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Testing Variation in the Relationship Between Cranial Morphology and Total Body Length in the American Alligator (*Alligator mississippiensis*)

Crocodilian populations are commonly monitored through the use of nighttime surveys where the size of individuals encountered is estimated by a visual estimate of head size and relating that measure to total body length (Chabreck 1966; Hutton 1987; Fukuda et al. 2013). This is done to determine size-class distribution and to provide information on size and age structure of target populations, which is a key component in the proper management of crocodilians (Verdade 2000). Magnusson (1983) suggested that a sample of animals should be captured and measured in order to establish relationships between estimates and animals' actual lengths and correct observer bias prior to conducting surveys (Verdade 2000).

Chabreck (1966) was the first to develop and use the method of estimating total length of American Alligators (*Alligator mississippiensis*) from estimating head size during nighttime population surveys. However, the data in which this method is based came from a relatively small (N = 54) sample of alligators from the same geographic locality (i.e., coastal Louisiana). Specifically for American Alligators, the consistency of these morphometric relationships across all alligator size classes and sexes has not been comprehensively tested.

Changes in morphology are common among crocodilians (Hall and Portier 1994; Tucker 1997; Platt et al. 2009). It is postulated that these changes result from selective pressures to strengthen the skull and increase gape size for capturing larger prey as individuals mature (Dodson 1975; Hall and Portier 1994; Platt et al. 2009). Changes among crocodilian morphology also reflect dietary shifts that are associated with energetic requirements for rapid growth (Hutton 1987; Tucker 1997; Platt et al. 2009) and dietary partitioning also may occur among size classes of American Alligators (Delany and Abercrombie 1986; Saalfeld et al. 2011).

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In this study, we examine the relationship between cranial measurements and body measurements among and between different size classes and sexes of American Alligators. The objectives of the study were to 1) determine if variation in body measurements can be explained by variation in head measurements, 2) determine if this relationship is constant across sizes and sexes of alligators, and 3) make recommendations relative to size estimation of alligators based on objectives 1 and 2. We hypothesize that relationships between total length and cranial measurements are not constant across all size and sex categories.

Materials and Methods

Alligators were captured at Brazos Bend State Park, a 1982-ha park in Fort Bend County, Texas, USA (Fig. 1). We captured alligators using field methods similar to Chabreck (1963),

Fig. 1. Map of Brazos Bend State Park in Fort Bend County, Texas, where alligators were captured during 2012–2013.

Chabreck and Joanen (1979), and Saalfeld et al. (2008), which encompassed a variety of methods including pole snares, hand capture, and swim-in live traps. Morphological measurements of total length (TL, cm; ventral tip of snout to tip of tail), eye-to-nare length (ENL, cm; length from nostrils to center of the frontal bone directly between the eyes), and total head length (THL, cm; dorsal tip of the snout to distal part of head scute) were collected and recorded as outlined by Saalfeld et al. (2008; Fig. 2). All length measurements were taken with a flexible tape measure. Sex of individuals ≥ 50 cm in length was determined by cloacal examination (Chabreck 1963). Sex of individuals <50 cm was not determined due to the difficulty of accurately assessing sex in first-year alligators (Saalfeld et al. 2008). Each captured individual was then uniquely marked using the marking techniques described by Eversole et al. (2014) to avoid duplication of measuring the same alligators. Alligators were subsequently released at the site of capture.

Statistical analysis.—We categorized alligators into the following size class categories based on TL: size class 1 = < 50 cm, size class 2 = 50.0–100 cm, size class 3 = 100.1–150 cm, size class 4 = 150.1–200 cm, and size class 5 = > 200.1 cm. The relationship between TL and head measurements was curvilinear; therefore, all analyses were performed on a log-log scale (commonly used in allometric studies). Measurements of total body length and head size are both random variables, and so model II regression would be appropriate to investigate these allometric relationships. However, a major goal in our study is to develop equations for managers to predict total body length of *A. mississippiensis* from head measurements. In this setting, therefore, it was appropriate to use model I regression to regress total body length on head measurements with the assumption that the conditional distributions of total body length for a given head size are normal and independent and head size measurements are independent with a distribution that is independent of the parameters of this regression (Rao 1965, Kutner et al. 2004, Smith 2009, Sokal and Rohlf 2012). We compared the equality of slopes among all size classes as well as between sexes within size classes 2 through 5 (Graybill 1976). The assumption of homogeneous variances of log(TL) within size classes across $\log_e$(ENL) or $\log_e$(THL) was assessed with the Breusch-Pagan test; variances were homogeneous on a log-log scale. Homogeneity of error variances among sizes classes was assessed with Bartlett's test—for both analyses, errors variances were heterogeneous; thus, tests of homogeneity of slopes among size classes, and between sexes for size classes 2–5, were analyzed with a linear mixed model that accommodated heterogeneous variances (Littell et al. 2006, SAS 2011). We considered results significant if $P \leq 0.05$. When testing for differences between male and female models, alligators of unknown sex were excluded.

