DEMOGRAPHIC AND GEOGRAPHIC VARIATION IN FOOD HABITS OF AMERICAN ALLIGATORS (ALLIGATOR MISSISSIPPIENSIS) IN LOUISIANA

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Abstract.—American Alligators (*Alligator mississippiensis*) are opportunistic carnivores and scavengers. However, composition of alligator diets often differs geographically, presumably because of geographic variation in food availability. Diet influences alligator body condition, growth, and reproduction because energetic and nutritional content varies among prey items. Therefore, information on geographic, demographic, and temporal variation in alligator food habits is important for monitoring current population status and predicting possible impacts due to habitat alteration or disturbance. This study compares food habits of 448 alligators of three sex-size classes from coastal marshes of southeastern and southwestern Louisiana. Overall, remains of crustaceans were the most frequently encountered prey category, followed by fish, mammals, reptiles, and birds. Stomachs from large males were more likely to contain remains of mammals and reptiles than were stomachs from small males and from females. Stomachs from southwestern Louisiana. Because alligator food habits vary among geographic locations and among sex and size classes, demographic parameters might also vary among alligator populations and also among sex and size classes within populations. The relationship between demographic parameters and food habits in alligators needs more investigation. In addition, because alligators are the top consumer in their trophic chain, they could serve as an indicator species for monitoring responses of coastal systems following habitat loss or disturbances such hurricanes.

Key Words.—American Alligator; Alligator mississippiensis; coastal wetlands; food habits; Louisiana

INTRODUCTION

Although American Alligators (Alligator mississippiensis) have been described as opportunistic predators (McIlhenny 1935; Delany and Abercrombie 1986; Wolfe et al. 1987), considerable variation in food habits exists among size (or reproductive maturity) classes (Delany and Abercrombie 1986; Wolfe et al. 1987), between sexes (Delany et al.1988; Delany et al. 1999), among seasons (Delany et al. 1988), among habitats (Chabreck 1972; McNease and Joanen 1977; Taylor 1986; Delany et al. 1999), and among locations (Kellogg 1929; Chabreck 1972; McNease and Joanen 1977; Delany 1990; Platt et al. 1990). In addition, the importance of various prey items at a single location might vary over time as a result of habitat alterations, disturbance, or management activities (Giles and Childs 1949; Valentine et al. 1972).

In Louisiana, coastal marshes comprise 72% of total statewide alligator habitat with the remainder occurring as inland lakes, swamps, and other habitat types (Joanen and McNease 1987). Significant losses of these coastal marshes resulting from natural and anthropogenic processes have occurred in recent decades (Boesch et al. 1983; Barras, J.A., P.E. Bourgeois, and L.R. Handley. 1994. Land Loss in Coastal Louisiana 1956-90. National Biological Survey, National Wetlands Research Center Open File Report 94-01. http://www.lacoast.gov

/cwppra/reports/LandLoss/index.htm [accessed June 15, 2009]) and have impacted alligator populations (Ruth Elsey, pers.comm.; Louisiana Department of Wildlife and Fisheries. 2008. FY 2007-2008 annual report. Available from <u>http://www.wlf.louisiana.gov/pdfs/about/07-08AnnualReport.pdf</u>. [Accessed 22 June 2009]).

Current rates of coastal marsh loss are greatest in southeastern Louisiana (Gagliano et al. 1981; Barras et al. 1994. *op. cit.*), a region that encompasses 62% of Louisiana's coastal marsh habitat (Joanen and McNease 1987). Food habits of alligators from southeastern Louisiana have received little attention when compared to those from southwestern Louisiana (Chabreck 1972; Valentine et al. 1972; McNease and Joanen 1977; Wolfe et al. 1987; Platt et al. 1990). In particular, no food habits data have been published for alligators from coastal marsh habitats in the Barataria-Terrebonne region in southeastern Louisiana, where marsh loss rates are greatest (Gagliano et al. 1981; Barras et al. 1994. *op. cit.*).

