

A Demographic Study of the Arrau Turtle (*Podocnemis expansa*) in the Middle Orinoco River, Venezuela

SOL C. MOGOLLONES^{1,2,4}, DIEGO J. RODRÍGUEZ¹, OMAR HERNÁNDEZ³, AND GUILLERMO R. BARRETO²

¹Instituto de Zoología Tropical, Facultad de Ciencias, Universidad Central de Venezuela, Apartado 47058, Caracas 1041-A, Venezuela [diego.rodriguez@ciens.ucv.ve; corresponding author];

²Laboratorio de Manejo y Conservación de Fauna, Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado 89000, Caracas 1080-A, Venezuela [guibarre@usb.ve];

³FUDECI, Palacio de las Academias, Av Universidad de Bolso a San Francisco, Caracas 1010-A, Venezuela [omarherpad@gmail.com];

⁴Present Address: University of Aberdeen, Zoology Building, Tillydrone Av, Aberdeen AB24 2TZ, Scotland, United Kingdom [sol_barrera@abdn.ac.uk]

ABSTRACT. – *Podocnemis expansa* (the giant South American or arrau turtle) is a freshwater turtle in critical risk of extinction, distributed along the Orinoco, Amazon, and Esequibo river basins. Protection of nesting beaches and headstarting of hatchlings has been in progress since 1989 on the Arrau Turtle Wildlife Refuge located in the Middle Orinoco River in Venezuela. The purpose of our study was to evaluate the population dynamics of the species in this refuge. We used data on the number of turtles and number of nests collected from 1989 to 2004 that were available from the Venezuelan Ministry of Environment as well as data collected by us in 2004. Also, we collected data in 2004 on sizes of individuals of known age. First, a somatic growth curve was constructed and used to transform size structure in age structure. Age-specific fecundity and survivorship were calculated. Finally, we constructed a size-dependent matrix model and used it to determine population status and to assess the effectiveness of alternative management options. According to our analyses, the population size and age structure have stabilized. The analyses also indicate that protecting the survivorship of juveniles and adults, more than fecundity, is the conservation action that could best reverse a population decline. We conclude that additional efforts focused on protecting juveniles and adults of the arrau turtle, such as reinforcement of illegal hunting controls, must be implemented in order to ensure the success of the conservation program.

KEY WORDS. – Reptilia; Testudines; Podocnemididae; *Podocnemis expansa*; turtle; conservation; size-dependent matrix model; management; demography; Venezuela

In long-lived iteroparous species, such as marine and freshwater turtles, the lack of information on survivorship and fecundity parameters has made the construction of population models challenging (Crouse et al. 1987), particularly for tropical freshwater turtles. Mark–recapture data from nesting females have been used to estimate demographic parameters for just a few species (Frazer 1983; Briceño-Dueñas and Abreu-Grobois 2000), and size-based matrix population growth models have been used to assess the effects of management policies and to project population growth rate (Crouse et al. 1987; Crouse 1999).

The giant South American or arrau turtle, *Podocnemis expansa* (Testudines: Podocnemididae) (Fig. 1), is distributed throughout the Orinoco, Amazon, and Esequibo river basins. In the Orinoco River, turtles nest communally on isolated beaches during January and April and show a high degree of fidelity for nesting beaches (Alho et al. 1979). The Middle Orinoco River in Venezuela contains some of the main nesting sites for *P. expansa*, although intensive harvest nearly extirpated the species (Paolillo 1982). The nesting concentrations once numbered hundreds of thousands of individuals (Humboldt 1820; Roze 1964; Pritchard and Trebbau 1984).

Podocnemis expansa in the Middle Orinoco River has decreased from an estimated 330,000 in 1800 (Humboldt 1820), to 123,622 in 1945 (Ojasti 1967), to a low of 700–1300 (data from the Venezuelan Ministry of Environment [MINAMB 2002]; Fig. 2) in recent years. Although these estimations are based on different protocols, they indicate a drastic decline in the population. The arrau turtle is a critically endangered turtle in Venezuela (Rojas-Suárez and Villas 2007; Rodríguez and Rojas-Suárez 2008) and a lower-risk/conservation-dependent species according to the IUCN Red List. The *P. expansa* population of the Middle Orinoco River has been actively managed by the Venezuelan government since 1989. A program of mass reintroduction of marked yearlings has been in place since 1994 in a joint effort of the Venezuelan Ministry of Environment (MINAMB); the Foundation for the Development of Physical, Mathematical and Natural Sciences (FUDECI); and a number of foundations and communities.

In the present study, we estimate demographic parameters of the Middle Orinoco arrau turtle population and construct a size-dependent matrix growth model in order to investigate the species' population status and the



Figure 1. An adult female *Podocnemis expansa* at the Arrau Turtle Wildlife Refuge in the Middle Orinoco River, Venezuela. (Photo by Claudia Ceballos.)

consequences of changing particular age parameters and to assess the effectiveness of the protection program policies.

METHODS

Study Area and Data Collection. — We studied *P. expansa* on mass nesting beaches and neighboring backwater zones in the Middle Orinoco River area, Venezuela. These temporary beaches are located inside a 17,431-ha Arrau Turtle Wildlife Refuge and Protective Zone as well as in a 24-km stretch of the Orinoco River (Fig. 3).