RESULTS

For analyses of total head length, 319 alligators were used (240 animals in size classes 2–5); for eye-to-nare length 324 animals were used (245 animals in size classes 2–5; Fig. 3). Individuals ranged from 25.0 cm to 365.3 cm TL.

TL as a function of THL or ENL

The relationship between $\log_e$(TL) and $\log_e$(THL) differed among all 5 size classes ($F_{4,104} = 4.39$, $P < 0.0026$); additionally, this relationship differed when alligators in size classes 2–5 were analyzed ($F_{3,111} = 3.98$, $P < 0.0098$) (Fig. 4). A model that included $\log_e$(THL), size class, and the interaction between $\log_e$(THL) and size class explained 98.2% of the variation in $\log_e$(TL). In general, increases in $\log_e$(TL) decreased with increasing size class. Expressed on the observed (i.e., linear) scale, total length changes $100(e^{(\hat{\beta}_1(\ln((100+p)/100)))}-1)$ percent for a p percent increase in total head length. Thus, for size class 1 total length increased 54% for a 50% increase in total head length, whereas for size classes 2 through 5, total length increased 48, 47, 44 and 40%, respectively, for a similar increase in total head length.

A similar model using $\log_e$(ENL), size class and their interaction explained 98% of the variation in log(TL). Although the relationship between $\log_e$(TL) and $\log_e$(ENL) differed ($F_{4,107} = 2.51$, $P = 0.0461$) when all size classes were analyzed, this

FIG. 2. Visual depiction of the morphological measurements of (a) eye-to-nare length (ENL), (b) total head length (THL), and (c) above water line length (AWLL) for alligators.

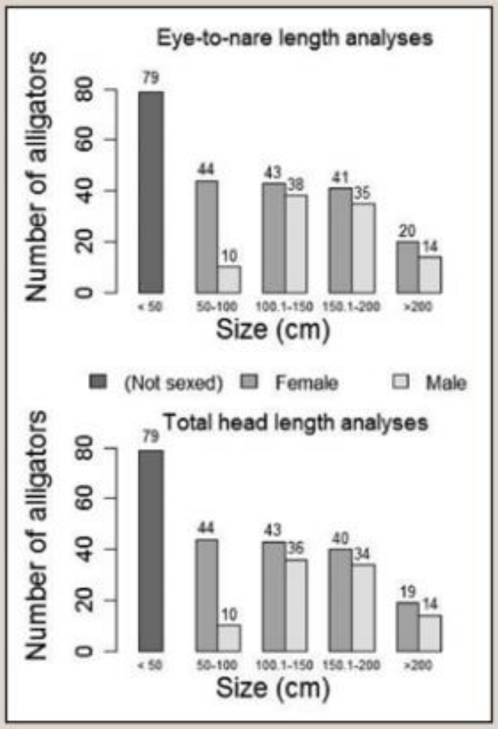

FIG. 3. Histogram highlighting the number of alligators of each sex and size class captured and measured for eye-to-nare length and total head length from Brazos Bend State Park, Texas, during 2012–2013.

