

# Size, sex and individual-level behaviour drive intrapopulation variation in cross-ecosystem foraging of a top-predator

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## Summary

1. Large-bodied, top-predators are often highly mobile, with the potential to provide important linkages between spatially distinct food webs. What biological factors contribute to variation in cross-ecosystem movements, however, have rarely been examined.

2. Here, we investigated how ontogeny (body size), sex and individual-level behaviour impacts intrapopulation variation in cross-ecosystem foraging (i.e. between freshwater and marine systems), by the top-predator *Alligator mississippiensis*.

3. Field surveys revealed *A. mississippiensis* uses marine ecosystems regularly and are abundant in estuarine tidal creeks (from 0.3 to 6.3 individuals per km of creek,  $n = 45$  surveys). *Alligator mississippiensis* captured in marine/estuarine habitats were significantly larger than individuals captured in freshwater and intermediate habitats.

4. Stomach content analysis (SCA) showed that small juveniles consumed marine/estuarine prey less frequently (6.7% of individuals) than did large juveniles (57.8%), subadult (73%), and adult (78%) size classes. Isotopic mixing model analysis (SIAR) also suggests substantial variation in use of marine/estuarine prey resources with differences among and within size classes between sexes and individuals (range of median estimates for marine/estuarine diet contribution = 0.05–0.76).

5. These results demonstrate the importance of intrapopulation characteristics (body size, sex and individual specialization) as key determinants of the strength of predator-driven ecosystem connectivity resulting from cross-ecosystem foraging behaviours. Understanding the factors, which contribute to variation in cross-ecosystem foraging behaviours, will improve our predictive understanding of the effects of top-predators on community structure and ecosystem function.

**Key-words:** *Alligator mississippiensis*, crocodylian, diet, ecosystem connectivity, estuary, food web, individual specialization, trophic coupling

## Introduction

Large-bodied top-predators exert pervasive top-down effects within food webs, thereby affecting ecosystem structure and function. Effects of these consumers are propagated by a range of mechanisms including consumptive and non-consumptive interactions with prey, and the translocation of nutrients, among others (Terborgh *et al.* 2010; Rosenblatt *et al.* 2013a). Large-bodied predators are often highly mobile and can link spatially distinct habitats while

acquiring prey, increasing connectivity between ecosystems. Predator-driven linkages have important ecological implications; for instance, these linkages are hypothesized to stabilize food webs by dampening population oscillation cycles (e.g. McCauley, Wilson & de Roos 1996; Loreau & Holt 2004; McCann, Rasmussen & Umbanhowar 2005). An understanding of factors regulating the occurrence and strength of predator-driven connectivity can inform predictions of when and where these species may influence structure and function of interconnected communities and ecosystems (e.g. Huxel & McCann 1998; Leroux & Loreau 2008; Rooney, McCann & Moore 2008).

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A rich body of literature exists regarding ecological implications and importance of cross-ecosystem linkages in the form of bottom-up subsidies, such as nutrients and prey (e.g. Polis & Hurd 1996; Huxel & McCann 1998; Jefferies 2000). Nutrient subsidies are most important when linkages are between nutrient-limited and more productive nutrient- or prey-rich ecosystems and can provide important subsidies (e.g. Polis & Hurd 1996; Aderson & Wait 2001; Barrett *et al.* 2005). For example, species of anadromous fish can transfer pelagic marine-derived nutrients to inland oligotrophic freshwater ecosystems (Bilby, Fransen & Bisson 1996). This subsidy is further mediated by the consumption of anadromous fish and translocation of nutrients via excretion by *Ursus arctos* Linnaeus 1758 (brown bear) and other predators to the surrounding terrestrial landscape (Hilderbrand *et al.* 1999; Helfield & Naiman 2001, 2006). More recently, however, the implications of ecosystem connectivity mediated by highly mobile top-predators has received increased attention due to the broad spatial scale over which their effects can be propagated and the range of other species that could be affected (Lundberg & Moberg 2003; McCauley & Young 2012). Mobile predators can exert strong top-down pressure in ecosystems, potentially inducing shifts in prey abundance, behaviour and habitat use. These effects can then cascade down food chains to influence primary producer abundances and distributions and result in changes in community structure and ecosystem function (Estes *et al.* 1998; McCoy, Barfield & Holt 2009; Burkholder *et al.* 2013; Nifong & Silliman 2013).

Within predator populations, individuals are known to vary in their use of habitat and food resources due to ontogeny, sex and individual specialization which can have significant implications for food web dynamics and community structure and function (e.g. McCauley, Wilson & de Roos 1996; Persson *et al.* 1998; Bolnick *et al.* 2011). Organisms with complex life cycles (Wilbur 1980), particularly common in species with extreme differences in body size through ontogeny, often undergo major changes in their ecology and behaviour (Werner & Gilliam 1984). Associated ontogenetic shifts in resource use can result from increased mobility (McCauley, Wilson & de Roos 1996), differential resistance or tolerance to abiotic stresses (Blanckenhorn 2000), or the release from gape limitation in larger individuals (Werner & Gilliam 1984; Scharf, Juanes & Rountree 2000). The effects of these ontogenetic shifts may increase ecosystem connectivity, as larger individuals have the ability to use a broader range of habitat types and prey resources. Alternatively, sexual dimorphisms and individual specialization may limit or promote ecosystem connectivity depending on the specific differences in behaviour and resource use among sexes and/or individuals (Araújo, Bolnick & Layman 2011; Bolnick *et al.* 2011). In this study, we examine short- (~1 month) and long-term (~1 year) intrapopulation variation in cross-ecosystem foraging behaviour of a mobile top-predator, *Alligator mississippiensis* Daudin 1801 (Ameri-

can alligator), in a coastal system of the south-eastern United States.

*Alligator mississippiensis* undergoes ten- to fifteen-fold increases in body size (i.e. total length) through ontogeny and can move great distances (10's of km) over both short and long temporal scales (Woodward *et al.* 1995; Lance *et al.* 2011; Rosenblatt & Heithaus 2011). *Alligator mississippiensis* inhabits a broad geographic range along the Atlantic coastal plain of the south-eastern United States, reaching from the Rio Grande River basin in Texas to the Albemarle Sound in North Carolina (Ross & Ernst 1994). Throughout its' native range, *A. mississippiensis* occupies a wide variety of freshwater habitats. While lacking lingual salt glands that are maintained in species of true crocodiles (family: crocodylidae) to assist in osmoregulation (Taplin & Grigg 1981; Taplin *et al.* 1982), *A. mississippiensis* frequent brackish (salinity 5 to 25 ppt) to fully marine (salinity > 25 ppt) habitats including tidal rivers and creeks, saltmarshes, mangroves, estuaries, beaches and dune swales (Mazzotti & Dunson 1989; Rosenblatt & Heithaus 2011; Nifong & Silliman 2013); even being sighted as far as 63 km from land (Else 2005). Given these observations and the physiological constraints *A. mississippiensis* face, it is apparent that while able to tolerate the higher salinities of marine and estuarine habitats, *A. mississippiensis* is reliant on freshwater for osmoregulation and survival. Thus, the movements of *A. mississippiensis* potentially establish a two-way linkage between coastal freshwater and marine/estuarine ecosystems as individuals that travel into marine/estuarine ecosystems must return to seek out fresh or low salinity water for osmoregulation.

The movement patterns of adult *A. mississippiensis* inhabiting coastal ecosystems have been studied in the Shark River Estuary of the Florida Everglades (Rosenblatt & Heithaus 2011; Rosenblatt *et al.* 2013b) and Sapelo Island, Georgia (Nifong, Layman & Silliman 2014) using acoustic as well as GPS telemetry. In each of these studies, researchers found individuals that travelled into marine/estuarine ecosystems always returned to fresh or low salinity habitats. While the temporal dynamics of the duration and frequency of trips to marine/estuarine habitats and return trips to low salinity habitats varied among populations and individuals, the overall pattern of repetitive back-and-forth movements between systems was consistent. However, these patterns have only been examined in adult individuals (mostly males), and little is known about intrapopulation variation in these behaviours.

