

Feeding across the food web: The interaction between diet, movement and body size in estuarine crocodiles (*Crocodylus porosus*)

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Abstract The estuarine crocodile (*Crocodylus porosus*) is an apex predator across freshwater, estuarine and coastal environments. The impact of a changing *C. porosus* population upon the ecosystem is unknown, but due to large ontogenetic changes in body mass (>1000-fold) their impact may be wide reaching and substantial. Here we investigated the relationship between diet, movement and body size in a population of *C. porosus* inhabiting a tidal river in northern Australia. Subcutaneous acoustic transmitters and fixed underwater receivers were used to determine the activity space and movement patterns of 42 individuals (202–451 cm in total length). There was no size-related spatial partitioning among different sized crocodiles. Large individuals (snout–vent length (SVL): 160 cm < SVL < 188.5 cm) did, however, exhibit a much larger activity space than other size classes. Diet and individual specialization was assessed using the composition of stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in tissues with different turnover rates. There was a quadratic relationship between body size and $\delta^{15}\text{N}$, suggesting that medium-sized individuals (110 cm < SVL < 160 cm) incorporated a greater proportion of high trophic prey into their diets than small (SVL < 110 cm) or large individuals (SVL > 160 cm). Tissue $\delta^{13}\text{C}$ composition on the other hand was positively correlated with body size, indicating that different size classes were trophically linked to primary producers in different habitats. Individual-level analyses showed that small crocodiles were generalist feeders while medium and large size classes specialized on particular prey items within the food webs they fed. The findings further our understanding of ontogenetic variation in *C. porosus* diet, and suggest that change in *C. porosus* population size or demographics may be influential at various levels across the local food web.

Key words: acoustic telemetry, discrimination factor, home range, stable isotope, apex predator.

INTRODUCTION

Estuarine crocodiles (*Crocodylus porosus*) are the largest and most geographically widespread species of extant crocodilian (Webb & Manolis 1989). Their geographic range currently stretches from the west coast of India to Sri Lanka, Bangladesh, the southern Malay Peninsula, throughout the Indonesian archipelago, north to the Philippines and Palau, then south through New Guinea to northern Australia, and east to Bismarck Archipelago, the Solomon Islands, New Hebrides, Fiji and

Vanuatu (Steel 1989; Webb & Manolis 1989). Throughout this range, *C. porosus* can be found in freshwater, brackish and marine habitats (Limpus 1980; Magnusson 1980; Magnusson *et al.* 1980; Webb & Manolis 1989; Letnic 2008; Campbell *et al.* 2010, 2013). Adult *C. porosus* are the apex predator in the environments they inhabit, and because individuals undergo a greater than 1000-fold increase in body size throughout their lifetime (Fukuda *et al.* 2008), they are likely to remove prey from a variety of trophic levels and food webs. Despite their possible role as a keystone species for trophic interaction, very little is known about the mechanisms that drive variation in their diet and where different sized *C. porosus* fit into freshwater, brackish, marine and adjacent terrestrial food webs.

As *C. porosus* grow, their snouts become proportionately broader with increased structural reinforcement (Busbey 1989, 1995), and they are able to produce increasingly powerful bite forces (Erickson *et al.* 2012, 2013). These ontogenetic changes in body size and cranial biomechanics are thought to play a major role in

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prey selection during the lifetime of an individual crocodile (Taylor 1979; Webb *et al.* 1991). To understand size-related variation in *C. porosus* diet, previous research has used direct observations of feeding behaviour and stomach contents analyses (e.g. Taylor 1979; Webb *et al.* 1991; Sah & Stuebing 1996; Whiting & Whiting 2011). These methods have identified many of the animals that *C. porosus* consume (Taylor 1979; Kar & Bustard 1981; Webb & Manolis 1989; Webb *et al.* 1991; Sah & Stuebing 1996; Whiting & Whiting 2011). However, they suffer from biases in digestion time and seasonal availability (Jackson *et al.* 1974) that misrepresent the significance of certain prey items within the overall diet. They are also poorly suited for determining the trophic position and dominant food webs of *C. porosus* across size classes, and describing individual-level feeding patterns such as individual specialization (wherein similar-sized individuals specialize on different prey; Roughgarden 1974; Bolnick *et al.* 2003).

The composition of stable carbon and nitrogen isotopes in animal tissues (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) reflects their diet. Specifically, tissue $\delta^{15}\text{N}$ compositions are a relative indicator of trophic position (DeNiro & Epstein 1981; Post 2002), and tissue $\delta^{13}\text{C}$ compositions reflect the habitats and food webs that animals use to acquire prey (DeNiro & Epstein 1978; Chisholm *et al.* 1983). Since different tissues turnover at different rates, the isotopic composition of different tissues in the same animal can provide insight into diet over multiple time frames (Tieszen *et al.* 1983; Hobson & Clark 1992; Dodge *et al.* 2011) and individual specialization (Bolnick *et al.* 2003; Newsome *et al.* 2009; Matich *et al.* 2011). In addition, stable isotopes can be coupled with individual tracking methods to describe spatial variation in diet (Rosenblatt & Heithaus 2011), which in turn could be used to determine whether size-related changes in an animal's movement patterns or feeding capabilities drive size-related variation in its diet.

Throughout northern Australia, different size classes of *C. porosus* have been observed to occur at different densities in upstream areas compared with downstream areas (Messel & Vorlicek 1986; Letnic 2008; Nichols & Letnic 2008). Although variation in physiology, morphology and feeding capability are considered to be the main drivers of size-related variation in the diets of *C. porosus* (Webb *et al.* 1991) – and for crocodilians in general (Brochu 2001) – the amount of variation that might also be associated with spatial partitioning within the same or adjacent habitats is poorly understood.

The objective of this study was to provide insight into the dietary ecology of *C. porosus* and the mechanisms driving variation in diet using underwater acoustic telemetry and stable isotope analysis of body tissues. Although stable isotope analysis has not yet been applied to *C. porosus*, it has been used to investigate dietary patterns in several other crocodilians. Nile crocodiles (*Crocodylus niloticus*) and broad-snouted

caimans (*Caiman latirostris*) were found to exhibit size-related variation in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions – indicating ontogenetic changes in diet (Radloff *et al.* 2012; Marques *et al.* 2013). By combining stable isotope analysis with movement data, American alligators (*Alligator mississippiensis*) were found to exhibit spatially structured diets (Rosenblatt & Heithaus 2011), with individuals inhabiting downstream areas feeding (partially) from marine food webs. This suggests that some crocodilians may have a key role in linking marine and estuarine food webs. Here, size-related variation in diet over both the short and the long term were investigated in *C. porosus* by sampling multiple tissues from a range of individuals within a single tidally influenced river system.

