

Reproductive Ecology of the Spectacled Caiman (*Caiman crocodilus*) in the Venezuelan Llanos

JOHN B. THORBJARNARSON

In the Venezuelan llanos, the reproductive cycle of the spectacled caiman (*Caiman crocodilus*) was constrained temporally by seasonal variation in water availability. Gonadal recrudescence in males and females began during the late dry season (April–May). Testicle mass peaks in May and June (early wet season), just prior to courtship. Peak spermatozoa levels were from June through Aug. Among vitellogenic females, ovarian mass and follicle size increased throughout the early wet season and peaked at the beginning of the nesting season (July–Aug.). Caiman were sexually size dimorphic with adult males (\bar{x} = 96.0 cm SVL, maximum 145.5 cm SVL) approximately 30–40% larger than females (\bar{x} = 72.0 cm SVL, maximum 99.0 cm SVL). Males were physiologically mature at 75 cm SVL (approximately 7 yr), but small mature males may not reproduce because of social factors. Females matured at minimum size of 60 cm SVL, but the mean size at first reproduction was 64 cm SVL (approximately 7 yr). Mean clutch size was 22.2 (\pm 5.8), and mean clutch mass was 1392 g (\pm 426 g). Clutch size and clutch mass, but not egg mass, were positively correlated with female SVL. An average of 54.3% of females > 60 cm SVL nested annually, but the reproductive frequency was size dependent. Female reproductive output increased both in absolute and relative terms as females grew. No evidence of a trade-off between egg size and clutch size was found.

En los llanos de Venezuela, el ciclo reproductivo de la baba (*Caiman crocodilus*) está temporalmente limitado por la variación en la disponibilidad de agua durante el año. En ambos sexos el recrecimiento de las gónadas comienza a finales de la estación seca (abril–mayo). El peso de los testículos alcanza su nivel máximo en mayo y junio (el comienzo de la estación de lluvia), poco antes de la época de cortejo. El nivel espermático alcanza su máximo entre junio y agosto. En hembras vitelgénicas, la masa de los ovarios y el diámetro de los ovulos aumentaron durante el comienzo de la estación de lluvia, llegando a su nivel máximo al principio de la época de nidificación. Se encontró dimorfismo sexual en adultos con los machos (\bar{x} = 96.4 cm SVL; máximo = 145.5 cm largo hocicio-cloaca (LHC) aproximadamente 30–40% más grandes que las hembras (\bar{x} = 72.6 cm LHC; máximo = 99.0 cm). Los machos alcanzan la madurez sexual en tallas cercanas a 75 cm LHC, y con aproximadamente 7 años de edad. Sin embargo, debido a factores sociales, machos de este tamaño no necesariamente se aparean. Las hembras empiezan a alcanzar la madurez sexual a los 60 cm LHC, pero el tamaño promedio de hembras reproduciéndose por primera vez es de 64 cm LHC (aproximadamente 7 años de edad). El tamaño promedio la postura es de 22.2 (\pm 5.8) huevos, y la masa promedio de la postura es de 1392 g (\pm 426 g). El número de huevos y masa de la postura, pero no la masa promedio de huevos, están relacionados con tamaño de la hembra (LHC). Un promedio de 54.3% de hembras mayores de 60 cm LHC se aparean cada año, pero la frecuencia es relacionada con el tamaño de la hembra. La inversión en reproducción (masa de la postura) aumentó en términos relativos y absolutos a medida que las hembras iban creciendo. Al controlar el efecto del tamaño de la hembra, no se encontró evidencia de una relación entre el número y el tamaño de los huevos en las posturas.

Recent reviews of life-history traits provide insight into ecological and evolutionary trends of turtles and squamates (Stearns, 1984; Dunham et al., 1988; Wilbur and Morin, 1988);

however, many aspects of crocodylian ecology remain poorly understood (Webb and Smith, 1987; Gans, 1989). Crocodylians exhibit a suite of life-history characteristics unique among liv-

ing vertebrates (large body size, long reproductive life span, the production of large numbers of relatively small eggs, and substantial parental care), but life-history analyses have been hampered by the lack of quantitative field studies.

The spectacled caiman (*Caiman crocodilus*) is a relatively small crocodylian, widely distributed throughout the Neotropical lowlands in a wide variety of habitats (Gorzula and Seijas, 1989). Previous studies of spectacled caiman reproduction largely have been restricted to nesting ecology (Crawshaw and Schaller, 1980; Ouboter and Nanho, 1987; Cintra, 1989). Other than the studies of M. Staton and J. Dixon (unpubl. data) and Ayarzagüena (1983), most information on the reproductive ecology of *C. crocodilus* is based on anecdotal accounts.

In the Venezuelan llanos, *C. crocodilus* inhabits a highly seasonal environment in which ground water levels vary extensively in accordance with seasonal rainfall (Staton and Dixon, 1975; Ayarzagüena, 1983). The goals of this study were to examine the seasonal timing of caiman reproduction, including seasonal variation in ovarian and testicular development, and stored lipids; and quantify the relationship between female size and egg and clutch characteristics. Previous studies of reptile life history have examined these relationships at interspecific (Stearns, 1984; Dunham et al., 1988; Iverson, 1992) and intraspecific (see Ford and Seigel, 1989) levels, and trade-offs between egg and clutch size is a basic tenet of life-history theory (Stearns, 1992). However, both egg and clutch size covary with female size, and few comparative studies of reptiles have examined these reproductive parameters using methods that take into account variation in female size (Ford and Seigel, 1989). Furthermore, reproductive frequency, a fundamental life-history parameter, rarely has been incorporated into reptile life-history studies (Iverson, 1992), producing a misleading view of reproductive output. Here, I use observed allometric changes in egg size, clutch size and reproductive frequency to determine size-related changes in the reproductive output of female *C. crocodilus*.