While many anecdotal accounts exist, few studies have directly assessed intrapopulation variation in the use of marine/estuarine habitats by coastal populations (e.g. Rootes *et al.* 1991; Rosenblatt & Heithaus 2011; Rosenblatt *et al.* 2013b; Nifong *et al.* 2014), and no studies have explicitly addressed variation in cross-ecosystem foraging behaviours between upland freshwater wetlands and marine/estuarine habitats in Atlantic barrier island systems. Here, using stomach content (short term) and

stable isotope (long term) analyses, we assess variation in the use of marine/estuarine ecosystems by *A. mississippiensis* in a population inhabiting a barrier island off the coast of Georgia, USA. Specifically, we asked the following questions: (i) Do coastal alligator populations use marine/estuarine habitat and prey resources to a significant degree? (ii) Does cross-ecosystem foraging vary through ontogeny and/or differ between sexes? (iii) Is there evidence of individual-level variation in cross-ecosystem foraging?

## Materials and methods

### STUDY SITE

This study was conducted within saltmarshes and upland ecosystems encompassed by the Sapelo Island National Estuarine Research Reserve (SI-NERR) and Georgia Coastal Ecosystems Long Term Ecological Research station at Sapelo Island, Georgia, USA (31.455779°N, -81.256115°W, Fig. 1). The 6777 ha barrier island system is the fourth largest of Georgia's barrier islands (Sullivan, Hurley & Mason 2008). Separated from the mainland by approximately 7 km of saltmarsh, lagoon and tidal

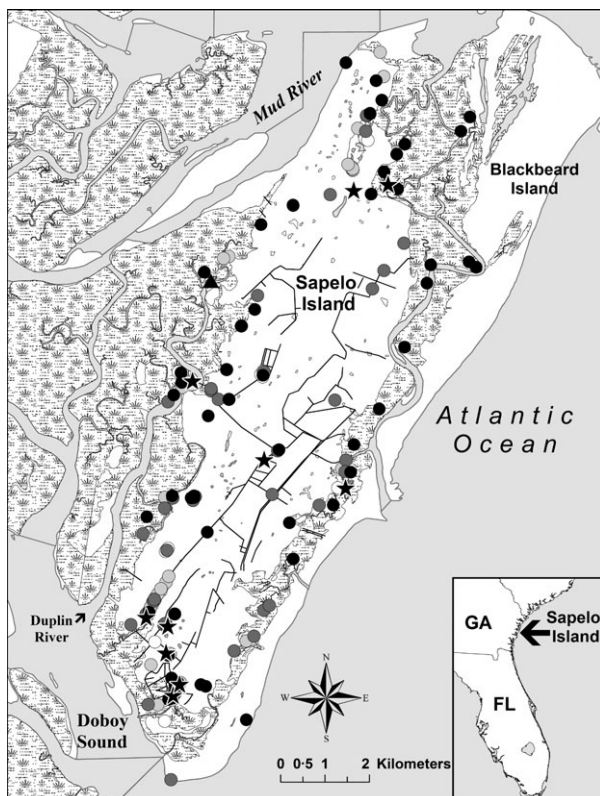
creek habitats, the 4411 ha of upland habitats are a mixture of maritime hardwood forest, pine savanna, scrub and dune ecosystems, as well as numerous freshwater wetlands, mosquito ditches, marshes and ponds. Sapelo Island is bordered by expansive tidal saltmarshes dominated by mono-specific stands of *Spartina alterniflora* Loisel to the west and the Atlantic Ocean and the smaller Blackbeard Island to the east.

### NIGHTLIGHT SURVEYS

We employed nightlight surveys to estimate relative abundance and identify general patterns in habitat use. Our methodology followed guidelines established by the Florida Fish and Wildlife Conservation Commission. Surveys were initiated 1 h post-sunset and were terminated prior to 0200 h. While travelling at slow speeds (~4 knots), we used one 200 000 candle power spot light (Brinkmann Corporation, Dallas, TX, USA) to identify eyeshines of individuals. Surveys were performed during the months of June to August of 2008 and 2009 within nine tidal creeks surrounding Sapelo Island. Surveys were repeated a total of five times in each creek, no less than 2 weeks apart to be considered independent (Woodward & Marion 1978). Each survey was performed by the same observers and same equipment (i.e. lights and boat) to avoid sighting bias among surveys. Observation of alligators during high tide was difficult due to complex morphology and tidal amplitude within tidal creeks (typical amplitude = 2–3 m); thus, we restricted surveys to within 2 h of low tide to control for tidal effects. Detectability of *A. mississippiensis* has not been quantified for saltmarsh habitats; therefore, we report raw counts of individuals per kilometre of creek surveyed. Raw count data should be considered highly conservative estimate of true population abundance/density. Furthermore, because of the relatively low the number of surveys per creek ( $n = 5$ ), we may have underestimate the amount of variation in number of individuals counted.

### ALLIGATOR CAPTURE AND TISSUE/FLUID SAMPLING

Alligators were captured opportunistically using standard crocodylian capture techniques (i.e. noose, snatch hook, hand). Following capture, morphometric measurements were taken [head length (HL), head width (HW), snout-to-vent length (SVL), total length (TL) and tail girth (TG)] to the nearest 0.01 cm and sex determined by cloacal examination and/or palpation. To establish long-term individual markings and analyse keratinized skin tissue for stable isotopes, three caudal scutes were removed using a sterile scalpel (one from each of the three caudal scute whorls in a systematic fashion corresponding to an individual-specific numeric code). Scute samples were immediately placed on ice and transferred to a -10 °C freezer until further processing. Aquatic habitats greater than 15 ppt salinity were classified as marine/estuarine (salinity was measured using STX-3 handheld refractometer at the site of capture, VEE GEE Scientific, Kirkland, WA), aquatic habitats with salinity ranging from 5 ppt to 15 ppt were classified as intermediate, and all aquatic habitats with salinity less than 5 ppt were classified as freshwater. Terrestrial habitats were classified as intermediate since they geographically lie between freshwater and marine/estuarine habitats and individuals captured in these areas are potentially moving between separate freshwater wetlands or between freshwater wetlands and marine/estuarine habitats.



**Fig. 1.** Map of Sapelo Island, Georgia. Filled circles are capture locations of individual *A. mississippiensis* (small juvenile-white, large juvenile – light grey, subadult – dark grey and adult – black). Black stars are primary producer and prey isotope sample collection sites. The black triangle is the location of SI-NERR hydrological monitoring station HD\_Hydro. Inset map indicates relative position of Sapelo Island on the south-eastern Atlantic coast USA.

## STOMACH CONTENT ANALYSIS

When possible, stomach contents were collected from captured individuals via gastric lavage (for full description see Fitzgerald 1989). The hose–Heimlich technique has been shown to be successful at removing 91 to 100% of stomach contents (for discussion of efficiency see Nifong *et al.* 2012). Diets of size classes were quantified using three measures: frequency of occurrence (% FO, proportion of stomachs containing one or more prey from a prey category divided by the number of stomachs), numerical abundance (%N, total number of prey items that belong to a prey category divided by the total number of prey) and gravimetric abundance (%M, total wet mass of a given prey category divided by the total wet mass of all prey recovered). Further details of stomach content analysis (SCA) are reported in Appendix S1 (Supporting information).