METHODS

Data collection

The study was conducted on a population of *C. porosus* inhabiting the Wenlock River, Cape York, Queensland, Australia (Fig. 1). The study area covered a 60 km stretch of the river, spanning from freshwater tidal reaches to macrotidal brackish water (see Pillans *et al.* 2008 for water quality data). In upstream areas, *Melaleuca* forests dominated the vegetation along the riverbanks. Further downstream, these forests were replaced by mangrove palm (*Nypa fruticans*). The region experiences little rainfall and slightly cooler temperatures during the dry season (January–April), and is inundated with rain during the wet season (May–December; RAAF Scherger and Skardon River stations; Australian Bureau of Meteorology 1988).

The crocodiles inhabiting this area range from hatchlings to adults (Messel *et al.* 1981), making it ideal for investigating size-related variation in diet. Crocodiles were head caught using a pole and noose or captured using baited traps throughout a 48 km freshwater stretch of river. The traps were floated on the water surface or placed at the water's edge along the riverbank. Each trap was baited with wild pig meat (*Sus scrofa*) and the trap door was activated by a trigger mechanism attached to the bait. Once captured, crocodiles were removed from the trap, manually restrained, and two parameters of body size (snout–vent length (SVL): distance from snout to the anterior tip of the cloaca; total length (TL)) were measured to the nearest millimetre using a tape measure.

Acoustic telemetry

In August 2008, 2009 and 2010, a total of 43 crocodiles were captured (mean SVL = 160.4 cm (range 100.6–239 cm); mean TL = 315.1 (range 202–451 cm)). Individuals were restrained and implanted with coded acoustic transmitters that emitted pulses at variable intervals between 90 and 120 s (98 × 16 mm, mass in air 36 g, VEMCO, Bedford, Nova Scotia, Canada; using methods in Franklin *et al.* 2009). Ten millilitres of local anaesthetic (Lignocaine, Troy Laboratories, Smithfield, Australia) were injected into the area of soft skin and muscle immediately behind the left forelimb. A 2 cm

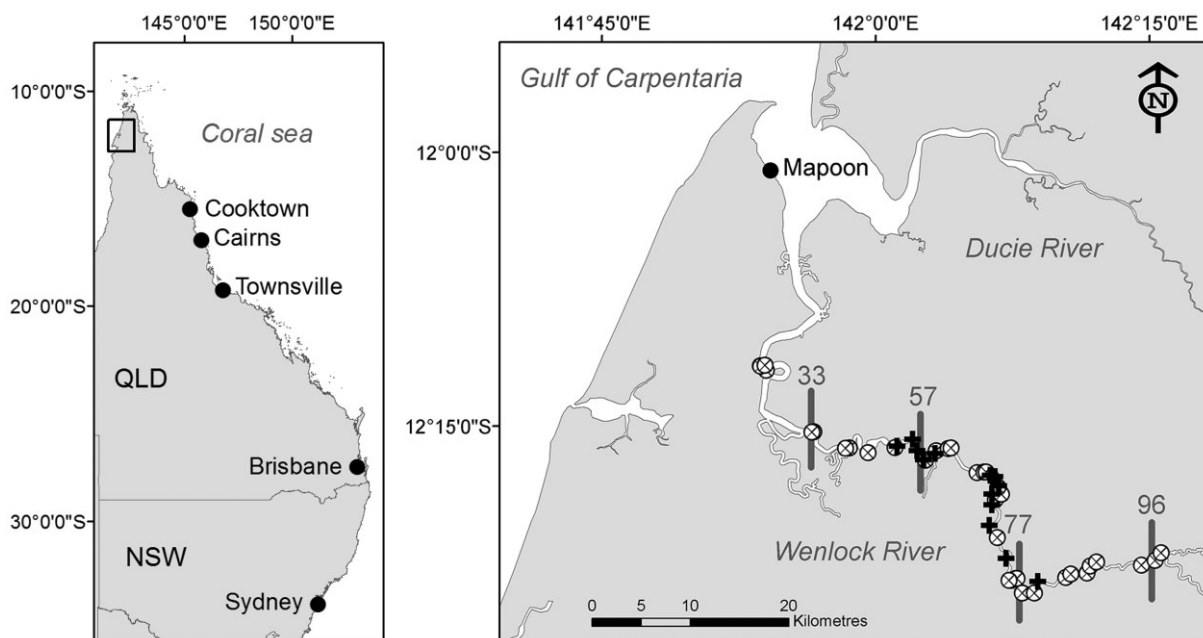


Fig. 1. The location of the study area. Open circles mark the locations of acoustic receivers. Crosses indicate the trap location sites along the river. Grey bars denote points at specific distances (km) along the river from the river mouth.

lateral incision was then made using a scalpel and the skin teased apart from the muscle by blunt dissection. The sterilized transmitter was inserted into the created pocket, and the wound closed by four to six interrupted sutures (cat-gut suture; Ethicon, Somerville, NJ, USA). This procedure was completed in less than 20 min, and the crocodiles were released at the point of capture. All surgical procedures were carried out using an aseptic technique.

To detect signals broadcast by the acoustic transmitters, an array consisting of 38 underwater acoustic receivers (VR2-W; VEMCO) was deployed throughout the study area (Fig. 1). Each receiver was attached to a cement anchor and moored to a fixed structure on the riverbank. The receivers were spaced between 2 and 4 km apart. To determine the detection range, an activated tag was towed behind a boat in a predetermined pattern around each receiver. The detection range was generally 400–600 m, and therefore, a crocodile could not pass along the river without the implanted transmitter being detected.

