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ORIGINAL PAPER

Morphometrics, sex ratio, sexual size dimorphism, biomass, and population size of the Nile crocodile (*Crocodylus niloticus*) at its southern range limit in KwaZulu-Natal, South Africa

Jonathan K. Warner[1,2] · **Xander Combrink**[1] · **Peter Calverley**[1] · **Garreth Champion**[1] · **Colleen T. Downs**[1]

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Abstract Animal body size and sex are requisite data for understanding population structure and demography. Little information exists regarding Nile crocodile, *Crocodylus niloticus*, morphometrics, sex ratios of wild populations, sexual size dimorphism and standing crop biomass. We captured 322 *C. niloticus* at Lake St Lucia and Ndumo Game Reserve, South Africa, the two largest crocodile populations at the southern extent of the species' range in Africa, and measured a suite of physical characteristics to create predictive models of body length from other morphological attributes and body mass. Our sample included 118 hatchlings, 91 subadults and 113 adults. Strong positive allometric relationships were found between body length metrics (total length and snout-vent length) and other morphometrics. All morphometric regressions were linear, with the exception of the relationship of body length to body mass, which was logarithmic. Among relationships of cranial morphology and body length, we found considerable individual variation among all size classes. The mean head width-to-head length ratio was 1.9 ± 1.6, and mean head length-to-total length ratio was 0.14 ± 0.005. The sex ratios for non-hatchling individuals at both populations were essentially 1:1, but adult sex ratios were male biased. We calculated a total standing crop biomass of 96,867.18 kg (161.45 kg/km) and 52,640.40 kg (1504.01 kg/km) for *C. niloticus* at Lake St Lucia and Ndumo Game Reserve, respectively, and an estimated 3650 non-hatchling individuals for the province of KwaZulu-Natal. The data presented here will help inform crocodile management and population surveys in South Africa, where *C. niloticus* is an important apex predator that partitions aquatic resources and occasionally comes into conflict with human beings.

Keywords Apex predator · Aquatic vertebrate · Crocodilian · Herpetology · Wetland

Introduction

Of the seven proposed crocodilian species in Africa (Shirley et al. 2014), the Nile crocodile, *Crocodylus niloticus* (Laurenti 1768), is the most iconic and widespread, ranging throughout sub-Saharan Africa to its continental southern range limit in subtropical KwaZulu-Natal, South Africa. As an apex predator, *C. niloticus* has extensive ecological influences on both aquatic and terrestrial food webs (Warner 2015). The species is also economically valuable in the commercial leather trade (Cott 1961; Blake and Jacobsen 1992). Despite the species' fearsome reputation, *C. niloticus* is still an understated human health concern in rural Africa where numerous communities share water resources with crocodiles, and fatalities likely number in the hundreds annually.

Crocodylus niloticus is currently under threat in South Africa and IUCN red-listed as Vulnerable (Marais 2014). In addition to traditional threats of habitat alteration and destruction (Leslie and Spotila 2001; Combrink et al. 2011) and poaching (Calverley and Downs 2014a), environmental pollution has emerged as an insidious new threat to *C. niloticus*, highlighted by the pansteatitis outbreak and resultant deaths of hundreds of crocodiles from the greater

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✉ Colleen T. Downs
downs@ukzn.ac.za

[1] School of Life Sciences, University of KwaZulu-Natal, P/Bag X01, Scottsville, Pietermaritzburg 3209, South Africa

[2] Present Address: Illinois Natural History Survey, Prairie Research Institute, University of Illinois, 1101 W. Peabody Dr., Urbana, IL 61801, USA

Olifants River watershed (Ferreira and Pienaar 2011; Lane et al. 2013).

In South Africa outside of the Kruger National Park, remaining viable crocodile populations are limited to northern KwaZulu-Natal Province, where the highest densities of *C. niloticus* occur in protected areas at Lake St Lucia within the UNESCO World Heritage iSimangaliso Wetland Park (Combrink 2014; Warner 2015), Ndumo Game Reserve (Calverley 2013) and at the Pongola River inlet at Pongolapoort (Jozini) Dam (Champion 2011; Summers 2015). Numerous smaller populations persist at the periphery of these areas, including uMkhuze Game Reserve, Tembe Elephant Reserve, Hluhluwe-iMfolozi Park, various waterbodies in greater iSimangaliso Wetland Park (Kosi Bay, Lake Sibaya, Lake Bhangazi North and South), and in the Enseleni, Zinkwazi and Tugela Rivers.

Knowledge of individual body size and sex is necessary data for analyses of animal population ecology and structure. Basic morphometric parameters (e.g., head shape, total length, mass) can help researchers answer complex questions about sexual size dimorphism (Shine 1986; Zamudio 1998), energetic constraints (Wikelski et al. 1997), hybridization (Brede et al. 2000), adaptation to different ecological niches (McMaster and Downs 2006; Ousterhout 2015), and the identification and conservation of cryptic species (Sanders et al. 2015; Davis et al. 2016). Conservation management of crocodilians in particular relies heavily on knowledge of individual body size and population size-class structure because size, rather than age, is the primary driver of demographic and reproductive processes (Webb and Smith 1987).

