Alligator Diet in Relation to Alligator Mortality on Lake Griffin, FL

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Abstract - *Alligator mississippiensis* (American Alligators) demonstrated low hatch-rate success and increased adult mortality on Lake Griffin, FL, between 1998 and 2003. Dying Lake Griffin alligators with symptoms of poor motor coordination were reported to show specific neurological impairment and brain lesions. Similar lesions were documented in salmonines that consumed clupeids with high thiaminase levels. Therefore, we investigated the diet of Lake Griffin alligators and compared it with alligator diets from two lakes that exhibited relatively low levels of unexplained alligator mortality to see if consumption of *Dorosoma cepedianum* (gizzard shad) could be correlated with patterns of mortality. Shad in both lakes Griffin and Apopka had high levels of thiaminase and Lake Apopka alligators were consuming greater amounts of shad relative to Lake Griffin without showing mortality rates similar to Lake Griffin alligators. Therefore, a relationship between shad consumption alone and alligator mortality is not supported.

Introduction

Alligator mississippiensis Daudin (American Alligators) have been affected by unknown factors on Lake Griffin, FL, causing low hatch-rate success and adult mortality (Ross et al. 2003, Schoeb et al. 2002). Alligator egg hatch-rate success dropped to 10% between 1994 and 1997 (A.R. Woodward, unpubl. data). Between November 1998 and December 2003, researchers recorded 439 dead alligators on Lake Griffin, of which approximately 98% were adults (D.A. Carbonneau, unpubl. data, (Fig. 1). Most alligator deaths occurred in spring, and over 100 individuals died that season in some years; however, alligator deaths were recorded all months of the year during bi-weekly surveys.

Between 1998 and 2003, we observed Lake Griffin alligators that were lethargic, unresponsive to human approach, and had uncoordinated behavior. Subsequently, these alligators may have died of drowning. Pathology examinations have shown that these Lake Griffin alligators were

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affected by severe neurological impairment of unknown causes (Schoeb et al. 2002). These included reduced nerve conduction velocity, degeneration of nerves and characteristic lesions of the torus semicircularis in the mid-brain. Organochlorine and organophosphate pesticides, heavy metals, West Nile virus, botulism, and infectious diseases were all investigated and rejected as being associated with this mortality event (Ross et al. 2002). Similar lesions and patterns of hatchling mortality and adult impairment as observed in Lake Griffin alligators have been seen in Great Lake salmonines that resulted from thiamin deficiency (Honeyfield et al. 2005). Because of this similarity in pathology, thiamin levels of Lake Griffin alligators were analyzed in 1999 and 2000. Thiamin levels in Lake Woodruff alligators also were analyzed as a reference representing unimpaired alligators. Lake Griffin alligators had lower thiamin levels than Lake Woodruff alligators and seriously impaired Lake Griffin alligators had lower thiamin levels than less seriously impaired specimens (Ross et al. 2002).

The cause of neurological impairment in salmonines was the abundance of prey rich in thiaminase, including *Alosa pseudoharengus* Wilson (Alewife), *Osmerus mordax* Mitchell (Rainbow Smelt), and *Clupea harengus membras* Linnaeus (Baltic Herring), which are all filter feeders (Tillitt et al. 2005). American Alligators are known to prey on fish throughout their range in Florida (Delany and Abercrombie 1986; Delany et al. 1988, 1999; Rice 2004). *Dorosoma cepedianum* Lesueur (Gizzard Shad), an abundant clupeid filter feeder, was available to alligators in many central Florida lakes. Because Lake Griffin alligators showed similar symptoms to salmonines—low tissue thiamin levels, reproductive failure, adult neural impairment, and

Figure 1. Annual alligator mortality in Lake Griffin, FL during 1998–2003, based on biweekly surveys.

brain lesions (Honeyfield et al. 2005, Schoeb et al. 2002)—and had access to similar prey fish types, we investigated alligator diets in Lake Griffin and nearby Lakes Apopka and Woodruff, where alligators did not demonstrate these characteristics. We hypothesized that elevated alligator mortality on Lake Griffin was due to a diet high in *D. cepedianum* with high levels of thiaminase causing a depressed level of thiamin in alligators.

