
USING SCAT TO ESTIMATE BODY SIZE IN CROCODILIANS: CASE STUDIES OF THE SIAMESE CROCODILE AND AMERICAN ALLIGATOR WITH PRACTICAL APPLICATIONS

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Abstract.—Models relating morphological measures to body size are of great value in crocodilian research and management. Although scat morphometrics are widely used for estimating the body size of large mammals, these relationships have not been determined for any crocodilian. To this end, we collected scats from Siamese Crocodiles (*Crocodylus siamensis*) and American Alligators (*Alligator mississippiensis*) to determine if maximum scat diameter (MSD) could be used to predict total length (TL) in these species. We obtained scats from 19 and 22 *C. siamensis* and *A. mississippiensis*, respectively, and evaluated the relationship between MSD and TL using logarithmic regression models. We found significant positive relationships between MSD and TL for both species. We attribute this relationship to anatomical constraints imposed on MSD by pelvic aperture width, which in turn correlates to body size. We found the MSD-TL relationship is similar for *C. siamensis* and *A. mississippiensis*. Our models can be used to increase precision of body size estimates in scat-based population surveys and dietary studies, and estimate the body size of nesting females.

Key Words.—*Alligator mississippiensis*; Crocodylia; *Crocodylus siamensis*; dietary study; dung; feces; nesting; population survey

INTRODUCTION

Knowledge of individual body size and the size-class structure of populations is fundamental for crocodilian research, management, and conservation because size rather than age is the primary driver of demographic and reproductive processes (Webb and Smith 1987; Warner et al. 2016). Obtaining accurate data on body size is challenging and generally involves capturing and measuring wild crocodilians (e.g., Webb and Messel 1978; Montague 1984; Hutton 1987; Warner et al. 2016; Labarre et al. 2017). The ability to infer body size of crocodilians, however, particularly of rare and cryptic species, without having to capture them is advantageous to biologists because of logistics, budgetary constraints, safety, and animal welfare issues associated with capturing animals (Montague 1984; Platt et al. 2009;

Marcip-Rios et al. 2012). This is particularly true with regards to large adult crocodiles, which not only pose a safety hazard to investigators, but are prone to mortality from severe anoxic acidosis brought on by prolonged struggle during capture (Seymour et al. 1987). Given these concerns, predictive models that relate indirect morphological measures to body size are obviously useful in studies of crocodilians (Platt et al. 2009; Marcip-Rios et al. 2012). These models allow estimation of body size from skulls and other remains (Webb and Messel 1978; Thorbjarnarson and McIntosh 1987; Hall and Portier 1994; Woodward et al. 1995; Platt et al. 2006), calibrated photographs (Choquenot and Webb 1987; Stewart 1988), heads observed during nocturnal spotlight counts (Fukuda et al. 2013), harvested skins (Webb et al. 2012), and tracks (Singh and Bustard 1977; Platt et al. 1990; Thorbjarnarson and Hernandez 1993;