Despite a legacy of conservation-based research on the species (Cott 1961; Pooley 1982a, b; Leslie 1997; Champion 2011; Calverley 2013; Combrink 2014; Summers 2015; Warner 2015), with the exception of Hutton (1987a, b, c) scant published information exists regarding morphometrics of free-ranging *C. niloticus*, sex ratios of wild populations, and sexual size dimorphism. In this study, we present an analysis of these variables from data collected in field studies. Additionally, we estimate the current metapopulation size and standing crop biomass of *C. niloticus* at its African range limit in KwaZulu-Natal based on recent ecological and population studies. Our findings are presented in light of their significance to crocodile research and management in South Africa.

Materials and methods

We captured *C. niloticus* during 2009-13 at Lake St Lucia and Ndumo Game Reserve, KwaZulu-Natal, South Africa, in conjunction with crocodile population surveys (Champion 2011), and studies of habitat use (Calverley 2013), spatial ecology (Combrink 2014), ecotoxicology (Warner et al. 2016) and stable isotope ecology (Warner 2015). The Lake St Lucia estuarine system is 67 km in total length and contains a main lake basin (6 km wide at capacity) connected to the Indian Ocean via a 27-km-long "Narrows" channel. Lake St Lucia is a highly dynamic environment over space and time with cyclical, but often unpredictable annual fluctuations between drought and high rainfall (Stretch et al. 2013). Due to a decade-long drought, at the time of our sampling the estuary mouth was closed and significant sections of the lake were hypersaline or exposed due to evaporation, thereby rendering the surrounding freshwater pools and feeder streams important habitat for crocodiles (Combrink et al. 2013). The 10,000-ha Ndumo Game Reserve is located on the southern Mozambique border, with the Usuthu and Phongola Rivers forming the northern and eastern boundaries of the reserve, respectively. During the rainy season (Nov–Mar), up to 40 % of the reserve may be inundated, including 12 permanent and semi-permanent floodplain lakes that host large congregations of crocodiles (Calverley and Downs 2014b). Lake St Lucia and Ndumo Game Reserve represent the two largest *C. niloticus* populations in KwaZulu-Natal.

We captured crocodiles at night and during the day, usually by direct noosing or snagging with a barbless weighted treble hook attached to Kevlar rope or fishing line (Combrink et al. 2012). Hatchlings were captured by hand in nursery areas in late February, March and early April within 30 days of nest emergence. After individuals were safely restrained and tissue samples were taken, we recorded the following measurements:

1. Total length (TL): distance from the tip of the snout to the tip of the tail, measured dorsally.
2. Snout-vent length (SVL): distance from the tip of the snout to the posterior margin of the cloacal vent, measured dorsally.
3. Head width (HW): maximum distance between the surangular bones at the level of jaw articulation.
4. Head length (HL): maximum distance between the tip of the snout to the posterior edge of the supraoccipital bone.
5. Neck girth (NG): maximum circumference of the neck, measured between the base of the skull and front legs.
6. Front-leg body girth (FBG): circumference of the pectoral region, measured immediately posterior to the front legs.
7. Middle body girth (MBG): maximum circumference of the middle torso.
8. Hind-leg body girth (HBG): circumference of the pelvic region, measured immediately anterior to the hind legs.

9. Tail girth (TG): maximum circumference of the tail posterior to the hind legs.
10. Horizontal–ventral scale girth (HVG): tail circumference where the two rows of horizontal tail scutes transition into a single vertical scute row.
11. Body mass (BM).

Head length, TL and SVL are used as body length indicators in many crocodilian studies (Fukuda et al. 2013), whereas NG, FBG, MBG, HBG, TG and HVG are volumetric indicators of body condition (Zweig et al. 2004). The body measurements collected during this study are consistent with other crocodilian morphometric studies (Webb and Messel 1978; Montague 1984; Hutton 1987a; Hall and Portier 1994; Platt et al. 2009, 2011), and for comparative purposes with other species, we generally followed the statistical approach of Hutton (1987a) and Platt et al. (2009, 2011). Cranial morphometrics (HW, HL) were measured with tree calipers for adults (±1 mm) and digital calipers for hatchlings (±0.1 mm). All other body measurements were collected using a fiberglass measuring tape or plastic sewing tape (±1 mm). Non-hatchling crocodiles were weighed in the field with a digital crane scale (±0.1 kg) attached to an adjustable aluminum tripod. Individuals were first stabilized with towing bands and then hoisted with a block and tackle until they were suspended from the ground, allowing accurate mass to be recorded (Appendix of Fig. 6). The mass of the bands and d-ring attached to the scale were subtracted from the total mass. Hatchling crocodiles were weighed with an Ohaus digital scale (±0.1 g). Non-hatchling *C. niloticus* were sexed by manual probing of the cloacal cavity (Brazaitis 1968).

We used regression analysis to determine predictive relationships between morphometric data (HW, HL, NG, FBG, MBG, HBG, TG, HVG, BM) and body size (TL and SVL), with the former treated as independent variables. For comparison with other crocodilian species, we also regressed the ratio of HL/HW against SVL, and the ratio of HL/TL against TL to examine potential ontogenetic changes in cranial morphology and the consistency of the HL/TL ratio across size classes (Tucker et al. 1996; Platt et al. 2009, 2011).