METHODS

The principal study site was Fundo Pecuario Masagual, a cattle ranch in the central Venezuelan llanos (Guárico state: 8°33'N, 67°37'W), approximately 50 km south of the town of Calabozo. The llanos was a highly seasonal environment with a well-defined wet season (May–Nov.) during which over 75% of the annual rainfall occurred. During the study period, total

annual rainfall ranged from 1448.1–1631.8 mm. A mean annual temperature of 26–28°C resulted in a Tropical Dry Forest plant association, as defined by the Holdridge system (Ewel et al., 1976). The ranch included approximately 8500 ha of mixed savannah/deciduous forest habitat west of the Guárico River at an elevation of 60–75 m above sea level. The dominant vegetation types graded from a low-stature deciduous forest located in the east, to an open palm savannah in the western portion of the ranch (Troth, 1979).

Reproductive tracts were obtained from fresh road-killed specimens ($n = 233$) from a highway adjacent to Masagual (Sept. 1984–May 1989); adult caiman from Masagual and the adjacent Flores Moradas ranch ($n = 72$) captured and killed under government permit between June 1986 and June 1987 (Licencia de Caza con Fines Científicas No. 001744, 9 June 1986, Ministerio de Ambiente y de Recursos Naturales Renovables); and 14 caiman found dead from natural causes. Sex, snout–vent length (SVL, measured to the posterior edge of the cloaca), total length, and weight of specimens were recorded. Mass of the lateral fat body, testes, and ovaries were determined on an O-Haus Triple Beam balance to the nearest 0.1 g, although gonad or fat body mass from road-killed specimens was not always measurable. The diameters of the six largest ovarian follicles in each ovary were measured with calipers to the nearest 0.1 mm. Vitellogenesis was determined by macroscopic examination of the ovarian follicles. Ovaries were examined for the presence of different sized follicles or corpora lutea. Oviducal eggs were weighed (0.1 g) and measured (length and width, 0.01 cm). Egg and clutch data were collected from nests ($n = 154$; Thorbjarnarson, 1991). Egg dimensions were measured with calipers to the nearest 0.01 cm, and egg weight was determined to the nearest 1 g. The diameter of the pelvic canal was measured to the nearest 0.1 cm from the rearticulated skeletons of sacrificed female caiman. Diameter was measured as pelvic canal width (straight-line distance between the ilio-ischium junctions) and pelvic canal depth (straight-line distance between the ventral surface of the vertebral centrum and the junction of the two ilea). Where appropriate, mean values are presented ± 1 SD.

Size-class distribution of the population was determined from 634 caiman captured by noosing, seining, or hand. Supplementary information on relative clutch mass and frequency of reproduction was collected from adult females equipped with radiotransmitters (Thorbjarnarson, 1991). Additional data on the max-

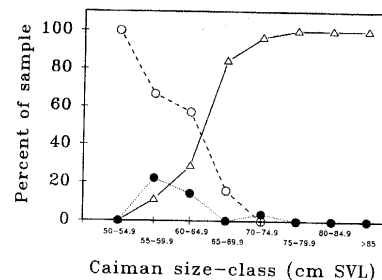


Fig. 1. Female caiman with distended (mature; solid line), partially distended (dotted line), and undeveloped (immature; dashed line) oviducts as a function of SVL size-class.

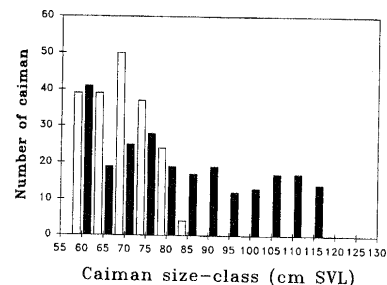


Fig. 2. Frequency distribution of DOR and captured male (dark bars) and female (open bars) caiman over 60 cm SVL.

imum size of adult caiman and testes mass were obtained from commercially harvested caiman on another cattle ranch, Hato Merecure, on the Arauca River, 150 km south of Masagual. Histological analyses of testes were performed for a sample of adult road-killed and sacrificed individuals. Testes were collected and preserved in 10% formalin, then prepared using standard histological techniques. Tissues were hematoxylin-eosin stained, mounted on glass slides and observed at 100 \times magnification.

RESULTS

Sexual maturity and adult size.—The smallest vitellogenic caiman examined measured 60.0 cm SVL (mean follicle diameter = 2.15 cm). The gross morphology of oviducts (immature: narrow, translucent less than 0.5 cm wide posteriorly and 0.3 cm wide anteriorly, mature: distended with conspicuous longitudinal convolutions in the posterior segment) also suggested sexual maturity at a minimum of approximately 60 cm SVL (Fig. 1). The oviducts of some females could not be readily classified as mature or immature and were recorded as partially distended. Most females attained reproductive maturity between 60 and 70 cm SVL, corresponding to 6–10 yr of age based on growth rates for this population (Thorbjarnarson, 1991). Average female size at first reproduction (50% of females with distended oviducts) was 64.0 cm SVL (approximately 7 yr). Only one female greater than 70 cm SVL had not reproduced. No females under 50 cm SVL showed signs of oviducal hypertrophy. Three of the four females under 65 cm SVL with partially distended oviducts were examined during the breeding season (July and Sept.).

Among females ≥ 60 cm SVL, mean snout-vent length was 72.6 cm (± 6.6 cm, $n = 134$) for live-captured females and 70.7 cm (± 6.8 cm, $n = 59$) for road kills (Fig. 2). The largest female examined on Masagual measured 86.1 cm SVL, but, in other parts of the llanos, females exceed this size (maximum = 99 cm SVL, Hato Merecure).