## STABLE ISOTOPE ANALYSIS

Stable isotope analysis is used to elucidate patterns in food webs structure and habitat use (Layman *et al.* 2012), as the isotopic composition of consumer tissues closely tracks the isotopic composition of the consumer's diet once adjusted for changes due to isotopic discrimination during metabolism (Deniro & Epstein 1978; Peterson & Fry 1987). The ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$  (expressed relative to a standard as  $\delta^{15}\text{N}$ ) is most often used to infer trophic position due to the preferential excretion of lighter  $^{14}\text{N}$  during protein synthesis and resulting stepwise enrichment of  $^{15}\text{N}$  in consumer tissues (Minagawa & Wada 1984; Post 2002), while the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  is used to indicate use of particular carbon pools and/or resources, since  $\delta^{13}\text{C}$  varies substantially across primary producers differing in photosynthetic pathways ( $\text{C}_3$  vs.  $\text{C}_4$ , O'Leary 1981) and changes relatively little during trophic transfers ( $1\text{‰} \pm 1\text{ SD}$ , (Peterson & Fry 1987; Tieszen *et al.* 1983). Detailed methods for stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) sample collection and analysis of *A. mississippiensis* keratinized scute tissue and representative prey and primary producers are reported in Appendix S1 (Supporting information).

## ESTIMATING PROPORTIONAL USE OF PREY RESOURCES

We used a Bayesian isotopic mixing model within the 'siar' package (version 4.2, Parnell & Jackson 2013) of R (hereafter SIAR) to estimate the proportion of prey resources contributing to the diet of *A. mississippiensis* subpopulation groups. The Bayesian framework used by SIAR allows for uncertainty to be incorporated into model parameters by allowing for variation in the isotopic signatures of consumers, end member sources (prey) and trophic enrichment factors – TEF (i.e.  $\Delta^{13}\text{C}$  and  $\Delta^{15}\text{N}$ , the change in isotopic value during metabolism and incorporation into consumer tissues, also known as discrimination factors Pecquerie *et al.* 2010). We used TEFs determined for *A. mississippiensis* keratinized scute tissue by Rosenblatt & Heithaus (2013):  $\Delta^{13}\text{C}_{\text{tissue-diet}} = 0.61\text{‰} \pm 0.12$  and  $\Delta^{15}\text{N}_{\text{tissue-diet}} = 1.22\text{‰} \pm 0.08$  (mean  $\pm$  SD). The TEFs reported for keratinized scute tissue of *A. mississippiensis* by Rosenblatt & Heithaus (2013) are similar to another species of alligatorid, *Caiman latirostris* Daudin 1801 (Broad-snouted caiman), reported by Marques *et al.* (2014). Given only one study has attempted to estimate these values for *A. mississippiensis*, little

is known about variation in TEFs due to age/size, sex, or habitat; however, due to the Bayesian framework of the SIAR model, this parameter's value is free to vary during every iteration and variation is incorporated into the uncertainty of the results.

Model fitting within SIAR is performed using a Markov chain Monte Carlo (MCMC) procedure, producing posterior probability distributions of plausible proportional contributions of sources (prey) to the consumer diet (for detailed formulation see (Parnell *et al.* 2010). We used 500 000 iterations in our MCMC with a burn-in of 50 000 and a thinning interval of 15, resulting in posterior distribution of 30 000 estimates of proportional source contributions to each subpopulation group. To increase model performance and reduce uncertainty in the model predictions (Phillips & Gregg 2003; Phillips, Newsome & Gregg 2005), isotopic values of prey were aggregated into one of two major categories, either freshwater/upland or marine/estuarine categories (similar to SCA). Prey species that have the ability to move between freshwater and marine/estuarine ecosystems (e.g. raccoons, wading birds, etc.) were categorized as marine/estuarine prey due to fact that their tissue isotope values closely resembled isotope values of prey which exclusively forage on marine/estuarine resources. For example, raccoon (*Procyon lotor* Linnaeus 1758) are known to forage within marine/estuarine habitats as well as upland forests and wetlands, but  $\delta^{13}\text{C}$  values (mean  $\pm$  SD,  $-19.7 \pm 1.3\text{‰}$ ,  $n = 12$ ) were similar to saltmarsh consumers such as *Armases cinereum* Bosc 1802 (Grey marsh crab,  $-18.1 \pm 2.0\text{‰}$ ,  $n = 8$ ) and *Ilyanassa obsoleta* Say 1822 (Mud snail,  $-17.6 \pm 0.7\text{‰}$ ,  $n = 3$ ) (see Table S2).

To assess differences in use of prey categories due to size and sex, we first grouped *A. mississippiensis* isotopic values into three size classes [juvenile (TL < 100 cm), subadult (100 < TL < 183 cm) and adult (TL > 183 cm)] based on previous dietary studies and known ontogenetic shifts in behaviour (e.g. Gabrey 2010). We then used threshold analysis to test for significant changes in mean and variance of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  due to total length (cm) within each of the three size classes. If a significant change was detected, we further subdivided the size class above and below the indicated size threshold. Size classes were further separated by sex prior to SIAR analysis. To examine contributions of freshwater/upland and marine/estuarine prey to the population diet, we first ran the SIAR model using isotope values of all individuals. We then estimated proportional end member contributions to the diet of each *A. mississippiensis* subpopulation group independently (i.e. males and females within each size class).

We compared SIAR model output resulting from two methods of calculating the mean and standard deviations for end member isotopic values used in the model. Firstly, a simple mean and standard deviation was calculated using isotopic values from all prey species identified across all individuals during SCA within each source group. We then calculated a weighed mean and standard deviation using the proportion of recovered prey biomass per size class as weighting factors in the calculation.

To assess significant differences in SIAR marginal posterior distributions resulting from the use of different end member value calculations, we used the following procedure: Firstly, for marginal posterior distributions of proportional diet contributions estimated using different end member value calculations given by X1 and X2, we defined a new transformed distribution  $Y = X1 - X2$ . The newly transformed distribution Y was

calculated using a numerical approximation of the joint density transformation (Hopkins *et al.* 2014). We then calculated the amount of probability (i.e. the area under the curve) less than zero  $P(Y < 0)$  and approximated two-sided  $P$ -values by calculating  $2 * P(Y < 0)$ . Significant differences were evaluated at  $\alpha = 0.05$ . All analyses were performed in R 3.0.1 (R Core Development Team 2013).

#### ESTIMATING NICHE SPECIALIZATION

To assess niche specialization and examine the potential for individual-level variation in foraging behaviours, we calculated the specialization index ( $\epsilon$ ) using posterior distributions from our Bayesian isotope mixing model (SIAR) analysis (for details regarding formulation of these metrics, see Newsome *et al.* 2012). Specialization index ( $\epsilon$ ) varies from 0 to 1 and measures the degree of dietary specialization at the population or group level, a value of 0 indicates consumers are complete generalists (i.e. feed on all available prey resources in equal proportions) and a value of 1 indicates consumers are ultra-specialists (i.e. feed on a small subset of available prey resources). Due to how  $\epsilon$  is calculated, this metric does not indicate which prey resource individuals specialize on. We first calculated  $\epsilon$  for the entire population and then calculated  $\epsilon$  separately for each subpopulation group (each sex within each size class) to draw comparisons.

## Results

#### NIGHTLIGHT SURVEYS AND ALLIGATOR CAPTURES

We performed nightlight surveys to estimate relative abundance of alligators in saltmarsh tidal creeks branching inward from two tidal rivers (Duplin and Blackbeard) surrounding Sapelo Island. Length of survey routes ranged from 2.2 to 11.8 km (mean  $\pm$  SD, 4.5 km  $\pm$  2.9,  $n = 9$ ). Daily mean water salinity during surveys was 27.8 ppt  $\pm$  3.7 (SD) ( $n = 180$ , measured by YSI 6600 data logger at SI-NERR hydrological monitoring station HD\_Hydro located on the northern end of the Duplin River, 31.478692°N 81.273011°W, Fig. 1). Mean ( $\pm$ SE) relative abundance at our study site ranged from 0.4  $\pm$  0.1 to 5.0  $\pm$  0.9 ind.km<sup>-1</sup> ( $n = 5$  for each survey route) and was 1.9  $\pm$  0.2 ind.km<sup>-1</sup> across all surveys ( $n = 45$ , Fig. 2). Correlation between mean relative abundance and length of survey route was non-significant (Pearson's:  $r = -0.52$ ,  $n = 9$ ,  $P = 0.15$ ).