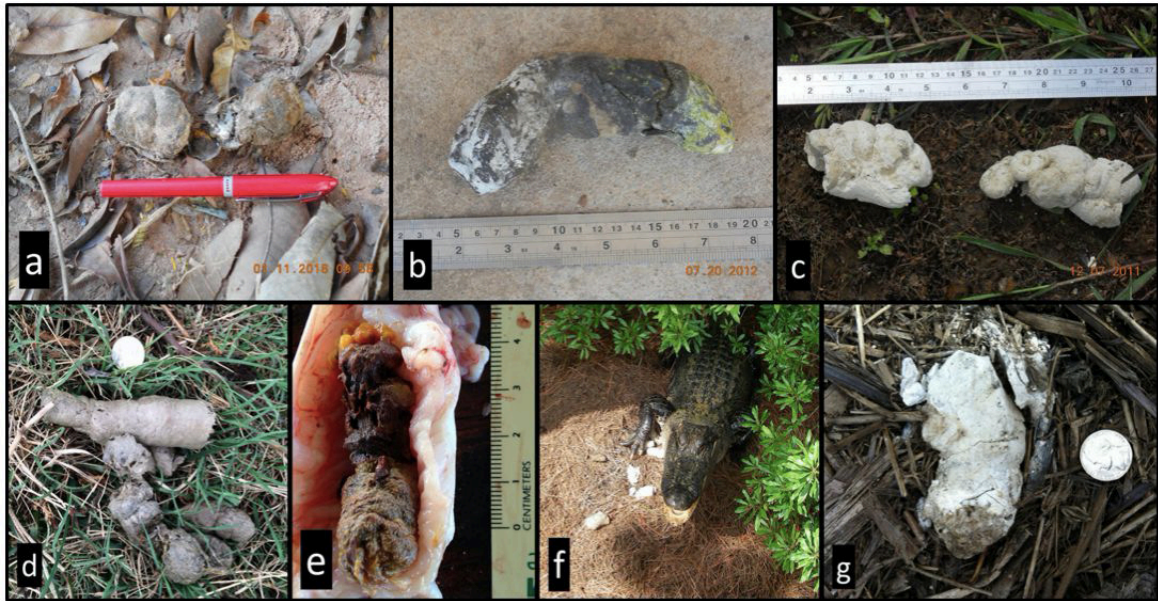


FIGURE 1. Crocodylian scat. (a–b) Fresh and (c) dried Siamese Crocodile (*Crocodylus siamensis*) scat photographed during population surveys of wetlands in Savannakhet Province, Laos. (d) Fresh American Alligator (*Alligator mississippiensis*) scat on a levee in coastal Louisiana, USA. (e) Distal end of the large intestine removed from an American Alligator with fully formed scat immediately prior to deposition. (f) Female American Alligator defending a nest; note dried scat (white) on top of nest mound. (g) Close-up of dried American Alligator scat on another nest mound. (a–c photographed by Steven G. Platt; d–e and g photographed by Ruth M. Elsey; f photographed by Matt Hamilton).

Swanepoel et al. 2000; Wilkinson and Rice 2000).

The use of scat (dung) morphometry as an indirect measure of body size in crocodylians has received surprisingly little attention from investigators. Crocodylian scat (Fig. 1) is distinctive in appearance (white-gray-brown solid organic matrix, fusiform with rounded terminus, and occasionally containing scales, feathers, and hair, but rarely bone), relatively easy to locate in the field, and can remain intact for months, and as such represents a potentially rich source of population data (Fisher 1981; Singh 2000; Bezuijen 2010; Milan and Hedegaard 2010; Brito et al. 2011). Simpson (2006) recommended using scat diameter to estimate individual body size of Siamese Crocodiles (*Crocodylus siamensis*) during population surveys but noted the relationship between scat diameter and body length had yet to be established. In lieu of predictive models, Bezuijen et al. (2013) used diameter measurements to assign individual scats to relatively broad size-classes (adults and juveniles) during population studies of *C. siamensis* in Lao, People’s Democratic Republic (PDR). Likewise, according to Singh (2000), the morphometry of intact scat can be used to determine the age-class (juvenile, young adult, large adult) of Mugger (*Crocodylus palustris*). Sam et al. (2015) distinguished individual crocodiles on the basis of scat diameter in combination with track length when estimating the size of small *C. siamensis* populations in Cambodia. Prasad et al. (2018) used the presence of scat and tracks to identify

occurrence hotspots when mapping the distribution of *C. palustris* at a wildlife sanctuary in India.

Scat morphometry is widely employed to estimate body size and age of elephants, ungulates, and primates (Coe and Carr 1983; Jachmann and Bell 1984; Putnam 1984; Reilly 2002; Morrison et al. 2005; Parnell 2006). For example, Jachmann and Bell (1984) determined the age-class structure of an African Elephant (*Loxodonta africana*) population in Malawi based on scat morphometrics, Reilly (2002) used measures of scat diameter to predict body size and age of Asian Elephants (*Elephas maximus sumatranus*) in Sumatra, and Parnell (2006) recommended using scat morphometrics to assess changes in the age-class structure of Lowland Gorilla (*Gorilla gorilla*) populations in central Africa. Although scat circumference was used in some studies of large mammals (e.g., Jachmann and Bell 1984), maximum scat diameter is easier to measure in the field and considered a more precise metric when related to body size (Reilly 2002; Morrison et al. 2005). Reilly (2002) suggested similar approaches might be useful for studying other species once the relationship between scat morphometry and body size has been determined.

An obvious first step towards successfully using scat morphometrics in field studies of crocodylians is to establish the relationship between scat morphometry and body size among this group. We present the results of a study to determine if a relationship exists between scat diameter and body size among a group of captive *C.*

siamensis, and both wild and captive American Alligators (*Alligator mississippiensis*). Our specific objectives were (1) to determine if scat diameter is related to total length [TL] in *C. siamensis* and *A. mississippiensis*, (2) present predictive models describing these relationships, and (3) determine if these relationships differ between the two species.

