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Maximum Size of the Alligator (*Alligator mississippiensis*)

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ABSTRACT.—The longest male and female alligators (*Alligator mississippiensis*) measured in Florida during 1977–1993 were 426.9 cm and 309.9 cm total length. The heaviest male and female alligators weighed 473.1 and 129.3 kg. A predictive model for calculating total length from head length is presented. Estimated total lengths for three large alligators described in the literature were substantially shorter than reported lengths. The longest alligator for which a total length can be corroborated from skull measurements was 454 cm. We discuss the plausibility of past reports of exceptionally large alligators with respect to verified lengths of specimens, harvest pressure, growth patterns, and longevity.

Maximum size of crocodilians is relevant from both evolutionary and ecological perspectives, and upper asymptotic size is important when describing growth patterns (Nichols et al., 1976; Chabreck and Joanen, 1979; Andrews, 1982; Brisbin, 1990). Aside from theoretical and practical applications, the maximum length attained by crocodilians has intrigued scientists, naturalists, and lay-persons for centuries (Pope, 1960; Guggisberg, 1972). However, most older records are difficult to validate, as discovered by Minton and Minton (1973) when reviewing accounts of larger reptiles and by Cott (1961) and Graham and Beard (1972) in their attempts to verify reports of large Nile crocodiles (*Crocodylus niloticus*). Moreover, Greer (1974) demonstrated that "record" size estimates reported for saltwater crocodiles (*C. porosus*) greatly exceeded sizes estimated from skull lengths.

Conant and Collins (1991) considered the average maximum total length (TL) for adult male American alligators to be 502 cm with the record TL being a 584 cm specimen reported by McIlhenny (1935). McIlhenny (1935) also described three other exceptionally long alligators of 562.6, 556.3, and 525.8 cm taken in Louisiana during the late 1800s. To our knowledge, however, no tangible evidence was preserved, nor did McIlhenny provide supporting morphological measurements from those animals to aid in the confirmation of reported lengths.

Several other large alligators have been reported, although none has approached the largest specimen reported by McIlhenny. Neill (1971) provided detailed measurements of a 531 cm alligator killed at Lake Apopka, Florida in 1956. Guggisberg (1972) referred to a 490 cm stuffed specimen in an exhibit in New Orleans, but did not included any additional measurements. Allen and Neill (1952) described a captive, 457 cm alligator ("Big George") that was caught at Lake George, Florida, but provided no description of how the alligator was measured. Cory (1896) apparently measured a 427 cm specimen from the St. Johns River, Florida and referred to the skull of an alligator killed on the Sebastian River, Florida, purported to be "a trifle over 16 ft." (488 cm). Barbour (1933) described a 64.0 cm skull in the Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts which appears to be the same skull described by Cory. Kellogg (1929) reviewed several early records of large alligators but provided no supporting measurements. Few other published records are available for large alligators, perhaps because most candidates were discounted because they were substantially shorter than McIlhenny's account.

Managed harvests and the propensity for hunters to seek credit for capturing the longest alligator have provided the opportunity to accurately measure a large sample of alligators. The objectives of this review are to: (1) document recent records from alligators measured in Florida, (2) quantitatively describe the relationship between head length (HL) and TL for predicting TL from head measurements, and (3) evaluate the plausibility of past reports of exceptionally large alligators.

METHODS

We reviewed reported skin length and TL data from 72,670 alligators that were harvested in Florida during 1977–1994. Although we were unable to directly measure all harvested alligators, hunters alerted Florida Game and Fresh Water Fish Commission (FGFWFC) biologists when large specimens were killed, and official measurements (taken by a biologist with a steel rule and recorded immediately) were obtained. Total length was measured as a straight-line from the tip of the snout to the tip of the tail. Snout–vent length (SVL) was measured from the tip of the snout to the posterior margin of

TABLE 1. Vital statistics of the largest male and female *Alligator mississippiensis* officially measured in Florida during 1977–94 in descending order of total length (TL).