Similar to other crocodilians, male *C. niloticus* attain greater body sizes than females (Cott 1961; Pooley 1982a; Hutton 1987b). To confirm this quantitatively, we used a *t* test to test the hypothesis that adult male SVL is significantly greater than adult female SVL (for free-ranging crocodiles in South Africa both sexes reach maturity at approximately 1400 mm SVL; Combrink 2014). We used a compressed sexual size dimorphism index (SDI) to quantify the degree of sexual size dimorphism between adult males and females (Lovich and Gibbons 1992; Platt et al. 2009, 2011). The SDI is a dimensionless number calculated by dividing the mean size of the larger sex by the mean size of the smaller sex and then adding one to this value if males are the larger sex, or subtracting one if females are larger (Lovich and Gibbons 1992). Although SDI can theoretically be based on any measurement or mass, we used SVL given its ubiquity in herpetological research and in keeping with previous crocodilian studies (Platt et al. 2009, 2011).

We estimated standing crop biomass (total mass of all individuals) for *C. niloticus* at Ndumo Game Reserve and Lake St Lucia by calculating the mean body mass for subadults and adults using the TL-BM regression equation, multiplied by the estimated number of individuals for each cohort for each population, and then summed to determine standing crop biomass (Thorbjarnarson 1988; Platt et al. 2009, 2011). The estimated number of individuals for each population was derived from spotlight and aerial survey data with correction factors (Calverley 2013; Combrink 2014). Biomass estimates for crocodilians are usually reported as kg/km of shoreline (Hutton 1987b; Thorbjarnarson 1988; Platt et al. 2009, 2011; Fukuda et al. 2011); we report biomass in both kg/km and kg/ha. Lake St Lucia is approximately 35,000 ha at mean lake level (Taylor 2006) with 600 km of shoreline observed during crocodile surveys (Combrink 2014). Shoreline length varies over time at the 10,117-ha Ndumo Game Reserve, as it is bordered by two meandering rivers and contains numerous ephemeral floodplain habitats. Taking into account the boundaries of the reserve and seasonal movement ecology of crocodiles at Ndumo Game Reserve (Calverley 2013), we established a shoreline length of 35 km for biomass estimates, although this number is likely an underestimate. Population size for the province of KwaZulu-Natal was aggregated from survey data in Champion (2011), Calverley (2013), Combrink et al. (2011), Combrink (2014) and unpublished reports of standardized aerial and spotlight counts.

Results

We captured 322 *C. niloticus* from Lake St Lucia and Ndumo Game Reserve for morphometric analyses (Fig. 1). Our sample included 118 hatchlings with a mean TL, SVL and BM (±SD) of 316 ± 25 mm (range 272–414 mm), 146 ± 12 mm (range 131–193 mm) and 73 ± 19 g (range 17–182 g), respectively. For 91 subadults captured, mean TL and SVL were 1958 ± 486 mm (range 753–2702 mm) and 1001 ± 258 (range 358–1392), respectively, and for 113 adults mean TL and SVL were 3172 ± 389 mm (range 2590–4136 mm) and 1710 ± 225 mm (range 1408–2460 mm), respectively. Mean BM for non-

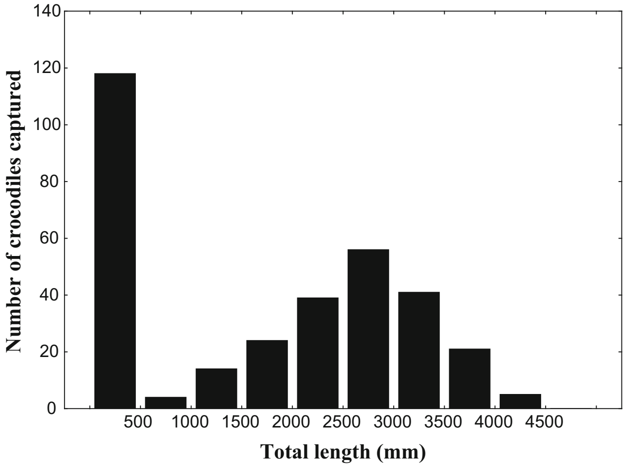

Fig. 1 Size-class distribution of 322 *Crocodylus niloticus* captured 2009–2013 at Lake St Lucia and Ndumo Game Reserve in KwaZulu-Natal, South Africa

hatchlings was 90.3 ± 70.6 kg (range 7.0–341.0 kg), and hatchlings were excluded from body mass regressions and biomass calculations due to extensive variance (Platt et al. 2009, 2011). Strong positive allometric relationships were found between body length metrics (TL and SVL) and other morphometrics ($r^2 \geq 0.91$); not all variables were recorded for each individual (Table 1; Figs. 2, 3). Morphometric regressions were linear, with the exception of the relationship of TL and SVL to BM, which was logarithmic (Table 1; Figs. 2, 3). For the relationships of HW/HL to SVL and HL/TL to TL we found considerable individual variation among all size classes, although there were slight negative linear trends for both relationships (Fig. 4). The mean HW/HL ratio was 1.9 ± 1.6 (range 1.39–2.50), and mean HL/TL was 0.14 ± 0.005 (range 0.12–0.16).