Based on the presence of spermatoocytes in the testes, the smallest physiologically mature male was 90.0 cm SVL ($n = 16$). However, this included only two individuals < 90 cm SVL, both examined during the nonbreeding season. Among animals whose testes were not examined histologically, enlarged testes with distended, fluid-filled epididymis were observed in caiman as small as 77.4 cm SVL. Assuming a minimum reproductive size of 75 cm SVL, males became sexually mature at an average age of 7 yr (Thorbjarnarson, 1991). Among males ≥ 75 cm SVL, mean size of live-captured males was 96.4 cm SVL (± 13.6 cm, $n = 113$; Fig. 2) and 94.9 cm SVL (± 13.6 , $n = 47$) for road-killed males. The largest male captured on Masagual measured 127.0 cm SVL, but the largest male examined in the llanos region was 145.5 cm SVL.

Seasonal ovarian cycle.—No annual differences in the timing of reproductive events were noted, so data were combined over the study period (Oct. 1984–May 1988). Nonvitellogenic adult females had two size classes of ovarian follicles (< 1 mm, and 2–3 mm diameter). Vitellogenesis began at the end of the dry season, with initial increase in mean ovarian follicle diameter in April–May (Table 1). Mean follicle size of vitellogenic females increased throughout the early wet season (May–July), peaking in July and

TABLE 1. MEAN MONTHLY OVARIAN FOLLICLE DIAMETER (cm) AND STANDARD DEVIATION FOR VITELLOGENIC AND NONVITELLOGENIC FEMALES.

Month	Vitellogenic			Nonvitellogenic		
	Mean	SD	n	Mean	SD	n
Jan				0.29	0.06	6
Feb				0.33	0.08	5
Mar				0.33	0.07	5
Apr	0.44	0.01	2	0.29	0.04	3
May	1.73	0.58	10	0.30	0.11	6
Jun	3.05	0.51	7	0.25	0.04	7
Jul	3.60	0.74	8	0.23	0.02	3
Aug	3.86	0.16	2	0.23	0.07	6
Sep				0.28	0.10	5
Oct				0.28	0.08	2
Nov				0.34	0.07	7
Dec				0.22	0.03	7

Aug. Paired ovary mass showed a similar seasonal pattern (Fig. 3).

The number of vitellogenic follicles declined as the reproductive season progressed, and the average size of follicles increased (Table 2). However, this reduction was only apparent among large females (> 75 cm SVL). Large females had more enlarged follicles than did small females ($F_{1,21} = 9.15, P < 0.01$). No significant difference in the production of ova was noted between right and left ovaries. There was no significant reduction in the proportion of vitellogenic adult females during the reproductive season (Table 3), suggesting that all vitellogenic females ovulated.

Ovarian follicles were shed into the oviducts at 3.7–3.9 cm in diameter. In two of five females with oviducal eggs, the number of corpora lutea exceeded the number of oviducal eggs (one and two missing ova), suggesting that some ova do not enter the ostium of the oviduct, and their fate remains unknown. Also, in two of five females ovarian displacement, or extrauterine migration (ova entering the opposite oviduct), occurred.

TABLE 2. MEAN NUMBER OF ENLARGED OVARIAN FOLLICLES BY MONTH FOR LARGE (≥ 75 cm SVL) AND SMALL (< 75 cm SVL) CAIMAN.

Month	Small females		Large females		All females	
	\bar{x}	n	\bar{x}	n	\bar{x}	n
May	25.0	2	40.3	4	35.2	6
Jun	25.8	4	32.0	2	27.8	6
Jul	18.7	3	32.5	2	24.2	5
Aug	25.5	2	26.0	1	25.7	3

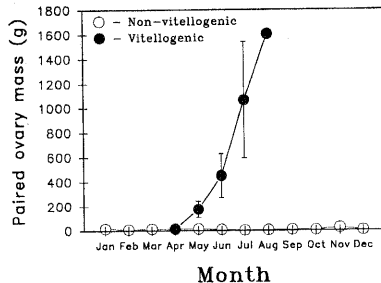


Fig. 3. Mean paired ovary mass by month for breeding and nonbreeding females.

Females had a variable number of intermediate sized ovarian follicles (to 2.2 cm diameter) shortly following ovulation. Three adult females had intermediate sized follicles (0.9–2.8 cm) in the late wet season or early dry season (3–5 months after ovulation), suggesting that nonovulated follicles enter an arrested growth phase or atrophy very slowly. One female had regressed corpora lutea visible in the ovary (2–3 months after ovulation). Intermediate sized ovarian follicles in females during the late wet and early dry season may be indicative of animals that ovulated in the previous reproductive season.

Most breeding females had shelled oviducal eggs by late July and Aug. (three of four reproductive caiman examined). Eggs encountered in the uterus were either completely shelled, or nearly so, and never were encountered in the anterior section of the oviducts. The mean date of finding females ($n = 7$) with oviducal eggs was 5 Aug. The mean date of oviposition varied from 12–17 Aug., suggesting that females retained eggs in their oviducts at least 7–12 days.

TABLE 3. NUMBER AND MONTHLY PERCENTAGE OF ADULT FEMALES (≥ 60 cm SVL) IN BREEDING CONDITION DURING THE PERIOD 1985–1988.

Month	Nonbreeding		Breeding	
	n	%	n	%
Apr	3	60.0%	2	40.0%
May	7	41.2%	10	58.8%
Jun	8	50.0%	8	50.0%
Jul	3	25.0%	9	75.0%
Aug	6	33.3%	12	66.7%
Sep	13	72.2%	5	27.8%
Total	40	46.5%	46	54.5%

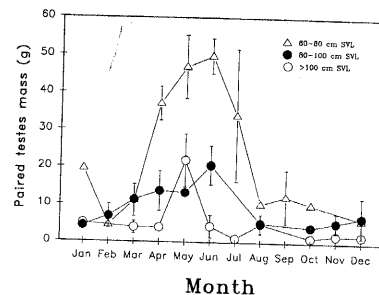


Fig. 4. Mean paired testicular mass by month for three size classes of caiman.