I.D.	TL (cm)	SVL (cm)	HL (cm)	WT (kg)	Sex	Date	Location	Source[a]	Official
89-7191	426.9		60.0	324.1	M	5 Jun 89	Apilachicola R.	N	S. Shea
89-4916	422.9	218.4	58.4	473.1	M	17 Apr 89	Orange Lk.	N	A. Woodward
83-3032	419.7	209.6		394.6	M	31 Mar 83	Lk. Dora	N	J. White
84-6716	416.6	226.0	55.9	317.5	M	25 Sep 84	Orange Lk.	H	A. Woodward
84-6839	408.9	215.9		294.8	M	13 Sep 84	Orange Lk.	H	A. Woodward
88-7667	406.4	213.4		349.3	M	12 Sep 88	Lk. Hancock	H	N. Wiley
88-8642	401.3	213.4		344.7	M	19 Sep 88	Lk. George	H	J. White
79-2934	381.0[b]	209.6		417.3	M	16 May 79	Lk. Jessup	N	J. White
81-0945	309.9	151.5			F	6 Oct 81	Lk. Smart	N	D. David
86-0738	304.8	157.5		115.7	F	5 Sep 86	Lk. George	H	J. White
88-8622	302.3	149.9		120.2	F	12 Sep 88	Lk. George	H	J. White
GFC40602	300.0	153.0	41.0		F	25 Jun 94	Lk. Apopka	R	A. Woodward
88-8574	299.7	157.5		111.1	F	9 Sep 88	Lk. George	H	J. White
GFC40650	299.0	150.0			F	25 Jun 94	Lk. Apopka	R	A. Woodward
GFC40604	298.0	155.5	41.0		F	26 Jun 94	Lk. Apopka	R	A. Woodward
85-8186	297.2	154.9		115.7	F	24 Sep 85	Orange Lk.	H	A. Woodward
88-8674	292.1	149.9		124.7	F	19 Sep 88	Lk. George	H	J. White
88-8667	289.6	147.3		129.3	F	12 Sep 88	Lk. George	H	J. White

[a] Obtained through: N = nuisance alligator harvest, H = managed hunts, R = research.
[b] Bobtailed.

the vent. Head length was measured from the tip of the snout to the posterior margin of the supraoccipital bone (Dodson, 1975). Weight (WT) was recorded with a spring scale or combination of spring scales hung parallel to each other and perpendicular to the long axis of the alligator. Although weighing scales were calibrated periodically, an error of up to 2% was possible due to variation in the performance and precision of scales. At least two of three length (TL, SVL, HL) measurements were obtained for all specimens. Our reported measurements may indicate more precision than actual because many were recorded in English units and converted to metric units.

We used measurements from 366 alligators ≥122 cm TL with complete tails, marked and released during 1987–1992 on lakes Apopka, Griffin, Jessup, Okeechobee, Orange, and Woodruff, to evaluate the relationship of HL to TL. Measurements from three large, male nuisance (threatening humans, pets, or livestock) alligators were added to the data set to enhance estimation of the allometry of larger alligators. Using ordinary least squares, the natural logarithm (log) of HL was regressed on log(TL). We regressed log(TL) on log(HL) to provide predictive models for estimating TL from HL. Initially, the model included terms for the effects of variables sex, area, and the sex × area interaction on the intercept and slope of the regression. Consistent with maintaining a hierarchial model, non-significant ($P > 0.10$) terms were removed so that the final model contained only significant terms. We tested the null hypothesis of slope = 1 within classifications defined by any significant sex, area, or sex × area effects to determine if the ratios of HL to TL changed with size of alligator. Homogeneity of variance was assessed by inspection of plots of internally studentized residuals vs predicted values. Normality was assessed using the Shapiro-Wilk statistic. We examined skulls in the Florida Museum of Natural History (FSM) collection and measured the TL and HL of a full museum mount of "Big George" (Allen and Neill, 1952). J. Rosado confirmed the HL of skull #34323 in the MCZ collection reported by Barbour (1933) and provided HL for other alligator skulls in that collection.

RESULTS

Recent Specimens.—The longest (TL) alligator measured in Florida since 1976 was a 426.9-cm male taken as a nuisance alligator from the Apalachicola River near Apalachicola, Franklin County, Florida (Table 1). The heaviest male alligator recorded (473.1 kg) was taken on Orange Lake (Table 1). The longest female alligator measured was 309.9 cm TL, and the heaviest weighed 129.3 kg (Table 1). Vital statistics of several other male and female specimens in excess of 400 cm and 289 cm are provided in Table 1.

