

EVALUATING THE RELATIVE EFFECTS
OF LIFE HISTORY STAGES IN THE CONSERVATION
OF THE AMERICAN CROCODILE (*Crocodylus acutus*)
IN FLORIDA

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ABSTRACT: A stage-structured matrix model for the endangered American Crocodile (*Crocodylus acutus*) in Florida was constructed using published data and biologically reasonable estimates. The baseline version of the model yields a population growth rate λ_d of 1.006, consistent with observations that the *C. acutus* population is slowly increasing in Florida. Elasticity or the proportional sensitivity of λ_d with respect to changes in annual survivorship indicates that annual survivorship of sub-adults (1 m – 2.25 m) has the greatest proportional effect on population growth. Annual survivorships can be affected by management and are, therefore, the parameters of most interest in this elasticity analysis. Simulated management scenarios further demonstrate the degree to which sub-adult annual survivorship can affect population growth. The finding that sub-adult annual survivorship has the greatest proportional effect on λ_d suggests that management efforts should be concentrated toward this stage of the American crocodile.

Key Words: Matrix model, American crocodile, *Crocodylus acutus*, conservation, elasticity

THE endangered American crocodile (*Crocodylus acutus*) is a broadly ranging species in much of tropical America, including a small and isolated population in southern Florida. This population has probably never been larger than 2,000 individuals since the beginning of the 20th century (Ogden, 1978). The population has declined due to habitat loss and human disturbance but is now slowly recovering (Ogden, 1978; USFWS, 1984, 1999). Current estimates range from 100–400 non-hatchlings (Ogden, 1978) to 500 individuals overall, of which 220 ± 78 are non-hatchlings (Kushlan and Mazzotti, 1989b).

There are a variety of hypotheses regarding the key factors affecting the recovery of *C. acutus* in Florida. Among those published are human disturbance (Kushlan and Mazzotti, 1989a; Moler, 1991), hurricanes (Ogden, 1978), interactions with alligators (*Alligator mississippiensis*; Moore, 1953), nest site availability, and desiccation and flooding of nests (Mazzotti et al., 1988; Mazzotti, 1989). A number of studies have also shown that salinity levels affect the survivorship of hatchling and juvenile *C. acutus* (Evans and Ellis, 1977; Ellis, 1981; Dunson, 1982; Mazzotti and Dunson,

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1984; Dunson and Mazzotti, 1989). However, the relative importance of hatchling and juvenile survivorship on population growth is unknown. Of all these effects, the most important may be human disturbance, which can manifest itself in many ways. While a number of individuals are killed on highways (Kushlan, 1988; Moler, 1991), a stable and growing population of *C. acutus* occurs in the disturbed cooling canals of the Florida Power and Light Company's Turkey Point nuclear power plant (Gaby et al., 1985). The relative importance of life history stages to population growth of *C. acutus* is poorly understood and needs to be investigated.

Modeling can relate the effects on individual life stages to the whole population, and thus assist in the identification of critical life history stages that can be targeted by management. These life stage specific effects can be investigated using stage structured models, such as matrix projection models. Matrix population projection models based on age were first introduced to biology by Bernardelli (1941), independently generalized by Lewis (1942) and Leslie (1945), and later generalized to stage-based models by Lefkovich (1965). Stage-based population projection matrix models (Lefkovich matrices) are particularly well-suited to long-lived organisms, e.g. loggerhead sea turtles (Crouse et al., 1987; Crowder et al., 1994), and killer whales (Brault and Caswell, 1993), including crocodiles, because age-specific demographic data are difficult to obtain and because survival and reproduction depend more upon size/stage than upon age.

Population modeling of crocodylians has concentrated primarily on simulating harvest strategies, not on the relative impacts of management strategies. Examples include harvest models of *A. mississippiensis* (Nichols et al., 1976; Rice, 1996), *C. niloticus* (Blomberg et al., 1982), and *C. johnstoni* (Smith and Webb, 1985). These models used large data sets and made fairly accurate predictions of population size. In one case (*C. johnstoni* simulation model, Smith and Webb, 1985) a sensitivity analysis was conducted on the input parameters. Their results showed that predicted population size was most sensitive to the measured error in egg survivorship, but this parameter also had the largest standard error of all the input parameters. They concluded that a better population size estimate would be gained by increased attention to the measurement of egg survivorship, presumably by lowering the measurement error associated with it, but they warned that using their results to assign relative importance to input parameters is "misleading". A proportional sensitivity analysis (elasticity) based on hypothesized true parameter values and not on measurement error would be needed to draw such a conclusion.