Every year during nesting season, which starts in February, personnel from MINAMB counted the number of nests and eggs inside each nest, in Playa del Medio, a beach in the Wildlife Refuge zone (Fig. 3). Assuming that each female reproduces once annually, nest counts are used to estimate female population size. The rearing and reintroduction program, in place since 1994, is managed as follows. Approximately 60 days after egg deposition, hatchlings are taken to rearing facilities where they are kept for a year. Yearlings are marked by cutting the first phalanx of a digit of the forelimb, with different digits for different years, and are then reintroduced at the natal beach. This mark allows aging of recaptured individuals, which are subsequently marked with an individual shell marking on recapture.

We captured turtles using standardized FUDECI methodology (Hernández and Espín 2006) in which one end of a fish net (120 × 5 m, with 5-cm mesh) was anchored on the beach and the other end tethered to a boat. Each netting consisted of a 60–80-m sweep, after which the net was taken to the shoreline, and the turtles captured in the sample were counted and analyzed. In 2004 we made a total of 140 nettings at 13 temporary beaches and sampled individual beaches on alternating days. Nettings were done from 0700 to 1200 hours and from 1500 to 1800 hours from 12 April to 14 May 2004.

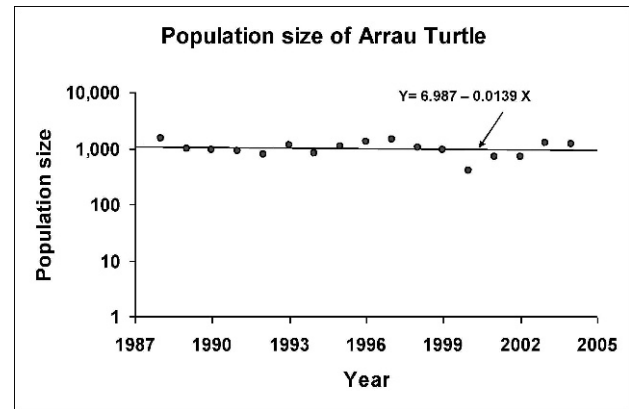


Figure 2. Population size of the arrau turtle in the Middle Orinoco River. Points are the natural logarithms of number of nests at Playa del Medio, a beach in the Wildlife Refuge zone. The line is the regression curve fitted to the points, which obeys the equation $y = 6.987 - 0.0139x$. The 95% confidence interval for the slope is $(-0.0480; 0.0203)$; the slope does not differ significantly from 0.

Every individual captured in the field, including unmarked turtles and previously marked turtles, was marked with individual marks in the marginal lamellae of the carapace, measured, weighed, and, when possible, sexed (Hernández and Espín 2006). In arrau turtles the sex can be determined when the size of the individual is larger than 175 mm curved carapace length, based on the length of the tail and the morphology of the anal groove in the plastron: this groove is V-shaped in females and U-shaped in males.

Age–Size Curve. — We graphed the curved carapace length (CCL) vs. the age of recaptured turtles from the headstarting program and fitted a logarithmic growth model (Fig. 4). This curve is necessary to transform size to age data and to relate size to the minimum age at first reproduction. The turtles used in this section were recaptured by us in 2004.

Estimation of Population Parameters. — Data used for the estimations were obtained from MINAMB (1990–1994, 2000–2002), FUDECI (1998, 2000–2003; Hernández and Espín 2006), and our fieldwork done in 2004. The data include the number of nests and clutch size from nesting beaches and size structure from turtles caught in the river with fishing nets.

Instantaneous Per Capita Growth Rate. — We obtained an initial estimate of the instantaneous per capita rate of increase, r , from annual census data. We applied Caughley's (1977) density-independent population growth equation to annual census data to determine the instantaneous rate of growth for this arrau turtle population. The slope of this linear regression corresponds to r (Fig. 2).

Fecundity. — There have been reports of a positive correlation between female size and clutch size in turtles (Ernst 1971; Gibbons et al. 1981), particularly in most freshwater turtles (Iverson 1991; van Loben Sels et al. 1997; Zuffi et al. 1999) and also for *P. expansa* (Meden