We determined the sex of 191 non-hatchling *C. niloticus* (96 female, 95 male). At Ndumo Game Reserve, we captured 35 subadult and 9 adult females, and 23 subadult and 20 adult males. The female-to-male observed sex ratio for all individuals at Ndumo Game Reserve was even (1:0.97), but the observed adult sex ratio was male biased (0.45:1). At Lake St Lucia, we captured 15 subadult and 37 adult females, and 5 subadult and 47 adult males, with an even sex ratio (1:1) for all individuals. The observed adult sex ratio was male biased (0.79:1). For both Ndumo Game Reserve and Lake St Lucia populations (which represent the majority of *C. niloticus* in KwaZulu-Natal), the observed sex ratio for all individuals was essentially even (1:0.99). Males were larger than females; the largest female SVL was 1782 mm, while 49 % of adult males captured were greater than 1800 mm. The mean SVL of adult males was significantly greater than that of adult females ($t = -6.52$, $df = 111$, $p < 0.001$; Fig. 5), and an SDI of 2.19 was calculated for the species.

Equation 18 from Table 1 was used to calculate standing crop biomass of *C. niloticus* at Ndumo Game Reserve (52,640.40 kg; Table 2) and Lake St Lucia (96,867.18 kg;

Table 1 Regression equations for predicting total length (TL) and snout-vent length (SVL) in millimeters for *Crocodylus niloticus* from other morphometric features (in mm except for body mass)

Equation no. and predictor *X*	Estimated value *Y*	Equation	R^2	*n*
1. TL	SVL	SVL = 0.55(TL) − 35.05	0.99	322
2. HW	TL	TL = 12.79(HW) + 90.30	0.99	322
3. HW	SVL	SVL = 6.99(HW) + 11.42	0.99	322
4. HL	TL	TL = 7.25(HL) − 7.234	0.99	322
5. HL	SVL	SVL = 3.96(HL) − 40.07	0.99	322
6. NG	TL	TL = 3.01(NG) + 589.92	0.96	204
7. NG	SVL	SVL = 1.72(NG) + 227.43	0.96	204
8. FBG	TL	TL = 2.71(FBG) + 466.43	0.98	80
9. FBG	SVL	SVL = 1.57(FBG) + 145.21	0.98	80
10. MBG	TL	TL = 2.24(MBG) + 407.31	0.98	80
11. MBG	SVL	SVL = 1.29(MBG) + 117.40	0.97	80
12. HBG	TL	TL = 2.89(HBG) + 362.26	0.97	80
13. HBG	SVL	SVL = 1.68(HBG) + 84.81	0.96	80
14. TG	TL	TL = 3.64(TG) + 354.14	0.95	204
15. TG	SVL	SVL = 2.07(TG) + 100.48	0.94	204
16. HVG	TL	TL = 8.47(HVG) + 107.01	0.94	80
17. HVG	SVL	SVL = 4.84(HVG) − 41.24	0.92	80
18. BM	TL	TL = 1722.24(logBM) − 393.97	0.91	47
19. BM	SVL	SVL = 990.81(logBM) − 344.71	0.91	47

HW head width, *HL* head length, *NG* neck girth, *FBG* front-leg body girth, *MBG* mid-body girth, *HBG* hind-leg body girth, *TG* tail girth, *HVG* horizontal–ventral scale girth, *BM* body mass (kg)