In this paper, I use a variety of published data to develop a stage-based population projection matrix model for *C. acutus* in Florida. Three primary areas are the current focus of *C. acutus* activity in Florida; the southern portion of Everglades National Park, Key Largo, and the Florida Power and Light Company's Turkey Point power plant. Data from published studies in all 3 areas were combined to parameterize the model. Using a prospective analysis (Horvitz et al., 1997), I addressed the question: which of the model parameters would have the largest effect on population growth? Elasticity analysis identifies the parameters having the greatest proportional effect on population growth and simulated management scenarios demonstrate these effects on *C. acutus* populations.

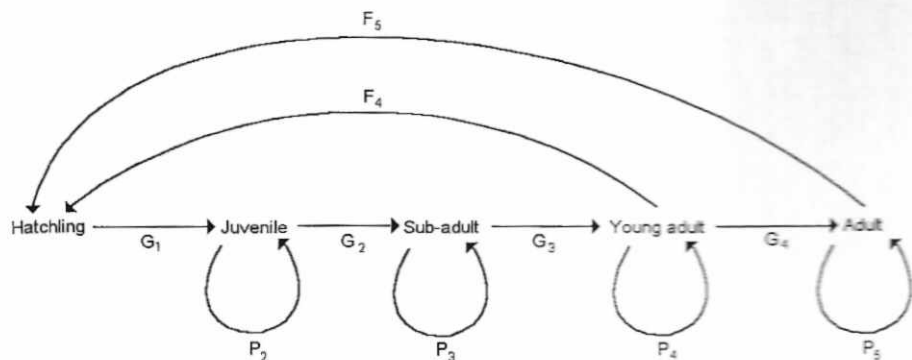


FIG. 1. Life cycle graph of *C. acutus*. P_i 's are the probabilities of remaining in stage classes, G_i 's are the transition probabilities of moving to the next stage classes and F_i 's are the number of hatchlings produced per female of stage i per year.

METHODS—The model—A stage-based matrix model for *C. acutus* was developed following the methods of Caswell (1989). Stage categories based on age, size (total length), and reproductive capacity were chosen for biological reasons in a similar way that has been done for plants (Horvitz and Schemske, 1995) and turtles (Crouse et al., 1987; Crowder et al., 1994; Heppell et al., 1996). Although approximate size and stage classes for *C. acutus* are referred to in the published literature, no general convention exists. Mazzotti (1983) and Kushlan and Mazzotti (1989b) referred to hatchlings (<0.5 m), subadults (0.5–2.5 m) and adults (>2.5 m). Gaby and co-workers (1985) used size classes of juvenile (60–120 cm), sub-adult (121–183 cm) and adult (>183 cm). From these categories and data from Moler (1991) I defined the following five stages for *C. acutus*: 1) "hatchlings" (<0.5 m, <1 year), 2) "juveniles" (0.5 m–1.0 m, 1 to <3 years), 3) "sub-adults" (>1.0 m–2.25 m, 3 to <10 years), 4) "young-adults" (>2.25 m–2.5 m, 10 to <12 years), and 5) "adults" (>2.5 m, 12 to 25 years). The hatchling stage defined here is consistent with Mazzotti (1983) and Kushlan and Mazzotti (1989b), but I divided their sub-adult stage into three stages. This division minimizes the probability of violating the assumption that all individuals within a stage have the same transition probabilities (Moloney, 1986). In Moler's (1991) 10-year study, *C. acutus* exhibits a change in annual survivorship at about 3 years of age, corresponding to a length of approximately 1.0 m. This split at the 1.0 m size results in two stages, juvenile and sub-adult. The "young-adult" stage was added because it has been observed that small (2.25 m–2.5 m), female *C. acutus* have reduced clutch size (Moore, 1953; Mazzotti, 1989). Finally I adopted the adult stage of Mazzotti (1983), Kushlan and Mazzotti (1989b) and others.

Figure 1 shows the five stage model life cycle graph for *C. acutus* where P_i is the probability of surviving and remaining in a stage i , G_i is the probability of surviving and growing into the next stage, and F_i is the fecundity of the stage i . Writing this as a matrix yields the basic form of the projection model for *C. acutus* (Eqn. 1):

$$A = \begin{bmatrix} 0 & 0 & 0 & F_4 & F_5 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix} \quad (1)$$

The diagonal (P_i) and subdiagonal (G_i) elements of A were calculated as a function of annual survivorship, p_i , and stage duration, d_i , (see Parameterization below and Table 1 for *C. acutus* estimates). P_i is calculated (Eqn. 2):

$$P_i = \frac{p_i(1 - p_i^{d_i-1})}{1 - p_i^{d_i}} \quad (2)$$

TABLE 1. Parameter sets for version 1 (the best estimate), version 2 (the minimum) and version 3 (the maximum). Units are as follows: size is total length in meters, d_i is in years, p_i has units of per year, and F_i are in units of hatchlings per year.

