Ontogenetic niche shifts in the American Alligator establish functional connectivity between aquatic systems

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ABSTRACT

Individual animals undergoing ontogenetic shifts in habitat use may establish a mobile link between discrete ecosystems via movement of energy, nutrients and matter, as well as through impacts on ecosystem and habitat structure. The American Alligator (Alligator mississippiensis) is a model species for studying ecological implications of ontogenetic niche shifts, because they grow in size by several orders of magnitude, and they play a critical role as both top predators and ecosystem engineers. We used equal trapping effort, radio telemetry and nest surveys to document ontogenetic habitat shifts of alligators between hydrologically isolated, seasonal wetlands and riverine systems. To estimate the degree of functional connectivity between systems, we quantified alligator biomass and nutrient excretion in both systems. Seasonal wetlands provided nesting and nursery sites for adult females and juveniles, which constituted 0.78 g/m^2 biomass and excreted 0.05 g/m^2/yr N, P, Ca, Mg, Na and K in that system. In contrast, the riverine system provided non-nesting habitat for adults and sub-adults of both sexes, totaling 0.18 g/m^2 biomass and excreting 0.01 g/m^2/yr of nutrients. Furthermore, sub-adults and adult females were documented moving across the terrestrial matrix, while adult males spent the duration of the study in the creek. Our results demonstrated that ontogenetic niche shifts in alligators establish connectivity between seasonal wetlands and riverine systems and with the surrounding terrestrial matrix. These findings have implications for the definition of jurisdictional wetlands under the US Supreme Court's 2001 SWANCC decision and highlight the importance of ecological, as well as hydrological, connectivity.

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1. Introduction

Species with complex life cycles are those in which individuals undergo major shifts in their ecology across different life history stages (Wilbur, 1980). Ontogenetic niche shifts are generally associated with a concerted shift in morphology, habitat and diet. Thus, juveniles and adults from a single population of a single species may utilize very different habitats and resources (Wilbur, 1980; Werner and Gilliam, 1984; Gillanders et al., 2003). An ecological consequence of ontogenetic niche shifts in animals is the establishment of links between juvenile and adult habitats through reproduction, growth, dispersal and death (Schreiber and Rudolf, 2008). The growth of individuals in juvenile habitat and their subsequent movement to and eventual mortality in adult habitat can result in substantial transfer of biomass, nutrients and energy between the systems (Deegan, 1993; Gibbons et al., 2006; Regester et al., 2006). The further growth of an individual in adult habitat and their return to juvenile habitat to reproduce establishes a second pathway for energy transfer between the systems (Gillanders et al., 2003; Regester et al., 2006).

The transfer of energy and nutrients across ecosystem boundaries through animal movement patterns can result in functional connectivity between otherwise discrete ecosystems (Gibbons, 2003; Gillanders et al., 2003; Helfield and Naiman, 2006). Functional connectivity among units in a landscape mosaic due to fluxes of energy, matter or organisms may in turn alter the structure and dynamics of the mosaic itself, resulting in a high level of ecosystem complexity (Cadenasso et al., 2006; Schreiber and Rudolf, 2008). Such horizontal transfers of biomass, energy, and nutrients have been demonstrated in studies of "mobile link" species that migrate across ecosystem boundaries, connecting otherwise separate food webs (Lungberg and Moberg, 2003; Helfield and Naiman, 2006; Kremen et al., 2007). Organisms that transport organic material, nutrients, and minerals across habitats often cause fluxes of resources from areas of high productivity to areas of low productivity (Polis et al., 1997; Stapp et al., 1999). They may also significantly influence the structure of the food web through their role as consumers or prey (Helfield and Naiman, 2006), or alter the

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physiochemical environment across habitats (Naiman et al., 1988). To identify mobile links due to ontogenetic niche shifts, information would be needed on differential use of habitats by distinct size classes of a population, and animal movements among habitats or landscape components (Beck et al., 2001).

As a species that has continuous growth, increases in size by four to five orders of magnitude over its lifetime, and exhibits allometric scaling in its morphology, the American Alligator (*Alligator mississippiensis*) provides an excellent model for studying ecological implications of ontogenetic shifts in habitat use (Polis, 1984; Werner and Gilliam, 1984). Positive allometry in snout length, jaw musculature, and bite force in alligators (Dodson, 1975; Erickson et al., 2003) is associated with increasing prey size as they grow. Hatchling alligators primarily subsist on insects, whereas juveniles (~61–122 cm total length; TL) begin to include crustaceans and fish in their diet (Delany, 1990; Platt et al., 1990). Around 120 cm TL, sub-adults undergo a second dietary shift and include larger vertebrate prey in their diet (Delany and Abercrombie, 1986; Delany et al., 1999). Negative allometry in limb lengths and mechanical properties of the femoral retractor muscles in alligators indicate a higher propensity for terrestrial locomotion in juveniles over adults (Dodson, 1975).