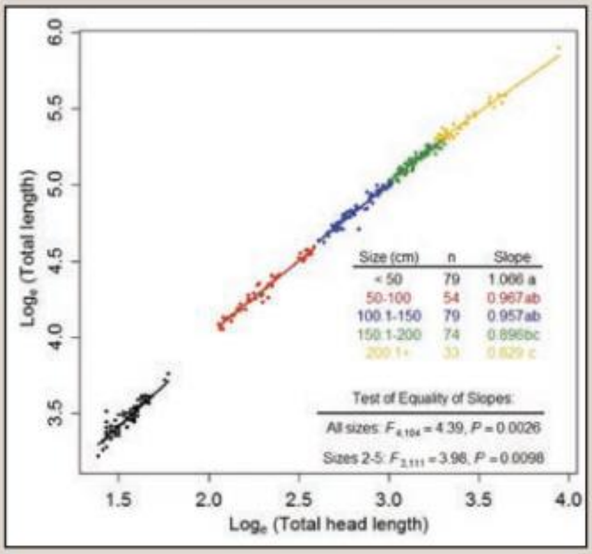

Fig. 4. Relationship between log$_e$(Total length) and log$_e$(Total head length) for N = 319 American Alligators in five size classes, with tests for equality of slopes among all five size classes and among size classes 2–5. Estimated slopes for each size class followed by the same letter are not significantly different ($P > 0.05$, protected pairwise tests).

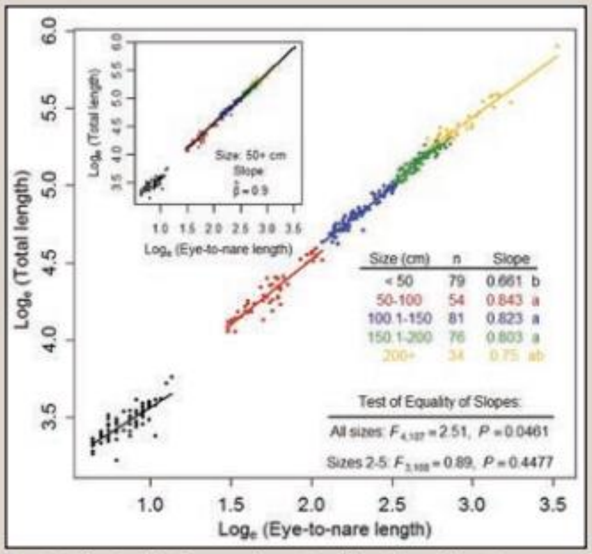

Fig. 5. Relationship between log$_e$(Total length) and log$_e$(Eye-to-nare length) for N = 324 American Alligators in five size classes, with tests for equality of slopes among all five size classes and among size classes 2–5. Estimated slopes for each size class followed by the same letter are not significantly different ($P > 0.05$, protected pairwise tests). Insert: estimated slope for size classes 2–5.

