REPRODUCTIVE CHARACTERISTICS OF THE ORDER CROCODYLIA

John B. Thorbjarnarson

NYZS The Wildlife Conservation Society,
Bronx, NY 10460, USA

ABSTRACT: Information on crocodilian egg and clutch characteristics is reviewed. The relationships between female size and egg mass, clutch size, and clutch mass are quantified, and the effects of nest mode, relative snout width, and family are examined. At the interspecific level, egg mass, clutch size, and clutch mass are strongly correlated with female size. However, larger species produce relatively smaller clutches and eggs. In most cases, similar relationships were found at the intraspecific level as well. Crocodylids are more variable in terms of nesting mode (hole and mound nesters) than alligatorids (all mound nesters). After correcting for differences in female length, no trade-off between clutch size and egg size was found at the interspecific level. The effects of family, snout width, and nest mode were also examined independent of female size. Clutch size and clutch mass were greater in the Alligatoridae than in the Crocodylidae and the Gavialidae. However, data on reproductive frequency suggest that crocodylids nest more frequently than alligatorids, and no significant difference in mean annual clutch mass was found between these two major phylogenetic groups. Narrow-snouted species lay significantly smaller clutches than other crocodilians. Consistent patterns of relative egg mass/clutch size variation were found within genera in the Alligatoridae. *Alligator* produces large clutches of small eggs. Tropical alligatorids have large relative clutch masses due to the production of relatively large eggs (*Melanosuchus* and *Paleosuchus*) or relatively large clutches (*Caiman*). Within the genus *Crocodylus*, the four species that inhabit strongly seasonal riverine or lacustrine environments are all hole nesters that invest relatively little in each reproductive bout (*C. intermedius*, *C. palustris*, and *C. johnsoni*) but may compensate with high reproductive frequencies. *Gavialis* may also follow this general pattern. Among the true crocodiles, two species have notably large clutch masses (*C. niloticus* and *C. porosus*). In terms of reproductive characteristics, *C. cataphractus* is the most unusual species, laying very small numbers of very large eggs.

Key words: Clutch size; Crocodylia; Life history evolution; Reproduction

COMPARATIVE studies of reptile life-history strategies have focused principally on squamates and chelonians (e.g., Congdon and Gibbons, 1990; Dunham et al., 1988; Elgar and Heaphy, 1989; Iverson, 1987, 1992; Stearns, 1984; Wilbur and Morin, 1988) and have revealed a remarkable variability in life-history characteristics of these relatively diverse groups of reptiles. Nevertheless, recent reviews of even these best known groups of reptiles acknowledge the incomplete nature of current life-history information (Dunham et al., 1988; Wilbur and Morin, 1988). The only prior assessment of the reproductive attributes of the Crocodylia (Greer, 1975) examined the relationship between clutch size and female size, but it did not treat other reproductive parameters and was hampered by a lack of information for several species. Greer (1975) also commented on the lack of information on intraspecific trends in size-specific fecundity. Over the last 20 yr, an increase in studies of crocodilian ecology has produced more detailed information, warranting a more thorough examination of crocodilian reproductive characteristics.

The finite energy resources that females have to invest in reproductive output can be classified using three parameters: egg mass, clutch size, and clutch frequency. The existence of a trade-off between egg size and clutch size is a basic tenet of much life-history theory and has generated a great deal of analysis and discussion (Sinervo, 1990; Smith and Fretwell, 1974; Stearns, 1977; Williams, 1966). A recent review of turtle reproductive correlates by Elgar and Heaphy (1989) found evidence for a clutch size–egg size trade-off at the interspecific level. Yet, surprisingly few studies have specifically addressed this question in other taxa (Roff, 1992). Simi-

larly, expected trade-offs between clutch mass and clutch (or breeding) frequency have been little studied (Elgar and Heaphy, 1989; Iverson, 1992). Iverson (1992) found that such a trade-off occurs among turtles and is influenced by environmental factors such as latitude (via the length of the breeding season) and potentially by the predictability of reproductive success (e.g., nest predation frequency).

The living members of Crocodylia (suborder Eusuchia) are divided among three phylogenetic lineages, classified as either families (King and Burke, 1989; Mook, 1934) or subfamilies (Romer, 1956; Steel, 1973), which have been separate at least since the Miocene (Steel, 1973). Crocodilians represent a small, relatively homogeneous group of reptiles characterized by large body size, delayed maturity, long reproductive life span, oviparity, one or fewer nest per year, and a tropical and subtropical distribution (Ferguson, 1985). Crocodilians are of additional interest because of their close phylogenetic relationship with birds (Perutz et al., 1981; Romer, 1956). Due to the small number of species (22), it is feasible to examine the reproductive attributes of the entire order, thereby avoiding taxonomic bias.

In this paper, I examine the effect of female size, family, and nest mode on crocodilian reproductive characteristics. Additionally, one of the few readily apparent morphological differences among crocodilians is snout shape, which is assumed to reflect variability in diet (and potentially related ecological differences). Accordingly, I also examine the effect of snout width on reproductive variables. Specifically, I address the following questions. (1) What is the interspecific effect of adult female body size on egg mass, clutch size, and clutch mass? (2) Independent of female body size, is there a trade-off between egg size and clutch size at the interspecific level? (3) Independent of female body size, what effects do family, nest mode, and snout width have on the relationship between egg mass and clutch size? (4) Independent of female body size, what effects do family, nest mode, and snout width have on clutch mass? (5) How does vari-

ability in reproductive frequency affect reproductive output?

I also examine the intraspecific effects of female body size on egg size and fecundity and summarize the results of field studies that have addressed these relationships within populations.

METHODS

For each of the 22 extant species of crocodilians, I compiled information on egg dimensions (length and width), egg mass, clutch size, clutch mass, and reproductive frequency (percentage of adult females nesting per year). Female size was quantified by means of mean adult female total length (TL) and mean adult female mass (BM). I used data from wild individuals or populations for most species, although in some cases the only data available for certain reproductive parameters were from captive individuals. I obtained information principally from published accounts but used some unpublished data.

In cases where mean egg mass was not reported, I estimated egg mass by one of the following methods (in descending order of preference): using the midpoint of the range of reported values, using values calculated from mean egg dimensions (length, width), or using values calculated from the midpoint of the range of reported egg dimensions. I calculated egg mass (EM) from linear egg dimensions [length (L) and width (W) in millimeters] using a formula [EM = $0.61(LW^2)$] modified from the equation for bird eggs developed by Romanoff and Romanoff (1949). Using 13 data sets from nine species for which mean egg mass and dimensions were known, the average error of values produced by this equation was -0.28%, ranging from -7.7% to $+5.0\%$.