Body condition analyses investigate an animal's energy store compared to its body size and are affected by abiotic and biotic components in their habitat (Green 2001). Delany et al. (1999) found differences in alligator condition among lakes in Florida and found that a high condition correlated with a fish-dominated diet. Because condition analyses indicate health of a population (Sutton et al. 2000) and it is unknown if thiamin deficiency affects alligator condition, we examined Lake Griffin alligator condition and compared it to alligator condition from Lakes Apopka and Woodruff.

Study Site

The study was conducted in Lake Griffin (Lake County—28°50'N, 81°51'W), Lake Apopka (Lake and Orange counties—28°37'N, 81°37'W), and Lake Woodruff National Wildlife Refuge (Volusia County—29°06'N, 81°25'W). Neither Lake Apopka nor Lake Woodruff were having unusual adult alligator mortality events and were chosen as comparative study lakes because of their lake characteristics. Lake Apopka has similar lake characteristics to Lake Griffin, and Lake Woodruff is a cleaner, more pristine lake for comparison. Lakes Griffin and Apopka are hypereutrophic, alkaline, polymictic, shallow water bodies and are a part of the Ocklawaha chain of lakes (Rice 2004). Throughout much of the early 1900s, both lakes were clear, macrophyte-dominated lakes; however, in the mid-1900s, both lakes dramatically changed due to water-level controls, diking and draining associated marshes, urban runoff, sewage, and agricultural effluents, resulting in eutrophication (Canfield et al. 2000, Woodward et al. 1993) as well as pesticide pollution (Heinz et al. 1991). Since the late 1990s, both lakes experienced restoration efforts to improve water quality. These efforts included planting native vegetation, fish removal to reduce phosphorus levels, restoration of marsh on surrounding muck farms, and implementation of a marsh flow-way system to filter the water (Fernald and Purdum 1998). Lake Woodruff National Wildlife Refuge, along the St. Johns River, is a macrophyte-dominated, eutrophic, alkaline lake (Rice 2004). Lake Woodruff has experienced little agriculture and urban development, and its alligator population had consistently high hatching rates (A.R. Woodward, unpubl. data) and low levels of adult mortality.

Methods

During 2001–2003, we captured adult alligators by capture dart and snare from airboats between 2000 and 0400 hours. Each alligator was

marked with two Monel self-piercing tags (National Band and Tag Co., Newport, KY), sexed by manual palpation, and weighed to the nearest 2 kg using a spring scale. Standard measurements including total length (TL), snout vent length (SVL), tail girth (TG), and head length (HL) were taken with a flexible tape to the nearest 0.1 cm.

Stomach contents were obtained predominantly from live adult alligators within 3 hours of capture using the stomach pumping “hose-Heimlich” technique described by Fitzgerald (1989) and modified by Rice et al. (2005). This technique reliably recovered most of the stomach content and allowed subsequent release of the alligator unharmed. Additional stomach samples were obtained during necropsy of alligators by other researchers.

Stomach-content samples were washed with water through a 0.5-mm nylon mesh strainer, preserved in 70% ethanol, and stored in the laboratory. Samples were sorted by prey group (fish, reptiles, mammals, birds, amphibians, gastropods, insects, crustaceans, or bivalves) and non-prey items. Prey items were then identified to the lowest possible taxa and minimum numbers of individuals by comparing to reference specimens and skeletons in the collection of the Florida Museum of Natural History (FLMNH).

All prey items were categorized as either freshly ingested (fresh) or not freshly ingested (old) to avoid over-representation of indigestible prey. Alligators are unable to digest chitin and keratin (Garnett 1985, Magnusson et al. 1987) and persistent animal parts such as hair, feathers, scutes, and snail opercula may be overrepresented and bias quantitative estimates of prey intake. Guidelines were established based on available literature to categorize each prey item as either fresh or old (Barr 1994, 1997; Delany and Abercrombie 1986; Janes and Gutzke 2002). The time range for prey to be categorized as fresh varied with each prey taxa, but ranged between 24 and 72 hours (Rice 2004). Only freshly ingested material was considered in this analysis. Live mass of fresh prey was estimated by allometric scaling (Brown and West 2000, Casteel 1974, Reitz et al. 1987), field data, and available published weight data for different groups (Burt and Grossenheider 1980, Dunning 1993, Hoyer and Canfield 1994). Fresh invertebrates (except for Gastropods) were weighed to the nearest 0.01 g.