A total of 181 individuals were captured (57 captured in freshwater, 48 within intermediate and 76 in marine/estuarine habitats, Fig. 1) between 16-May-2007 and 30-July-2010. Total length (TL) of individuals ranged from 37.7 to 315.5 cm (mean = 138.5 cm  $\pm$  66.9 SD), over an 8-fold difference, and sex ratio was male biased (2.2:1, male: female). Individuals captured within marine/estuarine habitats were larger than individuals captured in freshwater (Mann Whitney  $U$ -test:  $U = 2843.5$ ,  $P = 0.002$ , 95% CI of difference = 8–45 cm) and intermediate habitats ( $U = 2398.5$ ,  $P = 0.003$ , 95% CI of difference = 10–54 cm); TL of individuals captured in

freshwater habitats was not significantly different from individuals captured in intermediate habitats ( $U = 1363$ ,  $P = 0.97$ , 95% CI of difference = -19–18 cm, Table 1).

#### STOMACH CONTENT ANALYSIS

Stomach contents were analysed from a total of ninety-nine individuals during 2008 and 2009 with individuals grouped by size class, yielding samples from 15 small juveniles (TL < 79 cm), 22 large juveniles (TL = 79–100 cm), 34 subadults (TL = 100–183 cm) and 28 adults (TL > 183 cm). For prey items, we present findings at the family-level for ease of comparison, with the exception of insects which are grouped as aquatic or terrestrial and all bird species which are grouped into the Order Aves (Table S1, Supporting information). Prey items were also broadly classified as either freshwater/upland or marine/estuarine based on species known habitat use patterns and observations during isotope sampling (see Appendix S1, Supporting information for details). Small juvenile alligators were found to consume marine/estuarine prey (% FO = 6.7%) less frequently than large juveniles (59.1%), subadult (73.5%), and adult (78.6%) size classes (chi-squared test:  $X^2 = 24.65$ , d.f. = 3,  $P < 0.001$ ). This pattern was also evident in recovered prey biomass (%M, such that marine/estuarine prey comprised 8.9% of recovered prey biomass from small juveniles and marine/estuarine prey comprised 57.8%, 94% and 90% of prey biomass recovered from large juveniles, subadult and adult size classes, respectively (Table S1, Supporting information).

Combined, insects (both aquatic and terrestrial) and crayfish (cambaridae: *Procambarus* sp. Ortman 1905) were the most frequently consumed freshwater/upland prey for both small and large juveniles, occurring in 93.3% and 86.5% of contents, respectively. The most frequently consumed marine/estuarine prey taxa by large juveniles were marsh and mud crabs (sesamidae (marsh): *Armases cinereum*, FO% = 31.8%; panopeidae (mud): *Panopeus herbstii* Milne-Edwards 1834 and *Eurytium limosum* Say 1818, combined FO% = 27.3%). Subadult *A. mississippiensis* were found to mainly consume various marine/estuarine prey taxa (%M = 94%), ranging in size from small grass shrimp to larger mammal, bird and fish species (see Table S1 for family identification, Supporting information). While freshwater/upland prey only accounted for 6% of subadult prey biomass, their remains were frequently found, occurring in 67% of subadult contents (chiefly insects and crayfish). Adult *A. mississippiensis* consumed a range of prey sizes from both marine/estuarine and freshwater upland habitats. Frequently consumed larger marine/estuarine prey included invertebrates such as horseshoe crabs (%FO = 10.7%) and blue crabs (portunidae: *Callinectes sapidus* Rathbun 1896, % FO = 35.7%) and vertebrates such as raccoons (procyonidae: *Procyon lotor*, %FO = 28.6%), marsh rabbit (leporidae: *Sylvilagus palustris* Bachman 1837, %FO = 14.3%) and various wading/saltmarsh birds (ardeidae: *Egretta*

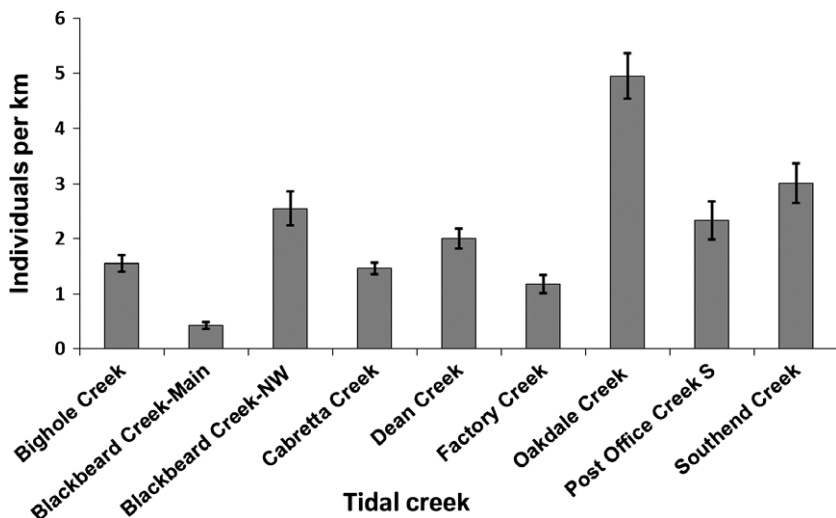


Fig. 2. Mean relative abundance (ind. km<sup>-2</sup>) of *Alligator mississippiensis* within nine saltmarsh tidal creeks surrounding Sapelo Island, Georgia surveyed in 2008 and 2009. Surveys were replicated five times in each creek transect ( $n = 5$ ). Error bars are  $\pm$  standard error (SE).

**Table 1.** Number of individuals ( $n$ ), number of males, number of females and the minimum, mean and maximum total length (TL, in cm) of *A. mississippiensis* captured in three habitats types at Sapelo Island, Georgia from 2007 to 2010. All upland wetlands and ponds with salinity <5 ppt were classified as freshwater, brackish wetlands (salinity range = 5–15 ppt) and terrestrial uplands were classified as intermediate habitats, and all aquatic habitats greater than 15 ppt salinity were classified as marine/estuarine habitats

Habitat type	$n$	No. Males	No. Females	Total length-TL (cm) min (mean) max
Freshwater	57	43	14	37.7 (129.9) 296.3
Intermediate	48	25	23	55.6 (119.9) 285.7
Marine/ estuarine	76	56	20	77.0 (156.7) 315.5

*thula* Molina 1782, snowy egret; *Bubulcus ibis* Linnaeus 1758, cattle egret; troglodytidae: *Cistothorus palustris* Wilson 1810, marsh wren; rallidae: *Rallus longirostris* Boddaert 1783, clapper rail, combined %FO = 17.9%). Large freshwater/upland prey of adult alligators included turtles (kinosternidae: *Kinosternon subrubrum* Bonnaterre 1789, mud turtle; emydidae: *Trachemys scripta* Thunberg 1792, pond slider, combined %FO = 14.2%) and mammals (cricetidae: *Oryzomys palustris* Harlan 1837, rice rat; muridae: *Sigmodon hispidus* Say and Ord 1825, hispid cotton rat, combined %FO = 28%). While larger prey were frequently found in adult stomach contents, small prey items accounted for a large portion of the numerical abundance and recovered biomass. In particular, grass shrimp (Palaemonidae: *Palaemonetes pugio* Holthuis 1949) accounted for 91% of the numerical abundance (2078 of the 2685 were recovered from a single individual) and 32% of recovered prey biomass in adult contents.

