exponential phases markedly separated in time (Figure 15). Earlier attainments of equilibrium phase, by 11% (year 85), with the maximal percentages being 76.8, and delayed attainment, by 27% (year 122), with the maximal

Figure 15. Response of population size to different sets of age-specific percentages of females nesting in a given year.

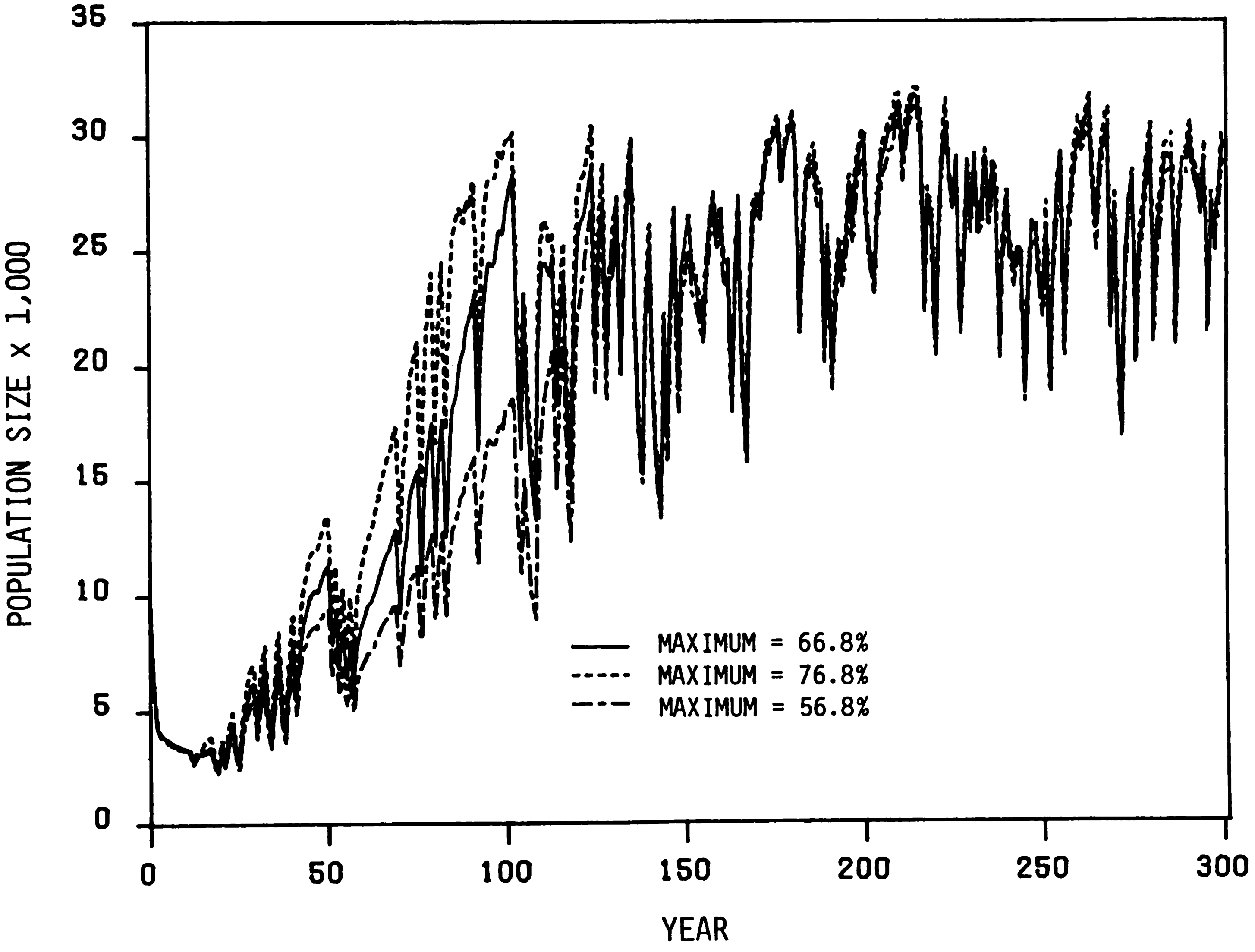

POPULATION SIZE x 1,000
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
YEAR
MAXIMUM = 66.8%
MAXIMUM = 76.8%
MAXIMUM = 56.8%

Figure 15.

percentages being 56.8 resulted. Respective measures of sensitivity of 0.76 and 1.81 were obtained. The numerical values for population size resulting from the maximal percentages of nesting females being 76.8 and 56.8 are in Tables 23 and 24, respectively.

Age-specific Clutch Sizes

Responsiveness to altered data on age-specific clutch sizes (CLUTCH) was gauged. Data for this parameter are derived from the cube root of clutch size, being linearly related to age of the crocodile. This is an adaptation from Cott (1961) and Graham (1968). Comparison was made of the population curve resulting from unchanged data with those resulting from increasing, and decreasing, these values by 15%. The 2 data sets so derived, ranging from 30.8 (10-year old females) to 75.0 (65-year old females), and from 22.8 (10-year old females) to 55.4 (65-year old females) markedly raised and lowered, respectively, both exponential and equilibrium phases of the population curves (Figure 16). As indicated, this is the result of a parameter that directly affects the number of young that in time reach maturity. The curve resulting from greater clutch sizes reached equilibrium phase earlier by a possibly negligible 7% (year 89), resulting in a measure of sensitivity of 0.49, while the curve resulting from the smaller clutch sizes delayed equilibrium by 25% (year 120), resulting in a measure of sensitivity of 1.67. The curve resulting from greater clutch sizes averaged 31,100 at equilibrium. This is an increase of 17% resulting in a measure of sensitivity of 1.16. The mean for the curve resulting from smaller clutch sizes is 22,100, a decrease of 17% resulting in a measure of sensitivity of

Figure 16. Response of population size to different sets of age-specific clutch sizes.

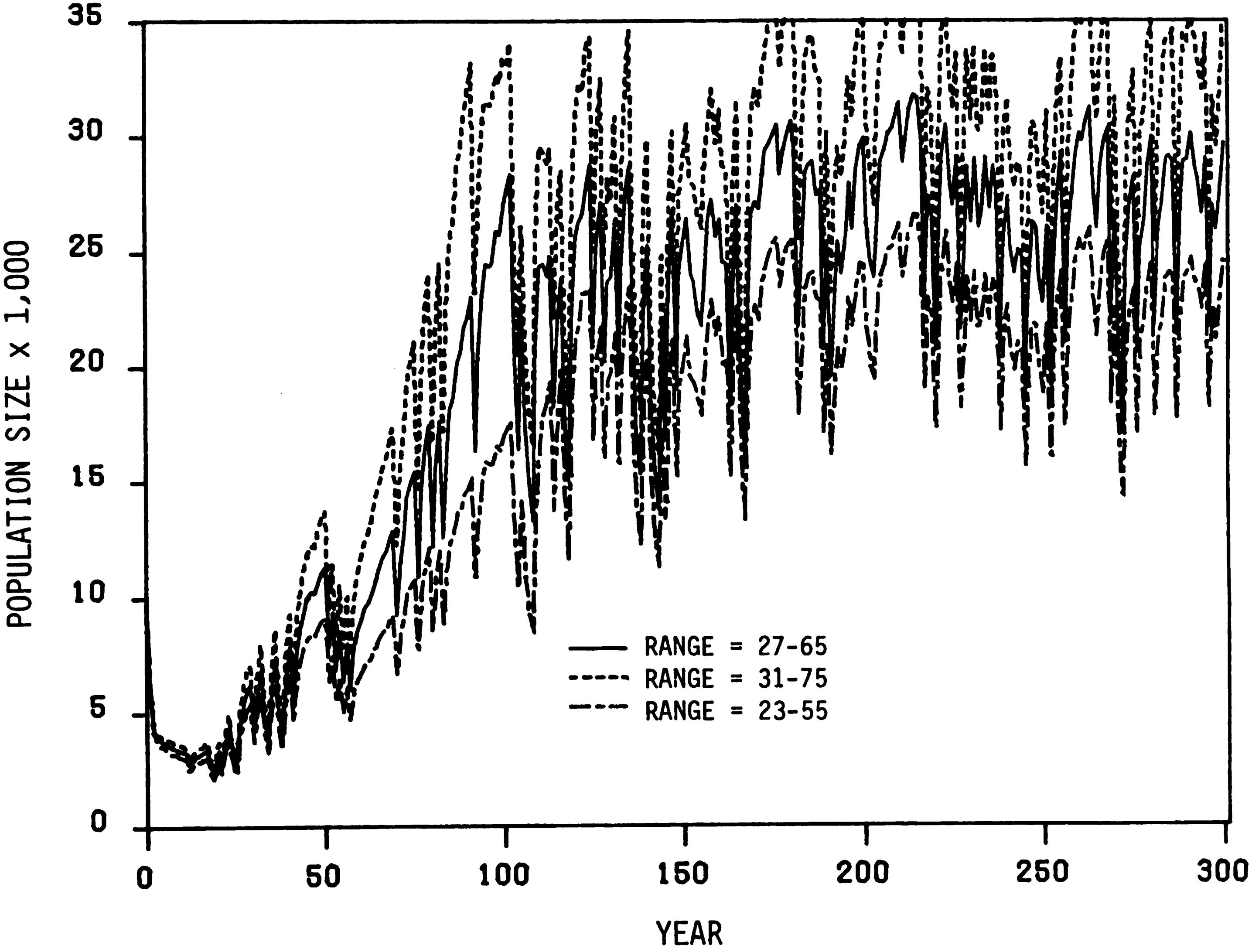

35
30
25
20
15
10
5
0
POPULATION SIZE x 1,000
0
50
100
150
200
250
300
YEAR
RANGE = 27-65
RANGE = 31-75
RANGE = 23-55

Figure 16.

1.11, respectively. Numerical values for population size, resulting from increasing and decreasing the original values for clutch size by 15%, are in Tables 25 and 26, respectively.

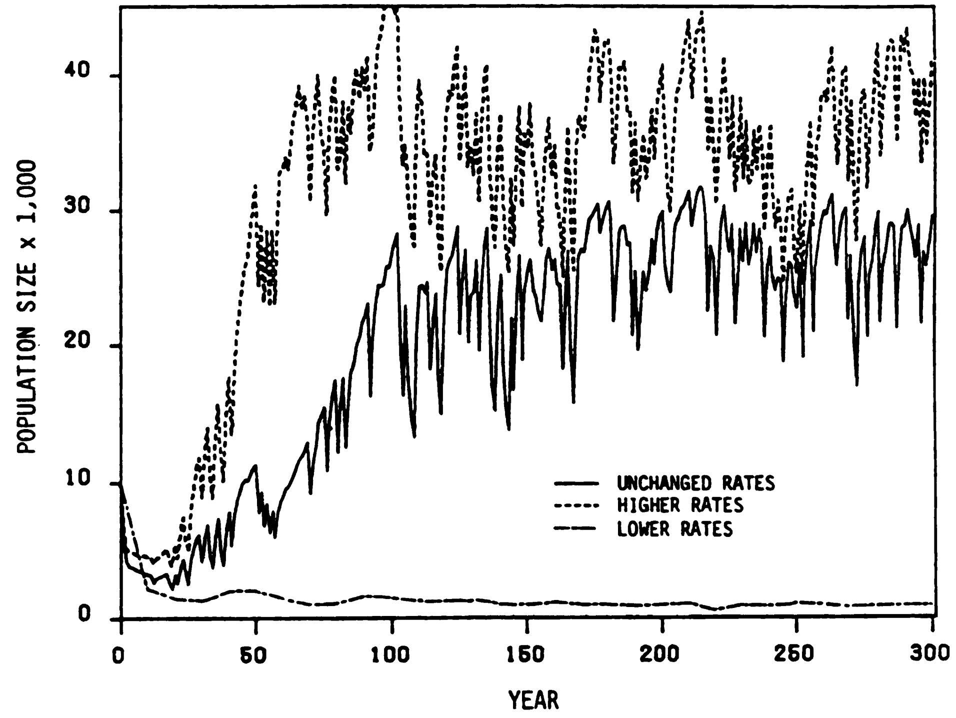
Age-specific Survival Rates

<u>Major Portions of Curve of Survival Rates</u>.--The model's response to varied age-specific survival rates (PSURV) for the first 20 years of life was tested. A set of high survival rates was obtained from the age structure in the 50th simulated year; a set of low survival rates consisted of values intermediate between those of the age structures in the 70th and 80th years.

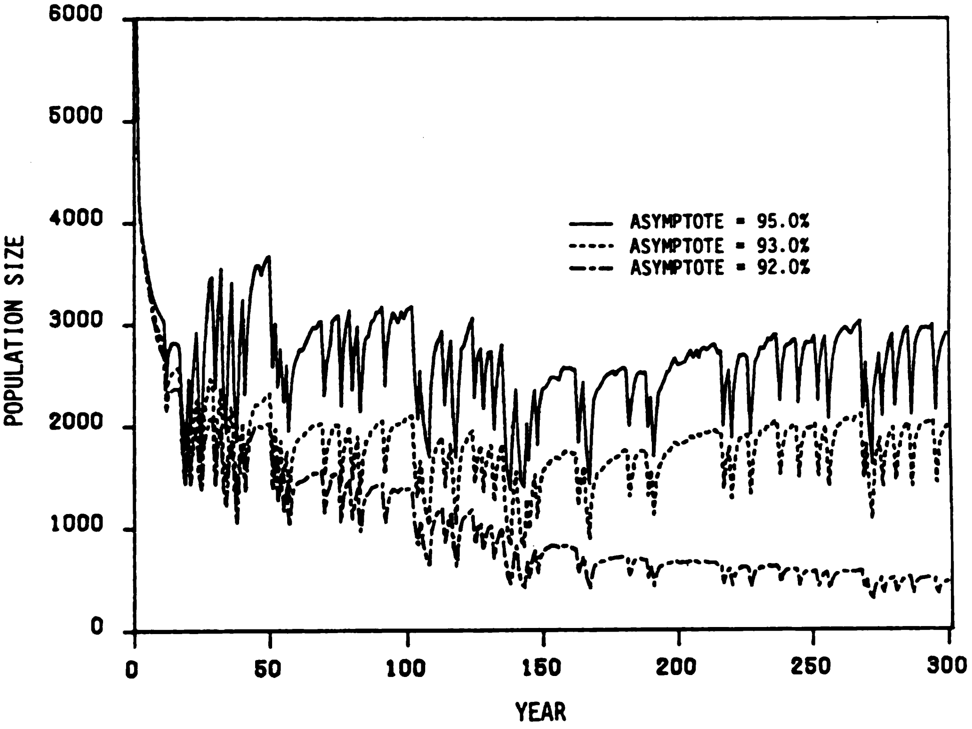
The higher survival rates, which on the average deviated from those originally used by 4%, resulted in a population curve that reached equilibrium phase earlier by 33% (year 64), effecting a measure of sensitivity of 8.15. The curve averaged 36,600 in the equilibrium phase and is thus 38% higher than that resulting from the originally used rates. The measure of sensitivity is 9.32. The population curve resulting from the lower set of survival rates, which on the average deviated from those originally used by 7%, soon dropped, to level off at 103 years. It is lower by 96%, i.e., 1,000, resulting in a measure of sensitivity of 14.4 (Figure 17a). Numerical values for population sizes derived from the age structure of the 50th simulated year, and from the age structure intermediate between that of the 70th and 80th simulated years, are in Tables 27 and 28, respectively.

Investigation of the model's response to age-specific survival rates (PSURV) lower than 99.0% (i.e., 95%, 93%, 92%, and 90%) in the asymptotic portion (age classes 22-51) of the curve of survival rates

Figure 17. Response of population size to (a) sets of changed survival rates in the first 21 age classes, and (b) sets of survival rates lowered from 99.0% in the asymptotic portion (age classes 22-51) of the curve of survival rates.


POPULATION SIZE x 1,000
0
10
20
30
40
0
50
100
150
200
250
300
YEAR
UNCHANGED RATES
HIGHER RATES
LOWER RATES

a


POPULATION SIZE
0
1000
2000
3000
4000
5000
6000
0
50
100
150
200
250
300
YEAR
ASYMPTOTE = 95.0%
ASYMPTOTE = 93.0%
ASYMPTOTE = 92.0%

b

Figure 17.

was also made. With the last value set the population size ultimately declined to below 10, and the result was not graphed.

The curve for population size resulting from asymptotic values of 92.0% shows a continuing downward trend. The curves resulting from asymptotic values of 95% and 93%, which are respective deviations of 4% and 6%, stay level after an early decline, at 2,600 and 1,800 respectively. The changes represent decreases in the population level, of 90%, resulting in a measure of sensitivity of 22.3, and of 93%, resulting in a measure of sensitivity of 15.4, respectively (Figure 17b). Numerical values for population sizes resulting from lowering the asymptotic survival rates to 95.0%, 93.0%, and 92.0% are in Tables 29, 30, and 31, respectively.

Constraint on Juvenile Survival.--As stated, Magnusson (1984, pers. comm.), from observation of the smooth-fronted caiman, and Messel et al. (1982, 1984), reporting on the estuarine crocodile, hypothesized that survival of juveniles is reduced by aggression of adults. Therefore, lowered survival rates (PSURV) for 6 age classes of crocodiles (being 5-10 years old, hence 1.5-2.5 m long) were entered into the model, to further gauge its response. These lowered survival rates were chosen arbitrarily; their mean (69.05) deviated 23% from that (89.32) of the original values, and reduced the population size by 90%, to 6,600 (Figure 18). (For this simulation PSURV(1) was set at 100.0.) The measure of sensitivity is thus 3.97. Numerical values for population size with unchanged data (PSURV(1) = 100.0), and with lowered juvenile survival, are in Tables 32 and 33, respectively.

Figure 18. Response of population size to arbitrarily lowered survival rates of juveniles (ages 5-10, 1.5-2.5 m long). (PSURV(1) was in this comparison set at 100.0.) Lowered survival of juveniles is believed to result from aggression by adults.

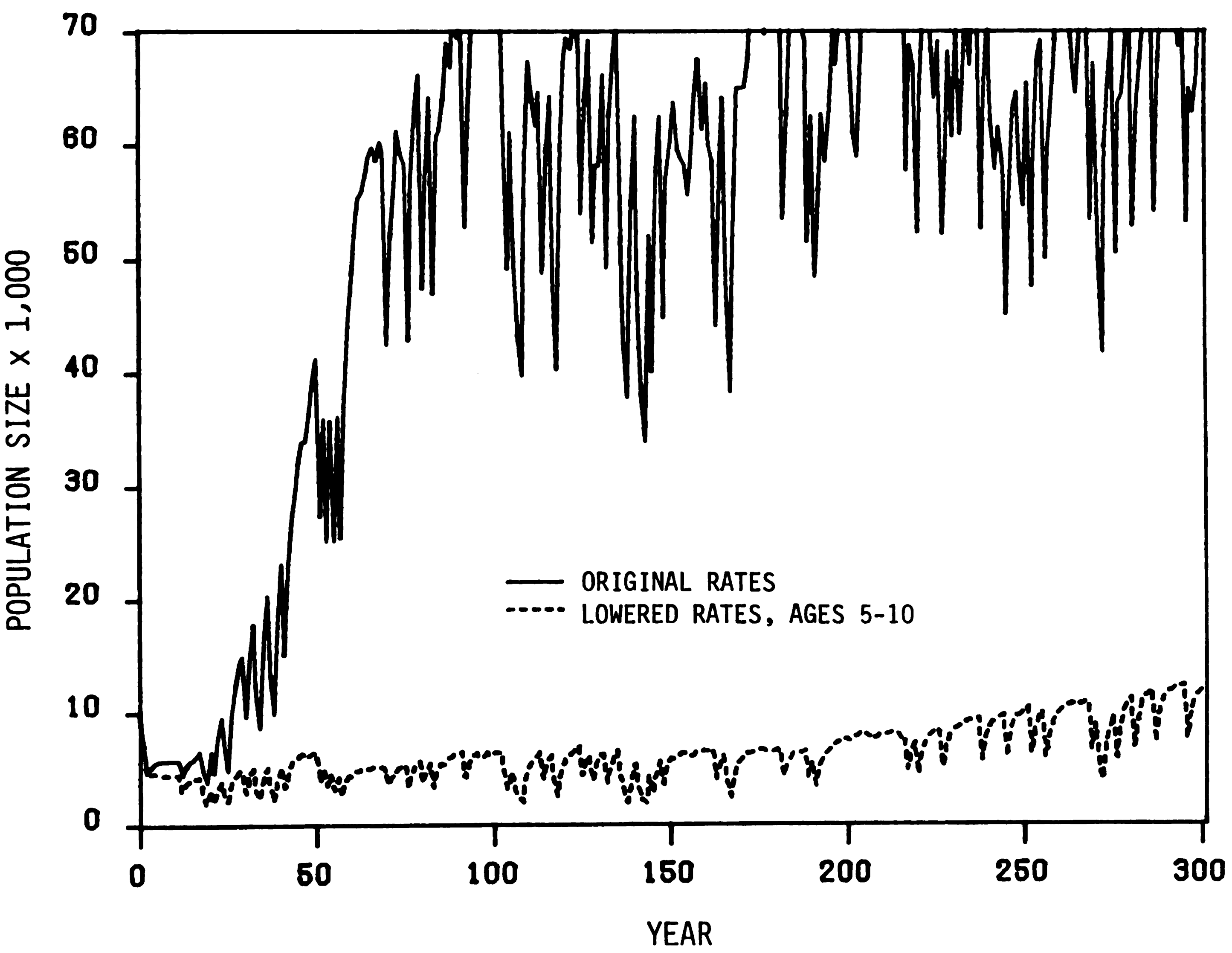

POPULATION SIZE x 1,000
70
60
50
40
30
20
10
0
0
50
100
150
200
250
300
YEAR
ORIGINAL RATES
LOWERED RATES, AGES 5-10

Figure 18.

Growth Rates of Crocodiles

Relation to Cannibalism.--The differing growth rates of crocodiles in different populations should have a bearing on the age spans that are subject to cannibalism. A given variable "TOTKIL", representing the number of cannibalized crocodiles, was originally spread over the first 3 age classes. Sensitivity of the model was tested by spreading this number over 4 age classes (ages 0-3) and over 11 age classes (ages 0-10), in accord with suggested growth rates of Graham (1976) and with low growth rates in Lake Turkana, Kenya (Graham 1968), respectively. They would, at any of these growth rates, be under 120 cm in length. Responses of the population curve ranged from 0% to slightly under 5%; sensitivity (its measures ranging from 0 to 0.1) to changes in this parameter is considered negligible.

It is believed that cannibalistic behavior begins in older age classes in populations where crocodiles grow more slowly, based on Cott's (1961) data. Responsiveness of the model to changed initial ages was tested. Specifically, initial ages of 11 and 18 (males and females, respectively) in accord with Graham's (1976) suggested growth rates, and of 35 and 46, respectively, with the low growth rates in Lake Turkana, Kenya (Graham 1968) were entered, for comparison with the originally used ages of 19 and 37, respectively. At these growth rates the crocodiles would have just reached 290 cm in length at the stated ages.

Simulation of earlier ages of cannibalistic behavior resulted in only slightly lower values for the exponential phase, and therefore delayed attainment of equilibrium phase by only 4% (year 100, the measure of sensitivity being 0.09). No change in attainment resulted from entry of later initial ages. The mean for the equilibrium phase of the curve resulting from earlier initial ages was 22,500, a decrease of 15%, resulting in a measure of sensitivity of 0.32. Simulation of later initial ages of cannibalistic behavior resulted in an equilibrium phase averaging 30,800, an increase of 16%, resulting in a measure of sensitivity of 0.30 (Figure 19). (The changes in initial age of males and females were averaged, resulting in -46.8% and 54.2% for growth rates of Graham (1976) and of Graham (1968), respectively.) The numerical values for population size at early and delayed initial ages of cannibalistic behavior are in Tables 34 and 35, respectively.

Relation to Initial Age of Egg Laying.--Initial age of egg laying is believed to vary inversely with growth rates of crocodiles. Initial ages of 13 (an increase of 30%) in accord with suggested growth rates of Graham (1976) and of 18 (an increase of 80%) in accord with Lake Turkana's low growth rates (Graham 1968) were entered and compared with the effect of the originally used age of 10, to gauge sensitivity of the model. With initial age of egg laying delayed to 18, attainment of equilibrium phase was delayed by 146% (year 236), resulting in a measure of sensitivity of 1.82. A delay to 13 years postponed attainment of equilibrium phase by 28% (year 123), resulting in a measure of sensitivity of 0.94 (Figure 20a). Respective population levels with these delays averaged 25,600 and 25,500, decreases of 3% and 4%, which, like the measures of sensitivity, may be considered negligible. This is the response of a parameter that only indirectly influences the number of hatchlings and their survival rates. (The equilibrium phase representing age 10 (Figure 20a), and that representing the original

Figure 19. Response of population size to changed growth rates, as expressed in initial ages of cannibalistic behavior. The curve labeled "MALES 11, FEMALES 18" results from suggested growth rates of Graham (1976); that labeled "MALES 35, FEMALES 46" results from the low growth rates in Lake Turkana, Kenya (Graham 1968).