Frequency of occurrence (percent of stomach samples containing a given prey type) and percent composition by live mass (percent of the diet each prey group or taxa represents based on estimated live-prey mass) were used to quantitatively analyze the fresh-diet data. The Kruskal-Wallis analysis of variance rank test was used to compare mean fish proportion in alligator diets among lakes, and when significant differences were found, the lakes were compared pair-wise using the Mann-Whitney U test.

Fulton’s condition factor ($K = W/L^3 * 10^n$, where W = mass of the alligator in kg, L = SVL in cm, and $n = 5$), was used to determine each alligators condition (Zweig 2003). Condition data were analyzed using a general linear model with the least significant difference (LSD) post-hoc

test. Values for both diet and condition data were expressed as the mean $\pm$ one standard error unless otherwise indicated. All statistical analyses were performed using SPSS software (SPSS 2000). Both diet and condition statistical tests used an alpha of 0.10, with the null hypothesis of no differences.

All analyses were performed on samples combined for all three years and then compared among the three lakes. However, Lake Griffin samples were quantitatively analyzed each year to compare the shad consumption year to year. Impaired Lake Griffin alligators were sampled along with normal Lake Griffin alligators during 2001. These samples were analyzed in the same manner as the other samples; however, these analyses were kept separate from normal Lake Griffin samples. No statistical analyses were performed on these samples due to small sample size. Results and discussion pertain to samples from normal (unimpaired) alligators among the lakes, unless indicated by stating that they were samples from impaired alligators.

Results

Stomach contents from 175 normal American Alligators ranging in size from 182 cm to 304 cm TL were collected from alligators captured at Lakes Griffin (n = 85), Apopka (n = 44), and Woodruff (n = 46) from March to October 2001, from April to October 2002, and from April to August 2003. Stomach contents from an additional 13 alligators were collected from impaired Lake Griffin alligators post-mortem during 2001 (Schoeb et al. 2002). The alligators ate a wide variety of vertebrate and invertebrate prey. Fish were the most important prey group in frequency of occurrence and percent composition by live mass for all lakes. Alligators from Lake Apopka had the highest occurrence of fresh fish (64%), followed by Lake Woodruff (57%) and Lake Griffin (44%) (Table 1). Fish made up an overwhelming percentage of the mass of alligator stomach samples from Lakes Apopka (90% of the diet) and Woodruff (80% of the diet). Total fish biomass for Lake Griffin alligators was 54% of the diet (Appendix 1). While fish were the predominant prey in all lakes, species composition and number of fish

Table 1. Percent occurrence of fresh prey in alligator stomachs collected from Lakes Apopka, Griffin, and Woodruff, FL during 2001–2003.

	Griffin (n = 85) % occurrence	Apopka (n = 44) % occurrence	Woodruff (n = 46) % occurrence
Fish	44	64	57
Reptile	14	7	2
Mammal	2	5	2
Bird	5	2	0
Amphibian	6	0	4
Gastropod	28	9	41
Bivalve	4	0	4
Crustacean	9	11	15
Insect	8	9	13

consumed varied among lakes. Catfish (Ictaluridae) were most commonly consumed in Lake Griffin, shad (Clupeidae) in Lake Apopka, and sunfish and bass (Centrarchidae) in Lake Woodruff (Appendix 1).