Where mean clutch size (CS) was not reported, I used the midpoint of the range of reported clutch size. Using 24 data sets from 10 species for which both mean clutch size and the midpoint of the range were known, the mean percent error was 1.14% (range -8.1 to 18.1%). If not reported, I estimated clutch mass (CM) by multiplying mean clutch size by mean egg mass. When mean (or individual) female mass

(FM) was not reported but female length was, I estimated mass from length–mass relationships for that species or a taxonomically similar one. Crocodilian length and mass equations were available for *Alligator mississippiensis* (Chabreck and Joanen, 1979), *Caiman crocodilus* (Ayarzagüena, 1983; Thorbjarnarson, unpublished data), *Crocodylus niloticus* (Graham, 1968; Hutton, 1984), *C. novaeguineae* (Montague, 1984), *C. acutus* (Thorbjarnarson, 1988), *C. johnsoni* (Webb et al., 1983a), and *C. porosus* (Webb and Messel, 1978). In the absence of data on mean or individual female lengths, I used the midpoint of the range of adult female lengths. Female length data presented as snout–vent length were converted into total length using formulae from either Chabreck and Joanen (1979), Hutton (1984), Thorbjarnarson (unpublished data: *Caiman crocodilus*), or Webb and Messel (1978). I calculated relative clutch mass (RCM) and relative egg mass (REM) as clutch mass and egg mass divided by female mass, respectively.

Nest mode (hole nester or mound nester) was assigned based primarily on information in Campbell (1972) and Greer (1970, 1971), with the one exception being *Crocodylus rhombifer*, where mound nesting was assigned based on more recent information (R. Ramos, personal communication). Relative snout width (snout length/snout width, measured just anterior to the orbits) was based on data in Brazaitis (1973) and Mook (1921); I classified species as either broad (snout length/width ≤1.5), intermediate (1.51–2.5), or narrow snouted (>2.5). Broad-snouted species included all the Alligatoridae plus *Crocodylus palustris*, *C. rhombifer*, and *C. moreletii*. Narrow-snouted species were *Gavialis gangeticus*, *Tomistoma schlegelii*, *Crocodylus cataphractus*, and *C. johnsoni*. Taxonomic classifications follow King and Burke (1989), with the exception of *Caiman yacare* being considered here as a subspecies of *Caiman crocodilus*.

Reproductive frequency was defined as the percentage of adult females that nest in any one year. I calculated annual clutch mass (ACM) by multiplying mean clutch mass by reproductive frequency.

As considerably more information was available for certain species (e.g., *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus niloticus*) than for others, data analyses were conducted using mean values for the reproductive parameters. I analyzed allometric trends by linear regression and the derivation of power formulas for each of the principal reproductive parameters (egg mass, clutch size, clutch mass) as a function of female mass.

To examine the effects of family, nest mode, and snout width on egg mass and clutch size, I characterized species according to the relationship between relative egg mass and relative clutch size. I used a geometric mean regression model (Sokal and Rohlf, 1981) to first regress egg mass and clutch size against mean adult female TL. Residual values for clutch size were plotted as a function of egg mass residuals for each of the 22 species. Residual values are referred to as relative egg mass and relative clutch size. I examined these plots to discern trends and identify major outliers in relation to the principal categorical variables. Trends were tested statistically using residual values in one-way analyses of variance.

A number of recent evaluations of comparative ecological studies have pointed out the problems associated with the use of species as independent values (due to shared ancestry: Harvey and Pagel, 1991). However, due to the small number of crocodilian species, use of higher taxonomic groupings (e.g., genera) was not statistically feasible. Nevertheless, in order to corroborate the effects of nest mode and snout width on reproductive parameters, I repeated these analyses within the most speciose genus (*Crocodylus*; 12 species). Statistical analyses were performed using CSS® (StatSoft, Inc.) software for microcomputers.

RESULTS

I located literature references for 269 accounts on all 22 species. Mean values are

TABLE 1.—Mean female size and reproductive parameters for all species.

Species	TL (cm)	FM (kg)	MTL (cm)	EM (g)	CS	CM (g)	RCM (%)	REM (%)
Alligatoridae								
Alligator mississippiensis	227	47.8	183	76.6	35.4	2712	5.7	0.16
Alligator sinensis	151	14.6	111	48.2	25.7	1239	8.5	0.33
Caiman crocodilus	143	10.9	115	62.9	24.4	1598	14.7	0.58
Caiman latirostris	161	14.6	130	76.2	31.4	2393	16.4	0.52
Melanosuchus niger	280	82.0	200	143.6	39.3	5644	6.9	0.18
Paleosuchus palpebrosus	108	5.9	105	68.6	13.3	912	15.5	1.16
Paleosuchus trigonatus	125	7.5	120	67.2	15.1	1015	13.5	0.90
Crocodylidae								
Crocodylus acutus	266	76.7	245	112.8	35.6	4016	5.2	0.15
Crocodylus cataphractus	232	50.5	192	146.0	19.5	2847	5.6	0.29
Crocodylus intermedius	299	107.9	258	110.4	39.8	4394	4.1	0.10
Crocodylus johnsoni	188	19.5	150	69.7	12.4	846	4.4	0.36
Crocodylus mindorensis	178	36.9	140	73.6	18.3	1347	3.7	0.20
Crocodylus moreletii	203	31.7	186	79.5	30.2	2401	7.6	0.25
Crocodylus niloticus	281	94.2	228	107.1	47.6	5098	5.4	0.11
Crocodylus novaeguineae	208	39.9	159	88.5	29.4	2602	6.5	0.22
Crocodylus palustris	232	42.7	175	99.5	23.4	2328	5.5	0.23
Crocodylus porosus	270	78.7	215	109.2	47.8	5220	6.6	0.14
Crocodylus rhombifer	219	57.5	195	104.3	25.4	2649	4.6	0.18
Crocodylus siamensis	232	42.5	192	106.9	28.4	3036	7.1	0.25
Osteolaemus tetraspis	131	18.8	101	55.0	12.3	677	7.7	0.63
Tomistoma schlegelii	305	119.0	250	139.9	31.8	4449	3.7	0.12
Gavialidae								
Gavialis gangeticus	341	147.0	303	161.4	38.9	6279	4.3	0.11

presented in Table 1 (the raw data are available from the author upon request).