Stage description	Size range	d_i (stage duration)	p_i (survivorship)	F_i (fecundity)
a) Version 1 parameters.				
1) hatchlings	<.5 m	1	0.2040	0
2) juveniles	(0.5 m–1.0 m)	2	0.6502	0
3) sub-adults	(>1 m–2.25 m)	7	0.7862	0
4) young adults	(>2.25 m–2.5 m)	2	0.90	5.99
5) adults	>2.5 m	25	0.90	7.63
b) Version 2 parameters.				
1) hatchlings	<.5 m	1	0.0680	0
2) juveniles	(0.5 m–1.0 m)	3	0.3640	0
3) sub-adults	(>1 m–2.25 m)	9	0.7076	0
4) young adults	(>2.25 m–2.5 m)	5	0.80	0.92
5) adults	>2.5 m	5	0.80	1.45
c) Version 3 parameters.				
1) hatchlings	<.5 m	1	0.4300	0
2) juveniles	(0.5 m–1.0 m)	1	0.7152	0
3) sub-adults	(>1 m–2.25 m)	6	0.8648	0
4) young adults	(>2.25 m–2.5 m)	1	0.99	15.76
5) adults	>2.5 m	40	0.99	15.44

and G_i (Eqn. 3):

$$G_i = \frac{p_i^{d_i}(1 - p_i)}{1 - p_i^{d_i}} \quad (3)$$

(Crouse et al., 1987). The population rate of increase λ_d (the dominant eigenvalue of A), the stable stage distribution (the right eigenvector of A associated with λ_d), and the reproductive value vector (the left eigenvector of A associated with λ_d) were calculated using EISPACk, a public domain subroutine.

Proportional sensitivities or elasticities measure the relative effects of proportional changes in various parameters on λ_d . Elasticity analysis is useful since it allows a comparison of the effects of various parameters that may not be on the same scale. The elasticities of λ_d for each parameterization of the model to their respective matrix elements (P_i , G_i , and F_i) were calculated using the computational form found in Crouse and co-workers (1987). Since the matrix elements are functions of annual survivorship (p_i) and stage duration (d_i), the elasticities of λ_d with respect to these parameters can be calculated (Eqn. 4):

$$E = \frac{\lambda_d(x + 0.01x) - \lambda_d(x - 0.01x)}{0.02\lambda_d} \quad (4)$$

(Crowder et al., 1994), where $\lambda_d(x \pm 0.01x)$ is the population growth rate λ_d calculated when parameter x (either p_i or d_i) is increased or decreased 1%. This form is an approximation, not an exact analytical form, as is the equation for elasticity to matrix elements given in Crouse and co-workers (1987). It was checked against a computational form (Wolff, 1997) and yielded nearly identical results that are accurate to approximately 4 decimal places.

Parameterization—General considerations—I adopted the “no holds barred methods of parameter estimation” (Caswell, 1989), using a mixture of methods to acquire parameter estimates. Most parameter estimates were based on a variety of published values, except annual survivorship (p_i) and stage duration

(d_i) of young adults and adults (see Stage duration and Annual survivorship sections below). Three versions of the model were developed using three sets of parameters that span the range of likely values. The baseline version 1 of the model was based on the means of published values for *C. acutus* in Florida, and my best estimates (Table 1a). In addition, minimum and maximum sets of parameters were created either by using the extremes of the reported range of values, or by adding or subtracting 10% of the parameter values used in version 1. This was done for all parameters except the stage duration (d_i) of hatchlings, juveniles, and sub-adults (see Stage duration and Annual survivorship sections below). The combination of the minimum and maximum parameter sets that yield the smallest and largest λ_d 's, were labeled version 2, the 'minimum', and version 3, the 'maximum', projection matrices. Table 1 includes all 3 parameter sets I used for analysis. Similar methods of combining means, point estimates and informed guesses have been used for other demographic models where few data were available, e.g., a Ridley sea turtle matrix model (Heppell et al., 1996), a desert tortoise model (Doak et al., 1994) and a *C. johnstoni* simulation model (Smith and Webb, 1985).