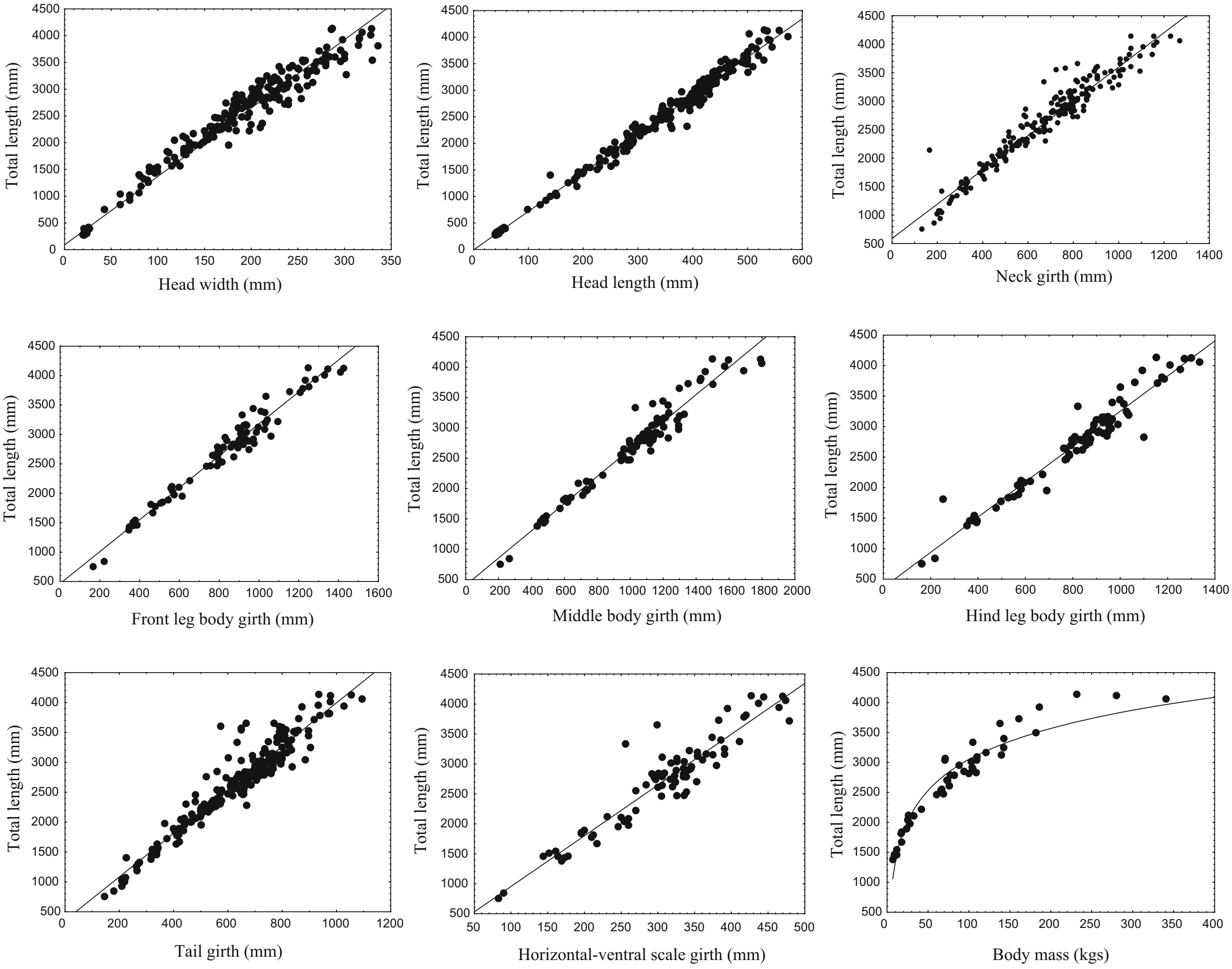

Fig. 2 Relationship between total length (TL) and all other morphometric parameters for *Crocodylus niloticus* captured 2009–2013 at Lake St Lucia and Ndumo Game Reserve in KwaZulu-Natal, South Africa

Table 3). These values were then divided by the respective ha of habitat and km of shoreline for both populations and reported in relation to other studies (Table 4). We estimate the total *C. niloticus* non-hatchling metapopulation size in KwaZulu-Natal to be approximately 3650 individuals, with Lake St Lucia (1005 ± 137 individuals; Combrink 2014), Ndumo Game Reserve (846 ± 59 individuals; Calverley 2013) and Pongolapoort Dam (549 individuals; Summers 2015) accounting for most crocodiles in the province.

Discussion

We did not include an assessment of morphometric variance between Lake St Lucia and Ndumo Game Reserve in our study because although these two populations are allopatric, there is a documented history in Zululand of *C. niloticus* being transported from source populations and released into foreign ones, particularly between uMkhuze Game Reserve, Ndumo Game Reserve and Lake St Lucia (Pooley 1982a, b). Furthermore, "problem" crocodiles captured by local conservation authorities in peripheral waterbodies outside of protected areas are frequently released at Lake St Lucia, as well as presumed farmed and pet escapees captured as far away as the uMsunduzi River near Durban (Warner et al. pers. obs.). Discussion of the conservation merit of these practices is beyond the scope of this manuscript, but any minor morphological or especially genetic difference(s) found between current Zululand *C. niloticus* populations are almost certainly not a reflection of ecological or evolutionary processes.

Similar to other morphometric studies of *C. porosus* (Webb and Messel 1978), *C. siamensis* (Chentanez et al. 1983), *C. novaeguineae* (Montague 1984), *C. niloticus* (Hutton 1987a), *C. moreletii* (Platt et al. 2009) and *C. acutus* (Platt et al. 2011), we found strong relationships