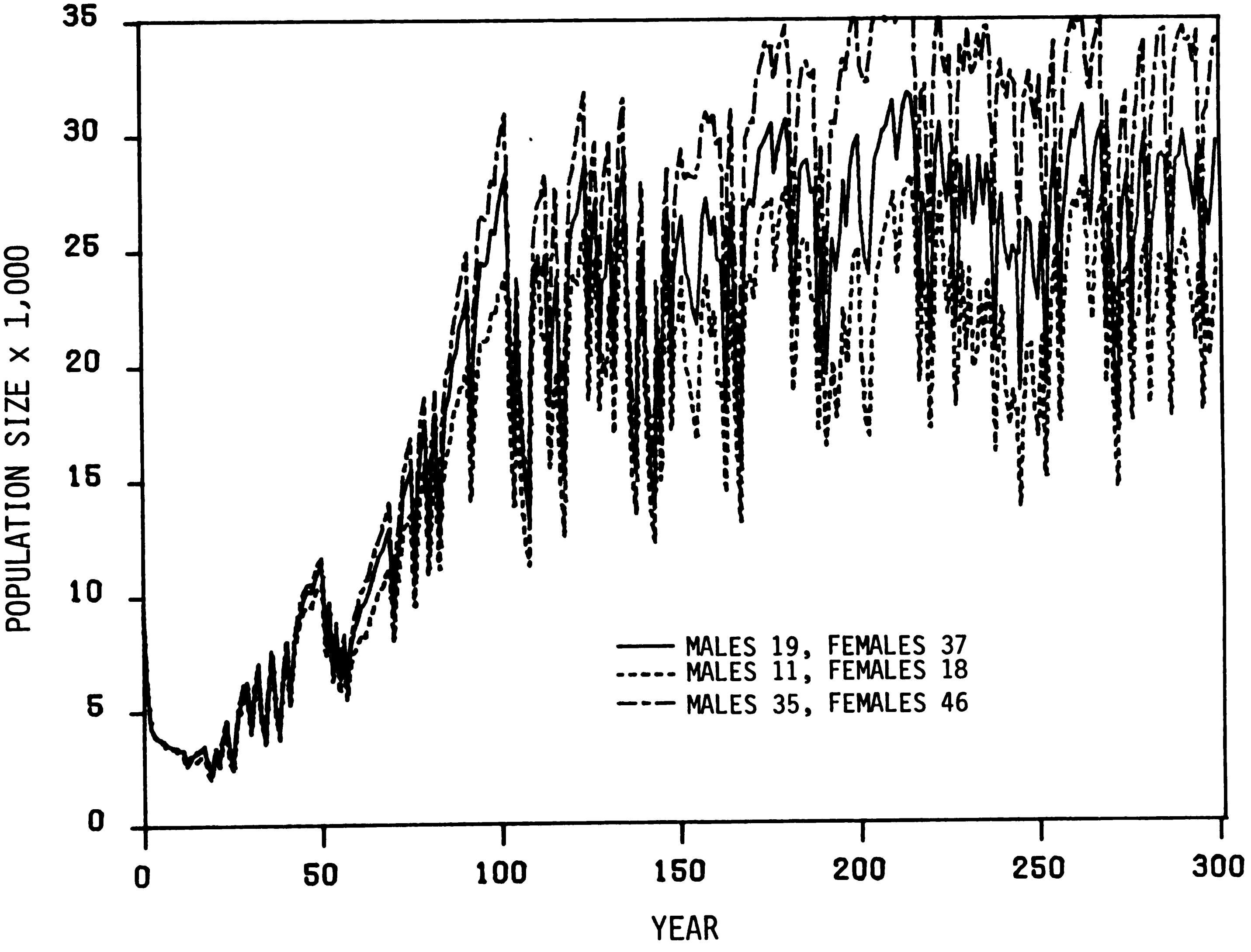
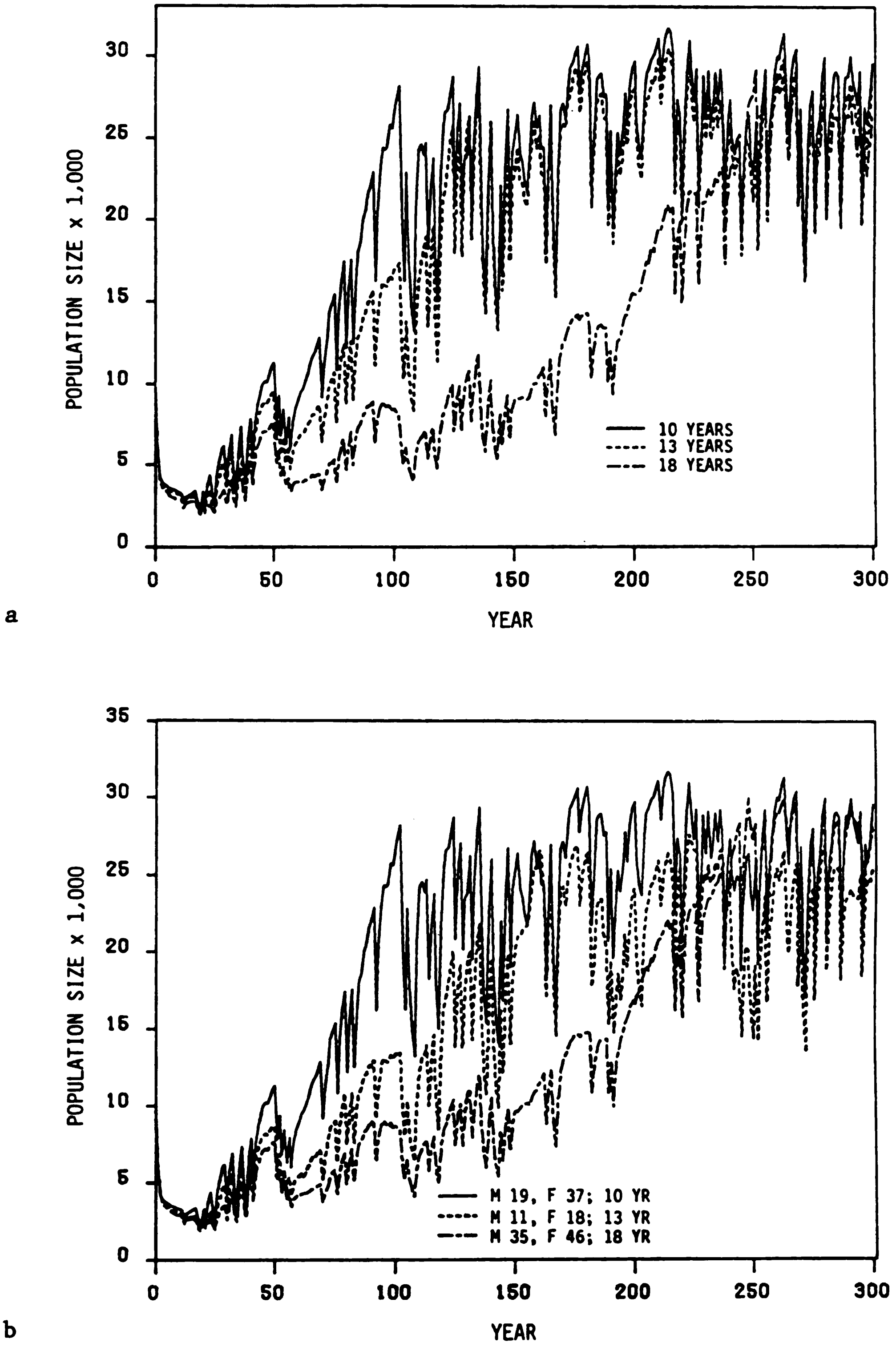

POPULATION SIZE x 1,000
35
30
25
20
15
10
5
0
0
50
100
150
200
250
300
YEAR
MALES 19, FEMALES 37
MALES 11, FEMALES 18
MALES 35, FEMALES 46

Figure 19.

Figure 20. Response of population size to changed growth rates, as expressed in initial age of egg laying, (a) singly, and (b) in combination with age spans cannibalized and initial ages of cannibalistic behavior. Initial ages of laying of 13 and 18 correspond with suggested growth rates of Graham (1976), and low growth rates in Lake Turkana, Kenya (Graham 1968), respectively. The curves labeled "10 YEARS" and "M 19, F 37; 10 YR" are identical.



POPULATION SIZE x 1,000
0
5
10
15
20
25
30
0
50
100
150
200
250
300
YEAR
10 YEARS
13 YEARS
18 YEARS
a
POPULATION SIZE x 1,000
0
5
10
15
20
25
30
35
0
50
100
150
200
250
300
YEAR
M 19, F 37; 10 YR
M 11, F 18; 13 YR
M 35, F 46; 18 YR
b

Figure 20.

population size in previous diagrams, prior to rounding off mean values, differ by a mere 0.03% from reducing the number of laying age classes from 56 to 48, for valid comparison with the 2 other data sets.) Values for population curves resulting from initial age of laying at 10, 13, and 18 are in Tables 36, 37, and 38, respectively.

It was felt that certain combinations of parameters pertaining to growth rates of crocodiles should also be run. Age spans cannibalized, initial ages of cannibalistic behavior, and initial age of egg laying were varied simultaneously, according to suggested growth rates of Graham (1976) and according to the low growth rates in Lake Turkana, Kenya (Graham 1968), to again test the model's response. There were again lowered exponential phases of the population curves, hence delay in attainment of equilibrium phase with the growth rates of Graham (1976) by 65% (year 158), and with the low growth rates in Lake Turkana, Kenya (Graham 1968) a delay of 147% (year 237). The former growth rates lowered the equilibrium phase to 23,400, a change of 12%, while the latter rates raised the equilibrium phase to 27,300, a negligible change of 3% (Figure 20b). The numerical values for population size resulting from the combination of age spans cannibalized, initial age of cannibalistic behavior, and initial age of egg laying, at the growth rates of Graham (1976), and the growth rates of Graham (1968), are in Tables 39 and 40, respectively.

Relation to Age Spans Being Hunted.--Prior to testing the model for sensitivity to changed age spans vulnerable to hunting, several alterations were made. Hunting was postponed 10 years, which had little impact on the population curve. Hunting mortality was also made to supersede natural mortality, up to a point, and this visibly raised the population curve.

Lower growth rates of crocodiles would delay the initial ages of vulnerability to hunting, and increase the number of years crocodiles remained vulnerable. The lower and upper length limits would be 120 cm and 190 cm, respectively. These length limits were reached at the age spans in Table 3. Hunting at the original growth rates made the population level stabilize (year 105) well below the initial population size, i.e., 1,800, a change of 93%. The effects of postponing and expanding age spans subject to hunting for both of the lowered growth rates, is a population size, averageing 2,700 when stabilized, an increase of 50% from that above (Figure 21a). Numerical values for population size resulting from age spans subject to hunting at the original growth rates, and those of Graham (1976) and of Graham (1968) are in Tables 41, 42, and 43, respectively.

Smaller means for the huntable male cohort, and the harvest, but apparently not the huntable female cohort, result from lower growth rates (Table 7). If the averages of the 2 huntable cohorts are added for each set of age spans, however, a progressive decrease is evident. There is an increase in number of years during which no hunting takes place.

A combination of the 4 parameters pertinent to growth rates of crocodiles was also used to test the model for sensitivity. Simultaneous alterations of data for all 4 parameters, in accord with suggested growth rates of Graham (1976), and with the low growth rates in Lake Turkana, Kenya (Graham 1968), were made and entered. Where level, the curve for the growth rates of Graham (1976) averages 4% lower than its counterpart in Figure 21a, and that for growth rates of Graham

Figure 21. Response of population size to changed growth rates, as expressed in age spans vulnerable to hunting, (a) singly, and (b) in combination with age spans cannibalized, initial ages of cannibalism, and initial age of egg laying. The curves labeled "MALES 4-7, FEMALES 5-9" and "M 4-7, F 5-9; M 11, F 18; 13 YR" result from the suggested growth rates of Graham (1976). Those labeled "MALES 11-19, FEMALES 11-20" and "M 11-19, F 11-20; M 35, F 46; 18 YR" result from the low growth rates in Lake Turkana, Kenya (Graham 1968).

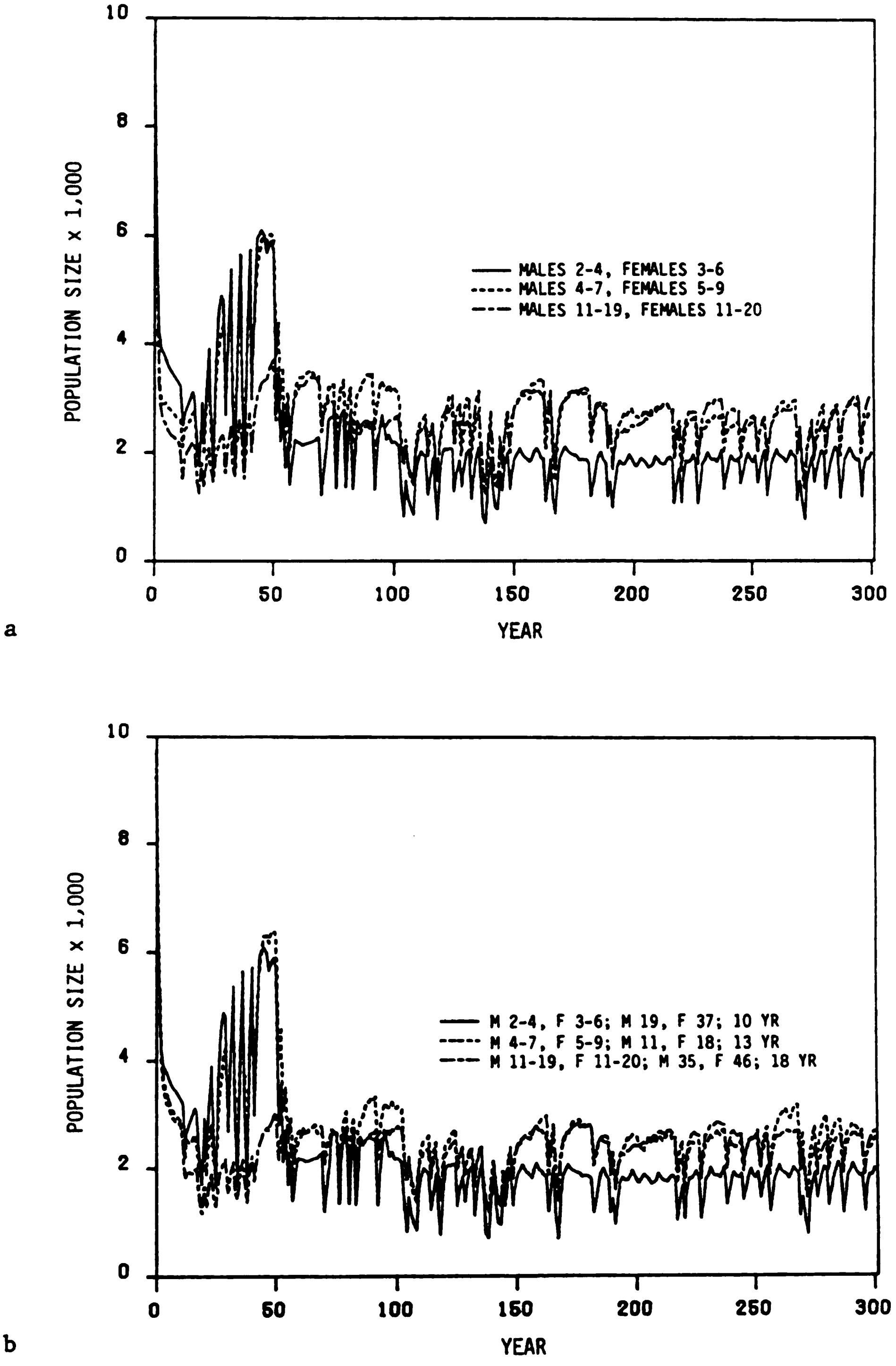

10
8
6
4
2
0
POPULATION SIZE x 1,000
MALES 2-4, FEMALES 3-6
MALES 4-7, FEMALES 5-9
MALES 11-19, FEMALES 11-20
0
50
100
150
200
250
300
YEAR
a
10
8
6
4
2
0
POPULATION SIZE x 1,000
M 2-4, F 3-6; M 19, F 37; 10 YR
M 4-7, F 5-9; M 11, F 18; 13 YR
M 11-19, F 11-20; M 35, F 46; 18 YR
0
50
100
150
200
250
300
YEAR
b

Figure 21

Table 7. Effects of hunting different age spans on means of huntable male cohort (HMPOP), huntable female cohort (HFPOP), and harvest (HUNT), and on number of years of no hunting.

Age spans	Mean of HMPOP[a]	Mean of HFPOP[a]	Mean of HUNT[a]	Years of no hunting[b]	
				No.	%
Males, 2-4[c] Females, 3-6	223	140	83	79	27
Males, 4-7[d] Females, 5-9	185	165	79	87	30
Males, 11-19[e] Females, 11-20	134	143	28	217	75

[a] Means are based on a sample of 59 years, beginning with year 11, then year 15, and every 5th year thereafter.

[b] Based on all 290 years during which hunting was simulated.

[c] Age spans at original growth rates.

[d] Age spans based on Graham's (1976) suggested growth rates for Okavango crocodiles.

[e] Age spans based on growth rates reported by Graham (1968) for crocodiles in Lake Turkana, Kenya.

(1968) thus averages 11% lower (Figure 21b). The changed growth rates caused respective population levels of 2,600 and 2,400, respective increases of 44% and 33% from that resulting from the original values. The curve resulting from growth rates of Graham (1976) averages slightly higher (8%) than that from growth rates of Graham (1968) in Figure 21b, unlike the the situation in Figure 21a. Apparently, in the long run, inclusion of changed data for the first 3 parameters depresses the population curve more, negligibly in the first case, but by a considerable percentage in the second, than hunting alone can do.

It appears from Figure 21 that hunting the youngest age classes lowers the population curve the most. The curve for population size labeled "M 2-4, F 3-6; M 19, F 37; 10 YR" is nearly the same as that resulting from hunting alone in Figure 21a (labeled "MALES 2-4, FEMALES 3-6"). (Prior to rounding the mean off to 1,800, it deviated from its counterpart in Figure 21a by -0.7%, due to reduction of the number of egg laying age classes, from 56 to 48, as in the other 2 data sets, for valid comparison.) Numerical values for population size at originally used growth rates, and at growth rates of Graham (1976) and Graham (1968), as expressed in the 4 parameters combined (48 egg laying age classes in each case) are in Tables 44, 45, and 46, respectively.

The huntable male cohort and the harvest again diminish with lower growth rates, while the mean of the huntable female cohort does not (Table 8). As before, a progressive decrease becomes apparent if the means of the huntable male cohort and the huntable female cohort are added for each growth rate. The 3 values above, for growth rates of Graham (1976), are noticeably lower in the present table, as is the mean for harvest at growth rates of Graham (1968). The number of

Table 8. Effects of different growth rates, simultaneously expressed in age spans cannibalized, initial ages of cannibalism, initial age of egg laying, and age spans hunted, on means of huntable male cohort (HMPOP), huntable female cohort (HFPOP), and harvest (HUNT), and on number of years of no hunting.

Growth rates	Mean of HMPOP[a]	Mean of HFPOP[a]	Mean of HUNT[a]	Years of no hunting[b]	
				No.	%
Original	223	140	83	79	27
According to Graham (1976)[c]	165	151	58	141	49
According to Graham (1968)[d]	134	145	16	252	87

[a] Means are based on a sample of 59 years, beginning with year 11, then year 15, and every 5th year thereafter.

[b] Based on all 290 years during which hunting was simulated.

[c] Suggested rates for Okavango crocodiles.

[d] Reported rates for Lake Turkana, Kenya.

years of no hunting increases, though at a somewhat greater rate than in Table 7.

CHAPTER 5

DISCUSSION

PRELIMINARY SIMULATIONS

Normal Conditions

The population level of roughly 21,000 is comparable to an earlier estimated prehunting population of 28,400, obtained by adding the initial population estimate (9,730) to the kills in Table 9. It was initially assumed that Wilmot took an estimated 14,400 crocodiles, instead of the present entry, making the total kill only 18,640. If Wilmot took about 10,000 crocodiles, as believed by Graham (1976, 1977), the prehunting estimate would be just below 24,000.

Crocodiles 0-3 years old normally comprised 50-85% of the entire population; they have a high mortality rate (Blake and Loveridge 1975, Graham 1968). This high mortality in any 1 year causes drastic declines in population size. Losses of hatchlings, which generally comprised 20-45% of the population, would certainly cause severe year-to-year fluctuations in population size.

Another important factor causing population fluctuations is the hatching rate of eggs. Two simulated phenomena, weather and predation by monitors, play a major role in determining this rate. Inclement weather, resulting in floods, can cause extensive destruction of eggs, sometimes eliminating the entire year's production (Pooley 1969b). Minor predation on eggs over many years is at least as destructive as mortality due to occasional floods.

Extreme Water Levels

The severe drought and flood simulations generated for the Okavango area are probably unrealistic. That the crocodile population placed under these unusually harsh conditions maintained itself at close to undisturbed (normal) levels over 300 years implies that the population is relatively insensitive to extreme water levels. The ability of female crocodiles to reproduce from ages 10 to 65 forms a population structure well buffered against recurring large losses of eggs and young.

Hunting

The larger population size obtained at a minimum of 500 huntable crocodiles might be explained by the roughly 36% fewer years of hunting when figures in Table 5 are averaged for both minimum numbers. That the ratio of nesting females to total population should be greater (5:100) at a minimum of 500 huntable crocodiles than at a minimum of 300 (3.75:100) is noteworthy. The difference might be an artefact of the program, changeable by raising the value for the number of females originally thought to saturate the nesting grounds (CCAP) above 1,360. It is also possible that fewer years of hunting enhances survival rates of females to a greater extent than survival rates of males. Because the females grow more slowly, their vulnerability to hunting lasts 1 year longer than that for the males. There is little difference between total harvest averages over 300 years (roughly 4% less at the 500 minimum, Table 5).

The best yearly hunt was realized at an efficiency of 0.3 at the 300 minimum, which also gave the fewest years without hunting.

However, according to Graham (1976, 1977), at least 200 crocodiles per hunting month are needed to make a profit. Hunting would be done from August to perhaps February (5-7 months) when the water level is low, so the crocodiles concentrate in the main channels. This means an annual harvest of 1,000-1,400 crocodiles, which far exceeds the simulated harvests (77-87 crocodiles per year, Table 5), and therefore appears unfeasible. Furthermore, such annual cropping rates approximate the destructive ones of 1958-1969, assuming B. Wilmot's total harvest was roughly 10,000-14,000.

Management Implications

Egg collection appeared more acceptable than hunting as a method of utilizing the crocodiles on the Okavango River. Commercial utilization of the crocodiles, on a sustained-yield basis, will motivate conservation; human sentiment alone is not likely to suffice (Bustard 1970, Blake and Loveridge 1975). Graham (1976, 1977) believed that without commercial harvesting, the Okavango crocodiles would be treated as pests and be eliminated.

Egg collection, followed by incubation and captive rearing, is the method of harvesting crocodiles in Zimbabwe (Blake and Loveridge 1975). The crocodiles are kept for 3 years, after which most are killed and skinned. The rest, representing 5% of the number of collected eggs, are released to maintain wild breeding stock. This percentage is believed to compensate adequately for lost natural recruitment to the population (Blake and Loveridge 1975). Nearly 80% of the collected eggs can be expected to hatch and about 50% of the hatchlings should reach age 3. In the wild, survival to that age is much less. Egg collection allows more production from the population because the high mortality of young is circumvented, and crocodiles of age 3 in a rearing station are nearly twice as long as those in the wild (Blake and Loveridge 1975). If well fed, crocodiles released at this age can be expected to have a high survival rate.

Blake and Loveridge (1975) suggested that at most 1,500 eggs be collected per rearing station annually in Zimbabwe. On the Okavango River, because of the average clutch size of 60.8 (Blomberg 1977), only about 25 nests would have to be robbed. For this reason and the believed adequacy of the 5% release, egg collection, and release of juveniles were not incorporated into the model. Greater numbers had lower hatching rates, probably because the rearing stations had more clutches than could be carefully managed at hatching time.

PRELIMINARY CONCLUSIONS

Commercial use of the Okavango crocodiles, on a sustained-yield basis, is viewed as a motivating force in conservation. On the basis of the described computer model, hunting could only play a minor role. It was concluded at this point that commercial use should take the form of captive rearing for the valuable skins, and that it should include the release of the number of 3-year old animals that represent perhaps 5% of the number of eggs collected. To increase income from the rearing scheme, there should be guided public tours of the rearing station.

The computer model should, at this point, be viewed only as a first approximation of the behavior of the crocodile population in the Okavango River. Discussion of results of further work, to make a second and presumably better approximation, follows.

SENSITIVITY TESTING

Results have been presented primarily in the form of curves representing size of the entire population. The model also produces numbers of nesting females for each year. Their curves are not presented, because of being artificially constrained by variable CCAP, set at 1,360.

The population size of 65,900 at equilibrium (Figures 12, 18), resulting from setting PSURV(1) at 100.0, merits some discussion. It should approximate the population size prior to the large-scale commercial hunting initiated in 1957. A pre-1957 population size of roughly 66,000 seems conceivable at this point, so an attempt was made to relate this population size to a reported harvest by the late B. Wilmot, significantly greater than the earlier reasoned estimate of 14,400. A. C. Campbell, former director of the Department of Wildlife and Tourism in Gaborone, Botswana, stated in a letter to R. I. G. Atwell of the Department of National Parks and Wildlife Management in Causeway, Zimbabwe, on August 9, 1973, that B. Wilmot (with whom he was acquainted) had killed an estimated 40,000 crocodiles. If it can be shown that this harvest is conceivable, then a pre-1957 population size of 66,000 must be conceivable. Regardless of total harvest, B. Wilmot was instrumental in depleting the population. That means that the pre-1957 population was probably in the tens of thousands. A lower order of magnitude appears impossible, and a population size of a higher order should have experienced little or no effect from the hunting.

A harvest of 40,000 crocodiles is incongruous with Graham's

(1976, pers. comm.) report that B. Wilmot hunted for 12 years with an annual quota of 2,000, which those who worked for him say he seldom filled. I have never seen whatever authentic records of B. Wilmot's harvests might exist; no one in the Department of Wildlife and Tourism in Gaborone mentioned such records. A. C. Campbell used the term "estimate" for the harvest in his letter, as indicated, and further stated that B. Wilmot operated in an estimated 1/6 of the Okavango Delta (which should roughly coincide with the present study area).

If B. Wilmot indeed killed roughly 40,000 crocodiles, despite seldom meeting his annual quota of 2,000, possibly his team shot far more crocodiles than they actually gaffed and loaded into the boats. A shot crocodile sinks and is lost if not gaffed within 5-10 seconds. An alternative explanation appears implicit in A. C. Campbell's letter, namely that the annual quota of 2,000 (to be reduced by 500 annually) was not imposed until 1967. This allows for an annual harvest of far more than 2,000 crocodiles prior to 1967, and therefore a total harvest of possibly 40,000.

If B. Wilmot killed 40,000 crocodiles, his and other harvests total 44,240 (in contrast to the previous estimate of 18,640), as shown in Table 9. The estimated pre-1957 population then becomes 44,240 + 9,730, or 53,970. The calculated mean population size of 65,900 at equilibrium exceeds this estimate by 22% when the model is run without hunting. As a kill of 40,000 crocodiles is conceivable, a pre-1957 population of roughly 66,000 is also conceivable.

Table 9. Hunting history of crocodiles on the Okavango River, with a large harvest by B. Wilmot assumed.

Year	Harvest	Enterprise	Source
1957	2,000	S. M. Lurie and Co. (Pty.) Ltd., Bulawayo, Zimbabwe	S. M. Lurie (1975, pers. comm.)
1958	800	"	"
1959	500	"	"
1958-1969	40,000 [a]	B. Wilmot	Assumed
1973	500	BGI, Francistown, Botswana	Taylor (1973)
1974	440	"	Blomberg and BGI
Total:	44,240		

[a] This number is an estimate. The information from different sources varies. B. Wilmot may have had a quota of 2,000 crocodiles per year; at any rate it was seldom filled (Graham 1976, pers. comm.), though it may have been raised the last few years. This makes 40,000 crocodiles seem incredibly high, unless many of those killed were not harvested. An alternative explanation is that the annual quota of 2,000 (lowered by 500 per year) was not applied until 1967 (Campbell 1973, in litt.). This allows for more than 2,000 crocodiles in each earlier year, hence for the possibility of a total kill of about 40,000.

Initial Population Size

The change in attainment of equilibrium phase with change in initial population size (age structure held constant) is evident in Figure 13, and shows desirable sensitivity. The measures thereof are 0.33 and 0.76 for the higher and lower estimates of population size, respectively. It is a positive feature of the model that the curves representing population size level off at seemingly identical values. Initial population size should not be a determinant of ultimate population size, so for this parameter the model seems to operate realistically.

Initial Age Structure

Response to changed initial age structure has been ascertained. It indicates that the model can be made a more reliable management guide for the Okavango crocodile population, if and when new field data can be collected for this parameter.