MATERIALS AND METHODS

Scats from *Crocodylus siamensis*.—We obtained scats from two groups of captive *C. siamensis* held at the Lao Zoo near Vientiane, Lao, PDR during 2011–2013. The first group (Group 1) consisted of 12 juvenile, subadult, and adult crocodiles (85–282 cm TL) selected from a large communal enclosure in December 2011. We measured each crocodile (see below), placed them in an individual pen, and provided them with food *ad libitum* on alternate days. We maintained crocodiles in these pens during January and February, and then returned them to the communal enclosure in early March 2012. In late April 2013, we selected a second group (Group 2) of 15 different crocodiles (92–257 cm TL) from the communal enclosure, which we measured, sequestered in individual pens, and fed *ad libitum* on alternate days. We held crocodiles from late April through July before returning them to the communal pen. The diet of both groups consisted of a mixture of freshwater fish, whole Domestic Chickens (*Gallus g. domesticus*), and occasionally rats (*Rattus* sp.) depending on availability.

Prior to being placed in individual pens, we determined TL (distance from the anterior tip of the snout to the posterior tip of the tail measured along the ventral surface) of each crocodile with a steel tape to the nearest 0.1 cm. We excluded crocodiles missing the distal portion of the tail (Webb and Messel 1978; Wilkinson et al. 2016) from our study. TL is a standard measure of body size and consistent with previous morphometric studies of crocodylians (e.g., Webb and Messel 1978; Platt et al. 2009, 2011; Wilkinson et al. 2016; Edwards et al. 2017).

We monitored individual crocodile pens at least once daily (usually before 1000) and recovered any scats present. We measured the maximum diameter of each scat (MSD) with a pair of dial calipers to nearest 0.1 mm. We excluded scats flattened or otherwise distorted by the crocodile after deposition (e.g., Milan and Hedegaard 2010) from our study. If multiple scats were deposited by the same crocodile during the penning period, we selected the scat with the greatest diameter for use in our analyses.

Scats from *Alligator mississippiensis*.—We collected scat from captive and wild *A. mississippiensis* during 2013–2018 at Rockefeller Wildlife Refuge (RWR),

a 28,700 ha protected area owned by the Louisiana Department of Wildlife and Fisheries in Cameron and Vermilion parishes, Louisiana, USA. Captive alligators ($n = 6$) we used in our study were neonates, juveniles, and subadults hatched from eggs collected on RWR, reared in controlled environmental chambers of varying size (Joanen and McNease 1976), housed in groups of three to 25 depending on body size and penning density, which we fed a commercial pelletized ration (1–2 times weekly). To collect scat, we transferred alligators to individual holding tanks and maintained them there until they defecated. We made daily inspections of holding tanks and removed and measured any scat present, after which we returned the alligators to the environmental chambers. In some cases, we captured wild alligators and temporarily maintained each in an individual pen until a fecal sample was produced, after which the animal was released ($n = 6$). We obtained additional scat from the lower gastrointestinal tract of wild alligators sacrificed for other studies ($n = 9$). We collected one scat sample from atop an alligator nest mound after capturing and measuring the attending female, and assumed this female deposited the scat.

We measured MSD with digital calipers and as with *C. siamensis*, distorted or flattened scats were not included in our analyses. Because composition of the diet can influence scat size and consistency (Weaver and Fritts 1979; Chame 2003), we acknowledge that using scats from both captive and wild *A. mississippiensis* could potentially bias our results, but considered this unavoidable owing to the difficulties of assembling a sufficiently large sample for analysis. Likewise, we recognize that differences in size and shape could exist between scats removed from the lower gastrointestinal tract and those recovered after defecation; however, any such differences were not readily obvious to us. We measured the TL of each alligator as described for *C. siamensis* and excluded alligators missing the distal portion of the tail from our study.