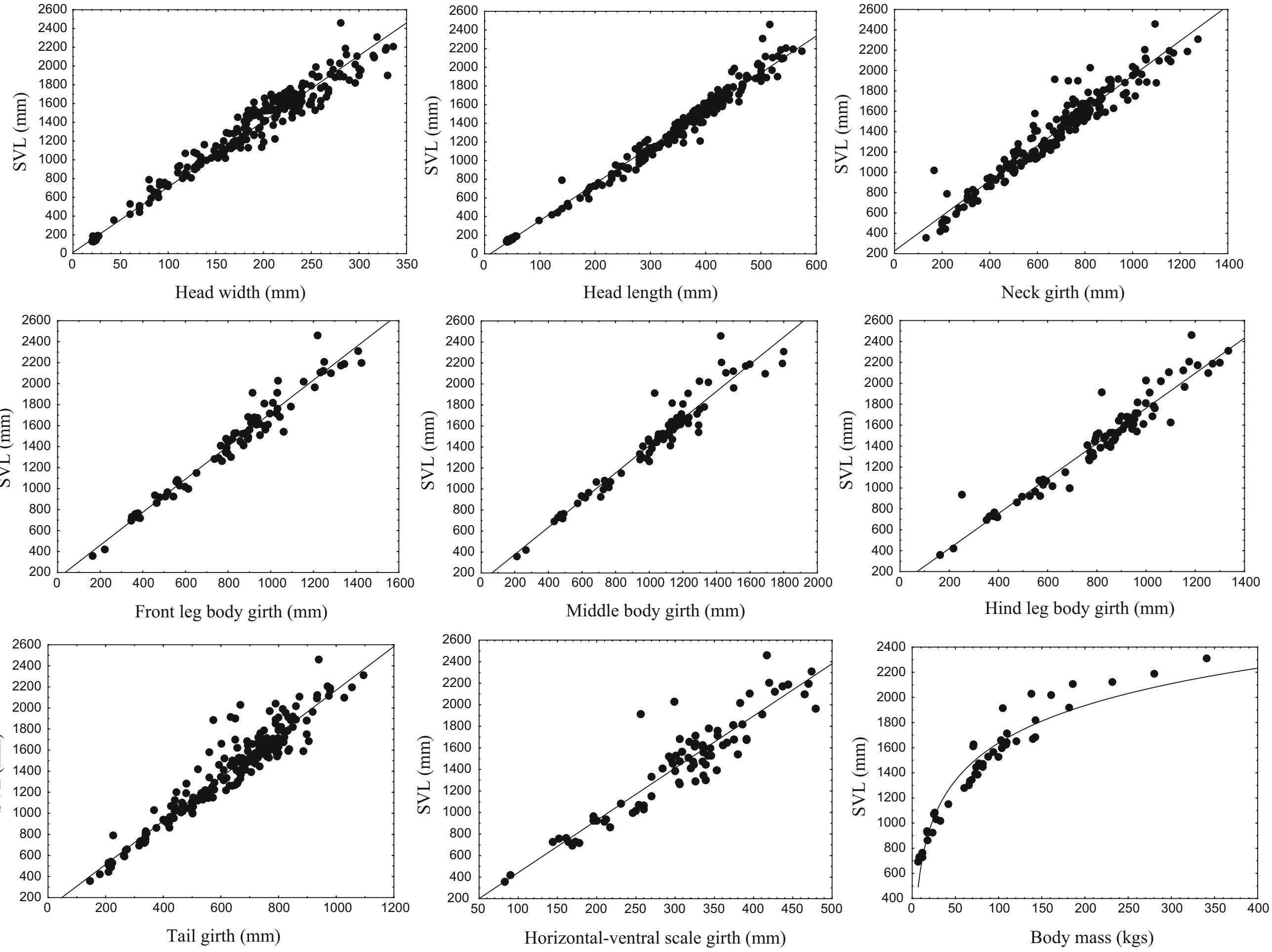

Fig. 3 Relationship between snout-vent length (SVL) and all other morphometric parameters for *Crocodylus niloticus* captured 2009–2013 at Lake St Lucia and Ndumo Game Reserve in KwaZulu-Natal, South Africa

between measures of body length (TL and SVL) and other physical attributes, with greater variance in body form found among larger individuals (Figs. 2, 3). The considerable individual variation found among all size classes for the relationships of HW/HL, HW/HL to SVL and HL/TL to TL revealed a significant degree of morphological plasticity for *C. niloticus* in KwaZulu-Natal. While such variability is not unusual for crocodilian hatchlings (Milnes et al. 2001; Murray et al. 2013; Fig. 4), our study adds to a growing body of literature that suggests there is an inherent high degree of variation between and among *C. niloticus* populations that probably exceeds that of all other crocodilian species (Salem 2011; Pearcy and Wijtten 2011; Hekkala et al. 2011; Nestler 2012). For example, Nestler (2012) found that based on statistical analyses of skull characteristics alone, *C. niloticus* in the Congo River Basin alone showed as much morphological variation as *C. porosus* did across the entirety of its geographic range (the most extensive among crocodilians). It is therefore possible that *C. niloticus* is actually a cryptic species complex consisting of multiple taxa (Hekkala et al. 2010, 2011), and the recent elevation of *C. suchus* in West Africa to specific status supports this (Hekkala et al. 2011). Additional morphometric and molecular data for *C. niloticus* across the species' range are needed to delineate potential taxa synonymized under *C. niloticus* and to properly address the region-specific conservation challenges these crocodiles face (Shirley et al. 2014). For southern Africa, the predictive models we present here (Table 1) will be helpful to future studies in assessing *C. niloticus* body length from skulls found in the field, detecting ontogenetic shifts in morphology, and estimating crocodile biomass at population and regional scales.

The neutral sex ratio found among non-hatchlings at both Ndumo Game Reserve and Lake St Lucia was unexpected. We hypothesized some degree of skewness among males and females simply because we could not capture and account for the sex of every individual in the population. Additionally, sex among *C. niloticus* embryos is determined by temperature (similar to other crocodilians),