These morphological and trophic shifts in alligators throughout their ontogeny are reflected in differential habitat use among size classes. Adult male alligators in coastal marshes are typically the largest individuals in a population and rely on deep, open water, likely in part because of the availability of large prey. Adult females typically use deep water only for breeding, and then return to more vegetated marsh to nest (Joanen and McNease, 1970, 1972; Taylor, 1984). Juveniles spend the first few years of their lives with their mothers near the natal site, and then begin to use a wide range of habitats (McNease and Joanen, 1974; Deitz, 1979). The tendency of juveniles to remain near their mother in vegetated marsh may be related to higher densities of invertebrate prey in that habitat as well as decreased exposure to predation and cannibalism (Rootes et al., 1991; Rootes and Chabreck, 1993; Lance et al., 2000).

Although these patterns of habitat use have been documented in contiguous coastal marshes, alligators in inland wetland systems remain relatively unstudied, and the range and connectivity of available habitats is markedly different in these systems (Ryberg et al., 2002). For example, in some upland systems in the southeastern coastal plain, deep, permanent bodies of water typically used by adult males are primarily found in creeks and rivers, whereas the vegetated marsh habitat favored by nesting females and juveniles primarily exists in hydrologically isolated, seasonal wetlands surrounded by a terrestrial habitat matrix. Alligators undergoing ontogenetic habitat shifts in this system may act as mobile links between the two aquatic systems.

In addition to using distinct habitats throughout different stages of their life history, alligators perform critical roles in the trophic and non-trophic processes of the systems they occupy. Alligators are opportunistic feeders that, as adults, become the top predators in the systems in which they live. In addition to substantial effects on the food web of these systems, alligators also act as ecosystem engineers, creating nest mounds as well as burrows and wallows that alter the hydrology of the system and provide refuge for many aquatic species during times of drought (McIlhenny, 1935; Craighead, 1968; Jones et al., 1994; Mazzotti and Brandt, 1994; Palmer and Mazzotti, 2004). Finally, as ectotherms, alligators are more efficient in energy transfer than birds or mammals (Burton and Likens, 1975). The ability of caiman to consume allochthonous nutrient inputs and transform them into useable nutrients for primary production *in situ* was hypothesized to play a critical role in the functioning of low-nutrient Amazonian mouth-lakes (Fittkau, 1970; Fittkau, 1973).

Herein, we test the hypothesis that ontogenetic niche shifts in alligators, which are an economically important game species in most US states where they occur, result in functional connectivity between two disjunct aquatic systems. Specifically, alligator movement patterns that accompany ontogenetic shifts in habitat use should result in alligators serving as mobile links between seasonal wetlands, surrounding terrestrial matrix and riverine systems. We predicted seasonal wetlands would provide the most suitable habitat for hatchling and juvenile alligators. At approximately 120 cm TL, the size at which ontogenetic shifts occur in all crocodilians (Fitzgerald, 1978; A. Subalusky and L. Fitzgerald, unpublished data), we predicted sub-adult alligators would begin to disperse across the landscape and into riverine systems. We also predicted adult females would migrate from the riverine system to nesting sites associated with wetlands.

We used equal trapping efforts in the two aquatic systems to test the prediction that wetlands were primarily inhabited by juveniles and adult females and the creek by sub-adults of both sexes and adult males, and we used radio telemetry to quantify movements between landscape components. We conducted nest surveys in the two systems to test our prediction that the wetlands provided preferred nesting habitat over the creek. Taken together, support for these predictions should establish the extent to which an ontogenetic niche shift occurs in alligators across these disjunct aquatic systems. Finally, we used total biomass measurements of the alligator population collected over all years of study, together with estimates of nutrient levels excreted by alligators, to quantify the degree to which these niche shifts result in the transport of nutrients and biomass across ecosystem boundaries, thus establishing functional connectivity between systems.

2. Methods

2.1. Study site

We conducted our study within the inland portion of the range of the American Alligator, on Ichauway, the outdoor laboratory of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia (Fig. 1). The study site is located within the Dougherty Plain physiographic region of the Lower Coastal Plain and Flatwoods ecoregion of the southeastern United States (McNab and Avers, 1994; Kirkman et al., 2000). In this region of the coastal plain, large lakes and expansive marshes are rare, and within our study site, bodies of water consist of creeks and rivers incised in limestone, and seasonal limesink wetlands with a hydroperiod driven by precipitation and evapotranspiration. These seasonal wetlands tend to be small, nutrient-limited habitats, in which the primary input is via decomposing litterfall (Watt and Golladay, 1999; Battle and Golladay, 2007).