Seasonal testicular cycle.—Testicular recrudescence began in April, at the end of the dry season (Fig. 4), with testes mass peaking during the early rainy season (May–June), dropping sharply in July–Aug., and remaining in a regressed state throughout the remainder of the wet season and the early dry season. Testicle mass was correlated with body size (Fig. 4). Large (120 cm SVL) males had maximum testes weights up to 60 g. Larger males (to 145 cm SVL) examined on other ranches had testes weighing up to 80 g in late April, indicating that maximum testes mass may exceed 100 g in very large males. Testicular recrudescence apparently began earlier in large and medium-sized males (March–April), than in small males (May; Fig. 4). During the reproductive season (May–Aug.), there was no significant difference between the mass of the right (mean 15.3 g, ± 10.1 , $n = 27$) and the left testes (mean 13.1 g, ± 9.3 , $n = 27$).

Moderate numbers of spermatozoa were in the seminiferous tubules of large males from mid-March but remained abundant into Aug. After Aug., there was a reduction in size of the seminiferous tubules and a proliferation of interstitial tissue. During this time, few or no spermatozoa were seen in the seminiferous tubules, although some were still observed in the efferent ductules. Spermatozoa were not observed from Nov. to Feb. ($n = 4$).

Seasonal fat cycle.—Wet mass of the lateral abdominal fat body was used as an index of stored lipids. To correct for differences in body size, a relative fat body mass (RFB) was expressed as a percentage of total body mass. Seasonal cycles in fat body mass were evident but differed between sexes. The mean RFB value for females was 0.48% of total body mass, that of males 0.14%. However, an analysis of covariance (SVL

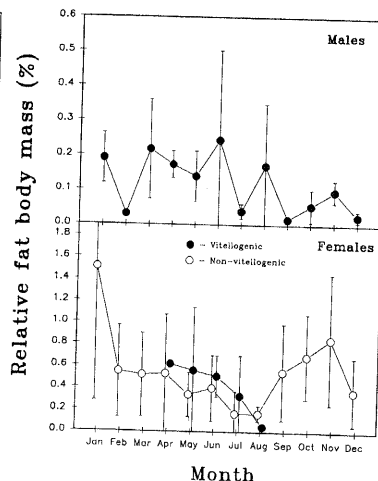


Fig. 5. Relative lateral fat body mass (fat body mass/body mass $\times 100$) among male caiman (top), and vitellogenic and nonvitellogenic females (bottom) by month.

as covariate) found no significant differences in fat body mass between the sexes ($F_{1,1,205} = 1.63, P = 0.20$). Female RFB (> 50 cm SVL) peaked in the late wet and early dry season (Fig. 5). RFB values declined during the dry season and the early wet season (Feb.–Aug.). Although the mean values of RFB during this period consistently were higher among breeding than nonbreeding females (Fig. 5), the differences were not significant (Kruskal-Wallis; $H_{1,45} = 0.60; P = 0.45$). Decline in RFB from the late dry to early wet season was significant (Kruskal-Wallis; $H_{4,46} = 9.68; P = 0.05$) for breeding and nonbreeding females. In the late wet season (Sept.–Nov.), the RFB increased in nonbreeding animals.

The seasonal RFB cycle of male caiman (> 60 cm SVL) exhibited considerable variability, but males tended to have high levels during the dry and early wet seasons (Jan.–June) and lower values in the mid to late wet season (July–Dec.; Fig. 5). The highest RFB values (and the most variable) were in June, at the height of the courtship and mating season.

Egg and clutch characteristics.—Mean caiman egg mass was 62.5 g (± 7.13 ; 38–85 g; $n = 1015$). Mean egg dimensions were as follows: length 6.45 cm (± 0.30), width 3.96 cm (± 0.14). Mean

TABLE 4. LEAST-SQUARE REGRESSION EQUATIONS FOR EGG SIZE AND FEMALE SIZE PARAMETERS. Clutch means of egg length (cm), width (cm), and mass (g) measurements were used for calculating correlations.

		n	r	P
Egg mass (EM)				
Egg length (EL)	EM = 19.50(EL) - 63.18	153	0.83	<0.001
Egg width (EW)	EM = 41.90(EW) - 103.68	153	0.84	<0.001
Clutch size (CS)				
Egg mass	CS = 0.241(EM) + 7.38	152	0.28	<0.001
Clutch mass	CS = 0.013(CM) + 4.54	152	0.94	<0.001
Clutch mass (CM)				
Egg mass	CM = 36.66(EM) - 875.07	152	0.57	<0.001
Clutch size	CM = 70.02(CS) - 157.16	152	0.94	<0.001
Female snout-vent length (cm)				
Egg length (cm)	EL = 0.008(SVL) + 5.93	25	0.20	0.312
Egg width (cm)	EW = 0.006(SVL) + 3.53	25	0.33	0.107

clutch egg mass ranged from 40.7–80.7 g. Mean egg mass varied significantly among years ($F_{4,144} = 0.474$; $P < 0.05$), with eggs from 1985 ($\bar{x} = 57.7 \pm 6.7$) significantly smaller than eggs from 1984 ($\bar{x} = 64.6 \pm 9.0$; LSD $P < 0.01$) and 1986 ($\bar{x} = 64.1 \pm 6.8$; LSD $P < 0.05$). Both egg length and egg width were significantly correlated with egg mass (Table 4). Egg mass (EM) was predicted from both egg length (EL) and egg width (EW) by the equation: $EM = 12.08 EL + 6.85 EW - 121.80$ ($n = 153$; $r^2 = 0.88$).