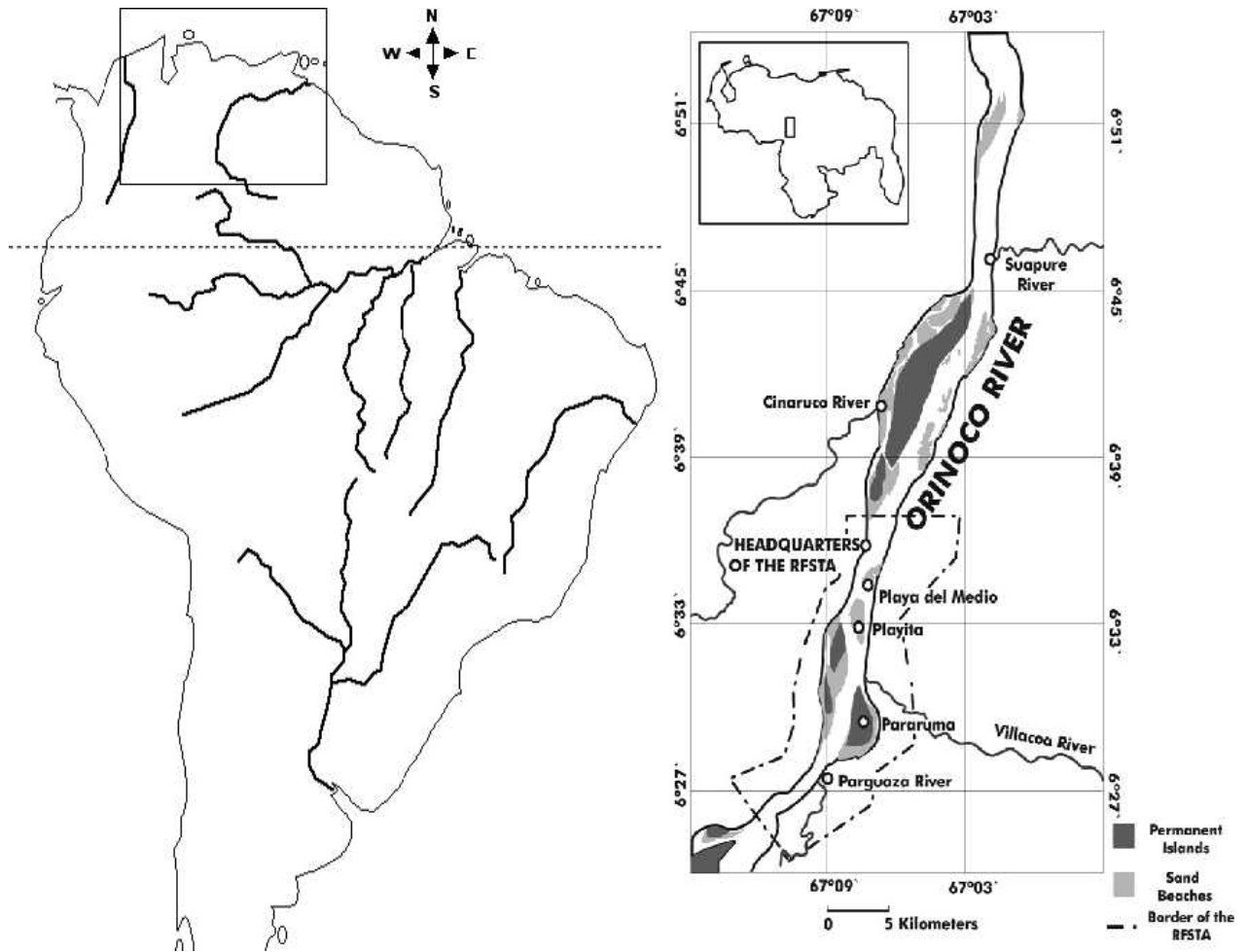


Figure 3. On the left, a map of South America showing a rectangle where the area of study is located. Note that the area is on the Orinoco River. On the right, a map of Venezuela showing the location of the Arrau Turtle Wildlife Refuge in the Middle Orinoco River. RFSTA is an abbreviation of Spanish words meaning Arrau Turtle Wildlife Refuge.

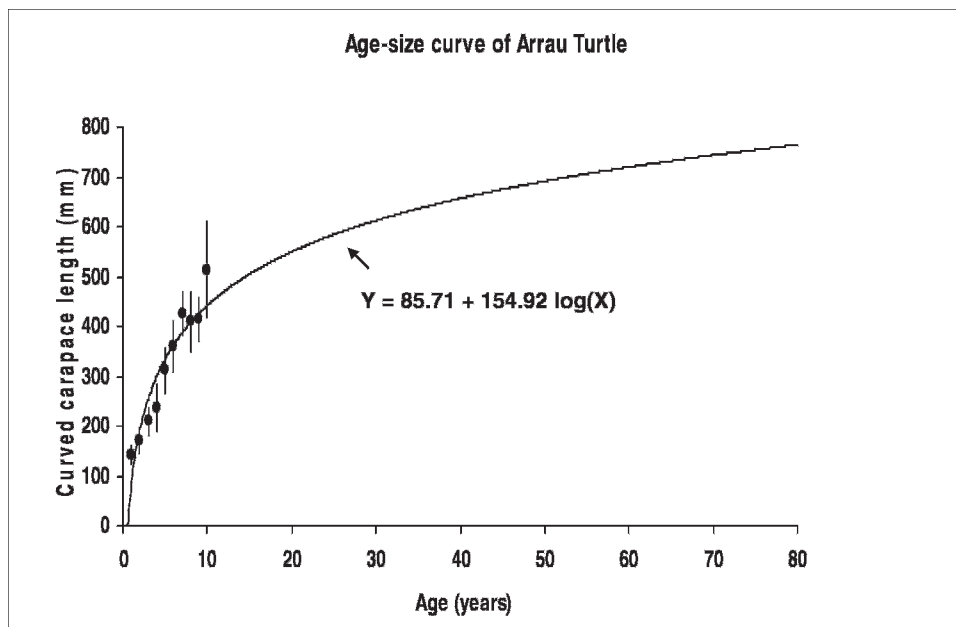


Figure 4. Relationship between age and size of recaptured female arrau turtles from the reintroduction program in the Middle Orinoco River. The points correspond to individuals recaptured in 2004. The curve was fitted to these points.

Table 1. Size categories and annual survival for the 5 size categories of arrau turtle females.