Fecundity, F_i —The census interval for the model is one year, with censusing in late August immediately after hatching. During a census interval, a female will mate, build a nest, and lay eggs, which hatch just prior to the next census. Stage 5 ("adult") fecundity (F_5 in Figure 1) was estimated using Kushlan and Mazzotti's (1989b) summary of previously published (up to 1982) and unpublished data on the nesting biology of *C. acutus* in Florida. Using their estimates of a mean clutch size of 38 eggs (range 15–56), a probability that a nest is successful of 0.783, the proportion of eggs that hatch given a successful nest of 0.575, and adult female survivorship during the interval, I estimated that 15.25 female and male hatchlings were produced per nesting female. Although Deeming and Ferguson (1989) claimed that female-biased sex ratios are likely in most crocodylian species, Thorbjarnarson (1997), using published data on 11 species of crocodylians, showed that a female-biased sex ratio is not supported. I assumed a 1:1 sex ratio for *C. acutus* in Florida (Kushlan and Mazzotti, 1989b; Moler, 1991), and since the model only follows females I divided the number of hatchlings per breeding female by two. This gave the estimated female hatchlings produced per reproductive female as $F_5 = 7.63$ for *C. acutus* in Florida (Table 1a). Finally, while it is possible that female *C. acutus* do not nest every year, currently there are no data to support an estimate of the proportion of females that do nest and, as will be apparent, the range of values for fecundity that I use in the minimum and maximum versions of the model would likely take this into account.

For the minimum and maximum estimates of F_5 I attempted to span the likely range of feasible fecundities for *C. acutus*. Using the ranges in Kushlan and Mazzotti (1989b), and including Ogden's (1978) estimate of 0.65 for the probability of a successful nest and female survivorship during the interval, a minimum fecundity estimate of 1.45 and a maximum of 15.44 were calculated (Table 1). Published data for *C. acutus* from other parts of its range report: 27 eggs in a single nest in Mexico (Aguilar and Casas-Andrew, 1991), a range of 19 to 41 eggs per nest in Colombia (Abadia, 1996), a mean of 22 eggs per nest (range = 9–36) in the Dominican Republic (Schubert et al., 1996), and a total fecundity value of 16.04 male and female hatchlings per nesting female in Haiti (Thorbjarnarson, 1988). These observations fall within the ranges that I used for *C. acutus* in Florida. In addition, a mean of 36.4 eggs per nest ($n=21$, $SD=13.93$, range = 15–75) was reported by Greer (1975) for *C. acutus* but the locations of the nests were not reported.

The fecundity estimates (F_4 , Fig. 1) for stage 4 (young breeders) were calculated similarly. Mazzotti (1989) observed a clutch of 22 eggs laid by a 2.28m female and Moore (1953) observed two captive female *C. acutus* of approximately 2.28 m laying clutches of 21 and 22 eggs. Given these limited data, I used a clutch size of 22 eggs per stage 4 female and the probability of any egg hatching of 0.450 (see above). After accounting for female survivorship during the interval, and growth into the large stage, this yielded a value of $F_4 = 5.99$ female hatchlings produced per stage 4 female per year for the version 1 model. For the minimum and maximum parameters of F_4 I reduced the appropriate estimates of the number of hatchlings produced per nest of stage 5 females by 50% and then adjusted these by survival and growth of stage 4 (Table 1).

Stage duration, d_i —The approximate durations of each stage (d_i 's of Table 1) were estimated for stages 1–3 using Moler's (1991) Figure 3. I approximated the age of first reproduction (at 2.25 m) to be 10 years based on Moler's (1991) Figure 3 and the stage durations of stages 1–3. Age of first reproduction

was estimated to be 13 years by both Lebuff (1957) and Ogden (1978) but Moler's (1991) data suggest that *C. acutus* can reach reproductive size (2.25 m) at age 9 years. Using this possible range of 9 to 13 years for the age of first reproduction, I set the stage durations for stages 2 and 3 in the minimum and maximum versions of the model (Table 1). For stages 2, 3 and 4 the minimum version has the longest stage durations and the maximum version has the shortest. This is because, for example, the greater the amount of time individuals remain in early life stages the less likely they are to survive to breed at full potential and the later they will start reproduction, thus reducing the population growth rate (λ_d).