Ichauway is an 11,600 ha reserve predominantly composed of longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) uplands interspersed with over 90 shallow, seasonal limesink wetlands. The site is bisected by 25 km of the Ichawaynochaway Creek, and bordered by 20 km of the Flint River on the eastern side and a small section of the seasonally dry Big Cypress Creek on the western side. We focused our sampling on the 25 km of the Ichawaynochaway Creek contained within Ichauway's borders and a subset of 13 seasonal wetlands in which we had consistently seen alligators over several years of survey. Our focal wetlands were primarily cypress-gum forests, although two were emergent marshes (Kirkman et al., 2000), and they ranged in size from 1.07 to 14.37 ha. These wetlands are consistently used by alligators due to both their longer hydroperiods and their proximity to other wetlands, as compared to other wetlands on site (A. Subalusky, unpublished data).
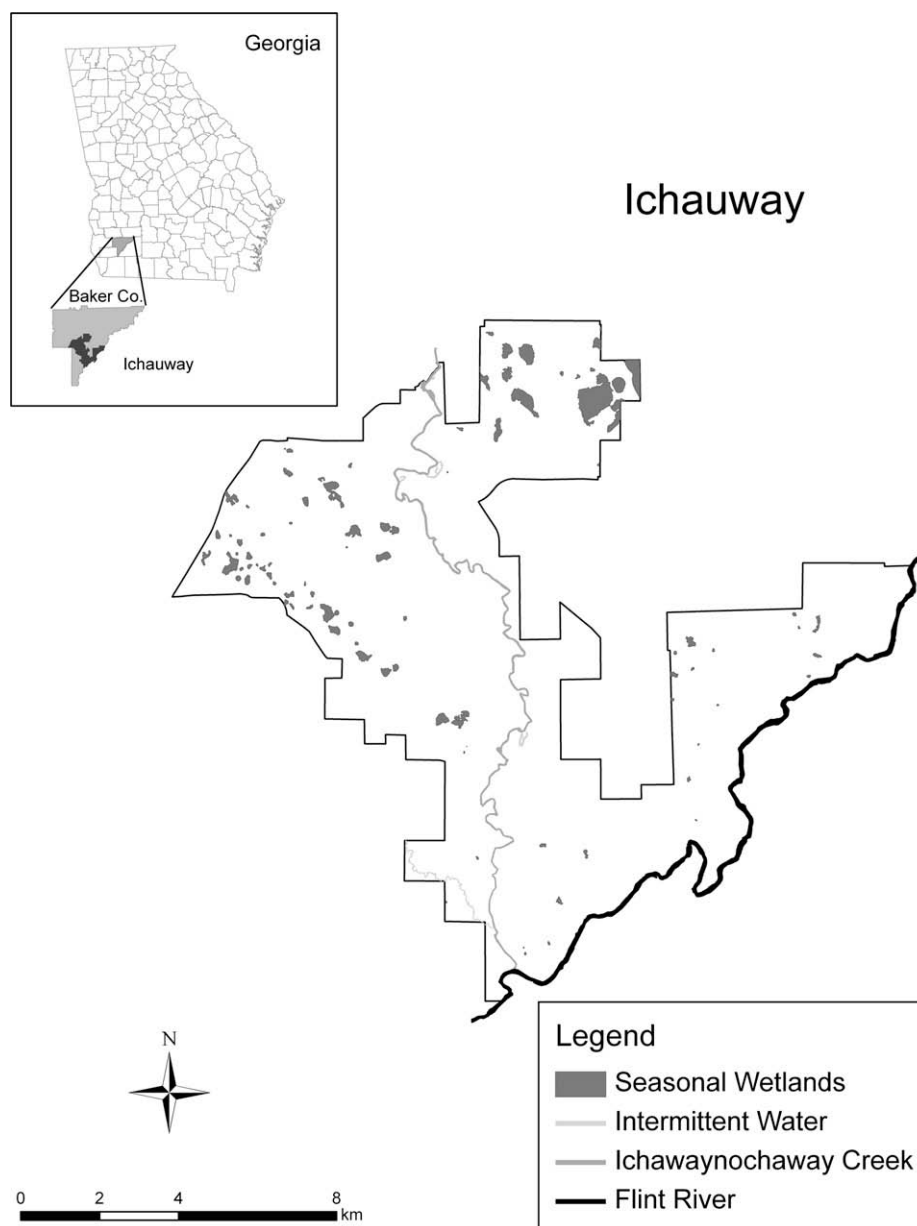
Fig. 1. Joseph W. Jones Ecological Research Center at Ichauway, Baker County, Georgia, USA. Ichauway is an 11,600 ha reserve of longleaf pine and wiregrass uplands interspersed with seasonal wetlands. The reserve is bisected by the Ichawaynochaway Creek and bordered by the Flint River on the eastern side and a small section of the intermittent Big Cypress Creek on the western side.