Age (y)	Size category	Size (mm)	Annual survivorship of an individual in the category
0	1: Eggs and hatchlings (up to yearlings)	50–140	0.584
1–10	2: Juveniles	141–450	0.44
11–28	3: Adults I	451–600	0.91
29–53	4: Adults II	601–700	0.93
> 53	5: Adults III	> 700	0.86

1960; Alho and Padua 1982; Valenzuela 2001). However, there are no such data for the arrau turtle in our study area. We assumed a constant average fecundity and calculated it as the average number of eggs per nest. We used the mean fecundity values found for females in the Middle Orinoco River since the beginning of the management plan. This value was corrected for the proportion of females found in the nests in order to make a growth model that considers only females. Knowing the mean number of eggs per nest (data from MINAMB) and considering that females make up 96% of hatchlings (C. Peñaloza, unpubl. data), the mean number of female eggs per nest was 90.46.

Survivorship. — Female size structure data are shown in the Appendix. Significance tests indicated that when a comparison is made between the size distributions of the population in years 1998, 2000, 2001, and 2004, only the frequency of 1 size class, that of 200–260-mm CCL in 2000, deviated from the rest (see Appendix). We concluded that size structure can be considered stable during this period of time. The size distributions were transformed to age distributions using Fig. 4. Because stability in size distribution implies stability in age distribution, we proceeded with the following calculations.

To obtain the adult age-specific survivorship, we followed Pielou (1977), which is based on the proportionality that exists between age structure profile and the probability profile of newborns to reach the different age categories, when the instantaneous growth rate is 0 ($r = 0$). Once this relationship is known, the calculation of the probability of an adult female to survive until the next year is immediate (Pielou 1977).

We applied Frazer's (1986) method to calculate the survivorship from birth to adulthood. This method uses the Lotka equation (Pielou 1977), the estimations of age-dependent survivorship and fecundity, and the instantaneous growth rate. To calculate the annual survival rate from hatching to adulthood, we proceeded as follows. Let p_x be the probability that a preadult aged x survives until age $x + 1$ and l_x the probability of a newborn to survive until age x . The probability of a newborn to survive until the next year was calculated as $p_0 = 0.584$. This value corresponds to the mean survival rate of the young during the first year as observed within the headstarting program (MINAMB) multiplied by the hatching success rate of eggs. It was assumed that the annual survival probability during the juvenile ages 1 and higher is constant. Let this probability

be p . Then, if l_α is the probability of a newborn to reach the first adult age, α being the age of first reproduction,

$$l_\alpha = p_0 p_1 p_2 \dots p_{\alpha-1} = p_0 p^{\alpha-1}$$

and p can be obtained from the expression

$$p = \left(\frac{l_\alpha}{p_0} \right)^{1/(\alpha-1)}$$

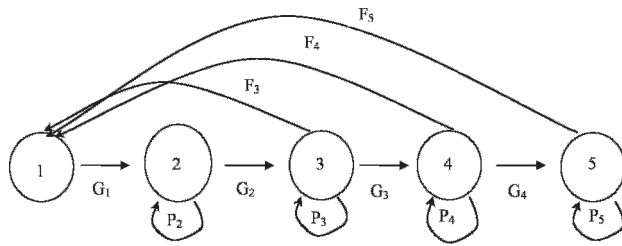
As will be explained later, we also constructed size categories by grouping several adult ages, and a similar method to that used for juveniles was used to calculate the annual survival of adults. Given any size category i , this survival probability is denoted σ_i .

We assumed that sexual maturity is reached at 11 years in females, based on reports from MINAMB, which we will find corresponding to a size of 450 mm CCL (Fig. 4). However, it is important to consider that some authors have reported maturation ages corresponding to sizes 500 mm and higher (Ramírez 1956; Alho and Padua 1982; Paolillo 1982). It has been proposed that the maturity of females depends on age and not size (Gibbons et al. 1981; Chaloupka and Limpus 1997; Limpus and Chaloupka 1997), but in arrau turtles, maturity has been considered as dependent on size, so Pritchard and Trebbau (1984) reported minimum reproductive size as 600 mm CCL, which corresponds to 563-mm straight-line carapace length (Hernández and Espín 2006). The case for age at maturity greater than 10 years of age (see also Jaffé et al. 2008) is supported by the lack of captures of any marked females from the headstarting program, which has been operating since 1994.

Size-Structured Matrix Growth Model. — We constructed a size-dependent matrix population growth model. This model is

$$\mathbf{n}_{t+1} = \mathbf{A} \mathbf{n}_t \quad [1]$$

where \mathbf{n}_t is the vector with the number of individuals in the various size categories at time t and \mathbf{A} the size-dependent projection matrix. Time t is measured in years. Table 1 shows the 5 size categories of the model. The limits of the adult categories were chosen in an arbitrary way, trying to span similar segments of age and size. It is important to consider that, as we are assuming the same annual survival and fecundity for reproducing adults, the limits chosen for these adult size categories will not change the population growth performance. Figure 5 shows the life cycle with the 5 size categories and the



$$\begin{bmatrix}
 0 & 0 & F_3 & F_4 & F_5 \\
 G_1 & P_2 & 0 & 0 & 0 \\
 0 & G_2 & P_3 & 0 & 0 \\
 0 & 0 & G_3 & P_4 & 0 \\
 0 & 0 & 0 & G_4 & P_5
 \end{bmatrix}$$

Figure 5. Life cycle graph and the corresponding size-classified population projection matrix for arrau turtles. Size categories are 1: eggs, hatchlings, and yearlings; 2: juveniles; 3: adults I; 4: adults II; 5: adults III.

projection matrix. In this matrix, F_i is the annual fecundity rate of the size category i , P_i is the probability that an individual in category i remains in this same category, and G_i is the probability that an individual in size category i grows to the next category. We followed the method of Caswell (2001) to calculate the numerical values of the elements of matrix A . This method assumes that the population has reached a stable size distribution as a consequence of having a stable age distribution. The method needs an estimation of the finite rate of increase λ (which is equal to e^r). To obtain F_3 , the number of eggs per nest was multiplied by σ_3 . To obtain the values of F_4 and F_5 , the number of eggs per nest was multiplied by σ_4 and σ_5 , respectively.