The somewhat earlier attainment of equilibrium phase, of the curve in Figure 14 resulting from the other normal population structure (narrow pyramid), can be attributed to a larger proportion of the females being of reproductive age. This also holds true for the curves resulting from the even age structure, in which the proportion of reproductive females is significantly greater than that in the previous data set, i.e., 84.9% vs. 5.5%, respectively.

The curves resulting from the inverted age structure reached equilibrium phase at roughly the same time as the curves resulting from normal age structures, though one might guess that it should happen very quickly as with the previously discussed structure. The reason is probably that a large proportion of reproductive females died too soon to effect an almost immediate attainment of equilibrium phase for population size. The oldest 5 age classes contained 57.2% of all individuals; the oldest 10 contained 76.9%. It is a positive feature of the model that varied age structures, with initial population size held constant, also resulted in seemingly identical values for the equilibrium phase.

An even age structure in a wild population would seem improbable at best, and then transitory, and the value of it in this analysis lies only in testing for sensitivity. The same may be generally true of an age structure that forms an inverted pyramid. As mentioned, however, Graham (1968) implied such structures around the unsheltered islands in Lake Turkana, Kenya, resulting from cannibalism exacerbated by a near-lack of sheltering emergent vegetation for the young. These populations were apparently maintained by recruitment of adults from the lake's shore, instead of by reproduction. Also, Watson et al. (1971) reported another population of crocodiles in the Grumeti River, Tanzania, that consisted apparently of little more than adult males that had moved in from Lake Victoria to avoid harassment by hunters.

Age-specific Percentages of Females Nesting in a Given Year

Conspicuous change in time of attainment of equilibrium phase, for population size (Figure 15) resulted from variation in the percentage of sexually mature females that nest in any given year. Good sensitivity of the model to variation in PERBRD is demonstrated, the measures thereof being 1.81 and 0.76, respectively, for maximal percentages of 56.8 and 76.8. Scanty observations in the field suggest that roughly 2/3 of the sexually mature females nest in a given season. This fraction probably rises somewhat above that, with increasing age (see Cott 1961:255). It seems a strength of the model that the equilibrium values for population size, resulting from different values for PERBRD, differ very little (see Figure 15). This parameter should not be a determinant of ultimate population size.

Age-specific Clutch Sizes

Desirable responsiveness to clutch sizes that, though changed, remain well within the actual range of sizes found in nature (roughly 23 to 75 due to the described changes), has been demonstrated. Therefore acquisition of age-specific clutch sizes from the Okavango River for entry into the model appears worthwhile.

It is noteworthy in Figure 16 that the time of attainment of equilibrium is delayed by smaller clutch size, and that equilibrium phases of the curves vary directly with clutch size. The measures of sensitivity for time of attainment were 1.67 and 0.49, for smaller and larger clutch sizes, respectively, and those for level of equilibrium were 1.11 and 1.16, respectively. Change in equilibrium level makes sense, as variation in this parameter mimics variation in PSURV (i.e., varying PSURV has the same effect as varying the survival rate of the eggs or young, or both), which is a limiting factor on ultimate population size.

Age-specific Survival Rates

Major Portions of Curve of Survival Rates.--Several tests of response to changed values for PSURV, for the first 20 years of life, and for the asymptotic values (see Figure 17) were run. Very noticeable changes in population size resulted. For the higher rates of survival in the first 20 years the measure of sensitivity was 8.15 in time of attaining equilibrium phase and 9.32 in the level of equilibrium. At lower rates of survival the measure was 14.4 in the level of equilibrium. For the asymptotic survival rates (ages 22-51) the measures of sensitivity were 22.3 at 95.0% and 15.4 at 93.0%. Good response to variation in this most important parameter is thus demonstrated. It appears very worthwhile to obtain data from the Okavango crocodiles, on age-specific survival, for entry into the model. Possibly males and females of any particular age class have differing survival rates. Any field study of survival rates should include sexing by the only known way, i.e., cloacal inspection (Graham 1976, 1977), of all animals possible. This will prove difficult at best, with very small crocodiles, however (Blomberg 1975).

PSURV is a key parameter in this model, in determination of a realistic population size at equilibrium phase, and in a realistic number of years for attainment thereof. Age-specific survival rates are intrinsically important to science, and are badly needed for sound management of crocodile populations (Graham 1968, 1976, 1977; Blake and Loveridge 1975).

Constraint on Juvenile Survival.--The preceding tests of sensitivity, involving altered data for various values of PSURV, significantly affected population size. Therefore the drastically lowered curve in Figure 18 can be expected. The measure of sensitivity for change in equilibrium phase was 3.97. It is not known what might be reasonable survival values for age groups 5-10; those used, as mentioned, were arbitrary due to lack of any field data. It therefore seems pointless to enter other hypothetical sets of survival data for these age groups. The purpose of this test, as indicated previously, was merely to ascertain the efficacy of varying juveniles' survival rates in regulating the the average height of the equilibrium phase. Such regulation might prove useful if a more reliable estimate of the population size prior to 1957, that is well below 54,000 (total in Table 9 + 9,730), can ever be reasoned out. If field data on low survivorship of juveniles is obtained and incorporated into the model, enhancement of survival rates of crocodiles 3-4 years old, or increase of age-specific clutch sizes, or some other adjustment, may become necessary for maintaining roughly 66,000 individuals, or whatever number seems correct, at equilibrium.

The rationale for hypothesizing a survival bottleneck for juveniles (Magnusson 1984, pers. comm.), as mentioned previously, is that when the crocodiles reach "medium length" (normally about 1.5 m in Crocodylus niloticus), they visually resemble adults enough to pose a territorial threat, or a sexual threat, or both, to them. The adults then might well attempt to kill the juveniles, or at least drive them to less suitable habitat, where mortality should be higher (Messel et al. 1982, 1984). Magnusson furthermore reasoned that large K-selected animals should produce few but large young (few small young, with more intense and protracted maternal care than is actually the case, is also conceivable), but that crocodilians instead produce many small young because the environment is unpredictable for the medium-sized individuals. The environment is normally saturated with large crocodiles, and room for a younger crocodile would usually exist only where an older conspecific has died.

In addition to his own evidence from *Paleosuchus trigonatus*, Magnusson (1984, pers. comm.) mentioned data from Webb and Messel (1977) that show increased scarring beginning at a snout-vent length of roughly 70 cm (roughly a total length of 1.4 m) in *Crocodylus porosus* in northern Australia. Cott (1961) reported similar results with *C. niloticus*. He and Webb and Messel (1977) suggested that the reason is either attempted cannibalism or other social interaction. Messel et al. (1984) stated that many juvenile *C. porosus* grow to about 1.5 m, but do not enter the adult segment of the population. Cott's (1961) statement that cannibalism in *C. niloticus* is acquired with age (which is written into the model) may also be relevant.

The incidence of injuries in the 1974-75 harvest from the Okavango River also increases toward greater length classes (Table 10). The small percentage of individuals at least 290 cm long, i.e., 1.7% of 241, suggests that most injuries resulted from aggression among juveniles, however. The proportion of injuries resulting from such aggression, and that resulting from adults attacking juveniles, probably vary with the proportion of adults in the population. Increased incidence of injuries toward greater length classes may be ambiguous evidence of intolerance for juveniles by adults.

Assuming the described constraint on juvenile survival, and supersessive hunting moratlity, it appears that hunting, within the previously mentioned length limits (120-190 cm), should not be postponed until the population attains equilibrium (although 10-15-year moratoria have been recommended in certain situations (e.g., Cott 1961; Becker 1974, pers. comm.)). Because skins are best within the mentioned length limits, and due to the constraint on survival, this

Table 10. Incidence of injuries,[a] attributable to intraspecific aggression, from the 1974 crocodile harvest on the Okavango River.

		Incidence	
Length class (cm)	No. examined	No.	%
25-124.5	48	4	8.3
125-149.5	78	5	6.4
150-174.5	47	7	14.9
175-325 [b]	68	13	19.1

[a] They consisted largely of amputations of portions of limbs and tails, and scarring.

[b] Individuals at least 250 cm long numbered 7 (10%), and individuals at least 225 cm long numbered 21 (31%) of this class.

would be the most economical stage in life to hunt crocodiles. It follows that the crocodile population that produces the greatest number of huntable individuals is at equilibrium. The greatest sustained yield is not from the population that has reached only about 50% of saturation (Magnusson 1983, pers. comm.).

Growth Rates of Crocodiles

Relation to Cannibalism.--The means of the population curves resulting from spreading TOTKIL (index of number of cannibalized crocodiles) over 4 age classes (ages 0-3), and over 11 age classes (ages 0-10), differed little from that due to spreading TOTKIL over 3 age classes (ages 0-2). Therefore only a slight sensitivity to variation in the number of age classes subject to cannibalism was ascertained. However, no data were collected from the Okavango River, and no smaller crocodiles were found in the stomachs of any of the 240 Okavango crocodiles dissected. The explanation may be that only 4 (1.7%) of these were over 290 cm long; 172 (71.7%) were under 175 cm long. Therefore cannibalism probably had negligible effect on the.Okavango River crocodile population. Other studies, e.g., Cott (1961) and Messel et al. (1984), have reported cannibalism.

Cannibalism on young, as programmed in this model, is highly speculative. Degree of sensitivity to changed data for this parameter is therefore of small significance, and this portion of the program should be rewritten, preferably following a detailed field study incorporating cannibalism. Thus the model points out a useful line of research. Even without a field study, cannibalism could well be rewritten to supersede natural mortality, but become additive to whatever extent it might surpass it. It would thus operate as hunting does in the model.

Figure 19 shows marked differences in equilibrium phases of the curves representing population size, due to variation in initial ages of cannibalistic behavior by large crocodiles (the measures of sensitivity for the growth rates of Graham (1976) and Graham (1968) being 0.32 and 0.30, respectively). This is viewed as a strength of the model. (The change in time of attainment of equilibrium was slight, however, measures of sensitivity being negligible for growth rates of Graham (1976) and 0 for those of Graham (1968).) It is believed that cannibalism is a potentially important, density-dependent, limiting factor on the population (Emmel 1973). In this context it is noteworthy that Graham (1968) reported possibly 100% cannibalism on young crocodiles around the unsheltered islands of Lake Turkana, Kenya, which indicates that the populations are maintained by recruitment of larger animals from the mainland (as mentioned).

<u>Relation to Initial Age of Egg Laying</u>.--Conspicuous delay in attainment of equilibrium phase, with measures of sensitivity being 0.94 and 1.82, and resulting from delaying initial age of egg laying to 13 and 18, respectively, and negligible differences in equilibrium phases, seem realistic. This parameter should not limit ultimate population size. It is apparent from Figure 20a that populations which differ in the initial age of egg laying have different time spans for recovery from any catastrophic event, e.g., overhunting. This age should be ascertained beforehand, preferably in tandem with age-specific percentages of nesting females and age-specific clutch sizes, for each Nile crocodile population in Africa that could become

subject to commercial hunting in the future.

Generally, variation of data for initial age of egg laying, combined with appropriately varied data for age spans cannibalized and initial ages of cannibalistic behavior, has noticebly changed the curves representing population size (Figure 20b) from what they were in the test solely of the first, and of the last (Figure 20a), parameter. Again, desirable sensitivity of the model to altered growth rates is demonstrated.

Relation to Age Spans Being Hunted.--Sensitivity of the model to changed growth rates, expressed in age spans subject to hunting, has been demonstrated in Figure 21a and in Table 7. It again appears worthwhile to obtain data on growth of wild crocodiles, for entry into the model.

In Table 7 it may be noteworthy that the mean for the huntable female cohort is less than that for the huntable male cohort by 36% for the original age spans, but only by 11% for the age spans based on Graham (1976), and is more by 8% for the age spans based on Graham (1968). This progression seems attributable in part to the increasing degree of overlap of male age classes with female age classes, as one reads down the table.

Lower means for the female cohort in the first and second growth rates are probably due to the females' longer age span of vulnerability to hunting, due to lesser growth rates (Cott 1961; Graham 1968, 1976, 1977). Beause the sexes are indistinguishable without cloacal inspection (Graham 1976, 1977), a somewhat greater harvest of females than of males may be unavoidable with an enforced upper length limit. If so, the proportion of females in the harvest, averaged over the years, may be an important factor in limiting the extent of allowable hunting, even at the low annual rates in Table 7.

The hunting rates in Table 7 are far below those of 1,000-1,400 implied by Graham (1976, 1977) to be minimal for economic profit. It should be realized that his rates are economical for the western style of hunting. Possibly, as suggested by W. E. Magnusson (1983, pers. comm.), and considered by Graham (1976), a local hunter network could harvest a far smaller number. This might approximate the hunting kill in the 3d column of Table 7, and be determined each year by a legal quota or limited number of hunting licenses. Some few additional licenses might also be sold, at higher prices, to tourists. If skins were then properly treated and sold to a reliable buyer, local hunters might still profit economically from an animal they otherwise would like to eliminate. This should result in a more positive attitude toward crocodiles among the local people (Graham 1976; Magnusson 1983, pers. comm.) than would ranching. Ranching would provide employment, though in Maun (Medem 1981), at least a day's journey by road from the Okavango River and upper delta. The local people might therefore, and because it would be European-owned, view the ranching as an enterprise in which they have too little influence. Especially difficult to understand or appreciate would be any legislation protecting crocodiles in their area, seemingly or actually for the mere benefit of an enterprise in Maun (Magnusson 1983, pers. comm.). The attitude of the local people is very important in long-term maintenance of the crocodile population. A local hunter network, once well organized, might be an alternative management scheme to crocodile ranching (which involves large overhead costs, and 10-12 years to recover the initial monetary outlay (Magnusson 1984)). Perhaps the most efficient way to exploit the crocodile resource, however, is to carry out both management schemes simultaneously.

Because Medem (1981) recommended that rearing stations (i.e., ranches, which depend on eggs or young collected in the wild) be turned into farms (which, by definition, depend on captive breeding stock), and because Magnusson (1984) stated that farming would reduce the incentive to maintain wild populations, a local hunter network might in the long run maintain this incentive (Magnusson 1983, pers. comm.). The local hunter network therefore should be seriously considered as a management tool for the Okavango crocodiles. This model might then prove useful in predicting allowable hunting rates.

The proposed hunting rates of 1,000-1,400 per year (Graham 1976, 1977) constitute 30-42% of B. Wilmot's destructive annual kill of 3,300, assuming he killed roughly 40,000 in 12 years. If this western style of hunting is used, it seems wise not to apply Graham's proposed rates before the population approaches or reaches equilibrium phase, resulting in maximal annual recruitment of huntable young. If, as suggested by Graham (1976, 1977), the comparatively dense human population along the Okavango River never again allows the crocodile population to reach its natural equilibrium, annually harvesting 1,000-1,400 crocodiles might well deplete the population. If Wilmot's total kill was only about 14,000, however, i.e., an annual mean of 1,200 in 12 years, Graham's proposed rates would, as stated earlier, certainly be unacceptable.

A response is evident, from Figure 21b, when all 4 parameters pertinent to growth are varied in accordance with the different growth rates. Desirable sensitivity to different growth rates is again demonstrated. In Figure 21b the equilibrium phase for population size resulting from Graham's (1976) growth rates averages slightly higher than that resulting from Graham's (1968) growth rates. One might expect the reverse, as the latter (lower) rates would result in fewer years of no hunting, however.

Small differences in means of huntable male and female cohorts, and of harvest, between Table 8 and Table 7, were obtained for original growth rates, prior to rounding off. The differences are meaningless, as the values in Table 8 result from reduction of number of egg-laying age classes from 56 to 48, as discussed. Generally, Table 8 reflects a more depressed trend in numbers of crocodiles, resulting from including the effects of varying all parameters, than what results from hunting alone. Again, sensitivity of the model to changed growth rates is demonstrated. It may be noteworthy that the mean for the huntable female cohort deviates from that for the huntable male cohort by -36% at the original growth rates. For the growth rates of Graham (1976) and Graham (1968) this mean deviates from that for the huntable male cohort by -11% and by +8%, respectively. This progressive increase in the ratio of females to males, like that in Table 7, would be attributable partly to the increasing overlap of huntable male age classes and huntable female age classes at lower growth rates.

It is felt, as an afterthought, that the efficiency of the hunter (EFFIC, subroutine HUNCR2) should be lowered from 0.3 to 0.12. The reason is that Messel et al. (1981, cited by Montague (1981b)) suggested that roughly 60% of the crocodiles present (and presumably of any cohort thereof) are seen at night, when most hunting takes place. It is then assumed that the hunter succeeds in killing roughly 20% of these.

A comment, in closing, regarding exceptionally low growth rates may be in order. Populations of stunted Nile crocodiles (at most 1.5-1.8 m long) exist in the Aswa, Ketchi, and other rivers in northern Uganda (Pitman 1952, Cott 1961). The arid environment forces the animals to estivate several months of the year (Pitman 1952), thus markedly limiting their food intake. It would be a positive feature of the model, were more of these populations' dynamics known, if entry of their growth rates effected successful execution.

CHAPTER 6

SUMMARY AND RECOMMENDATIONS

SUMMARY

Prior to certain alterations of the model, and tests of its sensitivity to changed data for several important parameters, the population leveled off at roughly 21,000. Achievement of this population size resulted from reducing the maximum rate of predation on eggs to 28%.

Imposition of 4 consecutive droughts every 20 years seemed not to significantly affect population size. However, this regimen of premature floods, severe enough to inundate a year's entire crop of eggs, often caused a noticeable decrease in population size every 20 years, though recovery was rapid. These simulations of drought and flood are believed unrealistically harsh, and the population's maintaining itself at close to normal levels over 300 years implies that it is relatively insensitive to extreme water levels. While drought intensified the rate of cannibalism on young, the loss to the population was less than that resulting from total flooding of eggs.

With 300 harvestable crocodiles (120-190 cm long) as minimal for allowing hunting, regardless of the hunter's efficiency (0.3-0.5), the population size leveled at roughly 1,400. At all efficiencies, the mean annual harvest was in the 70's to 80's; the highest averaged harvest was 87, with a minimal number of 300 and an efficiency of 0.3. Fewer years of hunting appeared to enhance survival of females more than that of males; the former had 1 additional year of vulnerability to hunting, due to lower growth rates. For economic profit, at least 200 crocodiles must be taken for each of 5-7 hunting months (Graham 1976, 1977). The resulting annual harvests of 1,000-1,400 far exceed the simulated harvests and approach the clearly destructive rates of 1958-69, assuming the latter totaled 10,000-14,000. Captive rearing from eggs collected in the wild (ranching) was considered a more acceptable alternative of commercial utilization.

Enhancement of the usefulness and reliability of the model is a desirable goal. Some needed changes of certain numerical values, and corrections and alterations in structure were made. Former Director of Botswana's Department of Wildlife and National Parks, A. C. Campbell, estimated that B. Wilmot, with whom he was acquainted, had during 1958-69 harvested 40,000 crocodiles. This number was judged conceivable, and compatible with an equilibrium phase of 65,900 crocodiles, resulting from a correction in the program. In addition, the response of the model to changed data sets, for a number of parameters, was tested, in order to determine the usefulness of obtaining and entering field data. When possible, a measure of sensitivity was calculated to quantitatively gauge the model's response.

All population curves except 1 were characterized by a dip well below initial size, over the first 24-123 years, reaching minima of 1,800-3,800 individuals. This may be attributed to the low number of sexually mature females at year 0 (1975) and rather low survival rates to age 10, at which fewer than 1% of the females lay eggs. These factors also postpone the time that equilibrium phase is reached.

Input of varied data sets for population size at year 0 (age structure held constant), for age structure at year 0 (population size held constant), for age-specific percentages of nesting females, and initial age of egg laying (treated later under growth rates) resulted in similar population sizes at equilibrium phase, i.e., 26,000-27,000. Lower (7,858) and higher (11,598) initial population sizes than that used originally (9,730), postponed (to year 110; measure of sensitivity = 0.76) and hastened (to year 90; measure of sensitivity = 0.33), respectively, attainment of equilibrium phase (originally year 96). Alteration of the population's age structure to a narrower pyramid than that originally used, to an even structure (diagrammatically rectangular), and to an inverted pyramid, hastened attainment of equilibrium phase to years 87, 9, and 88, respectively. Lowering and raising the maximal age-specific percentages (56.8 and 76.8, respectively, from 66.8) of females nesting in a given year postponed (year 122) and hastened (year 85), respectively, the attainment of equilibrium phase. (Respective measures of sensitivity were 1.81 and 0.76.) Appreciable sensitivity of the model to altered data for the preceding parameters was demonstrated, in terms of times of attainment of equilibrium phase. The similarity in equilibrium levels suggests realistic operation, as data for these parameters should not determine ultimate population size.

For the remaining parameters, namely age-specific clutch sizes, age-specific survival rates, and growth rates of crocodiles (with exception of initial age of egg laying), input of varied data sets usually resulted in changed years of attainment of equilibrium phase and in changed level thereof. The latter change can be expected from a parameter that directly affects the number of young that in time reach maturity. Age-specific clutch sizes, lowered and raised 15% from originally used values (27 in 10-year old females to 65 in

65-year old females), postponed (to year 120; measure of sensitivity = 1.67) and hastened (to year 89; measure of sensitivity = 0.49), respectively, attainment of equilibrium phase. Respective equilibrium levels were 22,100 (measure of sensitivity = 1.11) and 31,100 (measure of sensitivity = 1.16).

Lowered values for age-specific survival rates in the first 21 age classes (ages 0-20) simply caused the population to drop off at 1,000 (measure of sensitivity = 14.4), i.e., well below population size in year 0. Raised rates for these age classes hastened attainment of equilibrium phase to year 64 (measure of sensitivity = 8.15) and the equilibrium level to 36,600 (measure of sensitivity = 9.32). The lowering of the asymptotic survival rates (age classes 22-51 insofar as possible), from 99.0% to 95.0% and 93.0%, again made the population curves level off well below the initial population size, i.e., 2,600 (measure of sensitivity = 22.3) and 1,800 (measure of sensitivity = 15.4), respectively. When these survival rates were lowered to 92.0% the population curve declined over the entire time span. Good response to changes in age-specific survival rates is apparent. Survival rates of crocodiles aged 5-10 (1.5-2.5 m long), were lowered by 23% on the average, based on the hypothesis of increased aggression by adults toward juveniles. The response of the population curve was to level off well below the initial population size, at 6,600 (measure of sensitivity = 3.97), a decrease of 90% from the equilibrium of 65,900 used in this test. Evidence for this aggression as cause of lowered survival rates of juveniles is presented. Increased incidence of injuries with age of young crocodiles seems to be ambiguous evidence of such aggression, however.

Growth rates of crocodiles were expressed through the following parameters: age spans cannibalized, initial ages of cannibalistic behavior, initial age of egg laying, and age spans being hunted. Effects of changed data, representing the higher growth rates suggested by Graham (1976) and the lower growth rates of Lake Turkana, Kenya (Graham 1968) were noted for each parameter separately, and for certain combinations of these parameters. The population curve underwent only slight change from increasing the number of age classes vulnerable to cannibalism from 3 (ages 0-2) to 4 and 11 (ages 0-3 and 0-10, respectively). These crocodiles would be under 120 cm long. No data on cannibalism were obtained from killed crocodiles on the Okavango River, perhaps because only a small percentage of these were over 290 cm long.

Growth rates resulting in initial ages of cannibalistic feeding (lengths being 290 cm) in males at age 11 and in females at age 18 (due to faster growth in males) postponed attainment of equilibrium phase, perhaps negligibly, to year 100; the equilibrium phase was lowered to 22,500 (measure of sensitivity = 0.32). At the low growth rates, in which males became cannibalistic at age 35 and females at age 46, the year of attainment of equilibrium phase remained 96, but the population leveled off at 30,800 (measure of sensitivity = 0.30). Sensitivity to changes of initial ages of cannibalistic behavior is viewed as a strength of the model, as cannibalism is a potentially important limiting factor on a crocodile population.

Initial age of egg laying, delayed from the originally used 10 to 13 (Graham 1976), postponed the year the population reached equilibrium phase to 123 (measure of sensitivity = 0.94) and lowered the equilibrium phase to 25,500, a probably negligible 4%. A delay to age 18, corresponding to the low growth rates (Graham 1968) delayed attainment of equilibrium phase to year 236 (measure of sensitivity = 1.82), but lowered the equilibrium level insignificantly (by 3%). The response of the population curve appears typical for a parameter that does not directly affect survival rates, hence ultimate population size. Initial age of egg laying has a bearing on a crocodile population's recovery time after a catastrophic event, such as overhunting.

Age spans cannibalized, and initial ages of cannibalistic behavior and of egg laying, in combination, delayed attainment of equilibrium phase to year 158, and lowered the equilibrium phase to 23,400, at Graham's (1976) suggested growth rates. The latter change is 11%. At the low growth rates of Graham (1968) the equilibrium phase was reached in year 237, but was higher than that resulting from originally used values, by merely 3%.

Hunting at the originally used growth rates, at which males were aged 2-4 and females 3-6 (120-190 cm long), held the population well below its initial size, at 1,800, a change of 93% from 26,500. Postponing and expanding the age spans to 4-7 for males and 5-9 for females (Graham's (1976) suggested growth rates), and to 11-19 for males and 11-20 for females (low growth rates of Graham (1968)), the length span remaining constant, raised the population level to 2,700. Lower growth rates resulted in a progressive decrease in averages of the huntable cohort and an increase in the number of years when no hunting can take place.

Simultaneous alteration of data in all 4 parameters, for each growth rate, resulted in depressed population curves much like those resulting from varying age spans hunted only. The curve resulting from growth rates of Graham (1976) was lowered to 2,600 (a negligible 4%), that resulting from growth rates of Graham (1968) to 2,400 (11%). It appears that hunting the youngest (and shortest) age spans lowers the population curve the most. The trend in averages of the huntable cohort and in the number of years of no hunting is similar.

The model has responded noticeably to changed data for nearly all parameters tested. It should therefore have potential as a management tool. Further manipulation of it may be desired, and should include (1) redoing all simulations with PSURV(1) set at 100.0, (2) thoughtful rewriting of cannibalism on young in relation to growth rates, (3) experimenting with values of maximum numbers of nesting females in the population (CCAP) greater than 1,360, and (4) reducing the efficiency of hunting to 0.12. Input of field data for all parameters possible should increase the usefulness and reliability of the model as a guide to conserving the Okavango crocodile population. In reality, however, shortage of equipment, funds, and trained personnel might limit the acquisition of much of the desired field data. Some unanticipated changes in the model's mode of operation might become necessary, and ultimately the model will be outmoded. Nevertheless, it is felt to constitute an important step in the right direction, and that its implications should be applied as soon as possible.

RECOMMENDATIONS

It is assumed that commercial utilization of the Okavango crocodiles, on a sustained-yield basis, for the valuable skins, will motivate conservation. Prior to various corrections, alterations, and sensitivity testing of the model, it appeared that hunting at least 200 crocodiles per hunting month (1,000-1,400 annually) would again deplete the population, and that the method of utilization should therefore be captive rearing of young from eggs collected in the wild (i.e., ranching). This method is more efficient, relative to population size, because much natural mortality of young is eliminated.

It appeared that hunting could only play a minor role in utilization of the crocodile population. Ranching should include release of 3-year old animals constituting perhaps 5% of the number of eggs collected, and guided public tours to increase monetary income from the rearing scheme. Because the egg collection, with subsequent release, was assumed to have no adverse effect on the population, it was not incorporated into the model.