Size-frequency distributions of alligators taken during the 1981–1990 experimental harvests on Lochloosa, Newnans, and Orange lakes (Fig. 1) suggest that the probability of capturing alligators larger than 427 cm is low, and very unlikely for an individual >457 cm. From a

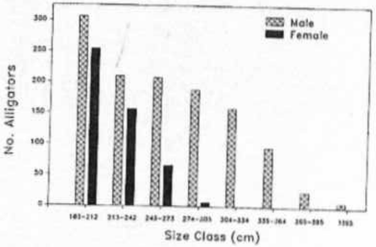

FIG. 1. Size distribution by sex of 1685 alligators ≥183 cm TL harvested during 1981–1990 on Lochloosa, Newnans, and Orange lakes, Florida.

population perspective, the size distribution of females relative to males (Fig. 1) indicates that females attain a substantially smaller maximum size than do males.

Allometric Relationships.—Residual plots in all regressions gave no indication of heterogeneity of variance, and the null hypothesis, H_0: residuals are normally distributed, was not rejected ($W = 0.988, P = 0.819$). Total length was strongly associated with HL for all sizes of alligators, but this relationship differed ($F_{2,362} = 5.172, P = 0.006$) by sex (Table 2, Fig. 2). The relationship between TL and HL did not differ ($F_{27,335} = 1.084$, $P = 0.357$) among areas. Head length was an excellent predictor of TL ($r^2 > 0.98$ for each sex) (Table 2). Head length was a constant proportion of TL for females but not for males (Table 2). The HL of a large male was a larger proportion of TL than the HL of a smaller male.

The final reduced model for log(TL) as a function of HL was parameterized as

$$\log(TL) = (\beta_0 + \delta\beta_1) + (\beta_2 + \delta\beta_3)\log(HL) + \epsilon \quad (1)$$

where

$$\delta = \begin{cases} 1 \text{ for females} \\ 0 \text{ for males} \end{cases}$$

and ϵ = experimental error, giving predicted log(TL) for each sex as

$$\log(TL) = 2.132494 + 0.95811(\log(HL))$$

for males

$$\log(TL) = 2.070667 + 0.98016(\log(HL))$$

for females

and the equation for the 95% confidence interval for log(TL) was

$$[2.132494 + 0.95811(\log(HL))] \pm 1.96\sqrt{0.0016496 - 0.000299(\log(HL)) + 0.0000447(\log(HL))^2}$$

for males

$$[2.070667 + 0.98016(\log(HL))] \pm 1.96\sqrt{0.0021933 - 0.000652(\log(HL)) + 0.0001019(\log(HL))^2}$$

for females.

Using the above model, the predicted TL for the 59.4 HL measurement reported by Neill (1971:265) was 422 cm (CI_{95}: 395,452) (Fig. 2). Thus, the upper limit of the confidence interval was 79 cm shorter than the reported TL of 531 cm. The predicted TL for the 64.0-cm HL measurement of the MCZ skull (#34323) reported by Cory (1896) and Barbour (1933) was 454 cm (CI_{95}: 424,485) (Fig. 2). The measured TL of "Big George" (413.0 cm) was somewhat larger than the predicted TL (402 cm) from the HL measurement (56.4 cm), but well within the 95% confidence interval (376,430). Both the measured and predicted lengths of Big George were ≥44 cm shorter than the 457-cm TL reported by Allen and Neill (1952).

DISCUSSION

The largest male alligators measured in Florida during 1977–1992 were substantially smaller than past reports (McIlhenny, 1935; Allen and Neill, 1952; Guggisberg, 1971; Neill, 1971) but were comparable to the longest officially

TABLE 2. Regression and test statistics for regressions conducted on head length (HL), total length (TL) and snout-vent length (SVL) for 385 alligators >120 cm TL captured on seven Florida wetlands during 1987–92.