Clutch size ranged from 4–36 ($\bar{x} = 22.2 \pm 5.57$; $n = 154$ clutches). There was no significant difference in clutch size among years ($F_{4,156} = 0.91$, $P = 0.46$). Clutch mass ranged from 201–2336 g ($\bar{x} = 1392 \text{ g} \pm 426.4$). Late clutches were heavier ($r = 0.19$, $P = 0.03$). No significant correlations were found between female size and egg mass, egg length, or egg width (Fig. 6; Table 4). Accordingly, as female size increased, egg mass (EM in g) declined relative to female mass (FM in g) ($EM = 27.10 FM^{0.09}$; $r = 0.22$). The width of female pelvic canals (PCW) was invariably smaller than pelvic canal depth and, thus, potentially more limiting to egg size. PCW (in cm) increased with female SVL ($PCW = 0.059 SVL + 0.168$; $r = 0.80$). The least-square regression lines for PCW and mean egg diameter intersected at a female SVL of 63.5 cm (Fig. 7). Clutch size and clutch mass were both significantly correlated with female SVL (Fig. 6). A partial correlation analysis (following Ford and Seigel, 1989) of egg and clutch attributes found that, independent of female size, as clutch size increased, there was no significant increase in egg mass or egg width, but there was a decrease in egg length (Table 5). Relative clutch mass (RCM) values were typically in the 10% to 16%

range with a mean of 13.9% ($n = 26$, ± 2.4). Clutch mass (CM in g) declined relative to body mass (FM in g) as female size increased ($CM = 1.46 FM^{0.74}$; $r = 0.70$).

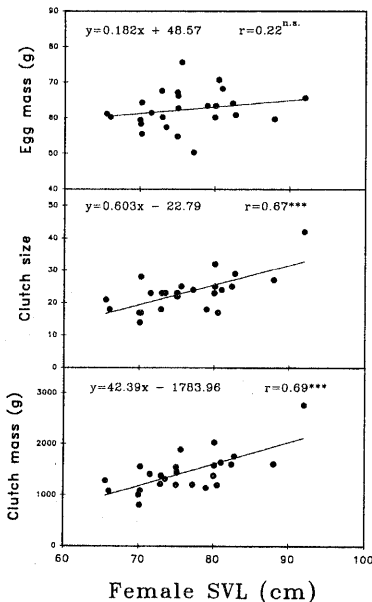


Fig. 6. Relationships between egg mass, clutch size, and clutch mass and female SVL (n.s. = $P > 0.05$, *** = $P < 0.001$).

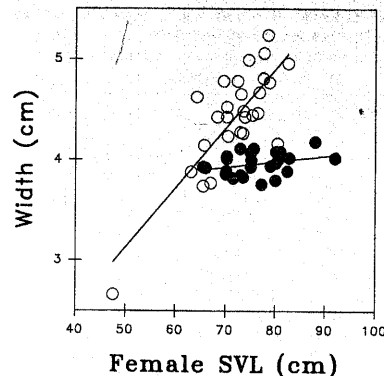


Fig. 7. The relationship between female SVL and egg width (filled circles) and minimum pelvic canal diameter (open circles).

TABLE 5. PARTIAL CORRELATION COEFFICIENTS BETWEEN THE INDICATED REPRODUCTIVE PARAMETERS AND CLUTCH SIZE; FEMALE SVL HELD CONSTANT.

Parameter	r_{pb}	n
Clutch mass	0.91**	25
Egg length	-0.48*	25
Egg width	-0.01	25
Egg mass	-0.12	25

* $P < 0.05$; ** $P < 0.001$.

clutch mass) for female caiman from 60–90 SVL (Fig. 9). Because the frequency of reproduction increased with female body size, mean annual reproductive rate increased allometrically at a faster rate than did clutch mass. As females grew, the relative mass of individual clutches declined, but mean annual reproductive output increased (Table 8).

DISCUSSION

Seasonal reproductive cycle.—The reproductive cycles of reptiles are influenced by environmental factors like temperature, photoperiod, rainfall, moisture, humidity, and food supply (Duval et al., 1982). Few data on tropical crocodylians are available, but among the more temperate species (e.g., *Alligator mississippiensis*), the reproductive season is constrained by temperature; and mean nesting dates are correlated with spring temperature regimes (Joanen and McNease, 1979, 1980; Kushlan and Jacobsen, 1990). In the lowland tropics, seasons are defined principally by variations in rainfall, and caiman in the Venezuelan llanos exhibit a reproductive cycle that is strongly correlated with the annual cycle of rains and flooding (M. Statton and J. Dixon, unpubl. data; Ayarzagüena, 1983; this study). Vitellogenesis and testicular

Frequency of reproduction.—Reproductive state was determined for 81 females [≥ 60 cm SVL; 28 road-killed (DOR); 30 sacrificed, 2 natural mortality (ND), and 21 radio-tracked females during the period 1985–1988; Table 6]. Among DOR, sacrificed, or ND specimens, only caiman examined during the reproductive season (May–Sept.) were used. The mean annual frequency of reproduction was 54.3%; ranging from 45% in 1985 to 69% in 1988, but no significant differences were noted among years ($F_{3,77} = 0.68$; $P = 0.57$). Frequency of reproduction (FR) was positively correlated with female size (SVL, in cm): $FR = 3.045 SVL - 170.110$; $r^2 = 0.945$ (Table 7).

Size-class distribution of breeding female population.—The size-class distribution of nesting females was estimated from clutch mass (using the female size-clutch mass relationship; Fig. 6) and from data on population size-class distribution (based on captures) and size-class specific reproductive effort (Table 7). Both techniques indicated that the modal breeding female size-class was 70–75 cm SVL, with the estimate based on clutch size having a larger range (Fig. 8). When compared with the size-class distribution of captured females, large females (> 80 cm SVL) are overrepresented in the nesting population (Fig. 8).