Longevity in crocodylians is notoriously hard to estimate, so I used a range that is reasonable. For version 1 of the model, the duration of stages 4 and 5 were arbitrarily chosen to be 2 and 25 years, respectively. For version 2, the minimum parameter set, I allowed stage 4 to have a duration of 5 years and stage 5 to have a duration of 5 years. For version 3, the maximum parameter set, stage 4 has a duration of 1 year and stage 5 is 40 years. The maximum possible life duration is 37 years in version 1, 23 years in version 2, and 49 years in version 3. Although there are no data on the longevity of adult *C. acutus* in the wild, there are accounts of other species of crocodylians living 40–56 years or more in captivity (Levy 1991), and thus 49 years seems to be reasonable for *C. acutus* in Florida.

Annual survivorship, p_t —Age-specific annual survivorship data, using minimum number known alive, is available for *C. acutus* from a 10 year mark-recapture study on Key Largo (Moler 1991). I converted Moler's (1991) age-specific annual survivorship data to stage-specific annual survivorship, by assuming that annual survivorship within a stage is independent of age. This resulted in estimates for the annual survivorship of stages 1 to 3. Because I am not aware of any published data for annual survivorship of stages 4 and 5, I chose the midpoint of Moler's (1991) estimate that *C. acutus* older than 5 years have annual survivorships between 0.80 and 1.00 (0.90).

To arrive at minimum and maximum estimates of annual survivorships I used other authors opinions and extreme estimates, when available. For hatchling annual survivorship I used the extremes of the range of 0.068–0.429 (Moler, 1991). The low value is consistent with both Brandt and co-workers (1995), who reported that over a 9 year period the mean hatchling annual survivorship was 0.085 at the Turkey Point site, and McIvor and co-workers (1994) who report that annual survivorship of hatchlings in Florida Bay is 0.10. For stages 2 and 3 I arbitrarily added 10% or subtracted 10% from the version 1 estimates for annual survivorship except the minimum for stage 2. The minimum for stage 2 (0.364, Table 1) was calculated using the data of Brandt and co-workers (1995: Table 1). For adults (stages 4 and 5) I set the range = (0.80–0.99) (modified from Moler, 1991) for annual survivorship for the minimum and maximum estimates of version 2 and version 3 of the model respectively (see Table 1).

Projection matrices—The population projection matrices for all three versions of the models were calculated from the appropriate parameter sets of Table 1. The best estimate, version 1, projection matrix is presented in Table 2. The population projection matrices for versions 2 and 3 are readily calculated from the parameter sets of Tables 1b and 1c, respectively.

Management simulations—Four simulated management scenarios (simulations A–C) were created as examples of the types of questions that can be addressed by this model and to provide an example of what the elasticity results mean. All simulations began with a total population of 500 individuals distributed according to the stable age distribution produced by version 1 of the model and were projected for 20 years by repeated matrix multiplication. Simulations A and B represented a hatch and release program by increasing fecundity 21% and maintaining that level of fecundity for 2 and 20 years respectively. Simulation C involved increasing sub-adult (stage 3) survivorship from 78% to 80.9% for all 20 years of the simulation, to simulate the effects of reducing road mortality. The fecundity increase in simulation B was chosen to produce a population growth rate close to that of simulation C.

TABLE 2. The population projection matrix for version 1 of the model.

Stage	Stage				
	1	2	3	4	5
1	0	0	0	5.99	7.63
2	0.204	0.394	0	0	0
3	0	0.256	0.738	0	0
4	0	0	0.049	0.474	0
5	0	0	0	0.426	0.892

uncertainty is not useful for making quantitatively accurate predictions for the population growth rate. However, it can be used to examine the proportional effects of the model parameters on population growth, or elasticity of λ_d to changes in the parameters.

The general pattern of elasticities for all matrix elements (P_i , G_i , and F_i) in all three versions of the model were similar, with one minor difference; thus, I present the elasticities of λ_d only for the matrix elements of version 1 (Fig. 2). For all versions the elasticities to P_3 and P_5 are larger than all other elasticities to matrix elements except for the elasticity to P_4 in version 2. This difference is due to the effect of the stage duration of stage 4 (d_4) on the elasticities of λ_d to P_4 . In version 1, where $d_4 = 2$, it is expected that λ_d would be more sensitive to changes in P_4 than when $d_4 = 1$ in version 3, since $P_4 = 0$ and elasticity is zero. Likewise, the elasticity of λ_d is still higher in version 2, where $d_4 = 5$. This result disappears if I set $d_4 = 3$ in version 2. These results showed that relatively small changes in P_3 and P_5 cause much greater changes in the population growth of *C. acutus* than proportionally similar changes to any of the other matrix entries.