Allometric Relationships

Egg size, clutch size, and clutch mass were positively correlated with female body size at the interspecific level (Fig. 1, Table 2). The power equations relating egg mass and clutch mass to female mass had exponential values <1 (Table 2), indicating that relative egg mass and relative clutch mass were inversely related to female size at the interspecific level. A multiple linear regression predicting clutch mass from egg mass and clutch size ($r^2 = 0.97$, $n = 22$) revealed that clutch size (standardized regression coefficient $\beta = 0.63$) accounted for a larger percentage of the total variance in clutch mass than did egg mass ($\beta = 0.49$), indicating that at the interspecific level clutch mass was increased principally by producing larger clutches and secondarily by laying larger eggs.

Among the six species for which data were available, reproductive frequency was not correlated with TL ($r = 0.26$, $P = 0.61$). Combining data for reproductive frequency and clutch mass, mean annual clutch mass was positively correlated with female TL (Fig. 2, Table 2).

Intraspecific (among populations) comparisons suffered from limitations of small sample size. Among six species for which sufficient data were available, a positive correlation between female size and egg mass was found in all species except one (*Caiman latirostris*), but the relationship was significant only in *Caiman crocodilus*, the species with the largest sample size (Table 3). Egg mass increased with female size in four of six studies (representing three of the four species) of individual populations (Table 4).

Intraspecific clutch size demonstrated a clearer allometry with female size than did egg mass, but again the analyses were hampered by small sample sizes. Of the
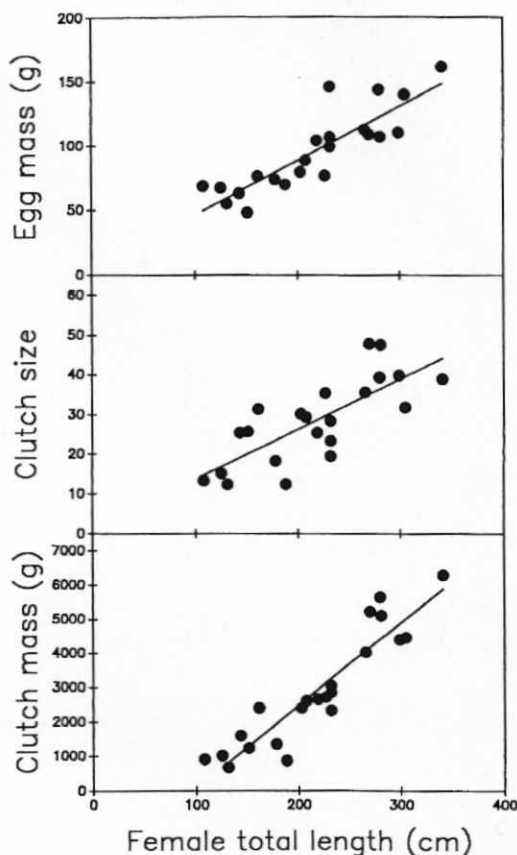
FIG. 1.—Relationships between egg mass (top), clutch size (middle), clutch mass (bottom), and female total length for crocodilians. Mean values for each of the 22 extant species.

TABLE 2.—Least-squares regression equations relating female total length (TL, in cm) to mean egg length (EL, in cm), egg width (EW, in cm), egg mass (EM, in g), clutch size (CS), clutch mass (CM, in g), and clutch variables at the interspecific level, and power equations relating egg mass, clutch size, clutch mass, and annual clutch mass (ACM, in g/year) to female body mass (BM, in kg). All regressions are significant at the 0.001 level.

Equation	r^2	n
EL = 0.106(TL) + 51.091	0.64	22
EW = 0.083(TL) + 27.977	0.72	22
EM = 0.423(TL) + 3.709	0.75	22
CS = 0.12(TL) + 1.092	0.58	22
CM = 24.109(TL) − 2341.630	0.85	22
EM = $31.62(BM^{0.29})$	0.74	22
CS = $7.43(BM^{0.35})$	0.60	22
CM = $241.36(BM^{0.64})$	0.81	22
ACM = $111.94(BM^{0.72})$	0.78	6

populations, a positive relationship between female size and clutch mass was noted in three of four studies, representing all three species for which data are available (Table 4). In the fourth study, the lack of a significant positive relationship was attributed to a small sample size ($n = 7$: Deitz and Hines, 1980).

Reproductive frequency was positively correlated with female size at the intrapopulation level in five of seven studies (Table 4).

Effect of Family, Nest Mode, and Snout Width

To examine the effects of family, nest mode, and snout width on reproductive characteristics, I conducted two analyses.
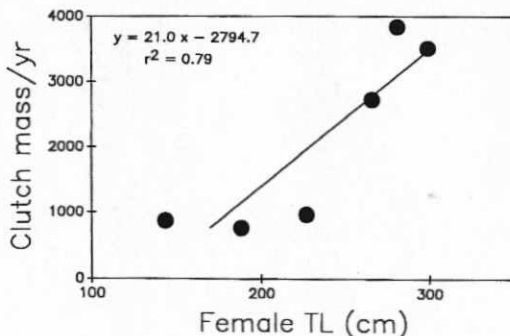

FIG. 2.—Mean annual clutch mass (clutch mass × reproductive frequency) as a function of female total length for six species of crocodilians.

six species examined, three had a significant positive correlation (Table 3). At the intrapopulation level, clutch size was positively correlated with female size in six of nine studies, representing all four species for which data are available (although for Alligator mississippiensis this was noted in only one of four studies: Table 4).

Intraspecifically, a significant positive relationship between clutch mass and female length was evident among three of the six species (Table 3). Two of the other three species (A. mississippiensis and C. niloticus) had high correlation coefficients and low values of P, which, given the small sample sizes, indicate a trend for increasing clutch mass. Only in Caiman latirostris was no relationship apparent. Within

TABLE 3.—Least-squares regression correlation coefficients between female length (cm TL) and egg mass (g), clutch size, and clutch mass (g) at the interpopulation level for six species of crocodilians. Numbers in parentheses are sample sizes and probability values.

Species	Egg mass	Clutch size	Clutch mass
Alligator mississippiensis	0.39 (5)	0.79 (5)	0.84 (5)
	(P = 0.56)	(P = 0.11)	(P = 0.08)
Caiman crocodilus	0.64 (12)	0.78 (12)	0.84 (11)
	(P = 0.02)	(P = 0.00)	(P = 0.00)
Caiman latirostris	0.15 (4)	0.16 (4)	0.15 (4)
	(P = 0.85)	(P = 0.84)	(P = 0.68)
Crocodylus niloticus	0.68 (4)	0.75 (7)	0.78 (5)
	(P = 0.32)	(P = 0.05)	(P = 0.12)
Crocodylus porosus	0.56 (6)	0.74 (6)	0.95 (6)
	(P = 0.25)	(P = 0.09)	(P = 0.00)
Crocodylus acutus	0.77 (4)	0.98 (4)	0.97 (4)
	(P = 0.23)	(P = 0.01)	(P = 0.03)

First, I examined the effects of these three categorical variables on the relationship between relative egg mass and clutch size. I then analyzed their effects on reproductive output, using clutch mass as a measure of reproductive investment.