2.2. Trapping effort

We used two different kinds of traps to sample the juvenile, sub-adult and adult components of the population—Tomahawk cage traps and trip-snare traps (Murphy and Fendley, 1974; Subalusky, 2007). We used an equal number of trap-nights in both systems (Subalusky, 2007). In 2005, we trapped sites for ten consecutive nights, between late June and mid-October, resulting in 1200 total trap-nights per system (wetlands vs. riverine). In 2006, we trapped for seven consecutive nights at half of all the sites, for a total of 420 trap-nights per system. We trapped from mid-May until early July, at which time we stopped trapping after the wetlands were mostly dry.

We took morphometric measurements on all captured animals, including snout-vent length and tail length, determined sex (Chabreck, 1963; Joanen and McNease, 1978), and marked animals using a tail scute notching scheme (Mazzotti, 1983) and a PIT tag

(passive integrated transponder; Biomark, Boise, Idaho). We considered alligators <120 cm total length (TL) juveniles, those >120 and <180 cm sub-adults, and alligators >180 cm reproductive adults (Joanen and McNease, 1980, 1989). We used SPSS 12.0 (SPSS, 2003) to test the data for normality using the Shapiro–Wilks test ($p = 0.586$), and we used t-tests and an analysis of variance (ANOVA) to compare size class distributions between the two systems. An alpha value of 0.05 was used for all significance testing.

2.3. Radio telemetry

When animals captured during the equal trapping effort or captured incidentally on site were >120 cm total length, we attached a radio transmitter to their nuchal scutes (Blackburn Transmitters, Nacogdoches, Texas). Transmitters weighed <200 g, <3.6% of the body mass of the smallest alligator in our study. Transmitters were attached with surgical-grade steel wire (2005) or braided Spectra

line (2006; Sully's Bowfishing Stuff, Lincoln, Missouri) threaded through the transmitter and through the holes drilled in the nuchal scutes (McNease and Joanen, 1974; Kay, 2004). The transmitter and attachments were covered with waterproof epoxy to improve hydrodynamic qualities and increase longevity of attachment.

Animals were tracked 1–3 times per week. Locations were obtained by taking compass bearings from 2 to 3 known locations and using program Locate II (Nams, 2000) to obtain the coordinates of their intersection. It was impossible to predict when overland movements would be made; therefore, we were unable to obtain fine-scale data on path tortuosity or the habitat matrix through which individuals moved. However, alligators were observed using all available habitats at different times throughout the study, from intact forest stands to roads to open fields, thus we used Euclidean distance to calculate the length of overland movements, as this measure provided the most parsimonious and conservative estimate of distance traveled. Locations within a water body were grouped into one point at the centroid of the wetland (to accommodate drastic changes in the perimeters of these wetlands during wet and dry seasons), and overland movement distances were calculated in ArcView 9.0 (Environmental Systems Research Institute, 2004) as the Euclidean distance from wetland centroid to centroid, or from wetland centroid to the nearest creek edge. Animals captured moving overland were assumed to be moving from the closest water body, which in all cases was a wetland. Movement distance was calculated from their capture location. We examined the number and distance of overland movements and the number of water bodies used as a function of sex and size class of the individual.

2.4. Nest surveys

Alligators typically nest in June and July and their nests hatch in August and September (Ruckel and Steele, 1984). Previous observations from our site indicate that alligators on Ichauway nest during the latter end of that timeframe, probably because the site is located north of where most nesting studies have been conducted, and nests hatch in early to mid-September (A. Subalusky, personal observation). We assumed a successful nesting event had taken place in a given year if we located a recently active nest with eggshell fragments or if we located a pod of hatchlings during or after September. If we located a pod of young <40 cm TL and with a mass <100 g before September, we assumed the nest hatched the previous year.

During 2005, we recorded locations of nests and pods of hatchlings. In 2006 we conducted systematic nest surveys in both the wetland and the riverine systems. We calibrated transect length along the creek to the average perimeter of a wetland, in order to equalize survey effort between the two systems. Two observers walked approximately 30-m wide transects along the ecotonal boundary of the wetlands and the creek searching for nests. Any potential nests were carefully approached and opened to determine whether eggs were present, and we searched for signs of eggshells or alligator paths in the near vicinity to include old or recently depredated nests.