Food habits of alligators in Florida often differ among lakes separated by only a few miles (Delany et al. 1999; Rice et al. 2007); therefore, food habits descriptions of alligators from southwestern Louisiana might differ from those of southeastern Louisiana. In addition, none of the published studies of Louisiana alligators compare food habits between sexes despite evidence for sex-related differences in Florida alligators (Delany et al. 1988; Delany et al. 1999). Because diet influences alligator body condition, growth, and reproduction (Chabreck 1972; Delany et al. 1999; Rice et al. 2007), information on geographic, demographic, and temporal variation in food habits is important for monitoring current population status and predicting possible impacts due to habitat alteration. This paper examines potential sexand size-related differences in food habits between alligators from the Barataria-Terrebonne region in southeastern Louisiana and those from southwestern Louisiana. These data can be useful in assessing impacts of continued marsh losses on alligator diets, as a baseline for comparison of effects of habitat alteration or disturbance, and in population models that incorporate growth, reproduction, and survival as a function of diet.

MATERIALS AND METHODS

Study area.-In conjunction with the Louisiana Department of Wildlife and Fisheries' (LDWF) Nutria (Myocastor coypu) management activities that began in November 2002 (Louisiana Department of Wildlife and Fisheries, unpubl. data; Gabrey et al. 2009), I collected alligator stomachs from cooperating hunters during the September alligator trapping seasons of 2002, 2003, and 2004. I collected stomachs from Lafourche and Terrebonne parishes in 2002; I added Cameron, Vermillion, and St. Charles parishes in 2003. Marshes in the southeastern parishes (Lafourche, Terrebonne, and St. Charles) are part of the Barataria-Terrebonne region and were included in LDWF's Nutria removal program, in which Nutria were harvested during the regular furbearer season (November to March) beginning in November 2002. Nutria removal was not in effect in marshes in the two southwestern parishes (Cameron and Vermillion). All marshes from which alligators were harvested are classified as fresh marsh except those in Lafourche Parish, which are classified as intermediate (Chabreck 1970).

Data collection.—Although Louisiana's alligator harvest regulations have no minimum length restrictions, alligator trappers target adults > 1.83 m; consequently, all stomachs analyzed were from adult alligators. Trappers capture alligators using hooks, typically baited with chicken parts, suspended above open water. Although wild birds (usually blackbirds or grackles) are used as bait occasionally, they can be differentiated easily from living birds ingested by alligators by the presence of shotgun pellet holes in the bait bird carcass. Trappers check trap lines daily; consequently, any prey consumed by a trapped alligator has been in its digestive system for up to a day. Harvested alligators were brought to a processing shed where they were tagged, measured, and sexed. I removed and froze stomachs after the carcasses were processed.

After thawing stomachs, I identified contents to the lowest taxon possible. Because most prev items were at least partially digested and therefore unidentifiable to lower taxonomic levels, I sorted prey remains into one of six broad categories (fish, mammals, crustaceans, birds, reptiles, and other), and recorded the total weight of each category in each stomach. Analysis of stomach contents can be biased by differences in rates at which various prey items are digested and voided from the digestive system (Delaney and Abercrombie 1986; Barr 1994, 1997). Therefore, metrics such as weight and frequency of occurrence under represent the importance of soft prey items (soft tissue, skin, etc.) in the actual diet and over represent the importance of hard prey items (exoskeletons, bone, fur, nails or claws, scales, etc.). Dietary reconstruction (Chabreck 1972; Wolfe et al. 1987) can overcome some of these biases; however, I was unable to use this method because of the indeterminate growth of fish and other prey items and the inability to identify individual prey items to species level. Consequently, I used simple presence/absence of each prey category in a stomach as the response variable for all analyses. Despite the limitations of using stomach contents to describe food habits, comparisons within this data set should be valid because all samples were subject to the same biases.

Statistical analysis.—I classified alligators as "large" if total length was greater than 2.44 m (8 feet) and "small" if total length was between 1.83 and 2.44 m (6–8 feet). Because only 4% (5 of 117) of females were > 2.44 m, all females were classified as small and are hereafter referred to as females. I considered a prey category "present" in a stomach if the total weight of that category was ≥ 0.1 g. Thus, I excluded those prey items represented by only a few hairs, scales, toenails, etc.