Covariation among variables.—Covariance among the independent variables (family, nest mode, and snout width) was evident. Nest mode was influenced by phylogeny (all alligatorids were mound nesters). Snout width was also highly influenced by family (ANOVA; $F_{2,18} = 10.43$, $P = 0.001$).

Clutch size and egg mass.—Residual (relative) values of egg mass, clutch size, and clutch mass are listed in Table 5. Plotting relative clutch size versus relative egg mass (Fig. 3) provided a convenient meth-

od for graphically analyzing the variability of reproductive characteristics. Higher ordinate values represented the production of larger than expected clutches (relative to female size). Increasing abscissa values indicated the production of larger than predicted eggs. Species in the upper left section of the graph produced many small eggs whereas species in the lower right laid few, large eggs. Relative clutch mass was greatest in the upper right hand corner of the graph and least in the lower left. I found no significant negative trend among these residual values ($r = -0.29$, $P = 0.19$), indicating the lack of a trade-off between egg size and clutch size.

Overall, members of the Crocodylidae were larger (Table 6) and exhibited a greater variability in nesting mode (hole

TABLE 4.—Summary of relationships between female size and reproductive parameters for crocodilians at the intrapopulation level. A plus indicates a significant positive relationship; a zero indicates no significant relationship.

Species	Egg size	Clutch size	Clutch mass	Reproductive frequency	Source[*]
Crocodylus niloticus		+		+	A
		+		+	B
	+	+		0	C
Crocodylus intermedius	+	+	+		D
Alligator mississippiensis	+	+			E
	0	0	0		F
	+	0	+	+	G
		0		0	H
				+	I
Caiman crocodilus	0	+	+	+	J

[*] Sources: A = Cott (1961); B = Graham (1968); C = Hutton (1984); D = Thorbjarnarson and Hernández (1993); E = Ferguson (1985); F = Dietz and Hines (1980); G = Wilkinson (1984); H = Joanen (1970) and Joanen and McNease (1980); I = Taylor et al. (1991); J = Thorbjarnarson (1994).
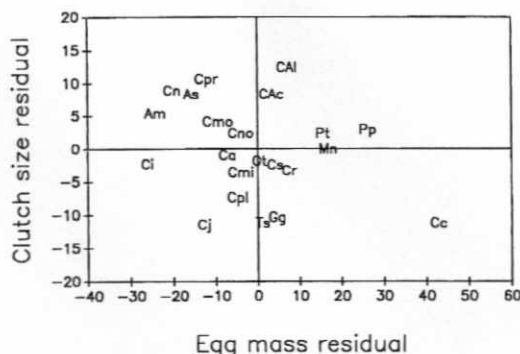
FIG. 3.—Residual values of clutch size as a function of egg mass residuals for each of the 22 extant species of crocodilians. Residual values were obtained from geometric mean regressions of clutch size and egg mass against female TL, respectively. **Alligatoridae**: Am = *Alligator mississippiensis*; As = *A. sinensis*; CAc = *Caiman crocodilus*; CAl = *C. latirostris*; Mn = *Melanosuchus niger*; Pp = *Paleosuchus palpebrosus*; Pt = *P. trigonatus*. **Crocodylidae**: Ca = *Crocodylus acutus*; Cc = *C. cataphractus*; Ci = *C. intermedius*; Cj = *C. johnsoni*; Cmi = *C. mindorensis*; Cmo = *C. moreletii*; Cn = *C. niloticus*; Cno = *C. novaequineae*; Cpl = *C. palustris*; Cpr = *C. porosus*; Cr = *C. rhombifer*; Cs = *C. siamensis*; Ot = *Osteolaemus tetraspis*; Ts = *Tomistoma schlegelii*. **Gavialidae**: Gg = *Gavialis gangeticus*.

and mound nesters) than the alligatorids (all mound nesters). The monotypic Gavialidae was represented by *Gavialis gangeticus*, a large hole nester. Before correcting for differences in body size, there were no significant differences in clutch size among the three families (ANOVA; $F_{2,19} = 0.58$, $P > 0.05$: Table 6). Graphic analysis of residual values for egg size and clutch size of the three phylogenetic lineages (Fig. 4) suggested that, with two exceptions (*C. niloticus* and *C. porosus*), the alligatorids tended to produce larger clutches than the crocodylids and *Gavialis*. The analysis of variance of residuals indicated a significant effect of family on clutch size (Table 7). Although mean egg mass varied significantly among the three families (ANOVA; $F_{2,19} = 4.67$, $P < 0.05$: Table 6), after correcting for female TL, no phylogenetic differences were found (Table 7).

Using the residual values for egg mass (Table 5), I classified species according to their egg size as below average, average
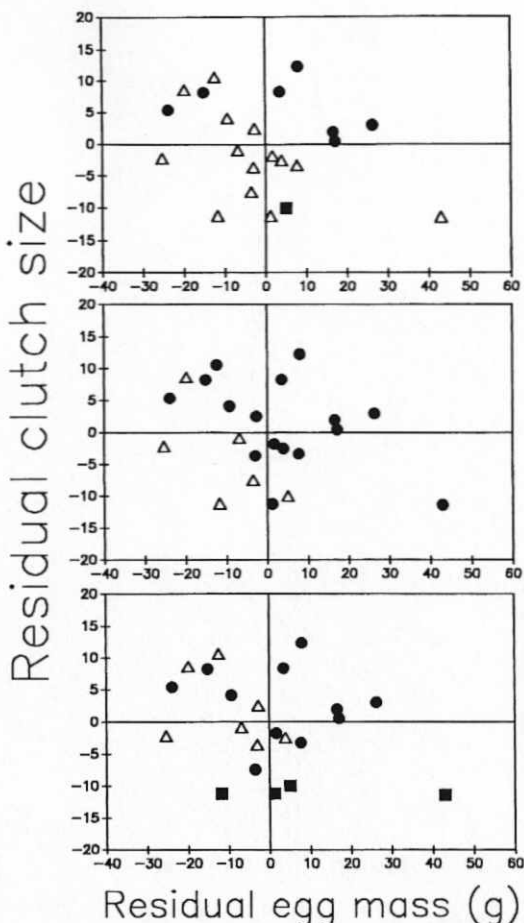

FIG. 4.—Effect of family (top), nest mode (middle), and snout width (bottom) on the relationship between relative clutch size and relative egg mass for crocodilians. Family: open triangles = Crocodylidae; filled circles = Alligatoridae; filled square = Gavialidae. Nest mode: open triangles = hole nesters; filled circles = mound nesters. Snout width: filled circles = broad snouted; open triangles = moderate snouted; filled squares = narrow snouted.