Appreciable change in time of attainment of equilibrium phase, which itself changed immaterially from 26,500, from changed data for population size and for age structure in year 0, and for age-specific percentages nesting in a given year, suggests a realistically operating computer model. The value of reasonably accurate estimates of the crocodile population's size and age structure is potentially accurate prediction of the time of attainment of equilibrium phase. Seasonal monitoring of the number, and of at least approximate lengths, of nesting females, followed by estimation of the population's size and age structure, should make the field data on the last of the above parameters available. Censusing the population by airplane is unworkable on the Okavango River; night counts by helicopter might work well, but could prove cost-prohibitive (Graham 1976, 1977). A marking scheme, described later, might be useful in estimation of population size. Collection of field data for the last parameter, for entry into the model, would be desirable.

Appreciable change in time of attainment of, and level of, equilibrium phase resulted from data on age-specific clutch sizes, changed within the range found in nature. Entry of field data should therefore be desirable for the model. Use of an approximate length-age relationship of aerially photographed females, each with its own clutch size (Graham et al. 1976), should provide data on age-specific clutch sizes.

Appreciable change in the population curves resulted from changing the first 21 age classes, and the asymptotic portion, of the curve of age-specific survival rates. This indicates that it is worthwhile to obtain data in the field, for this most important parameter, for entry into the model. Because males and females in a given age class might well have differing rates of survival, animals captured and marked in a field study should be sexed (difficult at best with very small animals (Blomberg 1975)). A large-scale program of capturing, individually marking, and recapturing the following year, would be needed. Animals should be measured for snout-vent length at least. Animals of all lengths that can be safely handled (up to roughly 240 cm) by 2 trained persons should be captured. From the recapture program, the following year, data would be obtained on growth, from which an approximate age-length relationship can be derived. A new marker, perhaps a collar differently colored from that used in the previous season, should then be secured onto each animal. The observed ratio of old to new markers should then be used to estimate the total number surviving of those captured in the previous year, to reduce the overestimate of mortality resulting from the impossibility of recapturing all survivors. Age-specific survival rates is perhaps the most important parameter in establishing the model's credibility and reliability. Acquisition of the data, though expensive in terms of time, money, and energy, is urged. Acquisition might well be repeated, possibly every 5 years, as long as the population is recovering from the earlier, destructive, hunting rates.

There is evidence, in other crocodilian populations, of markedly lowered survival of juveniles, resulting from aggression by adults. For this reason, and the assumption of supersessive hunting mortality, it is felt that allowable hunting (lengths being 120-190 cm) not be postponed until the population has reached equilibrium phase. Such postponement means foregoing economic gain. Restriction of hunting to juveniles results in skins of optimal condition (Magnusson 1983, pers. comm.). It also protects the breeders, and it follows that the greatest sustained hunting yield will come from a population at equilibrium phase.

The effect of cannibalism on young in the model is highly speculative, as no data from the Okavango River were obtained. It is felt that this portion of the computer program should be rewritten, preferably supplemented by a telemetry study of survival of the youngest animals, before and after a substantial proportion of adults has come about. Thus the model points out a useful line of research.

A study of incidence of cannibalism by various length classes of adults, to determine initial age, may never again become feasible, unless it is restricted to stomach analysis of killed nuisance crocodiles. These will increase in number if the population is allowed to approach or reach its pre-1957 size. A more expensive alternative would be to extract stomach contents of live, restrained, and possibly tranquilized, crocodiles. This has been done by Taylor et al. (1978) with *Crocodylus porosus*, of 28-180 cm total length, to date.

Because initial age of egg laying has a bearing on time spans of recovery from a catastrophe, it, preferably in tandem with age-specific percentages of nesting females and age-specific clutch sizes, should be ascertained for all Nile crocodile populations that might be subjected to hunting in the future. The initial age would come from derivation of an approximate age-length relationship from growth rates (mentioned earlier), and from aerial photogrammetry, of nesting females, as recommended by Graham et al. (1976).

The females' lower growth rates will likely result in somewhat greater harvest of females than of males, with enforcement of an upper length limit. This seems unavoidable, as crocodiles generally cannot be sexed without cloacal inspection. The proportion of females in the harvest, averaged over the years, may become an important factor in setting the legal limit on the size of the harvest.

Sensitivity to changed data for growth rates, as expressed in initial ages of cannibalistic behavior and egglaying, and age spans vulnerable to hunting, has been ascertained. It therefore appears worthwhile to obtain data in the field on these 3 parameters for entry into the model.

Allowable annual hunting rates indicated by the model are far below the 1,000-1,400 implied to be needed for economic profit in the western style of hunting (Graham 1976, 1977). An alternative might be a well-organized local hunter network (Graham 1976; Magnusson 1983, pers. comm.), with provision for a limited number of hunting licenses for tourists, to harvest an approximation of what the model indicates to be allowable. A more favorable attitude by the resident people toward crocodiles would thus result, which is needed to help ensure the crocodile population's long-term survival.

Ranching (rearing from eggs or young collected in the wild) as a simultaneous way of commercial utilization is also recommended. A likely shortcoming that must be considered, however, is that the employment it provides will be at least a day's journey (i.e., Maun (Medem 1981)) from where the crocodiles are, and people living along the Okavango River itself might not be involved. Other shortcomings (Magnusson 1984) are (1) large overhead costs, (2) 10-12 years to recover the initial monetary outlay, and (3) likely conversion to farming (dependent on captive breeding stock, and therefore reduces the incentive to maintain wild stock). Well before this conversion is completed, the local hunting network should be organized and active.

If farming largely or entirely replaces ranching, the incentive for long-term maintenance of the wild population might remain sustained by hunting. The model could well before then prove useful in predicting allowable hunting rates. However long ranching lasts, it should be done simultaneously with hunting, to bring about the most efficient commercial utilization of crocodiles. It is far better to initiate ranching and organization of a local hunter network, to provide incentives for conserving the crocodile population now, than to frantically, and at great expense and difficulty, try to save it from extinction some decades later.

Assuming B. Wilmot harvested approximately 40,000 crocodiles during 1958-1969, which would make the prehunting population of roughly 66,000 (produced after certain necessary changes in the model) seem likely, the proposed western style of hunting 1,000-1,400 annually, would constitute 30-42% of Wilmot's destructive harvest, each year. Use of this style of hunting might be unwise prior to the crocodile population's attainment of the above equilibrium phase. If the comparatively dense human population never again allows the crocodile population to reach its natural equilibrium level, taking 1,000-1,400 annually might well deplete the population.

APPENDICES

APPENDIX A: COMPUTER PROGRAM

APPENDIX A: COMPUTER PROGRAM

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      PROGRAM CROC(INPUT,OUTPUT,TAPE 8,TAPE 9)
      DIMENSION PSURV(66), FPOP(66), PERBRD(66), CLUTCH(66), EGGS(66)
      DIMENSION KIL(66), VAL1(12), VAL2(13), VAL3(10), WLEV(11)
      DIMENSION ATPOP(410), ANNFEM(410)
      DIMENSION MPOP(66),FHKIL(66),MHKIL(66),NATMORT(66)
      REAL MHKIL, MPOP, MHATCH, NATMORT
      REAL MEEG, IEM, NORMAL1, NORMAL2, NORPRED, M2, KIL, NNEST, M3
      LOGICAL VALUE,CRHUNT,INPRNT
      DATA PSURV/42.3,50.4,55.0,63.1,77.3,87.6,88.0,88.8,89.2,90.7,91.6,
     +92.8,94.1,95.0,95.7,96.7,97.3,97.6,97.8,98.3,98.7,30*99.0,92.
     +0,85.0,78.0,71.0,64.0,57.0,50.0,43.0,36.0,29.0,22.0,15.0,9.0,1.0,0
     +.0/
      DATA FPOP/2465.,1043.,525.,280.,216.,56.,34.,26.,2*12.,15.,2*4.,15
     +.,7.,4.,7.,17*4.,0.,6*4.,0.,4.,0.,4.,0.,4.,0.,3*4.,0.,4.,0.,4.,0.,
     +4.,0.,4.,3*0.,4.,2*0.,4./
      DATA PERBRD/10*0.,.42,.98,1.7,3.4,5.4,7,9,10.2,13.2,16.3,21.1
     +,24.3,28.7,32.6,40.6,44.4,47.9,51.5,54.4,56.8,58.5,59.7,60.9,62.1,
     +63.3,64.4,65.6,29*66.8/
      DATA CLUTCH/10*0.0,2.993,3.0123,3.0216,3.0409,3.0602,3.0795,3.098,
     +3.1181,3.1374,3.1567,3.1760,3.1953,3.2146,3.2339,3.2532,3.2725,3.2
     +918,3.3111,3.3204,3.3397,3.3590,3.3783,3.3976,3.4169,3.4362,3.4555
     +,3.4748,3.4941,3.5134,3.5327,3.5520,3.5713,3.5906,3.6099,3.6292,3.
     +6485,3.6678,3.6771,3.6964,3.7157,3.7350,3.7543,3.7736,3.7929,3.812
     +2,3.8315,3.8508,3.8701,3.8894,3.9087,3.9280,3.9473,3.9666,3.9859,4
     +.0052,4.0245/

C     INITIALIZE THE POPULATION FOR START AT YRS=0.

      DO 121 K=1,66
  121 MPOP(K)=FPOP(K)
      DO 111 K=1,66
  111 FHKIL(K)=MHKIL(K)=0.
      TPOP=0
      DO 16 K=1,66
      TPOP=TPOP+FPOP(K)+MPOP(K)
   16 CONTINUE
      DO 125 K=1,66
  125 KIL(K)=0.
      JJ=1 $ ATPOP(JJ)=TPOP $ ANNFEM(JJ)=82.0

C     PRINT RESULTS AT THIS TIME. TPOP,FPOP.

      YRS=0.
      PRINT 200
  200 FORMAT (*1*,*A POPULATION STUDY OF FEMALE CROCODILES IN THE OKAVAN
     +GO RIVER, BOTSWANA, AFRICA.*,///)
      PRINT 207
  207 FORMAT (*0*,130(1H*))
      PRINT 300
  300 FORMAT (*-*,*A FLAG EQUAL TO 0 MEANS THAT A NORMAL YEAR TOOK PLACE
     +.*/,* *,*A FLAG EQUAL TO 1 MEANS THAT A DROUGHT OCCURRED.*,/,* *,*
     +A FLAG EQUAL TO 2 MEANS THAT A FLOOD TOOK PLACE IN THAT YEAR.*)
      PRINT 206
      DO 202 I=1,66
      J=I-1
  202 PRINT 201, FPOP(I), J, I
  201 FORMAT (* *,*THERE ARE *,F8.0,* FEMALE CROCODILES BETWEEN THE AGES
     + OF *,I2,* AND *,I2,*.*)
      PRINT 203, YRS, TPOP
  203 FORMAT (*0*,*AT YEAR *,F4.0,* THERE WERE *,F10.0,* TOTAL CROCODILE
     +S IN THE POPULATION.*)
      PRINT 206
  206 FORMAT (*0*,130(1H*),//)

C     INITIALIZE PARAMETERS.

      INPRNT = .FALSE.
      IRNLGTH=300
      NORMAL1=5
      NORMAL2=7
      MEEG=0.072
      IEM=0.236
      NORPRED=0.06
      CCAP=1360. $ BABY=500.
      SMALL1=0. $ DIFF1=.25 $ K1=11
      VAL1(1)=0.0 $ VAL1(2)=0.008 $ VAL1(3)=0.039 $ VAL1(4)=0.07
```

```
      VAL1(5)=0.175 $ VAL1(6)=0.46 $ VAL1(7)=0.72 $ VAL1(8)=0.83
      VAL1(9)=0.915 $ VAL1(10)=0.96 $ VAL1(11)=0.98 $ VAL1(12)=1.00
      SMALL2=20. $ DIFF2=10. $ K2=12
      VAL2(1)=0.0 $ VAL2(2)=0.0 $ VAL2(3)=0.0 $ VAL2(4)=0.01
      VAL2(5)=0.05 $ VAL2(6)=0.085 $ VAL2(7)=0.185 $ VAL2(8)=0.235
      VAL2(9)=0.255 $ VAL2(10)=0.275 $ VAL2(11)=0.28 $ VAL2(12)=0.28
      VAL2(13)=0.28
      SMALL3=-1.5 $ DIFF3=.5 $ K3=9
      VAL3(1)=5. $ VAL3(2)=3.6 $ VAL3(3)=2.3 $ VAL3(4)=1.0
      VAL3(5)=.2 $ VAL3(6)=.2 $ VAL3(7)=.2 $ VAL3(8)=.2
      VAL3(9)=.2 $ VAL3(10)=.2
      DO 1 I=1,66
      PSURV(I)=PSURV(I)/100.
      PERBRD(I)=PERBRD(I)/100.
    1 CLUTCH(I)=CLUTCH(I)**3
      DO 313 I=1,66
  313 NATMORT(I) = 1. - PSURV(I)
      WLEV(1)=-1.5
      DO 2 I=2,4
    2 WLEV(I)=WLEV(I-1) + .375
      WLEV(5)=WLEV(6)=WLEV(7)=0.
      DO 3 I=8,11
    3 WLEV(I)=WLEV(I-1) + .6875

C     EXECUTION PHASE FOR 300 YEARS.

      DO 100 M=1,IRNLGTH
      CRHUNT = .FALSE.
      IF(CRHUNT) 103,104
  103 IF(M.LE.10) CRHUNT = .FALSE.
  104 YRS=YRS+1.
      JJ=JJ+1

C     RANDOM WEATHER VARIABLE ASSIGNED A VALUE.

      RANNUM=RANF(0)
      KK=RANNUM*10+1
      FLAG=0.
      IF (KK.LT.NORMAL1) FLAG=1.
      IF (KK.GT.NORMAL2) FLAG=2.
      F1=0.
      IF (FLAG.NE.2.) GO TO 4
      F1=TABLIE (VAL1,SMALL1,DIFF1,K1,WLEV(KK))

C     NUMBER OF EGGS FIGURED.

    4 TEGGS=0.
      TOT=0.
      VALUE=.FALSE.
      DO 5 K=1,56
      EGGS(67-K)=FPOP(67-K)*PERBRD(67-K)*CLUTCH(67-K)
      TOT=TOT+(FPOP(67-K)*PERBRD(67-K))
      IF(TOT.LE.CCAP)GO TO 5
      M2=3 $ M3=.1
      VALUE=.TRUE.
      GO TO 18
    5 TEGGS=TEGGS+EGGS(67-K)
   18 ACLUTCH=TEGGS/TOT
      HOLD=TEGGS-(TEGGS * F1)
      NNEST=HOLD/ACLUTCH
      F2=TABEXE (VAL2,SMALL2,DIFF2,K2,NNEST)
      ANNFEM(JJ) =  TOT

C     TOTAL HATCH MINUS MORTALITY.

      HATCH=TEGGS-(TEGGS * (IEM + MEEG + F2 + F1))
      IF (VALUE) HATCH=(HATCH-(HATCH * M3))
      MHATCH=FHATCH=HATCH/2.

C     EACH AGE CLASS IS NOW ADVANCED 1 YEAR.
```

```
      IF(CRHUNT) CALL HUNCR1 (YRS,MPOP,MHATCH)
      IF(FHATCH.LT.0.)FHATCH=0.
      SAVE=FPOP(1)
      FPOP(1)=FHATCH
      DO 15 K=2,66
      HOLD=FPOP(K)
      FPOP(K)=SAVE
   15 SAVE=HOLD
      IF(CRHUNT) CALL HUNCR2 (FHKIL,MHKIL,FPOP,MPOP)
      IF (FLAG.NE.0.) GC TO 6
      F3M1=1.
      GC TO 7
    6 F3M1=TABLIE (VAL3,SMALL3,DIFF3,K3,WLEV(KK))

C     CANNIBALISM FIGURED ON THE 0-2-YEAR OLD CROCODILES.

    7 AMPOP=AFPOP=BCROCKS=0.
      DC 8 K=38,66
    8 AFPOP=AFPOP + FPOP(K)
      DO 9 K=20,66
    9 AMPOP=AMPOP+MPOP(K)
      DO 10 K=1,3
   10 BCROCKS=BCROCKS+FPOP(K)+MPOP(K)
      PREDPOP=AMPOP + AFPOP
      IF (VALUE) 12,11
   11 IF (BCROCKS.LT.BABY) M2=0
      IF (BCROCKS.GE.BABY) M2=1
   12 TOTKIL=(PREDPOP*F3M1*M2*NORPRED)/2.
      KIL(1)=TOTKIL * .6
      KIL(2)=TOTKIL * .3
      KIL(3)=TOTKIL * .1
      CO 135 K=1,3
      IF((FPOP(K)*PSURV(K))-KIL(K)-FHKIL(K).LT.0.) GO TO 13
      FPOP(K)=(FPOP(K)*PSURV(K))-KIL(K)-FHKIL(K)
      GO TO 135
   13 FPOP(K)=0.
  135 CONTINUE
      IF(CRHUNT) 112,113
  113 DO 14 K=4,66
   14 FPOP(K)=FPOP(K)*PSURV(K)-FHKIL(K)
      DO 114 K=1,66
  114 MPOP(K)=FPOP(K)
      GO TO 226
  112 DO 116 K=4,7
      IF(FHKIL(K).GE.(FPOP(K)*NATMORT(K))) GO TO 117

C     IN THIS CASE HUNTING MORTALITY IS LESS THAN NATURAL MORTALITY,
C     AND REPLACES IT.  THE PROBABILITY OF SURVIVAL OF THOSE NOT
C     KILLED IS THEREFORE INCREASED, NECESSITATING CALCULATION OF A
C     HIGHER VALUE FOR PSURV(K).  IT IS USED IN FIGURING THE SIZE OF
C     THE AGE CLASS, FPOP(K).  BOTH VARIABLES ARE THEN USED IN RETURN-
C     ING TO THE ORIGINAL VALUE OF PSURV(K).

      FSURV(K) = 1 - ((FPOP(K)*NATMORT(K) - FHKIL(K))/FPOP(K))
      FPOP(K) = (FPOP(K)*PSURV(K)) - FHKIL(K)
      PSURV(K) = ((((FPOP(K)+FHKIL(K))/PSURV(K)) - FHKIL(K))/((FPOP(K)
     ++FHKIL(K))/PSURV(K))) - NATMORT(K)
      GC TO 116

C     IN THIS CASE HUNTING MORTALITY EQUALS OR EXCEEDS NATURAL MORTAL-
C     ITY, OF WHICH IT REPLACES 95 PERCENT.  THEREAFTER HUNTING MORTAL-
C     ITY IS ADDITIVE TO NATURAL MORTALITY.

  117 FSURV(K) = PSURV(K) + .95*NATMORT(K)
      FPOP(K) = FPOP(K)*PSURV(K) - FHKIL(K)
      PSURV(K) = PSURV(K) - .95*NATMORT(K)
  116 CONTINUE
      DO 118 K=8,66
  118 FPOP(K) = FPOP(K)*PSURV(K) - FHKIL(K)
      CALL HUNCR3 (PSURV,KIL,MHKIL,MPOP,NATMORT)

C     FIGURE TOTAL POPULATION FOR THE YEAR.
```

```
  226 TPOP=0.
      DO 17 K=1,66
      TPOP=TPOP + FPOP(K) + MPOP(K)
   17 CONTINUE
      ATPOP(JJ)=TPOP

C     PRINT INFORMATION AND RESULTS FOR YEAR PROCESSED.

      IF (INPRNT) 102,100
  102 IF (CRHUNT) 101,136
  101 IF (M.LE.10) GO TO 136
      IF (M/50*50.NE.M) GO TO 100
  136 DO 205 I=1,66
      J=I-1
  205 PRINT 201, FPOP(I), J, I
      PRINT 204, TOT,YRS
  204 FORMAT (*0*,*THERE WERE *,F6.0,* SEXUALLY MATURE FEMALES NESTING I
     +N YEAR *,F4.0,* .*)
      PRINT 203, YRS, TPOP
      PRINT 303. KK
  303 FORMAT (*0*,*THE RANDOM NUMBER FOR THIS YEAR WAS *,I2)
      PRINT 306,FLAG, F1, F2, F3M1, M2
  306 FORMAT (*0*,*THE VALUE OF THE FLAG WAS *,F3.0,/,*0*,*THE VALUE OF
     +F1 WAS *,F7.3,/,*0*,*THE VALUE OF F2 WAS *,F7.3,/,*0*,*THE VALUE O
     +F F3M1 WAS *F7.3,/,*0*,*THE VALUE OF M2 WAS *F4.0)
      PRINT 304, WLEV(KK)
  304 FORMAT (*0*,*THE WATER LEVEL FOR THIS YEAR WAS *,F5.2)
      PRINT 305, TEGGS, FHATCH, BCROCKS, PREDPOP, TOTKIL
  305 FORMAT (*0*,*THE TOTAL NUMBER OF EGGS FOR THIS YEAR WAS *,F8.0,/,*
     +0*,*THE TOTAL FEMALE HATCH WAS *,F8.0,/,*0*,*THE TOTAL NUMBER OF B
     +ABY CROCODILES WAS *,F8.0,/,*0*,*THE TOTAL NUMBER OF OLDER CROCODI
     +LES PREYING ON THE YOUNG WAS *,F8.0,/,*0*,*THE TOTAL KILL ON THE B
     +ABY CROCODILES WAS *,F8.0)
      PRINT 206
  100 CONTINUE
      PRINT 339
  339 FORMAT (*-*,2X,*TOTAL*,9X,*NESTING*,/,* *,*POPULATION*,6X,*FEMALES
     +*,/,* *,10(1H-),6X,7(1H-),//)
      PRINT 340, (ATPOP(I), ANNFEM(I), I=1,JJ)
  340 FORMAT (* *,2X,F7.0,7X,F7.0)
      WRITE(8,341)(ATPOP(I),I=1,JJ)
      WRITE(9,341)(ANNFEM(I),I=1,JJ)
  341 FORMAT(F7.0)
      END


C     THIS FUNCTION WILL CALCULATE VALUES FOR PERCENT MORTALITY
C     DEPENDING ON THE WATER LEVEL FOR A GIVEN YEAR. IN FLOOD YEARS
C     THIS MORTALITY WILL AFFECT THE NUMBER OF EGGS PRODUCED. IN
C     DROUGHT YEARS THIS MORTALITY WILL AFFECT THE HATCHLINGS AND THE
C     1-AND 2-YEAR OLD CROCODILES.

      FUNCTION TABLIE(VAL,SMALL,DIFF,K,DUMMY)
      DIMENSION VAL(13)
      DUM=AMIN1(AMAX1(DUMMY-SMALL,0.0),FLOAT(K)*DIFF)
      I=1.0+DUM/DIFF
      IF(I.EQ.K+1) I=K
      TABLIE=(VAL(I+1)-VAL(I))*(DUM-FLOAT(I-1)*DIFF)/DIFF+VAL(I)
      RETURN
      END


C     THIS FUNCTION WILL CALCULATE MONITOR LIZARD PREDATION ON EGGS,
C     DEPENDING ON THE NUMBER OF NESTS IN ANY GIVEN YEAR.

      FUNCTION TABEXE (VAL,SMALL,DIFF,K,DUMMY)
      DIMENSION VAL(13)
      DUM=DUMMY-SMALL
      I=MIN0(MAX1(1.0+DUM/DIFF,1.0),K)
      TABEXE=(VAL(I+1)-VAL(I))*(DUM-FLOAT(I-1)*DIFF)/DIFF+VAL(I)
      RETURN
      END


C     THIS IS THE FIRST OF 3 SUBROUTINES CALLED WHEN HUNTING OF CROCO-
C     DILES IS TO BE SIMULATED.  IT PRINTS YEAR NUMBER AND ADVANCES
```

```
C      EACH AGE CLASS OF MALES 1 YEAR.

       SUBROUTINE HUNCR1 (YARS,MCOHORT,MPIP)
       DIMENSION MCOHORT(66)
       REAL MCOHORT, MPIP
       PRINT 206
   206 FORMAT(*0*,130(1H*),//)
       PRINT 843,YARS
   843 FORMAT(*0*,*YEAR *,F4.0)
       IF(MPIP.LT.0.)MPIP=0.
       SAVE=MCOHORT(1)
       MCOHORT(1)=MPIP
       DO 115 K=2,66
       HOLD=MCOHORT(K)
       MCOHORT(K)=SAVE
   115 SAVE=HOLD
       RETURN
       END


C      THIS IS THE SECOND OF 3 SUBROUTINES CALLED WHEN HUNTING OF
C      CROCODILES IS TO BE SIMULATED.  IT OMITS HUNTING IN ANY YEAR
C      THAT THE SIZE OF THE TOTAL HUNTABLE COHORT DOES NOT EXCEED
C      A SPECIFIED NUMBER, "NONHUNT".  IT ALSO OMITS HUNTING OF EITHER
C      SEX IF ITS HUNTABLE COHORT SIZE DOES NOT EXCEED 0.  OTHERWISE
C      HUNTABLE FEMALE AND MALE COHORT SIZES ARE PRINTED AND ADDED.
C      THE SUM IS MULTIPLIED BY "EFFIC", A DECIMAL FRACTION THOUGHT TO
C      BRACKET THE HUNTER'S EFFICIENCY.  THIS GIVES "HUNT", THE ACTU-
C      AL NUMBERS HUNTED, WHICH IS ALSO PRINTED.  THIS NUMBER IS IN
C      TURN PARTITIONED INTO THE NUMBERS OF EACH SEX HUNTED.  LASTLY
C      THE NUMBERS IN EACH AGE CLASS OF EACH SEX ARE OBTAINED.

       SUBROUTINE HUNCR2 (FHUNKL,MHUNKL,FCOHORT,MCOHORT)
       DIMENSION FHUNKL(66),MHUNKL(66),FCOHORT(66),MCOHORT(66)
       REAL MHUNKL,MCOHORT,NONHUNT,MHUNT
       NONHUNT=300. $ EFFIC=.3 $ FLAGG=0. $ HFPOP=HMPOP=0.
        THPOP=0.
       DO 112 K=4,7
   112 HFPOP=HFPOP+FCOHORT(K)
       DO 1111 K=3,5
  1111 HMPOP=HMPOP+MCOHORT(K)
       PRINT 1112,HMPOP,HFPOP
  1112 FORMAT (*0*,*HMPOP= *,F7.0,6X,*HFPOP= *,F7.0)
       THPOP=HMPOP+HFPOP
       IF(THPOP.GT.NONHUNT)GO TO 420
       FHUNKL(4)=FHUNKL(5)=FHUNKL(6)=FHUNKL(7)=0.
       HUNT=0.
       MHUNKL(3)=MHUNKL(4)=MHUNKL(5)=0.
       GO TO 413
   420 HUNT=THPOP*EFFIC
       IF(HFPOP.GT.0.)GO TO 411
       FHUNT=0.
       FHUNKL(4)=FHUNKL(5)=FHUNKL(6)=FHUNKL(7)=0.
       FLAGG=1.
   411 IF(HMPOP.GT.0.)GO TO 412
       MHUNT=0.
       MHUNKL(3)=MHUNKL(4)=MHUNKL(5)=0.
       GO TO 4133
   412 MHUNT=(HMPOP/THPOP)*HUNT
       IF(MHUNT.GT.HMPOP)MHUNT=HMPOP
       DO 117 K=3,5
   117 MHUNKL(K)=(MCOHORT(K)/HMPOP)*MHUNT
  4133 IF(FLAGG.EQ.1.)GO TO 413
       FHUNT=(HFPOP/THPOP)*HUNT
       IF(FHUNT.GT.HFPOP)FHUNT=HFPOP
       DO 116 K=4,7
   116 FHUNKL(K)=(FCOHORT(K)/HFPOP)*FHUNT
   413 CONTINUE
       PRINT 421,HUNT
   421 FORMAT(*0*,* TOTAL HARVEST OF CROCODILES IS *,F8.0)
       RETURN
       END


C      THIS IS THE THIRD OF 3 SUBROUTINES CALLED WHEN HUNTING OF
C      CROCODILES IS TO BE SIMULATED.  IT FIRST SETS THE NUMBER OF
C      CANNIBALIZED MALES EQUAL TO THE NUMBER OF CANNIBALIZED FE-
C      MALES, BY AGE CLASS.  IT THEN SUBTRACTS THE NUMBER CANNIBAL-
C      IZED AND THE NUMBER HUNTED FROM RESPECTIVE AGE CLASSES OF
```

```
C     THE MALE COHORT.