Stable isotopes

To investigate dietary variation in the local population, a different cohort of crocodiles was trapped during August 2011 ($n = 18$; mean SVL = 124.7 cm (range 59–188.5 cm); mean TL = 246 cm (range 118–366.5 cm); Fig. 1) along the same stretch of river monitored by the acoustic receiver network. Blood plasma, red blood cells, collagen and keratin tissue samples were collected from this cohort for stable isotope analysis. These tissues were selected to provide insight into the crocodiles' diets over a large time frame and minimize harm to the animal (see Discussion for likely assimilation rates). Following the capture and restraint of a given crocodile, a 5 mL blood sample was taken from the cranial sinus and a dorsal 1 cm sample of the vertical scale

was collected from the first single scale crest of the tail (Frey 1988; Frey & Salisbury 2001; *sensu* the first 'single caudal verticil'; Brazaitis 1987) using a scalpel. Blood samples were heparinized and centrifuged at 1000 g for 5 min. Blood plasma was removed with a pipette from the red blood cells. All tissue samples were frozen at -20°C within a few hours of sampling.

To facilitate interpretation of diet, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of animal tissues need to be corrected using diet–tissue discrimination factors (DeNiro & Epstein 1978, 1981). Because no discrimination factors had previously been derived for *C. porosus* (but for other crocodilians, see Caut 2013; Rosenblatt & Heithaus 2013), these factors were experimentally determined using eight crocodiles (approximately 1.4 years old; mean 36.1 ± 0.8 cm SE SVL) obtained from a farm. These crocodiles had been fed a mixed diet of kangaroo and chicken meat in (roughly) constant proportions for their entire lives. Upon arrival at The University of Queensland, St. Lucia Campus, these animals were relocated to a large open enclosure, and were fasted for 14 days as they became acclimatized to their new surroundings. Although extended periods of fasting can alter $\delta^{15}\text{N}$ tissue compositions in some species (Hobson *et al.* 1993; Cherel *et al.* 2005), this is not universal (Kempster *et al.* 2007). Given that ectotherms often experience extended periods between meals, this short fasting period is unlikely to have induced any $\delta^{15}\text{N}$ enrichment. After the fasting period, the crocodiles resumed feeding on the same diet they had received at the farm. The food the crocodiles received in the new enclosure was acquired from the farm, and thus the crocodiles were in isotopic equilibrium with this diet. Thirteen days later, blood and scale crest samples were collected from these animals (using methods described for the wild crocodiles), and samples were also taken from their food ($n = 3$).

Tissue and diet samples were dehydrated and homogenized in preparation for mass spectrometry. Blood plasma

Table 1. Summary of *Crocodylus porosus* acoustic telemetry data

Year monitored	Number of crocodiles	Size range (SVL cm)	Total number of detections	Number of receivers	Mean detections per receiver
2009	19	101.1–214.1	77 077	15	5138
2010	32	100.6–239	70 961	24	2956
2011	23	100.6–228	89 720	10	4722
Total	42	101.1–228	237 758	34	7204

Data represent the crocodiles, receivers and detections associated with the dry seasons from 2009 to 2011. Most crocodiles were monitored for multiple years. Receiver units were sometimes replaced with other units in similar locations, and in these cases, the replacement units were not added to the counts.

samples were oven dried (80°C for > 48 h). Red blood cell samples from the captive animals were freeze dried (–15°C for > 96 h), and those from the wild animals were oven dried (80°C for > 48 h). All blood plasma and red blood cell samples were homogenized using mortar and pestles, and test tube pestles. Separate collagen and keratin samples were dissected from scale crests. Each of these samples was thinly diced, homogenized in 3 mL distilled water using an Ultra-Turrax disperser, oven dried (80°C for > 48 h) and further homogenized using test tube pestles, and mortar and pestles. Diet samples were prepared using methods described for collagen and keratin.

A small amount from each sample (0.5–0.9 mg) was encapsulated into tin foil cups for mass spectrometry. Samples were analysed in three batches using a continuous flow isotope ratio mass spectrometer (Micromass Isoprime Eurovector EA300, Manchester, UK) using nitrogen (IAEA-N-1; ammonium sulphate; 0.4 $\delta^{15}\text{N}$ ‰; calibrated against atmospheric nitrogen) and carbon (IAEA-CH-6; sucrose; –10.449 $\delta^{13}\text{C}$ ‰; calibrated against Vienna Pee Dee Belemnite) standards. To assess precision within batches, standards were interspersed throughout each batch ($n = 11, 18, 8$) to yield $\delta^{15}\text{N} = -11.5 \pm 0.1, -11.6 \pm 0.3, -11.5 \pm 0.1$ ‰ SD and $\delta^{13}\text{C} = 0.5 \pm 0.2, 0.4 \pm 0.1, 0.5 \pm 0.2$ ‰ SD. To assess precision between batches, replicates from a token tissue sample ($n = 1$ per batch) were included in each batch to yield $\delta^{15}\text{N} = 0.5$ ‰ SD and $\delta^{13}\text{C} = 0.2$ ‰ SD. The elemental ratios of carbon to nitrogen isotope abundance (C : N ratio) in all tissue samples (one sided t -test, $t_{98} = -10.951, P < 0.001$) were within acceptable limits for aquatic samples (<3.5). Similarly, the C : N ratios for dietary samples (mean -14.1 ± 1.76 ‰ SD $\delta^{13}\text{C}$; mean 3.86 ± 0.13 ‰ SD $\delta^{15}\text{N}$; mean C : N = 3.8 ± 0.26 SD) were within acceptable limits for terrestrial samples (<4.0). Thus variation in lipid content was not large enough to influence results (Post *et al.* 2007; Logan *et al.* 2008). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of samples were expressed using delta notation (δ^{X} ; see DeNiro & Epstein 1978).

Data analyses

Movement and activity space

Acoustic telemetry data were used to characterize the location and size of each crocodile's activity space along the river (Table 1) in a geographic information system framework.

Like many other tropical river systems, the Wenlock River floods during the wet season. Preliminary investigation revealed that during this period, tagged crocodiles frequently travelled upriver, beyond the extent of the receiver network. To ensure these movements and any associated movements during the very early and late parts of the dry season did not bias the results, we limited our analysis to telemetry data recorded during the July–September period of 2009, 2010 and 2011. As crocodiles remained within the main trunk of the river during the study period, we treated the study area as a one-dimensional space: distance along the Wenlock River from its river mouth. The location of each receiver was expressed as the shortest distance along the river to its coordinates from the river mouth (similar to 'linear distance' methods by Dwyer *et al.* in press). To represent frequency of usage along the river, we used the duration of time that an individual remained near each receiver station, rather than raw detections (Campbell *et al.* 2012; Dwyer *et al.* in press). Here, an event was initiated by the first detection of a transmitter at a new receiver and terminated when no further detections for that transmitter were recorded within a 1 h timeout window.