Variables				Intercept		Slope			
Dependent	Independent	Sex	N	Estimate	SE	Estimate	SE	r^2	*P*-value for H_0: slope = 1
LOG_HL	LOG_TL	Male	175	−2.1750	0.03807	1.0342	0.00713	0.9909	<0.0001
		Female	191	−2.0169	0.05455	1.0019	0.01047	0.9820	0.8593
LOG_TL	LOG_HL	Male	175	2.1325	0.02246	0.9581	0.00669	0.9909	<0.0001
		Female	191	2.0707	0.03238	0.9802	0.01010	0.9820	0.0502

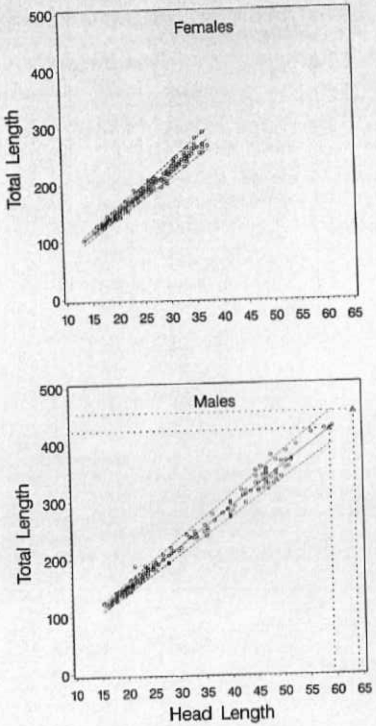

FIG. 2. Scatter plots of the relationship of total length to head length for male (N = 175) and female (N = 191) alligators measured in Florida during 1987–1992. The open triangles and small dashed lines represent the relationships between head length measurements of the Barbour (1933) and Neill (1971) skulls and estimated total lengths.

measured alligator [429.3 cm (14 ft. 1 in.)] in recent (1972–1992) hunts in Louisiana, from >250,000 measured alligators (T. Joanen, pers. comm.). The longest reported alligator harvested in annual hunts in Texas was a 416.6-cm specimen (Cooper et al., unpubl. data), and, in Georgia, the longest alligator measured was 411.5 cm (S. Ruckel, pers. comm.)

Total length of the longest female alligators in our sample were substantially larger than those reported in Louisiana (McIlhenney, 1935; Joanen et al., 1984) but similar to those documented in South Carolina (Wilkinson, unpubl. data). Large females in our sample were generally from eutrophic or hypereutrophic lakes which provide a rich nutritional base for growth.

The 64.0-cm skull reported by Barbour (1933) yielded the longest estimated TL [453.6 cm (14 ft. 10 in.)] for any specimen that we evaluated. The recounted TL (approx. 488 cm) by Cory (1896) was 35 cm greater than the estimated TL but only 3 cm greater than the upper limit of the confidence interval. The 59.4-cm skull reported by Neill (1971) yielded a TL estimate of 422 cm (13 ft. 10 in.), which was close to the largest specimens measured in recent years, but 109 cm short of his claim of 531 cm. "Big George" was estimated to be ≤413 cm (13 ft. 7 in.) which was ≥44 cm short of the 457-cm length asserted by Allen and Neill (1952). Thus, on the basis of the predictive relationship between TL and HL, we found our estimates of TL to be consistently shorter than TL reports of "record" alligators by naturalists.

McIlhenny (1935) speculated that exceptionally large alligators such as those he described were "... larger than normal, and were very old individuals, probably older and larger than alligators will ever again attain." Kellogg (1929) came to a similar conclusion about the perceived decreasing abundance of large alligators during the early 1900s. This contention is still widely held and is apparently based on the premise that skin hunting reduces survival of alligators substantially to preclude a significant number from attaining maximum longevity. Intertwined in this premise are several assumptions about past hunting intensity, and alligator growth and longevity.

Hunting Intensity.—We contend that for hunting to profoundly reduce the probability of alligators attaining maximum biological size, most populations of alligators would have to be easily accessible to hunters, hunting pressure would have to be constant and intense over extended periods, hunting pressure would have to be extremely high, and large alligators would have to be highly sought after and susceptible to hunting.

It is only within the last 50 years, with the advent of airboats and marsh buggies, that many marshes have been easily accessible to hunters. However, most wooded swamps continue to pose a barrier to boats of all types, making hunting of alligators in those habitats difficult. Since 1970, alligators have been protected on all state parks, national wildlife refuges, and national parks, except for the occasional removal of nuisance alligators. Thus, populations in many areas have been insulated from hunting for at least 25 years.