      SUBROUTINE HUNCR3 (CHANSRV,KANN,MHUNKL,MCOHORT,NATUMOR)
      DIMENSION CHANSRV(66),KANN(66),MHUNKL(66),MCOHORT(66)
      DIMENSION MKANN(66),NATUMOR(66)
      REAL KANN,MKANN,MHUNKL,MCOHORT,NATUMOR
      DO 10 K=1,66
10    MKANN(K)=0.
      MKANN(1)=KANN(1)
      MKANN(2)=KANN(2)
      MKANN(3)=KANN(3)
      DO 123 K=1,2
      IF((MCOHORT(K)*CHANSRV(K))-MKANN(K)-MHUNKL(K).LT.0.)GO TO 113
      MCOHORT(K)=(MCOHORT(K)*CHANSRV(K))-MKANN(K)-MHUNKL(K)
      GO TO 123
113   MCOHORT(K)=0.
123   CONTINUE
      DO 11 K=3,5
      IF ((MCOHORT(K)*CHANSRV(K)) - MKANN(K) - MHUNKL(K).LT.0) GO TO 12
      IF (MHUNKL(K).GE.(MCOHORT(K)*NATUMOR(K))) GO TO 13

C     IN THIS CASE HUNTING MORTALITY IS LESS THAN NATURAL MORTALITY,
C     AND REPLACES IT.  THE PROBABILITY OF SURVIVAL OF THOSE NOT
C   KILLED IS THEREFORE INCREASED, NECESSITATING CALCULATION OF A
C   HIGHER VALUE FOR CHANSRV(K).  IT IS USED IN FIGURING THE SIZE OF
C   THE AGE CLASS, MCOHORT(K).  BOTH VARIABLES ARE THEN USED IN RE-
C   TURNING TO THE ORIGINAL VALUE OF CHANSRV(K).

      CHANSRV(K) = 1 - ((MCOHORT(K)*NATUMOR(K)-MHUNKL(K))/MCOHORT(K))
      MCOHORT(K) = (MCOHORT(K)*CHANSRV(K)) - MKANN(K) - MHUNKL(K)
      CHANSRV(K) = ((((MCOHORT(K)+MHUNKL(K))/CHANSRV(K)) - MHUNKL(K))/(
     +(MCOHORT(K) + MHUNKL(K))/CHANSRV(K))) - NATUMOR(K)
      GO TO 11

C   IN THIS CASE HUNTING MORTALITY EQUALS OR EXCEEDS NATURAL MORTAL-
C   ITY, OF WHICH IT REPLACES 95 PERCENT.  THEREAFTER HUNTING MORTALITY
C   IS ADDITIVE TO NATURAL MORTALITY.

13    CHANSRV(K) = CHANSRV(K) + .95 * NATUMOR(K)
      MCOHORT(K) = MCOHORT(K) * CHANSRV(K) - MKANN(K) - MHUNKL(K)
      CHANSRV(K) = CHANSRV(K) - .95 * NATUMOR(K)
      GO TO 11
12    MCOHORT(K) = 0.
11    CONTINUE
      DO 124 K=6,66
124   MCOHORT(K)=MCOHORT(K)*CHANSRV(K)-MHUNKL(K)
      RETURN
      END
```

APPENDIX B: VARIABLES IN PROGRAM

APPENDIX B: VARIABLES IN PROGRAM

Table 11. List of variables in program CROC.

Name	Definition
ACLUTCH	Average clutch size per nesting female (TEGGS/TOT).
AFPOP	Size of cohort of cannibalistic female crocodiles (ages 37-65).
AMPOP	Size of cohort of cannibalistic male crocodiles (ages 19-65).
ANNFEM	Number of nesting females, subscripted by JJ (below). It gets each year's value from TOT (below) before TOT is reset to 0 in the main do loop, so that the number can be printed outside the main do loop.
ATPOP	Population size, subscripted by JJ (below). It gets each year's value from TPOP (below) before TPOP is reset to 0 in the main do loop, so that the number can be printed outside the main do loop.
BABY	A minimum number of crocodiles (constant at 500) of ages 0-2, which if not met sets a density factor (M2), hence the rate of cannibalism, at 0.
BCROCKS	Number of 0-2-year old crocodiles, which are subject to cannibalism.
CCAP	Number of females at first believed to saturate the nesting grounds (constant at 1,360).
CLUTCH	Cube root of clutch size (age-specific). It is cubed prior to use in the main do loop.
CRHUNT	Logical parameter with which to opt for simulated hunting (set at ".TRUE." or ".FALSE.").
DIFF1	One of several factors (constant at 0.25) to generate a value for F1 (below). It is the argument for dummy variable DIFF in function subprogram TABLIE.
DIFF2	One of several factors (constant at 10.) to generate a value for F2 (below). It is the argument for dummy variable DIFF in function subprogram TABEXE.

Table 11 (cont'd.).

Name	Definition
DIFF3	One of several factors (constant at 0.5) to generate a value for F3M1 (below). It is the argument for dummy variable DIFF in function subprogram TABLIE.
EGGS	Number of eggs produced by a given age class of females, dependent on survival and clutch size for the age class.
F1	Percentage egg mortality due to premature flood. Its value, except when 0, is obtained via function subprogram TABLIE.
F2	Percent egg mortality relative to number of nests, due to monitor lizard predation. Its value is obtained via function subprogram TABEXE.
F3M1	Multiplier of cannibalism rate, dependent on water level. Its value is obtained via function subprogram TABLIE, except during normal weather ("FLAG = 1") when it is 1.
FHKIL	Number of females killed by hunting, by age class. It is the argument for dummy variable FHUNKL in subroutine HUNCR2.
FLAG	Variable assigned a value of 0 in case of normal weather, 1 in case of drought, and 2 in case of flood. These values depend in turn on the value of KK (below) which originates from generation of a random number.
FPOP	Size of female portion of population. It is the argument for dummy variable FCOHORT in subroutine HUNCR2.
FHATCH	Number of female hatchlings, i.e., HATCH/2.
HATCH	Number of hatchlings produced (TEGGS - (TEGGS * (IEM + MEEG + F2 + F1))).
HOLD	Dummy variable standing for: (1) total number of eggs - percentage lost to premature flood (TEGGS - TEGGS * F1)), also (2) number of females in any given age class (FPOP(K)) except the first, later assigned to dummy variable SAVE, when advancing each

Table 11 (cont'd.).

Name	Definition
	age class one year.
I	Subscript used in designating ages of crocodiles and categories of other variables prior (mostly) to the main do loop.
IEM	Intrinsic egg mortality (constant at 0.236).
INPRINT	Logical parameter, making optional the printing of certain information toward the end of each iteration of the main do loop.
IRNLGTH	Number of iterations (usually 300) in the main do loop, representing number of years.
J	Subscript designating an age class 1 year younger than I (above), i.e., J = I - 1.
JJ	Counter for each year simulated by the model, used as a subscript for ATPOP and ANNFEM (above).
K	Subscript used in designating age classes of crocodiles, and certain variables pertaining to age classes.
K1	One of several factors (constant at 11) to generate a value for F1 (above). It is the argument for dummy variable K in function subprogram TABLIE.
K2	One of several factors (constant at 12) to generate a value for F2 (above). It is the argument for dummy variable K in function subprogram TABEXE.
K3	One of several factors (constant at 9) to generate a value for F3M1 (above). It is the argument for dummy variable K in function subprogram TABLIE.
KIL	Number of 0-2-year old female crocodiles cannibalized; it differs with age class (TOTKIL * .6, * .3, * .1, respectively). It is the argument for dummy variable KANN in subroutine HUNCR3.
KK	Random number, used each year to determine a value for FLAG (above), which determines weather

Table 11 (cont'd.).

Name	Definition
	conditions. It is also a subscript for WLEV (below), and turns RANNUM (below) into a random number from 1 to 11.
M	Index for the main do loop, designating the number of years simulated. Its highest value is IRNLGTH.
M2	Density-dependent factor influencing rate of cannibalism on 0-2-year old crocodiles; possible values are 0 if the crocodiles number fewer than 500, and 1 if a least 500. A value of 3 is assigned if the number of nesting females exceeds the arbitrary carrying capacity (CCAP) of 1,360.
M3	Factor used in decrementing the hatch by 0.1 when the number of nesting females exceeds the arbitrary carrying capacity (CCAP) of 1,360.
MEEG	Minor extrinsic egg mortality (constant at 0.072).
MHATCH	Number of male hatchlings, i.e., HATCH/2. It is the argument for dummy variable MPIP in subroutine HUNCR1.
MHKIL	Number of males killed by hunting, by age class. It is the argument for dummy variable MHUNKL in subroutines HUNCR2 and HUNCR3.
MPOP	Size of male portion of population. It is the argument for dummy variable MCOHORT in subroutines HUNCR1, HUNCR2, and HUNCR3.
NATMORT	Natural mortality by age class, equal to 1.0 - PSURV (below). It is the argument for dummy variable NATUMOR in subroutine HUNCR3.
NNEST	Number of surviving nests, obtained by number of eggs surviving flood, divided, by average clutch size (HOLD/ACLUTCH). It is one of several variables used to generate a value for F2 (above), and is the argument for dummy variable DUMMY in function subprogram TABEXE.
NORMAL1	Criterion (constant at 5) for random number KK; if

Table 11 (cont'd.).

Name	Definition
	KK is less, FLAG (above) = 1, which means drought.
NORMAL2	Criterion (constant at 7) for random number KK; if KK is greater, FLAG (above) = 2, which means premature flood.
NORPRED	Normal cannibalism rate on 0-2-year old crocodiles (constant at 0.06).
PERBRD	Percent of sexually mature females that are nesting, by age class.
PREDPOP	Size of cannibalistic cohort of the population (AMPOP + AFPOP, see above).
PSURV	Probability of survival to a given age class. It is the argument for dummy variable CHANSRV in subroutine HUNCR3.
RANF(0)	Random number generator, intrinsic to FORTRAN.
RANNUM	Random number obtained by use of RANF(0) (above).
SAVE	Dummy variable used to save the numerical value of the first age class of females (FPOP(1)), later set equal to HOLD (above) when advancing a given age class of females (FPOP(K)) to the next age class (FPOP(K + 1)).
SMALL1	One of several factors (constant at 0.) to generate a value for F1 (above). It is the argument for dummy variable SMALL in function subprogram TABLIE.
SMALL2	One of several factors (constant at 20.) to generate a value for F2 (above). It is the argument for dummy variable SMALL in function subprogram TABEXE.
SMALL3	One of several factors (constant at -1.5) to generate a value for F3M1 (above). It is the argument for dummy variable SMALL in function subprogram TABLIE.
TEGGS	Cumulative number of eggs for the year, resulting from production by each age class producing eggs.

Table 11 (cont'd.).

Name	Definition
TOT	Number of sexually mature females nesting (TOT + (FPOP(67 - K) * PERBRD(67 - K))), accumulated by year classes. This variable is within the main do loop, and gets reinitialized at 0 with every iteration, and therefore lacks a subscript.
TOTKIL	Index of total number of 0-2-year old crocodiles cannibalized ((PREDPOP * F3M1 * M2 * NORPRED)/2). It is partitioned by differing proportions into different age classes (see KIL above).
TPOP	Size of population (TPOP = MPOP(K) + FPOP(K)), accumulated by year class. This variable is within the main do loop, and gets reinitialized at 0 with every iteration, and therefore lacks a subscript.
VAL1	An array from which a value for F1 (above) is obtained by interpolation. It is the argument for dummy variable VAL in function subprogram TABLIE.
VAL2	An array from which a value for F2 (above) is obtained by interpolation or extrapolation. It is the argument for dummy variable VAL in function subprogram TABEXE.
VAL3	An array from which a value for F3M1 (above) is obtained by interpolation. It is the argument for dummy variable VAL in function subprogram TABLIE.
VALUE	Logical parameter, set at ".FALSE.", but reset at ".TRUE." if the accumulated number of nesting females exceeds 1,360 (i.e., CCAP, above), and if so it effects decrementation of HATCH (above) by 0.1 and effects (via M2 = 3) a higher value for TOTKIL (above).
WLEV	A water level index, and array of values used to generate a value for F1 and F3M1 from function subprogram TABLIE. It is then subscripted by KK (above), and is the argument for dummy variable DUMMY in TABLIE.
YRS	Counter for each iteration (representing a year) of the main do loop; it is one less than JJ (above).

Table 12. List of variables in function subprogram TABLIE.

Name	Definition
AMAX1	A function, intrinsic to FORTRAN, that returns a real maximum value of 2-500 arguments in an array of real numbers.
AMIN1	A function, intrinsic to FORTRAN, that returns a real minimum value of 2-500 arguments in an array of real numbers.
DIFF	Dummy variable for arguments DIFF1 and DIFF3 in program CROC, being the difference between adjacent elements in DUMMY (below). It is an element in generating a value for VAL (below).
DUM	Dummy variable that temporarily holds a value. It is the amount by which the DUMMY (below) argument is larger than SMALL (below), and it is converted to 0 if it is less than SMALL.
DUMMY	Dummy variable for argument WLEV(KK) in program CROC, and the array that is the basis for interpolation in generating a value for VAL (below).
FLOAT	A function, intrinsic to FORTRAN, that transforms an integer to a real value.
I	The interval within which the DUMMY argument is found.
K	Dummy variable for arguments K1 and K3 in program CROC, and the number of intervals between elements in DUMMY (above). It is an element in generating a value for VAL (below).
SMALL	Dummy variable for arguments SMALL1 and SMALL3 in program CROC, and the smallest element in DUMMY (above). It is an element in generating a value for VAL (below).
VAL	Dummy variable for arguments VAL1 and VAL3 in program CROC, and the array from which a value is returned to F1 and F3MI, respectively, in program CROC.

Table 13. List of variables in function subprogram TABEXE.

Name	Definition
DIFF	Dummy variable for argument DIFF2 in program CROC, being the difference between adjacent elements in DUMMY (below). It is an element in generating a value for VAL (below).
DUM	Dummy variable that temporarily holds a value. It is the difference between the DUMMY (below) argument and the minimum of the argument array, SMALL (below).
DUMMY	Dummy variable for argument NNEST in program CROC, and the array that is the basis for interpolation in generating a value for VAL (below).
FLOAT	A function, intrinsic to FORTRAN, that transforms an integer to a real value.
I	The interval within which the DUMMY argument is found. It is held within the limits of 1 and K (below).
K	Dummy variable for argument K2 in program CROC, and the number of intervals between elemets in DUMMY (above). It is an element in generating a value for VAL (below).
MAX1	A function, intrinsic to FORTRAN, that returns as an integer result the largest value of 2-500 arguments in an array of real numbers.
MIN0	A function, intrinsic to FORTRAN, that returns as an integer the smallest value of 2-500 arguments in an array of integer numbers.
SMALL	Dummy variable for argument SMALL2 in program CROC, and the smallest element in DUMMY (above). It is an element in generating a value for VAL (below).
VAL	Dummy variable for argument VAL2 in program CROC, and the array from which a value is returned to F2 in program CROC.

Table 14. List of variables in subroutine HUNCR1.

Name	Definition
HOLD	Dummy variable standing for number of males in a given age class (MCOHORT(K)) except the first, later assigned to dummy variable SAVE, when advancing each age class one year.
MCOHORT	Size of male portion of population. It is the dummy variable for argument MPOP in program CROC.
MPIP	Number of male hatchlings. It is the dummy variable for argument MHATCH in program CROC.
SAVE	Dummy variable used to save the numerical value of the first age class of males (MCOHORT(1)), later set equal to HOLD (see above) when advancing a given age class of males (MCOHORT(K)) to the next age class (MCOHORT(K + 1)).
YARS	Counter for each iteration (representing a year) of the main do loop in the calling program, CROC (within which all subroutines are called). It is the dummy variable for argument YRS in program CROC.

Table 15. List of variables in subroutine HUNCR2.

Name	Definition
EFFIC	Efficiency of hunter (constant at 0.3).
FCOHORT	Size of female portion of population. It is the dummy variable for argument FPOP in program CROC.
FHUNKL	Number of females killed by hunting, by age class. It is the dummy variable for argument FHKIL in program CROC.
FHUNT	Female fraction of population actually hunted ((HFPOP/THPOP) * HUNT).
FLAGG	Variable initialized at 0, but set at 1 whenever HFPOP (below) equals 0, so as to avoid simulated hunting of females.
HFPOP	Huntable portion of female cohort (3-6 years old, 120-190 cm long).
HMPOP	Huntable portion of male cohort (2-4 years old, 120-190 cm long).
HUNT	Harvest, i.e., huntable cohort of population times efficiency (THPOP * EFFIC).
MCOHORT	Size of male portion of population. It is the dummy variable for argument MPOP in program CROC.
MHUNKL	Number of males killed by hunting, by age class. It is the dummy variable for argument MHKIL in program CROC.
MHUNT	Male fraction of population actually hunted ((HMPOP/THPOP) * HUNT).
NONHUNT	The number (constant at 300) which must be exceeded by the huntable cohort (THPOP, below) if hunting is to take place in any one year.
THPOP	Total huntable cohort of the population (HMPOP + HFPOP).

Table 16. List of variables in subroutine HUNCR3.

Name	Definition
CHANSRV	Probability of survival to a given age class. It is the dummy variable for argument PSURV in program CROC.
KANN	Number of 0-2-year old female crocodiles cannibalized. It is the dummy variable for argument KIL in program CROC.
MCOHORT	Size of male portion of the population. It is the dummy variable for argument MPOP in program CROC.
MHUNKL	Number of males killed by hunting, by age class. It is the dummy variable for argument MHKIL in program CROC.
MKANN	Number of 0-2-year old male crocodiles cannibalized; each age class is set equal to the corresponding age class of KANN (see above).
NATUMOR	Natural mortality by age class. It is the dummy variable for argument NATMORT in program CROC.

APPENDIX C: YEARLY VALUES FOR POPULATION SIZE

APPENDIX C: YEARLY VALUES FOR POPULATION SIZE

Table 17. Values for population size at original values for all parameters (Figure 13).

9730.					
6489.	7816.	27672.	26476.	26195.	26082.
4268.	9324.	28379.	24051.	24572.	19170.
3930.	6827.	20258.	23707.	23890.	24318.
3808.	8459.	16351.	22434.	27223.	27524.
3735.	6324.	22977.	21741.	28950.	29301.
3599.	7972.	17579.	24244.	29476.	20999.
3513.	6025.	14838.	26434.	30165.	25736.
3446.	7791.	13305.	27280.	30370.	27405.
3393.	8592.	20801.	25675.	30856.	29181.
3320.	9078.	24361.	26460.	31473.	30108.
3253.	9534.	24486.	24551.	28860.	29777.
2706.	9721.	23915.	24488.	30312.	30729.
2991.	10195.	24775.	18270.	31203.	31273.
3095.	10717.	18252.	24515.	31815.	27470.
3197.	11209.	22091.	27043.	31728.	25961.
3319.	11688.	23867.	19516.	29756.	28767.
3397.	11971.	17916.	15857.	22511.	29876.
2635.	12549.	15014.	23061.	27423.	30338.
2267.	12901.	22433.	26676.	26480.	21891.
3360.	9219.	25610.	27155.	20699.	26743.
2616.	11461.	26259.	26884.	25540.	20220.
3756.	12761.	26650.	28328.	29254.	17030.
4403.	14328.	27727.	29414.	30507.	24663.
3157.	14918.	28832.	29667.	27917.	27128.
2571.	15462.	20865.	30095.	26984.	28232.
4420.	10897.	25439.	30535.	29110.	20568.
5294.	14464.	27186.	28318.	21592.	25183.
5978.	16293.	20230.	29405.	25342.	26305.
6163.	17516.	23684.	30169.	28645.	28783.
4233.	12229.	23881.	30729.	26240.	30011.
5898.	15550.	26395.	29529.	29055.	21677.
6898.	17660.	19636.	21738.	26025.	26907.
4763.	12522.	24273.	25340.	26699.	27159.
3743.	16487.	27465.	28496.	29051.	28994.
6194.	18144.	28705.	28758.	26911.	29170.
7411.	18697.	20911.	28925.	28737.	28866.
5136.	20119.	17163.	27471.	27669.	21331.
3995.	20750.	15276.	27699.	20616.	26824.
6631.	21684.	22589.	20734.	25741.	28885.
7851.	22185.	25302.	25483.	27380.	28975.
5442.	23055.	18748.	19622.	25101.	30153.
7618.	16279.	15501.	23091.	24020.	28562.
8758.	20519.	13826.	25468.	25064.	28151.
9458.	23059.	22900.	24062.	24729.	26621.
9943.	24506.	16742.	25531.	18799.	29053.
10208.	24367.	23658.	27948.	23442.	21645.
10155.	24522.	26766.	26907.	26249.	27011.
10718.	25934.	19302.	28541.	26046.	25918.
11079.	25763.	24128.	29579.	23769.	27675.
11294.	27390.	25408.	29969.	22744.	29656.

Table 18. Values for population size at low estimate of initial size (Figure 13).

7840.					
5300.	6464.	22880.	26423.	25872.	26123.
3471.	7723.	23461.	23865.	24300.	19225.
3191.	5653.	16748.	23589.	23615.	24350.
3097.	7020.	13517.	22470.	27464.	27547.
3044.	5245.	18989.	21959.	28937.	29321.
2940.	6628.	14528.	24227.	29323.	21039.
2875.	5003.	12263.	26327.	29936.	25771.
2843.	6480.	10996.	27853.	30136.	27427.
2839.	7150.	18766.	25856.	30611.	29201.
2840.	7554.	22745.	26574.	31227.	30124.
2846.	7931.	24673.	24642.	28634.	29845.
2299.	8081.	25923.	24594.	30731.	30838.
2616.	8467.	25071.	18361.	31315.	31414.
2692.	8890.	17849.	24661.	31803.	27603.
2751.	9285.	21516.	27067.	31678.	25719.
2819.	9667.	23457.	19504.	29711.	28745.
2828.	9887.	17289.	15820.	22479.	29959.
2197.	10349.	14263.	23242.	27384.	30467.
1892.	10626.	21157.	26197.	26440.	21972.
2753.	7599.	24578.	27016.	28658.	26888.
2155.	9431.	25361.	26151.	25499.	20314.
3063.	10493.	25706.	28030.	29201.	17103.
3580.	11777.	26697.	29292.	31122.	24386.
2581.	12261.	27745.	29624.	28206.	27124.
2109.	12711.	19912.	30114.	27167.	28083.
3599.	8965.	24499.	30574.	29243.	20504.
4305.	11900.	26182.	28356.	21685.	25248.
4862.	13408.	19350.	29443.	25157.	26409.
5017.	14420.	23085.	30161.	28778.	28538.
3455.	10071.	23631.	30666.	26352.	29775.
4812.	12814.	25834.	29415.	29133.	21554.
5633.	14560.	19070.	21644.	26120.	26011.
3895.	10325.	23645.	25179.	26784.	27214.
3064.	13607.	26967.	28270.	29109.	29076.
5078.	14983.	28364.	28952.	27173.	29262.
6083.	15445.	20520.	28872.	29305.	28964.
4192.	16627.	16756.	27302.	27945.	21376.
3280.	17155.	14879.	27424.	20788.	26154.
5459.	17933.	21813.	20553.	25854.	28584.
6494.	18350.	25149.	25540.	27468.	28829.
4482.	19073.	18534.	19600.	25169.	30067.
6284.	13463.	15274.	23233.	24066.	28488.
7230.	16975.	13610.	25315.	25081.	28079.
7811.	19077.	21573.	23807.	24720.	26551.
8214.	20275.	16468.	25186.	18818.	28981.
8435.	20159.	23126.	27522.	23410.	21582.
8392.	20284.	25761.	26283.	26180.	26951.
8859.	21451.	18472.	28423.	26508.	25871.
9160.	21307.	23373.	29282.	23934.	27637.
9341.	22401.	24690.	29617.	22822.	29623.

Table 19. Values for population size at high estimate of initial size (Figure 13).

11614.					
7617.	9024.	28875.	26530.	26068.	25961.
5034.	10743.	29366.	24386.	24613.	19112.
4538.	7868.	21459.	23987.	23421.	24253.
4315.	9719.	17621.	22819.	27112.	27470.
4179.	7273.	22342.	22241.	28988.	28673.
3982.	9141.	17834.	24687.	29553.	20690.
3849.	6921.	15504.	26335.	30244.	25221.
3754.	8940.	14154.	27607.	30417.	27195.
3706.	9867.	21969.	25681.	30873.	29119.
3665.	10442.	25483.	26602.	31450.	30110.
3624.	10989.	25459.	24623.	28850.	29862.
3051.	11229.	24598.	24726.	30299.	30869.
3390.	11803.	25441.	18429.	31176.	31451.
3538.	12432.	19010.	24439.	31766.	27637.
3704.	13023.	22551.	26867.	31659.	25753.
3880.	13596.	24627.	19470.	30402.	28786.
3989.	13935.	18662.	15869.	22809.	30005.
3972.	14615.	15752.	22945.	27534.	30513.
2633.	15027.	22894.	26507.	26518.	21971.
3951.	10726.	26397.	26976.	20720.	26889.
3060.	13339.	27179.	26765.	25544.	20289.
4423.	14850.	27458.	28226.	29243.	17064.
5193.	16670.	28519.	29312.	31174.	24325.
3707.	17348.	29622.	30252.	28270.	27037.
3007.	17974.	21546.	30369.	27220.	27983.
5194.	12662.	26084.	30659.	29288.	20425.
6223.	16796.	27839.	28353.	21715.	25136.
7021.	18910.	20809.	29413.	25157.	26288.
7227.	20321.	23955.	30144.	28732.	28751.
4956.	14187.	23798.	30679.	26295.	29951.
6893.	18024.	26462.	29452.	29084.	21617.
8050.	20457.	19839.	21729.	26071.	25920.
5557.	14509.	24464.	25393.	26697.	27058.
4364.	19084.	27714.	28637.	29031.	28875.
7201.	20992.	29584.	28958.	27108.	29045.
8605.	21626.	21452.	29197.	29203.	29401.
5932.	23264.	17542.	27795.	27827.	21571.
4642.	23989.	15571.	27517.	20726.	26825.
7685.	25067.	22773.	20685.	25740.	29277.
9125.	25646.	25844.	25673.	27327.	29026.
6307.	26652.	19082.	19748.	25036.	30034.
8817.	18825.	15722.	23342.	23948.	29000.
10131.	23728.	13977.	25410.	24965.	28242.
10937.	26666.	22005.	24180.	24614.	27194.
11496.	28342.	16758.	25198.	18753.	29210.
11802.	28186.	23569.	27976.	23346.	21752.
11741.	28369.	26428.	26169.	26127.	26967.
12388.	30009.	18783.	28095.	25911.	25848.
12800.	28831.	23897.	29528.	23631.	27987.
13041.	29241.	25098.	29471.	22609.	30965.

Table 20. Values for population size at initial age structure as a narrow pyramid (Figure 14).

9722.					
6820.	9504.	28985.	25983.	26186.	26096.
4757.	11207.	29727.	23936.	24581.	19190.
4487.	8301.	21792.	23625.	23919.	24329.
4320.	10288.	17961.	22494.	27277.	27531.
4180.	7762.	22784.	21978.	29020.	29368.
3990.	9884.	18249.	24434.	29546.	21045.
3869.	7498.	15915.	26081.	30226.	25400.
3794.	9839.	14569.	27366.	30412.	27293.
3773.	10949.	22499.	25443.	30874.	29175.
3759.	11654.	25982.	26570.	31468.	30148.
3765.	12321.	25690.	24400.	28838.	29832.
3172.	12629.	25084.	24504.	30272.	30794.
3647.	13314.	25641.	18270.	31152.	31350.
3879.	14055.	19257.	24265.	31755.	27541.
4144.	14749.	23136.	26698.	31665.	26037.
4449.	15413.	24806.	19343.	30417.	28866.
4632.	15796.	18866.	15766.	22837.	29992.
3492.	16557.	15962.	22921.	27575.	30461.
2953.	17007.	23583.	26560.	26560.	21963.
4613.	12098.	26648.	27073.	20762.	26833.
3509.	15024.	27691.	26850.	25597.	20275.
5187.	16695.	27386.	28314.	29306.	17068.
6114.	18701.	28829.	29435.	30558.	24715.
4304.	19423.	29402.	29708.	27964.	27180.
3454.	20075.	21488.	30165.	27040.	28283.
5999.	14142.	26273.	30588.	29181.	20604.
7190.	18680.	28101.	28344.	21647.	25230.
8093.	20982.	20950.	29433.	25112.	26357.
8313.	22502.	24044.	30181.	28729.	28837.
5685.	15730.	23804.	30705.	26320.	30064.
7894.	19912.	26996.	29461.	29140.	21713.
9207.	22554.	20094.	21712.	26104.	26048.
6348.	16023.	24977.	25346.	26778.	27201.
4978.	21009.	28311.	28551.	29134.	29034.
8174.	23076.	29466.	28840.	26992.	29207.
9731.	23761.	21398.	29040.	28819.	28898.
6711.	25546.	17507.	27614.	27745.	21356.
5259.	26334.	15536.	27816.	20676.	26850.
8621.	27514.	23110.	20797.	25814.	28909.
10207.	28151.	25789.	25563.	27453.	28966.
7065.	29261.	19001.	19666.	25161.	30130.
9827.	20687.	15616.	23143.	24072.	28527.
11248.	23813.	13852.	25495.	25113.	28112.
12084.	26567.	21470.	24076.	24772.	26581.
12618.	27952.	16417.	25530.	18835.	29011.
12846.	27842.	23191.	27934.	23477.	21625.
12657.	27849.	26138.	25992.	26280.	26978.
13193.	28749.	18579.	28510.	26072.	25881.
13481.	28403.	23362.	29552.	23786.	27635.
13613.	29315.	24493.	29943.	22754.	29617.

Table 21. Values for population size at even initial age structure (Figure 14).