The activity space of each crocodile was characterized by fitting a nonparametric Gaussian kernel density estimator to the location of each receiver, weighted by the length of time that the crocodile remained near it. Bandwidths were selected using methods in Sheather and Jones (1991). These kernels were used to predict the occupancy of each crocodile at 1028 equidistant points located between the furthest upriver and downriver receivers that detected the crocodile (buffered by three times the bandwidth used for the kernel). Based on these points, the location of each crocodile's activity space was calculated as the average distance along the river, weighted by the relative amount of time that the crocodile was predicted to have spent there. The size of each crocodile's activity space was calculated as the distance between points located at the 2.5 and 97.5 percentiles, weighted as described for the location measures. For crocodiles that were only detected at a single receiver, the size of their activity space was set according to the receivers' detection range (500 m). For crocodiles monitored over multiple years, activity space measures were calculated for each year using separate kernels.

The relationship between activity space location, size and body size was investigated using linear mixed-effects models. Full models were fitted with quadratic and linear terms for body size and accommodated the non-independence of measurements from the same year using random intercept

terms. They were tested for assumptions of residual normality and homoscedasticity using graphical methods and subject to backwards stepwise term deletion routines to derive term significance and minimal adequate models (terms retained when $P < 0.05$; see Murtaugh 2009 for evaluation). Models used to assess term significance were fitted using maximum likelihood. Minimal adequate models were refit using restricted maximum likelihood for parameter estimation and graphical presentation.

Diet–tissue discrimination factors

Discrimination factors ($\Delta^*X_{\text{Tissue Type}}$; Eqn 1) were determined for each tissue type as the difference between the average tissue $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ composition sampled from the captive animals $\overline{\delta^*X_{\text{Tissue Type}}}$ and samples taken from their diet $\overline{\delta^*X_{\text{Diet}}}$. Standard errors were calculated using the standard deviation of tissue ($\text{SD}_{\delta^*X_{\text{Tissue Type}}}$) and diet ($\text{SD}_{\delta^*X_{\text{Diet}}}$) sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions and the number of tissue ($n_{\text{Tissue Type}}$; blood plasma $n = 6$; red blood cells $n = 7$; collagen $n = 7$; keratin $n = 8$) and diet samples ($n_{\text{Diet}} = 3$; Eqn 2). These discrimination factors were used to correct the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of tissue samples collected from the wild crocodiles (expressed as $c\delta^{13}\text{C}$ and $c\delta^{15}\text{N}$; Eqn 3).

$$\Delta^*X_{\text{Tissue Type}} (\%) = \overline{\delta^*X_{\text{Tissue Type}}} - \overline{\delta^*X_{\text{Diet}}} \quad (1)$$

$$\text{SE}_{\Delta^*X_{\text{Tissue Type}}} (\%) = \sqrt{\frac{\text{SD}_{\delta^*X_{\text{Tissue Type}}}^2}{n_{\text{Tissue Type}}} + \frac{\text{SD}_{\delta^*X_{\text{Diet}}}^2}{n_{\text{Diet}}}} \quad (2)$$

$$c\delta^*X (\%) = \delta^*X - \Delta^*X_{\text{Tissue Type}} \quad (3)$$

Wild crocodile tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions

Linear mixed-effects models were fit to the $c\delta^{13}\text{C}$ and $c\delta^{15}\text{N}$ composition of 18 wild *C. porosus*, accommodating the non-independence of samples from the same individual using random intercept terms. Full models contained tissue type, linear and quadratic terms for body size, and all possible interactions between them as fixed effects. These models were then checked for their conformity to parametric assumptions and subject to routines to derive term significance and minimal adequate models (see previous page). Tissue samples collected from one wild crocodile were excluded from all analyses because their $c\delta^{15}\text{N}$ compositions were outliers (Cook's distance > 0.7).

Individual specialization in diet was assessed by calculating the total amount of isotopic variation in the wild *C. porosus* (total niche width (TNW)) and separating it into intra-individual variation (within individual component (WIC)) and inter-individual variation (between individual component (BIC); Roughgarden 1974). The WIC : TNW ratio describes the degree of individual specialization in a group of animals. As this ratio approaches zero, it indicates a greater degree of individual specialization. The composition of $c\delta^{13}\text{C}$ and $c\delta^{15}\text{N}$ in the crocodile tissues were analysed separately to determine whether individuals specialized on a specific

aspect of their diet. The absolute value of tissue $c\delta^{13}\text{C}$ compositions were used for analysis since negative numbers were not permitted. To ensure that size-related variation in diet did not bias this analysis, crocodiles were binned into three size classes (small: $\text{SVL} < 110$ cm, medium: $110 \text{ cm} < \text{SVL} < 160$ cm, large: $160 \text{ cm} > \text{SVL}$) and measures were derived for each size class. Monte Carlo samples (100 000 replicates) were used to determine whether the WIC : TNW ratios deviated from random expectations.

Software

Numerical analyses were performed in ArcGIS 10.0 (ESRI, Redlands, CA, USA) and R (version 2.15.3; R Development Core Team 2011). Spatial data were processed using the gdistance (van Etten 2012), raster (Hijmans & van Etten 2012), rgeos (Bivand & Rundel 2012), sp (Bivand *et al.* 2008) and VTrack (Campbell *et al.* 2012) R packages. Statistical analyses used the influence.ME (Nieuwenhuis *et al.* 2011) and lme4 (Bates *et al.* 2011) R packages. Individual specialization analyses were performed using the RInSp (Zaccarelli *et al.* 2013) R package.

RESULTS

Crocodile movement and activity space

The average activity space of the wild crocodiles monitored using acoustic telemetry during the beginning of the dry season was located 69.22 km from the river mouth and spanned across a 17.05 km section of river. There was no correlation between the location of a crocodile's activity space along the river and its body size (quadratic: $\chi^2_1 = 0.133$, $P = 0.716$; linear: $\chi^2_1 = 0.172$, $P = 0.679$; Fig. 2a). There was, however, a significant quadratic relationship between activity space size and body size ($\chi^2_1 = 6.225$, $P = 0.01$; Fig. 2b). The smallest and largest crocodiles in the acoustic dataset moved the shortest distances while undertaking routine behaviours, while the medium-sized crocodiles moved the farthest.