2.5. Biomass and nutrient calculations

Between 2002 and 2006, 174 individual alligators were captured on our study site, 90% of which were captured in seasonal wetlands and the remainder in the Ichawaynochaway Creek. A population estimate conducted in the seasonal wetlands resulted in an estimate of 133 individuals in the wetland population, which was close to the total 157 individuals captured in that habitat over the course of the study period (Subalusky et al., 2009). This estimate coupled with a significant decline in the number of unmarked

alligators captured or observed indicated the majority of the population appeared to have been captured and marked by the end of the study. Juvenile and sub-adult mass was obtained during capture events. Mass of adults was obtained when possible and these measurements were used to estimate mass of remaining individuals using linear regression ($y = 1146.1$ $x = 90332$; $R^2 = 0.975$). By classifying each individual according to the habitat in which they were captured, we were able to estimate total biomass of alligators of each size class in each habitat type.

We then calculated the approximate mass of N, P, Ca, Mg, Na and K contributed by alligators to each habitat on a daily and annual basis. We used data available on daily consumption rates for juvenile alligators (2.8% of body weight) and adult caiman and Nile crocodiles (0.6–0.8% of body weight) and daily amount of excreted nutrients for caiman (0.20–0.27‰ of their body weight under normal feeding conditions and 0.08–0.10‰ under starvation conditions) (Coulson and Hernandez, 1964; Fittkau, 1973). We also used percentage composition of each element as calculated by Fittkau (1973), and averaged between normal and starvation feeding conditions, to estimate levels of P and N, in particular. Due to similarities between all crocodilians in their biology, physiology and biochemistry, these levels of nutrient ingestion and excretion are likely attributable to American Alligators as well (Fittkau, 1973). Because juvenile alligators had a daily consumptive rate four times higher than larger caiman and Nile crocodiles, we multiplied the daily nutrient excretion levels for juveniles by four (Fittkau, 1973). As our study site is located in the northern part of the alligator's range, and alligators typically do not feed during the cooler months (October–March), we assumed 6 months of the year were under normal feeding conditions and 6 months were under starvation conditions. Our calculations do not include mortality, and are thus highly conservative. A mortality event, for example, would result in the input of their entire biomass to the nutrient cycle of that system, far outweighing annual excretion levels.

To calculate the area immediately affected by these biomass and nutrient inputs, we obtained area measurements of the wetlands and the creek from ArcView 9.0. Although there are over 90 seasonal wetlands on site, the majority of these are not used consistently by alligators. Therefore, we calculated wetland area using the subset of all seasonal wetlands on site in which an alligator burrow had been documented, indicating long-term or habitual use.

3. Results

3.1. Equal trapping effort

During 2005 and 2006, we captured 27 individuals in the two systems, ranging from 111.5 to 265.8 cm TL, with a mean TL of 188.2 cm (SD = 41.7; Table 1). Alligators captured in the creek (*n* = 14; mean TL = 231 cm) were significantly larger than those in the seasonal wetlands (*n* = 13; mean TL = 159 cm; Levene's test for equality of variances, $F = 0.092$, df = 25, $p = 0.764$; *t*-test for equality of means, $t = 4.834$, df = 25, and $p < 0.0001$).

Table 1
Summary statistics for American Alligators captured in the Ichawaynochaway Creek and within 13 seasonal wetlands on Ichauway, Baker County, GA, using equal trapping efforts between the two systems.

	Wetlands			Creek		
	Number	Mean TL (cm)	SD	Number	Mean TL (cm)	SD
Males	2	120.0	12.0	7	231.2	26.0
Females	11	165.7	27.6	7	200.0	27.8
Total	13	158.7	30.7	14	215.6	30.5

Because alligators are sexually dimorphic by size, differential habitat use by males and females could explain the larger size of the captured individuals in the creek system. Of the 14 alligators captured in the creek, 50% were female, while 84.6% of the 13 alligators caught in wetlands were female (one-sided Fisher's Exact Test, $\chi^2 = 3.635$, df = 1, $p = 0.066$; Table 1). For this study, the effect of sex on size was not significant ($F_{1,25} = 0.341$, $p = 0.565$). However, the effect of habitat type on size ($F_{1,25} = 33.817$, $p < 0.001$) was statistically significant as was the interaction between habitat and sex ($F_{1,25} = 9.443$, $p = 0.005$).

3.2. Radio telemetry

We radio-tracked 12 sub-adult females, two sub-adult males, three adult females and four adult males between 14 June 2005 and 31 October 2006. With the exception of two sub-adult males that left the study site after 27–29 days and could not be relocated, the subjects were monitored from 172 to 453 days, and the number of locations was between 19 and 102 (mean = 62 locations per individual). The number of recorded movements represents a known minimum (Table 2).