(within ±15 g of the expected value), and above average. Similarly, I classified species by clutch size (average defined as within ±5 of the expected). In the Alligatoridae, four distinctive patterns were found, and these patterns were consistent within genera (Fig. 3, Table 8). Both members of the genus *Alligator* laid large numbers of small eggs. The two species of *Paleosuchus* and *Melanosuchus niger* produced average numbers of large eggs. Both

TABLE 5.—Residual values of egg mass, clutch size, and clutch mass for each of the 22 species of crocodilians.

Egg mass		Clutch size		Clutch mass	
Crocodylus cataphractus	43.0	Caiman latirostris	12.3	Melanosuchus niger	1109
Paleosuchus palpebrosus	26.3	Crocodylus porosus	10.6	Caiman latirostris	968
Melanosuchus niger	17.1	Crocodylus niloticus	8.6	Crocodylus porosus	946
Paleosuchus trigonatus	16.6	Caiman crocodilus	8.3	Paleosuchus palpebrosus	873
Caiman latirostris	8.0	Alligator sinensis	8.2	Caiman crocodilus	644
Crocodylus rhombifer	7.7	Alligator mississippiensis	5.4	Crocodylus niloticus	537
Gavialis gangeticus	5.0	Crocodylus moreletti	4.1	Paleosuchus trigonatus	531
Crocodylus siamensis	3.9	Paleosuchus palpebrosus	3.0	Gavialis gangeticus	149
Caiman crocodilus	3.5	Crocodylus novaeguineae	2.5	Crocodylus sinensis	76
Osteolaemus tetraspis	1.7	Paleosuchus trigonatus	2.0	Osteolaemus tetraspis	36
Tomistoma schlegelii	1.2	Melanosuchus niger	0.5	Crocodylus novaeguineae	-51
Crocodylus novaeguineae	-2.7	Crocodylus acutus	-0.9	Crocodylus moreletti	-122
Crocodylus mindorensis	-3.0	Osteolaemus tetraspis	-1.8	Crocodylus acutus	-153
Crocodylus palustris	-3.5	Crocodylus intermedius	-2.2	Crocodylus siamensis	-245
Crocodylus acutus	-6.8	Crocodylus siamensis	-2.5	Crocodylus rhombifer	-292
Crocodylus moreletti	-9.3	Crocodylus rhombifer	-3.3	Crocodylus cataphractus	-434
Crocodylus johnsoni	-11.8	Crocodylus mindorensis	-3.6	Alligator mississippiensis	-438
Crocodylus porosus	-12.4	Crocodylus palustris	-7.5	Crocodylus mindorensis	-522
Alligator sinensis	-15.1	Gavialis gangeticus	-10.0	Crocodylus intermedius	-638
Crocodylus niloticus	-19.9	Tomistoma schlegelii	-11.2	Tomistoma schlegelii	-740
Alligator mississippiensis	-24.0	Crocodylus johnsoni	-11.2	Crocodylus palustris	-953
Crocodylus intermedius	-25.4	Crocodylus cataphractus	-11.4	Crocodylus johnsoni	-1284

TABLE 6.—Mean female size, egg mass, clutch size, and clutch mass as a function of family, habitat type, nest mode, and snout width (±SD). Corrected values have been adjusted by ANCOVA for differences in mean female TL between the compared groups. Significant differences among the mean uncorrected categorical variable are denoted by asterisks (* $P < 0.05$; ** $P < 0.01$).

	Family		
	Alligatoridae	Crocodylidae	Gavialidae
Female TL (cm)			
Mean**	170.7 (±61.0)	231.7 (±49.3)	341.0
Egg mass (g)			
Mean*	77.6 (±30.6)	100.2 (±25.4)	161.4
Corrected	96.7	94.3	110.7
Clutch size			
Mean	26.5 (±9.8)	28.7 (±11.3)	38.9
Corrected	34.3	26.3	18.2
Clutch mass (g)			
Mean	2216 (±1659)	2995 (±1473)	6278
Corrected	3463	2608	2962

	Nest mode	
	Hole	Mound
Female TL (cm)		
Mean*	267.8 (±53.2)	198.3 (±58.9)
Egg mass (g)		
Mean	110.2 (±29.6)	90.4 (±31.4)
Corrected	86.5	99.3
Clutch size		
Mean	33.0 (±12.8)	26.8 (±9.7)
Corrected	26.0	29.4
Clutch mass (g)		
Mean	3830 (±1950)	2546 (±1491)
Corrected	2519	3038

	Snout width		
	Broad	Intermediate	Narrow
Female TL (cm)			
Mean	182.9 (±57.0)	247.7 (±43.3)	266.5 (±69.2)
Egg mass (g)			
Mean*	83.3 (±26.1)	101.2 (±14.6)	129.3 (±40.7)
Corrected	98.3	90.4	110.9
Clutch size			
Mean	25.1 (±9.3)	35.3 (±10.8)	25.7 (±11.9)
Corrected	31.1	30.9	18.3.
Clutch mass (g)			
Mean	2233 (±1420)	3673 (±1416)	3610 (±2305)
Corrected	3232	2947	2383

species of *Caiman* laid large numbers of average-sized eggs (Fig. 3, Table 8).

The speciose genus *Crocodylus* exhibited a variety of reproductive patterns. Six of 12 species (plus *Osteolaemus tetraspis*) laid average numbers of average-sized eggs (Table 8). Two species (*Crocodylus palus-*

tris and *C. johnsoni*) produced small clutches of average-sized eggs. One species laid average numbers of small eggs (*C. intermedius*), and *C. cataphractus* represented the extreme extension toward the small-clutch, large-egg end of the spectrum. *Crocodylus niloticus* followed the

TABLE 7.—Statistics and probability values from analyses of variance of geometric mean residuals of egg mass, clutch size, and clutch mass, testing for differences in among family, nest mode, and snout width. All species were included.