I used logistic regression (PROC LOGISTIC, in SAS 9.1. SAS Institute. Inc., Carv. North Carolina) to determine which explanatory variables (region, size, and their interaction) affected the probability that a particular prey category was present in a stomach (Agresti 1996). A separate analysis was conducted for each prey category (fish, mammals, crustaceans, reptiles, and birds). For each of the five analyses, I began with the "saturated model" as the initial regression model and then used the backwards elimination option in PROC LOGISTIC to remove non-significant explanatory variables (Agresti 1996). The initial model included REGION (southeastern or southwestern), SIZE (large male, small male, or female), and the REGION*SIZE interaction as the explanatory variables and PRESENCE (1 if item was present, 0 if item was absent) of a prev category in a stomach as the dependent variable. I removed explanatory variables if the probability of a greater Wald's χ^2 was ≥ 0.05 . If the resulting logistic

	Southeastern			Southwestern			
	Large males $n = 117$	Small males $n = 177$	Females $n = 99$	Large males $n = 9$	Small males $n = 28$	Females $n = 18$	
Fish	44	49	47	67	71	67	
Mammals	47	23	24	33	43	22	
Crustaceans	53	84	73	22	7	6	
Reptiles	26	8	14	56	21	21	
Birds	8	5	10	0	11	11	
Other	18	21	25	11	11	17	

TABLE 1. Percentage of stomachs from 448 American Alligators that contained ≥ 0.1 g of remains of six prey categories. Stomachs were collected from southeastern and southwestern Louisiana during annual trapping seasons in September 2002, 2003, and 2004.

regression equation contained a significant effect (other than intercept), I used the CONTRAST option in PROC LOGISTIC to compare odds ratios and calculate their 95% confidence intervals. Finally, I used the resulting logistic regression equation to calculate the "predicted" relative frequencies (and 95% confidence intervals) of a stomach containing a prey category. Although I collected stomach samples over three years, I pooled all data across years and did not include YEAR as an effect in the logistic regression models because of small yearly sample sizes from southwestern parishes (0 in 2002, 31 in 2003, and 48 in 2004).

RESULTS

Characteristics of alligators harvested.—I collected stomachs from 553 alligators during the September hunting seasons of 2002, 2003, and 2004, most of which (> 80%) I took from alligators harvested during the first week of the 30-day trapping season. I excluded from analyses 10 stomachs lacking data for sex, length, or parish, and 95 stomachs that contained trace amounts (< 0.1 g) or no prey items. Of the remaining 448 stomachs, I collected 28% (*n* = 126) from large males, 46% (*n* = 205) from small males, and 24% (*n* = 117) from females.

Ninety-three percent (117/126) of the large male stomachs, 86% of the small male stomachs (177/205), and 85% of the female stomachs (99/117) came from the three southeastern parishes. I collected 393 stomachs from the three southeastern parishes (75 in 2002, 157 in 2003, and 161 in 2004) compared to 55 from the two southwestern parishes (0 in 2002, 25 in 2003, and 30 in 2004).

Stomach contents.—Crustaceans (crawfish, crabs, shrimp, and unidentified), fish, and mammals were the most frequently recorded prey categories for stomachs collected from the three Southeastern parishes compared to fish, reptiles, and mammals for the stomachs collected from the two Southwestern parishes (Table 1). Identifiable fish remains included Catfish (Ictalurus spp.), Bowfin (Amia calva), and Alligator Gar (Atractosteus spatula); identifiable mammal remains included Nutria and Muskrat (Ondatra zibethicus). Identifiable reptile remains included turtles, snakes (Crayfish Snake [Regina rigida], other unidentified species), and other alligators. Identifiable bird remains included Barred Owl (Strix varia) and Common Moorhen (Gallinula chloropus). Other prey items included insect or insect parts, snails, spiders, and clams.