Data analyses.—We performed statistical analyses using R version 3.3.1 (R Development Core Team 2016). We tested the assumptions of normality (Shapiro-Wilk Test) and homoscedasticity (Levene's Test) for each species data set (Legendre and Legendre 2012). Our data were normally distributed and homoscedastic. The relationship between MSD and TL appeared curvilinear for both *C. siamensis* and *A. mississippiensis*, and the curvilinearity of these relationships could not be transformed to fit a simple linear regression. We therefore used a log-linear model of the form $Y = A + B(\log X) \pm \text{standard error (SE)}$ to determine the predictive relationship between MSD (in mm) and TL (in cm), and we treated MSD as the independent variable that we regressed against TL. Our selection of the log-

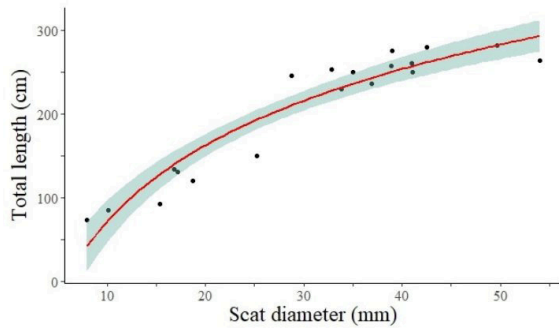


FIGURE 2. Bivariate plots showing total length (TL) as a function of maximum scat diameter (MSD) in the Siamese Crocodile (*Crocodylus siamensis*) where $TL = 131.58 + 70.98(\log MSD) \pm 23.73$ standard error. Shaded area represents 95% confidence interval.

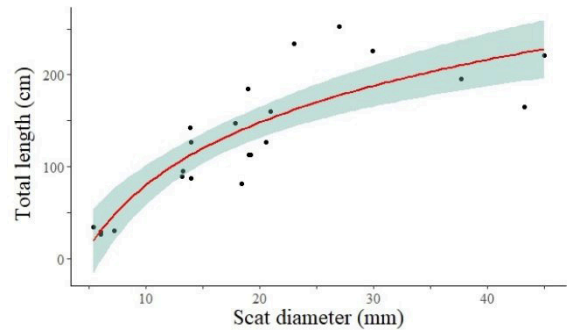


FIGURE 3. Bivariate plots showing total length (TL) as a function of maximum scat diameter (MSD) in the American Alligator (*Alligator mississippiensis*) where $TL = 98.46 + 79.90(\log MSD) \pm 36.44$ standard error. Shaded area represents 95% confidence interval.

linear model was based on comparisons of the adjusted r^2 and associated P -value. The standard error of the estimate is given by the square root of the residual mean square (Zar 2009). To determine if the relationship between MSD and TL differed between *C. siamensis* and *A. mississippiensis*, we compared the slopes of the regression lines for each species using an Analysis of Covariance (ANCOVA) with MSD as the covariate (Dytham 2003). We considered differences significant at $P \leq 0.05$.

RESULTS

We obtained one to three undamaged, measurable quality scats from 19 of 27 (70.3%) *C. siamensis* individually penned at the Lao Zoo. Fourteen crocodiles produced single scats, while two and three crocodiles each produced three and two scats, respectively. For crocodiles that produced multiple scats ($n = 5$), the intra-individual variability in scat diameter ranged from 0.01 to 0.10 of the MSD for that individual. The TL of crocodiles that produced scats ranged from 73 to 282 cm and MSD ranged from 8.0 to 54.0 mm. We found a significant positive relationship between MSD and TL ($F_{1,17} = 161.8, P < 0.001; r^2 = 0.90$) in *C. siamensis* (Fig. 2; Table 1). We obtained single, undamaged, and measurable quality scats from 22 *A. mississippiensis* ranging in TL from 26.5 to 252.7 cm at RWR. The MSD of our sample ranged from 5.4 to 45.0 mm. We found a significant positive relationship between MSD and TL ($F_{1,20} = 55.90, P < 0.001; r^2$

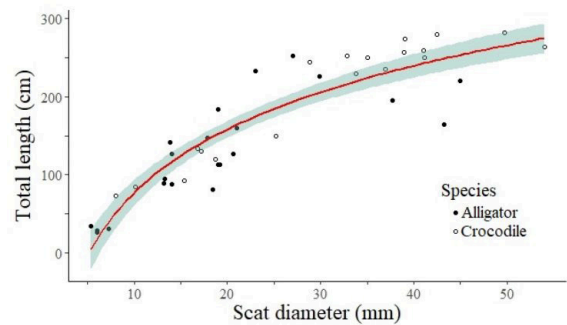


FIGURE 4. Bivariate plot showing total length (TL) as a function of maximum scat diameter (MSD) for the combined data sets of the Siamese Crocodile (*Crocodylus siamensis*) and the American Alligator (*Alligator mississippiensis*), where $TL = 117.32 + 76.86(\log MSD) \pm 32.93$ standard error. Dark circles = *Alligator mississippiensis*, open circles = *Crocodylus siamensis*, and shaded area represents 95% confidence interval.