Proportion of fish (by estimated fresh biomass) in individual alligator stomachs ranged from 0 to 100%. Lake Apopka alligators had the highest mean proportion of fish in their diet (mean = $79.9\% \pm 6.76$), followed by Lake Woodruff (mean = $59.4\% \pm 7.5$) and Lake Griffin (mean = $48.5\% \pm 6.05$) (Fig. 2). Proportion of fish in alligator stomachs differed among lake ($P = 0.006$), and proportion of fish in alligator stomachs from Lake Apopka was greater than those from Lakes Griffin ($P = 0.002$) and Woodruff ($P = 0.018$). Proportions of fish in Lakes Griffin and Woodruff alligator stomachs were not significantly different ($P = 0.403$).

The predominant prey group consumed by Lake Griffin alligators each year was fish, ranging from 43–68% of the diet (Table 2). Fresh shad (*D. cepedianum* and *Dorosoma* spp.) represented 38% of the diet of samples from Lake Griffin in 2001, making Clupeidae the predominant family of fish consumed that year. However, no shad were identified in any 2002 samples, and a single old shad was identified in one sample in 2003 (Table 2) (and catfish (Ictaluridae) were the predominant family of fish consumed by Lake Griffin alligators that year (Table 3).)

Other vertebrate prey groups (reptiles, mammals, birds, and amphibians) and invertebrates were found less frequently in alligator stomachs in all the lakes (Table 1), and reptiles were the most commonly consumed vertebrate prey after fish. Turtles were the most common reptiles consumed by the alligators, but alligators also consumed aquatic snakes, and we saw evidence (FWC marking tags) of alligator remains in stomachs (Rice 2004). We

Figure 2. Mean fish proportion ($\pm$ SE) in alligator stomach contents among Lakes Griffin, Apopka, and Woodruff during 2001–2003.

observed no evidence of fresh alligators in stomachs. Alligator eggshells were found in 2 Lake Griffin alligator samples (one female and one male alligator) and in one sample from a female alligator on Lake Woodruff.

Alligator-condition scores (K) for all Lake Griffin alligators ranged from 1.63 to 3.70 (mean = 2.66 ± 0.045), while K for all Lake Apopka alligators ranged from 2.15 to 4.13 (mean = 2.99 ± 0.059), and the K for all Lake Woodruff alligators ranged from 1.86 to 3.08 (mean = 2.48 ± 0.041) (Fig. 3). The condition of alligators differed among lakes ($P < 0.001$).

Impaired alligator samples

Thirteen stomach samples from impaired alligators were collected from Lake Griffin during 2001 and they exhibited some similarities and some differences to normal Lake Griffin alligator diets. Eight of the 13 samples contained only old prey, and most (6) were almost completely empty. The proportion of stomach samples containing old prey (62%) was higher than that of normal Lake Griffin samples (26%) (Rice 2004). Fresh prey identified in these samples included fish, reptiles, and invertebrates, similar to samples from normal alligators. Two of the 5 samples containing fresh prey contained multiple specimens of *D. cepedianum*, and 7 of the 8 samples containing old prey contained prey remains that could not be identified beyond fish.

Table 2. Lake Griffin alligator stomach content samples by year showing the proportion of fish consumed and the proportion of shad in alligator diets during 2001–2003. Note that 8 out of 10 shad in 2001 were identified as *D. cepedianum*, and that the one shad found in all the 2003 samples was not considered fresh, and therefore no biomass estimations were made.

Year	# samples	Total biomass (g)	Total fish biomass (g)	% Fish biomass	# Shad	% Shad biomass
2001	24	12,312.4	7875.2	64	10	38
2002	42	18,568.4	7998.1	43	0	0
2003	19	6566.7	4436.2	68	1	0
All years	85	37,447.5	20,309.5	54	11	12

Table 3. Lake Griffin alligator fish consumption by year and family, including minimum number of individuals (MNI) identified and estimated mass in grams of fresh fish consumed during 2001–2003.