The methods in Caswell (2001) also allow estimating the stable size distribution and the reproductive values of the size categories of the population when the stable size distribution has been reached.

Sensitivity and Elasticity Analyses. — Sensitivity measures the change in the value of λ as a consequence of a unit change in an element of the matrix A and is used to evaluate the effects of errors made in the estimation of such an element (Crouse 1999). This analysis is performed by measuring the slope of the finite rate of growth λ as a function of a given element of matrix A and thus amounts to the absolute effect on λ of a change in that matrix's element (Benton and Grant 1999). Elasticity analysis measures the fractional effect on λ as a consequence of a unit fractional change in an element of the matrix A . It measures how much λ is affected by a given percentage of change in an element of the matrix and thus allows comparison of the relative importance of each element of the projection matrix for the finite rate of increase (Mills et al. 1999). The sensitivities and elasticities were calculated following Caswell (2001).

RESULTS

Age-Size Curve and Population Parameters. — We collected a total of 716 turtles in 2004. Of these, 470 were headstarted, and 451 could be sexed. The sex ratio at birth is strongly biased toward females, with 11.1 females for each male. This ratio is oddly high, and this would raise questions about the possibility of maintaining a stable population. However, turtles do not make stable pair bonds between sexes, and females have multiple matings (Pearse and Avise 2001), which can prevent a decrease in population size because of a high female proportion.

The age-size curve is shown in Fig. 4. To fit the logarithmic equation to the experimental data, we did a linear regression of the size versus the logarithm of age. We also applied the von Bertalanffy growth model (Schoener and Schoener 1978) to the known-age turtle data (S. Mogollones, unpubl. data), but it was discarded because the logarithmic model provided a better fit. Marking of yearlings before reintroduction started in 1995, which is why 10 years is the age of the oldest recaptured turtles (in 2004) in Fig. 4. The logarithmic curve was fitted to turtles ranging from 1 to 10 years and then extrapolated to older ages. This of course can introduce an error; however, the error would be mainly at high ages at which, because of the flattening of the curve, there would not be much difference between sizes at different ages. The size of 700 mm would be reached at approximately age 80 years, which is the age we are considering as maximum longevity, following Hernández and Espín (2006).

The abundances of nesting females during the years 1988–2004 are shown in Fig. 2, as is the regression line fitted to the logarithm of the number of nesting females. These data are from MINAMB. From the fitting, it follows that $r = -0.0139$, and $\lambda = 0.99$. It is not possible to test the deviation from linearity of the points in this figure, because there is only 1 value of abundance for each year. But assuming that such deviation is not statistically significant, it is possible to measure the 95% confidence interval for the slope, equal to r , which is $(-0.0480; 0.0203)$. This confidence interval indicates that the instantaneous growth rate does not differ significantly from zero and that the finite rate of increase can be considered equal to 1. There is clear evidence that the population size has stabilized since 1989.

The estimations of survivorship are shown in Table 1. The pattern of annual survival for the arrau turtle in the Middle Orinoco River coincides with what is expected in this type of organism with high longevity and delayed sexual maturity: once adulthood is reached, annual survivals are high.

Size-Structured Matrix Model. — Growth matrices are shown in Table 2. Of hatchlings, 58.4% survive and grow enough during 1 year to enter the juvenile category; 43.98% of juveniles stay in that category after 1 year, and

Table 2. Population growth matrices, stable size distribution, reproductive value, and finite rate of increase for the growth matrix, of the arrau turtle.

Matrix	$\begin{bmatrix} 0 & 0 & 82.3186 & 84.1278 & 77.7956 \\ 0.584 & 0.4398 & 0 & 0 & 0 \\ 0 & 0.0002 & 0.8876 & 0 & 0 \\ 0 & 0 & 0.0225 & 0.9141 & 0 \\ 0 & 0 & 0 & 0.0159 & 0.9268 \end{bmatrix}$				
Category	Stable size distribution	Reproductive value		Finite rate of increase	
1	0.4533	0.0051		0.9287	
2	0.5414	0.0081			
3	0.0022	23.8731			
4	0.0003	251.7686			
5	0.0028	204.7775			

0.02% grow enough to enter the next category (adults I). Each year, 2.25% of adults I enter the next category (adults II), and 88.76% stay in the same category. An individual of adults I each year produces 82.32 females, which enter in the first category. A total of 91.41% adults II stay in the same category, and each individual produces 84.13 females, which enter the first category the next year. Finally, 92.68% of females belonging to the last category (adults III) stay in the same category yearly, and 1 female in this category produces 77.80 females entering the first category the next year.