#### STABLE ISOTOPE ANALYSIS

Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of dominant primary producers in marine/estuarine ecosystems were significantly

more enriched in both  $^{15}\text{N}$  and  $^{13}\text{C}$  relative to dominant freshwater/upland primary producers ( $t$ -test:  $t = -15.16$ , d.f. = 52,  $P < 0.001$  and  $t = -44.57$ , d.f. = 104,  $P < 0.001$  for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively, Table 2). Isotopic values of prey within each ecosystem reflected differences in isotopic values of dominant primary producers with marine/estuarine prey species more enriched in  $^{15}\text{N}$  and  $^{13}\text{C}$  relative to freshwater/upland prey species (Fig. 3 and Table S2). Values of producers and prey items were similar to values reported in previous studies in the same system (Peterson & Howarth 1987; Brittain *et al.* 2011).

A total of 181 *A. mississippiensis* (76 juvenile, 49 subadult and 56 adults) were analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Fig. 3). We further separated juveniles into small ( $n = 39$ , TL < 79 cm) and large ( $n = 37$ , TL = 79–100 cm) subdivisions as our threshold analyses identified a significant change in the mean and variance of  $\delta^{13}\text{C}$  at 79 cm TL ( $P < 0.001$ ) and evidence of differences in the diet of these two subdivisions during SCA (Table S1, Supporting information). All subpopulation groups were further separated by sex. To assess intrapopulation variation in *A. mississippiensis* cross-ecosystem foraging patterns, we estimated the proportion of marine/estuarine and freshwater/upland prey resources in the diet of subpopulation groups using a Bayesian-based isotopic mixing model (SIAR). Different calculations for end member means and standard deviations produced similar resource contribution estimates; we found just one significant difference (between diet estimates for small juvenile males) among all 16 pairwise comparisons (Table S3). Since few differences were found between model outputs using end member values weighted by % recovered prey mass or simple mean calculations, we choose to concentrate on SIAR results using end member values weighted by % recovered prey mass per size class. These end member values are likely a better representation of the prey isotope values utilized by *A. mississippiensis* subpopulation groups since they rely on direct estimates from dietary data recovered during the time of the study.

At the population level, we estimated *A. mississippiensis* consume freshwater/upland prey in slightly greater proportion (median proportional contribution estimate = 0.63, 95% Bayesian credible interval – BCI = 0.58–0.68) than marine/estuarine prey (median = 0.37, 95% BCI = 0.31–0.41). Estimated proportional resource contributions to the diet of *A. mississippiensis* size classes through SIAR analysis were highly correlated with both recovered mass (%M) and frequency of occurrence (%FO) from stomach contents ( $r = 0.85$ , %M;  $0.90$ , %FO). In general, cross-ecosystem marine/estuarine foraging increased with increasing body size. Median proportional contribution estimates for marine/estuarine prey values ranged from 0.05 (95% BCI = 0.0–0.19) for small juvenile females to 0.76 (95% BCI = 0.68–0.84) for adult males (Fig. 4 and Table S4). Diet of small juveniles was estimated to be comprised chiefly of freshwater/upland prey (freshwater/upland estimated contribution for females: median = 0.95, 95% BCI = 0.81–1.00; males: median = 0.82, 95% BCI = 0.74–0.92). Diets of large juvenile and subadult females were estimated to use marine/estuarine prey in greater proportion than males (females: median = 0.54 and 0.51 vs. males: median = 0.33 and 0.36, for large juveniles and subadult, respectively). Adult females, similar to adult males, were estimated to heavily rely on marine/estuarine prey (median = 0.71, 95% BCI = 0.62–0.79).

#### NICHE SPECIALIZATION ( $\epsilon$ )

We used posterior distributions produced by our SIAR mixing model analyses to calculate the specialization index ( $\epsilon$ ) to examine niche specialization and inform individual-level variation in diet. We found at the population level, *A. mississippiensis* were mostly niche generalists ( $\epsilon = 0.26 \pm 0.05$ , mean  $\pm$  SD), as such the diet of the majority of individuals is expected to be comprised of similar proportions of freshwater/upland and marine/estuarine

prey. However, the magnitude of  $\epsilon$  in conjunction with predictions from the SIAR model and dietary data indicates some individuals were niche specialists concentrating on either freshwater/upland or marine/estuarine prey resources. When assessing niche specialization separately for sexes within size classes, however, mean estimates of  $\epsilon$  ranged widely from 0.10 to as high as 0.87 (Table 3). Niche specialization was highest in small juveniles ( $\epsilon = 0.87 \pm 0.10$  and  $0.64 \pm 0.09$  for females and males, respectively) and lowest in subadults ( $\epsilon = 0.10 \pm 0.08$  and  $0.22 \pm 0.09$  for females and males, respectively). Mean estimates of  $\epsilon$  for large juveniles and adults were low to moderate (range = 0.23–0.51), indicating a high degree of variation in foraging patterns of individuals within these subpopulation groups.