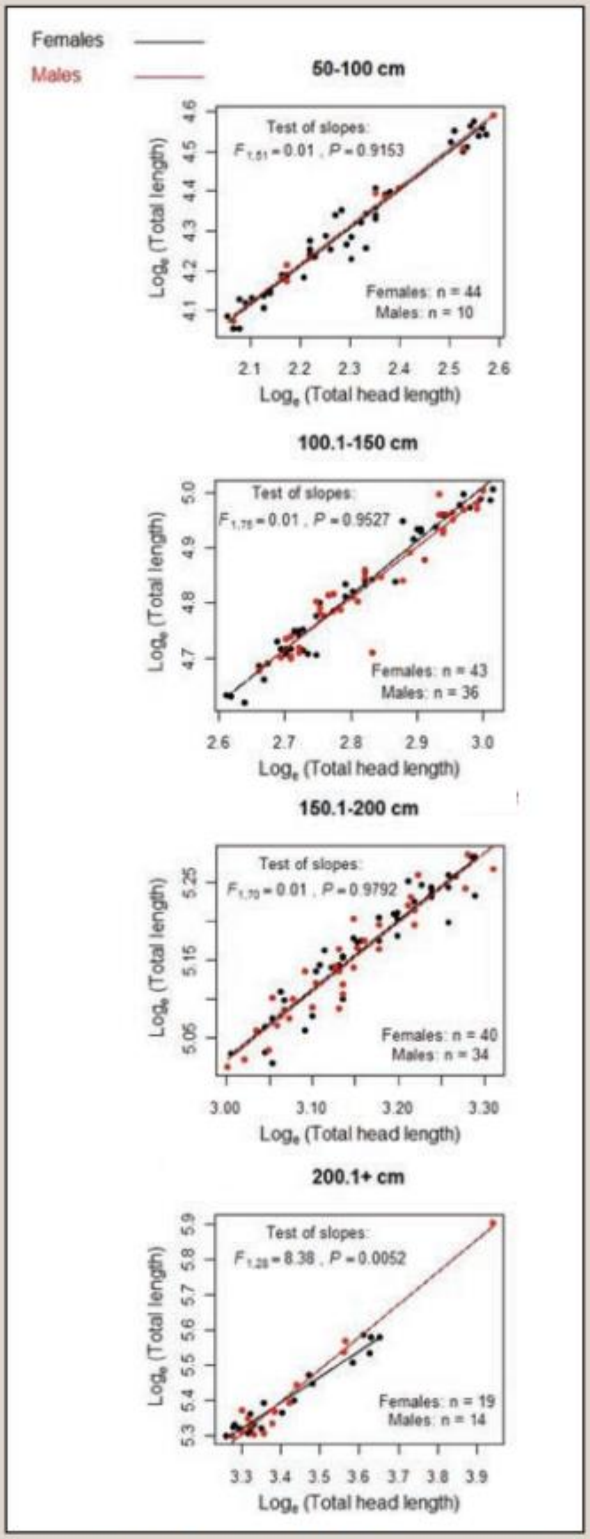

Fig. 6. The relationship between log$_e$(Total length) and log$_e$(Total head length) for male and female alligators for various size classes of alligators captured from Brazos Bend State Park during 2012–2013.

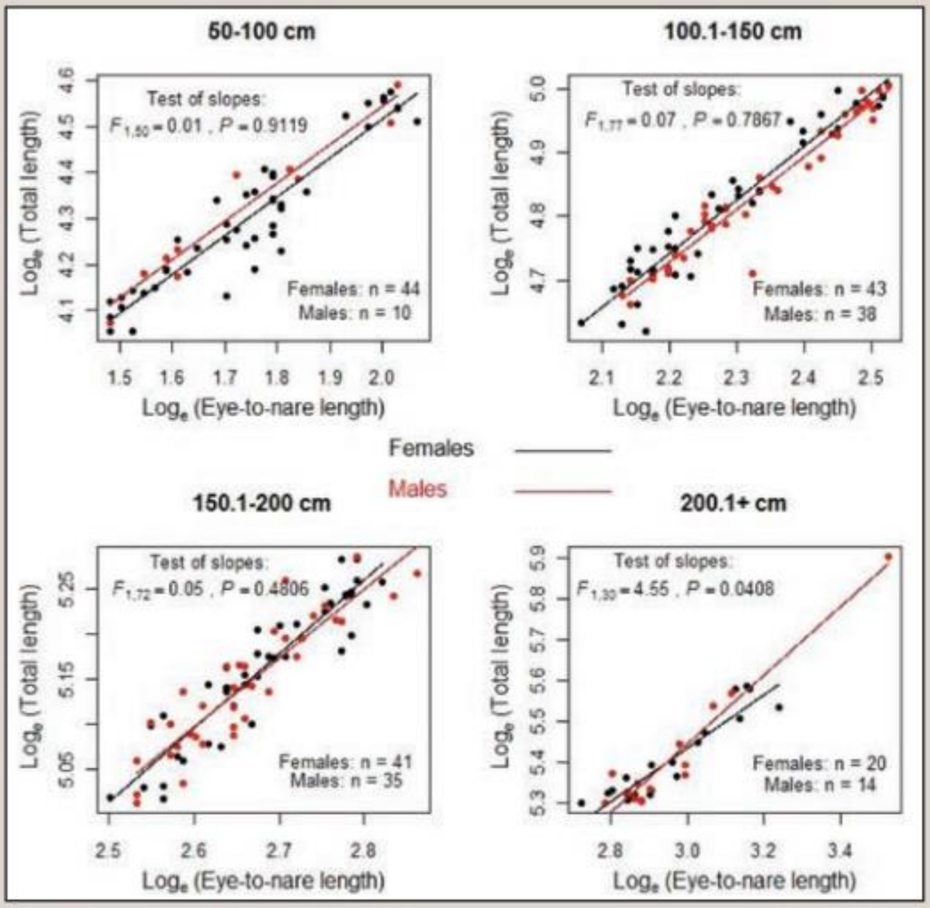

FIG. 7. The relationship between $\log_e$(Total length) and $\log_e$(Eye-to-nare length) for male and female alligators for various size classes of alligators captured from Brazos Bend State Park during 2012–2013.

relationship was stable ($F_{3,1108}$=0.89, P = 0.4477) across size classes 2 through 5 (Fig. 5). When regressed across size classes 2 through 5, the estimated slope was $\hat{\beta}_1 = 0.9$, so that total length increased 44% for a 50% increase in eye-to-nare length (Fig. 5, insert); for size class 1, total length increased 31% for a 50% increase in eye-to-nare length.