The size-specific effect of reproductive effort and clutch mass on caiman fecundity was determined by calculating mean annual reproductive output (frequency of reproduction \times

TABLE 6. PERCENTAGE OF FEMALES OVER 59.9 cm SVL BREEDING, AS DERIVED FROM FOUR SAMPLE POPULATIONS. All samples taken during the months May–Sept. over the period 1985–1988. DOR = dead on road, ND = natural mortality, radio = radiotelemetry female.

	DOR	Sacrificed	ND	Radio	Total
Sample size	28	30	2	21	81
Minimum SVL (cm)	60.0	60.0	77.4	61.0	60.0
Maximum SVL (cm)	86.1	82.8	80.5	82.5	86.1
Mean SVL (cm)	70.1	73.4	79.0	76.5	73.2
SD SVL (cm)	7.5	5.5	1.6	5.2	6.6
No. breeding	14	16	1	13	44
% breeding	50.0	53.3	50.0	61.9	54.3

TABLE 7. FREQUENCY OF REPRODUCTION OF FEMALE CAIMAN ≥ 60 cm SVL BY SIZE-CLASS AND YEAR. Data are presented as number breeders/sample size and percent breeding.

Size-class (cm SVL)	1985	1986	1987	1988	Total
60-65	0/1 0.0%	1/3 33.3%	1/3 33.3%	0/5 0.0%	2/12 16.7%
65-70	1/2 50.0%	0/5 0.0%	3/4 75.0%	0/0 0.0%	4/11 36.4%
70-75	1/2 50.0%	5/8 62.5%	5/9 55.6%	2/2 100.0%	13/21 61.9%
75-80	0/0 0.0%	2/7 28.6%	6/9 66.7%	3/3 100.0%	11/19 57.9%
80-85	1/1 100.0%	5/5 100.0%	1/5 20.0%	6/6 100.0%	13/17 76.5%
85-90	0/0 0.0%	1/1 100.0%	0/0 0.0%	0/0 0.0%	1/1 100.0%
Total	3/6 50.0%	13/29 44.8%	16/30 53.3%	11/16 68.8%	44/81 54.3%

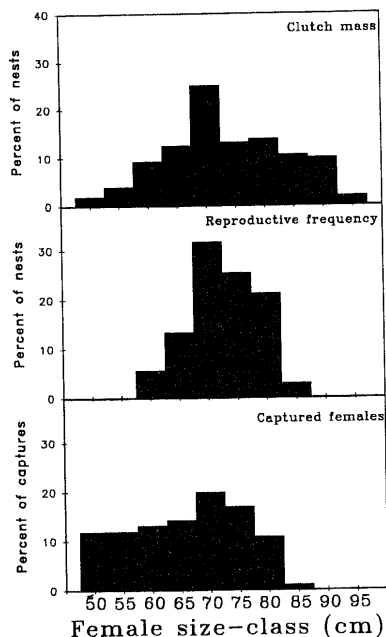


Fig. 8. The predicted size-class distribution of the nesting female population (as calculated from clutch mass and the reproductive frequency of females) compared to the overall female size-class distribution (based on captures).

recrudescence begin in the late dry season (April), two to three months prior to the peak period of courtship and mating, and approximately four months before the peak nesting period (M. Staton and J. Dixon, unpubl. data; Thorbjarnarson, 1991). Ovulation and peak sperm motility occurred during the early wet season, coincident with the dispersal of caiman from dry season lagoons and the establishment of breeding territories by males (Thorbjarnarson, 1991).

Because of the annual fluctuation in llanos water levels, and the physiological limitations of the breeding schedule (e.g., the time required for gonadal recrudescence, ovulation, and egg incubation), timing of caiman reproduction is critical. After the onset of gonadal recrudescence in the late dry season, caiman begin courtship and mating in the early wet

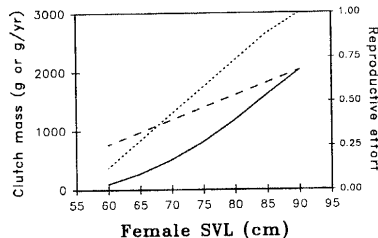


Fig. 9. The relationship between clutch mass [dashed line (g)], reproductive frequency [dotted line], and mean annual reproductive output [solid line (g/wr)] and female SVL.

season, following dispersal from the permanent water lagoons, and oviposition occurs during the peak of the annual savannah water levels. Given the interrelationship between reproductive hormone levels, gonadal recrudescence, and courtship (Lance, 1989; Kofron, 1990), changing the onset of breeding in the llanos, either earlier or later, would likely result in decreased reproductive success. An earlier onset would necessitate that courtship and mating take place during the late dry season under high population density conditions, which interfere with courtship and mating (Thorbjarnarson, 1991). Crowding and the resulting stress may also negatively effect nesting success (Elsej et al., 1990). Earlier onset of breeding and nesting also would increase the probability of nest flooding (M. Staton and J. Dixon, unpubl. data). Alternately, studies of caiman nesting and hatching ecology on Masagual suggest that delaying onset of breeding would reduce reproductive success by increasing the probability of nest depredation and neonatal mortality (Escalona, 1991; Thorbjarnarson, 1991).

Delaying courtship activities until after seasonal flooding results in a more predictable environment for nesting. Rainfall and the extent of savannah flooding vary among years. In some years, flooding is minimal, and caiman reproductive success (nesting success and neonatal survival) would be expected to be low. If ovulation is a response to copulation or courtship, as suggested by Lance (1989), engaging in courtship and mating only after significant flooding provides a mechanism to avoid investment in reproduction during extremely dry years (when dispersal is greatly delayed or does not occur). Alternatively, courtship and mating activities during the dry season would commit females to ovulating and nesting regardless of environmental conditions. In 1988, the rains on Masagual were delayed; but extensive flooding occurred by late June to early July, and nesting levels were high. However, in the year following the end of this study (1989), rains were very late, flooding did not occur until mid to late July, and nesting levels were very low (M. Muñoz, pers. comm.). These observations suggest that, if caiman disperse by early July, normal nesting can take place; but, if dispersal is delayed, nesting levels may be severely diminished.