	2001		2002		2003	
	MNI	Mass (g)	MNI	Mass (g)	MNI	Mass (g)
Total fish	22	7875	24	7998	9	4436
Ictaluridae	6	2044	13	4620	5	2389
Clupeidae	10	4618	0	0	0	0
Lepisosteidae	2	1003	2	2075	2	1411
Centrarchidae	1	150	4	183.1	1	635
Poeciliidae	2	0.2	1	0.4	0	0
Cyprinodontidae	0	0	2	8.6	1	1.2
Cichlidae	0	0	1	700	0	0
Amiidae	0	0	1	411	0	0
Unidentified fish	1	60	0	0	0	0

Discussion

This study confirmed previous studies indicating alligators are opportunistic carnivores that consume a variety of prey (Chabreck 1972, Delany and Abercrombie 1986). Fish were the dominant prey group for alligators in all three lakes in this study; however, the species of fish consumed differed among lakes. This may be due more to habitat differences that support a different composition of fish species rather than dietary preference.

Our hypothesis that alligator mortality on Lake Griffin was due solely to a diet high in *D. cepedianum* with high levels of thiaminase causing depressed levels of thiamin in alligators was not supported by this study. Lake Griffin alligators did have depressed thiamin levels and were consuming a large proportion of shad that had high levels of thiaminase in 2001 (Ross et al. 2003). The drop in mortality at Lake Griffin coincidental with the shift in diet away from shad to catfish (Ichthyuridae) does support the hypothesis, but Lake Apopka data does not support it. In addition, Lake Apopka alligators consistently ate large quantities of shad, also containing high levels of thiaminase (Ross et al. 2003), throughout the study, but there was no unusual adult mortality occurring on Lake Apopka.

The drop in consumption of shad in Lake Griffin alligator diets after 2001 was most likely due to shad removal by the St. Johns River Water Management District (SJRWMD). Just prior to Spring 2002 alligator sampling, almost 500,000 kg of *D. cepedianum* and an estimated 12,000 kg of *Lepisosteus* spp. (Gar) were removed from Lake Griffin as part of lake restoration and management efforts to reduce phosphorus levels (Walt Godwin, St. Johns River Water

Figure 3. Mean condition ($\pm$ SE) of alligators from Lakes Griffin, Apopka, and Woodruff during 2001–2003.

Management District, Palatka, FL. unpubl. data). Shad removal likely altered fish populations and certainly changed size distributions of shad in the lake and thus, their availability to alligators. Shad netting efforts ceased in February 2003 due to absence of large shad in the catch.

Alligator mortality on Lake Griffin was unusually high compared to other Florida lakes from 1999 through 2001 (Fig. 1—note that this figure includes only Lake Griffin data); however, by 2003, the number of alligators dying was not very different from typical mortality levels (D.A. Carbonneau, pers. comm.). Several factors in and around Lake Griffin occurred in 2002 that could have affected this decrease in alligator mortality: water levels rose sharply in early 2002 after heavy winter rains in 2001, the marsh flow-way restoration system was reactivated, large quantities of shad and gar were removed, and water quality improved as indicated by reduced chlorophyll levels (Rice 2004). Whether alligator mortality was linked to these events is uncertain. However, a significant change in the species composition in alligator diets coincided with these events.

Alligator condition can be affected by diet, prey density, alligator density, habitat, ambient temperatures, or other factors (Delany et al. 1999, Taylor 1979, Zweig 2003). Alligator condition in this study was different among lakes, and Lake Griffin alligator condition ranged between the condition of alligator on Lakes Apopka and Woodruff and appeared to be a healthy size. Insufficient measurements were taken during 2001 to compare the condition of impaired and normal alligators from Lake Griffin. However, impaired Lake Griffin alligators did not appear to be thinner or have a lower condition than normal Lake Griffin alligators.

Thiamin deficiency in crocodilian farms has occurred; however, little has been mentioned on how or if this deficiency affects body condition. Huchzermeyer (2003) described thiamin deficiency in crocodilians, but does not mention if body condition was affected. Jubb (1992) reported on thiamine deficiency in hatchling *Crocodylus porosus* Schneider (Saltwater Crocodile) and mentioned that hatchlings affected by thiamine deficiency were the largest in their clutch group. We did not see evidence of poor body condition in impaired or normal Lake Griffin alligators, and it may be that this deficiency caused a rapid onset of impairments that did not affect their condition.