Since the matrix elements were functions of the lower level parameters, d_i and p_i , elasticities of λ_d to these parameters may be more useful for assessment of management decisions on population growth (Crouse et al., 1987). Elasticities of λ_d to annual survivorship (p_i) are presented in Figure 3 for all three versions. The general pattern of elasticities of λ_d to p_i 's were similar for all three versions, and the qualitative results were the same. Sub-adult annual survivorship (p_3) had the largest elasticity of λ_d in all three versions. Adult annual survivorship also showed high elasticities of λ_d .

Elasticities of λ_d to stage duration were all small and usually negative. All elasticities to stage duration for all 3 versions fell within the range of -0.194 to 0.074 , which are comparable to the values found by Crouse and co-workers (1987) in their elasticity analysis on loggerhead sea turtles and were small relative to the elasticities of annual survivorship for stages 3 and 5 (Fig. 3).

Results of simulations—Version 1 of the model was projected for 20 years to provide a baseline projection to compare to simulations A–C. Figure 4 shows the results of the 20-year projections in terms of the non-hatchling population. Version 1 has a $\lambda_d = 1.006$ which indicates slow population growth; the simulated population increased from 220 to 248 non-hatchlings in 20 years. Figure 4 also includes the

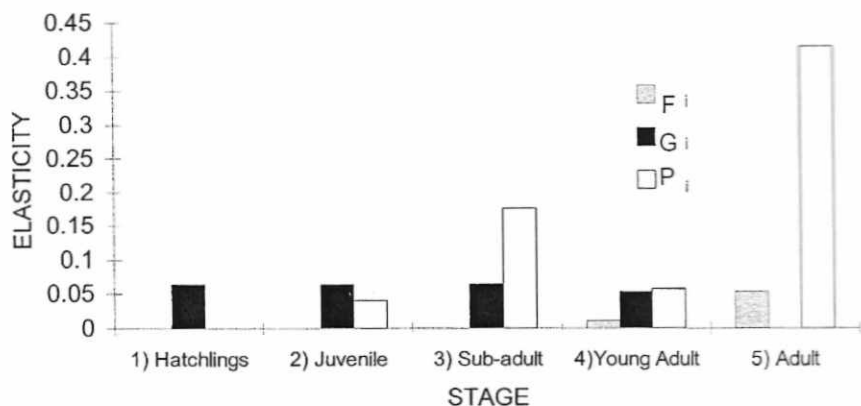


FIG. 2. Elasticities of λ_d with respect to the matrix elements for version 1. Versions 2 and 3 have a similar qualitative pattern of elasticities, with the largest elasticities due to P_i 's for stages 3 and 5, except for the addition of a large elasticity due to P_4 in version 2 (see text for details).

results of the four simulated management scenarios (A–C). Of these, increasing sub-adult annual survivorship to 80.9% (simulation C) yielded the highest population growth rate, $\lambda_d = 1.0192$, while increasing fecundity 21% over all 20 years (simulation B) yielded a similar λ_d (1.0188). At the end of the 20 year projection increasing fecundity 21% (B) resulted in a greater total non-hatchling population (see Fig. 4) but it would eventually be surpassed by simulation C if the projection length was increased sufficiently. The simulated 2 year hatch and release program (A) resulted in a short term increase in the non-hatchling population but soon returns to nearly baseline levels resulting in only a 2.8% increase over baseline (version 1) in the simulated population by year 20.

DISCUSSION—Elasticity analyses and simulations using the best estimate version of the model of the American crocodile (*C. acutus*) strongly suggest that annual survivorship of sub-adults (individuals 1 m–2.25 m) has the greatest effect on population growth rate. The same qualitative result was found in all versions of the model (Fig. 2). This conclusion is supported by similar models and empirical data that show the greatest effect on population growth rate of sub-adult or young adult survivorship for other large, long-lived species such as sea turtles (Crouse et al., 1987; Crowder et al., 1994; Heppell et al., 1996), desert tortoises (Doak et al., 1994), killer whales (Brault and Caswell, 1993), and long-lived birds, e.g. the spotted owl (Lande, 1988) and Hawaiian dark-rumped petrel (Simons, 1984). Because annual survivorship is a parameter that management can affect, it is more appropriate to examine the elasticity of λ_d to this parameter than to matrix elements which are functions of both annual survivorship and stage duration, such as the elasticity of λ_d to the probabilities of sub-adult and adult stasis (P_i , Fig. 2). In any case, for *C. acutus* in Florida, management practices that may increase annual survivorship of sub-adults (e.g. reducing road mortality) would probably also increase annual survivorship for all stages >1 m total length, which would increase P_5 as well.