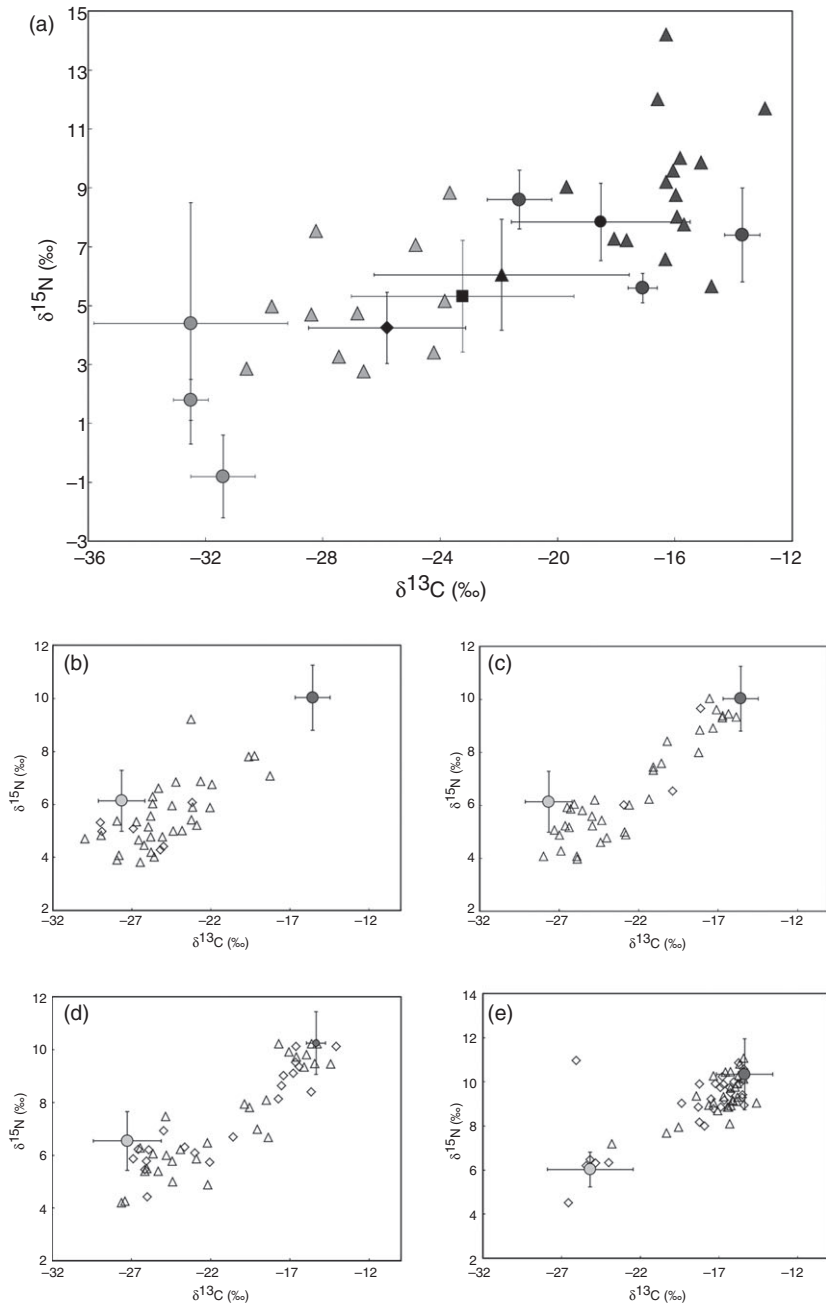
## Discussion

### THE EFFECT OF BODY SIZE ON CROSS-ECOSYSTEM FORAGING BEHAVIOUR

During nightlight surveys, all sizes of *A. mississippiensis* were observed within marine/estuarine habitats (although, young-of-year [hatchlings] and small juveniles were rarely observed) with a higher abundance of individuals being observed in smaller (< 5 m width) tidal creek sheds in close proximity to freshwater wetlands and ponds (Figs 1 and 2). Individuals captured in marine/estuarine habitats were on average larger than those captured in freshwater and intermediate habitats. Stomach content analysis revealed at the population level, *A. mississippiensis* consumes a wide variety of both freshwater/upland and marine/estuarine prey species (Table S1, Supporting information); however, the prevalence of marine/estuarine prey items greatly differed through ontogeny. Marine/estuarine prey were least frequently observed in small juvenile (TL < 79 cm) stomach contents (%FO = 6.7%); only one small juvenile contained six individuals of a

**Table 2.** Mean  $\pm$  SD  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of dominant primary producers in marine/estuarine and freshwater/upland habitats of Sapelo Island, Georgia

Primary producer species	$\delta^{15}\text{N}$ (‰) mean $\pm$ SD ( <i>n</i> )	$\delta^{13}\text{C}$ (‰) mean $\pm$ SD ( <i>n</i> )	Source
<b>Marine/estuarine</b>			
<i>Spartina alterniflora</i> (Saltmarsh cordgrass)	7.4 $\pm$ 1.6 (5)	–13.7 $\pm$ 0.6 (5)	This study
<i>Ulva</i> sp. (Sea lettuce)	5.6 $\pm$ 0.5 (3)	–17.1 $\pm$ 0.5 (3)	J.C. Mearz unpubl. data
Plankton	8.6 $\pm$ 1.0 (4)	–21.3 $\pm$ 1.1 (56)	Rau 1982; Gearing <i>et al.</i> 1984
<i>Juncus roemerianus</i> (Black Needle Rush)	4.5 $\pm$ 0.9 (4)	–25.5 $\pm$ 1.3 (4)	This study
<i>Borrchia frutescens</i> (Bushy seaside tansy)	0.9 $\pm$ 1.2 (4)	–27.0 $\pm$ 0.71 (4)	Brittain 2009
<i>Salicornia depressa</i> (Virginia glasswort)	4.4 $\pm$ 0.9 (4)	–27.4 $\pm$ 0.9 (4)	Brittain 2009
<b>Freshwater wetlands/Uplands</b>			
<i>Spirogyra</i> sp. (Freshwater algae)	4.4 $\pm$ 4.1 (4)	–32.5 $\pm$ 3.3 (4)	This study
<i>Carex</i> sp. (Sedge grass)	1.6 $\pm$ 0.7 (3)	–28.4 $\pm$ 1.6 (3)	This study
<i>Panicum</i> sp. (Switch grass)	1.8 $\pm$ 0.7 (3)	–32.5 $\pm$ 0.6 (3)	Brittain 2009
<i>Eupatorium capillifolium</i> (Dog fennel)	–1.6 $\pm$ 0.4 (3)	–28.0 $\pm$ 0.2 (3)	Brittain 2009
<i>Quercus virginiana</i> (Live oak)	–0.8 $\pm$ 1.4 (5)	–31.4 $\pm$ 1.1 (5)	This study
<i>Quercus nigra</i> (Water oak)	0.8 $\pm$ 0.6 (6)	–31.5 $\pm$ 0.1 (6)	Brittain 2009
<i>Sereoa repens</i> (Saw palmetto)	1.3 $\pm$ 0.6 (6)	–30.5 $\pm$ 0.6 (6)	Brittain 2009



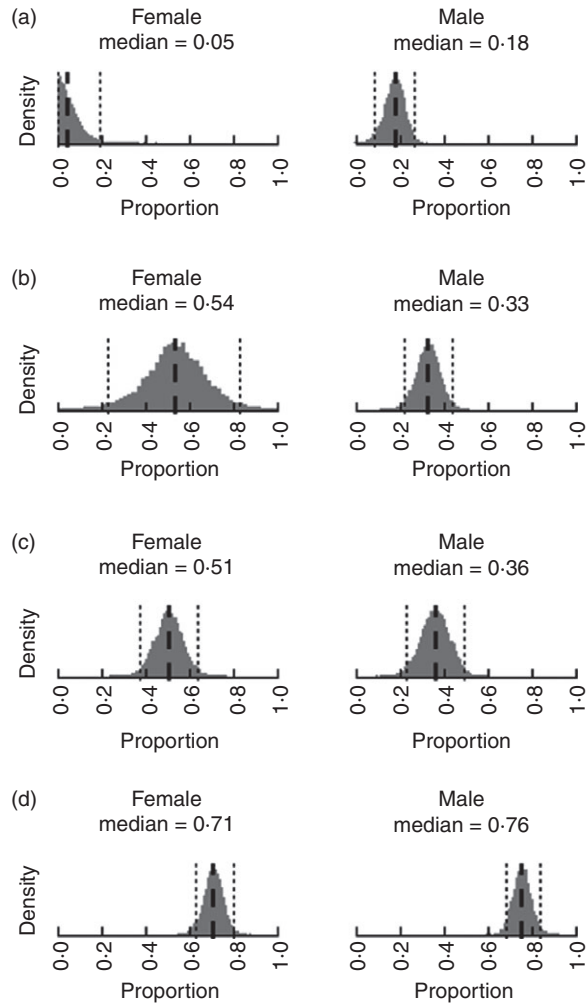
**Fig. 3.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of (a) mean values for *A. mississippiensis* subpopulation groups [black diamond is small juvenile (TL < 79 cm), black square is large juvenile (TL = 79–100 cm), black triangle is subadult (TL = 100–183 cm), and black circle is adult (TL > 183 cm)], marine/estuarine primary producers (dark grey circles), marine/estuarine prey species (dark grey triangles), freshwater/upland primary producers (light grey circles), and freshwater/upland prey species (light grey triangles). Error bars ( $\pm 1$  standard deviation) are not included for prey species for simplicity (see Table S2), (b) small juvenile individuals (open triangles – males and open diamonds – females) and mean SIAR end member values (light grey circle–freshwater/upland prey and dark grey circle – marine/estuarine prey), (c) large juvenile individuals and mean SIAR end member values, (d) subadult individuals and mean SIAR end member values, (e) adult individuals and mean SIAR end member values. Mean values of trophic enrichment factors (TEFs) were added to prey and end member values to correct for isotopic discrimination.

marine/estuarine crab, (sesamidae: *Armases cinereum*), which are known to inhabit saltmarshes and brackish wetlands as well as border habitats in terrestrial uplands (Buck *et al.* 2003). Frequency of marine/estuarine prey in *A. mississippiensis* stomach contents increased in larger size classes and were most frequently observed in subadult and adult contents (%FO = 94% subadults; 90% adults).