```
 9730.

18435.      21885.      30761.      26548.      26230.      26088.
12466.      25811.      31714.      24454.      24628.      19187.
17727.      20031.      23287.      24129.      23913.      24332.
20017.      23823.      19199.      23010.      27229.      27531.
22446.      18820.      23494.      22464.      28946.      29360.
21115.      25542.      19020.      24422.      29404.      21042.
21972.      19417.      16680.      26354.      30023.      25387.
23201.      24949.      15289.      27113.      30192.      27267.
24575.      26444.      23606.      25535.      30625.      29143.
26703.      26280.      27510.      26345.      31212.      30111.

27410.      27445.      26952.      24464.      28611.      29890.
18550.      24985.      25974.      24425.      30694.      30914.
24152.      26807.      26250.      18273.      31269.      31510.
26077.      28708.      19709.      24500.      31755.      27700.
27327.      29784.      23180.      27035.      31582.      25819.
28262.      30404.      25017.      19551.      30320.      28857.
27872.      27943.      18978.      15918.      22780.      30077.
19530.      28070.      15985.      23206.      27497.      30587.
15514.      26201.      23616.      26185.      26471.      22030.
22163.      19682.      27004.      27070.      20698.      26947.

16650.      24485.      27953.      26254.      25512.      20342.
22094.      26790.      28105.      28237.      29195.      17115.
24285.      28778.      28949.      29549.      31102.      24364.
17498.      25613.      29649.      29891.      28741.      27084.
14188.      24429.      21523.      30371.      27427.      28032.
20937.      18690.      26152.      30826.      29397.      29470.
23558.      24814.      27861.      27895.      21789.      25188.
25583.      27040.      20773.      29327.      25211.      26335.
25842.      28533.      24396.      30239.      28807.      28800.
18486.      20683.      23794.      30848.      26359.      29995.

23977.      23351.      26751.      29632.      29150.      21655.
27273.      27202.      19922.      21795.      26109.      25956.
19516.      20026.      24735.      25268.      26776.      27093.
15756.      25345.      27976.      28342.      29123.      28914.
22093.      25231.      29758.      28866.      26988.      29085.
24453.      27253.      21487.      29191.      25814.      28776.
18075.      29082.      17509.      27783.      27742.      21272.
14922.      27733.      15508.      27481.      20686.      26743.
21529.      29287.      22565.      20629.      25809.      28792.
23186.      27978.      25694.      25553.      27444.      28846.