Five of the 14 sub-adult animals spent the duration of the study at the location where captured. Another five individuals used more than one wetland and made multiple overland movements. The remaining four moved overland between multiple wetlands and the creek. Of the group of 14, four individuals moved through two to three wetlands in a short period of time, staying less than 10 days at each one before staying in the creek or a wetland for a substantial amount of time. The movements of two other individuals were seasonal, starting and ending in one wetland, but moving into a separate wetland to over-winter.

Of the three adult females, one spent the duration of the study in the wetland in which she was captured. The other two were captured in the creek, moved into a complex of two wetlands for a period of 1–3 months, and then moved back into the creek. One of the females was gravid when captured on the creek and moved into a wetland shortly thereafter, where she stayed for the duration of the nesting season.

All of the adult males spent the duration of the study either on the Ichawaynochaway Creek in which they were captured or in the Flint River. No movement overland or use of seasonal wetlands was recorded for adult males at any point in the study.

3.3. Nesting surveys

We documented eight nesting events in seasonal wetlands in 2005. Four observations were made during the fall of 2005, two during early spring of 2006, which were presumed to be 2005 nests, one nest was under construction in 2005 but never used, and one nesting attempt was assumed due to the gravid female alligator who was radio-tracked to a seasonal wetland. In contrast,

we observed no active or recently active nests or pods of hatchlings on the creek.

Systematic nest surveys were conducted between 19 July and 8 August 2006. The one active nest we located through our systematic survey methods was at the edge of a seasonal wetland. The low overall nesting activity in 2006 was likely due to drought (Georgia Automated Environmental Monitoring Network, 2007). Almost all of the wetlands were completely dry, except for the water remaining in the alligator burrows and wallows. We monitored the nest weekly throughout the remainder of the incubation period; however, it was eventually depredated. Other observations in the region suggested widespread alligator nest failure in 2006 (A. Subalusky, personal observation; B. West, personal communication).

3.4. Biomass and nutrient calculations

Total biomass of alligators captured from 2002 to 2006 was 1293.7 kg. Alligators in seasonal wetlands constituted 722.8 kg, or 0.778 g/m^2, and those in the creek constituted 570.9 kg, or 0.180 g/m^2. Although juveniles comprised 72% of the individuals captured, they only accounted for 8.7% of the total biomass. Adults, on the other hand, constituted 13% of the individuals captured and 73.0% of the total biomass. Sub-adults, the remaining 15% of the population sampled, were almost exclusively captured in wetlands, and comprised 18.3% of the total biomass (Table 3).

The total annual input of N, P, Ca, Mg, Na and K by alligators into wetlands was 44.96 kg, or 0.05 g/m^2/yr. N constituted 0.03 g/m^2/yr, and P excretion was 0.01 g/m^2/yr. Total nutrient input into the creek was 24.95 kg, or 0.01 g/m^2/yr. N accounted for 5.0E−03 and P was 8.3E−04. Due to their higher rates of ingestion and metabolism, juvenile alligators contributed a disproportionate amount to the wetlands, totaling 18.6 kg, or 0.02 g/m^2/yr. Adults contributed 0.018 g/m^2/yr (16.6 kg) to the wetlands and 0.008 g/m^2/yr (23.9 kg) to the creek. Sub-adults excreted 0.011 g/m^2/yr (9.8 kg) to the wetlands and 1.2E−04 g/m^2/yr (0.39 kg) to the creek (Table 3).

4. Discussion

The results converged on the conclusion that alligators substantiate a form of functional connectivity among the seasonal wetland, terrestrial, and creek–river systems in this region, and this connectivity is a consequence of the ontogenetic niche shift in habitat use as alligators grow. Functional connectivity is established not only by movements of sub-adult alligators across the landscape among wetlands and eventually to the creek and river, but also by females that migrated from the creek to nest in wetland areas.

The use of seasonal wetlands as nursery sites was supported by the different densities of juveniles and adults in the two aquatic habitats. The significant interaction between sex and habitat on

Table 2
A summary of individual American Alligators tracked, the number and type of water bodies used, and the number and distance of overland movements (calculated as Euclidean distance between wetland centroids or between wetland centroid and nearest creek edge).

Sex	Size class	Number of individuals	Number of water bodies used (wetland, creek, river)	Movements from wetland to creek Total (range)	Movements from creek to wetland Total (range)	Movements between wetlands Total (range)	Overland movements Min (mean) max	Distance of overland movements (m) Min (mean) max
F	Sub-adult	12	0–5, 1, 0	4 (0–1)	1	15 (0–5)	0 (1.6) 5	218 (749) 1588
M	Sub-adult	2	1–2, 0, 0	0	0	5 (2–3)	2 (2.5) 3	216 (588) 835
F	Adult	3	1, 1, 0	2 (0–1)	2 (0–1)	7 (2–5)	0 (3.7) 7	257 (436) 756
M	Adult	4	0, 1, 1	0	0	0	0	0

Table 3
Summary of the total number of individuals captured in seasonal wetlands and the Ichawaynochaway Creek on Ichauway, Baker County, GA from 2002 to 2006, including the average and total biomass measurements and total levels of N, P, Ca, Mg, Na and K excreted on a daily and annual basis for each size class. Individuals are grouped according to the habitat in which they were first captured.