Stable isotopes

Discrimination factors were calculated for blood plasma, red blood cells, collagen and keratin tissues using samples from the captive crocodiles (Table 2). The $\Delta^{15}\text{N}$ values were greater than 1‰ (Student's *t*-tests: all $P < 0.01$), and the $\Delta^{13}\text{C}$ values were not different from 1‰ (Student's *t*-tests: all $P > 0.05$).

The composition of carbon and nitrogen stable isotopes in the wild crocodile tissues (Appendix S1) correlated with body size. Tissue $c\delta^{15}\text{N}$ composition formed a quadratic relationship with body size ($\chi^2_1 = 7.293$, $P = 0.006$; Fig. 3). This quadratic

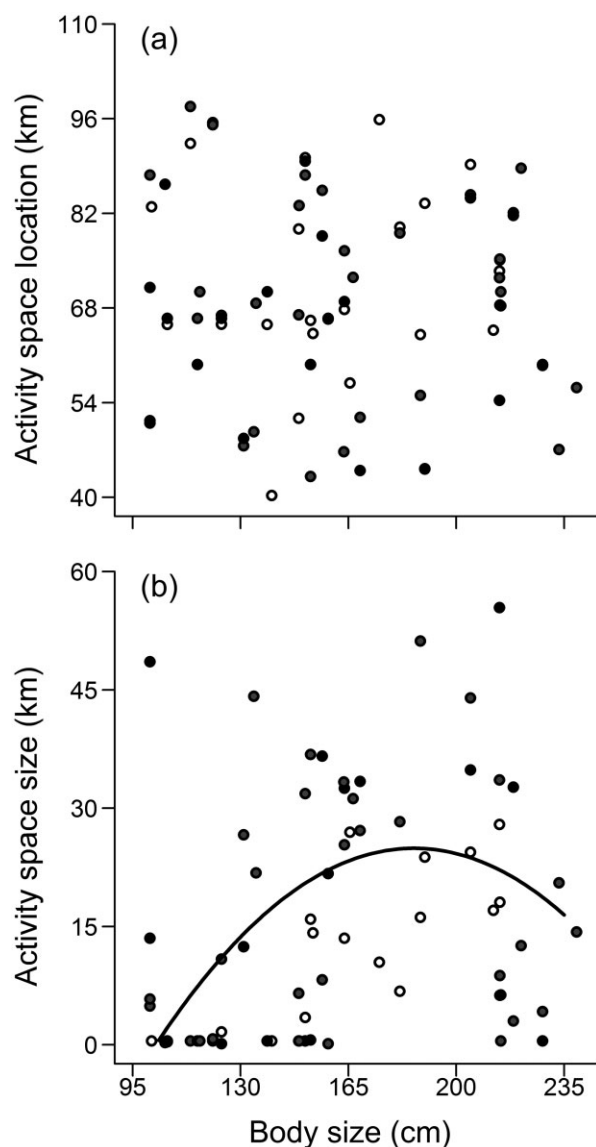


Fig. 2. Movement and home range patterns of *Crocodylus porosus*. (a) No evidence was found to indicate that body size (snout-vent length (SVL)) was correlated with activity space location (distance along river from river mouth), and (b) the relationship between body size (SVL) and activity space size (length of river occupied). Open circles are for measures calculated from detections in 2009, and filled circles are for measures from 2010 (grey) and 2011 (black). Fixed effects for activity space size = $(-0.004 \times \text{body size}^2) + (0.132 \times \text{body size}) - 98.374$.

relationship indicates that the medium-sized crocodiles had diets with greater $\text{c}\delta^{15}\text{N}$ values than those of smaller and larger crocodiles. There was no evidence to suggest that the relationship between $\text{c}\delta^{15}\text{N}$ composition and body size differed among blood plasma, red blood cells, collagen, or keratin tissues ($\chi^2_{10} = 6.585$, $P = 0.764$). The $\text{c}\delta^{13}\text{C}$ composition of crocodile tissues was linearly correlated with body size (quadratic:

Table 2. Diet-tissue discrimination factors for various *Crocodylus porosus* tissues

Tissue Type	Discrimination factor (‰)	
	$\Delta^{13}\text{C}$	$\Delta^{15}\text{N}$
Blood plasma	0.8 ± 1.0	2.7 ± 0.1
Red blood cells	0.6 ± 1.0	1.9 ± 0.1
Collagen	2.0 ± 1.0	3.3 ± 0.3
Keratin	1.4 ± 1.0	3.0 ± 0.5

Data represent mean and standard error (SE) for each discrimination factor.

$\chi^2_8 = 10.415$, $P = 0.237$, linear: $\chi^2_4 = 16.673$, $P = 0.002$; Fig. 4). Similar to $\text{c}\delta^{15}\text{N}$, the relationship between $\text{c}\delta^{13}\text{C}$ and body size did not differ among the tissue types ($\chi^2_3 = 0.644$, $P = 0.886$).

The tissue $\text{c}\delta^{13}\text{C}$ and $\text{c}\delta^{15}\text{N}$ WIC : TNW ratios were derived for each size class (Table 3; Fig. 5). All size classes had large $\text{c}\delta^{15}\text{N}$ WIC : TNW ratios, indicating that none of the crocodiles specialized on prey at particular trophic positions. However, the medium- and large-sized crocodiles had small WIC : TNW ratios for their tissue $\text{c}\delta^{13}\text{C}$ compositions, suggesting that they specialize on prey from specific habitats or food webs.

DISCUSSION

This study complements anecdotal observations and stomach content analyses by demonstrating that body size predicts the diet of *C. porosus* (Taylor 1979; Kar & Bustard 1981; Webb & Manolis 1989; Webb *et al.* 1991; Sah & Stuebing 1996). The study further shows that not only do *C. porosus* become trophically linked to primary producers in different habitats as they grow, but medium- and large-sized individuals also specialize on different prey within these food webs. In addition, no evidence was found to suggest that the crocodiles exhibit size-related spatial partitioning. These results tentatively suggest that in areas of high abundance along the Wenlock River, the impact of *C. porosus* may be considerable given the diverse range of potential prey items indicated by their isotopic composition.