Seasonal changes in mass of the lateral fat body were evident among both male and female caiman, but the pattern was sexually dimorphic. Female caiman utilize stored lipids throughout the dry season, and the decrease in relative fat body mass among vitellogenic females during

TABLE 8. ESTIMATED RELATIVE CLUTCH MASS (RCM) AND RELATIVE REPRODUCTIVE OUTPUT (RRO) FOR DIFFERENT SIZED FEMALES. RRO represents the mean annual clutch mass expressed as a percentage of female body mass.

Female SVL (cm)	RCM (% body mass)	RRO (% body mass)
60	14.9	1.88
65	15.0	4.16
70	14.6	6.26
75	13.9	8.11
80	13.1	9.69
85	13.9	12.36
90	11.6	11.63

the early wet season is consistent with mobilization of energy for reproduction. However, this trend was also seen in nonvitellogenic females, suggesting that lipids are also being used for maintenance. No such tendency was found among males, who exhibited what Derickson (1976) suggested was the typical pattern for tropical reptiles living in a seasonal environment, with the largest relative fat body masses found during the late dry and early wet season (March–June). Because no seasonal differences in the quantity of food consumed were found in this population (Thorbjarnarson, 1993), it is unlikely that changes in lateral fat body mass were related to food availability. The low stored lipid levels among males in the wet season may reflect increased energy demands associated with the establishment and maintenance of territories, courtship, and mating.

Sexual maturity and size-specific fecundity.—The size of males at sexual maturity is variable within and among populations of crocodylians. Caiman on Masagual are capable of producing sperm at approximately 75 cm SVL. However, some smaller individuals likely become sexually mature. Ayarzagüena (1983) reported sperm from two males measuring 69.5 and 73.5 cm SVL on the nearby Hato El Frio, in Apure state. In captivity, successful mating (the fertilization of eggs) of male *C. crocodylus* has been reported for individuals measuring 165 cm TL (approximately 87 cm SVL; Hunt, 1969), 150 cm TL (approximately 79 cm SVL; Alvarez del Toro, 1969) and 143 cm TL (approximately 76 cm SVL; Holmback, 1981).

Nevertheless, among wild animals, sexual maturity is less clear cut, because males may be physiologically mature (i.e., producing viable sperm) but excluded from mating by dominant males (McIlhenny, 1935; Modha, 1967; Joanan and McNease, 1975). Thus, the size at which

males begin to engage in courtship and mating depends on population density and size-class distribution, and probably habitat type. On Masaguara, small adult male caiman (approximately 70–80 cm SVL) bellowed, a behavior typically associated with the establishment of breeding territories (Thorbjarnarson, 1991). Evidence from radiotelemetry revealed size-specific differences in caiman movement patterns (Thorbjarnarson, 1991). Large males (> 100 cm SVL) dispersed short distances and apparently monopolized the preferred breeding habitats close to the dry season lagoons where the density of females was highest. Males < 90 cm SVL did not disperse large distances from the dry season lagoons but tended to have large home ranges, indicating they may not establish breeding territories. Males in the 90–100 cm SVL dispersed greater distances than larger and smaller males and appeared to be relegated to marginal areas for breeding. As males grow, they may undergo a shift in seasonal movement patterns that reflects their size mediated ability to participate in mating activities.

Although female *Caiman crocodilus* in the llanos attain sexual maturity at a smaller size (60 cm SVL) than do males, both sexes mature at approximately the same age (approximately 7 yr; Thorbjarnarson, 1991). The minimum size of sexual maturity of caiman on Masaguara agrees well with other estimates made for the Venezuelan llanos (Ayarzagüena, 1983) but is somewhat smaller than the minimum size (67.7 cm SVL) noted by Staton and Dixon (1977) for the same population.

Previous examinations of fecundity among crocodilians have dealt principally with the positive relationship between female size and clutch size (Greer, 1975); however, fecundity is also manifested in the frequency of breeding (Iverson, 1992). Estimates of reproductive output need to incorporate both parameters. In this study, relative clutch mass, which has been used in some studies of reptiles as a measure of reproductive output (Tinkle and Hadley, 1975; Jackson, 1988), decreased with female size. However, once annual reproductive frequency was incorporated, reproductive output, both in absolute and relative terms, increased with female size. For crocodilians, another important component of reproductive output is energy devoted to parental care, which is common, if not ubiquitous, in the group (Shine, 1988) but difficult to quantify.

Relatively little is known about the annual breeding frequency of crocodilians, and the few reports available largely represent single-year estimates that do not address the question of

female size-specific effects. Studies of *Crocodylus* have generally reported high annual nesting values: 90% (*C. johnsoni*; Webb et al., 1983), 87.6% (*C. niloticus*; A. Graham, unpubl., 1968), approximately 80% (*C. intermedius*; Thorbjarnarson and Hernández, 1993), 72% (*C. acutus*; Mazzotti, 1983), and 63.8% (*C. acutus*; Thorbjarnarson, 1988). Work on American alligators has suggested somewhat lower values: 68.1% (Louisiana; Chabreck, 1966), 63% (Louisiana; Joanen and McNease, 1980), 29.9% (Rootes and Chabreck, 1993), 29% (Florida Everglades; Kushlan and Jacobsen, 1990), 28% (Louisiana; Taylor, 1984), 25.3% (Louisiana; Taylor et al., 1991), 25% (South Carolina; P. Wilkinson, unpubl.), and < 10% (North Carolina; Lance, 1989).