Variable	Egg mass	Clutch size	Clutch mass
Family	$F_{2,19} = 0.50$	$F_{2,19} = 5.04$	$F_{2,19} = 4.93$
	$P = 0.62$	$P = 0.02*$	$P = 0.02*$
Nest mode	$F_{1,20} = 3.80$	$F_{1,20} = 2.47$	$F_{1,20} = 3.17$
	$P = 0.07$	$P = 0.13$	$P = 0.09$
Snout width	$F_{2,19} = 2.50$	$F_{2,18} = 10.05$	$F_{2,18} = 2.43$
	$P = 0.11$	$P < 0.01**$	$P = 0.11$

pattern for *Alligator* of large numbers of small eggs, and *Crocodylus porosus* followed the pattern for *Caiman* of large clutches of average-sized eggs. *Gavialis gangeticus* was grouped very closely with *Tomistoma schlegelii*, with both producing small numbers of average-sized eggs (Table 8). No crocodilians were found in the highest (large number of large eggs) or lowest (small number of small eggs) reproductive effort categories.

Most crocodilians are mound nesters (16 of 22 species: Table 1); however, on average, hole nesting species were larger ($F_{1,20}$ = 6.38, $P = 0.02$: Table 6). No significant differences in nest modes were found in mean egg mass, whether uncorrected (ANOVA; $F_{1,20} = 1.78$, $P > 0.05$) or corrected for female size (Table 7), although the latter approached significance ($P = 0.07$). The same was true for clutch size (Table 7, Fig. 4).

Mean egg mass was smallest in broad-snouted species and greatest in narrow-snouted species (ANOVA; $F_{2,18} = 4.45$, $P < 0.05$), but when corrected for differences in female TL, these differences disappeared (Fig. 4, Table 7). Mean uncorrected clutch size was unaffected by snout width (ANOVA; $F_{2,18} = 2.21$, $P > 0.05$), but when corrected for female body size (Table 7), longirostrine species laid significantly smaller clutches than other crocodilians (Fig. 4, Table 6).

In order to examine the effects of nest mode and snout width on crocodilian reproductive characteristics without the confounding influence of phylogeny, I repeated these ANCOVA analyses within the genus *Crocodylus*. The results were similar to those obtained for the entire order (Ta-

ble 9), with the effect of snout width on clutch size being the only significant factor.

Clutch mass.—When differences in female body size were statistically removed by using residual values in the analyses of variance, the alligatorids produced significantly larger clutch masses than the crocodylids or *Gavialis* (Table 7). I arbitrarily classified species' clutch mass as large, average (±500 g of the expected value), or small (Table 5). Within the Alligatoridae, *Melanosuchus*, *Paleosuchus*, and *Caiman* produced large relative clutch masses. *Alligator* had average values of relative clutch mass. Within the genus *Crocodylus*, relative clutch mass was largest in *C. porosus* and *C. niloticus*; small in *C. mindorensis*, *C. intermedius*, *C. palustris*, and *Tomistoma schlegelii*; and extremely small in *C. johnsoni* (Table 5).

Mean clutch mass was not affected by snout width (Tables 6, 7). Although Fig. 4 suggests a tendency for hole nesters to have smaller reproductive outputs, this difference was not significant (Table 7). These findings suggested that the observed phylogenetic differences in clutch mass (large in Alligatoridae, small in Crocodylidae) are not simply a reflection of differences in nest mode. This inference was supported by the analysis of relative clutch mass for hole versus mound nesters within the genus *Crocodylus* (Table 9).

Reproductive Frequency

The majority of the data on crocodilian reproductive frequency represents single-season data points determined using a number of different methods (Table 10). Nevertheless, reproductive frequency of

TABLE 8.—Classification of the Crocodylia according to relative size of eggs and clutches. Average values were arbitrarily defined as ±15 g (egg mass) and ±5 (clutch size) of the expected values (see Table 5).

Clutch	Egg mass		
	Small	Average	Large
Large	*Alligator mississippiensis*, *Alligator sinensis*, *Crocodylus porosus*	*Caiman crocodilus* *Caiman latirostris*, *Crocodylus niloticus*	None
Average	*Crocodylus intermedius*, *Crocodylus moreletii*, *Crocodylus mindorensis*, *Osteolaemus tetraspis*	*Crocodylus novaeguineae*, *Paleosuchus trigonatus*, *Melanosuchus niger* *Crocodylus acutus*, *Crocodylus rhombifer*, *Crocodylus siamensis*	*Paleosuchus palpebrosus*
Small	None	*Crocodylus palustris*, *Gavialis gangeticus* *Crocodylus johnsoni*, *Tomistoma schlegelii*	*Crocodylus cataphractus*

TABLE 9.—Statistics and probability values from analyses of variance of geometric mean residuals of egg mass, clutch size, and clutch mass, testing for differences among nest mode and snout width. Genus *Crocodylus* only.

	Egg mass	Clutch size	Clutch mass
Nest mode	$F_{1,10} = 3.66$ $P = 0.08$	$F_{1,10} = 0.25$ $P = 0.63$	$F_{1,10} = 1.31$ $P = 0.28$
Snout width	$F_{2,9} = 1.95$ $P = 0.20$	$F_{2,9} = 4.57$ $P = 0.04*$	$F_{2,9} = 2.07$ $P = 0.18$

the alligatorids ($\bar{x} = 40.9\%$ per annum) was significantly smaller than for the crocodylids ($\bar{x} = 78.3\%$) (Mann-Whitney U test, $Z = -2.12$, $P = 0.03$). However, because all the crocodylids for which data were available were hole nesting species, and all alligatorids are mound nesters, this may also reflect nest mode related differences. I tested for differences in mean annual clutch mass (residual clutch mass × mean annual reproductive frequency) between the Alligatoridae and the Crocodylidae and found no significant difference (ANOVA; $F_{1,3} = 0.39$, $P = 0.58$). Mean annual clutch masses were Alligatoridae = 1823 (±59 g, $n = 2$) and Crocodylidae = 2260 (±49 g, $n = 4$).

DISCUSSION

Allometric Trends in Reproduction

Comparative studies of many groups of vertebrates have revealed how life-history characteristics of species may covary with body size (Blueweiss et al., 1978; Calder, 1984; Peters, 1983; Reiss, 1989). Adult female crocodilians are a good group for addressing the role of size in life-history variation, as they span a large size range from the relatively diminutive dwarf caiman (*Paleosuchus palpebrosus*; approximately 110 cm TL) to *Gavialis gangeticus*, *Tomistoma schlegelii*, and several species of *Crocodylus* that regularly exceed 3 m TL. Interspecific comparisons demonstrate a clear trend for larger females to lay larger eggs and to have larger clutches in terms of both number of eggs and total clutch mass. A similar relationship has been noted among turtles (Congdon and Gibbons, 1985; Elgar and Heaphy, 1989; Iver-

TABLE 10.—Reported population values of reproductive frequency among crocodilians.