TABLE 2. Results of logistic regression analyses on the probability of an American Alligator stomach containing remains of five prey categories. REGION refers to two geographic locations (southeastern and southwestern Louisiana); SIZE refers to three size and gender classes (large males, small males, and small females). Effects in bold type were retained in the final logistic regression model.

Prey category	Effect	df	Wald χ^2	$P > \chi^2$
E' 1	DECIONISCIZE	2	0.07	0.07
FISH	REGION*SIZE	2	0.06	0.97
	REGION	1	8.90	<0.01
	SIZE	2	0.97	0.61
Mammals	REGION*SIZE	2	4.13	0.12
	REGION	1	1.25	0.26
	SIZE	2	18.56	<0.01
Crustaceans	REGION*SIZE	2	6.93	0.03
	REGION	1	37.19	< 0.01
	SIZE	2	0.51	0.77
Reptiles	REGION*SIZE	2	0.63	0.73
	REGION	1	7.39	<0.01
	SIZE	2	20.04	<0.01
Birds	REGION*SIZE	2	0.58	0.75
	REGION	1	0.32	0.57
	SIZE	2	2.62	0.27

Prey category	Comparison	Odds ratio	95% C. I.	Wald χ^2	Significance level
Fish	Southwestern vs. Southeastern	2.51	1.37-4.60	8.90	< 0.01
Mammals	Large males vs. Small males	2.51	1.57-4.02	14.67	< 0.01
	Large males vs. Females	2.71	1.56-4.69	12.61	< 0.01
	Small males vs. Females	1.08	0.64-1.83	0.08	0.77
Crustaceans					
Southeastern	Large males vs. Small males	0.22	0.13-0.38	30.18	< 0.01
	Large males vs. Females	0.42	0.24-0.75	8.70	< 0.01
	Small males vs. Females	1.91	1.06-3.47	4.57	0.03
Southwestern	Large males vs. Small males	3.71	0.44-31.26	1.46	0.23
	Large males vs. Females	4.86	0.38-62.60	1.47	0.22
	Small males vs. Females	1.31	0.11-15.79	0.045	0.83
Large males	Southwestern vs. Southeastern	0.25	0.05-1.27	2.78	0.10
Small males	Southwestern vs. Southeastern	0.015	0.003-0.067	30.36	< 0.01
Females	Southwestern vs. Southeastern	0.022	0.003-0.17	13.19	< 0.01
Reptiles	Southwestern vs. Southeastern	2.59	1.30-5.13	7.39	< 0.01
*	Large males vs. Small males	3.87	2.11-7.09	19.03	< 0.01
	Large males vs. Females	2.46	1.28-4.69	7.38	< 0.01
	Small males vs. Females	0.64	0.32-1.26	1.70	0.19

TABLE 3. Comparison of odds ratios, 95% confidence intervals, and Wald χ^2 for the probability that an American Alligator stomach from Louisiana contained one of five prey categories. Significance levels < 0.05 indicate that the reported odds ratio differs from unity.

Presence of these prey items was considered incidental to capture of other prey; therefore, I did not use this category in further analysis.

Logistic regression and odds ratios.—The REGION main effect was significant and remained in the regression model for the analysis of fish (Table 2). The deviance comparing this reduced regression model to the saturated model indicated no significant lack of fit ($\chi^2 = 1.03$, df = 4, P = 0.91). The odds ratio comparing relative frequency of fish in stomachs from southwestern parishes with those from southeastern parishes was 2.51 (Table 3), indicating that stomachs from southwestern parishes were about 2.5 times more likely to contain fish than were stomachs from southeastern parishes (Fig. 1).