17337.      29782.      18979.      19654.      25152.      30005.
22934.      21758.      15648.      23174.      24058.      28404.
25475.      24834.      13927.      25563.      25089.      27992.
26730.      28347.      22097.      24152.      24728.      27095.
27396.      30001.      16819.      25070.      18823.      29204.
26119.      30127.      23650.      27760.      23437.      21711.
27213.      30225.      26692.      25949.      26221.      26986.
28520.      31204.      18970.      29535.      26004.      25878.
29260.      31221.      23881.      29594.      23696.      27623.
29734.      31509.      25040.      29988.      22708.      29603.
```

Table 22. Values for population size at inverted initial age structure (Figure 14).

9736.					
12813.	9530.	29406.	26809.	26193.	26092.
6966.	12169.	29837.	24630.	24734.	19200.
8948.	8829.	21805.	24204.	23542.	24364.
9528.	11872.	17897.	22966.	27239.	27590.
9527.	8602.	22786.	22372.	29107.	28793.
8967.	11576.	18135.	24782.	29652.	20773.
8562.	8358.	15722.	26401.	30335.	25311.
8202.	10982.	14318.	27634.	30487.	27284.
7844.	11892.	22198.	25684.	30933.	29203.
7401.	12172.	25704.	26765.	31497.	30184.
6878.	12307.	25665.	24842.	28892.	29963.
4902.	12081.	24791.	24778.	30335.	30983.
5287.	12207.	25560.	18470.	31205.	31564.
5145.	12405.	19075.	24385.	31788.	27758.
4925.	12608.	22551.	27390.	31674.	25868.
4700.	12837.	24523.	19743.	30417.	28906.
4399.	12933.	18619.	16026.	22820.	30126.
3478.	13366.	15739.	22956.	27534.	30631.
3003.	13618.	22871.	26474.	26513.	22056.
3488.	9942.	25836.	26923.	20717.	26988.
2946.	12137.	26994.	26663.	25527.	20365.
3477.	13439.	26958.	28099.	29197.	17130.
3748.	15057.	28564.	29200.	31095.	24411.
3036.	15729.	29351.	30188.	28749.	27131.
2656.	16393.	21440.	30339.	27437.	28080.
3851.	11696.	25890.	30636.	29349.	20497.
4431.	15623.	27685.	28354.	21753.	25218.
5043.	17728.	20778.	29453.	25438.	26366.
5360.	19235.	23980.	30238.	28836.	28829.
3883.	13477.	23890.	30798.	26332.	30025.
5461.	17410.	26703.	29597.	29087.	21673.
6522.	20010.	20023.	21828.	26064.	25973.
4595.	14158.	24857.	25320.	26684.	27109.
3682.	19008.	28292.	28435.	29011.	28926.
6276.	21139.	29550.	28980.	27093.	29097.
7665.	21523.	21527.	29324.	29193.	28789.
5280.	23750.	17668.	27405.	27823.	21281.
4140.	24622.	15718.	27415.	20736.	26706.
7157.	25824.	23283.	20635.	25764.	29239.
8655.	26484.	26533.	25744.	27366.	29020.
5922.	27561.	19491.	19779.	25085.	30050.
8491.	19336.	15996.	23067.	24010.	29026.
9882.	24462.	14187.	25337.	25045.	28278.
10761.	27514.	21899.	24199.	24698.	27235.
11384.	29230.	16767.	25265.	18814.	29268.
11743.	29021.	23921.	28064.	23444.	21783.
11748.	29155.	26919.	26258.	26249.	27028.
12540.	30785.	19061.	28196.	26038.	25909.
13163.	29475.	23878.	29629.	23748.	27642.
13730.	29843.	25301.	29566.	22721.	29941.

Table 23. Values for population size at PERBRD increased by 15% (Figure 15).

9738.					
6479.	9285.	29770.	26540.	26287.	27159.
4263.	11380.	30198.	24358.	24671.	19776.
3954.	8210.	22193.	24119.	24231.	24723.
3818.	18339.	18329.	23132.	27622.	28056.
3718.	7666.	23285.	22491.	29513.	29240.
3563.	9936.	18618.	24912.	30095.	21082.
3462.	7414.	16255.	26442.	30744.	25843.
3394.	9889.	14898.	27784.	30787.	28156.
3351.	10998.	22781.	25655.	31836.	30058.
3321.	11744.	26161.	26999.	31882.	30854.
3298.	12424.	26481.	24826.	28994.	30239.
2747.	12776.	25486.	24682.	31109.	31067.
3127.	13462.	25720.	18432.	31589.	31860.
3321.	14289.	19413.	24454.	32150.	28308.
3518.	14932.	23188.	27587.	32104.	26612.
3721.	15632.	25387.	19853.	30795.	29312.
3832.	16860.	19247.	16137.	23139.	30468.
2880.	16838.	16247.	23359.	27784.	31280.
2428.	17374.	23666.	27073.	26772.	22484.
3693.	12262.	27488.	27516.	20966.	27497.
2826.	15338.	28132.	27138.	25858.	20728.
4160.	17117.	28371.	28468.	29738.	17424.
4926.	19306.	29326.	29718.	31663.	24584.
3469.	20215.	30488.	29944.	28615.	27174.
2783.	21876.	22145.	30538.	27037.	28497.
4925.	14696.	26547.	30967.	29056.	20800.
5966.	19683.	28783.	28744.	21700.	26038.
6751.	22293.	21489.	29761.	25360.	27211.
6951.	24852.	24559.	30515.	29074.	29345.
4718.	16645.	24281.	31204.	26385.	30511.
6664.	21470.	27416.	29421.	29227.	22059.
7827.	24581.	20391.	21785.	25975.	26741.
5348.	17216.	25171.	25622.	26965.	27895.
4164.	22973.	28260.	28552.	29447.	29671.
7005.	25531.	30810.	29195.	26844.	29729.
8448.	26328.	21703.	29691.	29022.	30115.
5764.	26985.	17686.	28047.	28527.	22117.
4472.	26288.	15644.	27943.	21129.	27344.
7597.	27286.	22923.	20942.	26170.	29156.
9099.	26929.	26282.	26177.	27642.	29296.
6217.	28093.	19240.	20856.	25308.	30677.
8887.	20280.	15786.	23637.	24257.	29035.
10210.	23872.	14083.	25620.	25231.	28541.
11826.	26809.	22294.	24513.	24916.	27664.
11703.	28138.	16919.	25961.	18968.	29759.
12853.	28199.	23384.	28320.	23885.	22158.
11991.	28172.	26988.	26701.	26183.	27496.
12744.	29333.	19075.	29142.	26298.	25613.
13218.	28972.	24153.	30060.	24276.	27776.
13495.	28859.	25292.	30293.	23219.	30301.

Table 24. Values for population size at PERBRD decreased by 15% (Figure 15).

9730.					
6474.	8557.	18302.	25035.	25507.	25687.
4260.	7735.	18674.	23136.	24052.	18839.
3865.	5694.	13468.	22727.	23025.	23733.
3706.	6882.	10951.	21801.	26629.	26716.
3610.	5194.	14990.	21011.	28097.	28349.
3461.	5449.	11606.	23682.	28563.	20386.
3368.	4921.	9878.	25562.	29317.	24990.
3314.	6210.	8902.	26971.	29478.	27009.
3294.	6797.	14593.	25951.	30495.	28958.
3280.	7136.	17523.	25917.	30786.	29945.
3217.	7458.	18865.	23444.	28022.	29313.
2658.	7552.	19683.	23822.	30014.	29997.
2916.	7884.	20632.	17969.	30695.	30571.
3069.	8252.	14589.	23748.	31298.	26847.
3181.	8595.	18860.	28656.	31265.	25008.
3215.	8920.	21225.	19315.	29536.	28005.
3246.	9045.	15197.	15753.	22277.	29400.
2542.	9418.	12264.	23198.	27062.	30077.
2282.	9616.	18903.	26272.	26066.	21602.
3122.	6973.	22270.	27127.	26379.	26506.
2476.	8568.	22985.	26285.	25135.	19957.
3431.	9476.	24487.	28089.	28730.	16764.
3961.	10564.	25795.	28835.	30406.	23994.
2903.	10901.	26864.	29523.	28039.	26411.
2462.	11256.	18815.	30039.	26790.	27475.
3970.	8044.	23995.	30428.	28823.	20051.
4683.	10572.	25561.	27896.	21375.	24760.
5256.	11842.	18580.	29434.	24501.	26016.
5414.	12692.	23955.	30160.	28215.	27879.
3762.	8954.	26386.	30787.	25731.	28895.
5176.	11229.	27131.	29167.	28512.	20964.
6019.	12701.	19457.	21417.	25637.	25222.
4216.	9096.	24031.	24739.	26107.	26373.
3353.	11834.	27750.	27806.	28384.	28289.
5399.	12911.	29808.	28323.	26019.	28449.
6405.	13268.	21181.	28571.	28059.	28262.
4477.	14187.	16926.	26938.	27232.	20854.
3544.	14562.	14858.	26895.	20268.	26073.
5763.	15181.	21437.	20091.	24842.	28141.
6778.	15455.	24681.	24628.	26770.	28312.
4738.	16019.	18166.	18947.	24620.	29505.
6547.	11417.	14980.	22254.	23411.	28080.
7505.	14158.	13348.	24578.	24840.	27649.
8065.	15839.	20566.	23416.	24198.	26532.
8477.	16762.	15866.	24444.	18408.	28789.
8643.	16595.	22136.	26961.	22951.	21370.
8588.	16611.	24930.	25381.	25257.	26553.
9047.	17476.	17965.	27682.	25477.	24934.
9362.	17275.	22749.	28746.	23588.	27023.
9408.	18009.	23808.	28975.	22061.	28813.

Table 25. Values for population size at CLUTCH increased by 15% (Figure 16).

9730.					
6608.	9438.	33181.	30544.	30465.	31085.
4328.	11435.	34089.	28055.	28619.	22673.
4067.	8320.	24861.	27854.	27037.	28301.
3992.	10538.	20411.	26718.	31545.	32103.
3948.	7806.	26155.	26027.	33990.	33454.
3830.	10057.	20831.	28792.	34049.	24149.
3759.	7512.	18096.	30564.	35183.	29633.
3703.	9943.	16524.	32058.	35462.	32318.
3658.	11082.	25626.	29719.	36770.	34541.
3588.	11790.	29614.	31221.	36861.	35507.
3526.	12437.	29360.	28709.	33480.	34848.
2902.	12754.	28846.	28438.	35913.	35844.
3237.	13414.	29502.	21267.	36459.	36719.
3371.	14136.	22079.	28166.	37195.	32622.
3495.	14827.	26609.	31633.	37156.	30677.
3638.	15505.	28543.	22819.	35628.	33811.
3746.	15966.	21670.	18535.	26749.	35165.
2862.	16781.	18316.	26730.	32115.	36136.
2437.	17329.	27223.	30901.	30995.	25947.
3702.	12242.	30812.	32186.	24251.	31717.
2844.	15337.	32176.	31318.	29945.	23896.
4176.	17147.	31985.	32611.	34435.	20079.
4944.	19355.	33681.	33932.	35881.	28347.
3493.	20287.	34342.	35262.	32809.	31340.
2810.	21119.	25042.	35368.	31170.	32852.
4966.	14728.	29895.	35625.	33634.	23975.
6016.	19720.	32548.	32941.	25068.	30006.
6821.	22331.	24289.	34901.	29442.	31362.
7037.	24088.	28245.	35238.	33796.	33816.
4779.	16675.	27231.	35794.	30707.	35142.
6755.	21487.	30893.	34580.	33987.	25406.
7942.	24512.	23116.	25464.	30222.	30831.
5427.	17232.	28713.	29531.	30634.	32147.
4226.	22969.	32410.	33446.	33833.	34164.
7146.	25497.	34576.	34243.	30974.	34202.
8616.	26333.	25017.	34429.	33535.	34615.
5874.	28488.	20415.	32850.	32615.	25434.
4553.	29559.	18091.	32435.	24204.	31408.
7719.	31001.	26875.	24328.	29990.	34446.
9257.	31886.	29876.	30251.	31661.	34111.
6325.	33246.	22050.	23225.	28968.	35466.
8964.	23228.	18144.	27289.	27749.	34240.
10359.	27016.	16106.	29539.	28862.	33252.
11228.	30064.	24852.	28241.	28433.	32056.
11842.	31585.	19034.	29917.	21683.	34377.
12219.	31364.	26744.	32653.	27151.	25633.
12168.	31549.	30247.	30809.	30622.	31743.
12894.	32745.	21524.	33664.	30405.	29555.
13388.	32333.	27560.	34765.	27891.	32032.
13721.	33465.	29006.	35081.	26592.	34928.

Table 26. Values for population size at CLUTCH decreased by 15% (Figure 16).

9730.					
6371.	6324.	17292.	21393.	21667.	21797.
4208.	7409.	17627.	19417.	20069.	16000.
3794.	5462.	12729.	19265.	19435.	20460.
3624.	6558.	10360.	18519.	22663.	22838.
3523.	4983.	14138.	17846.	23993.	24162.
3368.	6125.	10963.	20105.	24427.	17375.
3268.	4692.	9340.	22002.	25098.	21285.
3190.	5904.	8423.	22918.	25254.	23084.
3125.	6429.	13806.	21366.	25765.	24662.
3051.	6737.	16530.	22139.	26215.	25496.
2979.	7039.	17772.	20052.	23932.	24953.
2510.	7127.	18537.	20247.	25180.	25529.
2745.	7451.	19438.	15193.	26004.	26012.
2819.	7810.	13762.	20437.	26622.	22846.
2900.	5142.	17779.	22568.	26612.	21281.
3000.	8461.	20009.	16285.	25135.	23822.
3050.	8611.	14338.	13225.	18934.	25002.
2408.	9000.	11580.	19149.	23086.	25573.
2099.	9204.	17870.	22022.	22158.	18375.
3020.	6671.	21111.	22680.	17314.	22535.
2390.	8220.	21774.	21956.	21365.	16974.
3339.	9109.	23179.	23414.	24397.	14262.
3867.	10165.	23282.	24352.	25859.	20390.
2825.	10495.	23439.	24976.	23852.	22435.
2333.	10821.	16720.	25400.	22786.	23350.
3882.	7727.	20366.	25606.	24504.	17047.
4586.	10154.	21767.	23452.	18163.	21047.
5154.	11367.	16048.	24663.	20810.	22111.
5311.	12175.	19302.	25319.	23961.	23691.
3701.	8588.	19756.	25585.	21837.	24568.
5067.	10752.	21463.	24336.	24181.	17825.
5890.	12150.	15787.	17916.	21755.	21452.
4120.	5704.	19666.	20875.	22021.	22014.
3273.	11301.	22239.	23485.	24004.	23854.
5280.	12310.	23465.	23972.	22001.	24088.
6260.	12657.	16942.	24139.	23734.	23977.
4370.	13536.	13811.	22948.	23044.	17690.
3456.	13862.	12249.	22915.	17159.	22149.
5598.	14429.	18103.	17079.	21038.	23926.
6582.	14670.	20695.	20975.	22580.	24084.
4604.	15190.	15258.	16153.	20847.	24712.
6353.	10842.	12580.	19027.	19822.	23707.
7259.	13437.	11216.	20757.	21036.	23438.
7805.	15001.	17354.	19903.	20492.	22535.
8175.	15854.	13369.	20855.	15592.	24484.
8343.	15714.	18615.	23068.	19417.	18155.
8294.	15743.	21199.	21721.	21837.	22593.
8712.	16526.	15208.	23402.	21783.	21226.
8959.	16346.	19263.	24482.	20015.	23014.
9076.	17054.	20045.	24467.	18740.	24543.

Table 27. Values for population size at raised PSURV values for the first 20 years of life (Figure 17a).

9738.					
7157.	24493.	44413.	37928.	35320.	30508.
5273.	29112.	45835.	33555.	31474.	24605.
5088.	23206.	37543.	32650.	29897.	30784.
4977.	28474.	33380.	30337.	34584.	34194.
4897.	22883.	34891.	27405.	37791.	36736.
4791.	28560.	31144.	31969.	39148.	28932.
4750.	23067.	28942.	35450.	39820.	34345.
4721.	29467.	27436.	36844.	41823.	35729.
4699.	32896.	36598.	32674.	42647.	38497.
4666.	33070.	39673.	34835.	44142.	38860.
4637.	38300.	37960.	30331.	38345.	38102.
4098.	33017.	34059.	29308.	41451.	40787.
4431.	34674.	34298.	25112.	43187.	42290.
4595.	36835.	29086.	32032.	43607.	36432.
4784.	38073.	32477.	36236.	44758.	33453.
5004.	39265.	34113.	28986.	40873.	37935.
5239.	37427.	28487.	25602.	34562.	40417.
4363.	38433.	25553.	33962.	38559.	40708.
3938.	36678.	33660.	37080.	34665.	32341.
5528.	30694.	36977.	36338.	39488.	38345.
4525.	35673.	38833.	35413.	35286.	31339.
6313.	38193.	38578.	37852.	38989.	27811.
7473.	39994.	40815.	40191.	41466.	35556.
5749.	35657.	42078.	42051.	36838.	38694.
4970.	34421.	33693.	43320.	33922.	39057.
8059.	29696.	37939.	42876.	38508.	31780.
9667.	36462.	40664.	38054.	31499.	36195.
11198.	38129.	33227.	40701.	33879.	37081.
11823.	40018.	34899.	42622.	38348.	40399.
8892.	33047.	32589.	42664.	32352.	42421.
12009.	33960.	37237.	40758.	36672.	34157.
13992.	38087.	30757.	33507.	31942.	39371.
10503.	31942.	36417.	35888.	32239.	39769.
8882.	37634.	39863.	40546.	35897.	42187.
13408.	35661.	40761.	40392.	33098.	42711.
15814.	39171.	33142.	41049.	36409.	42540.
11892.	40536.	29448.	37447.	34777.	35069.
10858.	38280.	27285.	37592.	28550.	40092.
15160.	40603.	34335.	31371.	33606.	42986.
17785.	38903.	37158.	36518.	36258.	41821.
13449.	41499.	30506.	30764.	31303.	43620.
18111.	34363.	27271.	33403.	28792.	40607.
20804.	35703.	25395.	35675.	30828.	39976.
22752.	39591.	32472.	32357.	28924.	36983.
24463.	42217.	27432.	33939.	24649.	39836.
25861.	43042.	34361.	37472.	29060.	33669.
26542.	44376.	37761.	33817.	31270.	39906.
28551.	45827.	30277.	37831.	31619.	35037.
30284.	45705.	35650.	39271.	27126.	38115.
31893.	46014.	34635.	40816.	25345.	41178.

Table 28. Values for population size at lowered PSURV values for the first 20 years of life (Figure 17a).

9730.					
6139.	1376.	1579.	1096.	1054.	1060.
3789.	1727.	1570.	1118.	1060.	713.
3273.	1228.	1059.	1131.	1062.	900.
2941.	1590.	815.	1126.	1085.	983.
2721.	1103.	1137.	1117.	1095.	1021.
2520.	1435.	814.	1095.	1065.	634.
2407.	911.	663.	1119.	1083.	823.
2341.	1276.	581.	1134.	1054.	927.
2303.	1409.	1017.	1128.	1069.	977.
2254.	1465.	1216.	1139.	1072.	1002.
2158.	1501.	1308.	1131.	1054.	1011.
1599.	1495.	1360.	1137.	1056.	1021.
1884.	1514.	1404.	709.	1053.	1023.
1934.	1532.	946.	952.	1047.	1004.
1971.	1542.	1214.	1048.	1011.	993.
2009.	1549.	1336.	652.	1013.	1005.
1968.	1535.	907.	467.	640.	1008.
1332.	1545.	631.	790.	842.	1011.
1032.	1535.	1068.	924.	912.	633.
1572.	1049.	1257.	982.	579.	833.
1059.	1293.	1303.	1010.	809.	538.
1587.	1400.	1370.	1039.	918.	397.
1800.	1495.	1418.	1056.	974.	707.
1359.	1518.	1448.	1065.	992.	812.
1162.	1539.	969.	1068.	1004.	894.
1712.	966.	1233.	1066.	996.	605.
1905.	1329.	1305.	1045.	624.	809.
2070.	1479.	891.	1046.	843.	893.
2071.	1561.	1163.	1045.	939.	946.
1346.	1059.	1271.	1042.	965.	976.
1961.	1340.	1305.	1027.	999.	655.
2112.	1491.	811.	696.	997.	843.
1355.	929.	1090.	858.	1010.	919.
1177.	1302.	1252.	934.	1029.	966.
1802.	1438.	1326.	962.	1024.	988.
2059.	1489.	817.	975.	1041.	1001.
1488.	1561.	582.	971.	1042.	619.
1052.	1584.	456.	972.	704.	835.
1732.	1618.	877.	661.	890.	921.
1987.	1624.	1094.	833.	967.	954.
1442.	1647.	742.	537.	988.	976.
1893.	1114.	514.	762.	999.	981.
2096.	1388.	469.	868.	1022.	984.
2185.	1525.	871.	912.	1032.	979.
2235.	1587.	614.	954.	699.	990.
2227.	1578.	933.	994.	891.	616.
2174.	1573.	1076.	1008.	980.	816.
2229.	1605.	720.	1041.	1018.	879.
2237.	1571.	978.	1064.	1028.	918.
2214.	1590.	1076.	1047.	1035.	941.

Table 29. Values for population size at asymptotic PSURV values lowered to 95% (Figure 17b).

9730.					
6479.	2580.	3163.	2379.	2606.	2903.
4249.	3008.	3188.	2427.	2619.	2249.
3874.	2387.	2444.	2471.	2629.	2603.
3710.	2769.	2076.	2479.	2704.	2798.
3594.	2240.	2547.	2478.	2747.	2897.
3421.	2611.	2093.	2450.	2669.	2066.
3291.	1954.	1849.	2530.	2738.	2410.
3199.	2423.	1696.	2580.	2673.	2679.
3137.	2606.	2377.	2563.	2743.	2824.
3084.	2690.	2698.	2585.	2776.	2893.
3040.	2760.	2816.	2552.	2747.	2918.
2471.	2749.	2870.	2560.	2779.	2962.
2739.	2812.	2937.	1833.	2796.	2985.
2814.	2880.	2205.	2249.	2804.	2929.
2820.	2934.	2619.	2439.	2721.	2911.
2815.	2978.	2844.	1759.	2740.	2977.
2754.	2973.	2161.	1415.	1994.	3012.
2128.	3033.	1682.	1983.	2409.	3039.
1804.	3035.	2410.	2244.	2551.	2175.
2468.	2305.	2762.	2346.	1879.	2630.
1921.	2641.	2787.	2377.	2326.	1962.
2593.	2809.	2984.	2430.	2563.	1624.
2934.	3037.	3000.	2469.	2685.	2332.
2105.	3073.	3064.	2498.	2697.	2528.
1695.	3096.	2283.	2520.	2711.	2721.
2717.	2205.	2689.	2537.	2674.	2095.
3147.	2765.	2770.	2503.	1930.	2507.
3450.	3012.	2161.	2537.	2380.	2695.
3465.	3150.	2553.	2560.	2629.	2832.
2380.	2363.	2715.	2576.	2678.	2908.
3142.	2734.	2735.	2556.	2774.	2204.
3552.	2986.	1962.	1995.	2752.	2596.
2462.	2142.	2343.	2265.	2795.	2769.
1923.	2679.	2652.	2435.	2864.	2897.
2958.	2866.	2792.	2500.	2845.	2949.
3416.	2890.	1979.	2531.	2907.	2981.
2371.	3033.	1575.	2521.	2914.	2104.
1850.	3060.	1364.	2534.	2247.	2607.
2834.	3127.	1989.	1984.	2605.	2837.
3253.	3131.	2367.	2291.	2775.	2916.
2313.	3182.	1866.	1699.	2799.	2971.
3013.	2406.	1437.	2117.	2802.	2970.
3335.	2787.	1391.	2325.	2849.	2978.
3497.	3020.	2019.	2387.	2861.	2958.
3580.	3129.	1651.	2456.	2228.	3003.
3590.	3055.	2130.	2535.	2572.	2148.
3499.	3019.	2360.	2539.	2758.	2604.
3603.	3125.	1809.	2613.	2831.	2750.
3655.	3056.	2204.	2666.	2826.	2854.
3676.	3152.	2366.	2599.	2824.	2919.

Table 30. Values for population size at asymptotic PSURV values lowered to 93% (Figure 17b).

9730.					
6473.	1606.	2086.	1589.	1818.	2027.
4237.	1980.	2099.	1627.	1827.	1507.
3843.	1530.	1563.	1659.	1836.	1786.
3659.	1860.	1297.	1674.	1875.	1932.
3520.	1435.	1658.	1681.	1900.	2005.
3328.	1759.	1319.	1670.	1880.	1396.
3174.	1268.	1137.	1712.	1911.	1692.
3054.	1638.	1030.	1743.	1893.	1870.
2962.	1790.	1506.	1739.	1921.	1963.
2882.	1859.	1728.	1745.	1936.	2008.
2811.	1902.	1816.	1726.	1925.	2028.
2266.	1901.	1856.	1723.	1942.	2056.
2466.	1933.	1896.	1208.	1952.	2071.
2524.	1964.	1392.	1476.	1959.	2048.
2558.	1989.	1676.	1599.	1928.	2044.
2577.	2008.	1825.	1135.	1936.	2079.
2491.	2004.	1361.	899.	1374.	2099.
1877.	2029.	1032.	1271.	1677.	2116.
1556.	2027.	1514.	1443.	1796.	1482.
2033.	1514.	1747.	1514.	1287.	1811.
1576.	1768.	1811.	1543.	1617.	1322.
2044.	1889.	1872.	1580.	1785.	1072.
2261.	1995.	1923.	1609.	1871.	1580.
1760.	2019.	1959.	1635.	1891.	1766.
1495.	2018.	1430.	1660.	1906.	1885.
2089.	1411.	1709.	1682.	1910.	1396.
2309.	1763.	1809.	1680.	1336.	1700.
2469.	1920.	1356.	1708.	1663.	1842.
2438.	2003.	1636.	1735.	1836.	1934.
1681.	1486.	1759.	1757.	1886.	1983.
2143.	1744.	1809.	1754.	1946.	1455.
2372.	1901.	1256.	1299.	1942.	1747.
1652.	1337.	1550.	1539.	1971.	1880.
1457.	1695.	1734.	1671.	2010.	1966.
1980.	1836.	1820.	1724.	2005.	2004.
2195.	1894.	1256.	1750.	2040.	2027.
1693.	1965.	976.	1752.	2047.	1398.
1274.	1983.	830.	1762.	1520.	1753.
1818.	2028.	1301.	1307.	1797.	1917.
2043.	2029.	1548.	1554.	1929.	1981.
1581.	2058.	1153.	1125.	1964.	2019.
1924.	1526.	870.	1443.	1975.	2025.
2084.	1795.	806.	1598.	2033.	2036.
2173.	1946.	1271.	1655.	2013.	2030.
2221.	2018.	986.	1701.	1501.	2054.
2223.	2013.	1345.	1745.	1773.	1435.
2239.	2012.	1517.	1755.	1912.	1761.
2282.	2054.	1100.	1798.	1970.	1882.
2309.	2041.	1403.	1830.	1979.	1955.
2325.	2081.	1538.	1814.	1983.	1996.

Table 31. Values for population size at asymptotic PSURV values lowered to 92% (Figure 17b).

9730.					
6470.	1392.	1380.	791.	659.	583.
4231.	1652.	1380.	809.	661.	431.
3826.	1271.	1021.	822.	661.	514.
3632.	1519.	941.	826.	671.	554.
3482.	1172.	1072.	822.	677.	574.
3277.	1400.	847.	806.	663.	398.
3104.	1021.	725.	819.	672.	476.
2966.	1290.	651.	827.	659.	529.
2855.	1392.	955.	820.	666.	554.
2757.	1435.	1092.	815.	668.	562.
2674.	1463.	1145.	800.	661.	566.
2148.	1458.	1168.	793.	662.	571.
2316.	1479.	1191.	558.	662.	572.
2358.	1503.	864.	673.	660.	564.
2376.	1522.	1043.	721.	643.	572.
2379.	1536.	1135.	514.	644.	575.
2357.	1538.	836.	407.	457.	577.
1748.	1560.	631.	565.	558.	579.
1429.	1561.	928.	636.	604.	404.
1858.	1152.	1071.	661.	430.	490.
1426.	1346.	1098.	668.	537.	357.
1824.	1437.	1132.	680.	588.	288.
1986.	1519.	1159.	688.	612.	422.
1570.	1531.	1175.	696.	615.	465.
1356.	1532.	849.	702.	618.	499.
1809.	1062.	1005.	708.	613.	366.
1964.	1319.	1049.	703.	427.	446.
2077.	1429.	783.	711.	538.	486.
2062.	1482.	936.	719.	591.	506.
1418.	1089.	1001.	724.	602.	516.
1796.	1274.	1016.	718.	617.	375.
1986.	1381.	707.	531.	613.	452.
1377.	968.	855.	637.	620.	489.
1209.	1218.	956.	680.	630.	507.
1653.	1312.	998.	693.	624.	517.
1857.	1342.	689.	697.	632.	523.
1406.	1392.	534.	692.	632.	359.
1048.	1400.	452.	690.	465.	447.
1587.	1419.	692.	512.	551.	486.
1834.	1420.	820.	606.	590.	500.
1357.	1432.	609.	438.	594.	505.
1732.	1053.	459.	562.	593.	508.
1901.	1241.	421.	617.	598.	510.
1979.	1338.	670.	629.	598.	508.
2013.	1379.	515.	640.	443.	507.
2012.	1365.	695.	651.	527.	354.
1989.	1355.	779.	651.	566.	428.
2013.	1379.	561.	664.	576.	462.
2022.	1360.	714.	673.	575.	475.
2023.	1385.	777.	660.	574.	480.

Table 32. Values for population size at original values for all parameters, but PSURV(1) raised to 100.0 (Figures 12 and 18).

9730.					
7569.	27509.	77776.	63804.	67406.	65451.
4812.	36012.	80540.	59637.	61181.	47669.
5170.	25266.	59440.	58948.	59014.	59283.
5462.	35802.	49240.	58374.	69125.	67760.
5667.	25217.	61235.	55650.	74819.	69292.
5780.	36231.	49458.	60003.	75659.	50189.
5747.	25500.	43356.	64433.	78312.	59590.
5779.	37909.	39781.	67508.	78193.	64166.
5796.	44355.	57408.	61374.	80966.	69207.
5759.	48731.	67465.	65553.	79523.	74286.
5741.	52550.	64370.	55990.	72596.	70107.
4492.	55373.	61736.	58581.	78355.	71317.
5230.	55828.	64700.	44118.	76141.	72219.
5607.	57520.	48811.	59146.	79290.	66888.
5915.	58981.	59463.	64095.	79593.	64573.
6240.	59761.	64360.	46783.	76759.	71090.
6586.	58685.	48266.	38339.	57721.	73361.
4708.	60227.	40362.	55644.	68822.	74648.
3815.	59505.	59794.	65015.	67036.	53452.
6516.	42559.	67741.	65027.	52469.	67254.
4714.	51903.	69424.	65140.	65321.	50121.
7688.	56538.	68423.	67540.	72072.	41771.
9509.	61322.	71429.	71293.	77421.	59840.
6307.	59252.	74649.	74963.	68462.	65630.
4810.	58344.	53965.	73825.	64087.	70105.
9703.	42924.	63854.	75460.	69161.	50645.
12359.	57205.	69262.	69844.	52322.	63717.
14329.	62734.	51551.	74738.	59943.	64592.
14902.	66254.	56234.	73872.	68206.	69530.
9635.	47557.	58213.	74816.	60776.	73082.
14629.	56569.	66256.	72930.	71029.	52868.
17666.	64241.	45224.	53594.	60931.	63032.
11531.	47119.	62527.	62736.	64903.	67260.
8615.	60863.	67870.	71826.	71551.	70971.
16269.	61348.	71444.	71510.	67123.	72573.
20348.	63960.	51956.	73138.	73489.	74276.
13229.	69015.	42570.	71164.	71902.	54093.
9824.	66863.	37818.	65162.	52712.	67280.
18520.	71639.	54759.	51671.	65814.	72912.
23177.	69491.	62516.	62546.	71135.	72625.
15100.	71777.	46223.	48382.	62203.	76633.
22798.	52920.	38141.	56026.	57849.	74178.
27047.	61033.	33960.	62627.	61664.	73590.
29863.	71137.	52119.	58566.	58273.	68635.
32071.	74538.	40126.	62703.	45146.	70684.
33925.	76003.	57677.	76100.	55619.	53362.
34071.	75353.	62552.	67119.	63315.	64928.
36868.	78171.	44901.	73354.	64547.	62931.
39196.	78047.	57104.	74745.	58076.	66234.
41307.	79184.	60020.	74927.	54694.	73179.

Table 33. Values for population size at constrained juvenile survival, and PSURV(1) raised to 100.0 (Figure 18).

9738.					
7396.	3868.	6431.	5865.	7652.	10281.
4443.	4952.	6473.	6125.	7799.	6291.
4588.	3535.	4285.	6327.	7889.	8438.
4656.	4502.	3200.	6397.	8053.	9478.
4576.	3185.	4668.	6399.	8168.	9963.
4441.	4204.	3269.	6104.	7767.	5980.
4444.	2595.	2503.	6340.	8839.	7679.
4492.	3846.	2096.	6482.	7697.	9063.
4526.	4376.	4177.	6512.	7974.	9742.
4528.	4662.	5183.	6595.	8884.	10039.
4484.	4806.	5708.	6608.	8861.	10300.
3078.	4882.	6055.	6671.	8111.	10535.
3750.	4982.	6381.	4872.	8140.	10653.
4013.	5061.	4121.	5476.	8142.	10582.
4157.	5112.	5471.	6112.	7690.	10563.
4236.	5153.	6143.	3718.	7869.	10694.
4262.	5158.	3919.	2487.	4869.	10769.
2662.	5208.	2584.	4490.	6513.	10846.
1864.	5220.	4754.	5409.	7219.	6651.
3211.	3635.	5797.	5789.	4451.	8843.
2051.	4258.	5858.	6018.	6312.	5572.
3268.	4558.	6336.	6298.	7369.	3887.
3897.	5061.	6734.	6472.	7946.	7362.
2812.	5262.	6981.	6573.	8165.	8473.
2276.	5449.	4379.	6625.	8418.	9638.
3718.	3342.	5809.	6639.	8173.	5812.
4379.	4687.	6083.	6564.	5867.	8641.
4806.	5334.	3082.	6585.	6998.	9988.
4808.	5689.	5389.	6608.	7956.	10749.
2959.	3758.	6152.	6617.	8291.	11134.
4353.	4891.	6198.	6577.	8582.	6788.
5084.	5534.	3747.	4308.	8733.	9384.
3069.	3374.	5851.	5443.	8948.	10589.
2365.	4758.	6106.	6829.	9152.	11251.
4226.	8416.	6594.	6277.	9198.	11539.
5126.	8469.	3938.	6387.	9365.	11846.
3321.	5855.	2693.	6475.	9437.	7224.
2177.	6095.	2040.	6568.	5774.	9832.
4254.	6305.	4093.	4282.	7748.	11023.
5214.	6398.	5389.	5539.	8663.	11512.
3373.	8531.	3379.	3492.	9806.	11762.
4838.	4255.	2255.	5103.	9168.	11990.
5682.	5454.	1958.	5098.	9478.	12173.
5989.	6082.	4335.	6337.	9689.	12216.
6168.	6378.	2843.	6665.	5945.	12366.
6295.	6121.	4678.	7036.	8881.	7559.
6043.	6059.	5616.	7241.	9135.	10035.
6278.	6482.	3603.	7518.	9613.	11035.
6378.	6173.	5130.	7724.	9766.	11580.
6401.	6487.	5869.	7417.	9980.	11856.

Table 34. Values for population size at initial ages of cannibalism of 11 for males and 18 for females (growth rates of Graham (1976)) (Figure 19).

9730.					
6482.	7289.	23471.	24009.	20299.	21116.
4263.	8591.	24069.	19971.	17546.	15021.
3926.	6301.	17206.	19342.	16876.	20036.
3783.	7643.	13905.	17819.	21349.	23269.
3712.	5750.	19110.	16669.	23314.	25172.
3534.	7215.	14730.	20453.	24489.	17463.
3444.	5474.	12502.	22958.	25444.	22227.
3372.	6968.	11250.	24004.	26101.	24094.
3325.	7548.	19207.	21211.	26798.	25945.
3218.	7882.	23238.	22348.	27467.	26993.
3048.	8288.	24815.	19213.	23999.	26637.
2576.	8173.	21367.	19152.	26077.	27672.
2859.	8718.	20861.	14356.	27488.	28205.
2774.	9319.	15514.	20666.	27990.	23922.
2857.	9836.	18284.	23190.	28231.	21854.
3056.	10314.	19728.	16357.	25958.	25077.
2957.	10370.	14902.	13111.	19234.	26484.
2350.	10970.	12567.	20359.	24047.	27270.
2060.	11215.	19577.	23372.	22132.	19073.