To facilitate the interpretation of the results, hereafter, wild crocodiles in the acoustic telemetry and stable isotope datasets will be referred to using four size classes (the three size classes used for the individual specialization analyses and a larger size class: small, $\text{SVL} < 110$ cm; medium, $110 \text{ cm} < \text{SVL} < 160$ cm; large, $160 \text{ cm} < \text{SVL} < 188.5$ cm; and very large, $\text{SVL} > 188.5$ cm). Individuals in each of these size classes were present in both datasets, with the exception of the largest size class for which only acoustic data were obtained. The $\text{c}\delta^{13}\text{C}$ and $\text{c}\delta^{15}\text{N}$ composition of the *C. porosus* in the study indicated that individuals

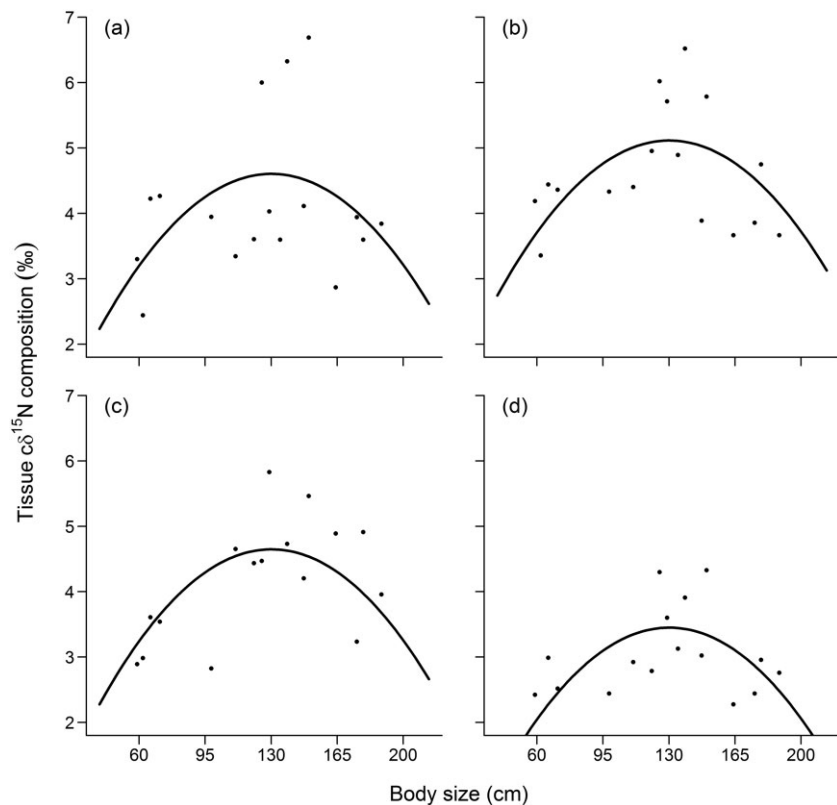


Fig. 3. The relationship between $c\delta^{15}N$ and body size (snout–vent length (SVL)) in *Crocodylus porosus*. (a) Blood plasma ($c\delta^{15}N$ (‰) = $(-0.0003 \times \text{body size}^2) + (0.074 \times \text{body size}) - 0.23$), (b) red blood cells ($c\delta^{15}N$ (‰) = $(-0.0003 \times \text{body size}^2) + (0.074 \times \text{body size}) - 0.28$), (c) collagen ($c\delta^{15}N$ (‰) = $(-0.0003 \times \text{body size}^2) + (0.074 \times \text{body size}) - 0.187$), (d) keratin ($c\delta^{15}N$ (‰) = $(-0.0003 \times \text{body size}^2) + (0.074 \times \text{body size}) - 1.385$). Coefficients are for fixed effects. Outlier excluded from analysis not shown.

Table 3. Measures of dietary niche width and individual specialization in *Crocodylus porosus*

Size class	Tissue composition									
	$c\delta^{13}C$					$c\delta^{15}N$				
	TNW	WIC	BIC	WIC/TNW	P	TNW	WIC	BIC	WIC/TNW	P
Small	1.178	0.666	0.512	0.566	0.056	0.63	0.455	0.175	0.723	0.271
Medium	7.735	0.569	7.166	0.074	<0.001	1.2	0.691	0.51	0.575	0.057
Large	1.561	0.497	1.064	0.318	0.003	0.623	0.55	0.073	0.883	0.665

Data represent total niche width (TNW), the within individual component (WIC) and between individual component (BIC) of niche width for three different size classes (small: SVL < 110 cm, medium: 110 cm < SVL < 160 cm, large: 160 cm < SVL < 188.5 cm). Significant *P*-values indicate that a given size class exhibits individual specialization.

consumed a range of diets according to their body size. While we do not have isotope data specific to prey in the Wenlock River, several recent studies in nearby river systems can be used to guide the interpretation of the crocodile isotope data. Small crocodiles typically had low $c\delta^{13}C$ and $c\delta^{15}N$ compositions (all samples mean -25.3‰ $c\delta^{13}C$ and 3.3‰ $c\delta^{15}N$) suggesting that they feed on herbivorous aquatic prey in riverine habitats (Jardine *et al.* 2012) and/or terrestrial prey that

feed predominantly on C-3 plants (cf. Vander Zanden & Rasmussen 2001; Murphy & Bowman 2009) such as herbivorous invertebrates (mean $-26.4 \pm 4.8\text{‰}$ SD $c\delta^{13}C$; mean $3.7 \pm 2.0\text{‰}$ SD $c\delta^{15}N$; TD Jardine, unpublished data, 2009, 2010). The tissue $c\delta^{13}C$ and $c\delta^{15}N$ compositions of the medium-sized crocodiles were greater than the small crocodiles (all samples mean -21.1‰ $c\delta^{13}C$ and 4.6‰ $c\delta^{15}N$). This indicates that they consumed similar diets to the small