The SIZE main effect was significant and remained in the regression model for the analysis of mammals (Table 2). The deviance comparing this reduced regression model to the saturated model indicated no significant lack of fit ($\chi^2 = 5.45$, df = 3, P = 0.14). The odds ratios comparing relative frequency of mammals in large males with small males and with females were 2.51 and 2.71 (Table 3), respectively, indicating that large males were about 2.5 times more likely to contain mammals than were the other size classes (Fig. 2). Small males and females were equally likely to contain mammal remains. The REGION*SIZE interaction was significant in the analysis of crustaceans (Table 2). The interaction model is the saturated model; therefore, there is no deviance or measure of lack of fit associated with this model. For stomachs collected in southeastern Louisiana, large males were less likely than both small males and females to contain crustaceans while small males were more likely than females to contain

crustaceans (Table 3, Fig. 3). For stomachs from southwestern Louisiana, all size classes were equally likely to contain crustaceans (Table 3, Fig. 3). However, the confidence intervals for the three odds ratios were extremely wide. Southwestern large males and southeastern large males were equally likely to contain crustacean remains (Table 3, Fig. 4). However, southwestern small males and southwestern females were 50–60 times less likely than were southeastern males and southeastern females, respectively, to contain crustacean remains (Table 3, Fig. 4). However, the confidence intervals for these odds ratios were very wide.

The REGION and SIZE main effects were significant and remained in the regression model for the analyses of reptiles (Table 2). The deviance comparing this reduced regression model to the saturated model indicated no significant lack of fit ($\chi^2 = 0.64$, df = 2, P = 0.73). The odds ratio comparing relative frequency of reptiles in stomachs from southwestern parishes with those from southeastern parishes was 2.59 (Table 3), indicating that stomachs from southwestern parishes were about 2.5 times more likely to contain reptiles than were stomachs from southeastern parishes (Fig. 1). The odds ratios comparing relative frequency of reptiles in large males with small males and with females were 3.87 and 2.46 (Table 3), respectively, indicating that large males were 2.5-3.8 times less likely to contain reptiles than were the other size classes (Fig. 2). Small males and females were equally likely to contain reptiles. No effects (except for the intercept) were significant for the analysis of birds (Table 2). Based on the intercept-only model, the predicted relative frequency of birds was 0.07 (95% C.I. = 0.05–0.10).



FIGURE 1. Predicted relative frequencies and 95% C.I. of presence of fish (top) and reptiles (bottom) in stomachs of American Alligator in southeastern and southwestern Louisiana. Frequencies were calculated from logistic regression models resulting from backwards elimination of non-significant effects (see Materials and Methods and Results for details).

DISCUSSION

Because I collected alligator stomachs during September only, my results do not necessarily reflect year-long food habits of American Alligators or seasonal changes therein. In addition, these data may not represent a true random sample as only those alligators that were in the presence of and attracted to bait were harvested. Therefore, comparisons with other studies should consider the time of year and manner (animals found dead, or captured with nooses, harpoons, or other devices) in which stomachs were collected.

Despite these limitations, this study suggests that food habits of adult American Alligators in southeastern Louisiana differ from those in southwestern Louisiana. Stomachs from adult alligators from the southwestern parishes were more likely to contain fish and reptile remains and less likely to contain crustacean remains than were stomachs from the southeastern parishes. Although I collected many more stomachs from southeastern than from southwestern Louisiana, my results agree with previous findings indicating that

alligator food habits differ among locations (Delany et al. 1999; Rice et al. 2007). Geographic variation in alligator food habits has generally been attributed to geographic differences in prey availability (McIlhenny 1935; Wolfe et al. 1987). Consequently, because prey species differ in their energetic and nutritional content (Cummins and Wuycheck 1971), population parameters such as growth, survival, and reproduction might vary among locations depending on the availability of calorically or nutritionally important prey items. The relationship between these demographic parameters and food habits in alligators needs more investigation.

Mammals (Muskrats and Nutria) typically make up a large proportion of the diet of adult alligators in coastal Louisiana (Chabreck 1972; Valentine et al. 1972; Wolfe et al. 1987). Mammal remains were present in about 30% of the stomachs analyzed in the present study and were equally likely to be consumed in both southeastern and southwestern Louisiana, suggesting that mammalian prey is an important dietary component numerically as well as nutritionally for adult alligators in Louisiana, regardless of location. In contrast, Florida alligators



□ Large males □ Small males □ Females

FIGURE 2. Predicted relative frequencies and 95% C.I. of presence of mammals (top) and reptiles (bottom) in stomachs of large male (> 2.44 m), small male (1.83–2.44 m), and female American Alligators. Frequencies were calculated from logistic regression models resulting from backwards elimination of non-significant effects (see Materials and Methods and Results for details).