Species	Reproductive frequency (%/year)	Location	Source[*]
Alligatoridae			
Alligator mississippiensis	68.1	Louisiana	A
	63	Louisiana	B
	29	Florida	C
	28	Louisiana	D
	25.3	Louisiana	E
	25	South Carolina	F
	<10	North Carolina	G
Caiman crocodilus	54.3	Venezuela	H
Paleosuchus trigonatus	<33	Brazil	I
Crocodylidae			
Crocodylus acutus	72	USA	J
	63.8	Haiti	K
Crocodylus johnsoni	90	Australia	L
Crocodylus intermedius	>80	Venezuela	M
Crocodylus niloticus	63	Zimbabwe	N
	87.6	Kenya	O

[*] Sources: A = Chabreck (1967); B = Joanen and McNease (1980); C = Jacobsen and Kushlan (1986); D = Taylor (1984); E = Taylor et al. (1991); F = Wilkinson (1984); G = Lance (1989); H = Thorbjarnarson (in press); I = Magnusson and Lima (1991); J = Mazzotti (1983); K = Thorbjarnarson (1988); L = Webb et al. (1983b); M = Thorbjarnarson and Hernández (1993); N = Hutton (1984); O = (Graham (1968).

son, 1992) and appears to be a general characteristic of vertebrates (Blueweiss et al., 1978; Peters, 1983).

Reiss (1989) predicted that the intra-specific scaling of relative parental investment increases with female body mass because larger females devote less energy to growth than do smaller individuals, and he supported this argument with information from isopods, aphids, and fish. However, data on lizards and one species of turtle suggest that relative reproductive output does not increase with age (Congdon et al., 1982). The question of whether relative reproductive expenditure changes during a female's reproductive lifetime has not been addressed with crocodilians, principally due to a lack of information on reproductive life span and on size- and age-specific fecundity. Theoretical arguments for the existence of an optimal egg (or neonate) size (Brockelman, 1975; Parker and Begon, 1986; Smith and Fretwell, 1974) predict that trade-offs between egg size and clutch size should occur, and that within a population no correlation between egg size and female size should exist. In some instances, egg size may be limited by physical factors such as the diameter of the pelvic canal (Congdon and Gibbons,

1987). Larger eggs produce larger hatchlings (Ferguson, 1985) and may increase neonatal survival by increasing competitive ability or by reducing predation (Congdon and Gibbons, 1985; Janzen, 1993). The data from the crocodilian literature do not support egg size optimality theory in the majority of cases (Table 4); the only study that provided unequivocal support was that of Thorbjarnarson (1994).

Although egg mass increases with female length at the interspecific level, it decreases relative to female mass. *Paleosuchus palpebrosus* produces eggs that average 1.18% of female mass, whereas the corresponding figure for *Gavialis gangeticus* is an order of magnitude smaller (0.11%). The result is that crocodilian neonates are all approximately the same size (20–30 cm TL, 30–100 g) even though adult female size varies greatly (100–350 cm TL, 6–150 kg). The allometric equations relating egg mass (EM) to female body mass (BM) among crocodilians [EM = $31.62(BM^{0.29})$], and for reptiles in general [EM = $0.41(BM^{0.42})$: Blueweiss et al., 1978], have smaller exponential values than the corresponding equations for birds [hatchling mass = $0.28(BM^{0.69})$] and mammals [neonate mass = $0.097(BM^{0.92})$: Blueweiss

et al., 1978; Peters, 1983]. These broad comparisons demonstrate that with increasing female size, birds and mammals increase neonate size to a much larger extent than do reptiles, which principally increase clutch size.

Because they are long-lived, iteroparous species, crocodilians may adjust short-term reproductive output in such a way that lifetime reproductive success is maximized, as has been suggested for turtles (Wilbur and Morin, 1988). Intraspecifically, female fecundity is manifested in two parameters: the frequency of reproduction and clutch size. In most cases, both variables increase with female body size, demonstrating a clear size-specific trend in fecundity. Crocodilians have nondeterminant growth, and females continue growing, albeit at a low rate, throughout their entire lives. Consequently, older females, by virtue of their larger size, are more fecund than younger ones. The effect of this fixed-sequence increase in fecundity may have important ramifications for life-history strategy (Philippi and Seger, 1989). For most species, egg (and offspring) size also increases with female size. If one makes the assumption that larger offspring experience lower rates of mortality (Janzen, 1993; Roff, 1992), then older, larger females of these species (e.g., *C. niloticus* and *C. intermedius*) not only are more fecund than smaller animals but potentially produce more fit offspring. However, this situation is complicated by the fact that a number of other fitness characteristics of juvenile crocodilians are defined by environmental conditions during incubation, especially temperature (Webb and Cooper-Preston, 1989), and this could potentially alter the nature of the relationship between offspring size and fitness. Nevertheless, it is clear that allometric trends in fecundity and offspring size need to be explicitly incorporated into discussions of the evolution of life-history strategies of long-lived species with indeterminate growth.

Ecological and Phylogenetic Correlates of Reproduction

Crocodilians have long been tacitly considered as a relatively homogeneous group in terms of life-history strategy, and little attention has been paid to variation in reproductive parameters within the order. Yet this variability does exist. For instance, it is interesting to note that *Osteolaemus tetraspis,* despite its morphological convergence with *Paleosuchus* (Magnusson, 1989) and its apparent preference for similar habitats, has a much smaller relative clutch mass. My examination of reproductive trends within the Crocodylia centered on two areas: the relationship between egg size and clutch size, and reproductive output. Given that females have finite energy that can be invested in reproduction, a trade-off between the number and size of offspring that can be produced would be expected (Congdon et al., 1982). Larger young presumably have an advantage in terms of survivorship (Janzen, 1993), but this comes at the cost of the female's fecundity (Sinervo, 1990). However, my analysis at the interspecific level failed to find a significant trade-off between values of egg mass and clutch size corrected for female size. In this respect, it may be significant that many unique or unusual (among reptiles) costs associated with crocodilian reproduction (e.g., nest defense, nest opening, protection of hatchlings) may alter the form of the relationship between egg mass and clutch size.

Analyses of the ecological and phylogenetic correlates of reproduction were hampered by the high degree of covariance of these attributes within the Crocodylia. Among crocodilians, nest mode, snout width, and phylogeny are all interrelated. For instance, all alligatorids are mound nesters. However, mound nesting is the dominant mode of crocodilian reproduction, and the few hole nesting species mainly inhabit seasonal habitats of rivers or lakes (Campbell, 1972). Hence, the mode of nesting of individual species may be constrained by phylogeny or may represent an adaptation to environmental conditions. Snout width is clearly related to phylogeny and may covary with preferred habitat type as well.