Other than the present study, the only information on annual variation in the frequency of reproduction comes from American alligators, which have lower, and in some cases more variable, values: Florida Everglades 16–58% over 7 yr (Kushlan and Jacobsen, 1990); Louisiana 33.3%, 12.5%, and 37.5% (Taylor, 1984), and 26.2%, 25.4%, 16.2%, and 25.3% (Taylor et al., 1991). Size-specific fecundity is also an important aspect of caiman population biology. In this study, breeding frequency was related clearly to female size, with larger females reproducing at more frequent intervals than smaller females. The little information on other crocodilians appears to confirm this relationship (Cott, 1961; P. Wilkinson, unpubl. data; Taylor et al., 1991); however, Joanen and McNease (1980) found no size-related difference in frequency of reproduction among 25 alligators in Louisiana.

As female caiman grow, the total amount of energy available for reproduction presumably increases because of greater lipid storage capacity and the reduced investment in growth (Congdon et al., 1982). Supplemental energy could be invested in increased offspring size, increased clutch size, or both. Among the caiman in this population, it was clear that increased investment in fecundity was favored over the production of larger offspring. Theoretical studies of the partitioning of energy resources available for reproduction predict a trade-off between the number and size of offspring (Smith and Fretwell, 1974; Brockelman, 1975), and the allometric trends in resource partitioning should reflect a trade-off between the advantages of higher fecundity versus the presumed benefits of increased neonatal fitness. Evidence for an inverse relationship between clutch size and offspring size has not been found in many intraspecific studies, attributed by Ford and Seigel (1989) to the failure to correct for differences

in female body size. Although the inverse relationship between caiman egg length and clutch size may suggest limitations on linear egg placement within the oviduct (Ford and Seigel, 1989), no evidence was found for a trade-off between egg size and clutch size. Small adult caiman appear to lay eggs as large as is physically possible given the limitations of the diameter of the pelvic canal, but, as females grow, egg mass does not increase significantly. Instead, increased energy availability is translated principally into larger clutch sizes, suggesting that the presumed fitness benefits of larger neonate size are equalled or exceeded by fitness reduction resulting from decreased fecundity.

Although trade-off between clutch and offspring size has become a central theme of much life-history theory, it rests heavily on the assumption that an offspring's fitness is directly related to its size. This relationship has been demonstrated for some reptiles (Ferguson and Fox, 1984; Sinervo, 1990); however, recent studies of crocodilians, which appear to universally have environmental sex determination (Ferguson, 1985; Deeming and Ferguson, 1988), suggest that a large component of neonatal fitness may be determined by conditions experienced by developing embryos within the nest. Independent of sex, incubation temperature has been demonstrated to affect the survival rate and the frequency of abnormalities of embryos, the weight of residual yolk and body size at hatching, and posthatchling growth rates (see Webb and Cooper-Preston, 1989). Because the environmental conditions for eggs in a nest are inherently unpredictable, developmental factors associated with environmental sex determination may act to uncouple the relationship between egg size and the potential for growth and survival of neonates.

Published information for populations of other crocodilians suggest that the relationship between female size and clutch and egg size vary considerably among and within species. As female size increases in *Alligator mississippiensis*, reports indicate that egg size and clutch size remain unchanged (Deitz and Hines, 1980), egg size but not clutch size increases (P. Wilkinson, unpubl.), or both egg size and clutch size increase (Ferguson, 1985). In *Crocodylus niloticus*, clutch size is known to increase with female size (Cott, 1961; Hutton, 1984; A. Graham, unpubl.), and Hutton (1984) suggests that egg size (egg length) also increases. In *Crocodylus intermedius*, both egg size and clutch size increase with female size (Thorbjarnarson and Hernández, 1993), but the relative increase in clutch size is greater; and, after controlling for female

size, no trade-off was found between egg and clutch size. Clearly, more information is needed before intraspecific trends in the covariation between egg and clutch size in the Crocodylia can be defined.

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DEPARTMENT OF WILDLIFE AND RANGE SCIENCES, SCHOOL OF FOREST RESOURCES AND CONSERVATION, UNIVERSITY OF FLORIDA, GAINESVILLE, FLORIDA 32611; AND FLORIDA MUSEUM OF NATURAL HISTORY, GAINESVILLE, FLORIDA 32611. PRESENT ADDRESS: NYZS-WILDLIFE CONSERVATION SOCIETY, BRONX, NEW YORK 10460-1099. Submitted: 14 Feb. 1993. Accepted: 15 Oct. 1993. Section editor: W. J. Matthews.

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Social Behavior and Operational Sex Ratios in the Viviparous Fish *Girardinichthys multiradiatus*

CONSTANTINO MACÍAS GARCÍA

Males of the sexually dimorphic goodeid *Girardinichthys multiradiatus* defend shoreline temporary courtship arenas where the operational sex ratio is strongly male biased. Any fish entering an arena is approached; males are challenged, and escalated fights may ensue, whereas females are courted. Heavily pregnant females spend long inactive periods at the water-land interface. Most courtship pairs are assortative by size and are often joined by fish of either sex. Interfering males either challenge or are challenged by the original male in a pair. Thus, both females and courtship arenas are sources of male-male combats. The frequency of male-male aggressive interactions and the degree of sexual dimorphism covary among populations, but the causes of these population differences are unknown.

The nature of biological processes can often be clarified using the comparative method (Harvey and Pagel, 1991). Appropriate tests can only be made once acceptable phylogenies are available for the taxa under scrutiny, but predictions derived from one taxon can be test-

ed by seeking evidence of the same phenomena in unrelated taxa. Here data on the social behavior of a viviparous fish belonging to the family Goodeidae are used to test predictions derived from studies on sexual selection in the family Poeciliidae.