3163.	8027.	22883.	23886.	17170.	23858.
2450.	10233.	24004.	22826.	21748.	17549.
3519.	11506.	23549.	25101.	25498.	14505.
4067.	12945.	25065.	26078.	27464.	21497.
2925.	13179.	25899.	26859.	23771.	23892.
2390.	13505.	18469.	26972.	22245.	24348.
4231.	9532.	22632.	27255.	25047.	17496.
4934.	12934.	24665.	24059.	18174.	21698.
5633.	14568.	18053.	26005.	20587.	22154.
5894.	15725.	20449.	27194.	24375.	24375.
4021.	10909.	19522.	27711.	20618.	25388.
5606.	13701.	22987.	25881.	24140.	18167.
6600.	15729.	16969.	18790.	19792.	21840.
4533.	11109.	22180.	21473.	20323.	22275.
3549.	14708.	24914.	24983.	23192.	24668.
5933.	15922.	26538.	25454.	20726.	24427.
7085.	16549.	18891.	25423.	23583.	24144.
4864.	17786.	15267.	22867.	22055.	17731.
3795.	18132.	13476.	22777.	16127.	22828.
6331.	18996.	20641.	16997.	20714.	24846.
7463.	19206.	23398.	21682.	22491.	24725.
5149.	20029.	17002.	16402.	18866.	25730.
7226.	14137.	13877.	18316.	17283.	23773.
8301.	17589.	12289.	20122.	18857.	22721.
8943.	19870.	19842.	17662.	17961.	20983.
9383.	21128.	14961.	19231.	13682.	24272.
9545.	21069.	21437.	22451.	18204.	17912.
9541.	21210.	24352.	20015.	20694.	23421.
10051.	22314.	17102.	22880.	20847.	20248.
10368.	22184.	21422.	24565.	17921.	22453.
10541.	23199.	22014.	25083.	16754.	24780.

Table 35. Values for population size at initial ages of cannibalism of 35 for males and 46 for females (growth rates of Graham (1968)) (Figure 19).

9730.					
6494.	8067.	30291.	29380.	32903.	32540.
4271.	9691.	31074.	28133.	32278.	24477.
3933.	7090.	22170.	28311.	32302.	29476.
3824.	8868.	17881.	28190.	34093.	32414.
3750.	6612.	23809.	28161.	35258.	34000.
3636.	8347.	18556.	28822.	35019.	25184.
3553.	6300.	15857.	30522.	35447.	29651.
3482.	8193.	14315.	31066.	34903.	32311:
3422.	9111.	22135.	30419.	35756.	34092.
3353.	9690.	25843.	31002.	36295.	34864.
3301.	10163.	27039.	29620.	34816.	34549.
2739.	10497.	27402.	29949.	36191.	35176.
3023.	10947.	28390.	22387.	36252.	35541.
3159.	11437.	20758.	28285.	36524.	33055.
3266.	11933.	25218.	31154.	35912.	31800.
3377.	12431.	27807.	22885.	35517.	33596.
3527.	12909.	20719.	18788.	27091.	34350.
2717.	13488.	17234.	26210.	31807.	35311.
2326.	14001.	24437.	29850.	32224.	26097.
3429.	9972.	28135.	30529.	25278.	31414.
2671.	12219.	28586.	30549.	30252.	24193.
3874.	13532.	29909.	32232.	33696.	20616.
4606.	15201.	30856.	32793.	35504.	28238.
3283.	16128.	31916.	33547.	33524.	30744.
2659.	16822.	23271.	34097.	32695.	31866.
4516.	11821.	28395.	33847.	33557.	23848.
5541.	15459.	29733.	32399.	25580.	29213.
6213.	17401.	22379.	33430.	30358.	31156.
6330.	18650.	27038.	34146.	33814.	33159.
4357.	13067.	28682.	34757.	32735.	34111.
6090.	16746.	29847.	33751.	34514.	25159.
7080.	18868.	22326.	25113.	32622.	30241.
4899.	13410.	26769.	29535.	32891.	32021.
3854.	17570.	30265.	32076.	34290.	34043.
6333.	19564.	31612.	32876.	33215.	34436.
7605.	20011.	23322.	33181.	34674.	34552.
5247.	21536.	19284.	32513.	34501.	25603.
4108.	22410.	17229.	32806.	25964.	30951.
6784.	23351.	24560.	24690.	31184.	33532.
8138.	24043.	27954.	29562.	33219.	34271.
5618.	24986.	20925.	23088.	32121.	34613.
7823.	17604.	17408.	27683.	31561.	34014.
8988.	22355.	15581.	30526.	32750.	34115.
9706.	25015.	23686.	30487.	32167.	33091.
10204.	26568.	18374.	31798.	24616.	34438.
10521.	26360.	25339.	33270.	29291.	25854.
10438.	26516.	28649.	32825.	31954.	30785.
11026.	28135.	20681.	34099.	32701.	31151.
11410.	27938.	26276.	35119.	31578.	33106.
11645.	29469.	28425.	34859.	30240.	34126.

Table 36. Values for population size at initial age of egg laying of 10 (Figure 20a).

9738.					
6461.	7800.	27544.	26456.	25998.	26076.
4254.	9302.	28240.	24020.	24398.	19196.
3914.	6811.	20163.	23650.	23696.	24305.
3795.	8436.	16276.	22393.	27538.	27480.
3724.	6308.	22860.	21695.	28973.	29292.
3591.	7936.	17493.	24216.	29317.	21015.
3506.	6003.	14768.	26403.	29930.	25737.
3441.	7746.	13244.	27250.	30110.	27384.
3389.	8532.	20694.	25625.	30563.	29159.
3316.	9025.	24245.	26404.	31175.	30090.
3248.	9493.	24625.	24464.	28584.	29846.
2702.	9685.	23935.	24423.	30677.	30844.
2987.	10160.	24730.	18244.	31252.	31407.
3091.	10682.	18212.	24479.	31722.	27602.
3193.	11173.	22014.	27017.	31534.	25716.
3315.	11651.	23794.	19507.	30246.	28746.
3393.	11934.	17864.	15858.	22735.	29962.
2631.	12511.	14971.	23072.	27418.	30468.
2264.	12863.	22351.	26681.	26395.	21965.
3356.	9191.	25508.	27153.	20649.	26870.
2613.	11430.	26592.	26145.	25425.	20296.
3751.	12726.	26756.	28012.	29119.	17085.
4397.	14288.	27724.	25315.	31020.	24333.
3153.	14875.	28774.	29654.	28634.	27059.
2567.	15418.	20833.	30159.	27319.	28006.
4414.	13865.	25371.	30655.	29293.	20454.
5286.	14424.	27099.	27784.	21723.	25183.
5969.	16250.	20177.	29212.	25418.	26324.
6154.	17466.	23613.	30127.	28856.	28806.
4227.	12193.	23796.	30759.	26374.	30029.
5889.	15501.	26288.	29577.	29139.	21670.
6887.	17599.	19571.	21740.	26076.	25985.
4756.	12480.	24676.	25374.	26729.	27126.
3737.	16435.	27607.	28588.	29061.	28944.
6183.	19080.	29436.	28856.	27143.	29105.
7398.	18626.	21279.	29920.	29280.	28818.
5098.	20036.	17369.	27568.	27939.	21293.
3988.	20661.	15411.	27788.	20774.	26758.
6619.	21599.	22646.	20764.	25822.	28799.
7867.	22093.	26057.	25483.	27425.	28867.
5433.	22954.	19161.	19609.	25136.	30022.
7605.	16211.	15754.	23951.	24021.	28412.
8743.	20440.	14003.	25377.	25021.	27985.
9441.	22962.	22064.	23936.	24644.	27075.
9925.	24395.	16831.	25392.	18789.	29173.
10188.	24263.	23690.	27788.	23356.	21693.
10136.	24423.	26764.	25862.	26111.	26981.
10698.	25822.	19041.	28340.	26450.	25867.
11057.	25645.	24119.	29332.	23863.	27613.
11270.	26971.	25374.	29731.	22763.	29592.

Table 37. Values for population size at initial age of egg laying of 13 (growth rates of Graham (1976)) (Figure 20).

9730.					
6416.	6593.	17085.	24418.	24703.	24755.
4231.	7676.	17358.	22357.	23168.	18193.
3844.	5664.	12601.	22301.	22532.	23130.
3686.	6708.	10294.	21175.	25662.	26261.
3589.	5101.	13825.	20797.	27423.	27858.
3435.	6166.	10797.	23106.	27519.	19957.
3336.	4765.	9242.	24823.	28535.	24083.
3278.	5856.	8359.	26157.	28358.	25959.
3247.	6313.	13433.	24347.	29265.	27798.
3218.	6595.	16057.	25201.	29997.	28954.
3190.	6860.	17290.	22856.	27100.	28603.
2621.	6889.	18073.	22699.	28758.	29472.
2929.	7173.	18949.	17283.	29717.	29836.
2988.	7496.	13476.	23089.	30514.	26194.
3034.	7783.	17421.	25472.	30094.	24643.
3078.	8075.	19641.	18593.	28760.	27243.
3013.	8185.	14108.	15253.	21643.	28358.
2416.	8543.	11421.	22169.	26138.	29200.
2124.	8723.	17740.	25585.	25147.	20988.
2799.	6389.	20962.	25956.	19690.	25540.
2289.	7913.	21695.	25611.	24263.	19285.
3052.	8813.	23240.	27169.	27838.	16231.
3469.	9899.	24640.	27766.	29593.	23325.
2621.	10280.	25736.	28582.	27277.	25612.
2216.	10694.	17959.	29256.	26018.	26530.
3614.	7624.	23109.	29174.	28904.	19392.
4290.	10207.	24715.	26576.	20763.	24035.
4896.	11541.	17794.	28170.	24112.	25240.
5116.	12440.	23213.	29057.	27367.	27406.
3572.	8709.	25562.	29651.	25017.	28186.
4998.	11053.	26359.	28280.	27691.	20420.
5882.	12573.	18808.	20754.	24946.	24818.
4088.	8932.	23299.	24231.	25535.	25582.
3233.	11702.	26891.	27181.	27590.	27718.
5333.	12783.	28722.	27625.	25715.	27635.
6387.	13118.	29334.	27766.	27392.	27859.
4419.	14008.	16281.	26217.	26479.	20473.
3471.	14344.	14264.	26393.	19728.	25279.
5811.	14936.	21514.	19653.	24097.	27565.
6902.	15184.	26074.	24232.	25922.	27381.
4766.	15683.	18724.	18556.	23883.	28378.
6652.	12158.	15100.	21704.	22768.	27391.
7652.	13752.	13276.	23957.	23770.	26738.
8270.	15311.	20313.	22734.	23398.	25784.
8669.	16178.	15639.	23629.	17822.	27801.
8826.	15972.	21546.	26141.	22222.	20682.
8731.	15896.	24175.	24605.	24867.	25676.
9165.	16593.	17455.	26855.	24710.	24412.
9405.	16343.	22052.	27870.	22656.	26298.
9477.	16940.	23179.	28067.	21132.	28397.

Table 38. Values for population size at initial age of egg laying of 18 (growth rates of Graham (1968)) (Figure 20a).

9738.					
6360.	5185.	8281.	9084.	15450.	29365.
4203.	5872.	8132.	9070.	15645.	21258.
3695.	4336.	6074.	9141.	15902.	26406.
3471.	4884.	5050.	9040.	16855.	27697.
3336.	3812.	6114.	9015.	17494.	28291.
3160.	4239.	4984.	9151.	17349.	20871.
3044.	3371.	4381.	9677.	18179.	24489.
2965.	3825.	4021.	10029.	18041.	26124.
2921.	3946.	5577.	10061.	18881.	27566.
2880.	3955.	6360.	10496.	19471.	28251.
2831.	4015.	6655.	10594.	19393.	27698.
2363.	3964.	6815.	10976.	20033.	28402.
2622.	4049.	7083.	8046.	20518.	28817.
2691.	4143.	5348.	10324.	20915.	25328.
2752.	4252.	6609.	11527.	20462.	23645.
2812.	4354.	7348.	8383.	20807.	26364.
2757.	4289.	5536.	6842.	15333.	27616.
2230.	4417.	4650.	10073.	18759.	28210.
1974.	4432.	6863.	11673.	19889.	20816.
2483.	3451.	8041.	12395.	14919.	25181.
2081.	4122.	8377.	12666.	18621.	19404.
2429.	4529.	8954.	13207.	20681.	16584.
2529.	5012.	9530.	13628.	21764.	22954.
2213.	5111.	10031.	13892.	21699.	25233.
2069.	5321.	7133.	14080.	21701.	25732.
2662.	3964.	9148.	14193.	21567.	19263.
2892.	5320.	9863.	13874.	15996.	23340.
3239.	6065.	7175.	14094.	19188.	24069.
3445.	6630.	9393.	14205.	21071.	26221.
2567.	4713.	10348.	14280.	21100.	27139.
3514.	6045.	10806.	14070.	21938.	20027.
4181.	6997.	7716.	10387.	21503.	23767.
3060.	4955.	9623.	12146.	21808.	24414.
2439.	6645.	11104.	13173.	22534.	26265.
4038.	7293.	11871.	13505.	22331.	26320.
4861.	7544.	8321.	13607.	23097.	26052.
3399.	8088.	6689.	13403.	23237.	19506.
2698.	8263.	5841.	13414.	17288.	24446.
4527.	8590.	8640.	10071.	21109.	26379.
5373.	8671.	10240.	12005.	23032.	26328.
3729.	8934.	7398.	9372.	23433.	27555.
5270.	8345.	5979.	11459.	23805.	25987.
6103.	7712.	5248.	12577.	24699.	25236.
6610.	8522.	8105.	12876.	25259.	23927.
6947.	8891.	6201.	13430.	18647.	26418.
7079.	8661.	8384.	14136.	23361.	19623.
7012.	8497.	9322.	14245.	26009.	24356.
7345.	8686.	6749.	14965.	27254.	22705.
7495.	8375.	8410.	15514.	27475.	24538.
7481.	8438.	9024.	15402.	27759.	26445.

Table 39. Values for population size at age spans cannibalized, initial ages of cannibalism, and initial age of egg laying at growth rates of Graham (1976) (Figure 20b).

9730.					
6409.	6015.	13297.	21010.	19641.	19186.
4226.	5864.	13448.	21044.	17396.	14182.
3839.	5072.	9795.	21472.	16440.	18444.
3660.	5838.	8017.	21520.	20927.	21501.
3566.	4476.	10308.	21824.	22730.	23670.
3369.	5337.	8155.	22600.	23411.	16717.
3263.	4157.	7038.	24329.	24453.	21048.
3196.	4976.	6396.	25523.	24611.	22528.
3170.	5233.	10240.	25444.	25298.	24846.
3107.	5405.	12240.	26597.	25977.	25492.
2975.	5607.	13012.	26633.	23027.	24726.
2476.	5386.	13338.	23293.	24809.	25864.
2781.	5713.	13970.	17183.	25792.	26623.
2657.	6094.	9987.	22263.	26408.	22180.
2695.	6403.	12854.	24572.	26164.	19877.
2804.	6703.	14609.	17805.	24675.	23352.
2561.	6644.	10477.	14472.	17700.	24926.
2107.	7024.	8477.	20952.	23789.	25754.
1688.	7126.	13571.	24060.	25620.	17829.
2557.	5211.	16212.	24309.	18236.	22628.
2892.	6690.	16898.	23022.	23416.	16433.
2789.	7573.	18040.	24776.	26290.	13438.
3115.	8578.	19183.	25789.	27655.	20673.
2361.	8709.	20067.	26403.	27089.	23360.
2001.	8956.	13885.	26794.	26679.	24234.
3385.	6341.	17894.	26945.	26494.	16944.
3948.	9747.	19254.	23104.	19116.	22980.
4570.	9941.	13756.	25088.	22699.	25126.
4847.	10800.	17716.	25925.	25081.	26543.
3350.	7457.	19304.	26441.	24658.	26991.
4678.	9343.	20146.	24085.	25701.	18741.
5562.	10786.	14272.	17733.	24556.	22829.
3831.	7578.	17801.	19268.	24814.	24317.
3007.	10025.	20491.	22976.	25829.	25518.
5044.	10822.	21841.	23446.	25327.	25510.
6063.	11173.	15387.	23489.	26608.	25304.
4164.	11902.	12267.	20789.	26695.	18166.
3249.	12041.	10715.	20425.	19561.	21883.
5483.	12525.	16163.	15259.	24502.	23437.
6505.	12560.	19389.	19416.	24488.	23722.
4472.	12970.	13931.	14717.	20552.	24152.
6242.	9188.	11228.	16492.	17564.	23644.
7170.	11078.	9862.	18592.	18945.	23555.
7734.	12387.	16173.	16895.	18312.	23489.
8079.	13083.	12172.	18305.	14489.	25042.
8148.	12911.	17340.	21212.	17900.	18448.
8077.	12816.	19907.	19064.	20349.	23537.
8450.	13264.	14028.	21828.	20110.	24835.
8640.	13033.	18309.	23638.	16322.	24662.
8664.	13377.	20182.	24209.	14345.	25625.

Table 40. Values for population size at age spans cannibalized, initial ages of cannibalism, and initial age of egg laying at growth rates of Graham (1968) (Figure 20b).

9730.					
6365.	5241.	8585.	9613.	17163.	28409.
4205.	5952.	8456.	9880.	17583.	20877.
3697.	4384.	6282.	10059.	17963.	25167.
3487.	4582.	5204.	10112.	18603.	27476.
3349.	3847.	6458.	10182.	19102.	28699.
3196.	4325.	5200.	10037.	18762.	21004.
3081.	3425.	4534.	10518.	19599.	24536.
2997.	3932.	4143.	10855.	19320.	26869.
2944.	4115.	5859.	11055.	20176.	28388.
2907.	4177.	6745.	11459.	20744.	29111.
2873.	4243.	7209.	11738.	20885.	29067.
2388.	4277.	7507.	12111.	21338.	29572.
2644.	4343.	7795.	8784.	21714.	29959.
2746.	4413.	5789.	11066.	22036.	28460.
2809.	4519.	7185.	12269.	21425.	27418.
2858.	4627.	8005.	8931.	21954.	28597.
2873.	4673.	5961.	7281.	16179.	29246.
2296.	4790.	4958.	10566.	19630.	29667.
2015.	4891.	7233.	12192.	21098.	21742.
2534.	3739.	8451.	12978.	15756.	26100.
2118.	4374.	8734.	13331.	19532.	20007.
2529.	4765.	9401.	13775.	21552.	16983.
2713.	5280.	9940.	14145.	22653.	23679.
2325.	5572.	10412.	14381.	22937.	25698.
2148.	5850.	7414.	14549.	23137.	27380.
2753.	4295.	9455.	14646.	22670.	20164.
3134.	5601.	10108.	14501.	16814.	24584.
3451.	6360.	7378.	14620.	20348.	26302.
3583.	6892.	9683.	14696.	22256.	27984.
2671.	4914.	10783.	14768.	22858.	28621.
3664.	6316.	11063.	14695.	23509.	20912.
4311.	7200.	7904.	10829.	23543.	25204.
3099.	5143.	9765.	12714.	23882.	26781.
2518.	6770.	11266.	13727.	24405.	28139.
4117.	7519.	12053.	14147.	24612.	28377.
4981.	7680.	8533.	14301.	25220.	28567.
3485.	8213.	6822.	14277.	25595.	20890.
2765.	8460.	5963.	14347.	18876.	25597.
4598.	8745.	8787.	10685.	23034.	27862.
5528.	8873.	10511.	12752.	25204.	28453.
3830.	5891.	7593.	9907.	26209.	29179.
5359.	6465.	6133.	12378.	26896.	28714.
6196.	7871.	5383.	13658.	27682.	28517.
6706.	8663.	8390.	14292.	28385.	27891.
7040.	9040.	6403.	14855.	28716.	28964.
7196.	8795.	8701.	15428.	25763.	21134.
7091.	8634.	9723.	15778.	28542.	25561.
7425.	8866.	7017.	16377.	30017.	25915.
7576.	8557.	8830.	16897.	28228.	27298.
7563.	8670.	9624.	16663.	27218.	28111.

Table 41. Values for population size at age spans hunted at original growth rates (Figure 21a).

9730.					
6489.	2826.	2184.	1990.	1740.	1964.
4268.	3590.	2111.	2079.	1825.	1463.
3930.	2210.	1259.	2001.	1910.	1657.
3908.	2734.	834.	1933.	1865.	1922.
3735.	1727.	1488.	1891.	1832.	2060.
3599.	2178.	1146.	1830.	1732.	1204.
3513.	1404.	976.	1969.	1745.	1464.
3446.	1845.	860.	2002.	1791.	1815.
3393.	2252.	1512.	2082.	1942.	1957.
3320.	2283.	1856.	2002.	1887.	2080.
3224.	2187.	2027.	1918.	1806.	1978.
2516.	2143.	1955.	1895.	1801.	1939.
2692.	2147.	1936.	1094.	1789.	1914.
2860.	2164.	1235.	1508.	1898.	1833.
2991.	2181.	1568.	1872.	1921.	1896.
3130.	2201.	1918.	1172.	1842.	2044.
3046.	2220.	1397.	887.	1077.	1972.
2199.	2268.	778.	1570.	1430.	1926.
1740.	2296.	1581.	1917.	1713.	1123.
2943.	1220.	2001.	2022.	1085.	1486.
2257.	1668.	2068.	2116.	1577.	1043.
3152.	2142.	2054.	2048.	1848.	770.
3921.	2616.	2088.	2007.	1822.	1469.
2438.	2661.	2075.	1978.	1886.	1734.
1647.	2671.	1294.	1954.	1975.	1941.
3676.	1357.	1638.	1935.	1841.	1450.
4625.	2076.	1863.	1870.	1057.	1655.
4910.	2715.	1378.	1884.	1448.	1897.
4835.	2769.	1686.	1884.	1601.	2054.
2709.	1370.	1985.	1871.	1878.	1985.
4166.	2068.	2061.	1826.	2031.	1320.
5398.	2719.	1139.	1188.	1909.	1589.
2937.	1333.	1473.	1452.	1872.	1852.
1678.	2027.	1923.	1773.	1890.	2039.
4346.	2613.	2094.	1936.	1837.	2128.
5657.	2448.	1347.	2021.	1961.	2024.
2999.	2547.	801.	1876.	2051.	1181.
1659.	2598.	714.	1810.	1347.	1552.
4448.	2596.	1436.	1191.	1595.	1889.
5740.	2561.	1893.	1458.	1867.	1985.
3004.	2557.	1372.	983.	1958.	2110.
4593.	1330.	994.	1487.	1858.	1991.
5952.	1884.	950.	1753.	1840.	1929.
6049.	2439.	1644.	1854.	1917.	1878.
6099.	2709.	1299.	1902.	1436.	1889.
6022.	2416.	1796.	1793.	1633.	1203.
5683.	2245.	2015.	1855.	1895.	1714.
5852.	2339.	1318.	1980.	2014.	1907.
5918.	2183.	1609.	1900.	1895.	1892.
5715.	2199.	1888.	1779.	1833.	2010.

Table 42. Values for population size at age spans hunted at growth rates of Graham (1976) (Figure 21a).

9730.					
6146.	3798.	3140.	2906.	2677.	2653.
3653.	4418.	3168.	3018.	2658.	2036.
3021.	2963.	2249.	3071.	2646.	2384.
2896.	3583.	1821.	3069.	2742.	2588.
2922.	2468.	2244.	3057.	2799.	2678.
2835.	3120.	1772.	2990.	2712.	1857.
2777.	2173.	1518.	3191.	2802.	2272.
2730.	2867.	1419.	3162.	2729.	2539.
2692.	3130.	2099.	3118.	2921.	2689.
2631.	3305.	2433.	3152.	2869.	2818.
2621.	3384.	2561.	3100.	2823.	2989.
2106.	3385.	2617.	3112.	2875.	2932.
2423.	3437.	2697.	2085.	2902.	2963.
2488.	3495.	2068.	2691.	2909.	2885.
2599.	3515.	2393.	2972.	2779.	2950.
2721.	3525.	2562.	1981.	2780.	2930.
2758.	3439.	1938.	1480.	1875.	2963.
2067.	3454.	1488.	2357.	2326.	2976.
1738.	3383.	2199.	2714.	2443.	1995.
2585.	2393.	2496.	2897.	1657.	2480.
1966.	2791.	2550.	2969.	2196.	1726.
2873.	2974.	2682.	3079.	2487.	1337.
3361.	3211.	2804.	3113.	2591.	2089.
2372.	3205.	2897.	3134.	2617.	2355.
1905.	3265.	2139.	3247.	2647.	2607.
3250.	2232.	2513.	3150.	2592.	1952.
3806.	2903.	2588.	3067.	1778.	2440.
4223.	3191.	1950.	3094.	2214.	2668.
4340.	3363.	2403.	3103.	2454.	2788.
2961.	2315.	2563.	3105.	2461.	2895.
4055.	2876.	2604.	3044.	2690.	2116.
4667.	3219.	1823.	2286.	2584.	2504.
3096.	2180.	2295.	2572.	2595.	2662.
2316.	2845.	2628.	2888.	2697.	2779.
3956.	3115.	2784.	2886.	2633.	2877.
4726.	3138.	1919.	2917.	2677.	2900.
3091.	3303.	1506.	2927.	2658.	1955.
2361.	3374.	1250.	2909.	1988.	2490.
4120.	3448.	1978.	2133.	2334.	2728.
4898.	3428.	2482.	2514.	2486.	2807.
3191.	3484.	1853.	1745.	2476.	2927.
4599.	2433.	1417.	2231.	2584.	2912.
5322.	2898.	1342.	2457.	2577.	2914.
5707.	3197.	2204.	2544.	2551.	2885.
5925.	3323.	1716.	2641.	1920.	2940.
5994.	3216.	2417.	2748.	2240.	1971.
5832.	3162.	2774.	2699.	2461.	2469.
6023.	3262.	2015.	2803.	2508.	2598.
6037.	3139.	2615.	2816.	2538.	2704.
5932.	3187.	2895.	2711.	2573.	2771.

Table 43. Values for population size at age spans hunted at growth rates of Graham (1968) (Figure 21a).

9730.					
6072.	2593.	2651.	2928.	2500.	2693.
3497.	3173.	2696.	3024.	2522.	2080.
2789.	2350.	2088.	3111.	2549.	2437.
2592.	2957.	1794.	3140.	2573.	2561.
2544.	2197.	2128.	3159.	2644.	2672.
2411.	2680.	1766.	3121.	2618.	1889.
2336.	2018.	1582.	3260.	2723.	2261.
2295.	2761.	1480.	3281.	2699.	2542.
2270.	3010.	1996.	3284.	2741.	2628.
2231.	3108.	2294.	3359.	2821.	2720.
2125.	3236.	2427.	3358.	2827.	2770.
1528.	3244.	2423.	3330.	2909.	2764.
1888.	3253.	2518.	2361.	2889.	2815.
2012.	3330.	1935.	2892.	2927.	2784.
2107.	3379.	2332.	3181.	2846.	2784.
2190.	3409.	2571.	2183.	2818.	2791.
2183.	3372.	1995.	1734.	2017.	2838.
1548.	3402.	1543.	2459.	2494.	2872.
1245.	3287.	2282.	2841.	2596.	2041.
1820.	2510.	2664.	2927.	1882.	2497.
1371.	2730.	2730.	2992.	2400.	1782.
1874.	2866.	2895.	3011.	2609.	1472.
2102.	2986.	3043.	3086.	2771.	2089.
1668.	2995.	3083.	3149.	2735.	2304.
1464.	2914.	2269.	3122.	2777.	2503.
1915.	2073.	2774.	3158.	2764.	1864.
2124.	2509.	2919.	3122.	1886.	2261.
2306.	2660.	2221.	3179.	2410.	2373.
2334.	2784.	2747.	3223.	2712.	2519.
1640.	2057.	2992.	3181.	2787.	2610.
2162.	2356.	2990.	3150.	2918.	1997.
2469.	2567.	2113.	2439.	2913.	2380.
1747.	1827.	2608.	2704.	2902.	2562.
1561.	2207.	2934.	2920.	2990.	2710.
2269.	2371.	3143.	2916.	2981.	2785.
2616.	2341.	2191.	2939.	2987.	2847.
1978.	2444.	1653.	2814.	2999.	2017.
1528.	2464.	1429.	2800.	2307.	2554.
2352.	2521.	2240.	2090.	2693.	2822.
2742.	2450.	2752.	2408.	2795.	2861.
2032.	2503.	1970.	1692.	2813.	2956.
2675.	1938.	1514.	2126.	2814.	2989.
2935.	2235.	1428.	2338.	2780.	3040.
3134.	2441.	2301.	2400.	2792.	2984.
3273.	2559.	1716.	2380.	2100.	3079.
3342.	2475.	2411.	2454.	2454.	2179.
3318.	2491.	2763.	2381.	2573.	2641.
3499.	2599.	2015.	2455.	2658.	2833.
3623.	2591.	2604.	2514.	2666.	2992.
3712.	2616.	2874.	2487.	2678.	3106.

Table 44. Values for population size at original age spans cannibalized, initial ages of cannibalism, initial age of egg laying, and age spans hunted (Figure 21b).

9730.					

6461.	2819.	2169.	1979.	1724.	1951.
4254.	3579.	2094.	2066.	1808.	1453.
3914.	2203.	1253.	1988.	1890.	1646.
3795.	2722.	830.	1919.	1841.	1909.
3724.	1720.	1476.	1879.	1808.	2046.
3591.	2146.	1139.	1820.	1718.	1195.
3586.	1391.	970.	1974.	1724.	1454.
3441.	1815.	854.	2111.	1774.	1803.
3389.	2206.	1498.	1979.	1914.	1945.
3316.	2170.	1842.	1947.	1853.	2066.

3220.	2170.	2011.	1886.	1774.	1965.
2512.	2131.	1942.	1868.	1768.	1927.
2688.	2135.	1922.	1190.	1755.	1901.
2856.	2153.	1227.	1731.	1850.	1821.
2987.	2171.	1559.	2002.	1895.	1885.
3126.	2191.	1907.	1150.	1802.	2032.
3042.	2211.	1389.	715.	1047.	1960.
2196.	2257.	774.	1479.	1395.	1915.
1738.	2287.	1572.	1849.	1679.	1116.
2939.	1217.	1989.	1962.	1065.	1477.

2254.	1656.	2057.	2069.	1555.	1037.
3147.	2135.	2042.	2006.	1820.	766.
3915.	2606.	2075.	1972.	1806.	1461.
2434.	2652.	2062.	1945.	1872.	1725.
1645.	2662.	1289.	1924.	1963.	1932.
3671.	1353.	1629.	1911.	1832.	1443.
4618.	2070.	1852.	1850.	1060.	1648.
4902.	2708.	1371.	1863.	1439.	1888.
4827.	2760.	1676.	1863.	1792.	2046.
2705.	1365.	1971.	1852.	1868.	1978.

4159.	2059.	2047.	1804.	2021.	1314.
5389.	2768.	1131.	1172.	1909.	1582.
2933.	1328.	1463.	1435.	1868.	1844.
1675.	2020.	1910.	1757.	1881.	2030.
4339.	2601.	2080.	1920.	1829.	2119.
5647.	2436.	1338.	2005.	1952.	2016.
2994.	2534.	795.	1864.	2042.	1176.
1657.	2582.	709.	1795.	1340.	1545.
4448.	2583.	1429.	1178.	1587.	1881.
5729.	2546.	1880.	1443.	1857.	1976.

2999.	2540.	1364.	970.	1948.	2181.
4585.	1326.	988.	1472.	1848.	1982.
5948.	1877.	944.	1733.	1829.	1920.
6037.	2424.	1632.	1834.	1936.	1869.
6087.	2690.	1291.	1783.	1426.	1880.
6009.	2481.	1783.	1774.	1623.	1197.
5671.	2234.	1999.	1837.	1882.	1706.
5841.	2325.	1309.	1959.	2002.	1898.
5905.	2167.	1597.	1878.	1883.	1883.
5701.	2185.	1876.	1766.	1822.	2081.

Table 45. Values for population size at age spans cannibalized, initial ages of cannibalism, initial age of egg laying, and age spans hunted, at growth rates of Graham (1976) (Figure 21b).

9730.					
6311.	4009.	3112.	2529.	2448.	2709.
4024.	4580.	3095.	2543.	2366.	2080.
3535.	3054.	2225.	2595.	2303.	2430.
3241.	3535.	1795.	2591.	2452.	2687.
3176.	2493.	2181.	2541.	2539.	2775.
3022.	2960.	1719.	2601.	2471.	1950.
2936.	2071.	1471.	2758.	2563.	2384.
2884.	2533.	1374.	2788.	2500.	2645.
2868.	2642.	2066.	2682.	2560.	2812.
2818.	2718.	2406.	2712.	2591.	2949.
2690.	2779.	2503.	2624.	2497.	3007.
2213.	2651.	2525.	2623.	2609.	3066.
2543.	2677.	2590.	1847.	2629.	3120.
2459.	2771.	1984.	2370.	2637.	2993.
2510.	2772.	2326.	2610.	2544.	2941.
2618.	2819.	2475.	1774.	2513.	3089.
2407.	2662.	1878.	1398.	1725.	3165.
1936.	2680.	1446.	2156.	2125.	3200.
1709.	2642.	2146.	2461.	2189.	2147.
2340.	2048.	2426.	2611.	1572.	2688.
1894.	2401.	2483.	2652.	2038.	1870.
2533.	2543.	2580.	2774.	2325.	1448.
2831.	2734.	2678.	2865.	2485.	2258.
2128.	2690.	2734.	2888.	2469.	2550.
1792.	2697.	2042.	2904.	2479.	2803.
3012.	1950.	2329.	2907.	2520.	2041.
3496.	2599.	2392.	2784.	1799.	2561.
4024.	2839.	1835.	2826.	2186.	2775.
4251.	3061.	2145.	2836.	2449.	2905.
2943.	2246.	2250.	2832.	2478.	3005.
4024.	2626.	2307.	2746.	2636.	2218.
4717.	2969.	1638.	2040.	2564.	2594.
3156.	2055.	2043.	2292.	2612.	2725.
2388.	2731.	2334.	2500.	2716.	2847.
4093.	2931.	2428.	2557.	2606.	2912.
4907.	2984.	1707.	2629.	2715.	2903.
3226.	3192.	1360.	2591.	2649.	1974.
2474.	3220.	1191.	2564.	2010.	2480.
4358.	3306.	1781.	1978.	2379.	2696.
5178.	3262.	2166.	2293.	2504.	2745.
3378.	3339.	1714.	1611.	2419.	2844.
4866.	2367.	1319.	2001.	2404.	2817.
5639.	2754.	1302.	2268.	2478.	2749.
6064.	3072.	1944.	2332.	2483.	2667.
6295.	3224.	1604.	2428.	1953.	2726.
6323.	3147.	2125.	2557.	2301.	1859.
6170.	3151.	2395.	2524.	2474.	2296.
6381.	3236.	1839.	2626.	2559.	2340.
6401.	3125.	2260.	2629.	2535.	2447.
6280.	3170.	2446.	2586.	2532.	2565.

Table 46. Values for population size at age spans cannibalized, initial ages of cannibalism, initial age of egg laying, and age spans hunted, at growth rates of Graham (1968) (Figure 21b).

9730.					
6365.	2165.	2744.	2442.	2435.	2640.
4205.	2602.	2760.	2531.	2454.	2006.
3697.	2121.	2156.	2601.	2470.	2330.
3487.	2519.	1859.	2632.	2528.	2505.
3349.	2062.	2247.	2658.	2569.	2601.
3196.	2488.	1798.	2629.	2532.	1887.
3081.	1785.	1510.	2747.	2604.	2228.
2997.	2303.	1502.	2819.	2576.	2469.
2944.	2461.	2016.	2838.	2651.	2605.
2907.	2578.	2188.	2908.	2699.	2595.
2543.	2655.	2300.	2930.	2617.	2630.
1827.	2663.	2354.	2977.	2663.	2678.
1930.	2710.	2330.	2149.	2697.	2719.
1923.	2754.	1812.	2566.	2723.	2697.
1907.	2789.	2132.	2803.	2665.	2689.
1570.	2813.	2307.	2029.	2623.	2657.
1992.	2789.	1824.	1642.	1925.	2686.
1438.	2803.	1426.	2224.	2326.	2703.
1173.	2784.	1987.	2535.	2494.	1960.
1658.	2204.	2257.	2668.	1861.	2351.
1274.	2445.	2309.	2641.	2230.	1787.
1703.	2564.	2404.	2712.	2480.	1504.
1513.	2627.	2471.	2772.	2626.	2016.
1495.	2652.	2519.	2813.	2680.	2217.
1285.	2678.	1965.	2842.	2643.	2386.
1773.	1884.	2272.	2777.	2617.	1887.
1991.	2335.	2357.	2749.	1895.	2149.
2117.	2555.	1897.	2772.	2360.	2315.
2171.	2606.	2207.	2784.	2619.	2432.
1560.	2036.	2336.	2794.	2701.	2504.
1921.	2351.	2369.	2771.	2790.	1956.
2119.	2551.	1740.	2179.	2754.	2288.
1563.	1851.	2076.	2366.	2816.	2443.
1431.	2298.	2313.	2517.	2665.	2553.
1919.	2476.	2356.	2569.	2857.	2599.
2166.	2429.	1707.	2500.	2820.	2630.
1740.	2543.	1391.	2478.	2820.	1903.
1377.	2583.	1231.	2476.	2211.	2315.
1950.	2638.	1798.	1866.	2524.	2513.
2230.	2655.	2135.	2155.	2662.	2601.
1787.	2702.	1723.	1618.	2684.	2655.
2209.	2128.	1362.	2204.	2605.	2665.
2444.	2437.	1342.	2198.	2628.	2605.
2591.	2635.	1915.	2274.	2637.	2615.
2692.	2748.	1610.	2255.	2088.	2663.
2750.	2715.	2064.	2317.	2317.	1940.
2719.	2630.	2298.	2337.	2483.	2350.
2866.	2741.	1815.	2394.	2557.	2505.
2973.	2709.	2214.	2439.	2569.	2616.
3040.	2796.	2411.	2414.	2576.	2691.

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