Although crocodilians expend considerable energy in parental care (Shine, 1988), I considered clutch mass to be a useful measure of overall reproductive

output by females. Interestingly, phylogeny was a significant factor in classifying both clutch size and clutch mass within the Crocodylia, with the Alligatoridae producing larger clutches than the Crocodylidae. However, the reproductive frequency of alligatorids was lower, and no significant differences in annual clutch mass were evident. These broad comparisons suggest that alligatorid reproduction is geared more toward the less frequent production of large clutches. Crocodylids, on the other hand, produce smaller clutches but at more frequent intervals.

The following example illustrates how different reproductive strategies can lead to similar levels of reproductive output and to the importance of information on reproductive frequency. *Caiman crocodilus* in the llanos of Venezuela (Thorbjarnarson, 1994), and *Crocodylus johnsoni* in northern Australia (Webb et al., 1983*b*) have very different reproductive strategies. Both species are similar in size (mean female length: *C. crocodilus* = 143 cm; *C. johnsoni* = 188 cm) and inhabit areas that undergo drastic seasonal reductions in the amount of wetland habitat, but *Caiman* produces an average clutch mass of 1600 g and individuals of *Crocodylus johnsoni* lay small clutches averaging 850 g. However, the estimated reproductive frequency for *C. johnsoni* is 90% whereas for *Caiman* it is much lower (54.3%). *Caiman* produces heavier clutches, but fewer females nest in any one year. Nevertheless, the mean annual output of both species (in mass of eggs per year) is approximately the same: *C. crocodilus* = 869 g/year; *C. johnsoni* = 765 g/year.

Although no significant relationship was noted between nest mode and clutch mass, the low probability values of the ANOVAs, given the limitations of the data set, may suggest a biologically significant trend for larger egg and clutch masses in mound nests. Much discussion has surrounded the ecological and phylogenetic significance of hole versus mound nesting species (Campbell, 1972; Greer, 1970, 1971; Ouboter and Nanhoe, 1987). Nest mode could potentially influence reproductive output via two mechanisms: the physical environment of the nest and frequency of nest predation.

The most apparent means by which clutch mass could be limited by the physical environment of the nest is by limitation of gas diffusion (Ackerman, 1980; Seymour, 1979; Seymour and Ackerman, 1980). Embryonic metabolism leads to hypercapnia and reduced oxygen availability in hole nests (Lutz and Dunbar-Cooper, 1984; Whitehead, 1987), but the few measurements on mound nests suggest good ventilation (Magnusson, 1982). Clearly, more work needs to be done on the gas exchange properties of mound versus hole nests before it can be determined if the physical environment of the nest influences clutch mass.

Alternatively, total clutch mass and breeding frequency may be influenced by rates of nest failure (e.g., predation, flooding). The larger clutch masses and less frequent breeding of mound nesters could theoretically reflect lower rates of nest failure and hence more predictable reproductive success. A similar situation has been suggested for temperate versus tropical turtles (Iverson, 1992; Wilbur and Morin, 1988). Mound nesting crocodilians tend to oviposit during periods of high water levels (Ouboter and Nanhoe, 1987), when nests are isolated and, presumably, more difficult to find. In contrast, the nesting habitat of hole nesters is frequently limited to specific areas with particular soil characteristics, and nests are frequently clumped (Cott, 1961; Webb et al., 1983*b*).

Aside from the fact that differences in general reproductive strategy were found between the two principal phylogenetic lineages, reproductive patterns differed among genera. Alligatorids that inhabit semi-temperate climates (*Alligator mississippiensis* and *A. sinensis*) were remarkable for their production of large clutches of small eggs. Given the low reported annual clutch frequencies for *A. mississippiensis*, these data suggest that the annual reproductive effort of *Alligator* may be among the lowest of all crocodilians. Tropical dwelling alligatorids were notable for their high reproductive output. It may be significant that *Paleosuchus*, which tends to inhabit relatively aseasonal habitats (when compared to some habitats regularly utilized by *Caiman*), achieves high

relative clutch mass by laying large eggs, and *Caiman* accomplishes the same by producing large clutches. However, the large relative clutch masses of these species do not necessarily imply a high reproductive output, as that parameter also depends on reproductive frequency. At this time, with few population data available for reproductive frequency of a tropical alligatorid (*Caiman crocodilus*: Thorbjarnarson, 1994; *Paleosuchus trigonatus*: Magnusson and Lima, 1991), this possibility cannot be realistically assessed. Nevertheless, the apparent trend within the Alligatoridae is for species that inhabit highly seasonal environments, either in terms of temperature (*Alligator*) or water availability (*Caiman*), to produce relatively large clutches.

Although it is difficult to assess adequately the preferred habitat type of many species of crocodilians, as they tend to be habitat generalists, it is interesting to note that many of the species of *Crocodylus* that inhabit highly seasonal habitats are hole nesters and have low clutch mass values (*C. palustris*, *C. intermedius*, and *C. johnsoni*). Of the five crocodilians in low reproductive output categories (average clutch and small eggs, or average eggs and small clutch), four are hole nesters in seasonal habitats (the three previously mentioned plus *Gavialis gangeticus*). This suggests that crocodilians in tropical, seasonal riverine or lacustrine environments tend to be hole nesters, have relatively low reproductive investment per nesting bout, and may compensate by having high reproductive frequencies. This latter point is supported by data from *Crocodylus johnsoni* (Webb et al., 1983*b*) and *C. intermedius* (Thorbjarnarson and Hernández, 1993). Although no data are available concerning wild populations of *C. palustris*, this is the only crocodilian known to lay regularly more than one clutch per year in captivity (Whitaker and Whitaker, 1984).

The unique reproductive strategy of *Crocodylus cataphractus* (small numbers of very large eggs) is difficult to assess as almost nothing is known about this species. Similarly, little is known about the ecology of *Tomistoma schlegelii*, which has a low relative clutch mass due to the production of a relatively small clutch. It would be convenient to dismiss these because of the lack of detailed studies if it were not for the fact that the relationship between snout width and clutch size was one of the strongest found in this study. The true narrow-snouted species (*Gavialis gangeticus*, *Tomistoma schlegelii*, *Crocodylus johnsoni*, and *C. cataphractus*) all produce relatively small clutches, yet there was no difference between the broad and intermediate snout-width groups. It is difficult to define this reproductive strategy in terms of a clutch size–egg mass trade-off because among this group only *C. cataphractus* has relatively large eggs, and these species span a broad range of preferred habitat types. These results suggest that there may be some inherent difference on the population ecology of narrow-snouted species that bears future investigation.

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