Isotopic mixing model results and the specialization index ( $\epsilon$ ) estimates corroborated stomach content findings, indicating small juveniles (TL < 79 cm) primarily consumed freshwater/upland prey resources (median estimated proportional contribution = 0.95 for females and 0.82 for males) and were relative niche specialists (mean  $\epsilon$  = 0.87 for females and 0.64 for males). Larger juveniles

(TL = 79–100 cm) and subadults (TL = 100–183 cm), however, exhibited a gradient of resource use patterns ranging from individuals predominately consuming freshwater/upland prey to predominately consuming marine/estuarine prey as indicated by a broad range in individuals' isotope values and heavily bimodal distribution of their isotope values near either end member (Fig. 3c,d). The majority of adult individuals (TL > 183 cm) were estimated to rely heavily on marine/estuarine prey (median estimated contribution = 0.69 for females and 0.74 for males), yet isotopic values of seven individuals (six females and one male, Fig. 3e) as well as moderate  $\epsilon$  values indicate some individuals may specialize on freshwater/upland prey resources.





**Fig. 4.** Marginal posterior distributions from SIAR mixing model analyses, coloured histograms (grey) are probability densities for the estimated proportion of diet comprised of marine/estuarine prey resources by *A. mississippiensis* subpopulation groups: (a) small juveniles (TL < 79 cm), (b) large juveniles (TL = 79–100 cm), (c) subadults (TL = 100–183 cm), and (d) adults (TL > 183 cm). Dashed lines are median values and dotted lines are 95% Bayesian credible intervals.

There are a number of plausible ecological and biological explanations for the observed patterns in *A. mississippiensis* resource use and subpopulation structure due to body size. Firstly, the increased reliance on marine/estuarine habitats and prey resources by larger sized individuals may be a consequence of increased competition for limited food resources in upland freshwater habitats. Interior freshwater aquatic ecosystems are small in size and support relatively few larger sized prey species, aside from a small number of terrestrial mammal and reptile species such as *P. lotor* (raccoon) and *Agkistrodon piscivorus* Lacépède 1789 (cottonmouth) which occasionally forage within freshwater habitats. Marine/estuarine habitats support a diversity of potential prey ranging from small invertebrates (such as shrimp and crabs) to larger vertebrates such as fishes, birds and mammals. Tamarack

**Table 3.** Mean  $\pm$  SD of specialization index ( $\epsilon$ ) estimated for each subpopulation group of *A. mississippiensis*. Individual specialization index ( $\epsilon$ ) was estimated from posterior distributions produced by SIAR isotopic mixing model analysis. Values of 0 denote complete generalist consumers (i.e. feed on all prey groups in equal proportions) and values approaching 1 denote ultra-specialist consumers (i.e. specialize on a subset of available prey)

Size class	Sex	$\epsilon$
Small juvenile	Female	0.87 $\pm$ 0.10
Small juvenile	Male	0.64 $\pm$ 0.09
Large juvenile	Female	0.23 $\pm$ 0.19
Large juvenile	Male	0.34 $\pm$ 0.11
Subadult	Female	0.10 $\pm$ 0.08
Subadult	Male	0.22 $\pm$ 0.09
Adult	Female	0.42 $\pm$ 0.09
Adult	Male	0.51 $\pm$ 0.08

(1989), studying a population of *A. mississippiensis* on Wassaw Island, Georgia, hypothesized that the metabolic demands of larger subadult and adult individuals could not be met by the amount of secondary production within interior freshwater and brackish wetlands; our results are consistent with this hypothesis. Similarly, Rootes *et al.* (1991) found *A. mississippiensis* inhabiting estuarine marshes in Louisiana grew faster and reached sexual maturity earlier than individuals within freshwater palustrine marshes, attributing higher growth rates to the increased quality of food resources within estuarine marshes. Additionally, the shift to a more heavily marine/estuarine-based diet in larger size classes could be explained by a combination of larger-bodied individuals' increased ability to capture larger sized prey, increased mobility (i.e. larger home ranges) and increased resistance to salinity stress.

It is well documented that ontogenetic changes in skull morphology, particularly increased size and subsequent increased crushing force of jaws, in crocodylians are associated with shifts in prey species composition (Wolfe, Bradshaw & Chabreck 1987). Increases in body size are also associated with higher mobility and larger home ranges in *A. mississippiensis* (Joanen & McNease 1972; McNease & Joanen 1974; Lance *et al.* 2011). While a number of studies conclude juvenile *A. mississippiensis* occupy larger home ranges than do subadult and adults (McNease & Joanen 1974; Taylor, Joanen & McNease 1976), their estimates likely include instances of long-distance dispersal and may not be accurate representations of true juvenile home range size (Lance *et al.* 2011).

Alligatorids (alligators and caimans) lack lingual salt secreting glands, which are present in true crocodiles (Taplin *et al.* 1982); therefore, they rely on behaviour and body morphology to minimize osmotic stress while using hyper-saline environments (Mazzotti & Dunson 1984; Jackson, Butler & Brooks 1996). Juvenile *A. mississippiensis* have been shown to have little resistance to osmotic stress and in fact, suffering losses in body weight

and mortality within 3 weeks when exposed to salinities > 15 ppt (Laurén 1985); however, the effects of and resistance to osmotic stress have not been thoroughly studied in individuals who regularly use hyper-saline environments. Lance *et al.* (2010) measured blood chemistry and stress hormones of adult *A. mississippiensis* following salt-water intrusion into freshwater Louisiana marshes by Hurricane Rita in 2005 and found elevated levels of blood osmolytes and corticosterone to persist for 10 months until increased rainfall returned salinities to normal levels. Lance *et al.* (2010) also found a negative relationship between corticosterone and total length 7 months after the intrusion event, indicating larger individuals may have recovered at a faster rate than smaller sized individuals. These data in conjunction with our findings indicate there may be a size limitation imposed upon the duration and extent to which *A. mississippiensis* can use high-salinity environments without suffering negative physiological consequences. Further research should be performed to examine the implications of physiological stress associated with the regular use of high-salinity environments and the behavioural as well as physiological mechanisms *A. mississippiensis* employ to mitigate this stress.

#### EFFECT OF SEX ON FORAGING PATTERNS

Movement patterns of *A. mississippiensis* are also known to differ between sexes, particularly in adults. Specifically, reproductively active adult females often maintain relatively small home ranges, remaining in close proximity to nesting sites and nursery ponds for a large portion of the year (Rootes & Chabreck 1993); whereas subadult and adult males may travel considerable distances to access mates and establish territories (Joanen & McNease 1972; Lance *et al.* 2011). Nest guarding and parental care by female crocodilians are common behaviours hypothesized to increase hatching success and juvenile survivorship (Kushlan & Kushlan 1980; Vliet 2001). While food quality and prey abundances for adult individuals are likely to be much lower in upland freshwater wetlands compared to marine/estuarine habitats, the positive benefits for reproductive success and juvenile survivorship may outweigh the cost of occupying suboptimal habitats by adult females. In the small juvenile size class, females were found to be more specialized on freshwater prey (mean  $\epsilon = 0.87$  and median proportional contribution = 0.95) than were males (mean  $\epsilon = 0.64$  and median proportional contribution = 0.82), but in large juvenile and subadult size classes, females consumed a mixed diet of both prey resource categories (median proportional contribution  $\approx 0.50$  for either prey category) and showed lower degrees of specialization than males (Tables 3 and S4). Conversely, adult females were found to be more specialized on either freshwater or marine/estuarine prey and demonstrated less of a mixed diet, offering further support that differences in foraging

patterns between adult sexes is likely to be linked to reproductive status.