Differences between sexes

The relationship between $\log_e$(TL) and $\log_e$(THL) differed between sexes only for size class 5 (Fig. 6). TL increased 34% and 45% for a 50% increase in THL for females and males, respectively. Similarly, the relationship between $\log_e$(TL) and $\log_e$(ENL) differed between sexes only for size class 5 (Fig. 7): TL increased 30% and 40% for a 50% increase in THL for females and males, respectively.

DISCUSSION

Our results suggest a strong relationship between $\log_e$(TL) and $\log_e$(THL) and an almost-equally strong relationship between $\log_e$(TL) and $\log_e$(ENL). However, the former relationship depended on size class whereas the latter relationship was independent of size class when alligators exceeded 50 cm. The relationship between ENL and TL is likely not size dependent because the ratio of ENL to TL does not change as alligators increase in growth and progress from one size class to the next. However, the ratio of THL and TL is not constant across size classes (i.e., these morphological characteristics do not increase proportionately with increasing size).

Relationships between $\log_e$(TL) and $\log_e$(THL) and $\log_e$(ENL) were consistent for male and female alligators greater than 50 cm long and less than 200 cm in total length. For alligators > 200 cm in length, however, estimated total length increased more rapidly for males than for females whether predictions were based on $\log_e$(THL) or $\log_e$(ENL).

During nighttime surveys, sex is also unknown to observers. If ENL is utilized along with morphological characteristics (e.g., width, thickness, bulkiness, and general appearance of the individual; Fukuda et al. 2013) observers may be able to more accurately estimate TL of alligators between 50 and 200 cm without the added error of sex or size differences that we found to be associated with THL. Woodward et al. (1995) also found that TL was strongly associated with THL, but their study did not compare the relationship between and among size classes or the relationship of TL to ENL. Nevertheless, we do not suggest to reject Woodward et al. (1995) based on our findings, but to add our findings to the existing knowledge to alligator morphometrics. However, we do believe it is possible that an inexperienced person conducting alligator surveys could mistakenly estimate the above water line length of alligators (Fig. 2c) as the total head length (Fig. 2b), which would result in an overestimation in alligator total length. We believe that eye-to-nare length, which uses the frontal bone between the eyes and is the highest point on an alligator's head, is a visually easier reference point from a distance than is the distal part of the head scute, which is the end point to measure total head length. Therefore, using ENL may reduce potential variation in estimating alligator total length during nighttime surveys. In contrast, it has been found that predictive models derived from small specimens tend to underestimate the TL of larger Saltwater Crocodiles (*Crocodylus porosus*) (Montague 1983; Platt et al. 2006; Fukuda et al. 2013).

Our results of model comparisons between sexes differed from those of Woodward et al. (1995), which found substantial variation between males and females for the relationship between TL and THL. It should be noted that a direct comparison between our results and those of Woodward et al. (1995) may not be entirely appropriate because their study was based primarily on larger alligators (e.g., individuals > 183 cm TL). Longitudinal growth has been found to slow substantially at different lengths for males (> 300 cm) and females (> 200 cm) (Chabreck and Joanen 1979). The large sample of alligators at and above these sizes obtained by Woodward et al. (1995) may explain why they observed results differing from those of our analysis For instance, the differences observed between sexes in size class 5 may be the result of physiological changes and subsequent decrease in growth of females. This decrease in female growth may result in differing TL to THL and ENL ratios than that of males, which explains the model inequalities.

The results of this study are similar to that of previous studies that found substantial allometric relationships between body length and cranial morphology of crocodilians (Montague 1983; Hutton 1987; Verdade 2000; Platt et al. 2009). Our coefficients of determination (r^2) were considerably high, indicating that a significant amount of variation in TL can be attributed to variation in THL and ENL. Although experienced observers often estimate TL based on multiple physical attributes, such as THL, ENL, head width, head thickness, overall bulkiness, and general appearance of the individual (Fukuda et al. 2013), cranial attributes exhibit a formidable relationship with TL; therefore, the method of using cranial estimates to estimate TL of alligators during nighttime surveys should be considered a reliable field technique. Our results will be useful in the study of museum specimens, trophy mounts, or poaching incidents in which oftentimes only the head or skull is available and information on sex and size class may not be available.

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