Harvest intensity has not been constant since the mid-1800s when commercial hunting be-

came widespread. Demand for alligator skins has fluctuated substantially over the last century, mainly due to shifting hide markets resulting from wars, fashion trends, and, most recently, trade laws (Kellogg, 1929; Allen and Neill, 1949; Kersey, 1976; Joanen and McNease, 1987). Consequently, even accessible alligator populations have experienced periods of minimal hunting intensity.

Hunting pressure on very large alligators subsided during the 1960s due to a shift in demand toward smaller skins (Hines 1979). Hunters maintain that the logistical problems involved with obtaining, skinning, preserving, hiding, and smuggling skins discouraged them from seeking larger (>300 cm) alligators during the 1960s. Furthermore, Webb and Messel (1979) and Woodward et al. (unpubl. data) found evidence that wariness of larger crocodilians increased with the size of the animal and with harassment, causing them to become more difficult to approach. The rapid appearance of >350-cm alligators during the early 1970s following protection (Palmisano et al., 1973; Hines and Woodward, 1980) further suggests that during the years of greatest persecution (1950–1970), large alligators were more common than observations indicated. Although evidence of past hunting intensity is fragmented and highly subjective, we believe that the available evidence suggests that there were adequate opportunities for a substantial proportion of alligators to grow with limited interference from hunting.

Growth Patterns.—Growth rate studies have shown that longitudinal growth slows considerably for male alligators >300 cm and females >200 cm (Chabreck and Joanen, 1979; Rootes et al., 1991; Woodward et al., unpubl. data; P. Wilkinson, unpubl. data). However, growth in mass may continue, possibly at the expense of longitudinal growth. It is likely that, at some point before alligators reach maximum age, maintenance costs exceed their ability to sustain growth and they stop growing (Brisbin, 1990). Recent growth studies in South Carolina (P. Wilkinson, pers. comm.) have shown that TL growth of male alligators >365 cm and female alligators >260 cm is virtually non-existent, thereby supporting this contention. Therefore, the limited evidence available suggests that growth in alligators is determinant.

Longevity.—The duration of exposure to hunting mortality can influence the probability of reaching maximum age. However, very little is known about longevity of wild alligators. Captive alligators can live as many as 57–70 yr (Honegger and Hunt, 1990; Ross, 1992; Snider and Bowler, 1992), although some have died of apparent old age at 34–40 yr (Kellogg, 1929). Under wild conditions, alligators are exposed to disease, fighting, and the debilitating effects of senescence (Comfort, 1979). Evidence is lacking that wild alligators can exceed 50 yr of age; therefore, a 40–50 yr maximum longevity seems reasonable.

It has been nearly 25 yr since alligators received effective protection against illegal hunting on a range-wide scale (Hines, 1979; Joanen and McNease, 1987). Based on longevity records and the occurrence of >350-cm alligators during the early 1970s, it is likely that a substantial contingent of alligators should have reached maximum size. The relative paucity of 425–430-cm specimens (Joanen and McNease, 1987; Woodward et al., unpubl. data) and lack of any larger specimens suggest that maximum growth is being attained for most individuals at lengths <430 cm.

Based on the data we reviewed and growth and aging patterns of alligators, we conclude that the probability that alligators exceed 457 cm (15 ft.) is extremely low. Whether *A. mississippiensis* >457 cm existed in recent times will remain a conundrum. Circumstances surrounding the measuring and recording of McIlhenny's "record" alligator and the lack of tangible evidence lend uncertainty as to its validity. Neill's (1971) detailed reporting of skull measurements and the preserved heads of Cory's (1896) and Allen and Neill's (1952) alligators help confirm the tendency of naturalists to exaggerate lengths. Similar disparities between reported lengths and TL predicted from HL measurements were found for saltwater crocodiles (Greer, 1974; Webb and Messel, 1978). In fact, Greer (1974) found that some TL predicted for *C. porosus* from skull measurements were as much as 3–4 m shorter than reported lengths. Webb and Messel (1978) cautioned against using extrapolation to estimate TL from HL because of the possibility of changing allometry. However, we found that the HL of longer male alligators was disproportionally longer than the HL of smaller specimens. Consequently, underestimation of TL from HL appeared more likely than overestimation.