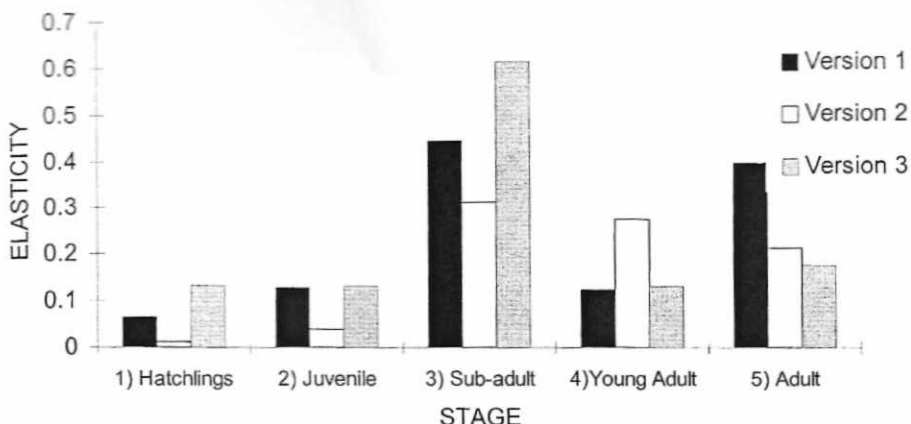


FIG. 3. Elasticities of λ_d with respect to annual survivorship (p_i) for all 3 versions. Elasticities are greatest for stage 3 sub-adults for all 3 versions.

Making quantitative predictions from models is risky (Crowder et al., 1994), and this is certainly true of this model. The estimates for adult annual survivorship are only rough estimates, and most of the remaining parameter estimates were derived from only a handful of studies. I assumed a 1:1 sex ratio even though the sex ratio of hatchling crocodilians is known to be affected by nest temperature (for reviews see Webb and Cooper-Preston (1989) and Deeming and Ferguson (1989)). I also assumed that survivorship is independent of age within a stage. This assumption does not allow for differential survivorship at younger ages within a stage. As more empirically derived data become available, a more quantitatively accurate model can be constructed. Matrix models have helped in understanding the relative impacts of management decisions on sea turtle life history stages (Crouse et al., 1987; Crowder et al., 1994). Crouse and co-workers (1987) and Crowder and co-workers (1994) showed, using elasticity analysis, that the annual survivorship of "large juvenile" loggerhead sea turtles had the greatest effect on population growth. This knowledge has redirected the efforts of management from focusing on headstarting to other critical life stages. Most crocodilians share a similar life history pattern with sea turtles and both have been subjected to both deliberate and incidental human impacts. It is not surprising to find similar matrix model results for *C. acutus* and those of sea turtles. Using the results of models like these to compare the value of alternative management strategies would further require an evaluation of the susceptibility of a given parameter to management (Nichols and Hines, 2002) and therefore the relative cost for a given effect (Nichols et al., 1976). In the case of crocodilians the effects of life history stages on population growth have not been systematically explored until now, although models of the type presented here are suggested by Nichols (1987).

Simulated management scenarios—The simulated management scenarios further strengthen the argument that sub-adult annual survivorship has the greatest proportional effect on population growth (see Fig. 4). These simulations demonstrate