The sensitivity of the rate of increase to changes in the elements of matrix A is shown in Fig. 6. Increases in the values of fecundity and in probabilities of transition and of permanence do not seem to affect the finite rate of increase. The only exception is with the probability of surviving and passing from category 2 to category 3, where increases result in a higher λ , and this effect is lower for higher ages of first reproduction. Also, increases in probability of permanence and annual survival of adults III have some effect on an increase in λ .

Most demographic parameters have little effect on λ in the elasticity analysis (Fig. 6), except for P and σ , which affect λ increasingly with each category.

DISCUSSION

Age-Size Curve. — The age-size curve of the arrau turtle shows the typical reptilian pattern, with fast juvenile growth followed by a decreasing growth rate until reaching sexual maturity and thereafter indeterminate growth of adults. In fact, Jaffé et al. (2008) have shown that this rate of body growth increased until approximately 150 days old, stabilizing at 0.15 mm/d after that and before 400 days old. The logarithmic model fitted to the experimental points does not have any clear biological meaning. However, it represents a good description of the data.

Similar studies using age-size curves have been done in tortoises and turtles (Germano 1988; Aponte et al. 2003) and used to construct size-based matrix population growth models (Andrews 1982; Frazer 1986).

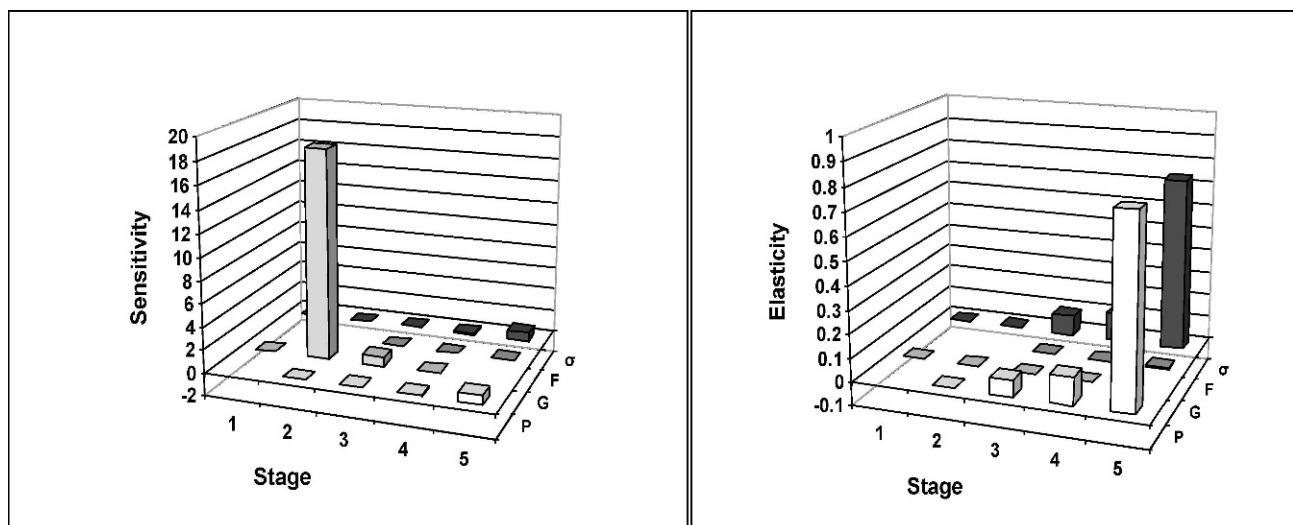


Figure 6. Sensitivities and elasticities of finite rate of increase (λ) to elements of size-based matrix, for the arrau turtle.

We have assumed an age at maturity of 11 years for female arrau turtles. Many freshwater turtles of large size mature at an age of 10 years or more. For example, *Chelodina longicollis* matures at 10 years and *Chelydra serpentina* at 20 years (Spencer 2001), and Hernández and Espín (2006) estimated 17 years for the arrau turtle in a similar study with fewer data than the present one. Delayed sexual maturity is a characteristic of life histories of long-lived vertebrates (Charlesworth 1980; Dunham et al. 1988; Charnov 1990). The benefits attributed to this trait are the increase in quality of the offspring, the increase in the number of newborn, and the decrease in the cost associated with reproduction.

Population Parameters. — The curve in Fig. 2 indicates that the protection program started at the end of the 1980s has been successful. We expect that the structure and size of the nesting female population will change when turtles from the reintroduction program, started in 1994, reach maturity.

The estimations indicate that only 0.02% of neonates reach adulthood. However, survivorships are high on attainment of adulthood. The value of preadult survivorship in the wild is probably overestimated, given that the yearlings reintroduced with the program of conservation have been taken into account. Also, human predation on arrau turtles in the Middle Orinoco River affects mainly juveniles whose mean linear carapace length is 289 mm (Hernández and Espín 2003).

A type II age survivorship curve has often been described for freshwater turtles (Wilbur 1975; Mitchell 1988). In this curve, mortality remains constant through the lifetime. However, the pattern of freshwater turtles adjusts better to a type III or type IV curve, in which the mortality is higher in eggs, hatchlings, and juveniles (Iverson 1991), as it has been in the present study. Annual survival of adults in freshwater turtles often exceeds 90% (Shine and Iverson 1995).