Size class	Number of individuals (wetland, creek)	Mass (kg) Mean (total)	Mass per unit area (g/m²) (wetland, creek)	Daily nutrient input per individual (g) (normal, starvation)	Annual nutrient input per individual (g)	Annual nutrient input per population (kg) (wetland, creek)	Nutrient input per unit area (g/m²/yr) (wetland, creek)
Juvenile	122, 4	0.89 (112.04)	0.117, 1.0E−03	0.84, 7.52E−05	152.56	18.61, 0.61	0.02, 1.9E−04
Sub-adult	25, 1	9.11 (236.94)	0.245, 3.0E−03	2.14, 1.93E−04	390.87	9.77, 0.39	0.01, 1.2E−04
Adult	9, 13	42.94 (944.77)	0.42, 0.18	10.09, 9.08E−04	1841.93	16.58, 23.95	0.02, 7.5E−03
Total	156, 18	1293.75	0.78, 0.18	–	–	44.96, 24.95	0.05, 7.9E−03

body size reflected the fact that only sub-adult males were caught in wetlands and only adult males were caught in the creek, and females of both size classes were caught in both systems. Furthermore, since we began working in this system in 2002, 78% of 157 alligators caught in seasonal wetlands were juveniles, 16% were sub-adults, and only 6% were adults (A. Subalusky, unpublished data). Of ten adults, only two were adult males. These findings corroborate the pattern elucidated by equal trapping efforts in both systems.

Nesting surveys further supported the hypothesis that seasonal wetlands provide suitable nursery sites for juveniles. All nesting attempts documented on Ichauway in this study were located in seasonal wetlands, whereas none were located in the riverine environment. Beck et al. (2001) defined a nursery as any habitat that contributes a greater amount of individuals to the adult population per unit area than other habitats in which juveniles occur. This may happen through any combination of four factors: higher density of juveniles, increased growth or increased survival of juveniles, and direct movement to adult habitats. In this study, we documented the first and fourth factors occurring in seasonal wetlands, indicating they operated as a nursery for alligators in this system (Beck et al., 2001; Gillanders et al., 2003). It is reasonable to predict that juvenile growth and survival would be higher in the wetlands than in the riverine system because the ephemeral nature of the wetlands results in a different predator guild than that present in the creek. Periodic drying prevents the establishment of large fish and precludes their use by many large alligators, both potential predators of juveniles. However, the wetlands are rich in invertebrates, which constitute the primary prey of juveniles (Delany, 1990; Platt et al., 1990; Battle and Golladay, 2001).

Overland movements were typically made by sub-adults undergoing an ontogenetic niche shift from wetland to riverine system, and by females moving into the wetlands in search of nesting sites. Sub-adults made the majority of their movements either among wetlands or from the wetlands to the creek, while adult females made equal movements between the creek and wetlands. In contrast, adult males made no overland movements during the course of this study and were never documented using seasonal wetland habitat. This suggests that breeding occurs in the riverine system, with adult females migrating overland between breeding and nesting sites.

We also demonstrated that alligators are transporting biomass and nutrients between the two systems, supporting our hypothesis that alligators serve as mobile links due to the ontogenetic shift in ecology that they experience (Deegan, 1993; Gibbons et al., 2006; Regester et al., 2006). Adult females migrate into wetlands and deposit eggs that have been nourished with nutrients from the riverine system. Juveniles grow in the wetlands and subsequently move into the riverine system as sub-adults with continued growth and

mortality in that habitat. The average mass of a sub-adult alligator was 9.1 kg, which is the amount of biomass accumulated in the wetlands and transported into the riverine system for each individual undergoing an ontogenetic shift in habitat. Using radio telemetry, we documented four sub-adult individuals moving from the wetlands into the creek, which resulted in a net shift of 36.4 kg biomass between these two systems, or an input of 0.01 g/m²/yr to the creek. This amount is a small nutrient input into a riverine system. However, when adult females return to the seasonal wetlands to nest and lay eggs, thus completing the cycle of biomass and nutrient transport between systems, they are contributing allochthonous nutrients to a system with otherwise very low input levels (Watt and Golladay, 1999; Battle and Golladay, 2007). The average mass of an adult alligator, 42.9 kg, is the biomass transferred from the river system into a single wetland when a female alligator returns to nest, in addition to the biomass of the 30–50 eggs she deposits, an occurrence we documented twice during our study. This corresponds to an input of 0.83 g/m²/yr to a single wetland, or as much as 0.2% of the annual litterfall input (410–582 g/m²/yr; Watt and Golladay, 1999).