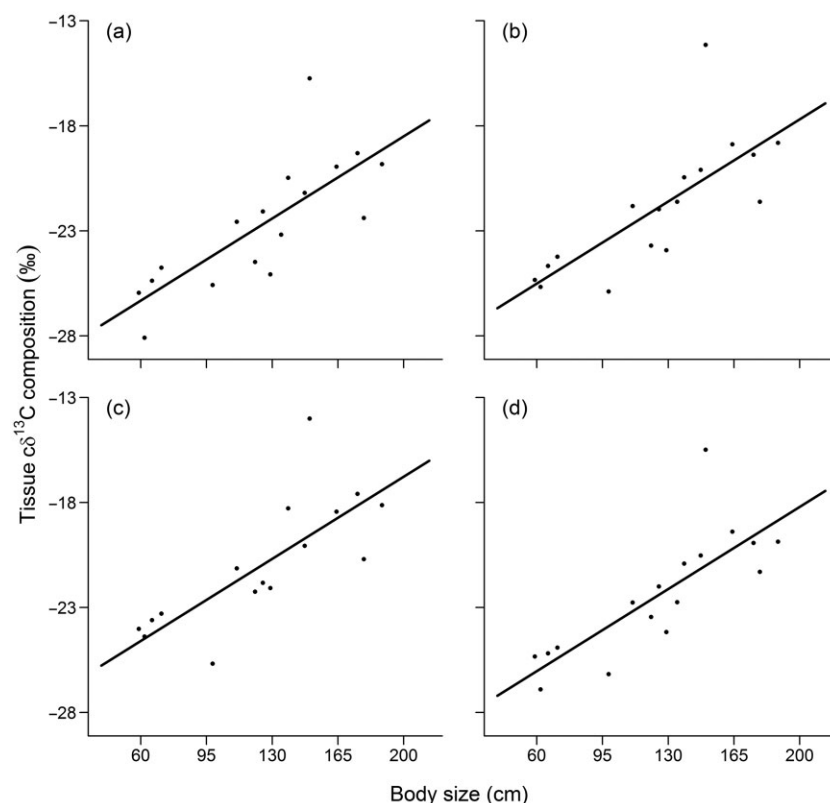


Fig. 4. The relationship between $\delta^{13}\text{C}$ and body size (snout–vent length (SVL)) in *Crocodylus porosus*. (a) Blood plasma ($\delta^{13}\text{C}$ (‰) = $(0.056 \times \text{body size}) - 29.674$), (b) red blood cells ($\delta^{13}\text{C}$ (‰) = $(0.056 \times \text{body size}) - 28.863$), (c) collagen ($\delta^{13}\text{C}$ (‰) = $(0.056 \times \text{body size}) - 27.945$), (d) keratin ($\delta^{13}\text{C}$ (‰) = $(0.056 \times \text{body size}) - 29.384$). Coefficients are for fixed effects. Outlier excluded from analysis not shown.

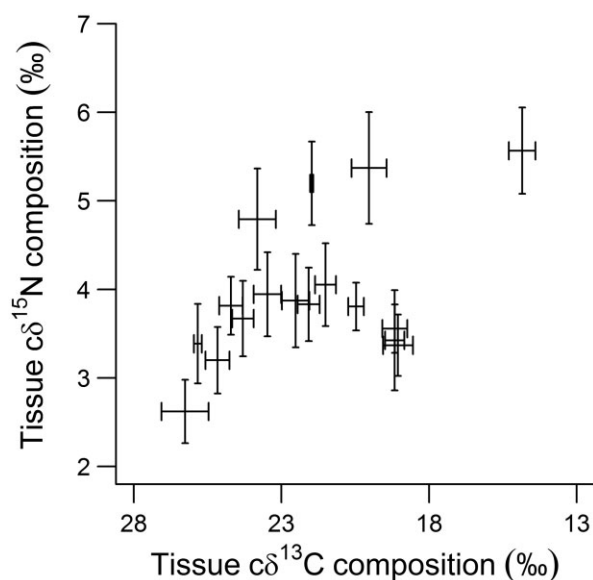


Fig. 5. The mean \pm standard error (SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each individual *Crocodylus porosus* based on blood plasma, red blood cells, collagen and keratin samples.

crocodiles, but supplemented their diets with prey from a slightly higher trophic level (cf. DeNiro & Epstein 1981; Post 2002; Abrantes & Sheaves 2010), such as predatory fishes (cf. Jardine *et al.* 2012).

The large crocodiles had greater $\delta^{13}\text{C}$ but lower $\delta^{15}\text{N}$ than the medium-sized crocodiles (all samples mean -19.7‰ $\delta^{13}\text{C}$ and 3.6‰ $\delta^{15}\text{N}$). These values for the large individuals can be derived from a mixture of three dietary sources known to be available in riverine landscapes. The first is terrestrial herbivores that consume C-4 grasses (Grocke *et al.* 1997; Murphy & Bowman 2009). Grazers of C-4 grasses are known to have high $\delta^{13}\text{C}$ (mean -14.1‰ $\delta^{13}\text{C}$) and low $\delta^{15}\text{N}$ ($<2\text{‰}$) in relatively wet savanna regions (Grocke *et al.* 1997; Codron *et al.* 2007) such as the Wenlock River. A second source is fish from temporary floodplain habitats (mean $-24.2 \pm 3.4\text{‰}$ SD $\delta^{13}\text{C}$; mean $8.6 \pm 1.5\text{‰}$ SD $\delta^{15}\text{N}$; TD Jardine, unpublished data, 2009, 2010). A final source is marine vertebrates that feed at low trophic positions (Post 2002; Abrantes & Sheaves 2010; Jardine *et al.* 2012), such as herbivorous fish (mean $-20.4 \pm 1.7\text{‰}$ SD $\delta^{13}\text{C}$; mean $8.0 \pm 0.6\text{‰}$ SD $\delta^{15}\text{N}$; TD Jardine, unpublished data, 2009, 2010). Large crocodiles therefore potentially consume prey from three distinct food webs and link terrestrial,

freshwater and saltwater ecosystems. These findings can be supported by anecdotal observations of large *C. porosus* consuming cattle, kangaroos, and marine and freshwater fish (Kar & Bustard 1981; Webb & Manolis 1989). Our interpretations were restricted to the feeding habits of *C. porosus* during the dry season. Since *C. porosus* in other areas have been shown to take advantage of seasonal prey abundance (e.g. *Pseudogobius* sp. in Taylor 1979), future studies will be required to characterize annual dietary variation in *C. porosus* inhabiting the Wenlock River.