In freshwater turtles, Iverson (1991) reports a survival rate of 0.229 in eggs (mean of 15 species), 0.672 in juveniles (mean of 7 species), and of 0.879 in adults (mean of 4 species). In general, our results coincide with previous freshwater turtle studies. Natural predators of adult turtles are not as common as on eggs, neonates, and juveniles (von Hildebrand et al. 1997), and this is probably the cause of the age survivorship profile described. The prohibition on capturing turtles in the refuge surely has also contributed to the high survivorship of adults in our study population.

The longevity of this iteroparous species and its high adult survivorship can compensate for the delayed maturation and the high mortality of eggs, thereby contributing to the population stability.

Size-Structured Matrix Model. — Size-structured population growth models have been built for loggerhead sea turtles (e.g., Crouse et al. 1987; Crowder et al. 1994) and Southern Great Barrier Reef green sea turtles (Chaloupka 2002). The matrix model in the present study

is a preliminary approach to predicting future population growth of the arrau turtle in the Middle Orinoco River. Stable size distribution is dominated by neonates and juveniles (Table 2) as is expected in populations with high preadult mortality and high fecundity (Pielou 1977). The high reproductive values of adult sizes and low ones of preadult sizes (Table 2) are explained by the fact that preadults do not reproduce and that annual survival is low in preadults and high in adults. According to Heppell (1998), this size-class distribution (mostly immature individuals) is also expected for long-lived, high-fecundity turtles like sea turtles and possibly the arrau turtle. The values of the rate of increase calculated as the dominant right eigenvalue of matrix **A** (Table 2) are very similar to the exponent of the slope of the straight line in Fig. 2, which indicates that calculations made with the 2 methods are consistent.

The sensitivity analyses in Fig. 6 indicate that the most important parameter to estimate accurately is G_2 . Elasticity analysis indicates that the population dynamics of the arrau turtle will be most affected by changes in P and σ , particularly those for older ages. Fecundity elasticity is very low. Then individual survival is more important than fecundity for the survival of the species. Annual survival probabilities (σ) of juveniles and particularly of adults have a large effect on population dynamics. These results coincide with those of Congdon et al. (1993), Heppell et al. (1996), and Heppell (1998). Eggs and hatchlings contribute very little to population growth because these stages are very short and their reproductive values are very low in comparison with other stages (Table 2). These results coincide with those of Benton and Grant (1999), who found in a group of species of turtles that neonate survivorship elasticities were low but that those of preadult and adult survival were high. These patterns of elasticities are apparently typical of these species' life history.

As we mentioned previously, many authors have found a positive relationship between female adult size and fecundity. We additionally performed the demographic analysis assuming a larger fecundity for larger females (S. Mogollones, unpubl. data). However, the results were similar to the present study. This may be due to the low fecundity elasticity. These results are a justification of our assumption of constant fecundity.

Conservation Management. — There is evidence that the population of arrau turtles in the Middle Orinoco River has maintained a constant population size and age structure as a consequence of the conservation plan started in 1989 in the Wildlife Refuge, previous to the start of the captive rearing and reintroduction program. The population seems to be constant in numbers of individuals and size structure. Since a population with high longevity, as is the case of the arrau turtle, needs a long time to stabilize both in population size and in age structure (Richardson and Richardson 1982; Caswell 2001), it is plausible that such stability was reached

previous to the reintroduction program. However, in spite of the conservation program, there is still turtle consumption in the area, targeting mainly juveniles (Hernández and Espín 2003). This would make the persistence of the arrau turtle dependent on the headstarting and reintroduction program.

Even if the captive rearing and reintroduction program continues, its effect on the adult population will not become apparent until 2012. Finally, it is important to point out that, because of the migratory habits of this species, the current conservation program in itself does not guarantee the persistence of the population. It is plausible that individuals migrate to areas where conservation policies are not applied. Further studies on turtle habitat use and human consumption of turtles will improve our understanding of the species' population dynamics in the area as well as the effects of the current conservation program.

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APPENDIX

Size structure of the arrau turtle population in the Middle Orinoco River. Data from 1998, 2000, and 2001 in the following figures come from MINAMB and FUDECI, whereas we collected 2004 data in the present study.

Size distributions are shown in Fig. A1. In 1998 the size class with the highest frequency was that of 221–240 mm, with a total absence of individuals larger than 300 mm. In 2000 we found individuals larger than 300 mm, and in 2001 we found individuals larger than 600 mm for the first time. All size classes are represented in 2004, and the one with the highest frequency was 141–160 mm.

In general, a displacement of frequencies to larger sizes seems evident for this data set. The size frequency in 2004 was compared with those of years 1998, 2000, and 2001. We found statistically significant interannual differences between the size frequencies ($\chi^2 = 93.206998$, degrees of freedom = 24, $p < 0.05$). We performed a residual analysis to determine which years and which age classes accounted for this difference. The only size class that deviates significantly was the 200–260-mm class for 2000 (Fig. A2).