$= 0.72$) in *A. mississippiensis* (Fig. 3; Table 1). Our comparison of the MSD-TL relationship between *C. siamensis* and *A. mississippiensis* found no significant interaction ($F_{1,37} = 3.500, P = 0.070$) between MSD and species. Because the effect of MSD on TL appears to be independent of species (i.e., the relationships for each species have similar slopes), we pooled the data from *C. siamensis* and *A. mississippiensis* and repeated our logarithmic regression analysis. We found a significant positive relationship ($F_{1,39} = 196.3, P < 0.001; r^2 = 0.83$) between MSD-TL in the combined (*C. siamensis* + *A. mississippiensis*) log-linear model (Fig. 4; Table 1).

TABLE 1. Logarithmic regression equations predicting Total Length (TL) from Maximum Scat Diameter (MSD) in Siamese Crocodile (*Crocodylus siamensis*), American Alligator (*Alligator mississippiensis*), and both species combined. Logarithmic regression equation of the form $TL = a + b(\log MSD) \pm$ standard error (SE). An asterisk (*) denotes $P < 0.001$.

	Intercept (a)	Slope (b)	\pm SE	r^2	F	n
<i>Crocodylus siamensis</i>	131.58	70.98	23.73	0.90	161.8*	19
<i>Alligator mississippiensis</i>	98.46	79.90	36.44	0.72	55.90*	22
<i>C. siamensis</i> + <i>A. mississippiensis</i>	117.32	76.86	32.93	0.83	196.3*	41

DISCUSSION

Our study demonstrates that a significant positive relationship exists between MSD and TL in *C. siamensis* and *A. mississippiensis*. As such, measurements of MSD can be used to reliably predict TL in *C. siamensis* and *A. mississippiensis* and probably other crocodylians as well. While previous workers have inferred the relative body size of crocodylians from scat morphometry (Singh 2000; Kanwatanakid-Savini et al. 2012; Bezuijen et al. 2013; Sam et al. 2015), our study is the first to confirm and quantify this relationship. The relationship between MSD and body size probably results from constraints imposed on scat diameter by the width of the pelvic aperture through which the large intestine passes en route to the cloaca (Richardson et al. 2002). The width of the pelvic aperture in turn allometrically scales to body size (Iverson and Hedrick 2018). Pelvic aperture diameter is also thought to constrain egg width in some crocodylians for the same reasons (Thorbjarnarson 1994; Larriera et al. 2004; Platt et al. 2008). In at least some species of turtles, this relationship appears to relax at larger body sizes (e.g., Rollinson and Brooks 2008), which may partly explain the curvilinearity of our data. Our results also indicate the slope of the MSD-TL relationship is similar for both *C. siamensis* and *A. mississippiensis*, possibly reflecting a more general underlying relationship among the Crocodylia.

Being able to reliably estimate the body size of crocodylians from MSD has several potential applications for research and management. First, our models can increase the precision of body size estimates in scat-based population surveys. Crocodile surveys typically rely on nocturnal spotlight counts to determine the relative abundance and demographic structure of populations (Bayliss 1987; Nichols 1987); however, spotlight counts are ineffectual or of limited use in some habitats (particularly densely vegetated wetlands and swift-flowing rocky rivers) and alternate methods such as track and/or scat surveys must be employed to assess populations (Simpson 2006; Kanwatanakid-Savini et al. 2012; Platt et al. 2014a; Sam et al. 2015). Scat surveys have been used to confirm occupancy (Thorbjarnarson et al. 2004; Sam et al. 2015; Whitaker 2015; Ouedraogo et al. 2016; Fellows 2019), determine encounter rates (Starr et al. 2010; Kanwatanakid-Savini et al. 2012; Sai et al. 2016), and broadly assign individuals to size- and age-classes (Bezuijen et al. 2013; Sam et al. 2015). Our models complement these approaches by allowing more precise estimates of body size, thereby providing greater insight into the size-class structure of difficult-to-survey populations, a critical consideration when evaluating the conservation status of rare and endangered crocodylians (e.g., Kanwatanakid-Savini et al. 2012; Platt et al. 2014a; Sai et al. 2016).