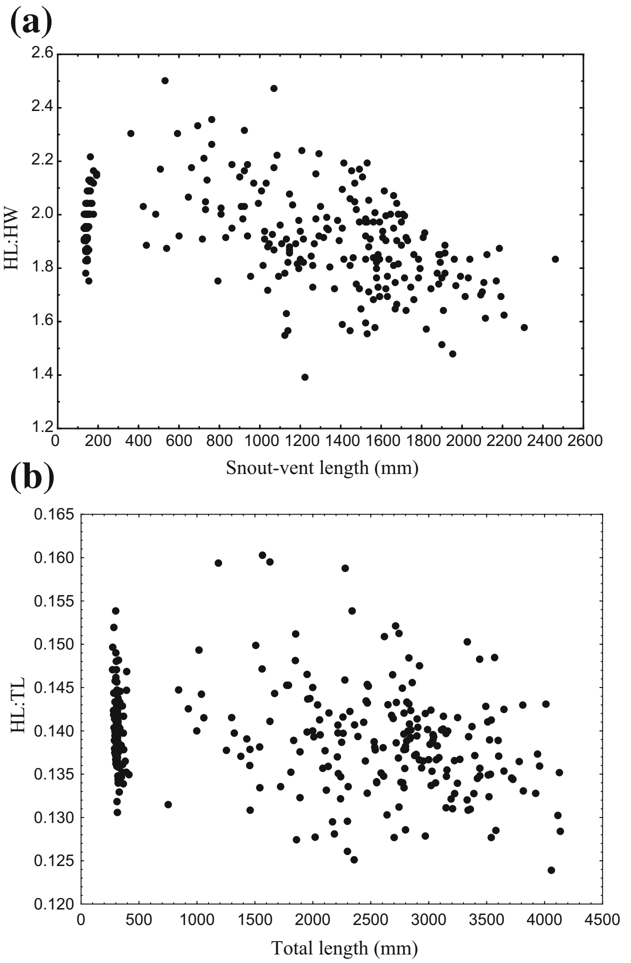

Fig. 4 Relationship of the ratio of **a** head length: head width (HL/HW) to snout-vent length (SVL), and **b** head length: total length (HL/TL) to total length (TL) for *Crocodylus niloticus* ($n = 322$) at Ndumo Game Reserve and Lake St Lucia, South Africa

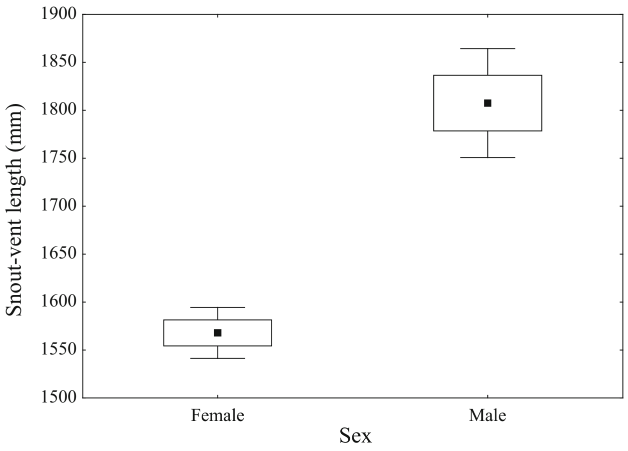

Fig. 5 Sexual size dimorphism for adult male ($n = 67$) and female ($n = 46$) *Crocodiles niloticus* in KwaZulu-Natal, South Africa quantified as the variance between snout-vent length means

and the nesting substrate and aspects of the species' nesting ecology differ substantially between the two populations (Calverley 2013; Combrink 2014). The observed even ratio we found for both populations is indicative that our sampling was probably truly random and reflective of the actual sex ratio, as observed deviations from a 1:1 pairing in reptile populations with temperature-sex determination is often due to sampling bias (Mrosovsky and Pieau 1991). However, intraspecific population biases do occur in crocodilians (Thorbjarnarson 1997) and for *C. niloticus* at the higher (colder) elevation of Lake Ngezi in Zimbabwe, Hutton (1987b) found a strongly female-biased sex ratio among all size classes and embryos.

Despite congruity in the overall sex ratio at Ndumo Game Reserve, the strong male bias we observed among adults is concerning with regard to long-term recruitment in the face of the ongoing *C. niloticus* population decline there (Calverley and Downs 2014a). For Lake St Lucia, Leslie and Spotila (2001) documented the shading effect of invasive triffid weed or paraffin bush (*Chromolaena odorata*) at *C. niloticus* nesting sites and warned that "unless immediate action is taken, a female-biased sex ratio in all nesting areas will result in eventual extirpation of the Nile crocodile from the Lake St. Lucia ecosystem." 15 years on, the sex ratios found in our study do not support this claim, and in fact we found a male-biased adult population. However, this should not diminish the ongoing serious threat of *C. odorata* invasion to suitable nesting habitat at Lake St Lucia, which requires active management in the form of plant removal and other proactive strategies.

The significant sexual size dimorphism we found for *C. niloticus* (Fig. 5), with males obtaining larger body sizes, conforms to the findings of previous research on the species (Hutton 1987a, b) and the normal trend among crocodilians (Webb and Messel 1978; Platt et al. 2009, 2011). Numerous hypotheses have been posited for the crocodilian size differential among sexes, but the most likely explanation is that female growth slows at sexual maturity so that resources can be diverted into reproduction, whereas large body size in males confers a fitness advantage in mating competition and territory defense (Platt et al. 2011). Across species males are approximately 20 % larger than females (Platt et al. 2009), and the SDI of 2.19 we calculated for *C. niloticus* is comparable to *C. moreletii* (2.12; Platt et al. 2009) and *C. acutus* (2.10; Platt et al. 2011). From an ancillary study of stable isotope analyses, we found no dietary differences between sexes that could be responsible for differences in growth (Warner 2015).