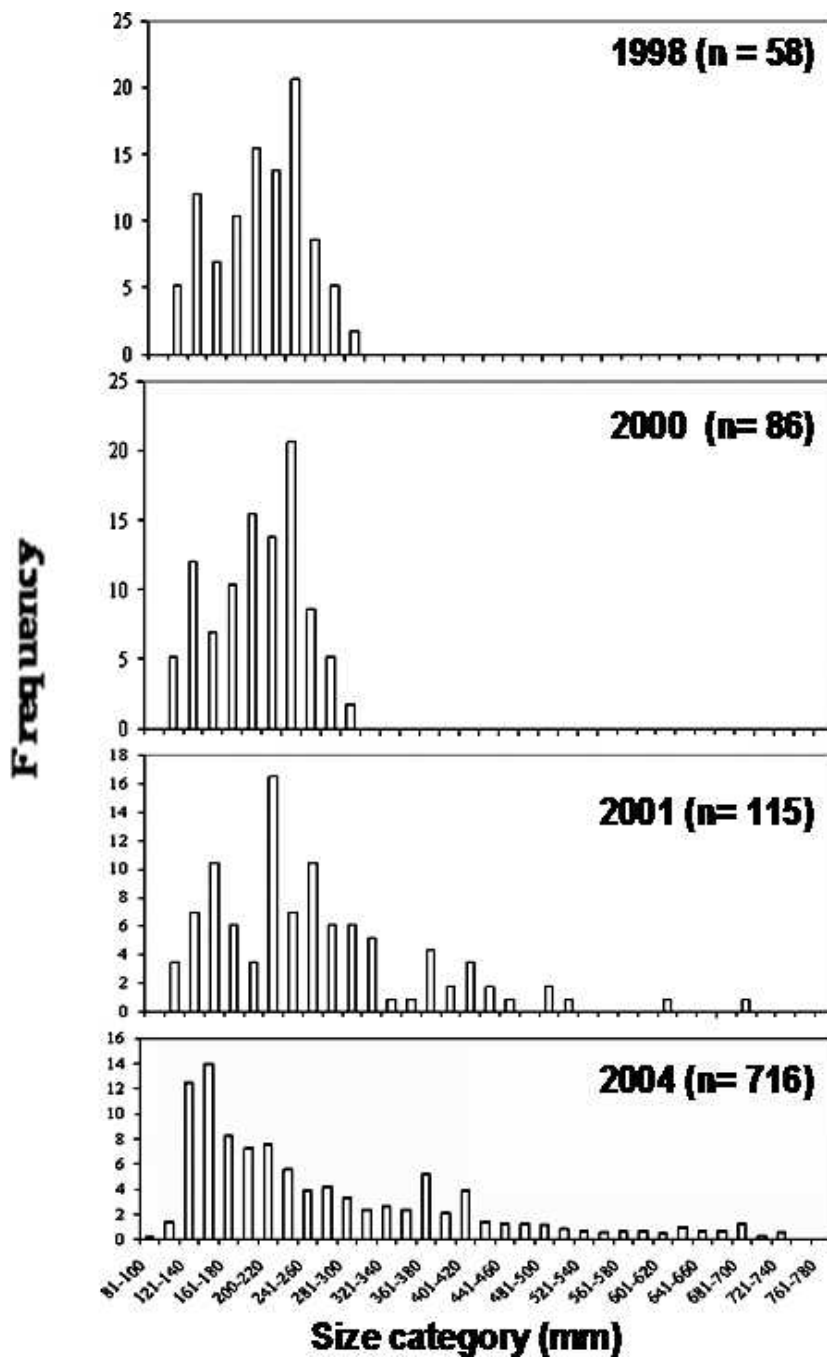


Figure A1. Frequency distribution of size classes of the arrau turtle population in the Middle Orinoco River in 4 years of study. Each graph indicates the year and sample size (in parentheses).

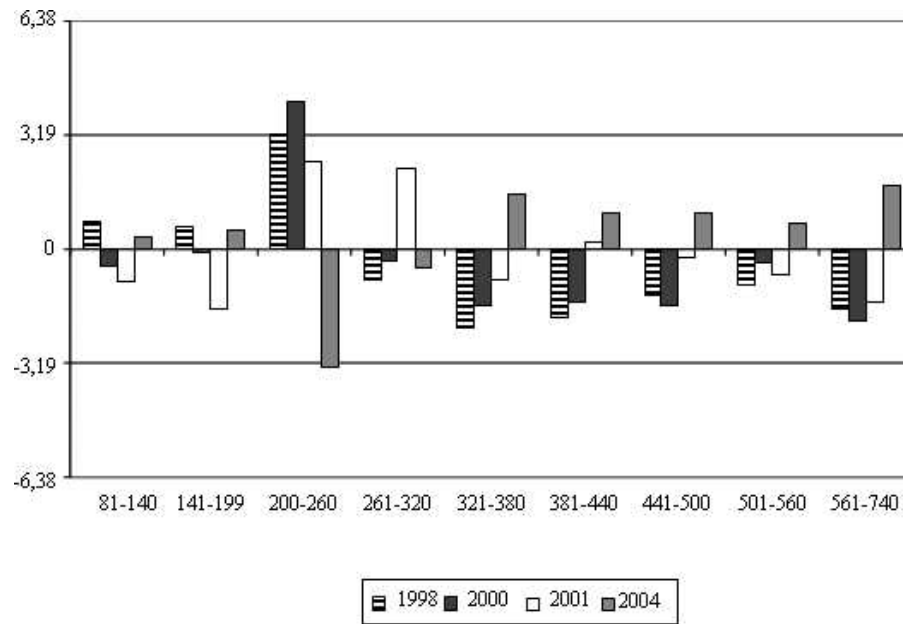


Figure A2. Standardized residuals for size classes of the arrau turtle population under study. Statistically significant values are those over 3.19 or under -3.19. A minus sign in the ordinate (−) indicates that the frequency was lower than expected and a plus sign (+) that it was higher than expected.