Lake Griffin alligators did have depressed thiamin levels and did consume *D. cepedianum* with high levels of thiaminase; however the combination of Lake Griffin alligators consuming less shad, the shad removal, and improving water quality all may have contributed to the number of impaired and dead Lake Griffin alligators observed and recorded by researchers decreasing after 2001. In addition, shad in Lake Apopka also had high levels of thiaminase (Ross et al. 2003), and Lake Apopka alligators were consuming greater amounts of *D. cepedianum* relative to Lake Griffin without showing mortality rates similar to Lake Griffin alligators (Appendix 1). An unknown factor that we did not detect in Lake Griffin may have contributed to the alligator mortality, and this unknown factor was not affecting Lake Apopka and therefore did not affect the alligators there. As of 2004, alligator mortality on Lake Griffin has returned to levels observed prior to the mortality event.

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Prey	Lake Griffin			Lake Apopka			Lake Woodruff		
	Mass			Mass			Mass		
	n	g	%	n	g	%	n	g	%
Catfish, <i>Pterygoplichthys</i> spp. Gill	1	250	2						
Undetermined Fish species	1	60	0.2						
Total fish	55	20,309.5	54.2	78	15,869	90	30	10,216	80
Birds									
Anhinga, <i>Anhinga anhinga</i> Linnaeus	1	1235	3.3	1	1235	7			
Double Crested Cormorant, <i>Phalacrocorax auritus</i> Lesson	2	3628	9.7						
White Ibis, <i>Eudocimus albus</i> Linnaeus	1	900	2.4						
Total birds	4	5763	15.4	1	1235	7	0	0	0
Reptiles									
Kinosternidae	1	105	0.3						
Stinkpot Turtle, <i>Sternotherus odoratus</i> Latreille in Sonnini and Latreille	6	385	1.0	1	35	0.2	1	108	0.6
Loggerhead Musk Turtle, <i>Sternotherus minor</i> Agassiz	2	150	0.4						
Redbelly Turtle, <i>Pseudemys nelsoni</i> Carr	1	1148	3.1						
Turtle, <i>Pseudemys</i> spp. Gray	1	13	0.03						
Gopher Tortoise, <i>Gopherus polyphemus</i> Daudin	1	582	1.6	1	113	0.6			
Florida Softshell Turtle, <i>Apalone ferox</i> Schneider	1	386	1.0						
Cottonmouth, <i>Agkistrodon piscivorus</i> Lacépède	1	686	1.8						
Brown Water Snake, <i>Nerodia taxipilota</i> Holbrook	1	300	0.8						
Mud Snake, <i>Farancia abacura</i> Holbrook				1	10	0.1			
Total reptiles	15	3755	10.0	3	158	1	1	108	0.6
Mammals									
Cotton mouse, <i>Peromyscus gossypinus</i> LeConte				1	40	0.2			
Eastern wood rat, <i>Neotoma floridana</i> Ord				1	291	1.6			
Hispid cotton rat, <i>Sigmodon hispidus</i> Say and Ord	1	155	0.4						
Raccoon, <i>Procyon lotor</i> Linnaeus	1	4705	12.6						
Round-tailed muskrat, <i>Neofiber alleni</i> True							1	289	1.8
Total mammals	2	4860	13.0	2	331	2	1	289	1.8

Prey	Lake Griffin			Lake Apopka			Lake Woodruff		
	n	g	Mass %	n	g	Mass %	n	g	Mass %
Amphibians									
Greater Siren, <i>Siren laceratina</i> Linnaeus	1	387	1				2	1325	8.2
Two-toed Amphiuma, <i>Amphiuma means</i> Garden in Smith	1	287	0.8						
Frog, <i>Rana</i> spp.	3	700.4	1.9						
Total amphibians	5	1374.4	3.7	0	0	0	2	1325	8.2
Gastropods									
Apple snails, <i>Pomacea paludosa</i> Say	64	1321.9	4.0	3	68	0.4	30	694.1	4.3
Total gastropods	64	1321.9	4.0	10	69	0.4	32	695.4	4.4
All other invertebrates combined	224	127.4	0.32	41	87.2	0.558	40	172.3	1.04