Table 2 Estimated standing crop biomass of non-hatchling *Crocodylus niloticus* for Ndumo Game Reserve, South Africa

Size class	Total length (mm)	Mean length (mm)	Predicted body mass (kg)	Population size	Estimated biomass (kg)
Subadults	750–2700	1955	23.12	440	10,172.80
Adults	2701–5000	3084	104.60	406	42,467.60
Total standing crop biomass (kg)					52,640.40
Biomass/ha (kg/ha)					5.20
Biomass/km shoreline (kg/km)					1504.01

Population size data extrapolated from Calverley (2013). Individual body mass estimated from Eq. 18 in Table 1. Biomass estimates based on 10,117 ha of habitat and 35 km of shoreline available to *C. niloticus* at Ndumo Game Reserve (see text for rationale)

Table 3 Estimated standing crop biomass of non-hatchling *Crocodylus niloticus* at Lake St Lucia, South Africa

Size class	Total length (mm)	Mean length (mm)	Predicted body mass (kg)	Population size	Estimated biomass (kg)
Subadults	750–2700	1967	23.50	266	6251.00
Adults	2701–5000	3203	122.62	739	90,616.18
Total standing crop biomass (kg)					96,867.18
Biomass/ha (kg/ha)					2.77
Biomass/km shoreline (kg/km)					161.45

Population size data extrapolated from Combrink (2014). Individual body mass estimated from Eq. 18 in Table 1. Biomass estimates based on 35,000 ha of habitat at mean lake level (Taylor 2006) and 600 km of shoreline (Combrink 2014) available to *C. niloticus* at Lake St Lucia

Table 4 Standing crop biomass estimates (kg/km of shoreline) for crocodilian populations

Species and locality	Estimated biomass (kg/km)	References
Crocodylus acutus		
Lake Etang Saumatre (Haiti)	66.6	Thorbjarnarson (1988)
Turneffe Atoll (Belize)	35.2	Platt et al. (2011)
Crocodylus moreletii		
Gold Button Lagoon (Belize)	187.2	Platt et al. (2009)
Crocodylus niloticus		
Lake Turkana (Kenya)	350.20	Graham (1968)
Upper Murchison Falls (Uganda)	75.3	Parker and Watson (1970)
Lower Murchison Falls (Uganda)	76.03	Parker and Watson (1970)
Lake Ngezi (Zimbabwe)	171.88	Hutton (1987b)
White and Black Umfolozi Rivers (South Africa)	124.97	Blake and Jacobsen (1992)
Olifants River excl. Flag Boshielo (South Africa)	14.74	Kleynhans and Engelbrecht (1993)
Flag Boshielo Dam (South Africa)	142.83	Botha (2006)
Lake St Lucia (South Africa)	161.45	This study
Ndumo Game Reserve (South Africa)	1504.01	This study
Crocodylus porosus		
Blyth River (Australia)	203.6	Fukuda et al. (2011)
Cadell River (Australia)	109.1	Fukuda et al. (2011)
Liverpool River (Australia)	104.5	Fukuda et al. (2011)
South Alligator River (Australia)	304.4	Fukuda et al. (2011)
West Alligator River (Australia)	146.1	Fukuda et al. (2011)
Wildman River (Australia)	370.3	Fukuda et al. (2011)

For Zululand, the largest female captured in this study was 3.22 m TL, which probably is close to the maximum female size for the region. Although male *C. niloticus* reach lengths of 5 m in the Kruger National Park in South Africa (D. Pienaar, pers. comm.), a 4-m male is an exceedingly large crocodile for the province of KwaZulu-Natal. For our study at Ndumo Game Reserve and Lake St Lucia, there were only five individuals captured >4.0 m, none of which were >4.2 m. However, at the outset of our research in 2009 two males >4.2 m (not included in morphometric analyses) were captured; a 4.30-m male from Pongolapoort Dam and a 4.72-m male from Ndumo Game Reserve. The latter, "Beauty," was a relatively famous crocodile in the region known for his enormous body size, severe facial scarring and reputation as a man-eater. Beauty was in noticeably poor body condition at the time of capture and died several months later at Lake Inyamithi in Ndumo Game Reserve, presumably of old age. From years of *C. niloticus* surveillance and monitoring data in Zululand, we find it unlikely that there are currently more than five crocodiles >4.3 m, and extremely unlikely that there are any individuals >5.0 m.

Our estimate of biomass for Lake St Lucia (161.45 kg/km) is comparable with other *C. niloticus* populations (Table 4), although it is important to note that given the current severe drought in the region most individuals are now restricted to southern portions of the lake exposed to freshwater inputs (e.g., the Nkazana stream mouth at Catalina Bay) and the 27-km-long Narrows channel. In light of the current adult bias at Lake St Lucia (Table 3), the survival of hatchlings to the subadult stage is a critical factor to the stability of the *C. niltocus* population over the next 20 years. For Ndumo Game Reserve, the biomass of 1504.01 kg/km we found is over four times the amount recorded for any other crocodilian population in the world (Table 4), but this is potentially due to a restocking program for the species in the late 1960s and early 1970s. Unless mitigative management actions are taken in the area, we predict the biomass at Ndumo Game Reserve to decline in the future primarily due to poaching and the destruction of nesting habitat (Calverley and Downs 2014a). The viable future of the estimated 3650 *C. niloticus* in KwaZulu-Natal will largely depend on proactive crocodile management practice and protection underpinned by continuing demographic and ecological studies at Lake St Lucia, Ndumo Game Reserve and Pongolapoort Dam.

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Compliance with ethical standards

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Appendix

See Fig. 6.

Fig. 6 Researchers taking morphometric measurements of *Crocodylus niloticus* in KwaZulu-Natal, South Africa

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