The possibility of giantism or acromegaly (disorder of growth hormone regulation) does exist. However, we were unable to find a description of this condition for vertebrates other than humans. Acromegaly in humans is usually accompanied by disproportionally larger growth of the hands and jaw, enlargement of the heart, and hypertension, which usually compromises health and can ultimately reduce survival (Norris, 1985). Thus, we believe it is highly unlikely that giantism can produce the longest alligators.

Based on our investigation, HL is an excellent index of TL in alligators. Further, because skulls and heads tend to be retained as museum specimens or trophies, they provide a reliable basis for validating alligator lengths. We did not conduct a thorough survey of museum specimens, and skulls may exist that are larger than the specimens reported here. We hope that scientists, naturalists, and curators will be able to use our data as a reference point for comparing existing or future specimens. The scientific community should avoid accepting claims of enormous crocodilians with no supporting evidence. For purposes of general reference, the largest verifiable size of published alligator specimens was estimated as 454 cm. For modeling growth patterns, asymptotic TL of a population of male American alligators would be the mean size at natural death, which would be somewhat shorter than record lengths and probably in the 350–400 cm range (Woodward et al., unpubl. data.).

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Three New Species of *Eleutherodactylus* (Amphibia: Leptodactylidae) from Paramos of the Cordillera Occidental of Colombia

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Abstract.—*Eleutherodactylus lasalleorum* and *E. satagius* are described from a high elevation páramo (3700–3850 m) in the northern part of the Cordillera Occidental of western Colombia. The former may be allied with frogs of the *E. leptolophus* group and the latter is the northern member of the *E. curtipes* group. *Eleutherodactylus xestus* is described from Cerro Tatamá (4050 m); it is another member of the *E. curtipes* group.

Resumen.—Se describe *Eleutherodactylus lasalleorum* y *E. satagius* del páramo (3700–3859 m.s.n.m) de la parte norte de la Cordillera Occidental de Colombia. Parece que *E. lasalleorum* es una especies del grupo *E. leptolophus* y que *E. satagius* es el miembro del grupo *curtipes* que se encuentra más al norte. Se describe *Eleutherodactylus xestus* del Cerro Tatamá (4050 m.s.n.m.), otra especie del grupo *E. curtipes*.

In the past twenty years, many areas of the Colombian cordilleras have been explored in search of eleutherodactyline frogs. During the past decade, the previously unexplored cloud forests largely have been inventoried as a consequence of searching for centrolenid frogs. Although high elevation (above 3500 m) frogs are known for much of Colombia and Ecuador, the western Andean cordillera of Colombia has no reported species (Duellman, 1979) because their island-like páramos have been inaccessible. Forty years ago, Philip Hershkovitz climbed to the Páramo de Frontino and collected two small frogs (FMNH 69719–20) that were misidentified as *Eleutherodactylus vertebralis* (Boulenger) by Cochran and Goin (1970:432). These two frogs are adult females but are now badly faded.

During the 1980s, two Colombian colleagues secured six additional specimens of *Eleutherodactylus* from this isolated páramo including two more specimens of the species collected by Hershkovitz and four specimens of yet another species. Additionally, two other Colombian colleagues ascended Cerro Tatamá, at the border between Chocó, Risaralda, and Valle del Cauca. Their objectives were botanical and geographical but they obtained a single specimen of an *Eleutherodactylus* from 4050 m elevation. Because it is also a species of one of the highland groups and because it helps to define the biogeographic pattern of the *curtipes* group, it also is described below.

Materials and Methods

Measurements were taken to the nearest 0.1 mm using dial calipers under a dissecting microscope. Terminology follows Lynch and Duellman (1980). Observations of skeletal material were made by dissection or from a skull prepared as a cleared and doubly stained individual.

Eleutherodactylus lasallorum sp. nov.
Fig. 1

Holotype.—Colegio San José Museo de Historia Natural (CSJMHN) 2474, an adult female from the Páramo de Frontino, Municipio de Urrao, Departamento de Antioquia, Colombia, 3850 m, obtained 30 December 1989 by M. A. Serna, A. Gómez, and M. Peña.