Scat-based population surveys are particularly well-suited for community conservation programs that rely on the participation of citizen-scientists with minimal formal training (Parnell 2006; Starr et al. 2010; Platt et al. 2014b). Scat surveys can be conducted throughout most of the year (except the wettest months); crocodile scat is conspicuous, easy to locate and unlikely to be misidentified, persists in the environment, can be collected and stored for extended periods (Simpson 2006; Platt et al. 2014a), and most importantly, scat diameter can be reliably measured by citizen-scientists in the field (Parnell 2006; Simpson 2006). This has been amply demonstrated by reports from Cambodia (Simpson 2006; Starr et al. 2010) and our experience in Lao, PDR (Platt et al. 2014b) where trained villagers participating in community conservation programs collect *C. siamensis* scats that are used to determine occupancy, monitor populations, and estimate the size of nesting female crocodiles (see below).

Our models can also be used to estimate the body size of nesting female crocodylians from scats deposited at the nest site. In crocodylians, fecundity and reproductive success are related to female body size (Ferguson 1985), which is therefore a metric of great interest to investigators (Thorbjarnarson and Hernandez 1993; Thorbjarnarson 1994; Platt et al. 2008). For a variety of reasons, determining the size of nesting female crocodylians can be challenging (Platt et al. 1990; Wilkinson and Rice 2000). Females may be absent or extremely wary when investigators are present at the nest (Platt et al. 1990; Wilkinson and Rice 2000), and moreover, capturing attending females at the nest can result in abandonment, thereby increasing the likelihood of nest loss to predators (Kushlan and Mazzotti 1989; Beauchamp et al. 2018). For reasons that remain unknown (but possibly related to pheromonal marking; see Liu 2013), however, female crocodylians frequently deposit scat at the nest (Hayes-Odom et al. 1993; Eversole et al. 2013; Liu 2013; Ferguson et al. 2016; Eversole and Henke 2018). If the assumption is made that scat found at a nest was deposited by the nesting female rather than another conspecific, diameter measures provide an indirect means to estimate body size without having to directly observe or capture the attending female.

Scat-based dietary studies offer another potential application for our models. Scat analyses are rarely used in studies of crocodylian diet (but see Casas-Andreu and Quiroz 2003; Simpson and Han 2004; Bezuijen 2010; Sam et al. 2015), in part because of biases associated with the differing digestibility of various prey types. Fish scales and chitinous (insects and crustaceans) and keratinous (feathers and mammal hair) remains are frequently recovered from scat samples, while readily digestible soft-bodied prey (anurans) and bones are

generally absent (Fisher 1981; Simpson and Han 2004; Bezuijen 2010). That said, differential digestion of prey types is a common source of bias in studies of crocodylian diet regardless of the method used to recover prey items (Jackson et al. 1974; Magnusson et al. 1987).

Scat analyses have been used for characterizing crocodylian diets (Simpson and Han 2004; Sam et al. 2015), although without a means to estimate the body size of individuals associated with particular scats, size-related dietary differences (e.g., Thorbjarnarson 1993; Tucker et al. 1996; Platt et al. 2006, 2013; Wallace and Leslie 2008) cannot be determined. Recognizing this limitation, previous workers have typically assigned scats to broad age-size classifications (juveniles or adults) based on diameter, with similarly broad categorization of the diet (Simpson and Han 2004; Bezuijen 2010). Our models can provide greater resolution to scat-based dietary studies by allowing more precise body size estimates to be assigned to individual scats, in turn making possible the detection of ontogenetic dietary trends, which are crucial for understanding the trophic ecology of crocodylians (Lang 1987; Grigg and Kirshner 2015). Bias associated with differing digestibility of prey can be minimized by analyzing differences within rather than among prey categories under the assumption that remains of different prey within any one prey category persist in the digestive tract for similar periods (Magnusson et al. 1987; Thorbjarnarson 1993; Platt et al. 2013).

In summary, our study demonstrates that a significant positive relationship between MSD and measures of TL exists in at least two species of crocodylians (*C. siamensis* and *A. mississippiensis*). Given the conservative body plan of the Crocodylia (Grigg and Kirshner 2015), we posit that this relationship likely applies to other members of the order. Research on other species is therefore warranted to develop species-specific predictive models for use in research and management.

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