#### EVIDENCE FOR INDIVIDUAL VARIATION IN FORAGING BEHAVIOURS

Individuals within a population often only use a subset of resources compared to the population as a whole regardless of size and sex, which carries important evolutionary and ecological implications for populations (Bolnick *et al.* 2003, 2011; Araújo, Bolnick & Layman 2011). Termed individual specialization, these differences in resource use and behaviour have been attributed to a variety of factors including but not limited to the degree of intra- and inter-specific competition (Svanbäck & Bolnick 2007; Bolnick & Ingram 2010; Araújo, Bolnick & Layman 2011), resource abundance and diversity (Bolnick *et al.* 2007; Araújo *et al.* 2009), habitat heterogeneity (Rosenblatt *et al.*, 2014), learned behaviours (Woo *et al.* 2008), genetic diversity and relatedness (Agashe & Bolnick 2010), as well as individual 'personality' (Bergmüller & Taborsky 2010). In the case of *A. mississippiensis* in this study, individual specialization can have both a positive and a negative effect on ecosystem connectivity depending on the particular behavioural strategy employed by specialized individuals. For example, in all size classes, there was some degree of specialization on freshwater/upland prey resources, indicated by moderate  $\epsilon$  values and the position of individuals' isotope values within the isotopic mixing space as well as dietary data (Table 3 and Fig. 3); these individuals may rarely venture into marine/estuarine ecosystems, thereby limiting predator-driven connectivity between these two ecosystems. On the other hand, individuals that specialize on marine/estuarine prey resources promote connectivity since these individuals require freshwater for survival and must return to freshwater ecosystems following cross-ecosystem foraging bouts. Specialization on marine/estuarine prey increased with increasing size and was more prevalent for females within large juvenile and subadult size classes, whereas adult males showed higher degree of specialization than adult females.

In general, coastal populations of *A. mississippiensis* have been found to exhibit a higher degree of individual-level dietary specialization compared to populations inhabiting inland lake ecosystems, likely due to the increased habitat heterogeneity and prey diversity found in coastal ecosystems (for detailed discussions, see Rosenblatt *et al.*, 2014). Beyond the intrinsic ecological attributes of coastal ecosystems, we hypothesize that multiple factors likely played a role in shaping individual foraging behaviours of *A. mississippiensis* within this population. Firstly, increased intraspecific competition for limited food supply, particularly in larger size classes, may force individuals to develop alternative foraging strategies for survival when freshwater prey resources become limited (e.g. Svanbäck & Bolnick 2007). Secondly, there is an evidence that crocodilians can learn specialized foraging

behaviours, such as tool use and cooperative hunting techniques, from conspecifics and/or parents (Dinets, Brueggen & Brueggen 2013; Doody, Burghardt & Dinets 2013). Therefore, genetic relatedness and learned behaviour may have contributed to the variation in individual behaviour, as *A. mississippiensis* exhibit parental care and juveniles can remain in family units (i.e. pods) for up to 3 to 5 years after hatching. Thirdly, differences in individuals' personality, in particular the degree of boldness or shyness, potentially contributed to differences in resource use and behaviour among individuals, particularly when foraging in novel or stressful environments (Wilson & Clark 1994; Sih, Bell & Johnson 2004). Future research explicitly testing these hypothesized causes for individual specialization in *A. mississippiensis* populations will inform as to when and where increased specialization can be expected.

#### IMPLICATIONS AND CONCLUSIONS

Our results have ecological implications for coastal ecosystems throughout the south-eastern United States. Data characterizing the role of *A. mississippiensis* in these ecological and economically important ecosystems (Nifong & Silliman 2013; Rosenblatt *et al.* 2013a; Nifong *et al.* 2014), and incorporating this knowledge into ecosystem management strategies, will promote better conservation practices in the face of accelerated change. Coastal freshwater wetlands, particularly those on barrier islands are often nutrient limited, as they are isolated from receiving riverine water inputs, are mostly ephemeral, and contain sandy, nutrient-poor substrates (Bellis 1995). By foraging in marine/estuarine ecosystems and returning to freshwater wetlands for rehydration, *A. mississippiensis* have the potential to deposit marine-derived nutrients through the excretion of waste products (Coulson & Hernandez 1964; Subalusk, Fitzgerald & Smith 2009). During this study, we observed accumulations of *A. mississippiensis* dung and excrement containing remnants of marine/estuarine prey in and around den sites within freshwater wetlands (Fig. S1, Supporting information). The translocation and deposition of nutrients via excretion of consumer waste products can greatly increase local primary production and support additional secondary production (e.g. Polis & Hurd 1996; Schmitz, Hawlena & Trussell 2010).

In addition to the transfer of nutrients, marine/estuarine prey subsidies to *A. mississippiensis* may provide the necessary resources to support higher population densities within freshwater wetlands than possible through the sole reliance on available resources in freshwater/upland ecosystems. Empirical and theoretical evidence demonstrate that more productive ecosystems can support higher biomass of consumers (e.g. Wootton & Power 1993). This subsidy, by increasing *A. mississippiensis* abundance in freshwater wetlands, may regulate a positive feedback loop maintaining freshwater wetlands through the habitat

engineering behaviours employed by *A. mississippiensis*. It is well documented that *A. mississippiensis* modify wetland habitats by excavating dens and shallow pools termed 'alligator holes', thereby increasing landscape heterogeneity and hydroperiod of freshwater wetlands (Craighead 1968; Campbell & Mazzotti 2004; Palmer & Mazzotti 2004). Den complexes and alligator holes were found within all freshwater wetlands inhabited by *A. mississippiensis* on Sapelo Island, Georgia (Fig. S2) and wetlands with alligator holes often maintained water levels higher and longer than wetlands without alligator holes (*personal observation*).

Top- and apex predators are in decline world-wide (e.g. Estes *et al.* 2011). Understanding the ecological roles they serve in communities is essential to predict consequences of these losses (Heithaus *et al.* 2008) and to design and implement effective conservation programmes to restore ecosystem functions that these predators regulate (e.g. Estes 1996; Sergio *et al.* 2008). Here, we have demonstrated that top-predators can provide linkages between spatially distinct food webs by foraging across ecosystem boundaries and that body size as well as other factors (i.e. sex and individual specialization) influence the degree to which predators' exhibit cross-ecosystem foraging behaviours. Given our findings, it will likely be important to incorporate a high degree of top-predator population subdivision into community and ecosystem models to increase both their accuracy and predictability.

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#### Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.j7049> (Nifong *et al.* 2014).

#### Author Contributions

JCN and BRS conceived and designed the project. JCN conducted the field and laboratory work. JCN and CL performed statistical analyses. JCN wrote the manuscript. BRS and CL provided editorial assistance.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Stomach content analysis (SCA) and stable isotope sample collection and analysis methods.

**Figure S1.** Photographs of alligator dung around wetlands.

**Figure S2.** Photographs of alligator dens and alligator holes in freshwater wetlands.

**Table S1.** Recovered mass, %M, numerical count (*n*), %N and frequency of occurrence (%FO) of prey taxa identified from stomach content analysis of *A. mississippiensis* captured from Sapelo Island, Georgia during 2008 and 2009.

**Table S2.** Number of samples (*n*), mean  $\delta^{15}\text{N}$  and mean  $\delta^{13}\text{C}$  of prey species identified from stomach content analysis and used in the calculation of end member means and standard deviation for use in SIAR mixing model analyses.

**Table S3.** One-sided *P*-values for pairwise comparisons between SIAR marginal posterior distributions estimated for subpopulation groups using two end member calculations: simple mean (.sm) and weighted mean by recovered mass (.rec).

**Table S4.** Median, standard deviation (SD) and 95% Bayesian creditable intervals for SIAR marginal posterior distributions of proportional prey resource contributions to the diet of *A. mississippiensis* subpopulation groups using two end member calculations.