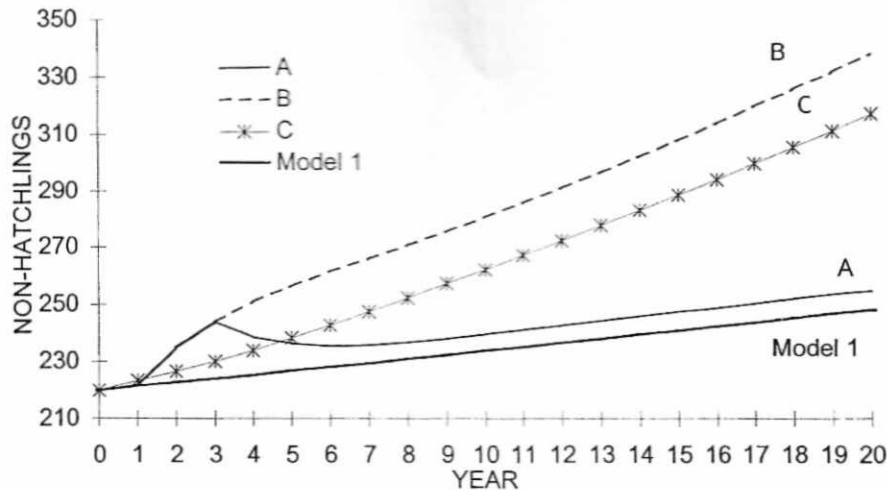


FIG. 4. 20 year simulated population projections based on four management scenarios (A-C). The version 1 of the model projection is included for a baseline comparison. Simulation A increased fecundity 50% and maintained that level of fecundity for 2 years. Simulation B increased fecundity 50% and maintained that level of fecundity for 20 years. Simulation C increased the annual survivorship of stage 3 from 78% to 84% for all 20 years of the simulation.

the relative effects on population growth of targeting particular life history stages of *C. acutus*. Increasing sub-adult annual survivorship a relatively small amount of 2.5% (simulation C) resulted in $\lambda_d = 1.019$. To approximate this level of population growth, a 21% increase in fecundity (simulation B) was needed. This is equivalent to collecting the eggs of 31.5% of the crocodile nests in Florida and incubating them in captivity with a survivorship to hatchling stage of 75%, as has been modeled for alligators (Nichols et al., 1976), before releasing them (assuming that wild and captive raised hatchlings have the same vital statistics). Hatch-and-release programs have been modeled for crocodylians and under some circumstances have been proposed as a viable management strategy, including for *C. acutus* in Florida (Behler, 1978; USFWS, 1984; Moler, 1991).

Simulation A represented a more realistic hatch and release management scenario. This 20-year simulation considered the effects of a limited 2-year hatch and release program and continued to track the population for 20 years. As expected, simulation A tracks simulation B (Fig. 4) for the first 3 years. At year 3, the non-hatchling population in simulation A declined as it moved back to the stable age distribution of version 1, eventually increasing again at about year 8 at the same rate as version 1. After 20 years simulation A resulted in 2.7% more non-hatchlings than version 1.

Moler (1991) noted that over an 11-year period 25 *C. acutus* (~two per year) died on the two highways that connect mainland Florida to Key Largo. Similar mortality figures are reported by Kushlan (1988) and Kushlan and Mazzotti (1989b). Many of the dead *C. acutus* are referred to as "adult". Thus I assumed that all were >1 m total length and were at least sub-adults in the stage classification presented

here. Increasing sub-adult annual survivorship from 78.6% to 80.9% in simulation C was approximately equal to saving two sub-adult *C. acutus* in the first year of the simulation. Reducing road mortality may be possible by installing bridges or box culverts in critical areas (USFWS, 1984). Most management plans that would cause an increase in the annual survivorship of sub-adults would likely result in an increase in the annual survivorship of all stages >1 m total length. Although this was not explicitly modeled in simulation C, the results of the elasticity analysis showed that increasing annual survivorship of the adult stage would also have proportionally large effects on population growth (see Fig. 3).

Although the results presented here showed that factors affecting hatchling survival had a small relative effect on population growth in *C. acutus* headstarting may in some cases be the only management choice. It can be of critical importance when trying to boost very small populations (Heppell, 1998). Headstarting can be problematic; for example, at Largo Enriquillo, Dominican Republic, a headstarting program for *C. acutus* failed due to personnel problems (Schubert et al., 1996). This population at one time was quite large (Thorbjarnarson, 1988) but has recently declined dramatically (Jackson, 1993; Schubert et al., 1996). It does appear that with increased protection, primarily by stopping illegal killing, this population may recover (Schubert et al., 1996), which is consistent with the results of the model presented here.

In summary, I believe that the future of *C. acutus* in Florida looks hopeful. Version 1, the best estimate of the parameters for the model, which is based to a large extent on published data, is consistent with observations that the Florida population of *C. acutus* is increasing. Complacency towards this population is not wise and hopefully the results of this modeling effort can help prioritize management efforts. Although they are difficult to obtain, estimates of the annual survivorship of large crocodylians in relation to management actions are needed. This lack of data limits our abilities to accurately predict the outcome of management decisions. In addition, the increasing human population of Florida will place increased pressure on *C. acutus* populations. Human-mediated disturbance could include road construction, increased road traffic and/or boat traffic, habitat destruction and Everglades restoration. Managers will be faced with difficult decisions and it is hoped that recognizing the relative effects of various life history stages, especially that of sub-adults and adults of *C. acutus*, will assist in future decision making.

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