In addition to transporting biomass between systems, alligators also excrete residual nutrients after metabolism, which can foster primary productivity in the system in which they reside (Fittkau, 1973). Our estimates showed the alligator population on Ichauway excreted 0.03 g/m²/yr nitrogen into seasonal wetlands, which was 0.72% of that contributed by litterfall (4.3–5.3 g/m²/yr) and 0.005 g/m²/yr phosphorous, which was 2.33% that of litterfall (0.22–0.77 g/m²/yr) (Watt and Golladay, 1999). Although a portion of nutrients contributed by alligators originate from local prey, another portion of nutrients is transported during habitat shifts. Nutrient transfer is particularly frequent during movements among multiple wetlands, which we documented in nine of the sub-adults and two of the adults that we radio-tracked. Furthermore, nutrients transported by adults may have originated in the terrestrial matrix surrounding the aquatic systems, as adult alligators take large terrestrial vertebrate prey. We observed raccoon (*Procyon lotor*) and Eastern harvest mole (*Scalopus aquaticus*) in the diet of alligators at Ichauway, and a variety of terrestrial prey are known from the diets of these opportunistic predators (Delany and Abercrombie, 1986; Delany et al., 1999). Hence, in addition to providing a functional link between seasonal wetlands and riverine systems, alligators also serve as mobile links between aquatic systems and the surrounding terrestrial matrix. In such small, nutrient-limited systems, allochthonous inputs such as these may play an important role in regulating their productivity (Fittkau, 1973; Polis et al., 1997; Watt and Golladay, 1999; Regester et al., 2006). These inputs also may be much more bioavailable than those provided by litterfall, which must first pass through the detrital cycle with a turnover rate of 2.2–2.4 yr (Watt and Golladay, 1999).

In addition to contributing to the net flux of productivity between otherwise disjunct aquatic systems, alligators probably influence seasonal wetlands most heavily through their role as top predator, and even more so as ecosystem engineers. Through the creation of burrows, wallows and nest mounds, alligators create habitat diversity and significantly alter the hydroperiod in these small systems, impacts that play a substantial role in the diversity and abundance of both plants and animals in the wetlands. Because alligators' use of seasonal wetlands is tied to dispersal from riverine waterways, these impacts are likely to be strongest in wetlands close to streams and rivers, or in wetlands that can be easily accessed from riverine systems via other "stepping stone" wetlands. In this study, average overland distance traveled was 591 m, suggesting that wetlands should be conserved within this proximity to one another or to riverine systems to promote alligator dispersal into the wetlands, which will in turn maintain important system processes. It is important to note that for other smaller or less vagile species, these minimum distances may be smaller (Semlitsch and Bodie, 2003).

When individuals rely on multiple habitat types throughout their lifetime, the conservation implications are numerous. In order to ensure persistence of the population, the discrete habitat types and their interconnecting matrix must be conserved to facilitate dispersal. In this case, multiple wetlands must be conserved within a relatively intact terrestrial matrix to allow alligators to move between systems. Preservation of dispersal patterns will, in turn, sustain important ecosystem processes impacted by the organisms, such as biomass and nutrient transport between systems and habitat diversification within the system.

Consideration of mobile link species and their contribution to the functioning and dynamics of ecosystems is increasing, but conservation at the landscape level has lagged behind. For instance, alligators are not the only species to move between multiple aquatic habitats that include seasonal wetlands. Similar phenomena have been documented for turtles (Burke et al., 1995; Tuberville et al., 1996; Joyal et al., 2001), salamanders (Scott, 1994; Gibbons, 2003), snakes (Seigel et al., 1995; Roe et al., 2004) and birds (Naugle et al., 2001; Amat et al., 2005). The 2001 US Supreme Court decision, Solid Waste Agency of Northern Cook County vs. United States Army Corps of Engineers (SWANCC), removed seasonal wetlands from federal protection under the Clean Water Act based on lack of hydrological connectivity to navigable waterways. However, as demonstrated in this study, seasonal wetlands are functionally connected to riverine waterways via the movement patterns of species that undergo ecological shifts during ontogeny. Moreover, some of these species, particularly crocodilians, turtles, and migratory birds, are of conservation interest or economically important. Conservation of species such as these requires protection of a matrix of seasonal wetlands, upland habitat, and navigable waterways. As exemplified by mobile link species driven by ontogenetic shifts, understanding ecosystem functioning and conservation at the landscape scale requires an approach that transcends ecosystem boundaries.

Acknowledgments

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