The low WIC : TNW ratios for tissue $\delta^{13}\text{C}$ compositions for medium- and large-sized crocodiles indicate that they specialize on prey that are trophically linked to primary producers in different habitats. In contrast, the small-sized individuals had large WIC : TNW ratios for their tissue $\delta^{13}\text{C}$ compositions. This result suggests that small-sized individuals trophically link different habitats, as reported in other populations where they consume tiny fish from aquatic habitats and insects from terrestrial habitats (Sah & Stuebing 1996). Because of the high connectivity among habitats within these wet-dry tropical landscapes, mediated by fish and other mobile prey (Jardine *et al.* 2012), food sources from all potential habitats would be available to crocodiles at all of our study points along the freshwater–marine interface. This would allow them to feed on prey according to their body size, regardless of where in the freshwater–marine continuum their activity space lies, and without having to travel to isotopically distinct habitats. Thus, as a population, *C. porosus* in the Wenlock River appear to link different habitats, with different individuals feeding in freshwater, terrestrial and marine food webs, but only small-sized individuals consume a considerable amount of prey from more than one of these food webs. Given that substantial size-related variation in diet was also detected, individual specialization probably has a lesser role in determining the diets of these crocodiles than their body size. Individual specialization and its consequences for habitat linkages in *C. porosus* require further investigation.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of multiple tissues reflects variation in diet over time (Tieszen *et al.* 1983). The duration of this snapshot relates to the difference in the assimilation rates of the sampled tissues, whereby using tissues with faster and slower turnover yields a larger window than using tissues with similar turnover. Although assimilation rates have not yet been derived for *C. porosus*, blood plasma has an average residence time of 90.9 days for $\delta^{13}\text{C}$ and 90.1 days for $\delta^{15}\text{N}$ and whole scale crests have an average residence time of 212.8 days for $\delta^{13}\text{C}$ and 149.3 days for $\delta^{15}\text{N}$ in *A. mississippiensis* (Rosenblatt & Heithaus 2013; converted from turnover rates using del Rio & Anderson-Sprecher 2008). Based on these assimilation rates, even a conservative estimate of assimilation rates in

C. porosus along with the isotopic composition of the *C. porosus* tissues would suggest that none of the size classes underwent a substantial change in diet at the start of the dry season (June–July). These patterns might be attributed to the cooler temperatures associated with the dry season, which could affect their activity levels and in turn their feeding strategies and diet.

Body size was not correlated with the location of a crocodile's activity space along the river. This result indicates that the population of *C. porosus* inhabiting the Wenlock River does not exhibit size-related spatial partitioning during the early-mid section of the dry season. However, only the movements of crocodiles between 160 and 240 cm SVL were monitored, and so any size-related spatial partitioning between smaller and larger sized individuals present in the study area would not have been detected by our analyses. Nevertheless, the movement patterns of the size classes that were monitored are in contrast to other Australian *C. porosus* populations in the Northern Territory (see Letnic 2008; Nichols & Letnic 2008). These different spatial patterns could be attributed to differences in their habitats because the Wenlock River ecosystem differs substantially from the grassy floodplain systems of the Northern Territory. Alternatively, these differences could be attributed to the use of different methods (tracking *vs.* spotlight survey counts), which only provide a snapshot of the population at a specific time interval and do not provide any index of movement or space use.

Large-sized crocodiles, whose movements were tracked by acoustic telemetry, had an activity space that was greater than the small, medium and very large crocodiles. This variation in space use may result from differences in feeding strategy and intra-specific aggression (adults of *C. porosus* often act aggressively towards smaller individuals; Messel & Vorlicek 1986). Very large crocodiles may have been able to monopolize specific parts of the river that provide them with access to key resources, such as riverbanks where they can ambush large terrestrial vertebrates that approach the river to drink (Kar & Bustard 1981), and as such would not need to forage over a large area. Large-sized crocodiles, on the other hand, may not have been able to access areas guarded by the very large crocodiles, and may therefore had to forage over a wider area, as observed in satellite telemetry studies (Campbell *et al.* 2013). As they traverse over large areas, based on the individual specialization analyses, the large-sized individuals seem to forage for resources from specific food webs. Further study is needed to determine the tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions of crocodiles in the very large size class to confirm this hypothesis.

This study has several limitations. First, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions of potential prey items in the Wenlock River were not sampled, and specific prey

items were not identified. But the diets of non-adult *C. porosus* have been well characterized by conventional analysis (see Taylor 1979; Webb *et al.* 1991; Sah & Stuebing 1996), and the main aim of the study was to provide unique insight into the feeding ecology of *C. porosus* to complement previous work. Second, the diet and movement data were not collected from the same set of crocodiles. However, each cohort involved a fairly large sample size and significant relationships were detected. Third, the discrimination factors were derived using a small sample size. This may introduce uncertainty into the discrimination factors and, in turn, the dietary analyses and interpretations regarding the wild crocodiles. However, the captive crocodiles were raised on a single diet since hatchlings which makes these discrimination factors comparable to those derived in other studies. Moreover, only the analyses that related to temporal variation in diet (i.e. differences in isotopic composition between tissues and their interaction with body size) would be compromised – the analyses regarding individual specialization and size-related variation in diet would be unaffected.

The tissue $\delta^{15}\text{N}$ compositions of the wild *C. porosus* indicate a change in diet at approximately 130 cm SVL. This change in diet also occurs in similarly sized *C. niloticus* (Radloff *et al.* 2012), even though these species occur in different habitats (Steel 1989) and consume different prey (cf. Cott 1961; Hutton 1987; Wallace & Alison 2008). Since these species are morphologically similar (Brochu 2001; Erickson *et al.* 2012, 2013), this shared diet change further suggests that ontogenetic development – presumably feeding behaviour – plays a major role in inter-specific size-related variation in diet for crocodilians.

Combining acoustic telemetry with stable isotope analysis showed that body size was a more important driver for variation in diet than size-related spatial partitioning. Different size classes consumed prey from different food webs and trophic positions, and individuals specialized in feeding on these specific prey items. This size-related and individual-level variation in diet will no doubt have implications for the influence that crocodile populations have on energy flow and prey densities along tropical savanna rivers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Wild *Crocodylus porosus* tissue sample and body size data.