appear to consume mammals much less frequently than do those in Louisiana (Delany and Abercrombie 1986;

Rice et al. 2007). Round-tailed Muskrats (*Neofiber alleni*), the most frequently encountered mammal in Florida alligator stomachs, are much less common and are not as widespread in Florida as are Muskrats and Nutria in Louisiana (Birkenholz 1972; Lowery 1974; Lefebvre and Tilmant 1992). In addition, Round-tailed Muskrats prefer shallowly flooded emergent vegetation rather than the open water and canals occupied by alligators (Schooley and Branch 2006).

Alligators frequently consume reptiles in both Louisiana and Florida, although to varying degrees (Delany and Abercrombie 1986; Wolfe et al. 1987). In the present study, reptile remains were present in 15% and 31% of stomachs from southeastern and southwestern Louisiana, respectively. These values are within the range of 10– 44% reported for other Louisiana studies (Chabreck 1972; Valentine et al. 1972; McNease and Joanen 1977). In addition, large males were more likely to contain reptile remains than were small males and females. These results are similar to those of Delany and Abercrombie (1986) who found that males consumed more reptiles than did females, and that turtles were the most important prey item for males larger than 3.0 m. They attributed the difference to differential habitat use because males spend more time in open water (Goodwin and Marion 1979) than do females and they are presumably more likely to encounter aquatic prev than are females. Females, on the other hand, spend more time in marsh or shoreline habitat near their nests than in open water (Goodwin and Marion 1979). In the present study, however, small males and females were equally likely to contain reptile remains and both were less likely than large males to contain reptile remains. If habitat use by small males is similar to that of large males and both differ from that of females, then the relative frequency of reptiles in stomachs of both groups of



□ Large males □ Small males □ Females

FIGURE 3. Predicted relative frequencies and 95% C.I. of presence of crustaceans in stomachs of large male (> 2.44 m), small male (1.83-2.44 m), and female American Alligators collected from Southeastern (top) and Southwestern (bottom) Louisiana. Frequencies were calculated from logistic regression models resulting from backwards elimination of non-significant effects (see Materials and Methods and Results for details).

males should have been similar to each other and different from that of females. Therefore, consumption of reptiles might be as much a function of alligator size as it is of habitat. Unfortunately, I only collected a few females larger than 2.44 m and therefore cannot test this hypothesis.

Recent hurricanes (Katrina in Buras in Plaquemines Parish in southeastern Louisiana in August 2005 and Rita in southwestern Cameron Parish in September 2005) drastically altered the vegetation of Louisiana's coastal marshes (Steyer 2008) resulting in significant damage to coastal alligator habitat and reduction in alligator populations (Louisiana Department of Wildlife and Fisheries. 2008. op. cit.). Hurricanes also affect the distribution and abundance of fishes and crustaceans (Roman et al. 1994), both of which are among the most important prey items for alligators in Louisiana (this study; Wolfe et al. 1987). While the most immediate and apparent effects of hurricanes on alligators appears to be nest loss due to flooding (Roman et al. 1994), a provided invaluable assistance sorting and identifying

dramatically altered prey base might have less obvious but possibly significant impacts on alligator populations. Because alligators are at the top of their trophic chain, they should be particularly sensitive to disturbances of lower trophic levels and therefore could serve as an indicator species in tracking responses of coastal systems following disturbances such as hurricanes. Comparative studies of pre- and post-disturbance alligator food habits data could provide significant insights into trophic relationships of coastal systems and their responses to disturbances.

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Gabrey.—Food habits of American Alligators.



FIGURE 4. Predicted relative frequencies and 95% C.I. of presence of crustaceans in stomachs of large male (> 2.44 m, top), small male (1.83–2.44 m, middle), and female (bottom) American Alligators collected from Southeastern and Southwestern Louisiana. Frequencies were calculated from logistic regression models resulting from backwards elimination of non-significant effects (see Materials and Methods and Results for details).

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